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“When a person doesn’t have gratitude, something is missing in his or her humanity”

- Elie Wiesel

This has been a long journey that cannot be resumed only by the document presented here, especially since this work was achieved in a completely different country (and Earth hemisphere) from where I used to live. It was not a trivial task to adapt to a new society, with different values and rules, while working on my doctorate. As such, the “human component” here in Montreal was crucial for my professional (and personal) achievement. I owe this to many people and being thankful costs very little and do lots of good for both the thankful and the thanked. The only risk is to forget to name someone that should be named. First, I am very grateful to have been supervised by Pedro R. Peres-Neto. He is a passionate scientist with endless ideas that he continuously shared with me and other students while allowing us to choose which one to pursue and how to conduct it. I would like to describe our interaction using a modified quote from Joshua Schimel’s book *Writing Science*: *“When I was a graduate student, I would sometimes go to my advisor, Pedro Peres-Neto, with what I thought was a simple question. Then we might spend weeks discussing issues that wandered all over the intellectual map and didn’t appear to fit on the straight road from my question to the answer. Many of the issues Pedro raised seemed irrelevant and extraneous. Over the years I worked with him, I came to understand what we were really doing in those conversations. Pedro saw more of the system and how it fit*

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To my family,
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RÉSUMÉ

Dénouer les divers facteurs influençant l'aire de répartition des espèces est un objectif de longue date en écologie. La dispersion est la clé pour comprendre la formation de ces aires de distribution et un nombre important d'études théoriques et empiriques s'est concentré à identifier les éléments affectant l'évolution des traits de dispersion. Cependant, il y a encore des lacunes dans nos connaissances concernant l'influence de processus tels que les interactions biotiques, la connectivité du paysage, l'adaptation locale et l'effet Allee sur l'évolution de la dispersion et des dynamiques des distributions des espèces. En générale, pour qu'une espèce étende son aire de répartition, les individus doivent être capables de se disperser dans une nouvelle région et ensuite de tolérer les nouvelles conditions abiotiques et biotiques rencontrées. Finalement, ils doivent pouvoir se reproduire pour soutenir une population viable. Alors que les approches statistiques (i.e., corrélatives) sont suffisantes pour évaluer l'importance des facteurs climatiques sur la distribution géographique d'une espèce (i.e., tolérance environnementale), elles sont moins efficaces pour les autres processus mentionnés ci-dessus. Par ailleurs, les échelles spatiales et temporelles sur lesquelles ces facteurs agissent font en sorte que l'utilisation d'approches expérimentales pour évaluer leurs effets est peu éthique, voir impossible. Conséquemment, je propose l'utilisation de modèles centrés sur l'individu (MCI) encadrés dans la théorie des métapopulations pour évaluer l'importance relative des processus influençant l'évolution de la dispersion et l'expansion des aires de répartition des espèces. Finalement, à travers l'étude de ces dynamiques, mon but est d'explorer les mécanismes structurant les patrons de biodiversité à large échelle. Les MCIs, par définition, prennent en compte la variation intraspécifique des traits et, de plus, ils tiennent compte des interactions adaptatives entre les individus et avec leur environnement. À ce titre, les MCIs fournissent l'agencement idéal pour évaluer comment les dynamiques écologiques et évolutives se déroulant aux petites échelles peuvent structurer des patrons écologiques aux larges échelles spatiales. Cette thèse est composée de trois chapitres utilisant les MCIs et un quatrième basé sur une base de données de zooplancton d'eau douce, qui sera utilisée pour tester quelques prédictions obtenues des MCIs. Le Chapitre I explore l'effet de la variation dans les degrés de connectivité des parcelles d'habitat dans des paysages sur l'évolution des stratégies de dispersion. Le Chapitre II vise à déterminer l'effet des facteurs abiotiques (niveau de connectivité et de fluctuations environnementales) sur la vitesse d'expansion d'une espèce à travers un paysage hétérogène. Plus précisément, j'évalue quelle des stratégies de dispersion denso-dépendante ou denso-indépendante induit des taux d'expansion plus rapides pour des espèces asexuées qui varient dans leur taux de croissance. Dans le Chapitre III, je développe un modèle multi-espèces pour comprendre comment les processus biotiques tels que l'effet Allee et la compétition interspécifique peuvent influencer l'expansion des aires de répartition des espèces à travers un paysage hétérogène.

J'explore également comment les gradients de diversité sont structurés par ces interactions. Pour terminer, dans le Chapitre IV, j'évalue comment la taille des aires de répartition et les gradients latitudinaux de diversité et d'aire de répartition (i.e., la loi de Rapoport) diffèrent entre les copépodes et les cladocères en utilisant une base de données sur la diversité et la distribution des microcrustacés d'eau douce dans plus de 1600 lacs au Canada. À cause de leurs modes de reproduction contrastés (cyclique parthénogénétique pour les cladocères et sexué pour les copépodes), ces deux clades diffèrent par rapport à leur susceptibilité à l'effet Allee et à leurs capacités de dispersion et d'adaptation locale.

Les résultats obtenus des MCIs fournissent des évidences par rapport à la façon dont les facteurs abiotiques et biotiques modulent l'évolution de la dispersion laquelle, à son tour, influence la taille des aires de répartition des espèces et les patrons de diversité à travers de larges échelles spatiales. Le Chapitre I démontre que différentes stratégies de dispersion peuvent évoluer en réponse à la structure spatiale du paysage. Le Chapitre II montre que la dispersion densité-dépendante permet une expansion plus rapide à travers un gradient environnemental seulement quand le taux de croissance des populations est élevé. Le Chapitre III illustre que l'effet Allee et la force de la compétition interspécifique peuvent moduler les gradients latitudinaux de diversité et d'aires de répartition. Finalement, le Chapitre IV démontre que les cladocères, des organismes ayant surtout une reproduction parthénogénétique et qui ne sont pas susceptibles à l'effet Allee, présentent, en moyenne, des aires de répartition significativement plus larges que les copépodes ayant une reproduction sexuée. Par ailleurs, les deux clades diffèrent énormément par rapport à leurs gradients latitudinaux de diversité et de répartition : le nombre d'espèces de cladocères décroît et leur aire de répartition moyenne s'accroît de manière importante vers les latitudes nordiques tandis que les copépodes ne présentent aucun patron latitudinal vis-à-vis de ces deux caractéristiques. Ainsi, cette thèse démontre que l'évolution de la dispersion et l'adaptation locale sont des facteurs clés pour comprendre la dynamique des aires de répartition (i.e., contraction et expansion) et que les processus qui se produisent aux petites échelles, tels que l'effet Allee et les interactions biotiques, peuvent influencer des patrons observables aux larges échelles spatiales comme la taille des aires de répartition des espèces et les gradients macroécologiques.

Mots-clés: Dynamiques des aires de répartition, zooplancton, gradient latitudinal de diversité, dispersion contexte-dépendante, structure du paysage, chevauchement de l'utilisation des ressources, loi de Rapoport

SUMMARY

Disentangling the multiple drivers underlying species geographic ranges has been a longstanding goal in evolutionary ecology. Dispersal is a key factor to understand range formation and there have been a number of theoretical and empirical studies focusing on the drivers of dispersal evolution. However, there are still some knowledge gaps regarding the interaction between dispersal evolution and other processes such as biotic interactions, landscape connectivity, local adaptation and Allee-effects in regulating range dynamics. For a species to spread its range, individuals first need to be capable of dispersing into a novel region, then tolerate the local abiotic and biotic environment and finally they should be able to reproduce in order to sustain a viable population. While statistical (i.e., correlative) approaches are enough to assess the importance of the environment on species geographic distributions (i.e., environmental tolerance), the same is not true for the above-mentioned processes. Furthermore, the spatial and temporal scales in which the processes regulating species ranges act make it unethical or impossible to evaluate them through experimental approaches. Therefore, I propose to use individual-based models (IBM) under a metapopulation framework in order to evaluate the relative importance of these drivers on dispersal evolution and range expansion. Ultimately, through the lenses of species range dynamics, I aim at exploring the mechanisms underlying large-scale biodiversity patterns. IBMs by definition account for intraspecific variation in traits and, more importantly, allow individuals to have adaptive interactions with each other and their environment. As such, IBMs provide the fundamental layout to evaluate how eco-evolutionary dynamics at small scales shape ecological patterns at larger scales. This thesis is comprised of three chapters using IBMs and a fourth that is based on a large-scale empirical dataset of freshwater zooplankton, which is used to test some predictions obtained from the models. Chapter I explores how landscapes with different degrees of connectivity among their habitat patches may affect the dispersal evolution. Chapter II investigates how abiotic factors influence the speed of range expansion across a heterogeneous landscape. Specifically I ask whether density-dependent (DD) or density-independent (DI) dispersal strategies induce faster range expansion rates to asexual species with varying growth rates in landscapes with different degrees of patch connectivity and levels of environment fluctuation. In Chapter III, I implement a multi-species model to understand how biotic processes such as Allee effects and interspecific competition may affect the range expansion of species across a heterogeneous landscape and, ultimately, how diversity gradients are structured by these interactions. Lastly, in Chapter IV, I evaluate how geographic range size (GRS) and latitudinal gradients in diversity and range-size differ between copepods and cladocerans using a large-scale dataset of freshwater microcrustacean species distributed across +1600 lakes in Canada. Given their contrasting mating system (cyclic parthenogenetic cladocerans and obligate sexual copepods), these two clades differ in their susceptibility to Allee effects, dispersal ability and capacity of adaptation.

Results obtained from the IBMs provide evidence regarding how abiotic and biotic factors modulate the evolutionary dynamics of dispersal, which in turn shape species geographic ranges and diversity patterns across large spatial scales. Chapter I demonstrates that different dispersal strategies may evolve in response to landscape spatial structure. Chapter II shows that DD dispersal only provides faster range expansion across an environmental gradient when population growth is high. Chapter III shows that both Allee-effects and the strength of interspecific competition modulate the steepness of latitudinal gradients in diversity and GRS. Finally, chapter IV shows that cladocerans, parthenogenetic species which do not suffer from mate-finding Allee effects, have a much larger ranges than sexual copepods. Both clades also have contrasting patterns regarding latitudinal gradients, in which the number of cladoceran species decrease and average GRS increase towards northern latitudes while copepods do not show any latitudinal pattern in either of these properties. Thus this thesis shows that dispersal evolution and local adaptation are of central importance to understand range dynamics (i.e., expansion and contraction) and that processes occurring at local scales such as Allee effects and biotic interactions may scale up to influence both species GRS and the structure of macroecological patterns.

Keywords: Range dynamics, zooplankton, latitudinal-diversity gradient, context-dependent dispersal, landscape structure, resource-use overlap, Rapoport's rule

INTRODUCTION

Why are there more species in the tropics than in higher latitude regions? Why are all species not able to adapt to every type of environment? Why do some species attain broad distributions whereas most do not? Can we understand biodiversity patterns through the mechanisms affecting species geographic range sizes? These are, among others, central questions in macroecology. Answering them will help understanding the patterns of diversity that are observed across Earth. In the present work, I will tackle a series of processes that contribute to species range dynamics. Among these processes, dispersal is a key component. Dispersal allows species to find new suitable habitats and affects the dynamics of adaptation to novel environmental conditions that they might encounter while expanding their geographic ranges. Moreover, dispersal is an evolvable trait influenced by the relative importance of factors that either improve fitness of dispersing individuals or increase the cost of dispersal. However, there are still many gaps in our understanding of how dispersal interacts with other processes such as Allee effects (i.e., decreased average individual fitness at low population density), landscape spatial structure and biotic factors and how these interactions shape macroecological patterns such as latitudinal diversity gradients and Rapoport's rule. Through a combination of computer simulations and analyses of empirical data from zooplankton communities, I explore some of these questions in a multi-scale framework, ranging from individual decisions up to large-scale distributional patterns.

Below, I give a brief overview on ecological and evolutionary processes driven by species dispersal at multiple ecological scales, their implication for species geographic ranges, and how they might influence the distribution of freshwater zooplankton. I then explain how the use of individual-based models can help to tackle some of these questions. Finally, I outline the main goals of the chapters from this thesis.

0.1 Multi-scale eco-evolutionary dispersal processes and their consequence for range dynamics

Dispersal is one of the most studied concepts in evolutionary ecology, especially given its various implications in ecological dynamics and longstanding impacts in evolutionary processes (reviewed in Bowler & Benton, 2005; Ronce, 2007; Travis *et al.*, 2013; Kubisch *et al.*, 2014). It is now widely accepted that dispersal is at the core of species geographic range formation (Sexton *et al.*, 2009). Most if not all species are capable of dispersing during some life stage and at a particular spatial scale, which allows them to persist in an ever changing environment (Ronce, 2007). Here I define dispersal as an active or passive attempt to move away from a natal/breeding population to establish into another breeding population, with potential effects for gene flow (Clobert *et al.*, 2009; Travis *et al.*, 2012). This process can be divided into three distinct stages: departure, transience and settlement (Bonte *et al.*, 2012; Travis *et al.*, 2012). As individuals tend to disperse to habitats around their natal population,

species are non-randomly distributed across space, generally forming cohesive geographic ranges (Rahbek *et al.*, 2007). The limits of species' geographic ranges are a result of the interplay between ecological and evolutionary process (Holt, 2003; Kubisch, 2012) that operate at a broad range of spatial and temporal scales, from small-scale decisions made at the individual level up to global climate drivers and major biogeographic events.

0.1.1 Dispersal evolutionary dynamics

In order to properly understand range dynamics, it is important to know how the different selective agents affect an individual's decision to disperse. Generally, individuals disperse in order to match their phenotype against prevailing environmental conditions as a way to improve their fitness (Ronce, 2007). However, dispersal is a risky behaviour, involving cost during both transfer (e.g., predation risk, failing to find suitable habitats) and settlement phases (e.g., lower competitive ability or fecundity compared to residents; Bonte *et al.*, 2012). Therefore, individuals may decide not to disperse if the risk of leaving a patch outweighs any fitness gains they might attain in another patch (Bowler & Benton, 2005). These findings, together with the fact that dispersal traits are heritable (Saastamoinen, 2008), imply that dispersal is subject to evolution (Bowler & Benton, 2005; Ronce, 2007). In addition, except for passive dispersal, dispersal decisions are generally non-random and rely on information (Ronce, 2007; Clobert *et al.*, 2009).

Species may disperse based on an assessment of local population density, a strategy named density-dependent dispersal (Poethke & Hovestadt, 2002; Travis *et al.*, 2009). On one hand, individuals will be more likely to leave crowded patches in order to avoid high competition for local resources (Hamilton & May, 1977; French & Travis, 2001; Bitume *et al.*, 2013). On the other hand, Allee effects (i.e., a decrease in average individual fitness when population density is low; Courchamp *et al.*, 1999) may reverse this tendency. For example, finding suitable mates for sexually reproducing species is a limiting factor; therefore leaving high-density patches may decrease an individual's chance of reproduction. Another process that affects dispersal evolution is environmental fluctuation; species dwelling in a habitat with large fluctuations (i.e., high variance) tend to have high dispersal rates in order to cope with temporal variability in resource availability (McPeck & Holt, 1992; Travis & Dytham, 1999) or simply to avoid local extinction (Poethke *et al.*, 2003). By spreading out offspring in a landscape in which conditions are highly stochastic, long-term average fitness is increased by lowering the temporal variance in fitness, a phenomenon named "bet-hedging strategy" (Philipi & Seger, 1989). Furthermore, high dispersal rates may be favoured due to spatial selection, a phenomenon that has been extensively studied in invasive species (Duckworth, 2008; Phillips *et al.*, 2010a). Spatial selection happens during range expansion, in which the most dispersive individuals are generally the ones found at the range border. Therefore, it is likely that they will mate with each other and thus produce highly dispersive offspring (Phillips *et al.*, 2010b). These individuals have higher fitness compared to

individuals from core populations due to the low competitive environment found at the expansion front, which results in an increased frequency in dispersive phenotypes (Brown *et al.*, 2013). Together, these processes promote a dramatic increase in the overall dispersal rate of the species. For instance, a study reported a five-fold increase in cane toads dispersal rates since the invasion began in Australia due to spatial selection (Phillips *et al.*, 2010b).

Ultimately, almost all species upon close inspection exhibit some degree of internal spatial structure, even in seemingly continuous habitat. Consequently, understanding the processes driving dispersal evolution can be undertaken in a metapopulation framework (i.e., spatially distinct populations linked by dispersal; Hanski & Beverton, 1994; Hanski, 1998). Whether an individual disperses or not between populations is contingent on the spatial structure of habitat patches, which regulates the flow of individuals across any given landscape (Baguette *et al.*, 2013; Grilli *et al.*, 2015). Therefore, landscape connectivity may have potential demographic consequences to local populations if it promotes asymmetric dispersal among them. If species are using a density-dependent dispersal strategy, landscape connectivity may indirectly influence dispersal evolution through its effects on population's demography. This process, however, remains to be tested.

0.1.2 Dispersal and metapopulation dynamics

Metapopulation population theory aims at understanding the colonization and extinctions dynamics of patchy populations (Hanski, 1998; Fortuna *et al.*, 2006). Species may persist regionally even if they go extinct in a local patch, which may be later recolonized by immigration from neighbouring populations. The species geographic range size is essentially the result of these dynamics, expanding or contracting depending on the relative importance of extinction and colonization (Kubisch *et al.*, 2016). Furthermore, dispersal among populations have important consequences for processes of local adaptation (Lenormand, 2002). Dispersal may allow populations to persist in unfavourable environments (i.e., negative net population growth) through source sink-dynamics (Pulliam, 1988). Depending on the harshness of the sink's environment, immigration may promote adaptation by increasing population size and genetic diversity, two pre-requisites for evolution by natural selection (Lenormand, 2002), thus allowing species to expand their ranges into previously unsuitable habitats (Holt & Barfield, 2011). However, dispersal may hinder local adaptation if mating between resident and immigrants imposes a reproductive cost and reduces the average individual fitness in the sink population, a process named migration load (Lenormand, 2002). Migration load can slow or prevent range expansion when an asymmetric flow of individuals from core to peripheral populations precludes these populations to adapt to novel environmental conditions encountered beyond the range border. Therefore, whether dispersal will

promote or prevent local adaptation is contingent on its intensity and the steepness of the environmental gradient.

0.1.3 Metacommunity dynamics, biotic interactions and their consequences for species geographic ranges

It is reasonable to assume that no single species lives alone in nature, therefore we use the metacommunity concept as the basic framework to understand how range dynamics may be affected by other species (Case *et al.*, 2005). Metacommunity theory is an extension of the metapopulation theory that aims at understanding the relative importance of abiotic factors, interspecific interactions and dispersal processes to both local community and regional pool assembly (Wilson, 1992; Leibold *et al.*, 2004; Henriques-Silva *et al.*, 2013; Fernandes *et al.*, 2014). For instance, metacommunity theory shows that species can co-exist regionally through dispersal even if a superior competitor drives an inferior competitor to extinction in a local community (Mouquet & Loreau, 2002). These effects compound over multiple species and determine the local and regional richness of a particular habitat patch or region, respectively. Similarly to metapopulations, dispersal effects on metacommunity dynamics are contingent on its intensity. For instance, the above-mentioned co-existence process is only possible at intermediary levels of dispersal. An inferior competitor may be driven to regional extinction if the superior competitor sustains high dispersal rates (Mouquet & Loreau, 2002). If competitive abilities are

similar, then community assembly may be contingent on priority effects in which the first species to colonize a new patch has an advantage over species colonizing later (Fukami, 2015). For instance, early colonizers may reduce the availability of local resources (e.g., light, space, nutrients) for later-arriving species, a process named niche pre-emption (Fukami, 2015). Finally, evolutionary dynamics may enhance priority effects if local adaptation of early colonizers improves their ability to monopolize local resources (Loeuille & Leibold, 2008; Urban *et al.*, 2008; Urban & De Meester, 2009; Vanoverbeke *et al.*, *in press*).

0.1.4 Range dynamics and large-scale diversity patterns

The identity and number of species distributed across the globe vary and understanding what drives these patterns has been a long-standing goal in macroecology and biogeography (Willig *et al.*, 2003). However, the ecological and evolutionary processes regulating these patterns operate at spatial and temporal scales in which experimental or manipulative studies are logistically unethical or impossible. As Haydon *et al.* (1993: p.117) stated: “The process of replication and repeatability, usually fundamental to the testing of scientific hypothesis, are not available for biogeographers”. Thus, correlative approaches (i.e., curve-fitting models) have dominated this field over the last decades (e.g., Currie, 1991; Hawkins *et al.*, 2003).

Unfortunately, so far there are no satisfactory explanations for the relative importance of mechanisms underlying diversity gradients given that multiple factors may show correlation, without necessarily having a causal link, with richness (Currie *et al.*, 1999; Peres-Neto & Legendre, 2010). As a consequence, there has been a recent shift to tackle this problem through more mechanistic models (e.g., Rahbek *et al.*, 2007; Rangel *et al.*, 2007; Gotelli *et al.*, 2009; Buschke *et al.*, 2015), consisting of a bottom-up approach where one explicitly simulates the mechanisms thought to underlie range dynamics and then evaluate if the outcomes of the model predict a pattern or fit empirical data (Grimm & Railsback, 2005; Gotelli *et al.*, 2009; Cuddington *et al.*, 2013). In these models, species will probabilistically spread across a landscape based on certain characteristics of available cells (e.g., their environment, proximity to cells occupied by the focal species). This process can be repeated for multiple species, where estimates of species diversity are computed based on the overlap of species ranges within each geographic cell (Rahbek *et al.*, 2007; Buschke *et al.*, 2015). In this case, the interactions of processes regulating multi-species range expansion will promote patterns of diversity across geographical cells according to their properties (e.g., their abiotic conditions, spatial isolation) (Gotelli *et al.*, 2009). Nevertheless, mechanistic models rely heavily on imposed responses in which desired outcomes are forced into the model. For instance, mechanistic-models generally constrain the range size of simulated species to follow a similar distribution of empirical range values (e.g., Buschke *et al.*, 2015). Further, mechanistic models assume that species are homogeneous entities, that is, composed of identical individuals. Therefore, they have

a limited capacity to account for eco-evolutionary dynamics because species lack intraspecific variation and adaptive responses. Trait variation has been recognized to be fundamental in classical work of niche evolution (Roughgarden, 1972; Grant & Grant, 2002), which is one way that species can expand their ranges (Davis & Shaw, 2001). Ecological processes are also affected by intraspecific variation. For instance, variation in phenotype-local environment matching may prevent species range from contracting in highly fluctuating environments by promoting persistence through portfolio effect (Bolnick *et al.*, 2011). Dispersal traits also show great variation among conspecifics (Stevens *et al.*, 2010), especially between core and marginal populations (Kubisch *et al.*, 2011) which may influence the speed of range expansion (Phillips *et al.*, 2010a). Neglecting intraspecific variation may thus hinder our ability to understand the multiple processes underlying species range dynamics (Stevens *et al.*, 2010; Bolnick *et al.*, 2011) and other large-scale ecological patterns (Araujo & Costa-Pereira, 2013).

0.2 Individual-based models in macroecology

Individual-based models (IBM) allow relaxing the above-mentioned assumptions. First, IBMs rely less on imposed responses because they allow complex interactions between their lower-level components and the consequent emergence of system-level properties from these interactions (Grimm & Railsback, 2005). Second, lower-level components in IBMs are, as suggested by their name, unique individuals with

characteristics that set them apart from every other individual. As a consequence, IBMs incorporate intraspecific variation by default. Finally, IBMs allow for individuals to exhibit adaptive response among them and between them and their environment. This approach stems from a general framework used in science known as “Complex Adaptive Systems” (CAS) which attempts to generate knowledge of a given system based on its interacting, adaptive agents (Levin, 1998; Railsback, 2001). Both intraspecific variation and the adaptive nature of lower-level components within IBMs provide the fundamental layout for an evolutionary perspective to be included in the model, that is, one that recognizes and explores the properties of ecological entities as a CAS whose components are subject to natural selection (Levin, 1998). This property is essential for understanding relationships and feedbacks between ecological and evolutionary processes (i.e., eco-evolutionary dynamics), especially given that it is increasingly recognized that evolution can occur on ecological timescales (Schoener, 2011). Therefore, spatially explicit IBMs are a useful tool to ask questions about macroecology patterns as they may incorporate dispersal, local adaptation, Allee effects, biotic interactions and many other processes involved in range dynamics (Travis & Dytham, 1998; Burton *et al.*, 2010; Kubisch *et al.*, 2013b; Kubisch *et al.*, 2014).

0.3 Study system

In the present work I propose to apply IBMs in a multi-scale framework to ask questions ranging from dispersal evolution, to abiotic and biotic factors influencing range dynamics and diversity patterns. Finally, I evaluate some of the predictions obtained from the IBMs on large-scale patterns in freshwater microcrustacean zooplankton. This taxonomic group is an interesting study system because it is composed of species that differ widely in breeding modes (Allan, 1976; De Meester, 1996), which have many implications for dispersal and local adaptation processes.

Cladocerans almost invariably reproduce through cyclic parthenogenesis, that is, several rounds of cloning interrupted by occasional sexual reproduction. Generally, females emerge at the beginning of the growing season and reproduce through amictic parthenogenesis (i.e., without fertilization) as long as environmental conditions are favourable (De Meester, 1996). When an environment starts to deteriorate, either by depletion of resources, overcrowding or the onset of unsuitable conditions (e.g., winter, drought), females produce males through parthenogenesis and haploid eggs, which are fertilized by males (De Meester, 1996). These sexual eggs represent the diapausing phase of cladocerans and will hatch as soon as favourable conditions are restored. In addition, some cladoceran species also have completely asexual populations, either through obligate apomictic parthenogenesis (Dufresne & Hebert, 1997) or self-fertilization (Hebert *et al.*, 2007) where female-

only populations are able to produce diapausing eggs. The capacity to reproduce asexually is a great advantage to cladocerans, as it improves their dispersal ability by allowing them to establish new populations with solely one individual (Havel & Shurin, 2004; Gray & Arnott, 2011).

The copepod mating system differs from cladocerans in its obligate sexuality. Fertilized eggs hatch into a larval phased called the nauplius. Subsequent larval and juvenile (i.e., copepodid) stages occur before reaching the adult phase, when individuals attain sexually maturity (Allan, 1976). During the mating phase, females may store sperm in a spermathecal sac, lessening the need for further breeding. The diapausing phase differ in the two main groups of copepods: calanoid copepods undergo diapause during the egg stage whereas the cyclopoid copepods encyst and diapause during juvenile stages, generally as C3-C4 copepodites (Fryer, 1996; Frisch, 2002). Given their life-cycle, copepods suffer from Allee effects when colonizing a new water body and experimental evidence has shown that cladocerans are better colonizers than copepods, as the latter are limited by mate-finding difficulties at low densities (Kramer *et al.*, 2008; Gray & Arnott, 2011; Frisch *et al.*, 2012).

Despite the island-like nature of lakes and ponds, which implies that they are generally isolated from one another by an inhospitable terrestrial matrix, freshwater microcrustaceans have shown incredible success at dispersing (Havel & Shurin, 2004; Frisch *et al.*, 2012). Dispersal occurs generally during the diapausing stage,

when the organisms may resist freezing, desiccation and even digestion, thus remaining viable through the harsh conditions of overland dispersal (Havel & Shurin, 2004). Cladocerans diapausing eggs are often enveloped by ephippial capsules that have spines, barbs or air-trapping dimples that improve buoyancy, which increase their capacity of hitchhiking via dispersal vectors (Fryer, 1996). With the exception of occasional free-swimming adult emigration through watercourses, dispersal mainly occurs passively, either *via* wind (Cáceres & Soluk, 2002; Horváth *et al.*, *in press*), human assistance (e.g., recreational boats, ship ballast tanks; Havel & Shurin, 2004) or animal vectors such as mammals and waterbirds (Figuerola *et al.*, 2005). Particularly, waterfowls are important animal vectors for long distance dispersal of zooplankton. For instance, studies have shown that the population genetic structure of some microcrustacean species is related to the north-south migration routes of these animals (Taylor *et al.*, 1998; Figuerola *et al.*, 2005).

Substantial ecological and evolutionary research has been done on zooplankton, especially at small scales. Zooplankton are used to understand how different processes such as local-adaptation (Van Doorslaer *et al.*, 2009; De Meester *et al.*, 2011), dispersal (Vogt & Beisner, 2011), biotic interactions (Lynch, 1979), Allee effects (Gray & Arnott, 2011) and priority effects (De Meester *et al.*, 2002; Louette & De Meester, 2007) affect community assembly. Larger scales studies have also been undertaken to disentangle the relative importance of local and regional processes underpinning the structure of multiple zooplankton communities (e.g., Pinel-Alloul,

1995; Pinel-Alloul *et al.*, 1995; Cottenie *et al.*, 2003; Beisner *et al.*, 2006). At continental and global scales, however, studies are scarce and show different results. For instance, Pinel-Alloul *et al.* (2013) and Hessen *et al.* (2007) showed that freshwater microcrustacean diversity is tightly related to energy-related variables whereas Mazaris *et al.* (2010) found only a weak relationship with environmental drivers. However, all these studies pooled both cladocerans and copepods in the same analysis. It is expected that they respond to different drivers due to their different mating system (Leibold *et al.*, 2010), which are known to have potential consequences for their susceptibility to Allee effects, dispersal capacity, and local adaptation processes (Hargreaves *et al.*, 2014; Grossenbacher *et al.*, 2015). As discussed previously, all these processes affect species range dynamics, thus we may expect that these two groups of species will differ in their geographic range size as well.

0.4 Thesis outline

The goal of this thesis was to explore the various factors affecting species range dynamics with IBMs and test some of these predictions on a large-scale dataset of freshwater microcrustaceans. To this end, the present work is comprised of four chapters, three using individual-based models and one with empirical data:

Chapter I – On the evolution of dispersal via spatial heterogeneity in connectivity

Chapter II – Range expansion depends on the interaction between dispersal strategies and population growth rate

Chapter III – Biotic processes during range expansion explain large-scale diversity gradients

Chapter IV – Mating system, climate and history interact in explaining macroecological patterns in freshwater zooplankton

In Chapter I the effect of variance in connectivity among patches on the evolution of density-dependent dispersal strategies was explored. I simulated landscapes that varied in their connectivity structure using network models. Landscapes ranged from all patches having the same number of connections to landscapes with high variability in connectivity (i.e., a few patches with many connections and many patches with a few connections). Landscapes were seeded with individuals exhibiting many different dispersal strategies and we evaluated which ones were selected across the different landscape configurations.

The goal of Chapter II was to investigate how abiotic factors such as landscape connectivity and environmental fluctuation would affect the spread rate of species with different dispersal strategies across an environmental gradient. We contrasted the range expansion speed of species with different levels of growth rates following either density-dependent or density-independent dispersal in landscapes with contrasting connectivity structures and degrees of environmental fluctuation.

Chapter III explored how biotic factors such as Allee effects and interspecific competition would influence the range expansion of multiple species on a heterogeneous landscape. Further, I was interested in evaluating how these effects on species range dynamics would influence emergent patterns of biodiversity across the landscape (i.e., latitudinal diversity gradient and Rapoport's rule). I simulated an out-of-the tropics model, in which I assumed that species originated in the tropics and expanded their ranges towards northern latitudes. Species were initially equivalent in respect to their dispersal capacity and environmental niche, but these traits were allowed to evolve during the simulation. I varied the degree of interspecific competition among species and I tested for Allee effects by contrasting two mating systems: asexual and sexual, in which the latter is subject to mate-finding difficulties at low densities. Ultimately, we measured the final range size of all species at the end of the simulation in each replicate and evaluated the steepness of diversity and range-size gradients across the landscape.

Chapter IV was conducted to test some of the predictions derived from the IBM in Chapter III on a large-scale dataset of freshwater zooplankton distribution in Canada. I first evaluated the geographic range size distribution of cladocerans and copepods. Given that they differ in their susceptibility to mate-finding Allee effects due to their different mating-systems, their range-size distributions should be similar to the ones predicted for the sexual and asexual species in the previous chapter for the asexual

and sexual species. Second, I analyzed the steepness of latitudinal gradients of diversity and geographic range size (i.e., Rapoport's rule) for each group. Given that their contrasting life-history traits may affect how they respond to environmental drivers and historical factors (i.e., dispersal limitation), it should translate into contrasting latitudinal-diversity gradients and Rapoport's rule.

To summarize, results obtained from the IBMs along chapters I to III provide evidence regarding how abiotic and biotic factors modulate the evolutionary dynamics of dispersal, which in turn shape species geographic ranges. Further, the multi-species model in chapter III uncovers previously overlooked factors regulating diversity patterns at large spatial scales. Chapter IV shows that some of these mechanisms, such as mate-finding Allee-effects, may have deep impacts on large-scale ecological gradients in freshwater zooplankton.

CHAPTER I

ON THE EVOLUTION OF DISPERSAL VIA HETEROGENEITY IN SPATIAL CONNECTIVITY

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1.1 Summary

Dispersal has long been recognized as a mechanism that shapes many observed ecological and evolutionary processes. Thus, understanding the factors that promote its evolution remains a major goal in evolutionary ecology. Landscape connectivity may mediate the trade-off between the forces in favour of dispersal propensity (e.g., kin-competition, local extinction probability) and those against it (e.g., energetic or survival costs of dispersal). It remains, however, an open question how differing degrees of landscape connectivity may select for different dispersal strategies. We implemented an individual-based model to study the evolution of dispersal on landscapes that differed in the variance of connectivity across patches ranging from networks with all patches equally connected to highly heterogeneous networks. The parthenogenetic individuals dispersed based on a flexible logistic function of local

abundance. Our results suggest, all else being equal, that landscapes differing in their connectivity patterns will select for different dispersal strategies, and that these strategies confer a long-term fitness advantage to individuals at the regional scale. The strength of the selection will, however, vary across network types, being stronger on heterogeneous landscapes compared to the ones where all patches have equal connectivity. Our findings highlight how landscape connectivity can determine the evolution of dispersal strategies, which in turn affects how we think about important ecological dynamics such as metapopulation persistence and range expansion.

1.2 Introduction

Dispersal is a key factor in both ecology and evolution (Ronce, 2007). From an ecological perspective, dispersal may affect population and community dynamics (Hanski, 1994; Mouquet & Loreau, 2002), rescue populations from extinction (Brown & Kodric-Brown, 1977), shape species distributions (Olden *et al.*, 2001), and allow species to track favourable environmental conditions and influence the rate at which species expand their ranges (Travis *et al.*, 2009). From an evolutionary perspective, dispersal can produce gene flow and depending on its magnitude, can preclude or promote local adaptation and speciation, increase or decrease local genetic diversity, mitigate the effects of drift in small populations and reduce mutation load (Roff & Fairbairn, 2001; Alleaume-Benharira *et al.*, 2006; Ronce, 2007). As such, natural selection is expected to act on traits associated with dispersal

(Clobert *et al.*, 2009; Stevens *et al.*, 2012; Bitume *et al.*, 2013; Fronhofer *et al.*, 2013).

Understanding what conditions promote dispersal evolution remains an active research topic in evolutionary ecology through theoretical models (Poethke & Hovestadt, 2002; Bach *et al.*, 2006; Massol *et al.*, 2011) and empirical studies (Galliard *et al.*, 2003; Bitume *et al.*, 2013; Waser *et al.*, 2013). On the one hand, these studies have shown that the evolution of high dispersal rates may be favoured by several mechanisms such as environmental fluctuations (e.g., to cope with temporal variability of resource availability; McPeck & Holt, 1992; Poethke *et al.*, 2003; Kubisch *et al.*, 2011), local extinction probability (Poethke *et al.*, 2003) as well as individual and kin competition (Hamilton & May, 1977; Gandon & Michalakis, 1999; Poethke *et al.*, 2007; Bitume *et al.*, 2013; Waser *et al.*, 2013). On the other hand, the fitness benefits of dispersing can be reduced by the associated risks such as dispersal costs and mortality (Bonte *et al.*, 2012), thereby promoting the evolution of lower dispersal rates (Travis & Dytham, 1999; Poethke & Hovestadt, 2002).

Despite this work, important gaps remain in our understanding of dispersal evolution in realistic landscapes. In natural landscapes, patch connectivity varies as a function of particular features such as topography, patch sizes, habitat types and distribution (Bonte *et al.*, 2010; Jacobson & Peres-Neto, 2010; Biswas & Wagner, 2012). Such spatial heterogeneity implies that habitat patches across landscapes are seldom

equally connected. Empirical evidence suggests that dispersal behaviour may undergo adaptive changes depending on landscape configuration (Bonte *et al.*, 2006; Schtickzelle *et al.*, 2006; Baguette & Dyck, 2007; Schtickzelle *et al.*, 2007). Moreover, heterogeneity in patch connectivity may affect regional persistence and patterns of extinction and colonization (Fortuna *et al.*, 2006; Economo & Keitt, 2008; Gilarranz & Bascompte, 2012) by promoting asymmetric flows of individuals across patches. In landscapes with heterogeneous levels of connectivity (i.e., some sites really well connected whereas others weakly connected), more connected patches receive more dispersers than more isolated patches, thus generating spatial variation in abundance and density within landscapes (Duputie & Massol, 2013). Therefore, the variance in connectivity across patches has the potential to change the dispersal cost/benefit trade-off through its effect on the spatial variation in population density. Because dispersal evolution is mediated in part by density-dependent intra-specific and kin interactions (Poethke *et al.*, 2007), heterogeneously connected landscapes might yield different selection pressures on dispersal traits than homogeneously connected landscapes.

So far, however, no study has investigated the potential effect of inter-patch variability in connectivity on the evolution of dispersal. Instead, most models have assumed rather simplistic spatial structures, where dispersal is either global (Gandon & Michalakis, 1999; Poethke & Hovestadt, 2002), local (i.e., nearest-neighbour; Travis *et al.*, 2009; Kubisch *et al.*, 2011) or a simple function of distance (Murrell *et*

al., 2002). In global dispersal models (i.e., spatially-implicit models), all dispersers merge into a global pool from which they are then randomly redistributed among patches. Local dispersal as is classically assumed in spatially-explicit models is modelled by creating a regular grid of habitat cells on which dispersers can move only to one, randomly chosen, neighbouring cell with equal probability. Finally, the modelling of dispersal based on dispersal kernels assumes that the probability to disperse from one patch to another is a decreasing function of their distances (Gros *et al.*, 2006; Büchi & Vuillemier, 2012). However, these models are generally based on a torus structure (i.e., no edge effects) and, when averaging the connectivity of each patch to all others, they suffer from the same assumption that all patches have an overall similar connectivity. As such, all these models assume one way or another a homogeneous landscape structure, i.e., all patches have equal connectivity, which is usually not the case in natural landscapes (Baguette & Dyck, 2007; Biswas & Wagner, 2012).

In the present study we address the following questions: (1) How does the spatial structure affects the evolution of dispersal strategies? (2) Does this effect depend on dispersal costs? and (3) Is the evolution of dispersal strategies adaptive? We show that differences in heterogeneity in patch connectivity within landscapes, coupled with density-dependent competition, lead to different evolutionary stable dispersal strategies. We set out to study the influence of landscape structure on the evolution of dispersal using an individual-based model (IBM) in which spatial networks with

varying levels of patch connectivity are used to represent different landscapes configurations. We assume density-dependent population dynamics and that individuals differ in their dispersal propensity but are otherwise identical. In addition, we also tested if the adaptation of a metapopulation to one landscape structure generates a specialized coalition of dispersal strategies such that it can resist invasion from metapopulations evolved on other landscape structures. In order to do so, we performed a series of contest simulations akin to reciprocal transplants experiments, where pairs of metapopulations evolved on different landscape types were confronted on their respective landscapes.

1.3 Methods

1.3.1 Landscape structure

The landscape structure of our IBM was modelled as four different types of network (Figure 1.1) of increasing heterogeneity: regular, random, exponential and scale free (Gilarranz & Bascompte, 2012) (note that landscape and network are used interchangeably). To understand the effects of network heterogeneity, all networks were set with the same number of nodes ($n_p = 1024$ patches), edges ($n_c = 4096$ connections) and average degree (8 connections per patch). The only factor manipulated across network types was the degree of heterogeneity (variance) in patch connectivity. Connections among patches are undirected, i.e., individuals may disperse both ways with equal probabilities between two connected patches. These

four types of networks provide a gradient in terms of the variance in connectivity across patches. Regular networks (Figure 1.1A) consisted of a simple regular grid where each patch was connected to its eight closest neighbours, representing a Moore neighbourhood in traditional spatially-explicit models (e.g., Travis *et al.*, 2009; Kubisch *et al.*, 2011). Regular networks were wrapped into a torus to avoid edge effects. Random networks (Figure 1.1B) were generated based on the Erdős and Rényi (Erdős & Rényi, 1959) random graph model: patches were connected at random, with equal probability, until the desired average number of connections per patch (degree = 8) was reached. This algorithm created variation in patch degree, so that the degree was Poisson distributed. Exponential networks (Figure 1.1C) were generated after Barabási and Albert (Barabási & Albert, 1999) but with an average degree of 8 rather than 2 as in their original framework. They were built by connecting five patches randomly and then adding new patches to the network one at a time and connecting them to one of the existing patches with equal probability until the maximum number of patches (1024) is reached. Finally, an average of 8 connections per patch was generated by repeating the second step 3 times. The exponential model creates asymmetry in patches' connectivity because initial patches will naturally have a higher degree and thus the network will exhibit an exponential degree distribution (Figure 1.2A). Finally, scale-free networks (Figure 1.1D) were also created by connecting five patches at random as in the case of exponential networks. However, in this case, new patches were added to the network with preferential attachment instead of equal probability until the desired number of

patches was reached. Preferential attachment is a process by which the probability to be connected to any existing patch is proportional to its degree (Barabási & Albert, 1999). Therefore more connected patches were more likely to become even more connected. Finally, an average of 8 connections per patch was built by adding connections one at a time between random pairs of nodes, with preferential attachment. Scale-free networks are the most heterogeneous landscapes due to preferential attachment, creating a degree distribution that follows a power law (Figure 1.2B; Barabási & Albert, 1999).

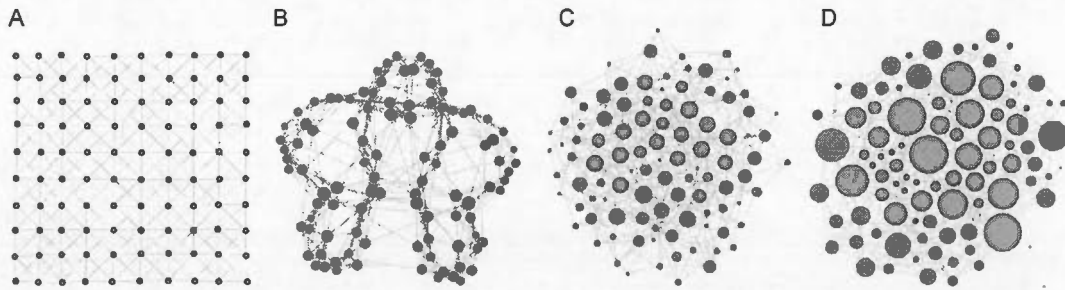


Figure 1.1. The four different spatial structures used for the simulations, from the most homogeneous to the most heterogeneous. Node size is proportional to its degree. (A) Regular network, (B) random network, (C) exponential network and (D) scale-free network. All networks were built with 1024 patches and included 4096 connections among patches, with an average of 8 connections per patch. The networks differ in terms of their degree variance and the average degree variance across the 200 replicates for each network is: (A) 0, (B) 0.14, (C) 19.42 and (D) 48.70.

1.3.2 Population dynamics

All patches were initially populated with a number of individuals equal to their equilibrium density (K). Individuals are haploid, asexually reproducing, and characterized by three dispersal traits (see “*Density-dependent dispersal*” section below). For each individual, the three dispersal traits were initially generated by drawing random values from a uniform distribution, hence assuring that a broad mix of genotypes were distributed across all network types at the start of each simulation and that the final outcome of the model would not depend on initial conditions. Genetic variation in traits important for dispersal has been documented (Roff & Fairbairn, 2001) such as evidence for additive genetic variation in morphological (e.g., body size, wing length; Roff & Simons, 1997), behavioural (e.g., propensity to initiate dispersal, duration of dispersal; Haag *et al.*, 2005) and physiological traits (e.g., enzymes associates directly with locomotion; Clark, 1990). As the genetic determinism of condition-dependent dispersal traits is poorly known, we used the classical one locus per trait approach. Each time-step of the simulation was then generated by the following sequence of events: density-dependent reproduction, death of adults (i.e., individuals are semelparous) and offspring dispersal (i.e., natal dispersal); therefore, we assumed no overlap between generations. Local population dynamics were based on a density-dependent reproduction function (Hassell, 1975), which is commonly used in simulation studies that evaluate density-dependent dispersal evolution

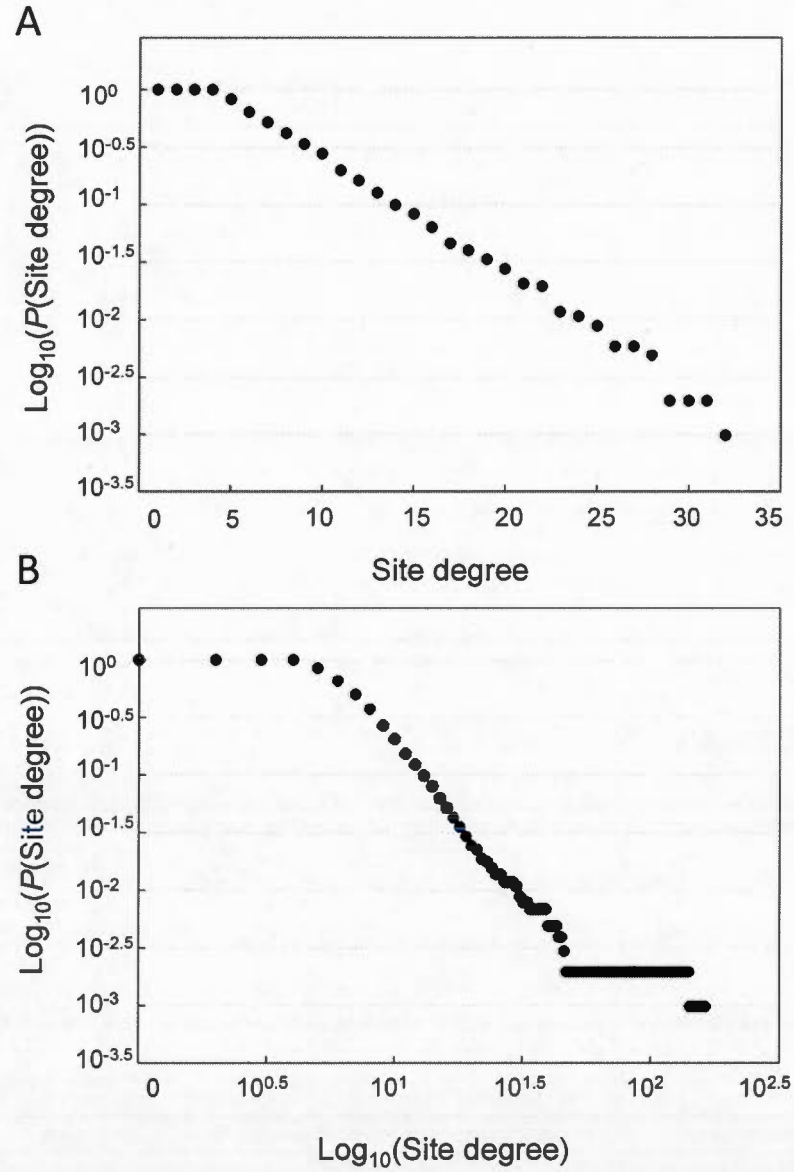


Figure 1.2. Degree distribution of (A) exponential and (B) scale-free networks. The degree distribution of exponential networks is visualized on a log-scale while the degree distribution of scale-free networks is visualized on a log-log scale.

(Poethke & Hovestadt, 2002; Kun & Scheuring, 2006; Travis *et al.*, 2009; Kubisch *et al.*, 2011) and has been successfully fitted to the dynamics of insect populations (Hassell, 1975; Bellows, 1981). In order to introduce demographic stochasticity into the model, every individual gave birth to a number of offspring drawn randomly from a Poisson distribution with mean λ , defined as:

$$\lambda = \mu(1 + aN_t)^{-b}$$

where μ is the intrinsic rate of local population growth, a is related to patch quality (see below), b describes the shape of the density-dependent competition affecting patches and N_t is the local population density in the patch. In the present study we used $b = 1$, which describes a contest competition (Travis *et al.*, 2009); note, however, that this parameter has little influence on dispersal evolution (Poethke & Hovestadt, 2002). The parameter a represents patch quality and is calculated as follows:

$$a = \frac{\mu^{1/b} - 1}{K}$$

so that the equilibrium population density is K for all patches across the landscape and therefore the environment is homogeneous. For all simulations K was set to 20. It should be noted that the reproduction (λ) varies only across patches due to local density (N_t). All other parameters were fixed and there were no genotype (i.e., trait) that could confer differential lifetime reproductive success, assuring that all individuals within a patch had the same fitness. As such, we assume equal strength for kin and intraspecific competition.

1.3.3 Density-dependent dispersal

After reproduction, all parents die and offspring disperse. The probability that an individual disperses d is controlled by three individual traits (D_0 , α and β) and depends on the local population density. This dispersal model represents organisms that can actively assess information about the quality of their natal patch in order to make dispersal decisions (Baguette & Dyck, 2007) and does not apply to passively dispersing organisms (e.g., wind-dispersed trees). However, the model assumes that movement is costly enough to preclude information gathering on the quality and number of potential target patches. Thus, dispersal decision depends solely on natal patch condition. Each dispersal trait is inherited by the offspring from its parent with a mutation probability $m = 10^{-3}$, and the magnitude was drawn randomly from a uniform distribution (D_0 [-0.1 – 0.1], α [-0.5 – 0.5], β [-5.0 – 5.0]) after Travis *et al.* (2009). The probability of dispersal is obtained from the sigmoid logistic function:

$$d = \frac{D_0}{1 + \exp[-(N_t - \beta)\alpha]}$$

where D_0 (range values: [0 - 1]) represents the maximum dispersal probability, β [0 - ∞] is the population density at which the dispersal probability reaches half of its maximum, α [0 - 10] describes the sharpness of the variation in dispersal probability at this inflection point and N_t is the population density at generation t . Note that we chose this flexible logistic function rather than simple single-parameter functions in order to introduce as few constraints as possible on the type of dispersal strategies

that can evolve (see Figure 1.3), given the increasing evidence that dispersal strategies are highly variable within a species (Cote & Clobert, 2007; Stevens *et al.*, 2010). The cost of dispersal is represented by a fixed mortality probability c when dispersing between patches. It accounts for the risks of dispersal (e.g. predation) and implicitly accounts for the energetic expense and other deferred fitness costs of dispersal (Bonte *et al.*, 2012). This scenario would apply when connectivity between patches is controlled by natural or anthropogenic obstacles rather than pure inter-patch distances and it was chosen to estimate the effects of connectivity independent of dispersal costs. However, in order to test if an interaction between mortality and connectivity could affect our initial results, we performed a second set of simulations that assumed a greater weight to the cost of dispersing from a less connected patch. This situation applies when individuals are dispersing randomly in all directions; as such, leaving a less connected patch would be riskier (i.e., less neighbouring patches) than leaving a highly connected patch. Individuals that survive the dispersal process ($1 - c$) enter one randomly chosen patch connected to the natal patch. Once all individuals have dispersed, they become adults and the next time-step begins.

1.3.4 Main simulations

We performed 200 replicates for each network structure assuming three levels of dispersal cost for the fixed-mortality scenario: no mortality (0%), low mortality (10%) and extreme mortality (50%), resulting in $n = 200 \times 4 \times 3 = 2400$ simulations.

In addition, 200 replicates for each network ($n = 200 \times 4 = 800$) were performed for the connectivity-dependent mortality scenario, which was estimated using a modified version of the connectivity metric from (Hanski *et al.*, 2000):

$$c = \omega D^{-\delta}$$

where the dispersal mortality c is a rational function of the degree (D) of the site from which the individual is emigrating (i.e., individuals leaving a more connected patch would have a lower mortality probability), ω controls the average mortality of the function and δ parameter is the effect of connectivity on the function and controls the shape of the kernel. We also tested a second scenario in which the probability of mortality was a property of the outward patch (i.e., destination) but results were qualitatively similar, thus we only present results from the following scenario. We chose the following parameter values for the dispersal mortality (c) function: $\omega = 1$ and $\delta = 0.9$. These values were chosen to constrain the mortality probabilities within the range of the ones used in the fixed dispersal mortality but without approaching the extreme mortality case (i.e., 50%). Dispersal mortality varied between 5% and 28% across patches in the exponential network and between 3% and 30% in the scale-free network.

The values used for all other parameters are presented in Table 1.1. Note that except for the regular network, in which connectivity for all sites is fixed, a different network for each replicate was generated for the other three types following their

Table 1.1. Initial parameter values used on the main simulations.

Parameter	Definition	Value
μ	Rate of population growth	1.5
b	Competition parameter	1
K	Equilibrium density	20
m	Mutation probability	0.001
c	Dispersal cost	0.0, 0.1, 0.5
D_0	Maximum dispersal probability	[0.0 – 1.0]
β	Inflection point (IP)	[0.0 – ∞]
α	Sharpness of the curve at the IP	[0.0 – 10.0]

respective generation rules described earlier (i.e., random, exponential and scale-free). The evolutionary dynamics of the dispersal traits were tracked for 40 000 generations (i.e., time steps), which allowed sufficient time for the metapopulation to attain an equilibrium strategy regardless of the initial conditions (see Appendix A). Note that we ran the scenario with connectivity-dependent mortality after the main simulations and we decided to reduce its duration to 15.000 generations in order to save computational time because the two most important traits (D_0 and β) reached stable equilibrium around this time step in the main simulation (Appendix A). In all simulations, data on trait values of all individuals across all sites were saved every 50 generations. In order to compare the evolutionary dynamics of different network structures and dispersal cost, we calculated for each replicate the mean of the three dispersal parameters across all patches at each generation. Afterwards, we computed the average and standard deviation of these means across the 200 replicates of each network - dispersal cost combination. In order to test the effects of network structure and dispersal costs (c), we used a two-way ANOVA using both these factors as fixed

predictors and the average values from the 200 replicates of each trait at the last time-step as the response variable. Further, if ANOVAs showed significant differences due to network structures, we applied post-hoc Tukey-Kramer tests to evaluate which types of networks and dispersal mortality treatments differed significantly in trait values. In order to explore the parameter space and the robustness of our results, we conducted a sensitivity analysis following Kubisch *et al.* (2011), which is present in Appendix B.

1.3.5 Contest simulations

Finally, in order to assess if a dispersal strategy selected in a particular network structure represented a regional adaptation to the landscape type they evolved, we tested if resident metapopulations could resist an invasion from metapopulations evolved on different networks. To do so, we performed a full factorial series of pairwise “contest simulations” between metapopulations evolved in different networks depicting one as the resident and the other as the invader. For each combination of resident – invader landscapes (4 types of landscape, hence 16 combinations), we randomly matched in a pairwise fashion the 200 resident metapopulations evolved in the first set of simulations to the 200 invaders metapopulations (e.g., 200 metapopulations that evolved on scale-free networks were randomly matched to the 200 evolved on regular networks, one by one) without repetition. Invasion from metapopulations evolved in the same type of network was

also performed to serve as control. The combination of 4 resident structures x 4 invader structures x 200 pairwise contests yielded 3200 simulations.

Each contest simulation was conducted as follows. First, a new landscape following the same rules but differing from the landscape on which the resident metapopulation evolved was created (e.g., if the resident population evolved in an exponential network, a new exponential network was created for this simulation). This was done to remove any possible advantage that the original landscape, in which the resident evolved, could provide during the contest. Second, each patch of this new landscape was populated with $K/2$ (i.e., 10) randomly selected individuals (without replacement) from the last generation (i.e., 40 000th timestep) of both resident and invader metapopulations. The simulations then proceed identically as the first set of simulation but only with dispersal mortality $c = 0.1$. These simulations ran for 25000 generations and results were saved at 50 time intervals. Results are presented in the form of average relative abundance of residents *versus* invaders across replicates. All simulations and statistical analyses were performed in Matlab (Mathworks 2014).

1.4. Results

Both spatial structure and dispersal mortality had a significant effect on the evolutionary dynamics and optima of the three dispersal traits. Figure 1.3 shows the average dispersal strategy selected in each network for each dispersal cost scenario as

well as the range of abundances of sites within networks, which regulates the realized dispersal rates of their metapopulations. It was only in the last scenario ($c = 0.5$) that the realized dispersal rates were below the potential dispersal rates because the local abundances were, except for the most connected patches in scale-free networks, below the threshold density (β) for dispersal propensity (Figure 1.3C). Two-way ANOVAs performed on the last time step across the 200 replicates of each structure indicated significant effects of network (regular, random, exponential and scale-free) and dispersal mortality (i.e., $c = 0, 0.1$ or 0.5) as well as their interaction for all three traits (Table 1.2; Figure 1.4). Post-hoc Tukey-Kramer tests indicated that differences among all networks were significant for all traits, except between regular and random networks and exponential and scale-free networks for the trait α (Appendix C1). Pair-wise comparison of dispersal mortality treatments indicated significant differences across all traits (Appendix C2). Finally, post-hoc Tukey-Kramer test in the interaction term showed that most were significantly different from one another (Appendix C3), with the following exceptions: network effects in the extreme dispersal mortality scenario ($c = 0.5$) and some comparisons of the interactions affecting the α trait (steepness of the curve at the inflection point). In all cases, differences in trait values were greater between homogeneously connected landscapes (random and regular) and heterogeneously connected landscapes (exponential and scale-free). This difference was due to the spatial variation in fitness (measured by the number of potential offspring λ) that occurred in heterogeneous networks

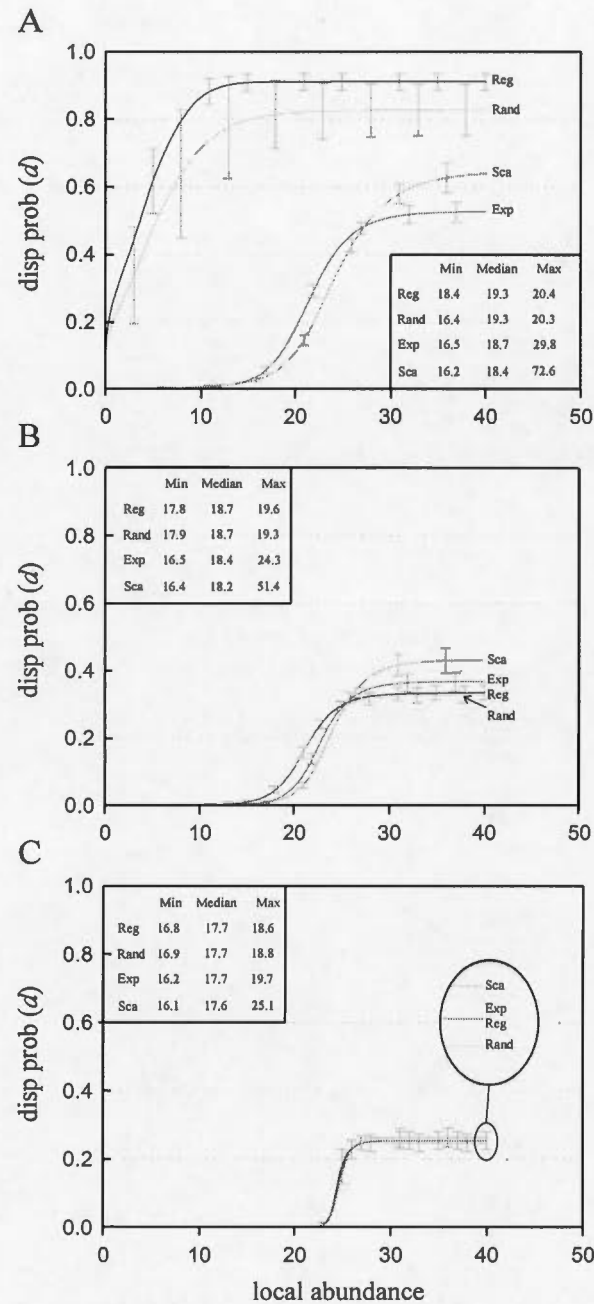


Figure 1.3. Average dispersal functions built from the three dispersal traits of all individuals at the last generation across the 200 replicates from simulations with (A) 0%, (B) 10% and (C) 50% dispersal mortality. These logistic functions represent the average dispersal strategy selected in each network and stand for the potential

dispersal rates. Average abundances of sites on the last time step were calculated across the 200 replicates for each network in order to evaluate the realized dispersal rates. Horizontal bars represent the standard deviation of the dispersal strategies across the 200 replicates. The numbers within the squares are the minimum, median and maximum abundances across sites in each network computed on the last time step. Reg = Regular network, Rand = Random network, Exp = Exponential network and Sca = Scale-free network.

Table 1.2. Results from two-way ANOVA. Network structure (Net) and dispersal costs (c) were used as fixed predictors and the average values from the 200 replicates of each dispersal trait at the last time step as the response variable. SS = sum of squares; MS = mean of squares; d.f. = degrees of freedom, F = F-Statistic; P = probability. Results from both predictors and their interaction were statistically significant under an alpha-level of 0.05.

Trait 1 – D_0					
	SS	MS	d.f.	F	P
Net	4.311	1.44	3	1087.84	<0.001
c	99.517	49.76	2	37671.98	<0.001
$c \times \text{Net}$	14.845	2.47	6	1873.19	<0.001
Residual	3.154	0.001	2388		
Total	121.827		2399		
Trait 2 – β					
	SS	MS	d.f.	F	P
Net	28880.6	9960	3	11609	<0.001
c	53481.4	26741	2	31166	<0.001
$c \times \text{Net}$	40181.5	6697	6	7805	<0.001
Residual	2048.9	0.001	2388		
Total	125592.4		2399		
Trait 3 – α					
	SS	MS	d.f.	F	P
Net	1551.4	517.134	3	180.73	<0.001
c	1743.1	871.557	2	304.59	<0.001
$c \times \text{Net}$	1778.3	296.388	6	103.58	<0.001
Residual	6833	2.861	2388		
Total	11905.9		2399		

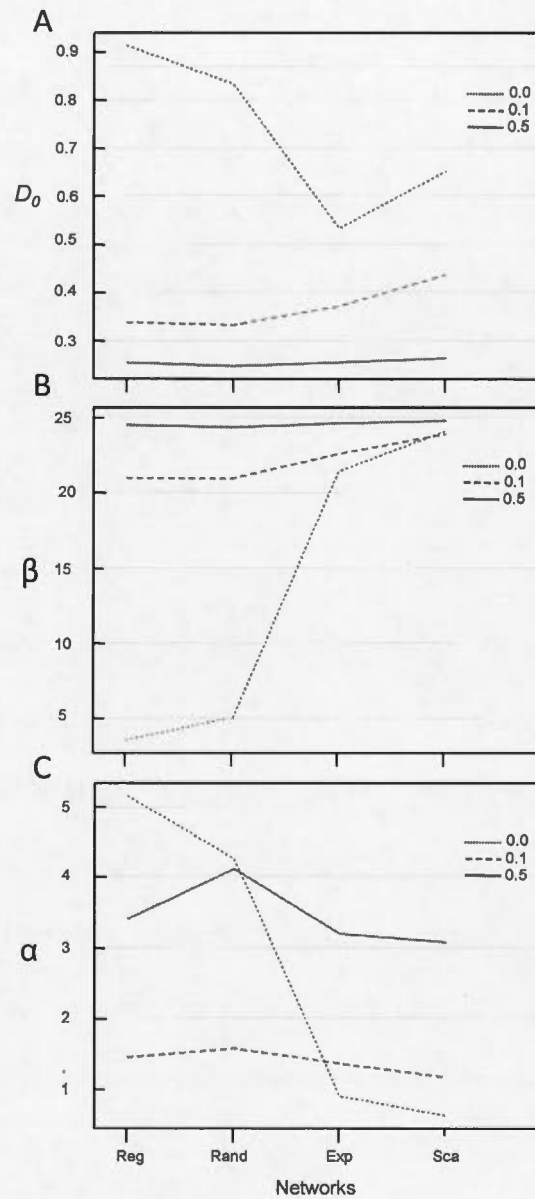


Figure 1.4. Results from two-way ANOVA. Network structure (x-axis) and dispersal costs were used as fixed predictors and the average values from the 200 replicates of each dispersal trait (A) D_0 , (B) β and (C) α at the last time step as the response variable (y-axis). Each line represents a different fixed dispersal cost ($c = 0.0, 0.1$ or

0.5). Reg = Regular network, Rand = Random network, Exp = Exponential network and Sca = Scale-free network.

(negative correlation between patch connectivity and λ ; Figure 1.5) but not in regular and random networks due to their null or low variance in patch degree, respectively (results not shown). In simulations with 10% dispersal mortality, selection favoured inflection point (β) values close to the equilibrium density (K) in random and regular networks, while in more heterogeneous landscapes (exponential and scale-free), selection favoured higher β values (Figure 1.5B). For all networks the α trait had the largest variability across replicates compared to the other dispersal parameters (see Appendix A). Finally, the trait that controlled the asymptote of the curve (D_0) was rapidly selected (see Appendix A) and presented higher values in heterogeneous landscapes in contrast to more homogeneous spatial structures (Figure 1.3B). The average dispersal function from the last generation across replicates clearly shows that different dispersal strategies were selected in each spatial structure (Figure 1.3B). Overall, metapopulations from regular and random networks had more similar dispersal strategies whereas metapopulations from exponential and scale-free networks were slightly different from each other and clearly different from the strategies selected in homogeneous landscapes (Figure 1.3B). As expected, when we increased dispersal mortality to 50%, all metapopulations adopted fairly similar dispersal strategies irrespective of landscape structure (low D_0 and high β values; i.e., low dispersal probability triggered only at high densities; Figure 1.3C). The second

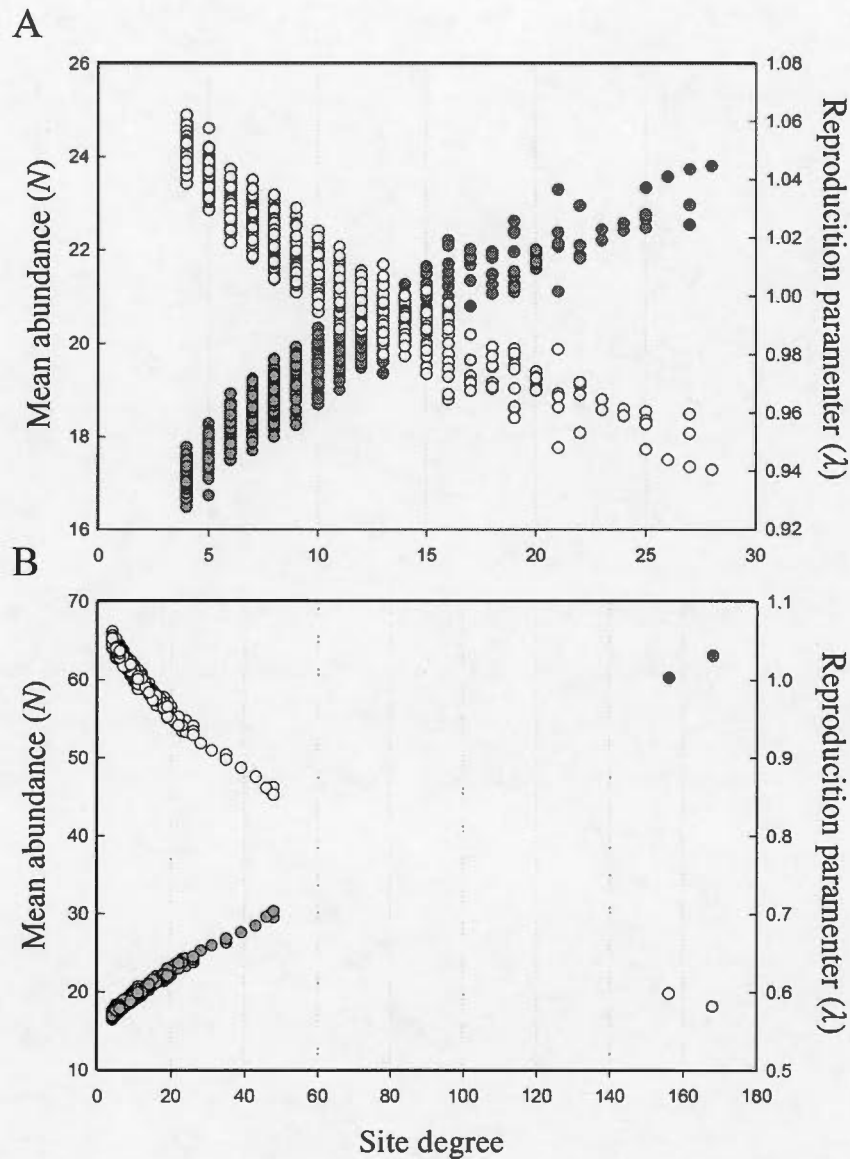


Figure 1.5. Relationship between site degree with the mean local abundance (gray circles) or the mean reproduction parameter (white circles) across the 40000 generations. The graphs represent one replicate from the (A) exponential network and one from the (B) scale-free networks in the 10% fixed dispersal mortality scenario. In general, patches with high degree support higher local abundance and produce lower mean fitness.

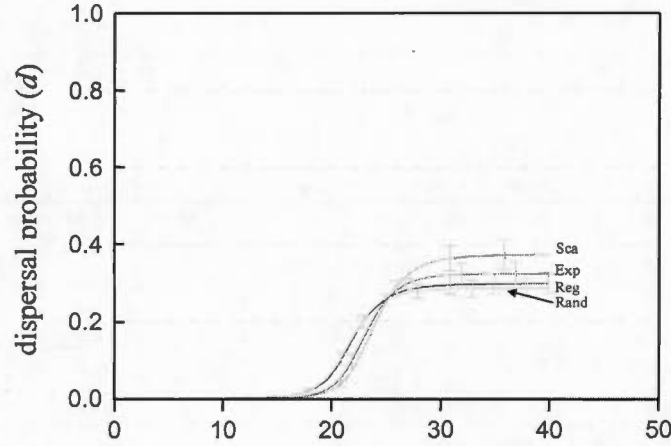


Figure 1.6. Average dispersal functions from the three dispersal traits of all individuals at the last generation across the 200 replicates from simulations with connectivity-dependent dispersal mortality. These logistic functions represent the average dispersal strategy selected in each network and stand for the potential dispersal rates. Horizontal bars represent the standard deviation of the dispersal strategies across the 200 replicates. Reg = Regular network, Rand = Random network, Exp = Exponential network and Sca = Scale-free network.

set of simulations with connectivity-dependent dispersal mortality shows that the results from our main simulation are robust and remain when we relaxed the assumption of fixed dispersal mortality. Selection favoured the inflection point (β) values close to the equilibrium density (K) in random and regular networks, while in more heterogeneous landscapes (exponential and scale-free), selection favoured higher β values (Figure 1.6). The trait that controlled the maximum dispersal probability (D_0) was also higher for heterogeneous landscapes compared to homogeneously connected ones (Figure 1.6). As in the main simulation, the α trait

had the largest variability across replicates in all networks compared to the other two traits, suggesting that it was not under strong selection. Note that the overall dispersal mortality probability in this simulation was 15.39% for both regular and random networks, and 15.22% and 15.19% for the exponential and scale-free networks, respectively. These values were calculated by weighting the dispersal mortality probability of each patch by its degree for each replicate and then taking the average across the 200 replicates. In general, the dispersal strategies selected in these simulations were fairly similar to the ones obtained in the 10% fixed dispersal overall dispersal mortality.

In simulations without dispersal costs ($c = 0$), the dispersal strategies selected in regular and random networks changed drastically in relation to the simulations with dispersal costs (Figure 1.3A); in contrast, exponential and scale-free networks remained fairly similar, except for the selection of higher maximum dispersal probability (D_0) values. The α trait increased sharply in homogeneously connected landscapes resulting in individual dispersal probability increasing at a slightly faster rate once the population threshold was reached in the patches of these landscapes. Moreover, β values decreased to ≈ 5 , selecting for a highly dispersive strategy where individuals migrated even when patches were empty. Again, the dispersal strategies selected in this set of simulations showed clear differences between homogeneously

(regular and random) and heterogeneously (exponential and scale-free) connected landscapes (Figure 1.3A).

Although there was one dispersal strategy clearly favoured by selection in each network structure, there were always multiple dispersal strategies at any one point in time that were maintained by a mutation-selection-drift balance. This was true regardless of dispersal mortality (Figure 1.7). Nevertheless, there were some differences in the magnitude of this variability. For instance, α had much greater variation across homogeneous networks in simulations without dispersal cost (Figure 1.7C) or very high cost (Figure 1.7I) compared to the ones with moderate cost (Figure 1.7C). In heterogeneous networks, the variability of this trait was slightly higher in simulations with moderate or high dispersal cost (Figure 1.7C, Figure 1.7I).

Results from the contest experiment between metapopulations evolved in different network types showed that, in general, the fitness advantage conferred by dispersal strategies of resident metapopulations was sufficient to resist invasion from individuals evolved in non-resident metapopulations (Figure 1.8). Resident metapopulations from regular networks only performed slightly better against

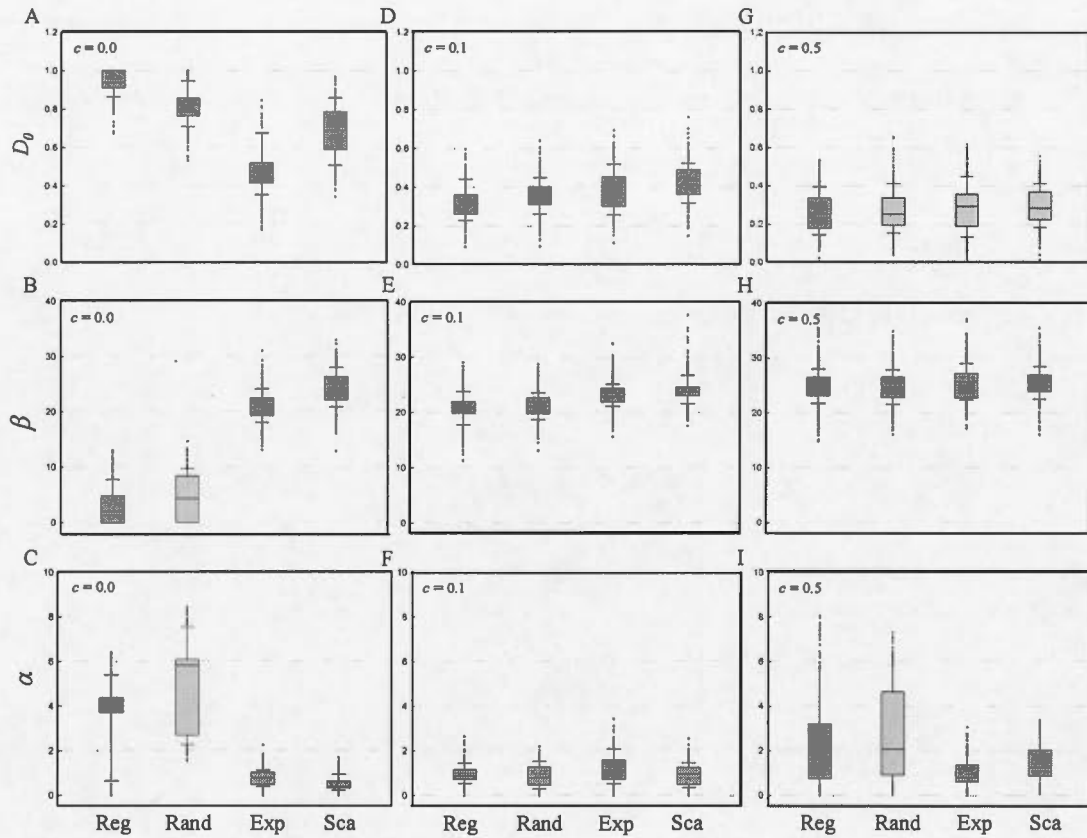


Figure 1.7. Box plots representing the distributions for the three dispersal parameters at equilibrium in the last generation. The bottom and top boundary of the box plots represent the 25% and 75% percentiles, respectively while the line within the box plots represents the median. Bottom and top whiskers outside box plots represent 10% and 90% percentiles. Data comes from one replicate of each network type. Columns represent, from left to right, simulations with no mortality ($c = 0$), simulations with 10% dispersal mortality ($c = 0.1$) and simulations with 50% dispersal mortality ($c = 0.5$). (A) (D) (G) D_0 = maximum dispersal probability; (B) (E) (H) β = inflection point; (C) (F) (I) α = steepness of the curve at the inflection point. Reg = Regular network, Rand = Random network, Exp = Exponential network and Sca = Scale-free network.

invaders from scale-free and exponential networks. In this case, the average proportion of residents (APR) ranged between 55 and 60%, while it was $\approx 50\%$ against random and control invaders. Resident random-network metapopulations had an advantage only against invaders from scale-free networks. Resident metapopulations from exponential networks outperformed invaders from random and

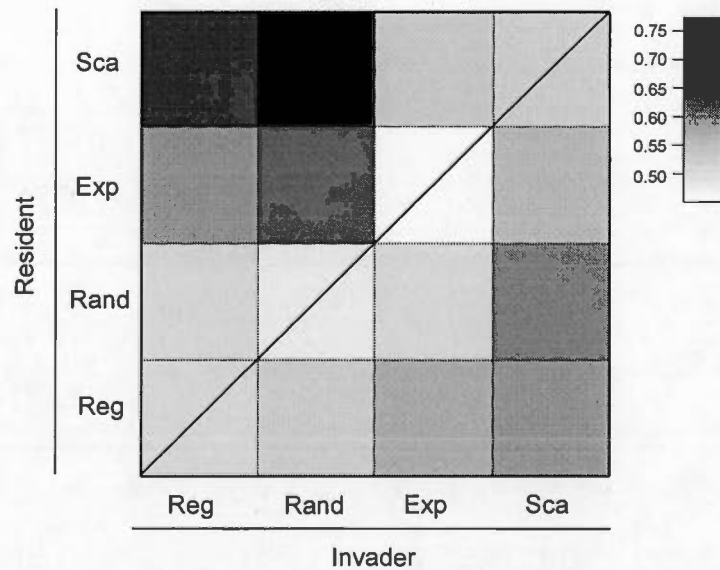


Figure 1.8. Results from contest simulations. Heatmap displaying the across-replicate average proportion of residents on the last timestep of each contest simulation. For instance, when the resident individuals were from scale-free networks, their final average proportion against invaders from regular networks was above 70%. The diagonal indicates control simulations and the average proportion of resident is, as expected, about 50% for all of them.

regular networks while it performed only slightly better than invaders from scale-free networks. Finally, resident metapopulations from scale-free networks clearly outperformed invaders from homogeneously connected networks (APR >70%) but were not able to win against invaders from exponential networks (APR $\approx$ 50%). Control simulations (i.e., invaders and residents from the same network type) behaved as expected, where both had similar odds of winning and the average proportion of each metapopulation across the 200 replicates was about 0.5. Moreover, the variation in dispersal traits within landscapes (Figure 1.7) was important in the contest simulations because, in some cases, it allowed the adaptation of invaders to a different selection pressure (i.e., different spatial structure) before being eliminated by the residents. The sensitivity analysis showed that under all tested scenarios the results were robust to parameter changes (Appendix B). The dispersal strategy adopted in each network across tested scenarios was fairly similar to the ones adopted in the original simulation with 10% dispersal cost.

1.5. Discussion

There is an increasing recognition that the spatial structure of landscapes influences evolutionary processes (Bonte *et al.*, 2006; Urban & Skelly, 2006; Baguette & Dyck, 2007; Büchi & Vuillemier, 2012). Indeed, the application of spatially-explicit as opposed to spatially-implicit models has shown that the spatial geometry between patches matters for dispersal evolution (Travis & Dytham, 1998), especially when the

environment is heterogeneous (Travis & Dytham, 1999; Poethke *et al.*, 2010; Büchi & Vuillemier, 2012). However, these models assume that patches are equally connected, which is not the case in natural landscapes (Baguette & Dyck, 2007; Baguette *et al.*, 2013). To our knowledge, this is the first study showing that variation in connectivity across patches also has important implications for dispersal evolution. Our results clearly indicate the possibility that landscape structure selects for different strategies (Figure 1.3) depending on the costs of dispersing.

Under extreme dispersal mortality (50%), selection favoured extremely sedentary individuals, which has been shown by previous studies (Poethke & Hovestadt, 2002; Poethke *et al.*, 2003; Kun & Scheuring, 2006). The high rate of dispersal mortality eclipsed the indirect costs of spatial variation in fitness on heterogeneous networks thus promoting dispersal strategies that were similar across all networks (Figure 1.3C). In contrast, different dispersal strategies were selected under low (10%) or zero dispersal mortality and we focus our analysis below on contrasting homogeneously and heterogeneously connected landscapes under these dispersal costs. Note that the conclusions taken from the model with a fixed 10% dispersal mortality are also valid for the connectivity-dependent dispersal mortality simulation as similar dispersal strategies evolved in both scenarios (Figure 1.6). In regular and random networks, under low dispersal mortality, selection favoured the evolution of somewhat sedentary individuals, which dispersed mostly once local abundance

reached the equilibrium density ($\beta \approx K = 20$) and, even then, with a somewhat low probability ($D_0 < 0.35$; Figure 1.3B). This is in agreement with other theoretical models, which have shown that if dispersal is a function of local density, almost no dispersal occurs when abundances are below the equilibrium density ($N < K$) in stationary populations (Poethke & Hovestadt, 2002; Kun & Scheuring, 2006; Travis *et al.*, 2009). Alternatively, when there was no dispersal cost ($c = 0$), selection favoured the evolution of highly dispersive individuals ($D_0 \approx 0.8-0.9$; $\beta \approx 5$; Figure 1.3A). These results were due to the fact that spatial variation in abundances (the only parameter influencing reproduction) was low in homogeneously connected landscapes as they all received, on average, a similar number of individuals from other patches. Therefore, the probability of dispersing into a better patch with lower abundances is similar to dispersing into an unfavourable patch. Consequently, when $c = 0.1$, the dispersal cost outweighs the small potential benefit of dispersing. In contrast, when there is no dispersal mortality, these homogeneously connected landscapes select for highly dispersive strategies due to the lack of both direct and indirect cost to dispersal (Figure 1.3A).

The novelty of the present study comes from networks with high variance in patch connectivity (i.e., exponential and scale-free), an aspect of landscape structure that has not been considered in previous studies, which clearly showed the potential for selection of alternative dispersal strategies. For instance, the importance of low

dispersal mortality as a selective force in dispersal traits is drastically reduced within heterogeneously connected landscapes. The strategy adopted by individuals in these networks was fairly similar between simulations with low dispersal cost ($c = 0.1$) and without it, differing only in the magnitude of maximum dispersal probability (D_0 ; Figure 1.3A, Figure 1.3B). Within such networks, highly connected patches receive a much greater number of immigrants than poorly connected ones. This asymmetric flow of individuals creates considerable variability in abundances (Figure 1.5), which in turn generates variability in density-dependent competition across patches. For instance, the most and least connected patches in the scale-free network have an average abundance over time of 65 and 16, respectively (Figure 1.5B). Therefore, individuals in isolated patches will only disperse when populations exceed their equilibrium density ($N > K$; $\beta \approx 22$ or $\beta \approx 24$ in exponential and scale-free networks, respectively; Figure 1.3A, Figure 1.3B) because there is a high probability to disperse into a highly connected and crowded patch (i.e., most patches are linked to them). Such a dispersal strategy incurs an additional cost to fitness compared to individuals that disperse at the equilibrium density. Therefore the former are more likely to disperse (i.e., higher D_0) when the patch reaches the threshold density (β) in contrast to individuals from homogeneously connected landscapes if there is a direct cost to dispersal (Figure 1.3B). However, in the absence of dispersal mortality ($c = 0$), individuals from heterogeneously connected landscapes have a lower D_0 than those in

homogeneous networks (Figure 1.3A), because the former still suffer an indirect cost from dispersal by potentially immigrating into an unfavourable patch.

Dispersal strategies can be considered as regional adaptations (Urban & Skelly, 2006), because they give a long-term fitness advantage to individuals at the landscape scale (i.e., network) while not having any adaptive value at the local scale (i.e., patch) (Hanski *et al.*, 2004). Indeed, the results obtained in the contest simulations reinforce the idea of a selective effect promoted by the landscape structure on dispersal strategies (Figure 1.8). Resident populations from homogeneous landscapes, where the selective pressure is lower, were more likely to be invaded than resident populations evolved in heterogeneous landscapes, which exert a stronger selection pressure. In these landscapes, invading populations from regular or random networks were, on average, not able to adapt their dispersal strategy fast enough and were maintained at a lower relative abundance compared to the resident populations. Note, however that they did outperform the heterogeneous landscapes in a few replicates, highlighting the importance of the variability in dispersal strategies across individuals (Figure 1.7).

The potential to adapt dispersal strategies to novel landscapes with different spatial arrangement of habitats should be relevant for species shifting their geographical ranges in response to climate change as well as invasive species extending their ranges to non-native regions (Travis *et al.*, 2013). Most species do not live in a

continuous homogeneous habitat, thus their ranges are constrained by dispersal dynamics (e.g., colonization and extinction) that are regulated by the availability of suitable habitat patches, their quality (e.g., size, resource abundance) and the connectivity among them (Kubisch *et al.*, 2014). Successfully predicting if species will be able to shift (or expand) their ranges is contingent on how they move across landscapes with different spatial configurations (Hodgson *et al.*, 2012). Populations at the core of the species' range most likely inhabit landscapes with low variance in connectivity among patches because more suitable habitats are available for them while populations at the edge should be coping with sparsely distributed habitat patches that potentially have a higher variance in connectivity. Thus, it is possible that different dispersal strategies are being selected between these populations (Travis *et al.*, 2009).

Empirical evidence indicates that landscape spatial properties can exert selection on dispersal traits (Matter *et al.*, 2009; Cote & Clobert, 2010). For instance, an increase in the degree of fragmentation across landscapes was significantly related to a monotonic reduction in dispersal propensity of *Boloria eunomia* butterflies (Schtickzelle *et al.*, 2006). However, butterflies in highly fragmented landscapes that did disperse were more likely to survive than migrants from more connected ones, indicating that an adaptive behaviour was adopted in order to reduce the costs of dispersing (Schtickzelle *et al.*, 2006). Other studies demonstrated that the degree of connectivity between patches affect the dispersal propensity in spiders (Bonte *et al.*,

2006) and lizards (Cote & Clobert, 2010). Moreover, Merckx and co-workers (Merckx *et al.*, 2003) showed experimentally that the dispersal propensity of speckled woods butterflies (*Pararge aegeria*) was higher or lower whether the individuals were born from parents sampled in woodland (less fragmented) or agricultural landscapes (more fragmented), respectively, suggesting that differences in dispersal propensity might have a genetic basis.

It should be noted that the results of our model are based on the assumption that dispersal propensity respond positively to density, which is commonly found in nature (Matthysen, 2005; Bitume *et al.*, 2013). However, many species exhibit no or a negative relationship between dispersal propensity and local density. Examples for these cases are rare sexual species where mate availability is an important factor for dispersal decisions (Shaw & Kokko, 2014), invasive species at the edge of their ranges (Taylor & Hastings, 2005) or cooperative species. These species may suffer from Allee effect and thus have a fitness disadvantage in low-density sites. In these cases, the sigmoid dispersal function used in our study should be inverted, where the asymptote of the curve (D_0) would occur at low densities and dispersal propensity would decrease as density increases. For instance, in the case of a rare sexual species, we may predict that heterogeneous landscapes would select for low dispersal rates (low D_0 and high β) due to the uneven distribution of individuals across patches. After colonizing highly connected patches, individuals would not emigrate from them

to avoid suffering from Allee effects in isolated low-density patches. These high-connectivity patches would behave like oceanic islands, in which losses of dispersal ability in colonists populations have been extensively document due to the high risk of emigrating from them (Carlquist, 1974). Conversely, in homogeneously connected landscapes, individuals should be spread more evenly across patches. In this case, it would become advantageous to disperse to find potential mates and one would expect selection to favour higher dispersal rates (higher D_0 and lower β).

1.6. Conclusion

In summary, we have shown that landscape connectivity can promote the evolution of dispersal strategies and, more importantly, that these strategies provide a long-term fitness advantage to the individuals at the regional scale. These results may highlight the importance of integrating the spatial context of habitat patches in order to predict how evolution affects the spread of species (Bonte *et al.*, 2010) and thus suggests important implications for the study of species invasiveness and range shift under climate change. Results also suggest the potential for the evolution of dispersal to influence metapopulation and metacommunity dynamics by altering the connectivity depending on regional landscape heterogeneity. We acknowledge that empirical dispersal data are difficult to obtain (Baguette & Dyck, 2007); however, we hope that experimental facilities designed to study dispersal such as the *Metatron* (Legrand *et*

al., 2012) and recent developments in spatial networks, least-cost-path analysis and other indirect methods to quantify dispersal and connectivity might address this issue (reviewed in Jacobson & Peres-Neto, 2010; Baguette *et al.*, 2013) and allow tests of the theoretical predictions demonstrated here.

CHAPTER II

RANGE EXPANSION DEPENDS ON THE INTERACTION BETWEEN DISPERSAL STRATEGIES AND POPULATION GROWTH RATE

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2.1 Summary

Understanding what constrain species geographical ranges have been a longstanding goal in evolutionary ecology. Notably, the eco-evolutionary dynamics of different dispersal strategies on range formation have received considerable attention from recent theoretical studies. It has been shown that density-dependent (DD) dispersal promotes accelerated emigration rates and wider geographical ranges compared to unconditional dispersal strategies (i.e., density-independent; DI). However, these predictions are based on models in which 1) there has been no consideration of population growth rates, 2) local adaption is assumed to be unimportant, and 3) patches across the landscape are equally connected. Here we relax these assumptions and use an individual-based model (IBM) to simulate species range dynamics in which both dispersal propensity and environmental tolerance are allowed to evolve (i.e., local adaptation is possible). We compared the range expansion speed of species following either DD or DI dispersal across an environmentally heterogeneous

landscape in which survival depends on their adaptation to the local environment (i.e., *via* stabilizing selection). This comparison was evaluated under a full-factorial design where we varied the degree of among-patch connectivity, the type of environmental fluctuation and population growth rates. Our results demonstrate that species with low population growth rates expand their range faster following DI dispersal while species with high growth rates perform better with DD dispersal but not in heterogeneously connected landscapes in which both strategies performed similarly. Finally, range expansion was generally slower in red-noise than in white-noise environmental fluctuations regardless of the dispersal strategy. Our results highlight that the evolutionary dynamics of local adaptation as well as changes in population growth rates and landscape structure can alter substantially the speed of range expansion under different dispersal strategies. As such, conclusions of previous models in which the general superiority of DD dispersal outperform DI dispersal in range expansion should be taken with reservation.

2.2 Introduction

Species' geographic ranges are the result of extinction and colonization dynamics regulated by environmental conditions, dispersal, demographic and evolutionary processes (Holt, 1997; Holt, 2003; Kubisch *et al.*, 2014), and represent the expression of a species' niche in space (Sexton *et al.*, 2009). Species generally inhabit environmental conditions where they exhibit positive net growth rates, i.e., the range

of habitat conditions to which they are adapted (Holt, 2003). Dispersal allows species to track their preferred environments provided that the landscape spatial structure is permeable enough for their movement (Baguette & Dyck, 2007). If environment changes to poor conditions and dispersal is not possible, populations may go extinct if they cannot adapt to the new environment (Opdam & Wascher, 2004). Thus, local adaptation and dispersal are key processes underlying range dynamics (Holt, 2003; Kubisch *et al.*, 2013b) and are crucial factors in determining species ability to respond to environmental changes, especially in fragmented landscapes (Opdam & Wascher, 2004; Kokko & López-Sepulcre, 2006; Travis *et al.*, 2013).

Notably, local adaptation and dispersal are known to feedback on each other (Holt & Gomulkiewicz, 1997). On one hand, dispersal determines the range of habitats that a species will experience, thus modulating the selection forces acting on its niche requirements (Holt, 2003). On the other hand, the spatiotemporal variation in habitat conditions will influence dispersal evolution (Poethke *et al.*, 2003; Bowler & Benton, 2005). Indeed, many organisms use cues about their own state (e.g., physiology, performance) and the environment to make dispersal decisions (Clobert *et al.*, 2009; Bocedi *et al.*, 2012). Notably, it has been shown that many species use population density (i.e., as a proxy for competition or number of mates) to decide whether to disperse or not (Bowler & Benton, 2005; Bitume *et al.*, 2013). For instance, dispersal is positively selected when kin or intraspecific competition for local resources is high (Hamilton & May, 1977; Kubisch *et al.*, 2013a) or to cope with high temporal

variability in habitat conditions (Poethke *et al.*, 2003). Conversely, temporally constant but spatially heterogeneous environments select against dispersal (Poethke & Hovestadt, 2002). Recently, theory on the advantages of informed dispersal over a random strategy in promoting regional persistence, range expansion and range size has been developed (Travis *et al.*, 2009; Kubisch *et al.*, 2011; Poethke *et al.*, 2011; Bocedi *et al.*, 2012). These models predict that species adopting density-dependent (DD) dispersal strategies have accelerated range expansion rates (Travis *et al.*, 2009) and wider geographic ranges (Kubisch *et al.*, 2011) than species that disperse randomly (i.e., density-independent; DI).

Although these models have provided a number of conceptual advances regarding the eco-evolutionary dynamics of dispersal, they assume that local adaptation is negligible. This premise is unlikely given the increasing number of studies showing that species are able to adapt rapidly to new environmental conditions (Al-Hiyali *et al.*, 1993; De Meester *et al.*, 2011), especially within timescales in which range expansion occurs (Davis & Shaw, 2001; Urban *et al.*, 2007). For instance, the evolution of earlier flowering time increased dramatically the fitness of populations at the northern expansion front of an invasive wetland plant species (Colautii & Barrett, 2013). Species invasion have been shown to be frequently accompanied by rapid morphological changes (Huey *et al.*, 2000; Dalrymple *et al.*, 2015), further highlighting the importance of local adaptation during expansion. In contrast, models evaluating the importance of dispersal strategies during range expansion either

consider an homogeneous environment (i.e., all patches are equal; Travis *et al.*, 2009) or spatiotemporal variation in carrying capacity, reproductive (or mortality) rates across patches to which adaptation is not possible (e.g., Poethke *et al.*, 2003; Kubisch *et al.*, 2011; Bocedi *et al.*, 2012). Moreover, most models investigating dispersal strategies during range expansion assume that all patches are equally connected (i.e., no variance in connectivity) (Travis *et al.*, 2009; Kubisch *et al.*, 2014). However, heterogeneity in landscape connectivity is rather the norm in nature, especially with current rates of habitat fragmentation, where more accessible patches will have more immigrants than isolated ones (Baguette & Dyck, 2007; Baguette *et al.*, 2013). Therefore, landscape connectivity influences variation in demographic processes among populations, which in turn may affect dispersal and niche eco-evolutionary dynamics, which are two key factors in species range expansion (Bonte *et al.*, 2006; Schtickzelle *et al.*, 2006; Hodgson *et al.*, 2012). Finally, models contrasting DD and DI dispersal during range expansion usually test for a single population growth rate value (Travis *et al.*, 2009; Kubisch *et al.*, 2011). However, given that DD dispersal is positively selected under high kin and individual competition (Hamilton & May, 1977; Poethke & Hovestadt, 2002), species with low and high population growth rates might differ regarding emigration rates under density-dependent and independent dispersal strategies.

In the present study, we aim at investigating how local adaptation, landscape connectivity and population growth influence the range expansion of species

following either DD or DI dispersal. To do so, we combined an individual-based model (IBM) frequently used in studies of dispersal evolution and range expansion (e.g., Poethke & Hovestadt, 2002; Kubisch *et al.*, 2011; Kubisch *et al.*, 2014) with assumptions from models that study adaptation to a continually changing environment for a single character (e.g., Burger & Lynch, 1995; Lande & Shannon, 1996). We predict the following outcomes: (1) density-dependent (DD) dispersal should promote faster range expansion for species with high growth rates because there should be a stronger positive selection for this strategy due to increased competition. Conversely, species with low growth rates will expand faster following a DI dispersal strategy because individuals will emigrate even at low densities; (2) DD dispersal should promote faster expansion rates than DI dispersal in heterogeneously-connected landscapes because the former strategy may confer adaptation to alleviate the fitness cost caused by among-patch variation in population density due to the asymmetric flow of individuals in these landscapes (see Chapter 1); (3) Given that in unpredictable environments there is no advantage to use information for dispersal decisions (Bocedi *et al.*, 2012), we predict that DD dispersal will lead to faster range expansion in scenarios with no environmental fluctuation while species using DI dispersal will expand faster under high environmental fluctuation.

2.3 Methods

We adapted early spatially explicit individual-based models with discrete generations and logistic population growth that have been frequently used in studies of dispersal evolution (Poethke & Hovestadt, 2002; Poethke *et al.*, 2007; Bocedi *et al.*, 2012) and range expansion (Travis *et al.*, 2009; Kubisch *et al.*, 2013b).

2.3.1 Landscape connectivity

To represent different degrees of connectivity, we considered two landscape types: one where all patches have similar number of connections and one with considerable variance in patch connectivity. The homogeneously connected landscape consisted of a rectangular grid containing 200 rows (y-dimension) x 30 columns (x-dimension), totalizing 6000 habitat patches connected to their eight closest neighbours (i.e., Moore's neighbourhood). To keep the number of patches equal to 6000 in the heterogeneously connected landscape, we increased the number of columns to 41 and made a number of patches unavailable to immigration to create barriers to dispersal and thus variance in connectivity (see Figure 2.1A). The number of available patches among rows was defined by an exponential distribution where only a few rows had very low number of patches available (creating bottlenecks in the landscape) whereas most rows had many patches available (Figure 2.1B). In both cases the borders in the y-dimension were wrapped in a torus to avoid edge effects whereas the borders from

the x -dimension have reflecting boundaries given that colonization took place along the columns of the matrix (Figure 2.1A).

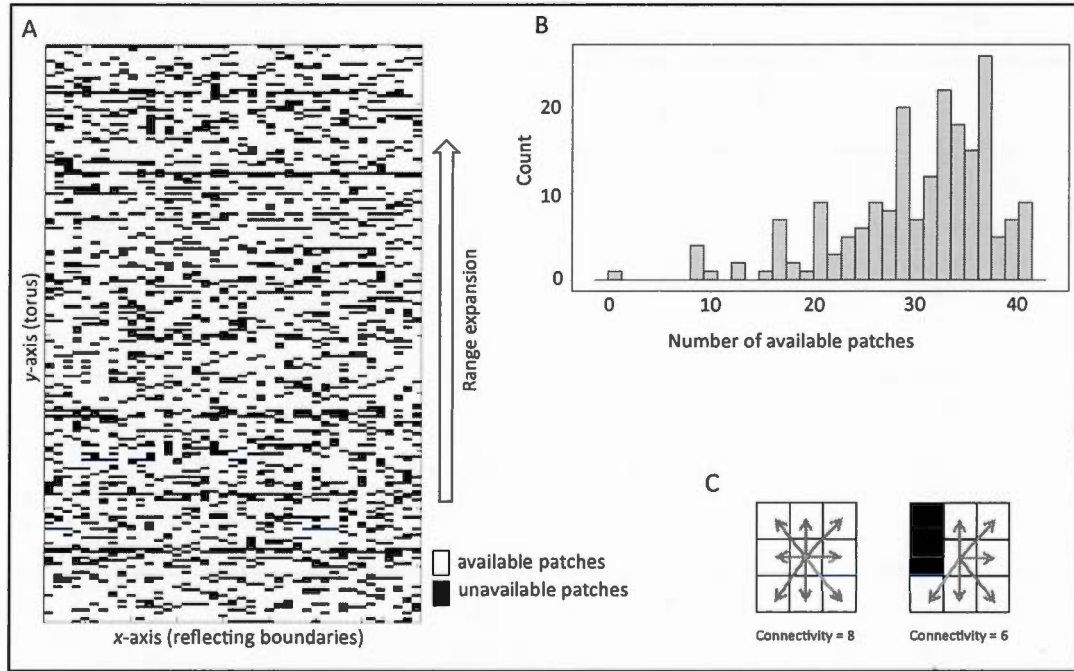


Figure 2.1. Structure of the heterogeneously connected landscape. (A) Spatial configuration of available and unavailable patches. Note that the exact structure was used across all replicates. Range expansion occurs along the y -axis. (B) Frequency distribution of available patches across rows from the y -axis (C) Patches are connected to their eight nearest neighbours minus unavailable patches; for instance, the second patch is near 2 unavailable patches, thus individuals emigrating from it may only choose among the six other neighbouring patches.

2.3.2 Environmental gradient

Each patch was characterized by an environmental value $e_{x,y}$ representing the optimum phenotype value for survival in that patch. The environment was generated

with the diamond-square algorithm (Miller, 1986), thus creating a spatially autocorrelated set of environmental values. These values were arbitrarily bounded between 0 and 15 and represent the steepness of the environmental gradient (Kubisch *et al.*, 2013b) where the largest variation occurs across the y -axis (see Figure 3.1 in Chapter III for an example). Note that all replicates started with the same environmental structure (i.e., same values across patches) as well. We tested three different scenarios of environmental stochasticity: 1) no temporal fluctuation (i.e., stable), 2) with auto-correlated temporal variability (i.e., red noise) and 3) with random temporal variability (i.e., white noise). Temporal variability in the environment was created through a first-order autoregressive process (Ruokolainen *et al.*, 2009) in which the environmental value e of the patch (x, y) at time $t+1$ was given by

$$e_{x,y,t+1} = e_{x,y,t} (1 + \varepsilon_{x,y,t}),$$

where ε is an environmental noise value defined as

$$\varepsilon_{x,y,t+1} = \kappa \varepsilon_{x,y,t} + \omega \sqrt{1 - \kappa^2},$$

where κ is the autocorrelation coefficient and ω is a random normal variable with mean 0 and a relatively small standard deviation 0.3. Under temporal autocorrelation, κ was set to 0.85 whereas under no temporal autocorrelation, κ was set to 0. For each patch (x, y) , its environmental value $e_{x,y}$ was constrained to vary between $[-1.5 \sigma_y, 1.5 \sigma_y]$ in which σ_y represents the standard deviation of environmental values across patches belonging to row y .

2.3.3 Individuals

Each individual was characterized by its dispersal phenotype d , environmental optima phenotype e_{opt} and patch location. The sequence of events at each time step was as follows: reproduction, adults perish (i.e., individuals are semelparous), offspring survival and dispersal; we therefore assumed no overlap between generations.

2.3.4 Genetics

We considered an explicit genetic structure for the phenotypic components for dispersal d and environmental optimum e_{opt} . Such as in Kubisch *et al.* (2014), the individuals carry a single allele value for the dispersal phenotype (i.e., d). The environmental optima phenotype (i.e., e_{opt}) was determined by additive genetic variation at multiple loci with no dominance or epistasis where the individual's phenotype is the sum of the allelic values over all n loci (Holt & Barfield, 2011). This approach was used by Burger and Lynch (1995) while studying adaptation to a continuous environment for a single character. Note that in preliminary simulations, while varying the number of loci from 1 to 6 we found that results were not affected (results not shown), so we considered a genetic structure with 3 loci. Alleles for d and e_{opt} inherited by the offspring had a small probability of mutation ($m = 10^{-3}$), in which a Gaussian-distributed random number with mean 0 and standard deviation 0.2 was drawn and added to the allele's value.

2.3.5 Reproduction

At each patch (x,y) at a given generation t , the average fertility of individuals $\mu_{x,y,t}$ was drawn from a lognormal distribution with mean μ and standard deviation σ ($= 0.05$) that created a small spatiotemporal variability in growth rates. We tested three different scenarios for growth rates: small ($\mu = 1.5$), intermediary ($\mu = 2$) and high ($\mu = 2.5$) fertility. All individuals were females and they gave birth to a number of offspring drawn from a Poisson distribution with mean $\lambda_{x,y,t}$ assumed to be independent of the individual's fit to the local environment.

2.3.6 Offspring survival

Offspring survival was regulated by environmental matching s_1 and local competition s_2 ; environmental matching was set as density-independent mortality and described by the following equation:

$$s_1 = \exp\left(-\frac{1}{2}\left(\frac{e_{opt} - e_{x,y}}{\eta}\right)^2\right)$$

where η denotes the niche breath of individuals which was set as 0.5 for all simulations and therefore assumed a Gaussian shape relationship between the individual's phenotype and the local environment. Offspring survival regulated by

local competition was simulated using Hassell (1975) density-dependent growth model:

$$s_2 = \frac{1}{1 + \left(\frac{\mu - 1}{K}\right) N_{x,y,t}}$$

where K refers to the equilibrium density while $N_{x,y,t}$ is the population size of patch (x,y) at generation t . The final survival probability was simply calculated as $s = s_1 s_2$. At each time step, a random uniform number between 0 and 1 was drawn for each individual, who died if this number was greater than s .

2.3.7 Dispersal

After survival, offspring dispersed with a probability d given by their dispersal phenotype. Individuals dispersed between adjacent patches such that species maintained their range cohesion and thus assuming biologically realistic processes regulating species' range expansion (e.g., environmental heterogeneity, dispersal limitation; Pulliam, 2000; Svenning & Skov, 2007). Dispersal followed either a density-dependent (DD) or a density-independent (DI) strategy. Under DI, individuals carried a dispersal allele varying between 0 and 1 that determined the probability of emigrating. DD dispersal was modelled using the density-dependent function developed by Poethke and Hovestadt (2002), in which there is no dispersal below the

threshold C_{TH} , and a non-linear increase in dispersal probability for densities above this threshold:

$$d = \begin{cases} 0 & \text{for } \frac{N_{x,y}}{K} \leq C_{TH} \\ 1 - \frac{C_{TH}K}{N_{x,y}} & \text{for } \frac{N_{x,y}}{K} > C_{TH} \end{cases}$$

The single allele value from their dispersal locus determined their critical threshold population density C_{TH} . At each time step, a random uniform number between 0 and 1 was drawn for each individual and dispersal occurred if this number was smaller than d . Individuals that dispersed had a mortality probability of $c = 0.2$, indirectly representing the various costs associated with dispersal such as predation risk, settlement failure, among others (Bonte *et al.*, 2012).

2.3.8 Model initialization and analysis

In all simulations, $K = 20$ individuals were distributed across patches within the area between $y = 1$ and $y = 10$ for 500 generations to allow for species to reach quasi-equilibrium dynamics. Dispersal alleles of each individual were drawn randomly from a uniform distribution between 0.8 and 1 in the DD scenario and between 0 and 0.2 in the DI scenario. These values were set by initial simulations and led to approximately similar dispersal rates in both scenarios (i.e., 20% dispersal rates). Initial values for the environmental optima alleles (e_{opt}) were chosen so that their sum

would be equivalent to the local patch's environment (i.e., individuals were perfectly adapted to their initial patch). After 500 generations, the remaining patches became available for the species to expand its range. The expansion phase was run for an additional 1000 generations.

We created a full-factorial design with environmental fluctuation, landscape connectivity, growth rates and dispersal strategies (Table 2.1) and, for each parameter combination, 20 replicates were performed. Expansion speed was measured as the outermost row (y -axis) in which the species was found at the end of the simulation, i.e., the range border location. We also measured emigration rates as the number of dispersers divided by the pre-dispersal population size, which was computed either for all populations across the landscape or for populations at the expansion front; the latter defined as the five rows of patches immediately preceding the northern range border. All simulations were performed in Matlab (Mathworks 2014).

Table 2.1. Simulation scenarios

Parameters	Scenario 1	Scenario 2	Scenario 3
Dispersal Strategy	Density-dependent	Density-independent	-
Intrinsic population growth rate (μ)	1.5	2	2.5
Landscape connectivity	Homogeneous	Heterogeneous	-
Environment	Stable	Red-noise fluctuation	White-noise fluctuation

2.4 Results

Whether DD or DI dispersal generated faster range expansions was dependent on the species growth rates (Figure 2.2). Species with low growth rates ($\mu = 1.5$) always dispersed faster following a DI dispersal strategy (Figure 2.2A) whereas species with high growth rates ($\mu = 2.5$) following a DD dispersal strategy expanded their range significantly faster only across the homogeneously-connected landscape either under a stable or white-noise environment (Figure 2.2C). Species with intermediary growth rates following a DI dispersal strategy exhibited faster range expansion under the stable and red-noise environment across homogeneously connected landscapes; no other statistical difference between dispersal strategies for the remaining scenarios was found (Figure 2.2B).

In general, these results supported our first hypothesis, which posited a faster expansion rate for the DI dispersal strategy under low growth rates whereas the DD dispersal would be favoured in species with high growth rates. In contrast, our second hypothesis was not supported given that greater variance in among-patch connectivity did not favour the expansion speed of species following DD dispersal for any combination of parameters (Figure 2.2). The only effect promoted by heterogeneously connected landscapes was to slow down the range expansion in comparison to homogeneously connected ones.

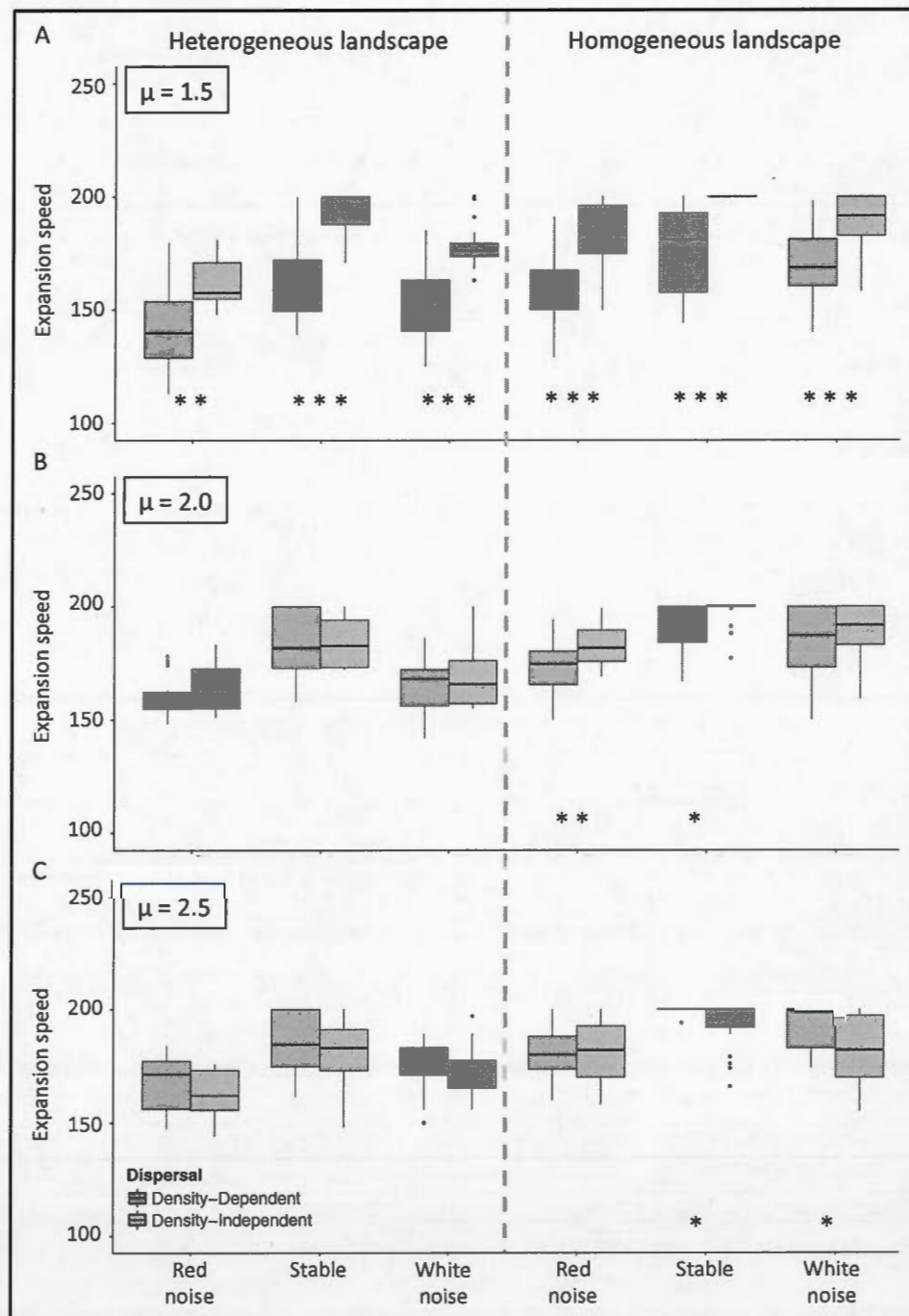


Figure 2.2. Boxplots depicting the overall expansion speed across all scenarios for species with (A) low, (B) intermediary and (C) high growth rates. Expansion speed was measured as the identity of the outermost row (y-axis) in which the species was

found at the end of the simulation. The bottom and top boundary of the box plots represent the 25% and 75% percentiles, respectively, while the line within the box plots represents the median. Top and bottom whiskers outside the box plots represent ± 1.5 times the distance between the first and third quartiles. Data beyond whiskers are outliers and plotted as dots. Significant differences between dispersal strategies within each scenario were tested using a two-sample *t*-test and *P*-values are represented as *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

However, this effect occurred regardless of whether the dispersal strategy was DD or DI (Figure 2.2). Our third prediction, i.e., DI dispersal favoured range expansion in fluctuating environments and DD dispersal favoured it in stable environments, was also not supported given that the degree of environmental fluctuation affected species ranges expansion speed similarly for both dispersal strategies. In general, species expanded their range faster in stable environments, followed by white-noise environments and the slowest range expansion occurred in the red-noise environmental models (Figure 2.2). This effect occurred similarly across different landscapes and species growth rates.

The analysis of emigration rates through time revealed an interesting pattern. In species with low growth rates ($\mu = 1.5$), evolution towards higher emigration rates occurred only at the expansion front, which was generally higher for the DI dispersal strategy (Figure 2.3). In species with intermediary growth rates ($\mu = 2$), both strategies evolved towards higher emigration rates at the expansion front (Figure 2.3)

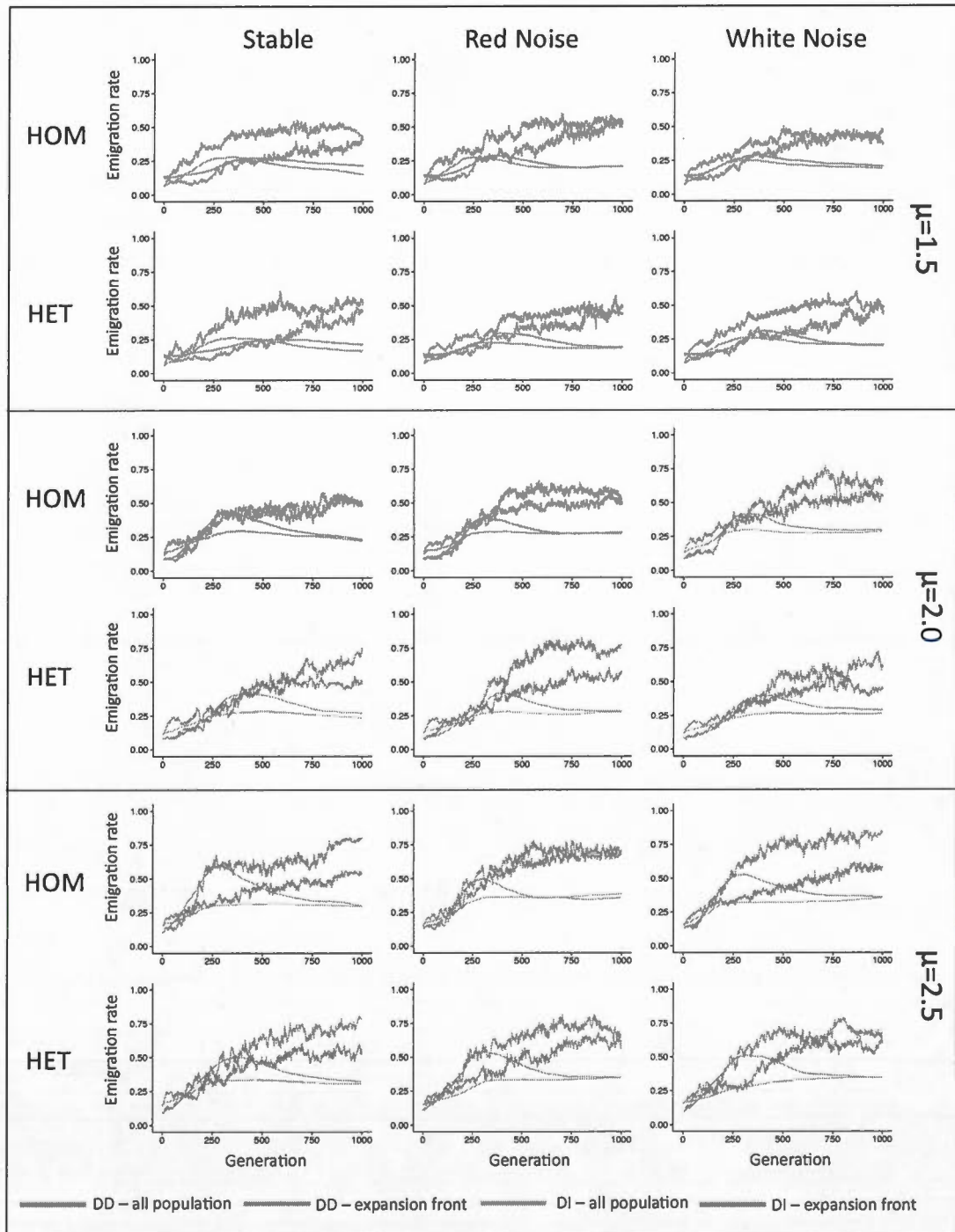


Figure 2.3. Emigration rates in both density-dependent (DD) and density-independent (DI) dispersal strategies for species with low (top panel), intermediary

(middle panel) and high (bottom panel) growth rates during the expansion phase. Lines in each plot represent average emigration rates, which were computed as the ratio of the number of dispersers and the pre-dispersal population size. Rates were computed across all populations (red (DD) and blue (DI) lines) or restricted to populations located in the first five rows at the expansion front (green (DD) and purple (DI) lines). Within each panel, top rows represent scenarios in homogeneously connected landscapes (HOM) while bottom rows represent scenarios in heterogeneously connected landscapes (HET). The left column depicts scenarios with stable environment; the middle column depicts scenarios with red-noise environmental fluctuation; the right column depicts scenarios with white-noise environmental fluctuation.

while when emigration rates were computed across all populations only the DD dispersal strategy evolved higher dispersal rates (Figure 2.3). Finally, for species with high growth rates ($\mu = 2.5$), DD dispersal always evolved higher emigration rates at both the expansion front and the entire range (Figure 2.3). The only exception was in the homogeneously connected landscape with red-noise fluctuation for which both DI and DD evolved similar emigration rates at the expansion front (Figure 2.3)

2.5 Discussion

In the present study, we investigated the conditions in which density-dependent (DD) and density-independent (DI) dispersal were favoured during range expansion across an environmental gradient. Range expansion was largely driven by a rapid evolution

of emigration rates at the expanding front (Figure 2.3). This process is known as spatial selection (Phillips *et al.*, 2010a), which is when highly dispersive individuals have a fitness advantage when emigrating to empty (i.e., competition-free) patches. Spatial selection was stronger for species with low population growth following DI dispersal whereas it was favoured in species following DD dispersal when they exhibited high population growth rates (Figure 2.3). This difference lies in an additional factor, which affects emigration rates during range expansion of species with high population growth rates but less so on species with low growth rates. It is known that marginal populations at the range expansion front have a strong kin structure, i.e., a progressive increase in relatedness due to repeated founder effects (Kubisch *et al.*, 2013a). Such process selects for higher emigration rates only when species follow a DD dispersal strategy. Because high growth rates enhance the effect of kin competition at the expansion front, DD dispersal had a strong increase in emigration rates for species with intermediary and high growth rates but not for species with low growth rates (Figure 2.3). Consequently, DI dispersal promoted significantly faster range expansion than DD dispersal for species with low population growth rates ($\mu = 1.5$) due to the absence of a strong kin structure at the expansion front. In species with intermediary growth rates ($\mu = 2$), both dispersal strategies led to similar range expansion speed across most scenarios, except within homogeneous landscapes with stable or red-noise environments, where DI dispersal still outperformed the density-dependent strategy (Figure 2.3). Finally, given the

increasing selective pressure of kin competition, faster range expansion was promoted by DD dispersal (compared to DI dispersal) only for species with high growth rates ($\mu = 2.5$) (Poethke *et al.*, 2007). However, such difference only occurred in stable and white-noise environments within homogeneous landscapes (Figure 2.3).

Interestingly, using a similar IBM, modelling a species with similar growth rates to the lowest value used in the present study ($\mu = 1.5$), Travis *et al.* (2009) reported faster range expansions for DD dispersal. However, their study differed in two major ways in relation to ours: 1) they modelled DD dispersal using a different function developed by Kun and Scheuring (2006) (used in Chapter I) and 2) they modelled a homogeneous environmental gradient. This difference could not be attributed to the dispersal function given that we also ran simulations with Kun and Scheuring (2006) function and it resulted in even slower range expansions compared to the DD function used in the present study (results not shown). Therefore, it is likely that the difference between our results lies in how the environment was simulated. Here we simulated a continuously-changing environment gradient (see Figure 3.1 in Chapter 3) that affects individuals survival probability (i.e., fitness) through stabilizing selection (e.g., Burger & Lynch, 1995). As such, our approach explicitly considers local adaptation during range expansion (Holt & Barfield, 2011), precluding populations at the expanding front to reach carrying capacity until individuals become locally adapted to the environment. This process slows down the range expansion of

species with low growth rates following density-dependent dispersal because it increases the lag between newly colonized habitat patches and the population reaching a threshold density required for individuals to start emigrating. Under a DI strategy, however, individuals disperse even if they are still not fully adapted to the local environmental and populations are below carrying capacity (Kubisch *et al.*, 2011; Bocedi *et al.*, 2012).

Contrary to what was initially predicted, landscape connectivity did not favour DD dispersal strategy during range expansion. In Chapter I, it was shown that DD dispersal could evolve in response to asymmetry in connectivity across patches due to spatial variation in demographic dynamics. However, this did not translate into faster range expansion for species following DD dispersal in heterogeneously connected landscapes. Given that we simulated an invasion of an empty landscape, the selective forces stemmed from the spatial variation in population density that could affect DD dispersal were not present during the expansion phase. DD dispersal should provide faster emigration rates than DI dispersal if the invaded landscape was already occupied by another competing species (Fronhofer *et al.*, 2015). In this case, the demographic dynamics of both species would be linked through competitive interactions and the spatial variation in the competitor's population density across landscapes with different connectivity patterns would provide the necessary selective forces to which DD dispersal (but not DI dispersal) could adapt.

Environmental fluctuation had the same effect across species with different growth rates and in both types of landscape structure. Species ranges expanded faster in stable environments but unexpectedly slower in the red-noise environmental model (i.e., positive temporal autocorrelation) compared to the white-noise model (Figure 2.2). Contrary to our original intuition (expectation), we now observed that this was the result of the red-noise model that created a sustained directional selection on the environmental optima phenotype over many generations, which narrowed the genetic variance of the population. Therefore, when the direction of the selection changed, the genetic load would suddenly increase and the lag between the population's average phenotype and the phenotypic optimum would be large enough for it to decline towards extinction (Lande & Shannon, 1996). Thus, under red-noise environmental fluctuation, suboptimal individuals were weeded out from the population, decreasing the population's genetic variance and thus increasing its susceptibility to changes in environmental conditions (Burger & Lynch, 1995). These local extinctions in turn slowed down range expansion. In contrast, when the environmental fluctuation was not temporally autocorrelated (i.e., white-noise model), there was no sustained directional selection on the environmental optimum, thus promoting a higher genetic variance, smaller genetic load, which safeguarded species against local extinction (Charlesworth, 1993). Despite the reduced average fitness due to the constant presence of sub-optimal individuals, random environmental variation selected for populations that had a lower fitness variance across generations, thus increasing persistence (Simons, 2011) and faster range

expansion. This implies that, for stochastic environments, the likelihood of a population to persist should depend on the frequency of environmental fluctuation through time (i.e., the size of each wavelength; Ruokolainen *et al.*, 2009), the duration of the organism's life-cycle relative to this frequency and how strong is the stabilizing selection on maladapted phenotypes (Burger & Lynch, 1995; Lande & Shannon, 1996).

Finally, there was an additive effect between landscape connectivity and environmental fluctuation independent of dispersal strategy. Heterogeneously connected landscapes have many poorly-connected patches (Figure 2.1) and, as such, their declining populations under environmentally-induced evolutionary load were less likely to be rescued from nearby populations (i.e., genetic rescue effect; Gomulkiewicz *et al.*, 1999). Ongoing habitat fragmentation, which increases variance in connectivity across habitat patches, may have thus a synergetic effect with climate change that enhances the extinction probability of isolated populations (Opdam & Wascher, 2004). Climate change is predicted to increase the variance in climatic conditions (Jentsch *et al.*, 2007), which may consequently amplify fluctuating selection experienced by populations. Habitat fragmentation reduces gene flow between populations to a point that the genetic rescue effect may be lost (Lowe *et al.*, 2005). In these conditions, populations may be increasingly at risk of extinction depending on how many generations are within the wavelength of the environmental fluctuation and how strong is stabilizing selection. Such synergetic effect may slow

down or even prevent species from shifting their ranges in face of climate change if dispersal does not evolve sufficiently to re-connect populations (Kubisch & Poethke, 2011).

2.6. Conclusion

In summary, we showed that whether density-dependent or density-independent dispersal underlies faster range expansion rates within a heterogeneous environment depend on the specific growth rates of the species while other factors were less important. Species with lower population growth rates disperse faster under a DI strategy because the forces that positively select for higher emigration (e.g., competition) rates in DD dispersal take a longer time to emerge while populations are maladapted. In contrast, at high growth rates the increasing intensity of kin and individual competition is enough to favour DD dispersal strategy. In a recent experimental study with protists, Fronhofer *et al.* (2015) showed that *Tetrahymena pyriformis*, the species with the highest growth rate among the three studied species, was the one that showed the highest increase in dispersal rates when placed in two-species metacommunities in comparison to the single-species control experiment, suggesting a strong dispersal reaction to competition. In contrast, the other two species with smaller growth rates reacted less strongly when coping with other competitors. It is plausible that these species favour environmental cues other than the density of co- or allo-specifics to make dispersal decisions. Future empirical studies

should therefore determine what type of cues individuals favour to make dispersal decisions across species with different levels of growth rates. Determining these cues will be key to improve our forecasting models regarding species range-shifts abilities under environmental change.

CHAPTER III

BIOTIC PROCESSES DURING RANGE EXPANSION EXPLAIN LARGE-SCALE DIVERSITY PATTERNS

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Will be submitted to PNAS

3.1 Summary

The latitudinal-diversity gradient (LDG), a decline in diversity from low to high latitudes, has attracted the attention of ecologists for decades. While its existence is undisputable, the mechanisms underlying such general pattern have been a longstanding source of debate. Much attention has been given to climatic, historical and evolutionary factors while biotic processes such as competition and Allee-effects are generally ignored. Here, we developed an individual-based model (IBM) simulating an out-of-the-tropics model (i.e., species expanding their ranges from the tropics to higher latitudes) to show how these two overlooked factors may modulate the steepness of the LDG. Given that we model the eco-evolutionary dynamics of species ranges, we also provide insights to the Rapoport's rule (i.e., an increase in average geographic range size (GRS) across the latitudinal gradient). First, our results show that Allee effects impacted negatively the sexual species GRS as local extinction increased due to mate-finding difficulties. Compounded over multiple

species, Allee effects promoted a smoother diversity decline across the spatial gradient due to a lower diversity at the landscape's southern portion that decreased the LDG's intercept, which did not happen for asexual species. Furthermore, interspecific competition had a strong effect on the steepness of the slope for both LDG and Rapoport's rule. Under intermediary competition, diversity (average GRS) declined (increased) smoothly across the spatial gradient. Species that dispersed earlier in the landscape were able to secure many patches through priority effects whereas late-arriving species were progressively precluded from expanding. Without interspecific competition, all species were able to extend their ranges and both ecological gradients disappeared. Under very strong interspecific competition, however, the landscape was mostly dominated by one species due to very strong priority effects while most species were restricted to the southern portion of the landscape. This created a very steep slope for both LDG and Rapoport's rule. Our results suggest that biotic processes may have important consequences for observed macroecological patterns and, more importantly, that ignoring these processes in species distribution models will likely result in biased or erroneous forecasting regarding species range-shift due to climate change.

To those who look at climate and the physical conditions of life as the all important elements of distribution, these facts ought to cause surprise, as climate and height or depth graduate away insensibly. But when we bear in mind that almost every species, ... would increase immensely in numbers were it not for other competing species...we

must see that the range of a species depending as it does on the ranges of others, will tend to be sharply defined. (Darwin, 1859)

3.2 Introduction

The latitudinal-diversity gradient (LDG), a negative relationship between species richness and latitude, is one of the most ubiquitous patterns in ecology (Willig *et al.*, 2003; Hillerbrand, 2004; Jablonski *et al.*, 2006). Hypotheses concerning the LDG generally invoke climate, historical events, tropical niche conservatism as well as differences in speciation and extinction rates across latitude as the main processes structuring this pattern (Wiens & Donoghue, 2004; Mittelbach *et al.*, 2007; Gillman & Wright, 2014; Schluter, *in press*). Although certainly important, they have overshadowed other potential mechanisms underlying the LDG (De Meester *et al.*, 2016). For instance, antagonistic species interactions (i.e., competition) through priority effects have also been put forward as a potential filter regulating the number of species able to expand their ranges from the tropics to high latitudes (Valentine *et al.*, 2008; De Meester *et al.*, 2016). This and other processes have so far received little attention, likely because it opposes a longstanding hypothesis, the Species Interactions-Abiotic Stress Hypothesis (SIASH; reviewed in Louthan *et al.*, 2015), which posits that northern limits of species ranges are determined by climatic factors while southern limits (e.g., tropical) are set mainly by biotic interactions (MacArthur, 1972; Gaston & Blackburn, 2000; Schemske *et al.*, 2009).

However, the generality of the SIASH has been contested (Louthan *et al.*, 2015; Cunningham *et al.*, 2016) and the idea that biotic interactions are stronger in the tropics has even been recently referred as a “zombie idea” (Moles & Ollerton, 2016). Indeed, meta-analyses found contradictory results regarding the latitudinal gradient in biotic interactions, either supporting (Schemske *et al.*, 2009) or refuting this pattern (Moles *et al.*, 2011). Moreover, other important biotic factors such as Allee effects and competitive interactions have not been included in these studies. It is well known that many species may form parapatric range margins in the presence of competitors (e.g., Bullock *et al.*, 2000; Cunningham *et al.*, 2009), especially if they are affected by Allee effects (Case *et al.*, 2005). Through their influence on range limits, competition and/or Allee effects could in turn influence the decline of species diversity across a latitudinal gradient (Valentine *et al.*, 2008; Chapter IV). In this study, we developed an individual-based simulation to demonstrate how these two processes could shape the steepness of latitudinal gradients. Our goal is to complement the existing body of theory regarding the LDG with what we found to be an important component (i.e., biotic factors) but that has been so far overlooked. We take a bottom-up approach by modelling species eco-evolutionary dynamics undergoing range expansion (Kubisch *et al.*, 2014). By doing so, we also provide new insights on the structuring of the Rapoport’s rule, another common latitudinal gradient that is characterized by an increase in species’ average geographic range size (GRS) from low to high latitudes (Rapoport, 1975). This pattern becomes salient when climatic seasonality correlates linearly with latitude (Stevens, 1989; Pintor *et*

al., 2015) but less so in other cases (e.g., species influenced by sea surface temperature; Jablonski *et al.*, 2013). Nevertheless, in most taxonomic groups there are a few widespread and many narrowly-distributed species (Gaston & Blackburn, 2000). Given the existence of many trade-offs related to resource-use, environmental tolerance and other traits (Stearns, 1989; Kneitel & Chase, 2004), fewer species should be able to evolve to become wide-range generalists, especially in highly seasonal environments. Therefore, there may be a common link between the mechanisms regulating range dynamics and large-scale ecological gradients such as LDG and Rapoport's rule (Stevens, 1989).

Species ranges result from fundamental demographic processes (e.g., birth, death and dispersal rates) that are influenced by both abiotic and biotic factors (Case *et al.*, 2005; Sexton *et al.*, 2009; Schurr *et al.*, 2012). One recurrent limiting factor is the presence of major dispersal barriers (e.g., mountain ranges, large rivers, oceans), though given enough time, most species are able to overcome these barriers; even the most isolated oceanic islands (e.g., Hawaii, the Galapagos) were eventually colonized by numerous terrestrial organisms. After immigration, individuals have then to tolerate the environment of the newly colonized region. Except in cases where the selection gradient is too severe (e.g., a terrestrial organism invading an aquatic environment or vice-versa), tolerating the local environment may occur either through pre-adaptation or *in-situ* adaptation assuming that populations have enough genetic variability for selection to be effective (Crawford & Whitney, 2010). Obviously, there

are many examples in which stable range limits are reached without dispersal barriers or severe environmental gradients. Two additional factors challenge range expansion. Given that invasions generally start with a few individuals, most species will need to overcome the Allee effect, which is a decrease in individuals' average fitness when populations are at low densities (Courchamp *et al.*, 1999). These effects are very common in sexually-reproducing species where individuals are required to find suitable mates to establish persistent populations (Courchamp *et al.*, 1999). Furthermore, species interact with other species often under limited resource conditions. These multiple and complex interactions have direct impacts on individuals' fitness and population dynamics, thus likely modulating the effect of abiotic conditions during range expansion (Case *et al.*, 2005; Svenning *et al.*, 2014; Louthan *et al.*, 2015). For example, interspecific interactions may preclude range expansion through competitive priority effects (Urban & De Meester, 2009) or by preventing local adaptation (Case & Taper, 2000). Alternatively, range expansion may be accelerated by enemy release (Keane & Crawley, 2002). The importance of competitive interactions should thus depend on how species overlap in their resource-use.

To understand what regulates biodiversity patterns requires understanding how population and community dynamics influence dispersal and local adaptation during range expansion (Schurr *et al.*, 2012; Kubisch *et al.*, 2014). These dynamics are largely influenced by density-dependent growth, which can be either negative (i.e.,

inter and intraspecific competition; Case & Taper, 2000; Case *et al.*, 2005; Kubisch *et al.*, 2013b) or positive (e.g., mate-finding Allee effects; Courchamp *et al.*, 1999; Shaw & Kokko, 2015). Here, we set out a model to investigate how density-dependent dynamics of multiple competing species expanding their ranges across a linear climatic gradient may shape diversity patterns and range-size distributions. We approach the problem with an individual-based model (IBM), which allows us to explicitly simulate adaptive interactions of individuals with one another and their environment, thus providing the fundamental layout for understanding how eco-evolutionary dynamics of low-level components (individuals) promote emerging patterns at higher scales. Our simulation revealed that the steepness of both GRS and diversity gradients is modulated by these density-dependent dynamics. These findings show a simple and potentially generalizable mechanism regulating the steepness of latitudinal gradients in GRS and diversity based on the resource-use overlap among species and, to a lesser extent, their susceptibility to Allee effects. Furthermore, we conclude by highlighting how these results could help improving forecast regarding the likelihood of species to shift their ranges following climate change.

3.3 Methods

Our simulation is based on the “out of the tropics” model, in which most taxa originated in tropical regions and then expanded their ranges towards higher latitudes (Jablonski *et al.*, 2006). There is ample evidence that most taxa originated in tropical

regions in the past (reviewed in Gillman & Wright, 2014), though new evidence indicates that this tendency may be shifting (Schluter, *in press*). Higher solar radiation (or temperature) at low latitudes reduce generation times and increase mutation rates, resulting in an accelerated selection on favourable mutants that in turn promote speciation (Rohde, 1992; Puurtinen *et al.*, *in press*). Further, Earth's climate underwent several oscillations that disproportionally impacted high-latitude regions, creating many glacial cycles and large extinction events in northern regions (Dynesius & Jansson, 2000), which in turn generated vacant niches that were posteriorly filled by tropical taxa expanding northwards (Jablonski *et al.*, 2006; Valentine *et al.*, 2008). Here, we base our simulations on a re-colonization process of multiple species expanding their ranges across a vacant latitudinal gradient.

3.3.1 Landscape and environment

We adapted a spatially explicit IBM used frequently in studies of species range dynamics (Kubisch *et al.*, 2014) and, for each scenario, we performed 20 replicates in which the range dynamics of 20 species were tracked (with the exception of the no competition scenario, where we simulated 10 species for computational speed; see more details in the 3.3.5 section). Initially, species were ecologically and evolutionarily equivalent but niche and dispersal traits were allowed to evolve. The simulated landscapes consist of a rectangular grid containing 200 rows (y-dimension) x 30 columns (x-dimension; i.e., 6000 individual patches), which are spatially

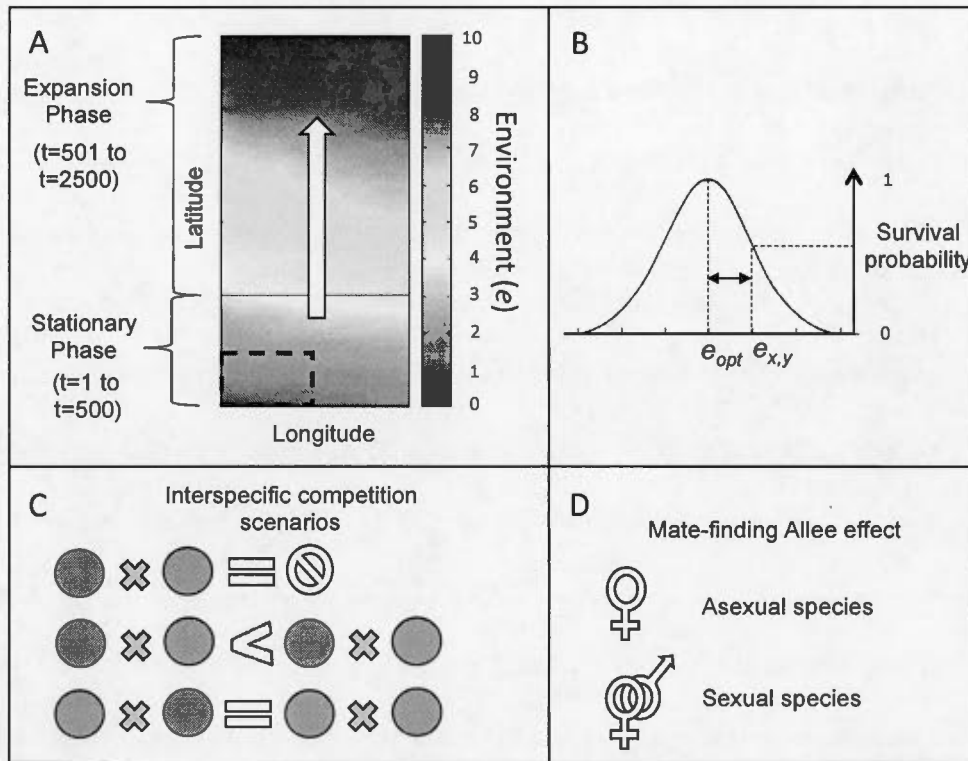


Figure 3.1. Environmental structure and tested scenarios. (A) Representation of the environmental structure in the landscape. Individuals are restricted to the area between $y = 1$ and $y = 50$ (i.e., where the black line crosses the landscape) for 500 generations (stationary phase) and then are allowed to expand for 2000 generation (expansion phase). The dashed square in the landscape represents a region, the scale in which diversity and GRS were measured in the analysis (see section 3.3.8). (B) Individuals survival depends firstly on how close their environmental optima phenotype (e_{opt}) matches the local patch's environment ($e_{x,y}$) and secondly (C) on the local density of conspecifics and allospecifics. Circle colours represent two different species to illustrate the three different scenarios tested for inter-specific competition: null, half the strength of intraspecific competition or equal to intra-specific competition. (D) We tested each of these scenarios with or without mate-finding Allee-effects.

connected to their eight closest neighbours (i.e., Moore neighbourhood). The borders in the y -dimension are wrapped into a torus to avoid edge effects whereas the borders from the x -dimension have reflecting boundaries (as the colonization process occurs along the y -dimension). Each patch is characterized by an environmental value $e_{x,y}$ (e.g., temperature), representing the optimum phenotype for survival in that patch. The environment was generated using the diamond-square algorithm (Miller, 1986), which creates a landscape with spatially autocorrelated environmental values. These values were arbitrarily bounded between 0 and 10 and aim at representing the steepness of the environmental gradient (Kubisch *et al.*, 2014) in which the largest variation occurs across the y -axis (i.e., the latitudinal gradient). Note that the same environmental structure (i.e., same values) was used in all replicates (see Figure 3.1).

3.3.2 Individuals

Each individual was characterized by its dispersal phenotype, environmental optima phenotype, species identity, gender (for the sexual scenario) and location in the landscape. Each time-step of the simulation was generated by the following sequence of events: reproduction, adults perish (i.e., individuals are semelparous), density-dependent (i.e., competition) and density-independent (adaptation to local environment) survival of offspring and dispersal; we therefore assumed no overlap between generations (see Figure 3.2).

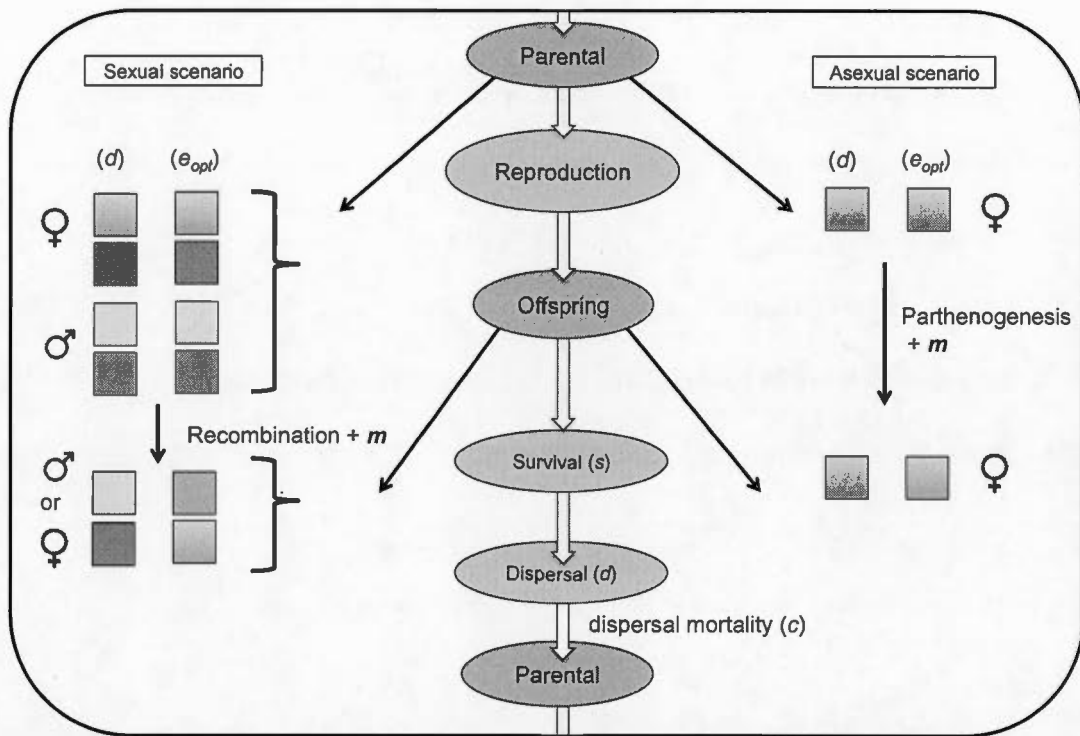


Figure 3.2. General workflow for the individual-based model. The coloured squares below sexual and asexual scenarios represent the alleles of an individual for both dispersal (d) and environmental optima (e_{opt}) phenotypes. In the sexual scenario, orange squares are male alleles whereas blue squares are female alleles and there is free recombination of alleles. In the asexual scenario there are only females and offspring inherit all alleles from the parental. In all reproductive events one offspring allele may mutate with a small probability (m).

3.3.3 Genetics

We modelled an explicit genetic structure for the phenotype components regarding dispersal (d) and environmental optimum (e_{opt}). In the sexual scenario, we used a diploid unilocus system for both dispersal and local adaptation genotypes such as in

Kubisch *et al.* (2014). Species in the asexual scenario had only one allele per locus (i.e., haploids). The value of the phenotype was computed as the average of the two-allele values for the sexual scenario, or the value of the single allele in the asexual scenario. Following previous models (Hovestadt *et al.*, 2010; Kubisch *et al.*, 2014), alleles from both traits (d and e_{opt}) inherited by the offspring had a small probability of mutation ($m = 1 \times 10^{-3}$), in which a Gaussian-distributed random number with mean 0 and standard deviation 0.2 was added to the allele's value.

3.3.4 Reproduction

At each patch x,y at a given generation t , the average fertility of individuals ($\mu_{x,y,t}$) was drawn from a lognormal distribution with mean μ and standard deviation σ , thus creating small spatio-temporal fluctuations in growth rates. The number of offspring was drawn from a Poisson distribution with mean $\lambda_{x,y,t}$ that was assumed to be independent of the individual's fit to the local environment. In the asexual scenario, all individuals were females and performed clonal reproduction in which offspring inherited all alleles from the parental female without recombination. The sexual scenario was characterized by a random pairing between one female and one male with free recombination of alleles inherited by the offspring. If there were more males than females, some males were not allowed to reproduce. If there were fewer males than females, then males could mate with more than one female (i.e., all males and

females will contribute to the next generation). In this scenario, an explicit Allee effect was present by default given that individuals of any species only reproduced if both sexes were present in a given patch x,y ; otherwise, no offspring were produced and the species went locally extinct in the next generation. Given that the number of females is only half of the population size in the sexual scenario (sex ratio 1:1), we halved the final number of offspring produced by all asexual females in order to standardize the number of offspring between the sexual and asexual scenarios.

3.3.5 Offspring survival

Offspring survival was regulated by two processes: 1) how close their environmental optima phenotype (e_{opt}) matched the patch environment ($e_{x,y}$). We assumed density-independent mortality following a Gaussian function:

$$s_1 = \exp\left(-\frac{1}{2}\left(\frac{e_{opt} - e_{x,y}}{\eta}\right)^2\right)$$

where η denotes the niche breath of individuals which was set as 0.5 for all simulations (Figure 3.1B); 2) offspring were subject to density-dependent competition with both conspecifics and allospecifics (i.e., individuals from other species). We tested three different scenarios for the strength of inter-specific competition using a modified version of Hassell (1975) density-dependent growth model:

$$s_2 = \frac{1}{1 + \left(\frac{\mu - 1}{K}\right) N_{x,y,t,i}}$$

where K refers to the equilibrium density and $N_{x,y,t,i}$ is the density of patch x,y at generation t perceived by species i . Across all scenarios we applied symmetrical interspecific competition in which the effect of species i on species j was similar to the effect of species j on species i .

In the first scenario, there was no interspecific competition and $N_{x,y,t,i}$ was simply computed as the number of individuals in the local population of species i . As such this scenario assumed no overlap in resource-use among species. Given the computational time-constraints involved in this scenario in particular, we reduced by half the number of species ($n = 10$) and the carrying capacity of patches ($K = 80$).

In the second scenario, we assumed that each species overlapped in 50% of their resource requirements with all other competing species and the perceived density of an individual from species i was set by the following equation

$$N_{x,y,t,i} = N_i + \frac{N_j}{2}$$

where N_i is the number of individuals of species i while N_j is the number of individuals of all other species. Classic competition theory predicts that co-existence is only possible for species that have the same resource requirements and the same environmental-related fitness, and if the strength of intra-specific is higher than inter-specific competition (MacArthur & Levins, 1967). This form of competition accounts

implicitly for stabilizing niche differences (e.g., resource partitioning, host-specific natural enemies; Chesson, 2000) where species limit themselves more than they limit others species, buffering species against local extinction by being advantageous under low abundances.

Finally, in the third scenario we assumed that species exhibited 100% overlap in their resource use (i.e., high competition) and therefore the $N_{x,y,t,i}$ was simply the total number of individual in a patch, regardless of species identities. This scenario implies equal strength for both inter and intra-specific competition. For all scenarios, the final survival probability was set as $s = s_1 s_2$. At each time step, a random uniform number between 0 and 1 was drawn for each individual, who died if this number was greater than s .

3.3.6 Dispersal

After survival, offspring individuals could disperse with a probability d given by their dispersal phenotype. Individuals dispersed between adjacent patches such that species maintained their range cohesion. Dispersal was modelled using a classic density-dependent function developed by Poethke and Hovestadt (2002), which has been shown to be adequate for individual-based simulations with discrete generation (Hovestadt *et al.*, 2010). It is characterized by the absence of dispersal below a certain

density C_{TH} , and a non-linear increase in dispersal probability for densities above this threshold.

$$d = \begin{cases} 0 & \text{for } \frac{N_{x,y}}{K} \leq C_{TH} \\ 1 - \frac{C_{TH}K}{N_{x,y}} & \text{for } \frac{N_{x,y}}{K} > C_{TH} \end{cases}$$

The single allele value (asexual) or the arithmetic mean of the two alleles (sexual) from the dispersal locus determined their critical threshold population density C_{TH} . At each time step, we drew a random uniform number between 0 and 1 for each individual; dispersal occurred if the number drawn was smaller than d .

3.3.7 Model initialization

In all simulations, the landscape was initially populated with the 20 species (except for the scenario without competition, which started with 10 species) that were distributed across all patches within the area between $y = 1$ and $y = 50$ (i.e., the “southern” most area of the landscape) for 500 generations to allow for species to reach quasi-equilibrium dynamics (i.e., stationary phase; Figure 3.1A). All patches were populated with K individuals set to 8 times the number of species (i.e., $K = 160$; or $K = 80$ in the no-competition scenario). Patches were populated with 8 individuals of each species (4 males and 4 females in the sexual scenario) thus assuring that there was no difference in their initial distributions and therefore no specific advantage to

any species during the expansion phase. Dispersal allele values of each individual were randomly drawn from a uniform distribution between 0.8 and 1, thus setting the initial emigration rate at approximately 20%. Environmental optima alleles values (e_{opt}) were chosen to be equivalent to the individual's starting patch environmental value ($e_{x,y}$) plus a random number drawn from a Gaussian distribution with mean 0 and a small standard deviation 0.2. As such, all species had equivalent niches at the start of the simulation. After the 500th generation, the remaining patches of the landscape became available for species to expand their ranges. The expansion phase ran for an additional 2000 generations. All simulations were performed in Matlab (Mathworks 2014).

3.3.8 Analysis

3.3.8.1 Geographic range size, niche and dispersal traits

At the end of each simulation, GRS of each species was measured as the number of patches occupied across the landscape and we plotted the histogram from the average GRS across replicates for each scenario (Figure 3.3). Moreover, we analysed the shape of the range-size distributions in each scenario by computing their skewness. In order to understand the impact of Allee effects and competitive interactions in the evolution of niche and dispersal traits during range expansion, we recorded, for each species, the average value of these traits in each generation and averaged these values across replicates within each scenario.

3.3.8.2 Spatial gradients

As in many macroecological studies, we evaluated diversity and geographic range size gradients at the regional scale. We divided the simulated landscape into equal-sized quadrates (15x4) containing 60 local patches each, resulting in a total of 100 regions (see Figure 3.1A). The diversity of each region was computed by pooling the number of different species found across their local patches and the region's GRS was computed as the average GRS value from the species present. Finally, we measured the steepness of the latitudinal-diversity gradient (LDG) and the Rapoport's rule as separate regression slopes of the regional diversity and the average GRS across species against latitude (i.e., the y position in the grid).

3.4 Results

3.4.1 Geographic Range Size

Our simulations show that both Allee effects and interspecific competition affect species GRS as well its steepness in relation to latitude. Interspecific interactions had the strongest effect: in the absence of competition, species were able to expand across the entire landscape whereas when interspecific competition was as strong as intraspecific competition, the landscape was mostly occupied by one or two species; the remaining species had a GRS restrained to the initial portion of the landscape. Consequently, in the two extreme scenarios (strong competition and no competition)

the skewness of range-size distributions became similar between sexual and asexual species (Figure 3.3B, 3.3C, 3.3E, 3.3F). The ability to avoid Allee effects in asexual-reproducing species allowed them to attain geographic range sizes that were, on average, 2.5 times greater than sexual species in the scenario with intermediary competition. This resulted in a highly skewed GRS distribution for sexual (skewness = 1.33) but not for asexual (skewness = 0.38) species under intermediate competition (Figure 3.3A, 3.3D).

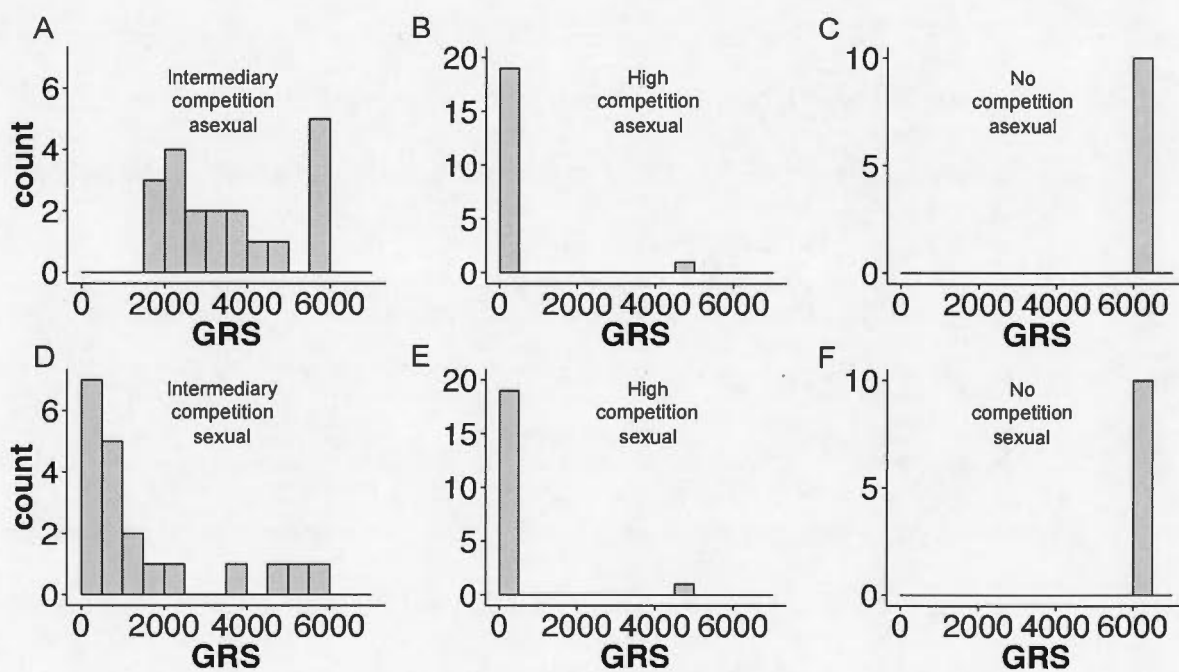


Figure 3.3. Count histograms from geographic range size (GRS) distributions across all scenarios. Species were ranked by GRS and average values were taken from the 20 replicates in each scenario. Asexual species under (A) intermediary, (B) high or (C) no competition. Sexual species under (D) intermediary, (E) high or (F) no competition.

3.4.2 Latitudinal-diversity gradients

In the intermediary competition scenario, a greater number of asexual species were able to expand their ranges across the landscape compared to sexual species. For instance, all 20 species were present in the regions between the 1st and the 60th rows of the y -axis across all replicates. In contrast, there was no single region where all 20 sexual species were present, suggesting that mate-finding Allee effects increases the risk of local extinction. These effects resulted in a smoother diversity decline across the latitudinal gradient for sexual species (Figure 3.4A, 3.4D). Consequently, the regression model between diversity and latitude was relatively weaker for sexual organisms (mean $R^2 = 0.80$) than asexual organisms (mean across replicates $R^2 = 0.94$; Table 3.1). In the absence of interspecific competition, the latitudinal gradient disappeared because all species were able to expand their ranges throughout the entire landscape (Figure 3.4C, 3.4F). Conversely, when interspecific competition was set to be as strong as intraspecific competition the latitudinal-diversity gradient became very steep (Figure 3.4B, 3.4E). In this case, the relationship between latitude and diversity became much weaker (mean R^2 asexual = 0.61; mean R^2 sexual = 0.58; Table 3.1) compared to the intermediary competition scenario.

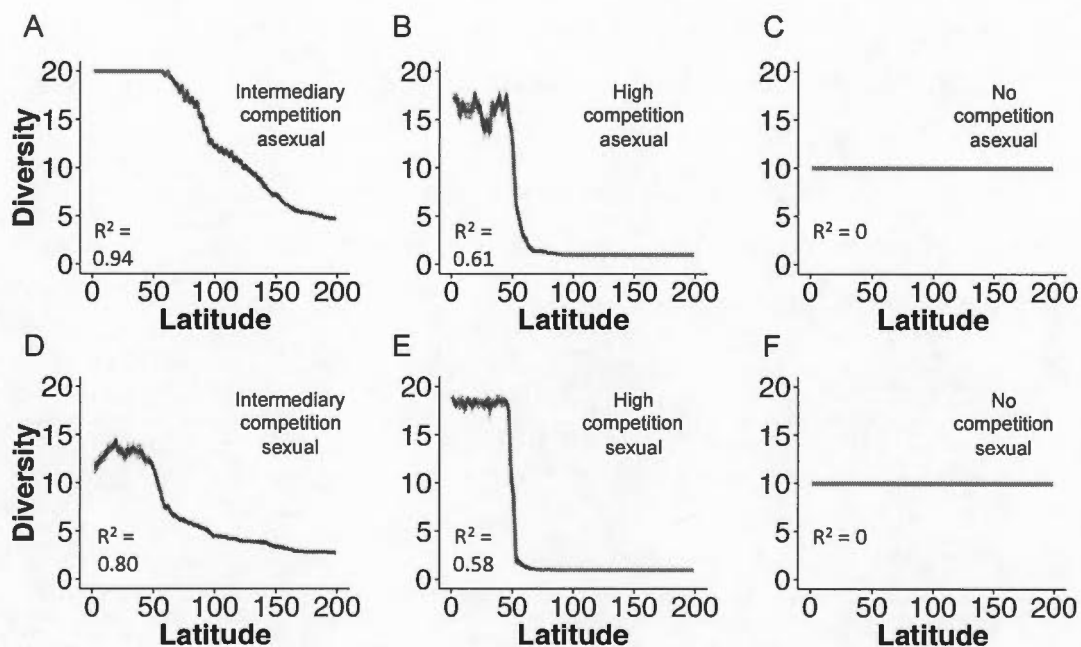


Figure 3.4. Relationship between species diversity and latitude (y-axis) across all scenarios. The red line and shaded region represent the mean and standard deviation across all replicates, respectively. Asexual species under (A) intermediary, (B) high or (C) no competition. Sexual species under (D) intermediary, (E) high or (F) no competition. Note that only 10 species were simulated in the scenario without interspecific competition. R^2 were computed from linear regressions between diversity and latitude.

3.4.3 Rapoport's rule

As expected, in the absence of competition, there was no spatial gradient in GRS (i.e., Rapoport's rule) given that all species were all able to expand across the entire landscape regardless of Allee effects (Figure 3.5C, 3.5F). When interspecific competition was as strong as intraspecific competition, the pattern was similar

Table 3.1. Results from linear regressions between diversity and latitude for each scenario in which the mean and standard deviation (std) were computed across replicates. IntComp = Intermediary competition scenario; HighComp = High competition scenario. a = intercept; b = regression coefficient; R^2 = coefficient of determination. Results from scenarios with no competition are not shown because regressions were not significant.

	Asexual IntComp	Asexual HighComp	Sexual IntComp	Sexual HighComp
a – mean	23.26	13.98	12.98	15.23
a – std	0.19	0.33	0.59	0.30
b – mean	-0.40	-0.35	-0.25	-0.39
b – std	0.01	0.01	0.02	0.01
R^2 – mean	0.94	0.61	0.80	0.58
R^2 – std	0.01	0.01	0.04	0.01

between asexual and sexual species, with a sharp increase in GRS beyond $y = 50$ (i.e., the limit of the simulation's initial phase). Note that in this case, only one species was able to expand its range across the landscape (Figure 3.5B, 3.5E). Both minimum and maximum averages GRS were similar between asexual and sexual species in this scenario. The average GRS reached higher values in the intermediary competition scenario, being slightly larger for both asexual species (Figure 3.5A, 3.5D). However, the minimum average GRS found in any given region was twice as large for asexual organisms (4000 x 2000 for sexual species) given that all 20 species were present in the regions between $y = 1$ and $y = 60$ (Figure 3.5A; 3.5D). Nevertheless, in both asexual and sexual scenarios the Rapoport's rule emerged, with a smooth increase in

the average GRS going towards the end of the landscape (Figure 3.5A, 3.5D).

Similarly to the diversity-latitude relationship, the GRS-latitude relationship was

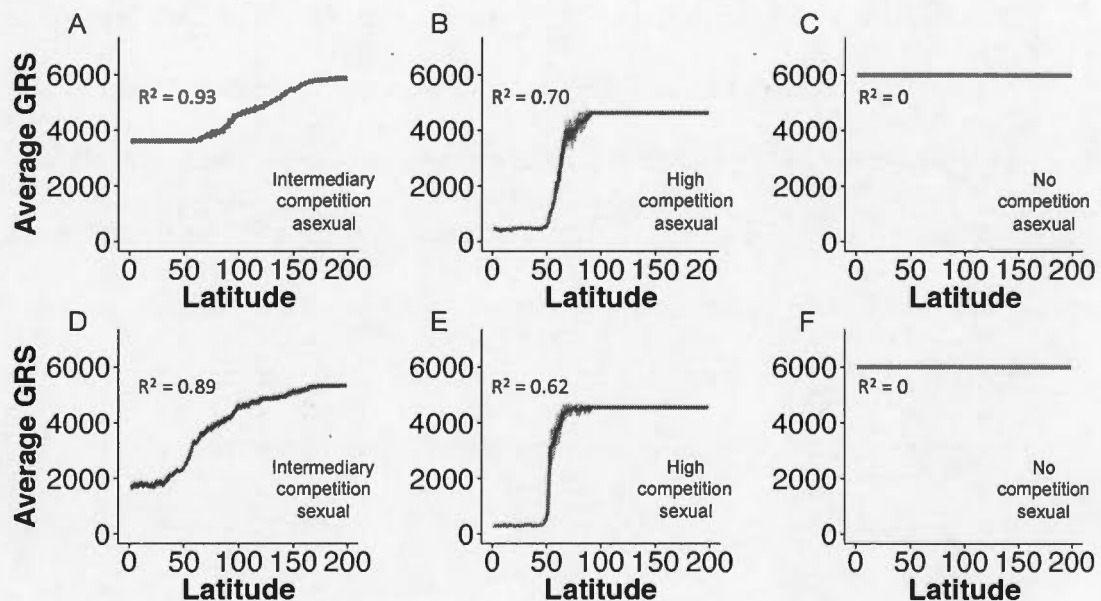


Figure 3.5. Relationship between average species GRS and latitude (y-axis) across all scenarios. Red line and shaded region represent the mean and standard deviation across all replicates, respectively. Asexual species under (A) intermediary, (B) high or (C) no competition. Sexual species under (D) intermediary, (E) high or (F) no competition. Note that only 10 species were simulated in the scenario without interspecific competition. R^2 were computed from linear regressions between average GRS and latitude.

stronger for intermediate-competition than high-competition scenarios (Table 3.2).

Moreover, the relationship was slightly stronger for asexual (average $R^2 = 0.93$) than sexual organisms (average $R^2 = 0.89$; Table 3.2).

3.4.4 Eco-evolutionary dynamics

In Figure 3.6, we present the expansion speed, dispersal rates and environmental phenotype (e_{opt}) of 20 replicates for 20 species ranked through their abundances. We observed that the species with the greatest expanding speed (red line in Figure 3.6A, 3.6D) underwent a major positive selection for dispersal, in which its emigration rates increased from ~ 0.1 to ~ 0.75 within the first 250 generations (red line in Figure 3.6B; 3.6E). This phenomenon is termed spatial selection (Phillips *et al.*, 2010a; Kubisch *et al.*, 2013a) and is reversed as soon as the species arrive at the margins of the landscape (usually between $t=250$ to $t=750$ in our simulations) when the dispersal

Table 3.2. Results from linear regressions between average GRS and latitude for each scenario in which the mean and standard deviation (std) were computed across replicates. IntComp = Intermediary competition scenario; HighComp = High competition scenario. a = intercept; b = regression coefficient; R^2 = coefficient of determination. Results from scenarios with no competition are not shown because regressions were not-significant.

	Asexual IntComp	Asexual HighComp	Sexual IntComp	Sexual HighComp
a – mean	3099.76	617.54	1723.52	834.23
a – std	55.04	156.02	172.00	183.71
b – mean	58.87	106.84	87.67	100.92
b – std	1.66	3.01	3.02	1.78
R^2 – mean	0.93	0.70	0.89	0.62
R^2 – std	0.01	0.05	0.03	0.05

rate is again selected towards its initial value (~ 0.1). Spatial selection is progressively weaker for subsequent species (i.e., pink to purple lines in Figure 3.6.B, 3.6.E) and practically disappears for late-arriving species. Likewise, evolution of the

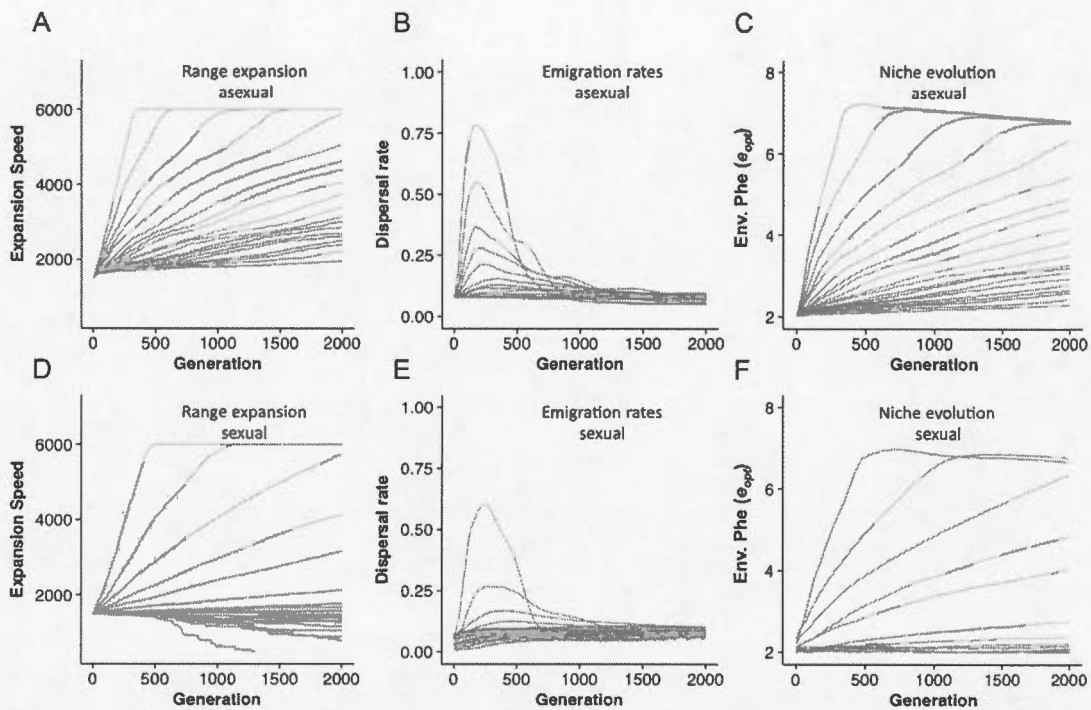


Figure 3.6. Results for range expansion speed (A, D), emigration rates (B, E) and niche evolution (C, F) for the intermediary competition scenario. Panels in the top and bottom rows refer to asexual and sexual species, respectively. Species were ranked by their abundances in all replicates and each colour represents the average values across replicates from each species. For instance, the red line in all panels represents the average value of the most abundant species across all replicates. Range expansion panels show the farthest patch in which the species was found in generation t . Emigration rate panels show the ratio between the number of dispersers and pre-dispersal population size for each species across time. Finally, niche evolution panels show the average value of the environmental optima phenotype (e_{opt}) for each species across time.

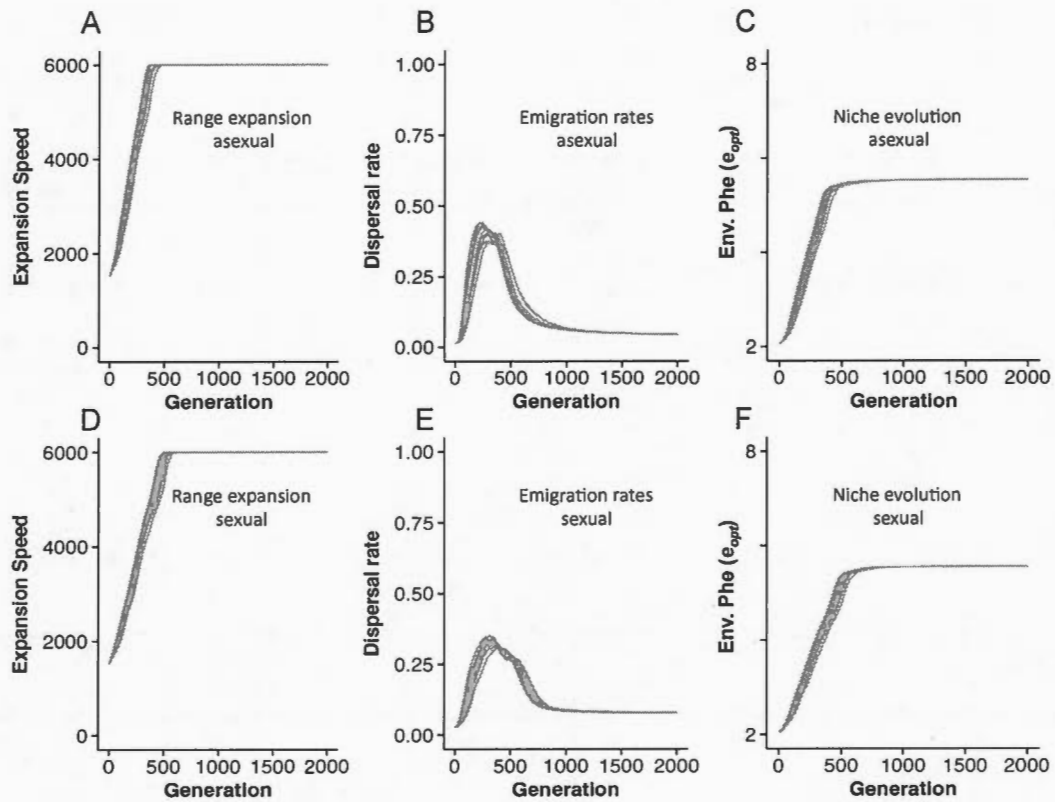


Figure 3.7. Results for range expansion speed (A, D), emigration rates (B, E) and niche evolution (C, F) for the scenario without interspecific competition. Panels in the top and bottom rows refer to asexual and sexual species, respectively. Species were ranked by their abundances in all replicates and each colour represents the average values across replicates from each species. Range expansion panels show the farthest patch in which the species was found in generation t . Emigration rate panels show the ratio between the number of dispersers and pre-dispersal population size for each species across time. Finally, niche evolution panels show the average value of the environmental optima phenotype (e_{opt}) for each species across time.

environmental optima phenotype (e_{opt}) is much faster for the first species colonizing the landscape and become increasingly slower for other species (Figure 3.6C, 3.6F). In the case when there was no interspecific competition (Figure 3.7), all species were able to expand their ranges and environmental niches (e_{opt}) across the entire landscape. The selection for higher dispersal rates was weaker (Figure 3.7B, 3.7E) for all species (~ 0.48 for asexual and ~ 0.3 for sexual) compared to the early-colonizing species in the intermediary competition scenario (Figure 3.6B, 3.6E), demonstrating the importance of both inter and intraspecific competition in influencing dispersal rates.

3.5 Discussion

In this study, we set out to evaluate how the strength of interspecific competition and the presence of mate-finding Allee effects would structure spatial patterns in diversity and GRS and affect the range dynamics of multiple species spreading into a heterogeneous landscape. We found that sexual species (i.e., under Allee effects) had smaller geographical ranges and their diversity and GRS gradients were smoother in contrast to asexual species. Further, the intensity of interspecific competition modulated both diversity and GRS patterns, promoting steeper gradients under strong interspecific competition than under intermediary or absence of competition. Disentangling the relative importance of factors shaping species distributions and, more broadly, large-scale diversity patterns, is a critical research topic in ecology

(Willig *et al.*, 2003; Hillerbrand, 2004). During past decades, a large body of research was concentrated towards understanding the relationship between species distributions and large-scale climatic gradients, especially given current concerns regarding potential species responses to changing environmental conditions (Hawkins *et al.*, 2003; Guisan & Thuiller, 2005). However, there is increasing evidence that biotic processes are as important as abiotic factors for both range dynamics and, potentially, for large-scale diversity patterns (Svenning *et al.*, 2014; Louthan *et al.*, 2015). Here we show how biotic density-dependent processes, such as competitive interactions and Allee-effects, may modulate the steepness of the LDG as well as Rapoport's rule, thus providing an alternative explanation for some of the most ubiquitous phenomena involving biodiversity patterns.

Mate-finding Allee effects not only hindered the colonization ability of sexual species but also subjected them to higher extinction rates (see Courchamp *et al.*, 1999) given that some species suffered range contraction in our simulation (Figure 3.6D). As a result, sexual species exhibited an average GRS much smaller than asexual species. Recent empirical studies corroborate our results; Grossenbacher *et al.* (2015) showed that selfing plant species had an average GRS twice as large as their outcrossing sister species and we show that (see Chapter IV) among freshwater microcrustaceans, cladocerans (cyclical parthenogenetic) exhibited GRS 1.7 times larger than copepods (obligate sexual). Taken together, these results suggest that mate-finding Allee effects may have strong negative effects on species range size.

Allee effects have recently gained attention on studies of range dynamics (Keitt *et al.*, 2001; Miller & Inouye, 2013; Shaw & Kokko, 2015), especially in the context of invasive species (Taylor & Hastings, 2005). Generally, Allee effects slow down or even prevent range expansion because populations at the edge of a species' range are at low densities (Taylor & Hastings, 2005; Hargreaves *et al.*, 2014). Note that mate-limitation Allee effects are not restricted to comparisons between asexual and sexual organisms. Any trait that increases the likelihood of reproduction may alleviate Allee effects (Shaw & Kokko, 2014) and allow species to increase their ranges (e.g., sperm storage in females, mating timing, sex-biased dispersal). For instance, species that mate before or during dispersal should have increased spread rates and larger range sizes compared to ones that mate after (Miller & Inouye, 2013). Furthermore, these local-scale Allee effects influence the shape of diversity gradients at larger scales. Although asexual species were more numerous to advance across the latitudinal gradient, the steepness of the diversity-gradient was stronger for them than for sexual species (Figure 3.4A; Figure 3.4D). This occurred because at the end of the simulation, all regions within the starting position (i.e., between $y = 1$ to $y = 50$) retained the maximum number of asexual species while this did not happen for the sexual species. Given that Allee-effects promote more spatially restricted distributions (i.e., smaller ranges), sexual species were more evenly spread across space, which decreases their diversity at both ends of the gradient and resulted in a smoother latitudinal-diversity slope. In chapter IV, it is shown that this pattern arises in freshwater zooplankton: copepods, which are susceptible to Allee-effects given

obligate sexuality, do not exhibit either LDG or Rapoport's rule because of their evenly spread and more restricted distributions. In contrast, cyclic parthenogenetic cladocerans showed a strong decline in diversity and an increase in range size along the latitudinal gradient. Nevertheless, the generality of this pattern is still an open question given that, to the best of our knowledge, no other study has contrasted macroecological patterns among groups with different susceptibility to Allee effects.

We developed a simple implicit way to represent different degrees of resource-use overlap among competing species and demonstrated that it has strong negative effects on the ability of species to spread their ranges. Early-arriving species had a series of advantages over other species. First, fast individuals (i.e., those with high d) at the expanding front had higher fitness because they benefited from a low competition *milieu* (i.e., spatial selection; Phillips *et al.*, 2010a). This creates a strong selection for highly dispersive individuals and increases the overall dispersal rate for species that expand their ranges earlier (Figure 3.6B, Figure 3.6E). Spatial selection has been empirically demonstrated in the cane-toad invasion in Australia (Brown *et al.*, 2013) as well as for experiments on range expansion on protists (Fronhofer & Altermatt, 2015). Note that this effect was stronger under intermediary competition (Figure 3.6B, 3.6E) compared to the one without it (Figure 3.7B, 3.7E). Indeed, dispersal rates have been shown to increase by orders of magnitude to cope with strong interspecific competition in experimental protist metacommunities (Fronhofer *et al.*, 2015). In addition to spatial selection, kin competition selects for increased dispersal

rates, especially at the front of the expanding range where kin structure is more prevalent due to frequent founder effects (Bitume *et al.*, 2013; Kubisch *et al.*, 2013a). These two processes allow species that disperse first into the empty landscapes, to spread their ranges much faster than later colonizers (Figure 3.6 A, Figure 3.6D) and, as a consequence, to build large populations (Fronhofer & Altermatt, 2015). Moreover, these species might not only experience a demographic release from resource limitation but also an evolutionary release from biotic constraints from other competitors (Yoder *et al.*, 2010; Vanoverbeke *et al.*, *in press*). By arriving earlier in a non-competitive environment, a species may adapt faster (Figure 3.6C, Figure 3.6F) to the local environment than late-arriving species (Urban & De Meester, 2009). Finally, given their large populations and longer time adapting to the environmental conditions at the expansion front, early colonizers are more likely to resist invasions of less-adapted individuals from other species through niche preemption (i.e., priority effects; Fukami, 2015).

The process in which an early-arriving species evolves to consume local resources, in such a way that decreases the establishment probability of competing species, has been coined the community monopolization hypothesis (De Meester *et al.*, 2002; Urban & De Meester, 2009). The importance of priority effects on range expansion will depend on how species overlap in their resource use. In our model, stronger competitive interactions resulted in a lower number of species being able to expand their ranges (Figure 3.4). For example, experimental evidence has shown that prairie

grassland species became less abundant when introduced into communities that were composed of other functionally similar species than in situations in which the recipient community was composed of species from other guilds (Fargione *et al.*, 2003). Thus, species range dynamics can be regulated by the extent of the competitive pressure of other species at the border of its range (e.g., Alexander *et al.*, 2015). All else being equal, it should be easier for a species to adapt to novel environmental conditions when the biotic resistance is low at the expansion front (Case *et al.*, 2005). The mechanisms discussed above (i.e., increase dispersal rates and resource monopolization; Figure 3.6) may also explain why some groups exhibit Rapoport's rule. Species that disperse earlier across the landscape undergo fast evolution of their dispersal rates and evolve to become widespread generalist species. This effect may explain why high-latitude species are more dispersive than tropical species (Jocque *et al.*, 2010). Species that disperse later are affected by competition and thus are precluded to evolve higher dispersal rates, do not experience environmental selection across the gradient and thus end up evolving smaller environmental niches. Thus, depending on the degree of resource overlap, priority effects may promote both LDG and Rapoport's Rule in clades that originated in the tropics and spread their ranges towards higher latitudes (Jablonski *et al.*, 2006; Valentine *et al.*, 2008).

Historically, the effect of biotic interactions on ecological dynamics has been widely thought to be restricted to local scales. The idea that they may also influence range

dynamics and large-scale patterns of diversity have only recently gained attention (Araújo & Luoto, 2007; Gotelli *et al.*, 2010; Svenning *et al.*, 2014; Fukami, 2015; Louthan *et al.*, 2015; Morales-Castilla *et al.*, 2015). Our results suggest that competition and Allee effects at local scales may scale up (i.e., small scale processes driving large scale patterns; Kissling & Schleuning, 2015) and could be major drivers regulating the steepness of LDG and Rapoport's rule. Theoretical studies show that range limits, in two-species models, are shaped due to an interaction between environmental gradients and competition, even if either species are capable of evolving its phenotype to invade the whole landscape (Case *et al.*, 2005). These so called "biotic barriers" are enhanced if both species become better locally adapted to the local environment from their share of the landscape (Urban & De Meester, 2009). Evidences for the effect of biotic barriers limiting species range expansion are plentiful in the field of invasion biology. On one hand, alien species may be precluded to invade a region by native species to which they did not evolve defence or competitive abilities (i.e., biotic resistance hypothesis; Levine *et al.*, 2004). On the other hand, invasive species may exhibit outstanding range expansion rates once they are transported into a region where there are no natural enemies (i.e., predators, parasites) or competitors (i.e., competitive release hypothesis; Brossley & Notzold, 1995). Together, both hypotheses (biotic resistance and competitive release) suggest that the intensity of biotic interactions may regulate the range expansion of invasive species. We argue here that the same principle may be applied to the expansion of

clades from the tropics towards higher latitudes. The stronger the competition within clades, the steeper their latitudinal gradient should be.

We propose a new mechanism behind the LDG, which complements already established theories. Current evidence show that tropics are both *cradle* and *museum* of species diversity, meaning that not only more species have originated in the tropics but they also tend to persist for longer period of times because the environment is relatively more stable (Dynesius & Jansson, 2000; Jablonski *et al.*, 2006; Mittelbach *et al.*, 2007). Then, several but not all taxa have expanded their ranges into extra-tropical regions. It has been argued that the failure of many taxa to expand outside tropical regions is due to their inability to adapt to colder climates, which acted as environmental barriers (i.e., tropical niche conservatism; Wiens & Donoghue, 2004). We suggest that in some instances the inability to adapt to colder climates may be a joint process of abiotic factors combined with biotic interactions. In other words, species may have failed to evolve the necessary adaptations not because they were inherently inapt (i.e., did not have the necessary genetic variability for selection to act), but rather due to the additive effects of the environmental selection and interactions with locally-adapted competitors (i.e., niche pre-emption; Fukami, 2015). Thus, it may be increasingly harder for late-arriving tropical species to adapt to northern climates given the need to evolve multiple dimensions of its niche simultaneously to cope with both abiotic stress and early-arriving competitors (Case *et al.*, 2005).

In order to rigorously evaluate this mechanism, we propose that future studies contrast the LDG steepness of clades that differ in the degree of resource overlap among constituent species. We predict that clades with high resource overlap would have a steeper decline in LDG because they would be more prone to high interspecific competition and priority effects (Vannette & Fukami, 2014). For instance, it was shown in Chapter IV that the latitudinal-diversity gradient is much steeper for cladocerans than copepods. It follows that most cladoceran species are generalist herbivorous and exhibit high resource overlap whereas copepods can better partition resources given that they are composed of specialized species with herbivorous, omnivorous and carnivorous diets (Guisande *et al.*, 2003; Barnett *et al.*, 2007). It is possible that differential diet overlap may have influenced how the LDG of these two groups were structured. Nevertheless, the generality of this mechanism remains to be tested with a broader number of clades across different biogeographic regions. Finally, our results may have important implications to forecast how different taxa will respond to climate change. Taxa or groups of species that exhibit greater overlap in their resource use may find climate-induced range shifts more challenging than taxonomic groups that exhibit smaller overlap (Alexander *et al.*, 2015). Likewise, groups of species in which diet-related traits are more labile may be better suited to perform climate-induced range shifts (Descombes *et al.*, 2015). These outcomes, however, will depend on how the strength of biotic interactions is mediated by abiotic conditions and how northern potential competitors will respond

themselves to climate change (Davis *et al.*, 1998; Taniguchi *et al.*, 1998; Louthan *et al.*, 2015).

3.6 Conclusion

Our simulation study suggests that biotic factors such as the Allee effects and competitive interactions may be as important as dispersal processes or environmental filtering in shaping diversity and geographic-range size gradients. Allee-effects hamper geographic range size because they increase extinction rates and decrease colonization rates. Further, we showed that the structure of these gradients might be created through spatial selection and priority effects (Phillips *et al.*, 2010a; Fukami, 2015; De Meester *et al.*, 2016). Species dispersing first across the landscape benefit from a low competition environment, allowing them to adapt faster to the environmental gradient and spread rapidly (i.e., increase their ranges) before competitors arrive. Later disperser species will not have this advantage and face both biotic and abiotic barriers. Finally, the importance of biotic interactions structuring these gradients will depend on the resource-use overlap among species. We hope that our results encourage macroecologists and biogeographers to test the predictions derived from these results and advance our understanding of the mechanisms underlying large-scale diversity gradients.

CHAPTER IV

CLIMATE AND HISTORY INTERACT IN EXPLAINING
DIFFERENTIAL MACROECOLOGICAL PATTERNS IN FRESHWATER
ZOOPLANKTON GROUPS WITH CONTRASTING LIFE-HISTORY
STRATEGIES

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4.1 Summary

Understanding spatial patterns of species diversity and distribution has been a longstanding goal in macroecology. Given that different groups of species share exclusive traits that affect how they respond to the environment, decomposing assemblages into smaller subsets of species that are internally homogeneous may allow us to better understand the mechanisms underlying diversity patterns over large spatial scales. Here, we investigated how freshwater microcrustaceans with contrasting susceptibility to Allee effects differ in the distribution of their Geographic Range Size (GRS) and diversity along latitudinal gradients, evaluating the importance of climatic and historical factors in explaining these differences. We hypothesized that sexual copepods would have a smaller GRS and that their distribution would be linked to historical processes due to mate-finding Allee effects during colonization.

Given that cyclic parthenogenetic cladocerans avoid these Allee effects, we predicted that they would exhibit a larger GRS and their distribution would be related to climatic factors rather than dispersal limitation. We used a database containing the presence-absence of freshwater zooplankton across 1665 Canadian lakes along a 40° latitudinal gradient. We computed GRS through minimum convex polygons encompassing all lakes in which each species was present. We pooled the diversity of lakes within watersheds and computed linear regressions models between watershed diversity and average GRS with the watershed' average latitude, distance from a glacial refugium and environmental variables. All analyses were performed separately for cladocerans and copepods. Cladocerans exhibited, on average, a GRS 70% larger than copepods. We found a strong relationship between cladoceran diversity (negative) and average GRS (positive) with latitude but none for copepods. Cladoceran macroecological patterns were mainly explained by climatic factors whereas the lack of latitudinal gradients in copepods was potentially due to the influence of a northern glacial refuge. Our results show that Allee effects are strongly and negatively associated to GRS, influencing the relative importance of environmental filtering and dispersal limitation on species distributions and diversity. We suggest that studies should avoid lumping species with large differences in their susceptibility to Allee effects in order to better disentangle the multiple processes affecting large-scale patterns.

4.2 Introduction

One of the oldest and most recognized patterns in macroecology is the latitudinal-diversity gradient (LDG), i.e., increasing species diversity from the poles to the equator. Despite its generality across taxa and habitat types (Hillerbrand, 2004), determining the mechanisms underlying the LDG has been challenging (see Mittelbach *et al.*, 2007 for a review on more than 30 hypotheses). Notably, climatic conditions have been often invoked given that temperature, precipitation and productivity are well correlated with species-richness patterns (Francis & Currie, 2003; Hawkins *et al.*, 2003). Historical hypotheses have also been put forward, suggesting that past environmental conditions and/or geographical barriers, which have shaped speciation and extinction rates as well as dispersal processes, may have longstanding effects on present-day species richness (Dynesius & Jansson, 2000; Baselga *et al.*, 2012). Disentangling these processes is difficult as contemporary environments are often correlated with past ones and likely both have played a role shaping present-day diversity patterns (Hortal *et al.*, 2011).

Evaluating how different groups of species (or species attributes) vary along the latitudinal gradient can provide valuable information on the relative importance of these drivers (Marquet *et al.*, 2004). Notably, one species attribute that has been shown to vary in a predictable manner across latitudinal gradients is their geographical range size (GRS): the average species GRS increases from southern to northern latitudes, a pattern known as Rapoport's rule (Rapoport, 1975; Stevens, 1989). As diversity is a property from the overlap of species geographic ranges within a region,

analyzing the spatial variation in GRS may improve our understanding of the processes underlying the LDG (Gaston, 2009; Blanchet *et al.*, 2013). Geographic ranges are shaped by both ecological and evolutionary forces and represent the expression of the species' realized niches in space (Gaston, 2009; Kubisch *et al.*, 2014). Species spread to new geographical locations when individuals disperse into new areas and are able to tolerate the local abiotic and biotic environment, generally requiring either pre-adaptation or *in-situ* adaptation (Sexton *et al.*, 2009). Given that most invasions start with a few individuals, they are subjected to Allee effects, which is a decrease in individuals' average fitness when population are at low densities (Courchamp *et al.*, 1999). In sexual organisms, mate-finding is one of the most common sources of Allee effects and known to slow down range expansions and even promote range contraction via local extinction (Kramer *et al.*, 2008; Shaw & Kokko, 2015). Another challenge in the range expansion of sexual species is the dispersal of maladapted individuals from core populations to the range border (Lenormand, 2002; Holt & Barfield, 2011). Such immigrants when mating with resident individuals may swamp out the effects of local adaptation with maladapted genes, a process known as migration load (Lenormand, 2002). Conversely, species that perform autonomous reproduction (e.g., selfing, parthenogenesis) may have a higher potential associated to range expansion because they avoid both migration load and Allee effects. However, asexual species lack mechanisms that increase the genetic variability of populations such as recombination and crossing over, potentially hindering their ability for local adaptation (Holt & Barfield, 2011; Kubisch *et al.*, 2014). Thus, species mating

strategies are likely to play an important role regulating both GRS and large-scale diversity patterns.

In this context, it would be interesting to contrast the spatial variation of GRS and diversity of taxa that are subject to similar abiotic and biotic conditions but have contrasting mating strategies. One organism group that allows such comparison is freshwater microcrustaceans (Allan, 1976; Leibold *et al.*, 2010). Cladocerans reproduce almost invariably through cyclic parthenogenesis, in which many phases of asexual reproduction with no genetic recombination are alternated with sexual reproduction while all copepods are obligate sexual species (Allan, 1976; De Meester *et al.*, 2002). Recent evidence in plants shows that outcrossing species have a much smaller GRS than selfing species (i.e., autonomous reproduction). The authors concluded that, despite having higher genetic variability, sexual species are subjected to Allee effects and are not able to expand their ranges as well as autonomous-reproducing species (Grossenbacher *et al.*, 2015). In their system it was not possible to evaluate the unique contribution of Allee effects in GRS because outcrossing species are also subject to migration loads. In contrast, in freshwater zooplankton, one can partially control for it because cladocerans and copepods perform sexual reproduction, which implies that both groups may be subject to migration loads from maladapted immigrants. However, cladocerans remain somewhat less subject to this effect given that they tend to reproduce asexually and due to their ability to prevent gene flow through niche pre-emption by established clonal populations (De Meester

et al., 2002). Nevertheless, the ability to reproduce through parthenogenesis suggests that cladocerans have higher dispersal rates than copepods because they evade mate-finding Allee effects during the colonization phase (see Table 1 for a review of evidence). Therefore, freshwater microcrustacean provides a strong system to test for the contribution of Allee effects on GRS and latitudinal gradients.

In the present study, we used a large dataset of freshwater microcrustaceans distributed along a latitudinal gradient spanning 40° across Canada (Pinel-Alloul *et al.*, 2013) to evaluate how the difference in susceptibility to Allee effects of cladocerans and copepods may affect their GRS as well as the steepness of their latitudinal gradients in diversity and range-size (Rapoport's rule). Like other freshwater organisms, the diversity of zooplankton in Canadian lakes is mainly the result of a recent (<15000 years) post-glacial range expansion of species located in glacial refugia across the United States during the melting of the glacial sheet (Hebert & Hann, 1986). By restraining our analysis within Canada, the potential effects of clade age on species GRS should not affect our results as both clades were well established long before the melting of the Pleistocene ice sheet given that the oldest fossil-record for both groups dates the Carboniferous (see Sun *et al.*, 2015 and references therein). Note that one high-latitude region remained unglaciated in North America (i.e., Beringian refugium in Alaska; Hebert & Hann, 1986), potentially influencing the steepness of latitudinal gradients if many species were able

Table 4.1. Empirical evidence showing that cladocerans have better dispersal capacity than copepods.

Evidence	Reference
Under low dispersal (i.e., low propagule pressure), copepods are less likely to establish in acidified lakes than cladocerans (i.e., interaction between local environment and Allee effect)	(Gray & Arnott, 2012)
After the removal of fish in historically fishless lakes in which their introduction led to the extinction of large-bodied copepods and cladocerans, only cladocerans were able to recover. This occurred despite the presence of copepod egg banks in these lakes, showing evidence for the Allee effects due to mate-finding difficulties	(Kramer <i>et al.</i> , 2008)
Both parthenogenetic cladocerans and rotifers had higher colonization rates than sexual copepods in newly constructed ponds	(Frisch <i>et al.</i> , 2012)
Most cladocerans produce an ephippia egg, which is much more resistant to desiccation and freezing than normal diapausing eggs (calanoids) or diapausing copepodid stages (cyclopoids).	(Havel & Shurin, 2004)

to re-colonize northern regions from this refugium. Given that both zooplankton groups had equal time to recolonize Canada after the Pleistocene glaciation, we propose the following predictions: (1) Cladocerans should exhibit a larger geographic range size (GRS) than copepods because the former have greater colonization abilities; (2) The diversity and GRS distribution of cladocerans should be more influenced by climate (i.e., environmental filtering) given that they are not dispersal limited while copepods should respond mostly to historical factors (i.e., dispersal limitation); (3) The differential response to environmental filtering and dispersal-limitation between the two groups should translate into contrasting patterns regarding both LDG and Rapoport's rule between these groups.

4.3 Methods

4.3.1 Data set

The dataset used in this study is based on a long-term sampling program (1961–1991) carried out by the Freshwater Institute of Fisheries and Oceans Canada. It contains the presence-absence of 83 crustacean zooplankton species distributed across 1665 lakes along the entire mainland Canada (42–80° N and 52–139° W) (Figure 4.1). Sampling took place once during the mid-summer, near the center of the lakes, therefore only pelagic species were sampled. As with any long-term large-scale data set, sampling effort was not equal across lakes, ranging from a single site in most lakes but up to 50 sites in very large lakes. The sampling method was similar across all lakes: zooplankton were collected with a Wisconsin plankton net (25 cm in diameter, mesh size of 53–77 mm) by vertical hauls from the lake bottom to the surface, or from a depth of 50 m in the deepest lakes (see Patalas, 1990; Patalas *et al.*, 1994 for information on the sampling design). While sampling might have missed some species because it did not cover the entire growing season, it has been shown recently that mean annual species richness correlates strongly with zooplankton diversity estimated on a daily basis (Shurin *et al.*, 2007). Further, variation in per-lake sampling effort may bias analyses performed at local scale, especially given that lake zooplankton diversity is influenced by factors that either operate at small and less predictable spatiotemporal scales or by relatively more stable and predictable large-scale factors (Pinel-Alloul, 1995; Pinel-Alloul & Ghadouani, 2007). Given that our interests are into the long-term processes that shaped more stable large-scale patterns, we considered regional variation (across watersheds; Figure 4.1) rather than small local variation at the lake level. In order to pool the lake data (e.g., species

occurrence, climatic factors) into watersheds, we downloaded watershed shape files from the global hydrography dataset HYDRO1K (USGS, 2012), which is available at <https://lta.cr.usgs.gov/HYDRO1K>. The drainage basins delineated in the HYDRO1K database consist of a hierarchical structure of 6 levels of increasingly smaller polygons based on topographic relief and hydrological flow direction related to elevation. For the analysis reported here, we used secondary watersheds and retained only the ones that had at least 20 lakes surveyed because it has been shown that > 90% of the species found in a region were usually found by sampling at least 20 lakes (Patalas, 1990). In total, 1500 lakes belonging to 26 watersheds were retained for analyses (Figure 1). Given that large-scale diversity-patterns may be scale-dependent (Rahbek, 2005), we tested the consistency of our results by evaluating the LDG and Rapoport's rule using tertiary watersheds (i.e., finer spatial grain) from the HYDRO1K database. Due to a greater degree of spatial sub-division, a fewer number of lakes (928 in total) across 25 tertiary watersheds were analyzed. We also performed another set of analyses by lowering the threshold to a minimum of 10 lakes per watershed, which retained 1219 lakes across 47 tertiary watersheds. In all analyses we removed any species from the dataset with less than 3 occurrences (8 species in total) because the metric used to compute the geographical range needs at least 3 data points (see "*Diversity and Geographic range size metrics*" section further

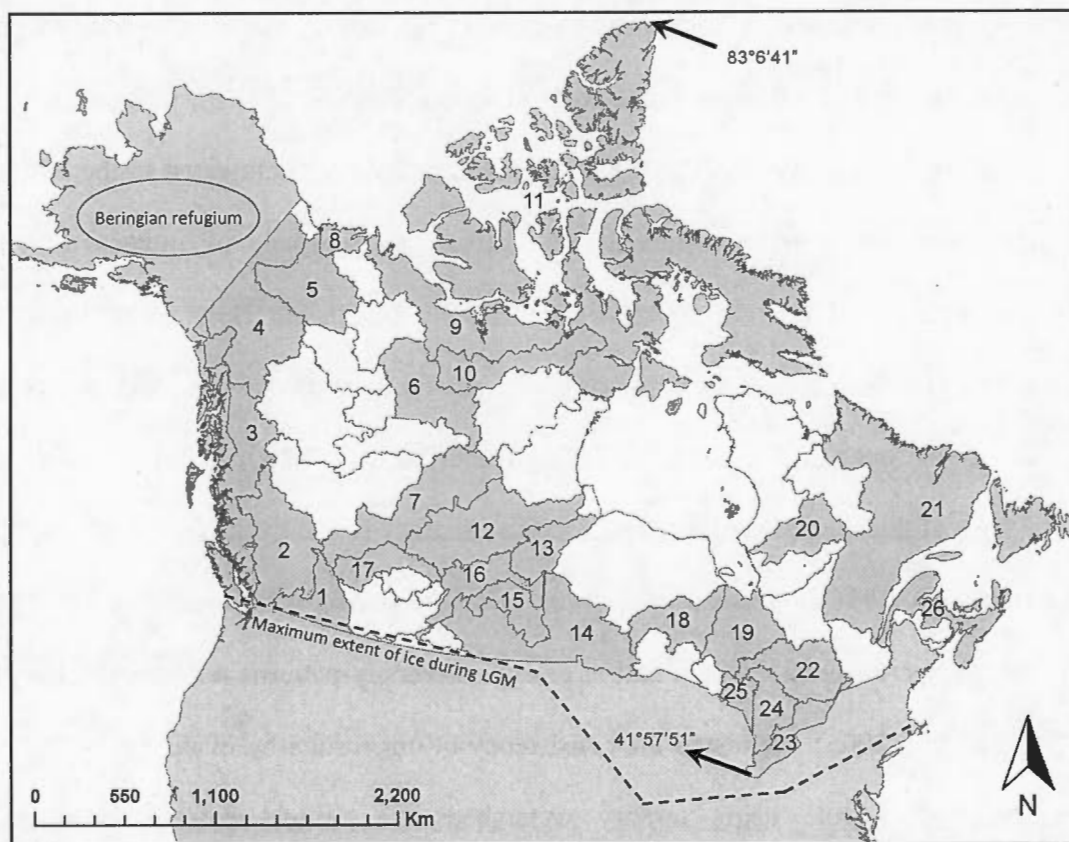


Figure 4.1. Map of Canada with the 26 watersheds retained for the analysis in light orange. The dashed line represents the maximum extent of the ice cover during the last glacial maximum (LGM); modified from Blanchet *et al.* (2013). The arrows represent the two extreme latitudes of Canada; southern arrow: Point Peele, Ontario; northern arrow: Cape Columbia, Ellesmere Island, Nunavut.

below for more details). In total, 75 species were retained for the main analyses. Note that, for the analyses based on tertiary watersheds, additional species were removed (3 for the 20 lakes rule and 1 for the 10 lakes rule) because all lakes in which they occurred were eliminated from the dataset.

4.3.2 Climatic and historical factors

Environmental data and geographic coordinates of each lake were obtained from Pinel-Alloul *et al.* (2013): Growing Season Length (days), Growing Degree Day above 10°C, Effective Growing Degree Day above 5°C, Mean elevation (m), Annual Potential Evapotranspiration, Total Annual Precipitation (mm), Mean Daily Global Solar Radiation, Mean Duration of Bright Sunshine (hours), Mean Annual Air Temperature (°C), Maximum Annual Air Temperature (°C), Mean Annual Vapor Pressure, Latitude and Longitude. To obtain values at the watershed level, we averaged variables across lakes within each watershed. Descriptive statistics for each variable are presented in Table 4.2. Furthermore, we computed the Euclidean distance between Alaska's centroid to each watershed as a variable to account for the potential historical effects of the Beringian refugium on current patterns of zooplankton diversity and GRS (see Figure 4.1).

4.3.3 Diversity and Geographic Range Size metrics

Species richness for each zooplankton group (copepods and cladocerans) at any given watershed was defined as all species found within their sampled lakes. To verify potential sampling biases across watersheds, we computed the first-order jackknife

Table 4.2. Mean $\pm$ standard deviation (STD), minimum (Min) and maximum (Max) values for each variable. Statistics were computed from values at the watershed level, which were computed by averaging the values across lakes within each watershed.

Variable	Code	Mean $\pm$ STD	Min	Max
Growing Season Length (days)	GSL	154.87 $\pm$ 44.98	43.57	214.29
Growing Degree Day above 10°C	GDD10	479.62 $\pm$ 208.86	0.64	1107.70
Effective Growing Degree Day above 5°C	EGDD	1147.85 $\pm$ 472.12	92.60	2017.83
Mean Elevation (m)	M_ELE	475.56 $\pm$ 361.88	25.72	1365.95
Annual Potential Evapotranspiration	APE	500.67 $\pm$ 156.52	163.38	780.75
Total Annual Precipitation (mm)	TAP	617.02 $\pm$ 343.57	172.67	1402.70
Mean Daily Global Solar Radiation	MDGSR	11.58 $\pm$ 1.34	8.98	13.19
Mean Duration of Bright Sunshine (hours)	MDBS	1930.65 $\pm$ 185.49	1571.35	2299.83
Mean Annual Air Temperature (°C)	MeanAT	4.42 $\pm$ 6.76	-10.54	13.25
Maximum Annual Air Temperature (°C)	MaxAT	-0.69 $\pm$ 6.24	-13.85	7.48
Mean Annual Vapor Pressure	MAVP	0.70 $\pm$ 0.12	0.48	0.90

richness index (Palmer, 1990), $S_{EST} = S_{OBS} + x(n-1)/n$, where S_{OBS} is the total number of species in the watershed, n is the number of lakes and x is the number of species that are present in only one lake (i.e, singletons; see also Pinel-Alloul *et al.*, 2013). We then calculated a Pearson correlation between watershed richness and the first-order jackknife richness index. Correlation coefficients were extremely high for both groups ($r = 0.97$ for cladocerans and $r = 0.95$ for copepods), suggesting that any sampling differences among watersheds across groups should not affect our results. The dataset contained different number of species for cladocerans ($n = 30$) and copepods ($n = 45$). As suggested by Baselga *et al.* (2012), we standardized the species richness of each group for all watersheds to avoid any bias in the latitudinal-diversity regression slopes:

$$S_{STD} = \frac{S_i}{S_{MAX}} 100$$

where (S_i) is the species richness in the i^{th} watershed and (S_{MAX}) is the maximum richness value of the corresponding group recorded across all 26 watersheds.

The geographic range size of each species (see Appendix D1 and Appendix D2) was estimated as the area of the minimum convex polygon (km^2) that encompasses all the lakes (independently of watersheds) in which a species was found to be present using the function *earth.poly* in the R package *fossil* (Vavrek, 2011). This metric has been shown to correlate quite well with other common measures of geographic range size (Quinn *et al.*, 1996) and was highly correlated with maximum latitudinal extent ($r = 0.93$) in our dataset. We obtained a value of GRS for each watershed by averaging the range size values of all their constituent species.

4.3.4 Statistical analysis

To determine the strength of the latitudinal gradients in richness and range size, we computed linear regressions between log-transformed watershed diversity (S_{STD}) and average GRS (*Range*) for each microcrustacean group on the mean latitude of lakes within a watershed (*Lat*). Additional regression models for latitudinal gradients were

performed for tertiary watersheds (see map in Appendix E1) to evaluate if results were scale-dependent (see Appendix E2 and E3). We verified the potential effect of the Berigian glacial refuge by regressing log-transformed GRS and diversity for each group on the distance from the refugium (*BER*). Finally, to estimate the importance of different environmental factors in explaining both diversity and GRS patterns for cladocerans and copepods, we computed multiple linear regression models with all environmental variables (see section “Climatic and Historical factors”) using a forward selection procedure proposed by Blanchet *et al.* (2008) through the R package *packfor*; selection of variables were on the basis of a significance level of 0.05 and probability values of partial contributions were estimated on randomization tests using 999 permutations (see Blanchet *et al.*, 2008 for more details). In all regression models we included log-transformed watershed area (*A*) as a covariate to control for size differences among watersheds. We tested residual normality by performing the Kolmogorov-Smirnov test with the Lilliefors correction using the R package *nortest* (Gross, 2015) and residual homoscedasticity through the Breusch-Pagan test using the R package *lmtest* (Hothorn *et al.*, 2014). Results from these tests are presented in Appendix F. One model failed the residual homoscedasticity test (cladoceran $GRS \sim BER + A$) and therefore we heteroscedasticity corrected it by the Huber-White method using the R package *car* (Fox & Weisberg, 2011). In order to better understand how cladocerans and copepods diversity gradients are structured across space, we used the beta-diversity metric based on the Sørensen index family developed by Baselga (2010), which decomposes the variation in species composition

(i.e., total beta-diversity; β_{sor}) into spatial assemblage turnover (β_{sim}) and differences in species composition due to differences in richness (i.e., nestedness; β_{nes}). These metrics were computed across secondary watersheds in order to have a global measure of beta-diversity using the R library “*betapart*” (Baselga & Orme, 2012).

Note that populations of the *Daphnia pulex* complex (*D. pulex*, *D. pulicaria* and *D. middendorffiana*) in northern latitudes switched their mating system from cyclic parthenogenetic to obligate asexuality (Decaestecker *et al.*, 2009). Given that we aimed at comparing cyclic parthenogenetic cladocerans with obligate sexual copepods to account for the effect of migration load, we repeated all the analyses without the species from the *Daphnia pulex* complex to verify if these species could have affected our results. Results from these analyses did not affect our main conclusions and are presented in Appendix G1, G2 and G3. Finally, to further evaluate the robustness of our results to sampling effort variation (see “Data set” section), we also performed a re-sampling technique to test how the relationship between diversity and latitude changed between the two groups if a subset of lakes were selected randomly from each watershed. Details and results from this analysis are presented in Appendix H and they show that the striking differences found between the two groups were not affected by potential sampling effort issues.

4.4 Results

Cladocerans exhibited on average a GRS 1.72 times larger than copepods ($t = 2.8699$, $P = 0.0054$). While the cladoceran GRS distribution was almost uniform (skewness = 0.1087), showing a similar number of species with small and large GRS (Figure 4.2B), copepod GRS distribution was heavily left-skewed (skewness = 0.7750), where most species exhibit small GRS (Figure 4.2A). Our second prediction was also supported because we found large differences in the steepness of latitudinal gradients for both watershed diversity and average GRS between cladocerans and copepods (Figure 4.3; Table 4.3). The diversity of cladocerans was strongly negatively related to latitude ($b_{LAT} = -0.034$; $Adj-R^2 = 0.617$; $P < 0.001$) while the same relationship was not statistically significant for copepods ($Adj-R^2 = -0.012$; $P = 0.442$; Table 4.3). The same pattern was found for average GRS, where cladoceran average GRS was strongly and positively related to latitude ($b_{LAT} = 0.014$; $Adj-R^2 = 0.706$; $P < 0.001$) but copepod average GRS was unrelated to latitude ($Adj-R^2 = 0.069$; $P = 0.167$; Table 4.3). The second set of analysis performed without the *D. pulex* complex did not change our results (Appendix G1). If anything, the pattern became stronger as the $Adj-R^2$ for the diversity-latitude relationship increased its from 0.61 to 0.69 ($b_{LAT} = -0.037$; $P < 0.001$) while the $Adj-R^2$ for the average GRS-latitude decreased by only 1% ($b_{LAT} = 0.015$; $Adj-R^2 = 0.691$; $P < 0.001$).

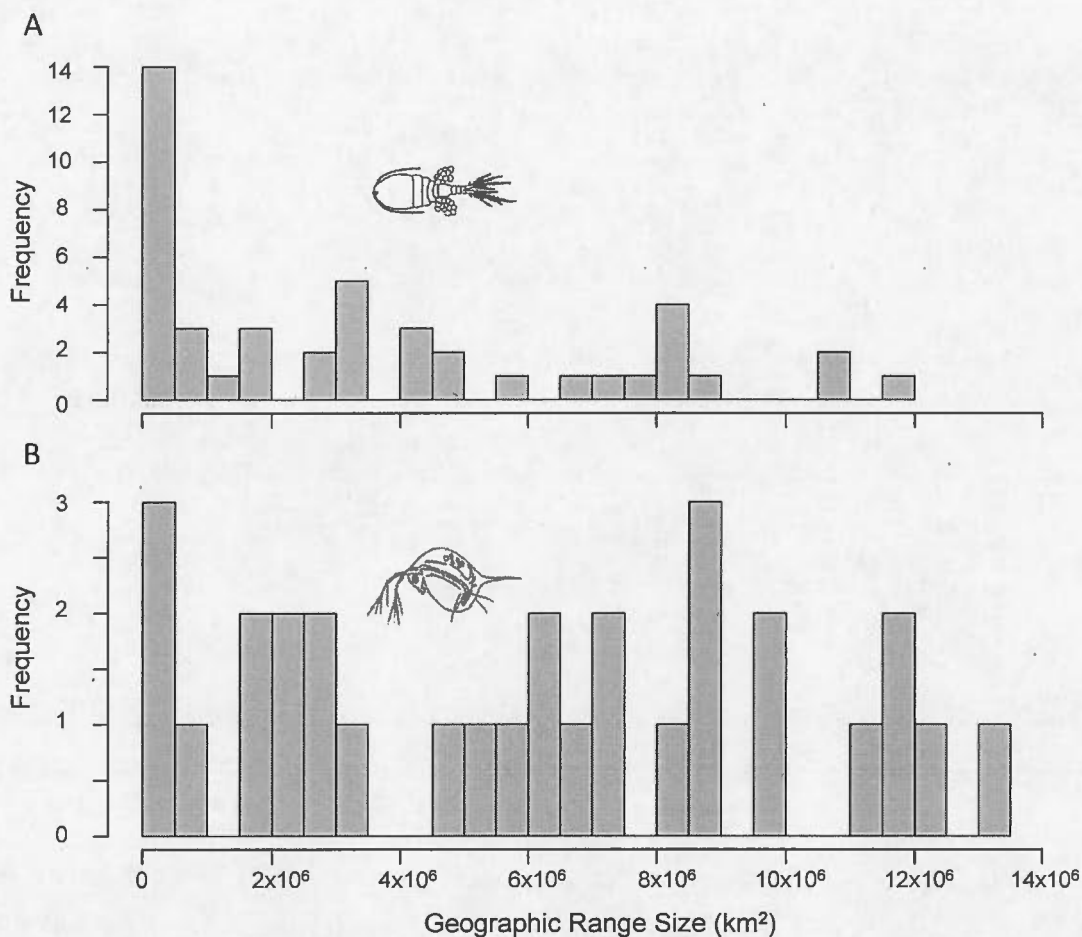


Figure 4.2. Frequency distribution of geographic range size for (A) copepods and (B) cladocerans. Note that the scale of the y-axis is different for each histogram.

Regression models between these two variables and the distance from the Beringian refugium (*BER*) showed no significant relationship with either cladoceran richness ($\text{Adj-R}^2 = 0.001$; $P = 0.37$) or average GRS ($P = 0.07$; Table 4.4). In contrast, copepods average GRS was positively related to the distance from the refugium ($b_{BER} = 0.002$; $\text{Adj-R}^2 = 0.19$; $P = 0.032$; Table 4.4), meaning that watersheds near the

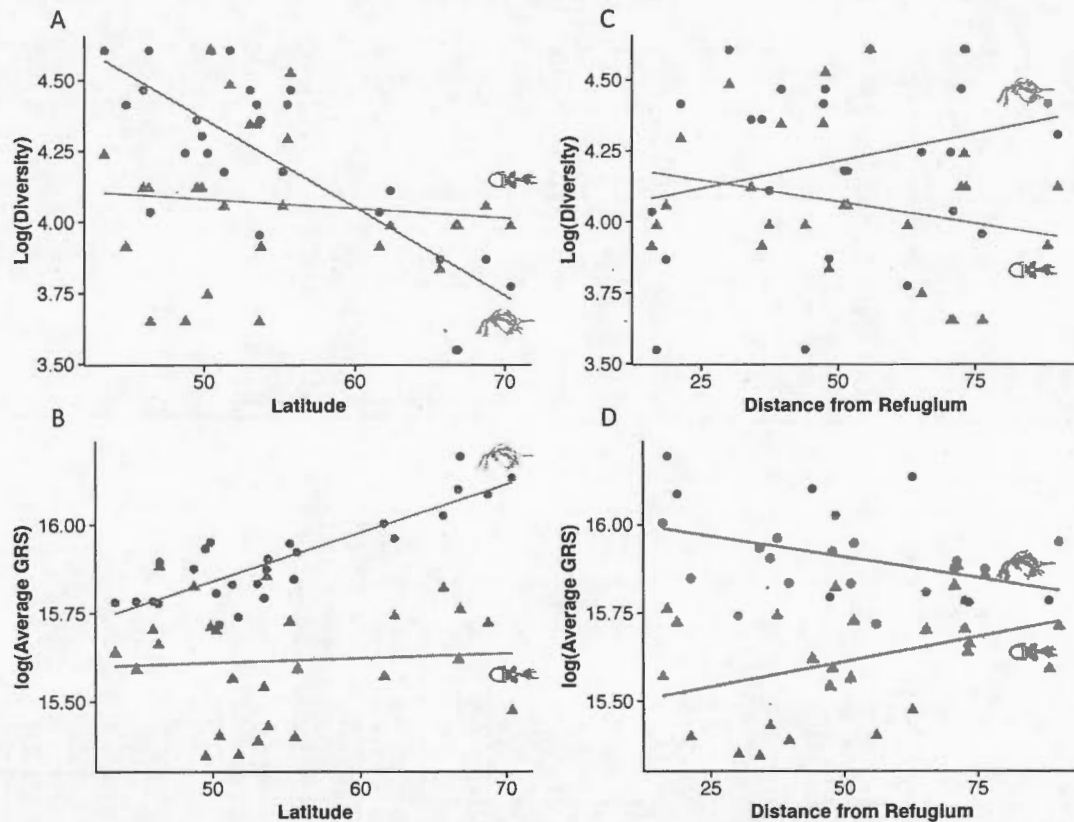


Figure 4.3. Relationship between watershed latitude and (A) its diversity or (B) average GRS for copepods and cladocerans. Relationship between watershed distance from the Beringian refugium and (C) its diversity or (D) average GRS for copepods and cladocerans. Red circles represent cladoceran data while green triangles represent copepod data. Each data point represents a watershed. Regression results for these slopes are presented in Table 4.2 and Table 4.3.

refugium had small-range copepod species compared to watersheds further east (Figure 4.3D). However, the diversity of copepods was unrelated to *BER* ($\text{Adj-R}^2 = 0.029$; $P = 0.27$; Table 4.4D), thus only partially supporting our third prediction regarding the relationship between copepods and cladocerans with historical factors

(i.e., dispersal limitation). The analysis performed for cladocerans without the *D. pulex* complex were not significantly changed in either diversity ($P = 0.118$) or average GRS ($P = 0.0636$; Appendix G2).

Table 4.3. Results from linear regression models between latitude and log-transformed watershed diversity (S_{STD}) and average geographic range size (GRS) with watershed area (A) as a covariable. *Global - P* = global probability; P_{INTER} = probability for the intercept; P_{LAT} = probability for latitude; P_A = probability for watershed area; b_{LAT} = coefficient for latitude; b_A = coefficient for watershed area. Significant P -values under an $\alpha = 0.05$ are highlighted in bold.

Group	Cladocera		Copepoda	
Response	S_{STD}	GRS	S_{STD}	GRS
F	21.14	31.1	0.846	1.936
<i>Global - P</i>	<0.00001	<0.00001	0.442	0.167
$Adj-R^2$	0.617	0.706	-0.012	0.069
Intercept	5.27	15.16	3.39	16.34
P_{INTER}	<0.00001	<0.00001	0.00022	<0.00001
b_{LAT}	-0.034	0.014	-0.006	0.004
P_{LAT}	<0.00001	<0.001	0.411	0.352
b_A	0.065	-0.002	0.082	-0.078
P_A	0.199	0.91	0.235	0.064

The results from the forward selection procedure showed a strong relationship between both cladoceran diversity (positive) and average GRS (negative) with variables related to temperature and productivity (Table 4.5). The only variable selected to explain cladoceran richness was Mean Annual Temperature (MAT; $b = 0.044$; $Adj-R^2 = 0.718$; $P < 0.0001$). Cladoceran GRS ($Adj-R^2 = 0.7376$) was negatively and strongly related to Mean Daily Global Solar Radiation (MDGSR; $b =$

Table 4.4. Results from linear regressions between the distance from the Beringian refugium (*BER*) and log-transformed watershed diversity (*S_{STD}*) and average geographic range size (*GRS*) with watershed area (*A*) as a covariable. *Global - P* = global probability; *P_{INTER}* = probability for the intercept; *P_{BER}* = probability for distance from the Beringian refugium; *b_{BER}* = coefficient for distance from the Beringian refugium; *P_A* = probability for watershed area; *b_A* = coefficient for watershed area. Significant *P*-values under an $\alpha = 0.05$ are highlighted in bold. *Given that the residuals from this model were not homoscedastic, we applied the Huber-White method, which gives heteroscedastic corrected estimates for the linear model.

Group	Cladocera		Copepoda	
Response	<i>S_{STD}</i>	<i>GRS</i> *	<i>S_{STD}</i>	<i>GRS</i>
<i>F</i>	1.02	--	1.383	3.995
<i>Global - P</i>	0.3762	--	0.2709	0.032
<i>Adj-R²</i>	0.001	--	0.029	0.1933
Intercept	4.48	15.52	3.44	16.26
<i>P_{INTER}</i>	<0.0001	<0.0001	0.000147	<0.0001
<i>b_{BER}</i>	0.003	-0.002	-0.003	0.002
<i>P_{BER}</i>	0.193	0.071	0.20	0.0435
<i>b_A</i>	-0.038	0.04	0.06	-0.06
<i>P_A</i>	0.615	0.36	0.31	0.073

-0.067; $P < 0.0001$) and weakly related to Total Annual Precipitation (TAP; $b = -0.0001$; $P = 0.0278$). When removing the *D. pulex* complex, the latitude-GRS relationship did not change and the same variables were selected in the forward-selection procedure. The diversity-latitude relationship changed slightly, as Growing Season Length (GSL) and MDGRS were selected instead of MAT (Appendix G3). However, both these variables are strongly correlated with temperature, generating

Table 4.5. Result from forward-selection regression models between environmental variables and diversity and average geographic range size (*GRS*) of watersheds for both cladocerans and copepods. *VAR1* and *VAR2* refer to the variables selected in the forward-selection procedure. MeanAT = Mean Annual Temperature; MDGRS = Mean Daily Global Solar Radiation; TAP = Total Annual Precipitation; MDBS = Mean Duration of Bright Sunshine; M_ELE = Mean Elevation; b_{VAR1} = regression slope for the first selected variable, b_{VAR2} = regression slope for the second selected variable; P_{VAR1} = probability for the first selected variable; P_{VAR2} = probability for the second selected variable; b_A = coefficient for watershed area; P_A = probability for watershed area. Significant *P*-values under an $\alpha=0.05$ are highlighted in bold.

Group	Cladocera		Copepoda	
Model	S_{STD}	GRS	S_{STD}	GRS
<i>VAR1</i>	MeanAT	MDGRS	MDBS	M_ELE
<i>VAR2</i>	--	TAP	--	--
<i>F</i>	35.82	24.43	3.569	13.73
Global - <i>P</i>	<0.0001	<0.0001	0.044	0.00012
Adj- R^2	0.718	0.7376	0.1705	0.5045
Intercept	3.52	16.76	1.85	16.43
P_{INTER}	<0.0001	<0.0001	0.0549	<0.0001
B_{VAR1}	0.044	-0.0669	0.0006	-0.0003
P_{VAR1}	<0.0001	<0.0001	0.023	0.0001
B_{VAR2}	--	-0.000103	--	--
P_{VAR2}	--	0.0278	--	--
b_A	0.06	-0.00168	0.082	-0.05584
P_A	0.166	0.9220	0.1668	0.056

similar interpretation. For copepods, richness was positively but weakly related to Mean Duration of Bright Sunshine ($b = 0.0006$; Adj- $R^2 = 0.17$; $P < 0.0001$) whereas Mean Elevation was strongly negatively related to their average GRS ($b = -1763.2$; Adj- $R^2 = 0.50$; $P = 0.0001$). Overall, these results support our third prediction regarding environmental filtering, which posited a strong relationship of cladocerans

to climatic factors but not for copepods. Finally, none of the regression models suggested a relationship with watershed area (Table 4.3; Table 4.4; Table 4.5; Appendix G1, Appendix G2; Appendix G3), indicating that the results were not an artifact from the species-area relationship. Finally, the beta-diversity analysis (see Appendix I) showed that the overall beta-diversity (β_{sor}) was slightly higher for copepods (0.86) than cladocerans (0.81) but the partitioning revealed important differences: 94% of the variation in copepod beta-diversity was due to pure spatial turnover ($\beta_{\text{sim}} = 0.81$) and only 6% from nestedness ($\beta_{\text{nes}} = 0.05$) whereas cladoceran beta-diversity variance was decomposed into 83% spatial turnover ($\beta_{\text{sim}} = 0.67$) and 17% nestedness ($\beta_{\text{nes}} = 0.14$).

4.5 Discussion

As predicted, cyclic parthenogenetic cladocerans exhibited a much greater geographic range size than obligate sexual copepods, with an average difference of 70% between the two mating systems. We thus added important evidence that mate availability can be a limiting factor during range expansion as previously established in plants by Grossenbacher *et al.* (2015). Further, these groups differed strongly in how they responded to historical (i.e., Beringian refuge) and climatic factors (Table 4.4; Table 4.5), probably due to their contrasting life-history. Cladoceran richness and GRS had opposite relationship with temperature, where watersheds with warmer

climates contained more species with smaller GRS than cold-climate regions, suggesting that environmental filtering is an important structuring factor for cladocerans at macroecological scales. Furthermore, dispersal-limitation seems not to affect their distributional patterns, especially given that the Alaska glacial refuge had no effect in either their diversity or GRS (Figure 4.3C, 4.3D). The strong influence of climate on cladocerans may explain the steep relationship between their richness and average GRS with latitude (i.e., LDG and Rapoport's rule; Figure 4A, 4B). These results persisted even when we removed the *D. pulex* complex (Appendix G1, G2, G3), which populations are known to have switched to obligate asexually (i.e., therefore are not affected by migration load) in northern latitudes (Dufresne & Hebert, 1997; Decaestecker *et al.*, 2009). In contrast, copepod richness was only weakly influenced by temperature-related. Together, these results suggest that environmental filtering is not an important structuring factor for copepod macroecological patterns. Note, however, that our results do not mean that environment is not important for individual copepod species distributions. Different species may have particular affinities for different portion of the environmental gradient, but the environment in itself do not explain the variation in number of copepods species across space. Further, copepod average GRS was related to elevation and it may be an indirect effect of the Rocky Mountains proximity to the Beringian refugium as we found a significant positive effect of the distance from the Beringian refugium and GRS for copepods (Figure 4.3D; Table 4.4). This suggests that some copepod species colonized north-western watersheds from this northern

refuge but due to their poor dispersal ability (see Table 4.1), they were unable to expand their ranges across eastern or southern Canada, particularly given that they are absent from these regions. Indeed, some copepod species may rely on surface-waters for dispersal (Stemberger, 1995) and species that survived the Pleistocene glaciation in the Beringian refugium were never in direct contact with the ice-front lakes that formed along the southern ice sheet (Stemberger, 1995). Moreover, dispersal through migrating waterbirds from the Beringian refugium towards north-eastern watersheds is limited because migratory routes are mainly along the south-north direction. As a consequence, many copepod species in the north exhibit small geographic ranges. For instance, five out of 14 copepod species present in the Arctic Archipelago (#11 in Figure 4.1) were found solely in this watershed or distributed in only two more other watersheds (Appendix D2). This may explain the absence of both Rapoport's rule and LDG in this group (Figure 4.3). The regional beta diversity analysis (Appendix I) also support these results, where most of the spatial variation in copepod species composition was unrelated to richness but to species ranges that do not overlap (i.e., high spatial turnover - β_{sim}). In contrast, cladoceran beta-diversity is partially driven by species loss (i.e., higher β_{nes}), with a clear decrease in species diversity from southern watersheds towards the Arctic (Figure 4.3A).

The striking differences found among macroecological patterns in cladocerans and copepods are to an important degree due to their mating system. We can exclude

differences in biogeographic history (e.g., one group colonizing preferentially from northern refugia while the other colonizing preferentially from southern refugia) between the two groups given that many studies have shown that they both colonized Canada from southern (e.g., Mississippian and Atlantic) and northern (e.g., Berigian) glacial refugia (Hebert & Hann, 1986; Stemberger, 1995; Figuerola *et al.*, 2005; Jeffery *et al.*, 2011). We acknowledge that cladocerans and copepods differ in a number of factors other than mating system such as environmental tolerances, propagules capacity to disperse (e.g., ephippia eggs vs diapausing eggs; Havel & Shurin, 2004) and diet niche overlap (Barnett *et al.*, 2007). Therefore, one cannot exclude the possibility that these differences may also have played a role in shaping the differences in macroecological patterns between the two groups. Nevertheless, mating system may be a critical factor because it influences many processes such as the susceptibility to Allee effects during earlier stages of colonization (Courchamp *et al.*, 1999; Kramer *et al.*, 2008; Gray & Arnott, 2012), how rapidly they can adapt to local conditions and monopolize resources (De Meester *et al.*, 2002; Urban & De Meester, 2009) as well as the number of generations needed during the growing season to produce diapausing eggs. Notably, with a few exceptions (Shurin *et al.*, 2000; Leibold *et al.*, 2010), research involving large-scale patterns in diversity and distribution of freshwater microcrustaceans often neglect the potential effects of these fundamental life-history differences (e.g., Hessen *et al.*, 2007; Mazaris *et al.*, 2010; Pinel-Alloul *et al.*, 2013). For instance, Mazaris *et al.* (2010) could not find either spatial or environmental predictors that accounted for zooplankton large-scale

compositional patterns and we suspect that it might be because they pooled both cladocerans and copepods in the same analysis. In contrast, Leibold *et al.* (2010) demonstrated that cladocerans respond more to local-scale lake environmental factors (e.g., limnological variables) while calanoid copepod distribution is related to biogeographic events. Our results corroborate their findings, and show that even at broader scales, cladocerans continue to respond strongly to the environment (e.g., large-scale climatic variables) because they are not dispersal-limited while copepod diversity seems to be more driven by historical factors (e.g., Beringian refugium).

We propose two complementary explanations for the decrease in cladoceran diversity but not copepod diversity across the latitudinal gradient at northern regions. The first one is directly related to their mating system whereas the second encompasses other differences in their life-history traits. Zooplanktons cope with winter conditions by going through a diapausing phase that resists freezing and drying (Havel & Shurin, 2004), providing long-term persistence in highly seasonal environments. However, cyclic parthenogenetic cladocerans only produce diapausing eggs during the sexual phase, meaning that they need at least two generations to produce those eggs. Lakes and ponds located in northern regions have short growing seasons and experience very cold temperatures, in which both cladocerans and copepods have a slower metabolism and take longer to complete their life cycles (Allan, 1976). Northern latitude conditions might thus exclude some cladoceran species because they are unable to complete twice their life cycle during the short growing season (Hebert &

Hann, 1986). Notably, some cladoceran species (e.g., *Daphnia pulex* complex) lose their ability to reproduce sexually at northern latitudes, becoming completely asexual either through obligate apomictic parthenogenesis (Dufresne & Hebert, 1997) or self-fertilization (Hebert *et al.*, 2007). Evidence shows that many cladocerans populations found in the Canadian high Arctic have switched to an asexual breeding system while southern populations from the same species remain reproducing through cyclic parthenogenesis (Hebert *et al.*, 2007). Therefore, cladoceran diversity towards northern latitude may be limited due to the inability of most species to transition their mating system towards obligate asexuality. In contrast, copepods are composed by two groups that have different adaptations to cope with overwintering. Cyclopoid copepods are able to produce resting eggs throughout the growing season and can encyst in the 4th copepodid instar, providing more insurance to cope with highly seasonal environments (Tash & Armitage, 1967). Calanoid copepods are mostly composed of univoltine species that produce a small number of eggs and may require as long as 3 months before reaching reproductive maturity (Tash & Armitage, 1967), which can make them particularly sensible to disturbances such as an early onset of winter conditions (Hebert & Hann, 1986). However, diaptomid calanoid copepods (e.g., *Hesperodiaptomus arcticus*) can attain reproductive maturity at greatly reduced body sizes but unchanged generation time in stressful environmental conditions (Anderson, 1971), thus allowing them to cope with environmental conditions at northern latitudes.

The second likely explanation for the macroecological patterns described in this study is related to the monopolization hypothesis, proposed by De Meester *et al.* (2002), and lately extended to multiple species (i.e., community monopolization hypothesis; Urban & De Meester, 2009; De Meester *et al.*, 2016). Here, we extend this idea to macroecological scales: suppose that a few lakes in northern watersheds were first colonized by a long-distance dispersal event (e.g., diapausing eggs carried in waterbird feathers, a process deemed to be important in zooplankton dispersal; Figuerola *et al.*, 2005). Furthermore, as cladocerans are not affected by mate-finding Allee effects during colonization they can spread across these regions through small-scale dispersal processes much more rapidly than copepods. In addition, rapid population growth rates due to asexual reproduction together with clonal selection enable early cladoceran colonizers to adapt quickly to the local environment (De Meester *et al.*, 2002). In contrast, copepod growth rates are slower and they do not undergo clonal selection due to obligate sexual reproduction, thus having a slower local adaptation process (De Meester *et al.*, 2002). Theory from eco-evolutionary metacommunity models predicts that local adaptation from first colonizers enhance priority effects precluding the establishment of later migrants through niche pre-emption (Urban & De Meester, 2009; Fukami, 2015). Indeed, recent experimental work has shown that this process occurs frequently in cladocerans (e.g., Louette & De Meester, 2007; Pantel *et al.*, 2015), especially given that most species in this clade are herbivorous (28 out of 30 in our dataset; Barnett *et al.*, 2007) and exhibit high niche overlap in their resource use (Guisande *et al.*, 2003). Due to the short growing season

and low productivity of northern latitude lakes, the few resources available cannot sustain many cladoceran species (Vogt *et al.*, 2013). Therefore, rapid dispersal, resource monopolization and high food niche overlap may be a second reason underlying the sharp decline in cladoceran diversity across the latitudinal gradient. The fact that cladocerans exhibited a strong Rapoport's rule, in which only large GRS species were present in northern watersheds (Figure 4.3B); suggests that these regions were colonized only by highly dispersive and/or competitive species. For instance, six out of 10 cladoceran species present in the Arctic Archipelago watershed (#11 in Figure 4.1) were also distributed across 20 or more other watersheds and the remaining four were located in more than 12 watersheds (Appendix D1). In contrast, copepods show a much greater variability in diet, containing many omnivorous, carnivorous and some herbivorous species (Barnett *et al.*, 2007), which allow them to consume a much broader range of resources and lessen the strength of competition. Indeed, experimental work evaluating amino-acid composition and stable isotopes signature has shown that copepods exhibit a much lower food niche overlap than cladocerans (Guisande *et al.*, 2003; Santer *et al.*, 2006). Cyclopoids copepods, for instance, may change opportunistically between resources depending on their relative abundance (Santer *et al.*, 2006). Taken together, the fact that copepods are more dispersal-limited (Stemberger, 1995) and that they use a much broader range of resources might preclude monopolization from a few copepod species and allow later colonizers or weaker competitors to persist in these environments.

Disentangling the main factors underlying species geographic ranges is pressing, especially given the predicted changes in future climatic conditions and the potential range shift processes that will follow. Most of the literature concerning range dynamics focuses on traits that influence species environmental tolerances and dispersal ability (Gaston, 2009; Sexton *et al.*, 2009). The results presented here show that mate-limitation Allee effects should also be considered to understand species range dynamics (Courchamp *et al.*, 1999; Shaw & Kokko, 2015). Thus, future studies should also focus on how traits that alleviate Allee effects (e.g., dispersal timing, female sperm storage) may influence how different group of species will cope with changing environmental conditions. In respect to zooplankton, our results suggest that cladocerans will be less affected by climate change given their broad distribution, resilience to extinction and capacity for adaptation (Van Doorslaer *et al.*, 2009). However, it is possible that completely asexual populations thriving in the Arctic could be replaced by cyclic parthenogenetic phenotypes as temperature and growing season length increase. Moreover, the number of cladocerans species in northern watersheds may also increase, but it will depend on the immigration of other trophic levels (i.e., new algae species) as well as the strength of resource monopolization from resident species in these lakes. Copepods, however, may face more difficulties, especially the species restricted to the Arctic region. Given their strong dispersal limitation, they may not have enough time to adapt to the changing conditions and these processes may profoundly modify the trophic networks of Arctic ecosystems.

4.6 Conclusion

In conclusion, the present study shows important differences in the macroecological patterns of copepods and cladocerans. Cladocerans species are generally widespread whereas most copepods have a spatially-restricted distribution. Furthermore, cladocerans show the usual decrease in species diversity towards northern latitudes associated with an increase in average GRS (i.e., Rapoport's rule) and are highly influenced by climatic conditions. Conversely, neither copepod diversity nor average GRS show any significant relationship with latitude and are not related to environmental factors, suggesting a stronger role of dispersal limitation and biogeographic events. We hope that our findings will encourage both empiricists and theoreticians to carry out work to better elucidate the effect of mating system and, more generally, Allee effects on these processes.

CONCLUSION

Understanding species range constraints has been a longstanding goal in ecology. Dispersal barriers and environmental conditions are often cited as the main drivers and are at the core of most species distribution models. It is therefore assumed that biotic interactions are not important, species are at equilibrium with climate, and dispersal is a fixed trait. Recently, however, these erroneous assumptions have been challenged. Recent evidence has shown that biotic processes may influence a variety of large-scale ecological patterns. We also know that species are not homogeneous entities, but rather a complex collection of individuals that show large variation in many traits – notably dispersal and environmental tolerance. More importantly, these traits have been shown to evolve faster than previously thought, and certainly within the timeframe under which range expansion occurs.

This thesis was therefore framed through a multi-scale bottom-up approach, in which I explicitly evaluated how abiotic and biotic factors influencing niche and dispersal evolution would shape species geographic ranges. The ultimate goal was to understand how these processes might affect diversity patterns at continental scales under the logic that biodiversity is a by-product of the overlap of multiple species ranges. These mechanisms were explored across three chapters using individual-based models (Chapter I to III), which differed in the primary conceptual underpinning and ecological scales in which such processes were considered. The

fourth chapter, in turn, was used to test predictions regarding biodiversity gradients derived from the multi-species model developed in Chapter III using a large-scale freshwater zooplankton dataset.

The main conclusion of my first chapter was that landscape connectivity could select for different density-dependent dispersal strategies. Such an effect was due to the spatial variation in demographic processes created by asymmetric dispersal between patches. Given that dispersal may evolve over short time-scales, connectivity should be considered to better predict how species would shift their ranges between landscapes with contrasting spatial structures.

In the second chapter, I explored the effects of landscape connectivity, environmental fluctuation, and population growth rates on the speed of range expansion for species following either a density-dependent (DD) dispersal strategy or a random dispersal strategy (i.e., density-independent; DI). Variance in connectivity slowed range expansion for both dispersal strategies. Further, whether DD or DI dispersal promoted faster range expansion depended on species population growth rate. Species with low growth rates spread their ranges faster following DI dispersal while species with high growth rates spread their ranges under DD dispersal. Given that individuals at the expansion front were initially maladapted, populations remained at low densities due to high mortality rates until favourable mutations occurred. In these conditions, only species with high growth rates were able to offset mortality rates to

build up the necessary population density that would favour higher emigration rates under DD dispersal. Our results show a previously unknown interaction between dispersal strategies and population growth rates, which could be empirically tested by identifying the primary cues used for dispersal decisions among species with different population growth rates.

In the third chapter, I up-scaled the individual-based model to multiple species in order to investigate the effects of biotic processes, such as inter-specific competition and mate-finding Allee effects, on species range expansion. Further, I analyzed the formation of spatial gradients in diversity (latitudinal-diversity gradient; LDG) and average geographic range size (Rapoport's rule). Mate-finding Allee effects had a large negative effect on geographic range size (GRS) that was in accordance with empirical evidence published in previous studies, as well as Chapter IV through the comparison of GRS from freshwater microcrustacean groups that differ in their susceptibility to Allee effects. In addition, Allee effects also regulated both LDG and Rapoport's rule by decreasing the intercept of their slope, an effect that did not occur in asexual species. Mate-finding Allee effects increased local extinction risk, which decreased the diversity of all regions, including the regions where species were initially seeded, creating a smoother diversity gradient. In contrast, all asexual species persisted in most regions where they were initially seeded, thus creating a steeper decline in diversity across the environmental gradient. Furthermore, I showed that the strength of interspecific competition modulated the steepness of latitudinal gradients

in both diversity and average GRS. This chapter shed light onto two overlooked mechanisms structuring large-scale ecological patterns. The generality of the LDG is already a settled question in ecology, although there is still an ongoing debate regarding its underlying mechanisms. The results provided by Chapter III imply that ecologists should go beyond this debate and start investigating how the slope varies across taxonomic groups with distinct ecological traits. This approach should provide a more mechanistic understanding on large-scale biodiversity patterns and potentially improve our predictions regarding how distinct clades will respond to future environmental change.

Finally, the steepness of latitudinal gradients in diversity and GRS between cladocerans and copepods was investigated in Chapter IV. These two microcrustacean clades have distinct mating systems that influence their susceptibility to Allee effects, dispersal ability and local adaptation processes, providing an interesting system to evaluate the predictions derived from Chapter III. Our results showed that cladocerans have, on average, much wider GRS than copepods, likely due to the avoidance of mate-finding Allee effects. Furthermore, cladocerans exhibit a sharp decline in diversity and an increase in average GRS across the latitudinal gradient. In contrast, copepods do not show any spatial variation in species diversity or GRS across the latitudinal gradient. Copepod species distributions were largely affected by dispersal limitation and proximity to a northern glacial refuge, the Beringian refugium. On the other hand, cladoceran distributions were mostly regulated by

climatic factors. These results support the prediction from Chapter III, namely that mate-finding Allee effects may influence large-scale ecological patterns such as geographic ranges and latitudinal gradients.

In conclusion, this thesis provides a robust framework to investigate eco-evolutionary dynamics of dispersal and local adaptation, along with their relationship to species ranges. By extending the framework to multiple species we were able to uncover new mechanisms regulating diversity patterns at large spatial scales. There is much work to be done though, especially to empirically validate predictions obtained from the modelling chapters, as well as to further enquire into the feedback between ecological and evolutionary processes regulating large-scale ecological patterns.

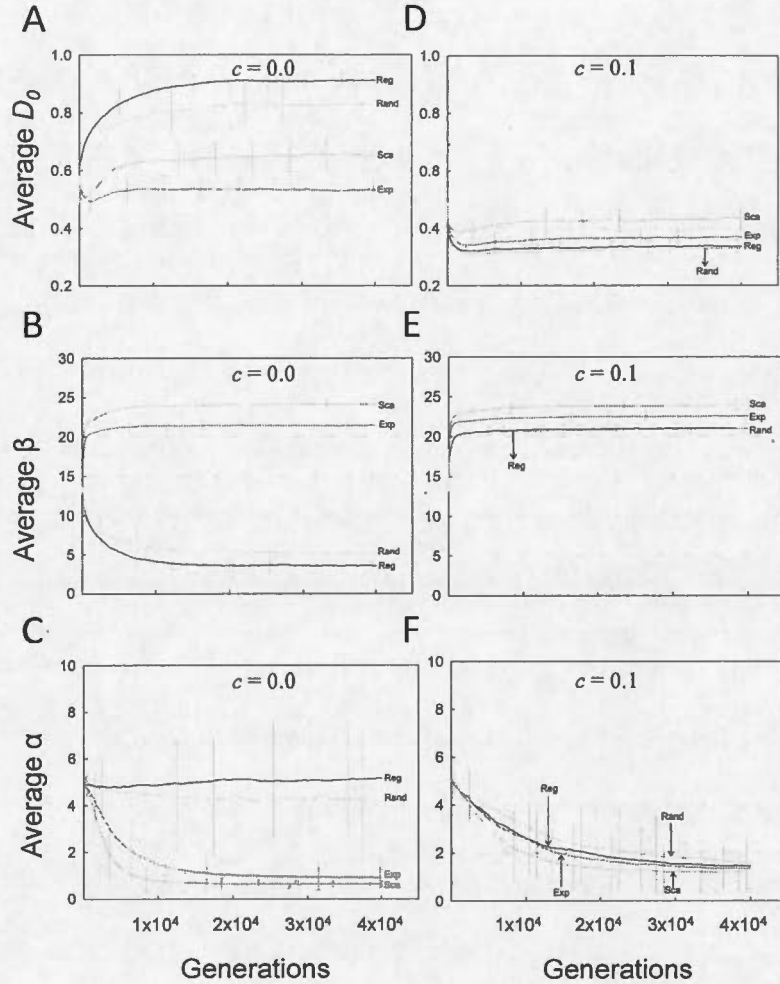
This thesis raises many interesting research topics for future studies for which I will provide three examples. 1) As dispersal influences the genetic structure and evolution of populations through gene flow, how does the selection of different density-dependent dispersal strategies based on landscape structure would affect other life-history traits? Given that different landscapes may exert weaker or stronger selective pressure on dispersal traits (Chapter I), what would be the consequence for genetic variability regulating other correlated traits? 2) Chapter II demonstrated that the relative importance of density-dependent and density-independent dispersal on emigration rates depends on population growth rates. It remains to be investigated if a species is able to change the types of cues (e.g., density of conspecifics, predators,

potential mates, climate) used to disperse at different levels of population growth rates. 3) Chapter III shows that in absence of competition all species are able to evolve their environmental niches. One could ask whether tropical niche conservatism results from an intrinsic inability of species to evolve the necessary adaptations for invading temperate regions (i.e., due lack of genetic variability) or a synergetic effect of abiotic and biotic factors that limit niche evolution through trade-off in important life-history traits.

It is my hope that the present work will inspire theoreticians and empiricists to carry out work on the mechanisms underlying species ranges and how these would in turn influence the diversity and distribution of species across space. Approaching macroecology through the lenses of range dynamics may be a worthwhile avenue of enquiry as I have shown in this thesis that it may lead to novel and interesting insights about large-scale ecological patterns.

APPENDIX A

CHAPTER I



Evolutionary dynamics of the dispersal parameters over 40000 generations for each network structure from the main simulations of Chapter I. (A) D_0 , (B) β and (C) α represent simulations ran with fixed dispersal mortality $c = 0$ while (D) D_0 , (E) β and (F) α represent simulations ran with dispersal mortality $c = 0.1$. The lines represent the mean value across the 200 replicates of the average parameter value across all individuals for each generation. Horizontal lines represent the standard deviation of these values across the 200 replicates. D_0 = maximum dispersal probability; β = inflection point; α = steepness of the curve at the inflection point. Reg = Regular network, Rand = Random network, Exp = Exponential network and Sca = Scale-free network.

APPENDIX B

CHAPTER I

A sensitivity analysis was performed in order to evaluate the robustness of our results regarding all relevant model parameters. We followed the methodology from Kubisch *et al.* (2011) and changed parameter values (K , b and μ) by $\pm 20\%$ and evaluated the values of dispersal traits that were selected in each landscape structure. The sensitivity analysis was only performed for $c = 0.1$ due to the high number of simulations required. However, the interpretation of our main results was robust to parameter changes for this dispersal cost scenario. We performed 200 replicates for each parameter change and computed the average values for each dispersal trait (D_0 , β and α) at the last time step. We then subtracted the average trait values obtained in each scenario from the average trait values obtained in the original simulation. Finally, we calculated sensitivity as the relative change of the trait value divided by the relative change of the according parameter. High sensitivity values indicate a higher magnitude in change on the trait value compared to the change in the parameter value. A positive sensitivity means that the effect on the trait value follows the direction of the parameter change (e.g., an increase in a parameter value causes an increase in a dispersal trait value). A negative sensitivity value indicates that the effect on the trait value is in the opposite direction of the change in the parameter value (e.g., an increase in a parameter value causes a decrease in a trait value).

The results obtained from this analysis show that across all network structures, D_0 was only slightly affected by the tested scenarios, remaining fairly similar to the values obtained in the original simulation. Changes in K and b presented a negative effect on D_0 while changes in μ had a very small effect on this trait. Overall, these results suggest an increase in the maximum dispersal probability (D_0) under conditions of lower carrying capacity or stronger competitive interactions. Moreover, across all tested scenarios, the sequence of D_0 values across networks remained similar to the original simulation, where scale-free networks presented the highest value while random networks selected for the lowest value. The second trait (β) was strongly positively affected by changes in K and b while not being affected by changes in parameter μ . In general, lower carrying capacities and stronger competition selected for smaller β values while higher carrying capacities and lower competition resulted in higher β values. The direction and magnitude of this effect was similar across all network structures. This is expected because β controls the threshold value in local abundance in which the probability of dispersing is half of its maximum. Decreasing the carrying capacity or increasing competition within patches decrease the threshold abundance in which an individual will be willing to disperse, independent on the network configuration. Finally, α was positively affected by an increase in b and negatively affected by both increases and decreases in the parameter μ . However, the effect of α on the dispersal function (d) is stronger only between the values 0 and 1 (Travis et al., 2009), and all changes on α due to model parameter

changes resulted in average α trait above 1, thus having little effect on the dispersal strategy.

Results from the sensitivity analysis for a change of $\pm 20\%$ of the relevant model parameters across all network types. The numbers outside the brackets represent the difference in trait values between original simulation and tested scenarios. The numbers in brackets denote the sensitivity of this difference for the given parameter. For instance, in the K -20% scenario in regular networks, D_0 has a sensitivity value of -0.59. The negative sign indicates that the change in the trait value is the opposite of the change in the parameter value. Thus, the value represents an increase in D_0 of 59% of the change in the K parameter. K is the carrying capacity of local patches, b represents the strength of local competition (where lower values denote stronger contest competition) and μ represents the growth rate of local populations.

	Regular					
	$K - 20\%$ $K = 16$	$K + 20\%$ $K = 24$	$b - 20\%$ $b = 0.8$	$b + 20\%$ $b = 1.2$	$\mu - 20\%$ $\mu = 1.2$	$\mu + 20\%$ $\mu = 1.8$
D_0	0.04 (-0.59)	-0.03 (-0.44)	0.05 (-0.76)	-0.03 (-0.52)	-0.03 (0.40)	0.01 (0.21)
β	-4.33 (1.03)	4.30 (1.03)	-5.24 (1.25)	5.30 (1.26)	0.37 (-0.09)	-0.11 (-0.03)
α	-0.16 (0.53)	0.19 (0.64)	-0.09 (0.30)	0.41 (1.41)	1.44 (-4.93)	-0.25 (-0.86)
	Random					
	$K - 20\%$	$K + 20\%$	$b - 20\%$	$b + 20\%$	$\mu - 20\%$	$\mu + 20\%$
D_0	0.04 (- 0.58)	-0.03 (-0.42)	0.05 (-0.73)	-0.04 (-0.56)	-0.03 (0.45)	0.01 (0.18)
β	-4.39 (1.05)	4.38 (1.05)	-5.31 (1.27)	5.24 (1.25)	0.14 (-0.03)	-0.14 (-0.03)
α	-0.16 (0.49)	0.25 (0.79)	-0.05 (0.15)	0.42 (1.33)	1.52 (-4.77)	-0.30 (-0.94)
	Exponential					

	$K - 20\%$	$K + 20\%$	$b - 20\%$	$b + 20\%$	$\mu - 20\%$	$\mu + 20\%$
D_0	0.04 (-0.52)	-0.03 (-0.45)	0.04 (-0.58)	-0.04 (-0.53)	-0.02 (0.21)	-0.01 (-0.10)
β	-4.64 (1.03)	4.52 (1.00)	-5.64 (1.25)	5.43 (1.20)	0.02 (-0.01)	-0.18 (-0.04)
α	-0.08 (0.30)	0.35 (1.27)	-0.06 (0.23)	0.62 (2.24)	1.55 (-5.64)	-0.16 (-0.59)

	$K - 20\%$	$K + 20\%$	Scale-free		$\mu - 20\%$	$\mu + 20\%$
	$K - 20\%$	$K + 20\%$	$b - 20\%$	$b + 20\%$	$\mu - 20\%$	$\mu + 20\%$
D_0	0.04 (-0.46)	-0.03 (-0.36)	0.04 (-0.50)	-0.04 (-0.49)	0.01 (-0.11)	-0.03 (-0.29)
β	-4.78 (1.00)	4.71 (0.99)	-5.85 (1.22)	5.63 (1.18)	0.32 (-0.07)	-0.32 (-0.07)
α	-0.13 (0.53)	0.05 (0.23)	-0.08 (0.33)	0.27 (1.13)	0.61 (-2.60)	-0.13 (-0.55)

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APPENDIX C1

CHAPTER I

Results from post-hoc Tukey-Kramer test on the two-way ANOVA for network structure. $u_{G1} - u_{G2}$ represent the difference in means from the group 1 (G1) and group 2 (G2). p = probability. In the table below, the differences between structures for the three dispersal traits were all significant, except between Regular and Random networks and between Exponential and Scale-free networks for α (steepness of the curve at the inflection point).

Trait 1 – D_0			
G1	G2	$u_{G1} - u_{G2}$	P
Regular	Random	0.031	<0.001
Regular	Exponential	0.116	<0.001
Regular	Scale-free	0.052	<0.001
Random	Exponential	0.085	<0.001
Random	Scale-free	0.021	<0.001
Exponential	Scale-free	-0.064	<0.001
Trait 2 – β			
G1	G2	$u_{G1} - u_{G2}$	P
Regular	Random	-0.440	<0.001
Regular	Exponential	-6.520	<0.001
Regular	Scale-free	-7.887	<0.001
Random	Exponential	-6.080	<0.001
Random	Scale-free	-7.447	<0.001
Exponential	Scale-free	-1.368	<0.001
Trait 3 – α			
G1	G2	$u_{G1} - u_{G2}$	P
Regular	Random	0.017	0.99
Regular	Exponential	1.512	<0.001
Regular	Scale-free	1.709	<0.001
Random	Exponential	1.495	<0.001
Random	Scale-free	1.692	<0.001
Exponential	Scale-free	0.197	0.181

APPENDIX C2

CHAPTER I

Results from post-hoc Tukey-Kramer test on the two-way ANOVA for dispersal mortality. $u_{G1} - u_{G2}$ represent the difference in means from the group 1 (G1) and group 2 (G2). p = probability. In the table below, the differences between dispersal mortality treatments for the three dispersal traits were all significant.

Trait 1 – D_0			
G1	G2	$u_{G1} - u_{G2}$	P
$c = 0$	$c = 0.1$	0.364	<0.001
$c = 0$	$c = 0.5$	0.477	<0.001
$c = 0.1$	$c = 0.5$	0.114	<0.001
Trait 2 – β			
G1	G2	$u_{G1} - u_{G2}$	P
$c = 0$	$c = 0.1$	-8.560	<0.001
$c = 0$	$c = 0.5$	-11.012	<0.001
$c = 0.1$	$c = 0.5$	-2.452	<0.001
Trait 3 – α			
G1	G2	$u_{G1} - u_{G2}$	P
$c = 0$	$c = 0.1$	1.341	<0.001
$c = 0$	$c = 0.5$	-0.715	<0.001
$c = 0.1$	$c = 0.5$	-2.056	<0.001

APPENDIX C3

CHAPTER I

Results from post-hoc Tukey-Kramer test on the two-way ANOVA for the interaction between mortality and network structure. The test was performed on 66 pairs related to the interactions for each trait. Due to the large number of results, we will only present the pairs of interactions that were not significantly different from one another (significance-level = 0.05).

Trait 1 – D_0 (Number of comparisons; significant = 60 / non-significant = 6)			
G1	G2	$u_{G1} - u_{G2}$	p
Regular/c=0.1	Random/c=0.1	0.005467732	0.9396517
Regular/c=0.5	Random/c=0.5	0.007608113	0.6276343
Regular/c=0.5	Exponential/c=0.5	-0.000107509	1
Regular/c=0.5	ScaleFree/c=0.5	-0.008816401	0.3887129
Random/c=0.5	Exponential/c=0.5	-0.007715622	0.6061808
Exponential/c=0.5	ScaleFree/c=0.5	-0.008708892	0.4088419
Trait 2 – β (Number of comparisons; significant = 58 / non-significant = 8)			
G1	G2	$u_{G1} - u_{G2}$	p
ScaleFree/c=0.0	ScaleFree/c=0.1	-0.20314969	0.5547676
Regular/c=0.5	Random/c=0.5	0.16056395	0.8527488
Regular/c=0.5	Exponential/c=0.5	-0.10609027	0.9925579
Regular/c=0.5	ScaleFree/c=0.5	-0.26043258	0.1755711
Random/c=0.5	Exponential/c=0.5	-0.26665421	0.149101
Random/c=0.5	ScaleFree/c=0.0	0.25928131	0.1808188
Random/c=0.5	ScaleFree/c=0.1	0.462431	0.000041
Exponential/c=0.5	ScaleFree/c=0.5	-0.15434231	0.8833773
Trait 3 – α (Number of comparisons; significant = 51 / non-significant = 15)			
G1	G2	$u_{G1} - u_{G2}$	p
Random/c=0.0	Random/c=0.5	0.14391	0.9994898
Exponential/c=0.0	ScaleFree/c=0.0	0.278386	0.8918839
Exponential/c=0.0	Regular/c=0.1	-0.54718	0.0558826
Exponential/c=0.0	Exponential/c=0.1	-0.46072	0.2151105
Exponential/c=0.0	ScaleFree/c=0.1	-0.2671	0.9167633
ScaleFree/c=0.0	ScaleFree/c=0.1	-0.54548	0.0575953
Regular/c=0.1	Random/c=0.1	-0.12644	0.9998543
Regular/c=0.1	Exponential/c=0.1	0.086461	0.999997
Regular/c=0.1	ScaleFree/c=0.1	0.280081	0.8877807
Random/c=0.1	Exponential/c=0.1	0.212902	0.9838988
Random/c=0.1	ScaleFree/c=0.1	0.406522	0.4040816
Exponential/c=0.1	ScaleFree/c=0.1	0.19362	0.9925968
Regular/c=0.5	Exponential/c=0.5	0.211313	0.9848308
Regular/c=0.5	ScaleFree/c=0.5	0.330389	0.7251875
Exponential/c=0.5	ScaleFree/c=0.5	0.119076	0.9999196

APPENDIX D1

CHAPTER IV

Occurrence (number of watersheds), Geographic Range Size (GRS) and presence in the Arctic archipelago (see Watershed 11 in Figure 4.1) of cladoceran species (indicated by X). The total number of watersheds (WS) is 26.

Species name	Occurrence	GRS (km ²)	Arctic archipelago
<i>Bosmina longirostris</i>	26	13420298.0	X
<i>Ceriodaphnia lacustris</i>	16	5880108.0	
<i>Ceriodaphnia quadrangula</i>	19	8871466.0	
<i>Ceriodaphnia reticulata</i>	9	2766761.0	
<i>Chydorus sphaericus</i>	26	11909970.0	X
<i>Daphnia ambigua</i>	11	2677235.0	
<i>Daphnia catawba</i>	7	1714730.0	
<i>Daphnia dubia</i>	9	2085952.0	
<i>Daphnia galeata</i>	4	768615.4	
<i>Daphnia mendotae</i>	23	7258309.0	
<i>Daphnia longiremis</i>	24	11525617.0	X
<i>Daphnia magna</i>	6	4547827.0	
<i>Daphnia middendorffiana</i>	12	8779165.0	X
<i>Daphnia parvula</i>	9	1868183.0	
<i>Daphnia pulex</i>	20	9608406.0	X
<i>Daphnia retrocurva</i>	18	5221963.0	
<i>Daphnia rosea</i>	12	6126944.0	X
<i>Daphnia pulicaria</i>	16	8415249.0	X
<i>Daphnia similis</i>	5	263364.0	
<i>Daphnia thorata</i>	3	181319.3	
<i>Diaphanosoma brachyurum</i>	17	7007613.0	
<i>Diaphanosoma leuchtenbergianum</i>	19	6628421.0	
<i>Eubosmina longispina</i>	16	11269232.0	X
<i>Eubosmina tubicen</i>	5	2425917.0	
<i>Holopedium gibberum</i>	26	12093279.0	X
<i>Leptodora kindtii</i>	23	9627942.0	
<i>Moina hutchinsoni</i>	3	124242.7	
<i>Ophryoxus gracilis</i>	9	3487153.0	
<i>Polyphemus pediculus</i>	21	8576857.0	X
<i>Sida crystallina</i>	10	6038167.0	

APPENDIX D2

CHAPTER IV

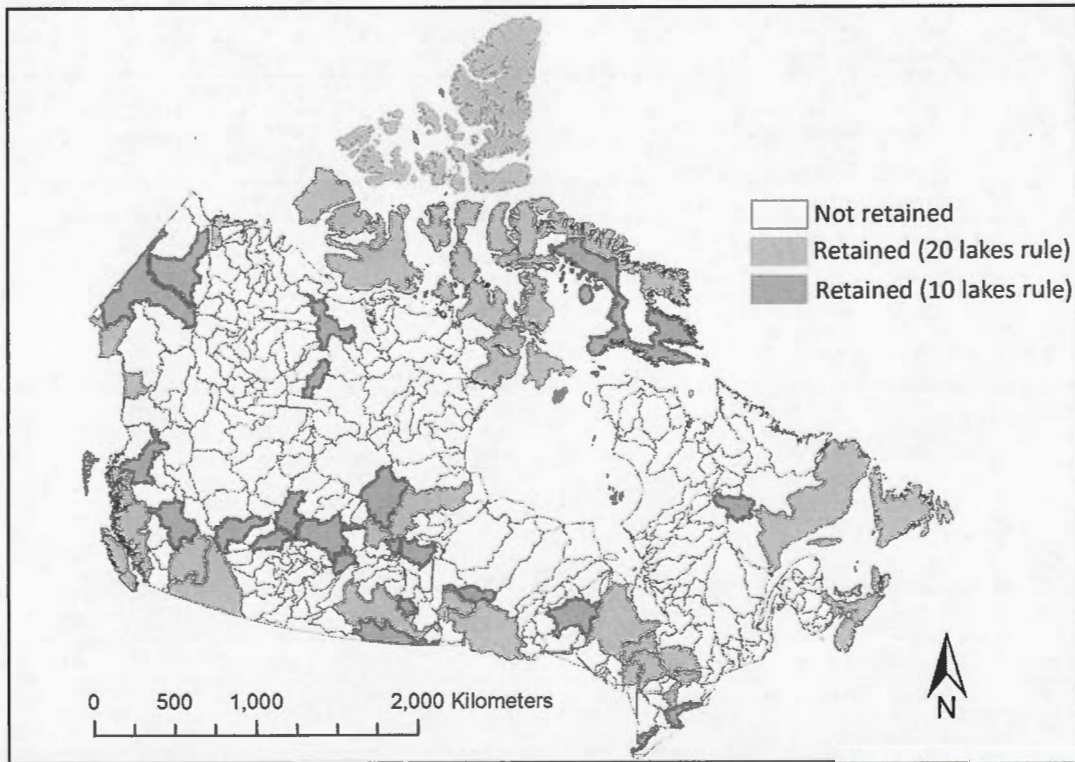
Occurrence (number of watersheds), Geographic Range Size (GRS) and presence in the Arctic archipelago (see Watershed 11 in Figure 4.1) of copepod species (indicated by X). The total number of watersheds (WS) is 26.

Species name	Occurrence	GRS (km ²)	Arctic archipelago
<i>Acanthodiaptomus denticornis</i>	10	1996942.0	
<i>Acanthocyclops vernalis</i>	24	10990976.0	X
<i>Acanthocyclops capillatus</i>	9	4609678.0	X
<i>Aglaodiaptomus clavipes</i>	1	16871.9	
<i>Aglaodiaptomus forbesi</i>	3	63066.8	
<i>Aglaodiaptomus leptopus</i>	8	3034744.0	
<i>Aglaodiaptomus spatulocrenatus</i>	4	1097693.0	
<i>Cyclops abyssorum</i>	1	3428.0	X
<i>Cyclops scutifer</i>	19	11916724.0	X
<i>Cyclops vicinus</i>	1	5343.5	X
<i>Diacyclops thomasi</i>	24	8389144.0	
<i>Epischura lacustris</i>	19	7026051.0	
<i>Epischura nevadensis</i>	8	4466224.0	
<i>Epischura nordenskiöldi</i>	2	49568.2	
<i>Eucyclops agilis</i>	13	10980500.0	X
<i>Eucyclops serrulatus</i>	9	4399282.0	
<i>Eucyclops speratus</i>	11	5543048.0	
<i>Eurytemora affinis</i>	1	8552.0	
<i>Eurytemora canadensis</i>	3	506836.7	X
<i>Hesperodiaptomus arcticus</i>	9	2619824.0	X
<i>Hesperodiaptomus eiseni</i>	3	3396190.0	X
<i>Hesperodiaptomus franciscanus</i>	2	186685.8	
<i>Hesperodiaptomus kenai</i>	3	168794.3	
<i>Hesperodiaptomus nevadensis</i>	5	234054.8	
<i>Hesperodiaptomus wilsonae</i>	1	269452.8	
<i>Heterocope septentrionalis</i>	9	3487335.0	
<i>Leptodiaptomus ashlandi</i>	17	6883844.0	
<i>Leptodiaptomus angustilobus</i>	10	3374168.0	X
<i>Leptodiaptomus connexus</i>	2	18645.1	
<i>Leptodiaptomus minutus</i>	17	7582199.0	X
<i>Leptodiaptomus nudus</i>	3	191845.5	
<i>Leptodiaptomus sicilis</i>	23	8439619.0	X
<i>Leptodiaptomus siciloides</i>	9	2872020.0	

<i>Leptodiaptomus tyrrelli</i>	6	849532.6	
<i>Limnocalanus macrurus</i>	16	8345121.0	X
<i>Macrocylops albidus</i>	16	8889381.0	
<i>Megacyclops magnus</i>	2	770660.7	X
<i>Mesocyclops americanus</i>	9	1959914.0	
<i>Mesocyclops edax</i>	16	4947557.0	
<i>Orthocyclops modestus</i>	11	1828766.0	
<i>Senecella calanoides</i>	8	4093188.0	
<i>Skistodiaptomus oregonensis</i>	22	8077237.0	
<i>Skistodiaptomus pygmaeus</i>	1	23388.6	
<i>Skistodiaptomus reighardi</i>	1	29.8	

APPENDIX E1

CHAPTER IV



Map depicting the tertiary watersheds selected in the analysis of LDG and Rapoport's rule. We applied two different rules to select watersheds. The first retained only watersheds with a minimum of 20 sampled lakes (dark orange; 926 lakes in 24 watersheds) similarly to the one used in the main analysis with secondary watersheds. Given that too many lakes were removed with this rule we performed a second analysis but decreased the minimum threshold to 10 sampled lakes (light orange, 1219 lakes in 47 watersheds). Regression results under this spatial scale are presented in Appendix E2 (dark orange watersheds) and Appendix E3 (light orange watersheds).

APPENDIX E2

CHAPTER IV

Latitude-diversity and Latitude-GRS relationships across tertiary watersheds with a minimum of 20 lakes per watershed. Results from linear regression models between latitude and log-transformed watershed diversity (S_{STD}) and average geographic range size (GRS) with watershed area (A) as a covariable for calanoids and cyclopoids. *Global - P* = global probability; P_{INTER} = probability for the intercept; P_{LAT} = probability for latitude; P_A = probability for watershed area; b_{LAT} = coefficient for latitude; b_A = coefficient for watershed area. Significant p -values under an $\alpha = 0.05$ are highlighted in bold.

Group	Cladocera		Copepoda	
Response	S_{STD}	GRS	S_{STD}	GRS
F	29.47	24.61	0.02117	4.297
<i>Global - P</i>	<0.0001	<0.0001	0.9791	0.02727
$Adj-R^2$	0.7123	0.6725	-0.09303	0.2228
Intercept	6.104895	15.252059	4.137491	15.671623
P_{INTER}	<0.0001	<0.0001	<0.0001	<0.0001
b_{LAT}	-0.034296	0.012602	-0.001676	0.001974
P_{LAT}	<0.0001	<0.0001	0.869	0.5744
b_A	-0.002727	0.002867	0.012432	-0.064582
P_A	0.935	0.833	0.854	0.0109

APPENDIX E3

CHAPTER IV

Latitude-diversity and Latitude-GRS relationships across third-level watersheds with a minimum of 10 lakes per watershed. Results from linear regression models between latitude and log-transformed watershed diversity (S_{STD}) and average geographic range size (GRS) with watershed area (A) as a covariable for calanoids and cyclopoids. *Global - P* = global probability; P_{INTER} = probability for the intercept; P_{LAT} = probability for latitude; P_A = probability for watershed area; b_{LAT} = coefficient for latitude; b_A = coefficient for watershed area. Significant p -values under an $\alpha = 0.05$ are highlighted in bold.

Group	Cladocera		Copepoda	
Response	S_{STD}	GRS	S_{STD}	GRS
F	31.45	36.94	0.406	3.552
<i>Global - P</i>	0.0001	<0.0001	0.6688	0.03714
$Adj-R^2$	0.5697	0.6098	-0.02651	0.09988
Intercept	6.027765	15.235882	3.739133	15.531084
P_{INTER}	<0.0001	<0.0001	<0.0001	<0.0001
b_{LAT}	-0.035510	0.012908	0.002864	0.004151
P_{LAT}	<0.0001	<0.0001	0.761	0.1740
b_A	0.019977	0.002488	0.034346	-0.052203
P_A	0.538	0.829	0.576	0.0107

APPENDIX F

CHAPTER IV

Results from Kolmogorov-Smirnov test with the Lilliefors correction and Breusch-Pagan test for all regression models in Chapter 4: latitude ($LAT + A$), distance from the Beringian refugium ($BER + A$) and environment variables selected in the forward selection procedure ($ENV + A$). The +A refers to the watershed area (A) included in the model as a covariable. Significant tests are highlighted in the bold. The only significant test was between Cladocera GRS with the refuge variable (BER).

Kolmogorov-Smirnov test (Normality of residuals)								
Group	Cladocera				Copepoda			
Response	S_{STD}		GRS		S_{STD}		GRS	
Statistic	D	P	D	P	D	P	D	P
$Lat + A$	0.116	0.4861	0.115	0.5036	0.089	0.8525	0.099	0.726
$BER + A$	0.148	0.146	0.100	0.7172	0.129	0.3129	0.119	0.441
$ENV + A$	0.0852	0.8977	0.102	0.6904	0.145	0.1679	0.129	0.3243
Breusch-Pagan test (Homoscedasticity)								
Group	Cladocera				Copepoda			
Response	S_{STD}		GRS		S_{STD}		GRS	
	BP	P	BP	P	BP	P	BP	P
$Lat + A$	1.4345	0.4881	1.388	0.4996	1.875	0.3916	1.8357	0.3994
$BER + A$	3.5566	0.1689	6.3178	0.0424	0.5422	0.7625	3.9619	0.1379
$ENV + A$	0.9443	0.6237	0.8245	0.8436	1.7867	0.4093	0.3633	0.8339

APPENDIX G1

CHAPTER IV

Regression analysis for cladocerans without the *D. pulex* complex. Results from linear regression models between latitude and log-transformed watershed diversity (S_{STD}) and average geographic range size (GRS) with watershed area (A) as a covariable. *Global - P* = global probability; P_{INTER} = probability for the intercept; P_{LAT} = probability for latitude; P_A = probability for watershed area; b_{LAT} = coefficient for latitude; b_A = coefficient for watershed area. Significant p -values under an $\alpha = 0.05$ are highlighted in bold. Both residual normality and homoscedasticity were tested similarly to the main analysis and results were not significant (results not shown).

	Cladocera (without <i>D. pulex</i> complex)	
Response	S_{STD}	GRS
F	29.99	28.98
<i>Global - P</i>	<0.00001	<0.00001
$Adj-R^2$	0.6987	0.6912
Intercept	5.98	15.01
P_{INTER}	<0.00001	<0.00001
b_{LAT}	-0.037	0.015
P_{LAT}	<0.00001	<0.00001
b_A	0.02	0.001
P_A	0.659	0.937

APPENDIX G2

CHAPTER IV

Regression analysis for cladocerans without the *D. pulex* complex. Results from linear regressions between the distance from the Beringian refugium (*BER*) and log-transformed watershed diversity (*S_{STD}*) and average geographic range size (*GRS*) with

watershed area (*A*) as a covariable. *Global - P* = global probability; *P_{INTER}* = probability for the intercept; *P_{LAT}* = probability for latitude; *P_A* = probability for watershed area; *b_{LAT}* = coefficient for latitude; *b_A* = coefficient for watershed area.

Significant *p*-values under an $\alpha = 0.05$ are highlighted in bold. Both residual normality and homoscedasticity were tested similarly to the main analysis. Again, the model (cladoceran *GRS* ~ *BER* + *A*) failed the residual homoscedasticity test and therefore we heteroscedasticity corrected it by the Huber-White method (results not shown).

	Cladocera (without <i>D. pulex</i> complex)	
Response	<i>S_{STD}</i>	<i>GRS</i>
<i>F</i>	2.352	3.113
<i>Global - P</i>	0.118	0.0636
<i>Adj-R²</i>	0.0975	0.1446
Intercept	5.051	15.41
<i>P_{INTER}</i>	<0.00001	<0.00001
<i>b_{BER}</i>	0.0053	-0.002
<i>P_{BER}</i>	0.083	0.059
<i>b_A</i>	-0.095	0.050
<i>P_A</i>	0.237	0.137

APPENDIX G3

CHAPTER IV

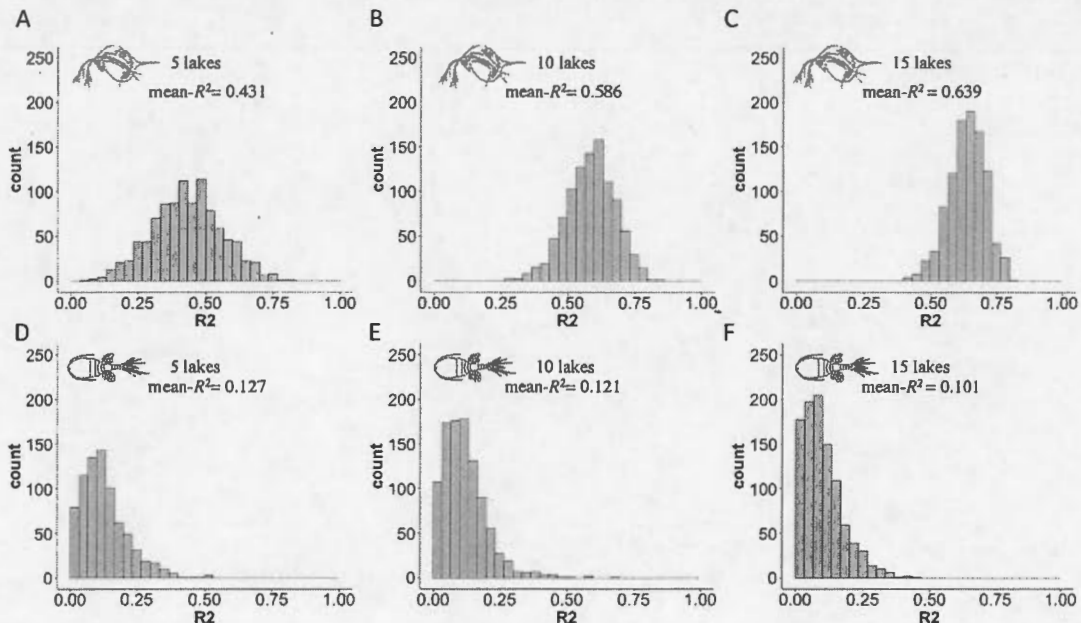
Regression analysis for cladocerans without the *D. pulex* complex. Result from forward-selection regression models between environmental variables and log-transformed watershed diversity (S_{STD}) and average geographic range size (GRS) with watershed area (A) as a covariable. $VAR1$ and $VAR2$ refer to the variables selected in the forward-selection procedure. GSL = Growing season length; $MDGRS$ = Mean Daily Global Solar Radiation; TAP = Total Annual Precipitation ; b_{VAR1} = regression slope for the first selected variable, b_{VAR2} = regression slope for the second selected variable; P_{VAR1} = probability for the first selected variable; P_{VAR2} = probability for the second selected variable; b_A = coefficient for watershed area; P_A = probability for watershed area. Significant p -values under an $\alpha=0.05$ are highlighted in bold. Both residual normality and homoscedasticity were tested similarly to the main analysis and results were not significant (results not shown).

	Cladocera (without <i>D. pulex</i> complex)	
Model	S_{STD}	GRS
$VAR1$	GSL	$MDGRS$
$VAR2$	$MDGRS$	TAP
F	33.78	23.05
$Global - P$	<0.0001	<0.0001
$Adj-R^2$	0.7973	0.7258
Intercept	1.663214	16.83
P_{INTER}	0.017	<0.0001
B_{VAR1}	0.004	-0.076
P_{VAR1}	0.0013	<0.0001
B_{VAR2}	0.099	-0.00013
P_{VAR2}	0.022	0.0428
b_A	0.055	0.0013
P_A	0.1852	0.9456

APPENDIX H

CHAPTER IV

In order to test if our results are robust to per-lake sampling effort variation, we developed a re-sampling procedure in which we randomly draw from each watershed a subset of 5, 10 and 15 lakes. We then computed the regional diversity metric (similarly to the original analysis) based on this subset of lakes for cladocerans and copepods. Further, we regressed this diversity of each group against the latitude of each watershed, always including the watershed area as a covariable. This technique was performed 1000 times for each subset size ($n = 5, 10$ or 15) and below we show the histograms of R^2 distribution for cladocerans and copepods for each subset size.



These histograms show that even through random selection of lakes the relationship between cladoceran diversity and latitude remain strong whereas for copepods it

remains weak. We are thus confident that our conclusions hold despite per-lake sampling effort variation.

APPENDIX I

CHAPTER IV

Beta-diversity analysis for copepods and cladocerans at the continental scale (i.e., across watersheds).

	Cladocera		Copepoda	
Metric	Value	% of total β -diversity	Value	% of total β -diversity
β_{sor}	0.81	100%	0.86	100%
β_{sim}	0.67	83%	0.81	94%
β_{sne}	0.14	17%	0.05	6%

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