Species' responses to an ever-changing world

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POPULÄRVETENSKAPLIG SAMMANFATTNING

En av naturens mest slående egenskaper är dess mångfald – fler än en miljon arter har till dags dato identifierats och klassificerats. Denna mångfald har inte bara ett inneboende värde utan förser oss människor med en mängd viktiga resurser genom vad som ofta kallas ekosystemtjänster. Många av dessa ekosystemtjänster är livsviktiga för vårt uppehålle och hjälper t ex till med att förse oss med rent dricksvatten, luftrening, pollinering och matproduktion. Tyvärr är denna mångfald idag hotad av människans ökande utbredning. På bara 200 år den mänskliga befolkningen ökat från en miljard människor till drygt 7 miljarder, och inom 30 år beräknas vi vara ytterligare cirka 2 miljarder fler. Samtidigt som vi blir allt fler som ska dela på resurserna som tillhandahålls av Jorden använder vi också allt mer resurser per capita. Många säger nu att vi befinner oss i det sjätte massutdöendet av arter, då frekvensen av utdöenden uppskattats vara över hundra gånger över det normala. Det största hotet mot biodiversitet är habitatförstörelse och i takt med att människans påverkan på ekosystemen intensifieras ökar också den andel av natur som hyser en mängd arter som börjar användas till jord- och skogsbruk. Det har uppskattats att ungefär hälften av alla däggdjur har förlorat fyra femtedelar av sina habitat - under de senaste hundra åren. Utdöenden till följd av habitatförstörelse riskerar också att vidare öka när förlusten av habitat kombineras med andra hot såsom antropogenisk klimatpåverkan, överfiske (och jakt) och invasiva arter. Hoten mot biologisk mångfald stannar dock inte vid dessa direkta hot. Varje störning som direkt kan påverka förekomsten av en art kan också påverka fler arter indirekt genom denna. Ingen art är isolerad från andra arter, utan alla arter ingår i ekologiska nätverk där olika organismer såsom t ex växter och djur interagera med och är beroende av varandra. Forskningen i den här avhandlingen syftar till att bättra vår förståelse på hur arter kan komma att påverkas av just klimatförändringar. Jag har studerat hur arters förmåga att förflytta sig kan öka eller minska en deras känslighet för klimatförändringar när de måste söka sig till nya habitat, men också själva störningen påverkar näringsväven och de sekundära effekterna av sådana störningar. Arter har också en viss plasticitet och möjlighet till förändring över tid genom evolution; detta kan också tänkas ge arter möjligheter att dämpa de negativa effekterna av klimatförändringar. Därför har jag också studerat hur näringsvävar kan tänkas formas över tid av just evolution. I de två första studierna (Paper I och Paper II) i avhandlingen visar jag på hur spridningsförmågan hos arter påverkar deras potentiella respons till klimatförändringar. I Paper I fann jag att när det finns en homogen distribution av potentiella habitat i landskapet, så har de allra flesta arter i studien möjligheter till att emigrera till nya habitat. I heterogena landskap är det dock större variation på utfallen beroende på arters spridningsförmåga och hur habitatet är aggregerade i landskapen får större vikt. Ett resultat av detta är också att det inte bara att den mängden tillgängligt habitat som är viktigt när vi försöker utvärdera en arts klimatkänslighet utan också hur detta är placerat i landskapet. Eftersom hastigheten av klimatförändringar är osäker och varierar över jordklotet studerade jag också hur olika hastigheter påverkade olika exempelarter. Klimatförändringens hastighet hade dock begränsad påverkan på huruvida population överlevde och både habitatens placering i landskapet och arters spridningsförmåga var viktigare. I Paper II använder jag data på fjärilen backvisslares (*Pyrgus armoricanus*) abundans i lokaler i Sverige över tid och data från en spridningsstudie för att modellera den möjliga framtida utbredningen av arten i Sverige. Denna studie visar att för arter med låg spridningsförmåga och få habitat följs inte den s k klimatiska nischen – det vill säga den utbredning som arten skulle nå om vi bara tog hänsyn till klimatförändringar. Det är ett exempel på hur kombinationen av klimatförändringar och begränsad tillgång av habitat kan samverka. I den tredje studien (Paper III) undersöker jag hur stabiliteten i små näringsvävar påverkas av autokorrelationen i omvärldsvariation och spridningen mellan populationer. Här pekar resultaten på att vissa arters interaktioner

med andra arter gör att deras respons till förändringar i omvärldsvariation skiljer sig från om man modellerar systemet som enskilda arter. Effekten av ökad autokorrelation på stabiliteten förändras också beroende på spridningen mellan populationer. För dessa arter fann jag att den lägsta stabiliteten för en population inte var när utbytet mellan populationer var som lägst, utan att stabiliteten kan påverkas negativt av ett lågt utbyte mellan populationer. Analys av resultaten visar att det beror på att dessa arter har en jämvikt som inte beror på omvärldsvariationen, medan andra arters jämvikt gör det. Resultaten understryker på så sätt att den rumsliga dimensionen i kombination med tid kan ha komplexa effekter på arters abundans och populationers stabilitet. I den fjärde studien (Paper IV) genererade vi ekologiska nätverk och jämförde sedan hur de simulerade nätverken skiljde sig åt beroende på om vi tog hänsyn till selektion eller inte. Vi använde en modell där interaktionerna mellan arter definierades utifrån en egenskap vilket var deras storlek. Här fann vi att om ett nätverk har många arter och de genererade arterna tillåts att förändras över tid så leder det till ett system med få arter på grund att konkurrensuteslutning där en art konkurrerar ut andra på grund av skillnader i arternas variation. Eftersom arterna kunde anpassa sig till sin omgivning så minskade inte bioproduktionen i näringsvävarna linjärt med att antalet arter minskade.

ABSTRACT

One of nature's most astonishing features is the diversity of life, as more than a million species has been identified and classified. This diversity not only have a intrinsic value, but sustains us humans through a multitude of ecosystem services. Many of these services are critical for our sustenance. In our current age this diversity is threatened however, in what sometimes is referred to the Earth's 6th mass extinction as the current frequency of species-extinction is estimated to be over a hundred times over the background rate. The largest threat to biodiversity is human land use and overexploitation. However, in the past decades we have seen the addition of another large threat that can also compound to the extinction rates - climate change.

In the first two studies (Paper I and Paper II), I show how species' dispersal ability might affect their response to climate change. In paper I, I found that when the potential new habitat of a species is homogeneously distributed in the landscape most species in the study were able to emigrate to new habitats. There was a larger variation in heterogenic landscapes where the outcome depended on both the dispersal ability of the species combined with how the habitat were specifically arranged in relation to the climatic optimum of the species. From this also follows that it is not only the amount of habitat that is important but also where the habitat is located in relation to other habitat. I also show that both dispersal ability and habitat might be more important predictors of a successful climatic shift of a species than the speed of climate change. In paper II, I use previously collected data of population abundances and dispersal of a butterfly (*Pyrgus armoricanus*) in Sweden to model its future distribution. Similar to Paper I we see that low habitat availability, as well as heterogeneous configuration together with low dispersal ability negatively impacts its range expansion.

In the third study (Paper III) I examine how the stability of species in small food webs is influenced by the autocorrelation of environmental noise and dispersal rates. I also let modeled basal species independently to see if stability differed when modeling species in isolation. I found that not only does the stability of species abundance depend on the environmental noise and dispersal rates, but the stability also changes non-linearly with changes in autocorrelation and dispersal rate. The lowest stability for a species were not necessarily at the lowest dispersal rate but at a low to medium rate. An analysis of the results shows that at least some species seem to have an equilibrium that is not determined by the autocorrelation of environmental noise. The results thus underline complex mechanisms that might influence the abundance and stability of populations.

In the fourth study (Paper IV) we generated ecological networks and compared how simulated networks differed, depending on if selection was included or not. Here we used an allometric model where growth rate, mortality and interactions between phenotypes depend on the body size of the phenotypes. We found that while removing implicit traits such as the intraspecific competition between individuals of the same species made the webs unstable and prone to lose many species during the simulation, networks became much more unstable when introducing selection on the body mass trait. The restructuring of networks due to evolution either led to competitive exclusion of species or a race between plants, with an evolutionary pressure to escape predators, and animals to become larger and larger.

Overall the research presented here give new insights into how species' dispersal ability together with landscape configuration and climatic shift might determine the future distributions of species. Not only is the future climate range of a species important, but

also the mechanisms that would affect a successful range shift. Of these mechanisms the dispersal ability and the distribution and availability of habitat in the landscape are the most important. It is also shown that dispersal ability is important to take into account when planning for conservation actions as to identify which potential habitat will better facilitate range expansion.

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Linköping, August 2020

List of papers

- I. J. Årevall, R. Early, A. Estrada, U. Wennergren, and A. Eklöf. (2018).
“Conditions for successful range shifts under climate change: The role of species dispersal and landscape configuration.”
Diversity and Distributions 24.11, pp. 1598–1611.
- II. J. Årevall, F. Gustafsson, E. Öckinger, and U. Wennergren. (2020).
“Future distribution of a specialist butterfly (*Pyrgus armoricanus*): exploring traits aiding range expansion.”
Submitted manuscript.
- III. J. Årevall, S. Gudmundson, and U. Wennergren (2020).
“Stability Patterns of Metacommunities in Colored Environments.”
Manuscript.
- IV. J. Årevall, G. Barabás, and A. Eklöf (2020).
“Evolution in food webs.”
Manuscript.

Contents

Abstract	iii
Acknowledgments	vii
List of Papers	ix
Contents	xi
1 Introduction	1
1.1 Species distribution modeling	1
1.2 Environmental fluctuations	2
1.3 Food web models and trait evolution	3
2 Aims	5
2.1 Aims of Paper I	5
2.2 Aims of Paper II	6
2.3 Aims of Paper III	6
2.4 Aims of Paper IV	6
3 Methods	7
3.1 Dispersal between patches	7
3.2 Allometric food web model and evolution	8
3.3 Generating environmental fluctuations	10
4 Main results and implications	11
4.1 Paper I	11
4.2 Paper II	12
4.3 Paper III	12
4.4 Paper IV	12
5 Discussion	15
5.1 Species distributions and climate change	15
5.2 Noise colour effects on metapopulation dynamics	16
5.3 Evolution structuring food webs	17

References	19
Paper I	27
Paper II	43
Paper III	85
Paper IV	105

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1

Introduction

1.1 Species distribution modeling

While a species' distribution can be considered at multiple scales, such as geographical, habitat or microhabitat scale, and I will here mainly refer to the geographical scale which is also commonly referred to as a species' range. Shared between the different scales is that all species' distributions are bounded by areas where a population cannot be maintained; be it because of physical limitations, biotic limitations, or a combination of the two.

As climate change the distribution for a species which is physically limited by environmental factors, such as temperature, wetness or dryness, can be expected to change. Thus, environmental variables, such as temperature, light availability, and wetness or dryness, are routinely used in ecology to predict the geographic distribution of both species and ecotypes. One type of species distribution model (SDM) is bioclimatic envelope models which use this association between climatic factors and known occurrences of species to create a set of conditions under which species are likely to occur. Envelope models go back to Grinnell (1917), who concluded that one important restriction of the distribution of the California thrasher (*Toxostoma redivivum*) was temperature conditions. This approach has also been successful, leading to findings of new populations (Feria A. and A. T. Peterson 2002; Bourg, McShea, and Gill 2005), assessing geographic ranges of invasive species (Broennimann et al. 2007; Villemant et al. 2011), and identifying historical sites of biodiversity (Waltari et al. 2007). These envelope models has also been used to

predict changes in species' distributions, and at large relied on the correlation between climatic factors and present distribution (Guisan and Zimmermann 2000; Araújo and A. T. Peterson 2012; Lawler et al. 2009). Lately however, the accuracy of such models has been extensively debated (Araújo and A. T. Peterson 2012; Thuiller, Münkemüller, et al. 2013; Wiens et al. 2009), owing to limitations such as species dispersal often being considered unlimited or nonexistent (A. Peterson et al. 2001; Thuiller, Lavorel, et al. 2005), the exclusion of population dynamics (Zurell, Jeltsch, et al. 2009), and in general leaving species-species interactions out. A limitation of considering species dispersal and colonization as something digital is that it will only give an estimate of best and worst case for a species. Recently there have been a development of "hybrid models" which combine the classical SDM approach with simple dispersal or population models (Ehrlén and Morris 2015). Models including dispersal and population dynamics have been shown to have higher predictive accuracy when forecasting species range shift, when compared to simpler SDM models that only account for change in climate (Zurell, Thuiller, et al. 2016; Fordham et al. 2018). A downside is that more complex models need more detailed data, such as species dispersal kernels and demographic processes.

1.2 Environmental fluctuations

One of the early mentions of environmental variation as a cause for coexistence go back to Hutchinson (1961). Hutchinson argued for environmental fluctuations as a possible explanation for the wide range of plankton species observed, despite the competition for resources. Sanders (1968) showed that diversity in marine fauna were correlated with the stability and the history of the physical environment. This concept is further developed in Huston (1979), who argued that while competitive exclusion is important, systems can be prevented from reaching a competitive equilibrium by periodic population reductions and environmental fluctuations. However, as Fox (2013) points out, adding these disturbances change the average mortality rate, and a correct control for a model such in Huston (1979)) would be a model with the same long-term average mortality. In spite of this, mathematical models have shown that two or more species can coexist as a function of temporal variation in the environment, but that non-linear effects is necessary (Levins 1979; Hsu 1980; Chesson and Warner 1981; Chesson 1994). There are two theoretical mechanisms of coexistence due to enviromental fluctuations, which are commonly refered to as the storage effect and relative nonlinearity (Chesson 2003). The storage effect mechanism refer to coexistence maintained when species have unique response to environmental conditions in a varying environment. The relative nonlinearity mechanism instead refer to when co-

existence is maintained through differences in species' response to variation in resource.

While in general Chesson (1994) is agnostic as to the autocorrelation structure of environmental fluctuations, all the examples use gaussian white noise. Environmental fluctuations are expected to be positively autocorrelated depending on the time-scale considered (García-Carreras and Reuman 2011; Vasseur and Yodzis 2004). Increased autocorrelation is referred to as increasingly red noise, while noise without any temporal autocorrelation is referred to as white noise (Halley 1996). The first theoretical studies on how the environmental noise colour affects population stability of species were done with single species models (Roughgarden 1979; May 1981). Generally the population stability decrease with increased redness, and the growth rate determines if the population and the environmental noise will have the same variance over time (Ruokolainen, Lindén, et al. 2009; Petchey, Gonzalez, and Wilson 1997; Lögberg and Wennergren 2012). This corresponds to how well a population track its environmental conditions. Population densities will track the environmental fluctuations better in red noise as change in said conditions is slower over time, compared to white noise. However, the effect on population dynamics are not necessarily transferred to models with multiple species. The response of species to environmental noise in food web models has been shown to be dependent on several factors, such as if species are generalist or specialists (Murdoch et al. 2002), the environmental sensitivity of species (Vasseur 2007), and the synchrony of species environmental responses (Ruokolainen and Fowler 2008a; Lögberg and Wennergren 2012).

1.3 Food web models and trait evolution

The relation between the structure of ecological communities and evolution is not entirely clear. One branch of theoretical models that explicitly link evolutionary dynamics and population dynamics are quantitative trait models. As a simplification of quantitative genetics these models use phenotypic traits that under selection pressures changes and influences species coexistence. One of the early quantitative genetic models were developed by Lande (1976) and Lande (1982) building upon the ideas in Simpson (1953) of an adaptive topography for phenotypic characters. This framework has since been extended to two and three species cases with Lotka-Volterra interactions (Slatkin 1980), and used to study character displacement. While some studies of small systems (Vellend 2006; Vasseur, Amarasekare, et al. 2011; Klauschies, Vasseur, and Gaedke 2016) show that trait adaptation can facilitate coexistence, Kremer and Klausmeier (2013) show that evolution on ecological timescales can disrupt an otherwise stable coexistence. There has also been few studies exploring if trait adaption facilitates coexistence in larger communities. Vellend (2006) indicate that in communities with clonal repro-

duction trait diversity promote coexistence, but a study with a modified model (Yamauchi and Miki 2009) showed that this only held true as special case and suggest that trait diversity (as an extended niche distribution) tends to reduce species diversity when interspecific competition is stronger than intraspecific competition. With evolution and population dynamics acting at the same time-scale Barabás and D’Andrea (2016) show that while evolution lead to decreased coexistence when measured as species richness, community pattern and community robustness can increase.

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2

Aims

The overall aim of this thesis is directed toward bettering our understanding on how species and biotic communities are affected by changes in climate. In each paper we focus on a few of the aspects which together determine how a species or community might be affected by external perturbations. These aspects range from modeling a single species at a time and how dispersal might mitigate negative effects of climate change, to how evolution affect communities formation and stability over time. In the following sections I outline the aims of each paper.

2.1 Aims of Paper I

In this study we developed a theoretical modeling framework to address the implications of habitat configuration coupled with dispersal capacity for successfully migrating during a climate-drive range shift. We vary the habitat aggregation, but not total availability, under scenarios of different rates of climate change and dispersal ability of species. We wish to know:

1. Does different habitat configurations impede or promote climate-driven range shifts
2. How does climate change and species' dispersal ability interact with habitat configurations?

2.2 Aims of Paper II

We used the framework from Paper I and investigate the potential future habitat for a specialist butterfly (*Pyrgus armoricanus*) and the butterfly's ability to track it's climatic niche. The climatic niche of the species were estimated using current species distribution and dispersal data from a mark-recapture study was used to estimate a dispersal kernel and model the range expansion of the species. We wish to know:

1. Will our model species (*Pyrgus armoricanus*) be able to expand its northern range limit and keep up with its climatic niche
2. How does the following traits influence range shift ability: degree of habitat specialization, growth rate, emigration propensity, establishment probability, and dispersal kernel shape

2.3 Aims of Paper III

Here we explore how the stability of resource species may respond to change in the autocorrelation of environmental variability. We apply white and red environmental noise on the metapopulations of a resource species in a food web, and as isolated single species when they are in a small food web. We then introduce dispersal between the patches to see how dispersal might interact with the environmental noise. We wish to know:

1. Does the response of a species to change in environmental noise and dispersal differ if we model a species in isolation versus as part of a community?
2. Do all resource species react similarly to changes in environmental noise and dispersal?

2.4 Aims of Paper IV

In this paper we use an eco-evolutionary model where we combine the ecological dynamics of interactions between species and the evolutionary process of natural selection stemming from said interactions. We generate allometric food webs, and compare the structure of resulting networks when including/excluding evolutionary processes acting on the species in the network. We wish to know:

1. How does evolutionary dynamics affect species richness in large food webs?
2. How might evolutionary dynamics change the density of the species in the food web?

3

Methods

3.1 Dispersal between patches

Dispersal refer to the movement from one location to another, and in this thesis this will in general mean animal dispersal from one habitat patch to another.

In Paper III dispersal between patches was simply modelled as a mass-action mixing process, and the rate of dispersal was simply a constant proportion of each population size. The dispersing part of the population leaving a patch q were equally distributed among other patches equally, without any sort of distance dependence (sometimes denoted as a global dispersal process). Population change was then modelled as

$$\frac{dN_i^q}{dt} = N_i^q \left(r_i + \sum_{j=1}^s \tilde{a}_{ij} N_i^q - d \right) + \sum_{w \neq q}^{n-1} N_i^w \frac{d}{(n-1)}, \quad (3.1)$$

where the superscript denotes the patch, d is the proportion of the population leaving for other patches, and n the number of patches.

In paper I and paper II the landscape was explicit, and the dispersal between the habitat patches in the landscape were distance dependent. For each individual dispersing from a patch i a sample was made from a distribution of all possible arrival probabilities. The probability of an individual from

patch i to patch j were defined by a normalized dispersal kernel of which the probability mass function (PMF) was given by

$$P_{ij} = \frac{e^{-(d_{ij}/a)^b}}{\sum_{j=1}^n e^{-(d_{ij}/a)^b}} \text{ for } j = 1, 2, \dots, n \text{ and } i \neq j, \quad (3.2)$$

where d_{ij} is the distance between patch i and j , a and b are width and shape parameters of the dispersal kernel, respectively; and n is the total number of patches. The dispersal kernel is normalized by dividing by the sum of all possible destinations, as to make the power mass function equal to one. In paper I the b parameter was set to 1, and thus the dispersal kernel was exponential (declining) function. The width parameter a was set to four different values, divided into "groups" roughly corresponding to four different European mammals of which some empirical data were available (*Pteromys volans*, *Rupicapra rupicapra*, *Lepus europaeus*, and *Ursus arctos*). In paper II data for dispersal had been collected in a previous mark-recapture study, and here the parameters a and b were estimated via Bayesian inference with a Hamiltonian Markov Chain Monte Carlo technique, using the RStan package in R. Each replicate in the simulations of the model then sampled the posterior distribution of a and b .

In Paper I the explicit landscape was generated using a spectral method to generate neutral point pattern landscapes (NPPL) as described by Lindström, Håkansson, and Wennergren (2011). The NPPLs are primarily defined by three parameters: the number of patches (n), a continuity parameter (γ) and a contrast parameter (δ). The continuity parameter determines the spatial autocorrelation over multiple scales, that is, if areas with similar patch density are located close to or far from each other. The contrast parameter defines the size of the difference between areas with dense or sparse habitat distribution, that is, is a measure of density dispersion.

3.2 Allometric food web model and evolution

As food webs increase in size and the number of interacting species increase the complexity of the food webs sharply increase. Collecting detailed data for all species' attributes and interactions quickly becomes unmanageable - in large food webs collecting binary data of interactions in cumbersome. Allometric food webs models seek to simplify the parameterization of large food webs through the use of allometry, which is the study of the relationship between body size and physiological traits. Yodzis and Innes (1992) created consumer-resource models based on energetic reasoning and allometric relationships, where most of the parameterization of the model were determined by body sizes and metabolic categories of the species. In a more recent paper (Berlow et al. 2009) the authors also let the interaction strenghts of species-species interactions scale with body size. Models similar to this has been used to

examined ecosystem functioning (Schramski et al. 2015; Schneider, Brose, et al. 2016) and stability in food webs (Brose, Williams, and Martinez 2006; Brose 2010; Schneider, Scheu, and Brose 2012).

In paper IV an allometric food web model from Schneider, Brose, et al. (2016) is used to describe the population dynamics, and adapted to include quantitative genetics. We chose this model since it and similar models have been extensively used, and since it is allometrically parameterized interactions between species mainly depend on the bodymasses of the species. The quantitative trait z (in this case the log body mass)

As in Barabás and D’Andrea (2016) we assume that the trait we model (in this case the logarithm of the body mass m) is governed by a very large number of loci contributing additively to the trait, and each locus has a very small effect. In this limit the trait distribution of a species is always normal and the trait distribution $p_i(z)$ is thus given by

$$p_i(z) = \frac{1}{\sigma_i \sqrt{2\pi}} e^{-\frac{(z-\mu_i)^2}{2\sigma_i^2}} \quad (3.3)$$

where μ_i is species i ’s mean log body mass and σ_i^2 its trait variance. The phenotypic variance is the sum of the additive genetic variance and an independent, non-heritable environmental variance. While not changing over time, we assume that this variance is species-specific. Since the shape and variance of the trait distribution does not change over time, the full distribution of a species i can be modeled with just the population biomass and mean trait value. If the species- and trait-dependent growth rates $r_i(z)$ of the species are given, then the dynamics of the species abundances and trait means can be expressed as

$$\frac{dN_i}{dt} = N_i \int p_i(z) r_i(z) dz, \quad (3.4)$$

$$\frac{d\mu_i}{dt} = h_i^2 \int (z - \mu_i) p_i(z) r_i(z) dz \quad (3.5)$$

(Barabás and D’Andrea 2016). Here t is time, h_i^2 is the heritability of the log body mass of species i , and $r_i(z)$ is the growth rate of species i phenotype z .

The per capita growth rates in Paper IV are based on the metabolic food web model of Schneider, Brose, et al. (2016), but written in terms of phenotypes:

$$r_i(z) = \varrho(z)G_i - x(z) + \sum_{j=1}^S e_j \int F(z, z') N_j p_j(z') dz' \quad (3.6)$$

$$-N_i \sum_{j=1}^S \int N_j p_j(z') F(z', z) dz', \quad (3.7)$$

where $\varrho(z)$ is phenotype z 's growth rate on a unit of abiotic nutrients in the absence of any species interactions, $x(z)$ is phenotype z 's mortality rate, G_i is a species-specific (as opposed to phenotype-specific) growth factor determined by nutrient availability, S is the number of species, e_j is a resource conversion efficiency (whose value depends only on whether the resource species j is a producer or itself a consumer), and $F(z, z')$ is the per-capita and per-biomass attack rate of phenotype z on phenotype z' . The feeding rate $F(z, z_0)$ is given by

$$F(z, z') = \frac{e^{-z} b(z, z')}{1 + \int T(z, \tilde{z}) \sum_{l=1}^S b(z, \tilde{z}) N_l^q p_l(\tilde{z}) d\tilde{z}}, \quad (3.8)$$

where the factor $e^{-z} = m_0/m$ converts the feeding rate from being per capita to per biomass; $T(z, z')$ is phenotype z 's handling time of phenotype z' (also depending on mean log body mass allometrically), and

$$b(z, z') = b_0 e^{\beta_C z + \beta_R z'} e^{-\frac{(z - z' - Z)^2}{w^2}} \quad (3.9)$$

is a phenotype-specific capture coefficient.

3.3 Generating environmental fluctuations

Environmental fluctuations, or environmental noise, were generated as $1/f^\beta$ noise by a spectral method (fast Fourier transform). This type of noise is a set of sine waves where the amplitudes for each frequency scale according to a power law (Halley 1996):

$$A^2(f) \propto 1/|f|^\beta, \quad f \neq 0 \quad (3.10)$$

where the square amplitude, A^2 , of a frequency f is proportional to $1/f^\beta$. The value of the exponent β will then indicate the noise colour.

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4

Main results and implications

Overall, the research give new insights into how species' dispersal ability together with landscape configuration and climatic shift might determine the future distributions of species. Not only is the future climate range of a species important, but also the mechanisms that would affect a successful range shift. Of these mechanisms the dispersal ability and the distribution and availability of habitat in the landscape are the most important.

4.1 Paper I

This study highlights the importance of accounting for interplay of species dispersal and landscape configuration when estimating future climate impact on species. We show that not only is the amount of suitable habitat important, but the realized distribution might also be crucial. Interestingly, the speed of climate change had limited effect on the survival of local populations and usually the landscape configuration and dispersal ability were more important. Compared with species distribution models, SMD, based on statistical correlations (Guisan & Zimmermann 2000, Thomas 2006) we show that these aspects are important for conservation efforts and identifying species vulnerable to climate change due the necessity of a range shift. In landscapes with homogeneous distribution of suitable habitat, even species with low dispersal ability will be expected to range shift. However, the population densities of species with high dispersal ability might decline initially due to the dispersal to unsuitable habitat. In heterogenous landscapes, with longer distances

between clusters of patches the outcome is more variable and does not only depend on the dispersal ability of the species but also where the habitat is located in landscape, leading to nonlinear effects on the population sizes and success of a climatic shift.

4.2 Paper II

In line with the implications from Paper I we found a large discrepancy between *P. armoricanus*' projected climatic niche and its future distribution predicted from our simulations. Despite having favorable climatic conditions *P. armoricanus* might have difficulties expanding its range in Sweden due to a combination of poor dispersal ability and low habitat availability; in the best case its range only expanded 16 km north compared to a 175 km expansion of the climatic niche under the RCP 4.5 climate scenario. The landscape configuration for *P. armoricanus* is highly heterogeneous, with the suitable habitat being primarily located in Southern Scania and Östergötland, and thus a high dispersal ability would be required to bridge the spatial gap. For species like *P. armoricanus* that have strict habitat requirements, like dependence on a specific host plant, restoration of potential habitat that might link important habitat clusters will be an important priority to mitigate future biodiversity loss. Habitat availability, dispersal ability and growth rate were traits that we identified as important for the butterflies' range shift. It was primarily the degree of habitat requirements and dispersal ability that influenced the extent of range shift, which conforms to the theory that species with general habitat requirements are less vulnerable to climate change (Melero 2016, pöyry 2009).

4.3 Paper III

From earlier findings we know that species might react differently to changes in environmental variability depending on if the species is incorporated in an ecological community or not (Gudmundson 2015). Introducing dispersal between identical communities we find further confounding effects such as that the effect of dispersal on stability differs in white and red environments. We found that the effect of increased autocorrelation on stability differs nonlinearly between different levels of dispersal. We find that even at very low dispersal rates dispersal can be beneficial yet be followed by a decrease in stability at low to medium dispersal rates. For the most connected basal species in both food webs used the minimum stability occurred.

4.4 Paper IV

Through incorporating heritable phenotypic variation in the species' body masses the resulting food web structure depends on both the intraspecific

variability, and the ability of species to evolve to both larger and smaller sizes. The inclusion of a heritable trait significantly alters some of the predictions based on evolutionary static food webs: species evolve larger body masses, communities end up with a significantly lower species diversity, and the pattern of the log body masses are much more even in the presence of evolution - both when compared to without evolution and random chance. This lead to a simpler community structure with more predictable species-species interactions.

A decorative element consisting of several thin, vertical black lines of varying heights, positioned to the left of the chapter title.

5

Discussion

The findings and contributions of the work presented in this thesis are discussed under three major headings: A) Estimate species response to climate change; B) Impact of noise colour and dispersal on population dynamics for species in small food webs; and C) Evolution of traits and the structuring of food webs.

5.1 Species distributions and climate change

In Paper I we extended the classical species distributions models (SDMs), not only taking climate ranges such as species' temperature tolerances into account, but also population dynamics and dispersal in explicit landscapes. It has previously been argued that classical SMDs can lead to problems of both under- and overestimation of species distributions, owing to the lack of models including population dynamics and dispersal (Araújo and A. T. Peterson 2012; Schurr et al. 2012). A species with limited dispersal ability can be prevented or delayed from reaching locations where its population can grow, leading to a discrepancy between possible species distributions and actual species distributions. Populations at the frontier might take time to reach equilibrium abundances, and might introduce further time-lag between colonization events and further dispersal. In Paper I we point out the importance of accounting for the interaction of species' dispersal ability and the landscape configurations, and assumptions such as in A. T. Peterson et al. (2002) that dispersal simply is non-existent, global, or continuous, is not fine-grained enough except in

the case where a species' distribution is constant or contracting in all three cases. Schloss, Nuñez, and Lawler (2012) showed that many species (9.2 % of mammals) in the Western hemisphere are likely to not be able to keep pace with climate change. We show similar results in Paper I, but also show there are differences depending on if the landscape is homogeneous or heterogeneous. Landscapes where it is longer between potential new habitat for a species might also take longer to reach, due to the decreased probability of migrating there. This leads to faster dispersal through homogeneous landscapes where habitat patches are well spread out and available.

A challenge when incorporating demographics and dispersal patterns into SDMs is often the lack of data. In Paper II we use a model species, *Pyrgus armoricanus*, of which we had both timeseries of abundance for several locations in Sweden, and dispersal data from a mark-recapture study. Apart from estimating the range shift for *P. armoricanus* we also examined scenarios where the butterfly had enhanced establishment probability, enhanced migration, and longer dispersal. We show that *P. armoricanus*' specific habitat requirements, and the low habitat availability coupled with long distances between patches, leads to a very modest possibility for range expansion. This is in line with a Fourcade and Öckinger (2017), attributing the discrepancy between suitable habitat and current habitat to spatial isolation. Furthermore, we compared the range expansions of two fictional butterflies which had more available habitat. While habitat specialization was the major determinant of how far north the butterfly reached, the other factors had little if any effect on range expansion. These results are in line with the theory that generalists will be less vulnerable to climate change (Melero, Stefanescu, and Pino 2016; Pöyry et al. 2009). While there was relative good data available for *P. armoricanus*, predicting the full effect of climate change on a species' distribution is complicated, as it depends on more species traits than we could take into consideration in Paper II. Increased temperature can induce changes in the life cycles of butterflies, affecting a wide range of traits such as voltinism, flight season, size, and host plant use (Bennett et al. 2015; Kharouba et al. 2014).

5.2 Noise colour effects on metapopulation dynamics

Earlier work has shown that how strong of an effect the noise colour of environmental fluctuations has on populations depends on the populations responsiveness to changes and the colour of the noise (Ripa and Lundberg 1996; Petchey, Gonzalez, and Wilson 1997; Cuddington and Yodzis 1999; Schwager, Johst, and Jeltsch 2006; Lögberg and Wennergren 2012). In single-species models where species have a fast response to environmental fluctuations (over-compensatory population dynamics) red noise is generally associated with a lower extinction risk of populations (Ripa and Lundberg 1996; Lögberg and

Wennergren 2012), while in slow-responding species extinction probability increases with increasing redness of the environmental noise (Laakso, Kaitala, and Ranta 2004). For a single-species model in a spatial setting a higher degree of synchrony between patches leads to increased extinction risk, regardless of whether the population dynamics are over- or undercompensatory (Lögdberg and Wennergren 2012). In multi-species models the population responses due to noise colour is more complex, since the responses also depend on the structure of the food web (Ripa and Ives 2003; Ruokolainen and Fowler 2008b). Gudmundson, Eklöf, and Wennergren (2015) compared the stability of species' populations when modelled as isolated species or part of a small food web. While there was no difference in population dynamics when exposed to white noise, in a red environment some species responded very differently with increased stability. In paper III we added further complexity by introducing an implicit spatial dimension. While dispersal between patches for a (isolated) single-species always lead to increased stability, this was not the case when species were part of a food-web. The same species that increased in stability with increased redness, also had higher stability with higher dispersal rates between patches. However, increased dispersal lead to a higher tracking error for local populations, as an increasing dispersal rate leads to a global averaging of the densities. This is in line with other studies showing that the stability of food webs may change as new levels of complexities are added (Brose, Williams, and Martinez 2006; Loreau 2010). In theory this might make populations more vulnerable if the dispersal is not continuous, as local densities would be further from their carrying capacity after dispersal events .

5.3 Evolution structuring food webs

In Paper IV we analyzed how the structure of food webs are affected when population parameters and feeding interactions are allometrically controlled, and species can evolve their body masses in response to their feeding interactions. An important difference in perspective between our model and the allometric models in e.g. Schneider, Brose, et al. (2016), Schneider, Scheu, and Brose (2012), and Heckmann et al. (2012) is that since in those models each species has a single unique body mass shared by all individuals belonging to this species, the model parameters can be chosen in such a way that they are species-specific. Thus, even though parameters and species interactions are determined by body masses, the fact that a species is uniquely associated to a single body mass value allows for describing parameters as belonging to specific species instead of specific phenotypes. In contrast, in our model individuals belonging to the same species are not equal as the species contain a distribution of body masses. Putting the model on a solid basis of phenotypes is vital, since our questions concern coexistence, diversity and community pat-

terns. If certain parameters depend on species identity, we might effectively add trait dimensions for each species identity. An example of this is intraspecific predator interference. In the original model of Schneider, Brose, et al. (2016) this term is adjustable via an interference parameter, but we had to set it to zero. Such intraspecific interference generally promotes coexistence (Barabás, Michalska-Smith, and Allesina 2017), which is no surprise since as a species may become more successful the relative strength of intraspecific competition would increase. Because this interference term is species-specific only, two different species will only interfere with their own individuals, with no cross-species interference, regardless of how similar the actual modelled trait of two species might be. One obvious result from our analysis is that biodiversity is significantly reduced when species are allowed to evolve their body masses. This result is in line with Barabás and D’Andrea (2016), who found that species richness was lower in the presence of trait variation, and in particular when the trait was heritable. In Paper IV we instead model feeding interactions between phenotypes, but also find that heritability always results in communities with fewer species. A strong trend found in our analyses was the selection of larger phenotypes, as larger individuals have smaller metabolic losses, and this could lead to communities with excessive body masses. In both our model and other models similar to Schneider, Brose, et al. (2016) this is made possible by the extremely low mortality rates coupled to large body masses. While lower mortality for large consumers is known from empirical studies (Enquist et al. 1999; Brown et al. 2004) the lack of any disadvantage for being large allows for large consumer populations to be sustained by very low consumption rates. In Paper IV we additionally show that hereditary body mass also influences community structures, as characterized by an increase of non-random spacing of species along the trait axis. This result is also in line of Barabás and D’Andrea (2016). They found that including heritability of a trait lead to more even distributions of species along the trait axis in communities of competing species. While in their model communities eventually settled at an equilibrium, in Paper IV we see dynamics that lead to species becoming larger and larger. One of the limitations of our models is the property that plants’ nutrient use is species-specific, and not phenotype specific. While body mass is undoubtedly an important trait structuring food webs, it is not the only one. Accounting for more traits requires an extension of the model to multidimensional trait spaces. Importantly, the model lacks any speciation, as species are assumed to always possess a normal distribution of phenotypes, regardless of the existence of multi-modal selection pressures or not.

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