

BUTTERFLIES IN CHANGING WEATHER CONDITIONS: IMPLICATIONS FOR
ECOLOGY AND CONSERVATION



SUSU RYTTERI

FACULTY OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES

UNIVERSITY OF HELSINKI

2021

Butterflies in changing weather conditions: implications for ecology and conservation

SUSU RYTTERI

LUOVA, Doctoral Programme in Wildlife Biology

Research Centre for Ecological Change

Faculty of Biological and Environmental Sciences

University of Helsinki

ACADEMIC DISSERTATION

To be presented for public discussion with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki, in Room 2402, Biocenter 3 (Viikinkaari 1), on the 30th of March, 2021 at 12 o'clock noon.

Supervised by: Assoc. Prof. Marjo Saastamoinen
Faculty of Biological and Environmental Sciences, University of Helsinki, Finland

PhD. Mikko Kuussaari
Biodiversity Centre, Finnish Environment Institute (SYKE), Helsinki, Finland

Members of the thesis advisory committee:

Prof. Jon Brommer
Department of Biology, University of Turku, Finland

PhD. Johan Ekroos
Centre for Environmental and Climate Research, Lund University, Sweden

PhD. Mar Cabeza
Faculty of Biological and Environmental Sciences, University of Helsinki, Finland

Reviewed by: PhD. Robert J. Wilson
Department of Biogeography and Global Change, National Museum of Natural Sciences, Madrid, Spain

Prof. Nicolas Schtickzelle
Earth and Life Institute – Biodiversity, Université catholique de Louvain, Louvain-la-Neuve, Belgium

Examined by: PhD. Toke Thomas Høye
Department of Bioscience – Biodiversity and Conservation, Aarhus University, Denmark

Custos: Assoc. Prof. Marjo Saastamoinen
Faculty of Biological and Environmental Sciences, University of Helsinki, Finland

ISBN 978-951-51-7141-2 (paperback)
ISBN 978-951-51-7142-9 (PDF)

<https://ethesis.helsinki.fi>

Unigrafia, Helsinki 2021

CONTENTS

Contributions	5
Abstract	6
Tiivistelmä	7
1 Introduction	8
1.1 Changing weather conditions.....	8
1.2 Effects of weather on insects	8
Box 1. Climate change and phenology.....	9
1.2.1 Direct effects of weather on insects	10
1.2.2 Indirect effects of weather on insects	10
Box 2. Complex life cycle makes insects vulnerable to climate change	11
2 Aims of the thesis	12
Box 3. Translocation as a conservation tool	13
3 Material and methods	14
3.1 Study systems.....	14
3.1.1 The Glanville fritillary.....	14
3.1.2 The Clouded Apollo.....	14
3.2 Data	15
3.2.1 Survey and monitoring data on the Glanville fritillary.....	15
3.2.2 Overwintering experiment on the Glanville fritillary	16
3.2.3 Mark-recapture data on the Clouded Apollo.....	16
3.3 Statistical analyses	17
4 Results and discussion	18
4.1 How do snow cover and spring onset timing affect overwintering survival, post-diapause larval survival, developmental time, pupal weight or sex ratio?.....	18
4.2 How does food deprivation at the pre-diapause stage affect overwintering survival under snowy and snowless conditions and at different spring onset timings?	20
4.3 Does the increasing exposure to freezing caused by shortened snow cover duration decrease metapopulation growth rates?.....	20
4.4 What are the impacts of spatial variation in weather and varying microclimates on larval development and survival, and host plant growth?	21
4.5 Do the local effects of weather and microclimate on larval development translate into metapopulation-level variations in population growth rates?	22
4.6 How do the larval body surface temperatures deviate from concurrent ambient temperatures and how does this affect larval feeding activity?	23
4.7 How do the weather conditions of the flight season alter the emigration and colonisation rates, residence times and dispersal distances within a metapopulation?.....	24
4.8 Is it possible to predict the spatial expansion of a translocated population in a novel landscape based on prior knowledge of the species' movement rate? How does the annually varying flight season weather affect the accuracy of the predictions?	25
5 Conclusions	26
6 Acknowledgements	27
7 References	28
Chapter I	35
Chapter II	51
Chapter III	67
Chapter IV	77

CONTRIBUTIONS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

- I** Susu Rytteri, Aapo Kahilainen & Marjo Saastamoinen (2021). **Effects of snow cover, spring onset timing, and individual condition on butterfly overwintering.** Manuscript.
- II** Susu Rytteri, Mikko Kuussaari & Marjo Saastamoinen (2021). **Microclimatic variability buffers butterfly populations against increased mortality caused by phenological asynchrony between larvae and their host plants.** *Oikos*, DOI: 10.1111/oik.07653.
- III** Mikko Kuussaari, Susu Rytteri, Risto K. Heikkinen, Janne Heliölä & Peter von Bagh (2016). **Weather explains high annual variation in butterfly dispersal.** *Proceedings of the Royal Society B: Biological Sciences*, 283(1835), 20160413.
- IV** Susu Rytteri, Mikko Kuussaari, Marjo Saastamoinen & Otso Ovaskainen (2017). **Can we predict the expansion rate of a translocated butterfly population based on a priori estimated movement rates?** *Biological Conservation*, 215, 189-195.

Table of contributions

	I	II	III	IV
Original idea	SR, MS	SR, MK, MS	MK	SR, MK, OO
Study design	SR, AK, MS	SR, MK, MS	MK, SR, RKH, JH	SR, MK, OO
Data collection	SR	SR	MK, SR, RKH, JH, PvB	SR, MK
Analyses	SR, AK	SR	MK	SR, OO
Manuscript preparation	SR, AK, MS	SR, MK, MS	MK, SR, RKH, JH	SR, MK, MS, OO

SR: Susu Rytteri, MS: Marjo Saastamoinen, MK: Mikko Kuussaari, OO: Otso Ovaskainen,

AK: Aapo Kahilainen, RKH: Risto K. Heikkinen, JH: Janne Heliölä, PvB: Peter von Bagh

© Susu Rytteri (Summary, Cover illustration)

© The authors (Chapter I)

© The authors, published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos (Chapter II)

© The authors, published by the Royal Society (Chapter III)

© Elsevier Ltd. (Chapter IV)

© Taneli Ilomäki (Layout)

ABSTRACT

The weather conditions of the globe are changing due to anthropogenic climate change. In addition to warming average and extreme temperatures, the variability of weather conditions is increasing. Both extreme precipitation and drought events are becoming more common and severe. Warming winter temperatures decrease snow cover duration in temperate, alpine and polar regions. These changes together with other anthropogenic environmental stressors, such as habitat loss and fragmentation, potentially have drastic ecological consequences. Insects as small, short-lived ectotherms are strongly affected by changing weather conditions. Their complex life cycles with immobile life stages make them particularly sensitive to the seasonal changes and microclimatic variations of weather.

In this thesis, I utilised long-term data from two butterfly systems to study the ecological effects of changing weather conditions and their implications for insect conservation. Firstly, large-scale metapopulation survey data from 1993-2019 on the Glanville fritillary (*Melitaea cinxia*) complemented with detailed field monitoring data and experimental data allowed the study on the larval biology. Secondly, mark-recapture data from 2000-2016 on a translocated population of the Clouded Apollo (*Parnassius mnemosyne*) enabled me to study the effects of weather on dispersal and colonisation in a novel landscape.

The larval stage of the Glanville fritillary studied in chapters I and II spans over ten months a year. Being specialised on two host plant species, larvae are sensitive to host plant mediated effects of weather in addition to the direct effects. In chapter I, I showed experimentally that larval overwintering survival was enhanced by snow cover and late spring onset. Post-diapause survival was higher and development faster after late spring onset. Degraded larval condition caused by pre-diapause food deprivation lowered overwintering survival especially under snowless conditions and early spring onset. The detrimental effect of snowless overwintering conditions on individual level were not reflected by metapopulation growth rates in the wild. Instead, metapopulation growth was enhanced by increasing growing season precipitation, which largely determines the larval food availability.

In chapter II, I found that microclimatic variation buffers populations against phenological asynchrony between post-diapause larvae and their host plants. In a detailed field monitoring study, larval growth was accelerated by warm microclimatic conditions, but larval survival was highest in cool microclimates. Host plant growth was poor regardless of the microclimate. Plant growth responds to the ambient temperature, while larvae in sunny microclimates can effectively thermoregulate reaching high body temperatures even under cold ambient conditions. According to metapopulation-level survey data, local population growth rates were highest in habitat patches with heterogeneous larval microhabitats situated on warm, southward slopes and cool, shaded sites.

In chapter III, I showed that flight season weather importantly alters annual dispersal rates of butterflies. Emigration rates were increased and residence times in a natal patch shortened by increasing solar radiation and proportion of exceptionally warm days, respectively. The average movement distance increased with the average temperature of the flight season. Additionally to warm and sunny weather, dispersal was enhanced by increasing conspecific density. Weather and intrinsic population variables together explained 79-91 % of the observed variation in dispersal.

In chapter IV, I simulated the spatial expansion of a translocated butterfly population in the novel release landscape based on prior knowledge of the habitat-specific dispersal rates in the source population. Dispersal rates were obtained from a spatially explicit movement model parameterised in a flight season with particularly high proportion of exceptionally warm days, and consequently the predicted colonisation rates in the release area were overestimated especially in predominantly cold flight seasons. Nevertheless, I managed to successfully predict the approximate rate and order of habitat patch colonisations.

Overall, my thesis highlights the multiple stressors climate change poses to insects via changes in weather conditions throughout the life cycle. Shortening snow cover duration and advancing spring onset may have both direct and trophic interaction mediated adverse effects for survival and development, and these effects are amplified by stressful weather conditions at earlier life stages. Warming flight season weather may importantly enhance dispersal and colonisation on high-latitude and –altitude range margins with a potential to accelerate range expansions. On the other hand, increasing variation in annual weather conditions may cause range retractions during years of unfavourable weather. Furthermore, increasingly variable weather makes conservation translocations more risky, as the success of an insect translocation project is often dictated by the weather following the release.

TIIVISTELMÄ

Ihmisen aiheuttaman ilmastomuutoksen myötä maapallon keski- ja ääriämpötilat nousevat, ja samalla sääolojen vaihtelut lisääntyvät. Sekä rankkasateet että kuivuusjaksot yleistyvät ja voimistuvat. Lauhkealla vyöhykkeellä, vuoroissa ja napa-alueilla talvien lämpeneminen lyhentää lumipeitteisen ajan kestoa. Sääolojen muutosten ja muiden ihmisperäisten stressitekijöiden – esimerkiksi elinympäristöjen vähenemisen ja pirstoutumisen – ekologiset yhteisvaikutukset voivat olla huomattavia. Sääolot vaikuttavat voimakkaasti hyönteisiin, koska ne ovat vaihtolämpöisiä ja lyhytikäisiä. Niiden monivaiheiset elinkierrat tekevät niistä herkkiä sään vuodenaikaisvaihtelun muutoksille. Erityisesti niiden liikkumiskyvyttömät elinkiertovaiheet ovat riippuvaisia niitä ympäröivästä mikroilmastosta.

Väitöskirjassani hyödynsin pitkiä aikasarjoja sääolojen vaikutuksista kahden eri päiväperhoslajin ekologiaan ja suojeluun. Toukkavaiheiden tutkimuksen mahdollisti laaja metapopulaatiotason kartoitusaineisto täpläverkkoperhosen (*Melitaea cinxia*) toukkapesien esiintymisestä Ahvenanmaalla vuosina 1993-2019. Täydensin kartoitusaineistoa lisäksi yksityiskohtaisella seuranta-aineistolla sekä kokeellisella aineistolla. Aikuisten perhosten paikallispopulaatioiden välisiä liikkeitä ja leviämistä uudelle alueelle pystyin tutkimaan hyödyntämällä merkintäjälleenpyyntiaineistoa Porvooseen istutetusta pikkuapollipopulaatiosta (*Parnassius mnemosyne*) vuosilta 2000-2016.

Täpläverkkoperhonen viettää 10 kuukautta vuoden mittaisesta elämästään toukkavaiheessa, jota tutkin kappaleissa I ja II. Toukat käyttävät ravintonaan vain kahta kasvilajia, ja erikoistuneisuus tekee niistä herkkiä sään suorien vaikutusten lisäksi myös sään aiheuttamille muutoksille ravintokasvien saatavuudessa. Kappaleessa I näytin kokeellisesti, että toukkien selviytymistä talven yli paransivat lumiset talvehtimisolosuhteet sekä myöhäinen kevät. Kevään myöhäinen alkua paransi myös toukkien talvehtimisen jälkeistä selviytymistä ja kehitystä. Talvehtimistä edeltänyt ja toukkien kuntoa heikentänyt ravintostressi lisäsi talvikuolleisuutta etenkin lumettomissa oloissa ja aikaisena keväänä. Lumisuus ei vaikuttanut metapopulaatioiden kasvukertoimeen luonnossa. Sen sijaan toukkien ravinnonsaantia parantava kasvukauden runsas sadanta lisäsi huomattavasti metapopulaatioiden kasvua.

Kappaleessa II minulle selvisi, että vaihtelevat mikroilmastot lisäsivät populaatioiden kasvua toukkien altistuessa ravinnon puutteelle niiden aktivoitua keväällä aikaisin ennen ravintokasvien kasvuunlähtöä. Yksityiskohtaisessa seuranta-tutkimuksessa lämmin mikroilmasto nopeutti toukkien kasvua, mutta lisäsi samalla niiden kuolleisuutta. Ravintokasvit eivät kasvaneet missään mikroilmastossa sään ollessa kylmä. Toukat taas säätelivät ruumiinlämpöään tehokkaasti aurinkoisissa mikroilmastoissa saavuttaen korkean ruumiinlämmön ja ravinnontarpeen myös kylmällä säällä. Metapopulaatiotason kartoitusaineiston perusteella populaatiot kasvoivat eniten elinympäristölaikuilla, joilla toukkia löydettiin vaihtelevista mikroilmastoista niin lämpimistä etelärinteistä kuin viileiltä, varjoisilta alueilta.

Kappaleessa III näytin, että lentokauden aikainen sää vaikuttaa voimakkaasti perhosten elinympäristölaikkujen välisiin liikkeisiin metapopulaatiossa. Perhoset viipyivät synnyinlaikullaan lyhyemmän ajan ja lensivät todennäköisemmin toiselle laikulle, kun lentokaudella oli paljon hellepäiviä ja auringon säteilyn määrä kasvoi. Lentokauden keskilämpötilan nousu johti pidempiin keskimääräisiin lentomatkoihin. Lisäksi laikkujenvälisiä liikkeitä lisäsi perhosten suuri yksilötiheys, joka yhdessä sääolojen kanssa selitti 79-91 % havaitusta vaihtelusta perhosten liikkeissä.

Kappaleessa IV simuloin istutetun perhospopulaation leviämistä istutusalueella perustuen tietoon lähdepopulaation perhosten liikkeistä erilaisissa ympäristöissä. Tieto perhosten liikkumiskäyttäytymisestä perustui ympäristökohtaisiin parametriestimaatteihin lentokaudelta, jolloin oli erityisen paljon hellepäiviä. Tämän seurauksena simulaatiomalli, joka ei huomioinut sään vaihtelua, ennusti todellista voimakkaampaa leviämistä etenkin sääoloiltaan kylminä lentokausina. Tästä huolimatta onnistuin ennustamaan melko tarkasti istutusalueen elinympäristölaikkujen asutusjärjestyksen ja perhosen leviämisenopeuden.

Kokonaisuutena väitöskirjani nostaa esiin useita stressitekijöitä, joita ilmastomuutoksen myötä muuttuvat sääolot aiheuttavat hyönteisille eri elinkiertovaiheissa. Lumipeitteisen ajan lyheneminen ja kevään alun aikaistuminen voivat johtaa sekä suoraan että muuttuvista biologisista vuorovaikutuksista johtuen lisääntyneeseen kuolleisuuteen ja kasvuun hidastumiseen, joita voimistavat aiemmissa elinkiertovaiheissa koetut stressitekijät. Lentokausien lämpeneminen voi lisätä huomattavasti leviämistä korkeammille leveysasteille, jotka ovat ilmastomuutoksen myötä muuttuneet sääoloiltaan suotuisemmiksi. Samalla sääolojen kasvavat vaihtelut voivat johtaa populaatioiden katoamiseen epäsuotuisan sään aikana ja vaikeuttavat hyönteisten siirtoistutuksia, joiden onnistuminen on usein kiinni istutusta seuraavista sääoloista.

1 INTRODUCTION

1.1 Changing weather conditions

Weather conditions vary spatially and temporally over a large gradient of scales. In addition to the geographical, seasonal and stochastic natural variations, there is a directional change going on. The high levels of anthropogenic greenhouse gas emissions cause warming average temperatures, increasing variability of temperature and precipitation, increasing frequency and intensity of extreme heat, precipitation and drought events, as well as decreasing frequency of cold extremes (Easterling et al. 2000, Coumou & Rahmstorf 2012, Dai 2013, IPCC 2014). Precipitation is increasing in the high latitudes and the equatorial Pacific, but decreasing in many dry mid-latitude regions (IPCC 2014, Cook et al. 2018).

In the Northern Hemisphere, the most prominent changes in weather conditions have taken place in winter (Pauli et al. 2013, IPCC 2014). Snow cover duration of the Northern Hemisphere has shortened with greatest reductions in spring snow cover extent, and these changes are expected to accelerate in the 21st century (Brown & Mote 2009, Choi et al. 2010, Brown & Robinson 2011, Zhu et al. 2019). There is an ongoing shift in the form of winter precipitation from snow to rain across the Arctic as well as other high-latitude regions (Bintanja & Andry 2017, Luomaranta et al. 2019). By the period 2040–2069, the average length of the thermal winter (the part of the year when daily mean temperature is below 0 °C) in northern Europe is expected to shorten by 30–60 days relative to 1971–2000 (Ruosteenoja et al. 2020). The number of days with frozen ground but without snow cover is predicted to increase notably in the western United States, Europe, the Tibetan Plateau and Mongolia (Zhu et al. 2019).

The onset times, durations and weather conditions of other seasons are also changing, while regional variations in these projections are considerable (Aalto et al. 2016, Allen & Sheridan 2016, Park et al. 2018, Ruosteenoja et al. 2020). For example, the onset of thermal spring is expected to advance more than the onset of thermal summer in parts of northern Europe including southern Finland, with over ten-day prolongation in the average extent of springs and falls by the mid-century (Ruosteenoja et al. 2020). Contrastingly, the average duration of the intermediate seasons is projected to remain constant in northern Finland, where the summers are lengthening at the same rate as the winters are shortening (Ruosteenoja et al. 2020). During the

thermal summer (as defined by Ruosteenoja et al. 2020), the mean temperatures exceed 10 °C, while in the intermediate seasons, temperatures fall between the threshold values of 0 °C and 10 °C. The changes in the average and variability of weather conditions, extreme weather events and the timing of thermal seasons have various consequences on natural systems, causing distributional and phenological shifts (Box 1), adaptations and extinctions across terrestrial, marine and freshwater taxa (Walther et al. 2002, Parmesan & Yohe 2003, Parmesan 2006, Cahill et al. 2013).

1.2 Effects of weather on insects

Effects of changing weather conditions on insects are numerous and divergent, and a current challenge is to identify the winners and losers of the ongoing climate change (Foden et al. 2019). Climate change happens globally, but populations and individuals respond to environmental conditions of much smaller scales (Bramer et al. 2018). Despite the rapidly growing body of literature on the ecological consequences of climate change, we still largely lack the understanding of the mechanisms by which changes in local weather alter the dynamics of populations. Insects, in particular, often have highly limited movement capacity and niche, and thus depend on micro-scale climatic conditions especially during immobile life stages (Box 2, Pincebourde & Casas 2019). Studying what happens at the micro scale relevant for given species is required to improve our understanding on the general effects of changing weather conditions and climate on insects (Bramer et al. 2018).

The ongoing climate change interacts with other anthropogenic stressors, which makes the current crisis far worse for insects and other organisms compared to climatic changes of the past (Warren et al. 2001, McLaughlin et al. 2002, Wilson et al. 2007, Brook et al. 2008, Fox et al. 2014, Oliver et al. 2015, Halsch et al. 2021). Complex and heterogeneous responses of species assemblages to changing weather are often associated with habitat heterogeneity (Fox et al. 2014, Bowden et al. 2015a, Koltz et al. 2018, Loboda et al. 2018, Nice et al. 2019, Platts et al. 2019). Indications exist for more uniform phenological than abundance response to changing weather conditions within communities (Stewart et al. 2020). In the Arctic, where climate change is most rapid, fly assemblages show decreasing abundance and diversity attributable to warming temperatures, even though responses of individual species are heterogeneous (Loboda et al. 2018). Decreased abundance, in turn, may lead to

Box 1. Climate change and phenology

Increasing temperature affects the timing of biological processes with the potential to break phenological synchronies of interacting organisms such as mutualists, competitors, or different trophic levels of food webs (Post et al. 2001, Parmesan 2007, Thackeray et al. 2016, Kharouba et al. 2018, Piao et al. 2019). The advancement of spring phenology and its potentially differing rates between interacting trophic levels are among the most-studied ecological effects of climate change and have been found across aquatic and terrestrial systems (Fig. 1, Durant et al. 2007, Møller et al. 2008, Post & Forchhammer 2008, Both et al. 2009, Saino et al. 2011, Doiron et al. 2015, Kankaanpää et al. 2018, Kharouba et al. 2018, Høye 2020). Current challenges in understanding the effects of climate change on phenological synchrony include assessing the baseline level of synchronisation: in many interacting species, asynchrony is a historically prevalent state, and hence the climate change may act to diminish the mismatch as well as to render it (Singer & Parmesan 2010, Kharouba et al. 2018).

While the rising spring temperatures seem to generally advance phenology across diverse taxa, winter warming causes divergent phenological responses. It accelerates the phenology of some species and impedes the phenology of others, particularly ones with chilling requirements that are not met due to the warming (Bosch & Kemp 2003, Zhang et al. 2007, Cook et al. 2012, Stålhandske et al. 2017, Marshall et al. 2020). The different rates and even directions of phenological shifts between interacting species may arise from these varying responses to a given climatic cue, or from the sensitivity to different climatic

cues that are not changing jointly (Doi et al. 2008, Ovaskainen et al. 2013, Chmura et al. 2019, Davies 2019). Increasing temporal variability of weather as well as ascending frequency and severity of extreme weather events pose a particular risk of emerging phenological asynchronies: evolutionary adaptation to abrupt and unexpected variations of weather conditions does not take place as it does to the gradual, directional change of average climatic conditions (Vázquez et al. 2017). These complexities create a challenge for scientists in search for generalisations, and many profound questions are yet to be answered (Kharouba et al. 2018): Which phenological interactions are changing most? How will they change? What is their biological relevance?

The biological relevance of altered synchronisation between interacting species varies widely with potentially critical alterations for the population dynamics of focal species (Bewick et al. 2016) or the food webs and ecosystem functioning (Deacy et al. 2017). On the other hand, phenological asynchrony with critical resources may decrease individual fitness without affecting population growth, as various other variables buffer populations against the adverse effects of mismatches (Johansson & Jonzén 2012). For example, phenological asynchrony with prey decreased fitness in great tits (*Parus major*), which in turn led to fitness gains by relaxing competition, and thus the population growth rate remained stable (Reed et al. 2013). Direct evidence of climate-induced trophic phenological asynchronies are scarce (Renner & Zohner 2018) in spite of broad meta-analyses suggesting that species of interacting trophic levels are shifting their phenologies at different rates (Parmesan 2007, Thackeray et al. 2016).

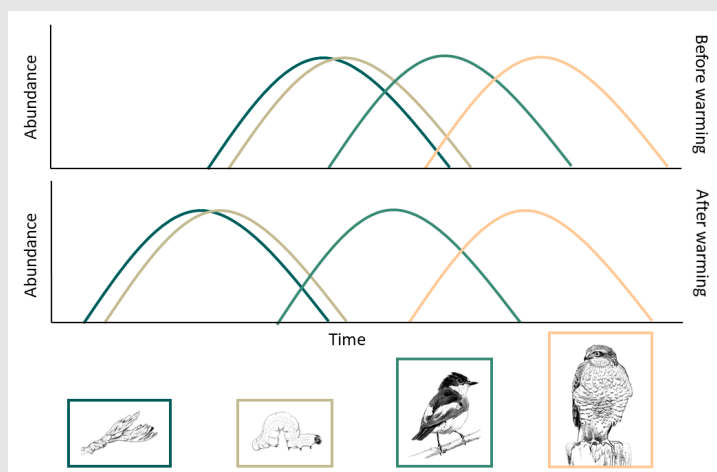


Figure 1. Both et al. (2009) showed that spring warming caused the oak bud burst and the peak abundance of oak-eating caterpillars to advance more than the peak abundance of passerine fledglings consuming the caterpillars. The peak abundance of passerine fledglings, in turn, advanced more than that of sparrow hawk fledglings consuming them.

reduced genetic diversity and adaptive potential of populations and species (Banks et al. 2013, Caplins et al. 2014). The rates of range shifts of invertebrates in Britain are best explained by taking into account the interaction between habitat availability and climate change (Platts et al. 2019).

Insects as short-lived ectotherms are predicted to be more strongly and negatively affected by the increased climatic variability due to climate change than longer-lived species such as birds and perennial plants (Morris et al. 2008). Long-term persistence of insect populations threatened by climate change and habitat loss requires conservation management. The resilience of vulnerable populations can, for example, be promoted by conservation actions that enhance the availability of macro- and microhabitats to allow niche and range expansions at the landscape scale (Fox et al. 2014, Oliver et al. 2015, Greenwood et al. 2016, Suggitt et al. 2018, Platts et al. 2019, Román-Palacios & Wiens 2020). Translocation of individuals to areas that have newly become climatically suitable, but are beyond dispersal distance of the focal species, may help overcome dispersal barriers when it is not possible via improvements of habitat connectivity (Box 3, Thomas 2011, Widhalm et al. 2020). Among insects, butterflies are a model group of the effects of climate change because of the extensive data available on their population trends over long periods and vast geographic areas (Parmesan et al. 2000, Eskildsen et al. 2015). Sedentary habitat or host plant specialist butterflies show greatest declines due to anthropogenic environmental change in general (Warren et al. 2001, Wilson et al. 2007, Eskildsen et al. 2015) and under climatic extremes in particular (De Palma et al. 2017).

A growing number of insects persist as metapopulations due to the ongoing habitat fragmentation (Tscharntke & Brandl 2004, Ribeiro et al. 2009, Hanski et al. 2017). The classical metapopulation theory assumes independent dynamics of local populations with frequent local extinctions and colonisations of currently unoccupied patches (Hanski et al. 1995). Theory predicts that increasing spatial synchrony of local colonisation and extinction events compromises the long-term stability of classic metapopulations (Hanski et al. 1995). Such increased spatial synchrony in population growth rates may be induced by the growing spatial synchrony in weather conditions caused by climate change, and especially by large-scale extreme weather events (Kindvall 1996, Tack et al. 2015, Kahilainen et al. 2018, Hansen et al. 2020, van Bergen et al. 2020).

1.2.1 Direct effects of weather on insects

Drawing generalisations on the effects of weather on insects is difficult if not impossible, because of the vast variety of responses to similar changes of weather within and among species assemblages. However, some general patterns emerge from the weather- and climate change-related ecological literature. Increasing temperature variability is particularly harmful for many insects, even for species that are affected positively by the warming average temperatures (Vasseur et al. 2014, Verheyen & Stoks 2019). This is demonstrated by the finding that rising maximum temperatures rather than rising average temperatures lead to increased extinction risk (Román-Palacios & Wiens 2020). Increasing frequencies of extreme heat contributed to local extinctions of bumble bees over two continents (Soroye et al. 2020). In aquatic damselfly larvae, a simulated extreme heat wave improved performance of surviving individuals, but increased mortality in one of two study species (Van Dievel et al. 2017).

Under stressful conditions, organisms face the trade-off between the response to stress and the allocation to growth and reproduction (Vázquez et al. 2017). Warming may decrease insect body size hence lowering fecundity and dispersal ability (Bowden et al. 2015b). Contrastingly, on a leading range edge, warming may enhance dispersal, and rapid poleward range shifts of insects have been reported in response to warming climate (Parmesan 1999, Chen et al. 2011a). In multivoltine insects, warming temperatures may increase voltinism (Altermatt 2010) with important demographic consequences: when growing degree days are not increased sufficiently to support an extra generation, the attempt results in a developmental trap where the last generation of the season fails to complete their development and population growth rate is consequently reduced (Van Dyck et al. 2015, Kerr et al. 2020). Contrastingly, when the warming is sufficient to support an extra generation, a demographic bonanza results, as another generation means an additional opportunity for population growth (Kerr et al. 2020).

1.2.2 Indirect effects of weather on insects

Changing species interactions are among the most important causes of population declines and extinctions related to climate change (Cahill et al. 2013). Insects are not only sensitive to the direct effects of weather conditions, but they also have to balance between the dual pressure of gaining resources and not becoming a resource for predators and parasitoids (Schmitz et al. 2016). Both hosts and natural enemies of insects are affected by the weather conditions as

Box 2. Complex life cycle makes insects vulnerable to climate change

Insects generally have complex life cycles with different life stages potentially responding contrastingly to climate warming (Kingsolver et al. 2011). Juvenile insects commonly experience highly different conditions than adult ones, due to differences in microhabitats, movement ability and seasonality (Fig. 2). Research often focuses on single life stages that are easiest to observe, such as the colourful adult butterflies or flashing adult fireflies, while other, more invisible life stages may be more sensitive to environmental change (Radchuk et al. 2013, T. R. Evans et al. 2019).

Insects experience global climate at local and micro scales, and thus their experience of climatic conditions may deviate importantly from macroclimatic conditions (Pincebourde & Casas 2019). Dependency on highly specific microclimates may increase their vulnerability to extreme climatic events (Pincebourde & Casas 2019). On the other hand, the availability of varying microclimates may buffer populations against the adverse effects of climate change

(Suggitt et al. 2012, Bramer et al. 2018). Immobile life stages of insects are not capable of behaviourally altering their microclimatic conditions (Van Nouhuys & Lei 2004). In ecological monitoring studies, there is a lack of recording climatic variables at a micro scale relevant for insects and particularly their immobile life stages (Bramer et al. 2018).

The responses of different life stages of British butterflies to extreme climatic events were studied by McDermott Long et al. (2017). They found that overwintering butterflies regardless their specific life stage were most vulnerable to extremely warm weather. Contrastingly, hot and dry weather during adult flight period enhanced population growth. Furthermore, univoltine species were sensitive to the adverse effects of heavy precipitation at the pupal stage. Previously, overwintering butterfly larvae have been shown to be negatively affected by warming temperature (Radchuk et al. 2013). Decreasing snow cover and winter warming have also led to reductions in butterfly population growth as well as in temperate forest beetle abundance and diversity (Matter & Roland 2017, Harris et al. 2019).

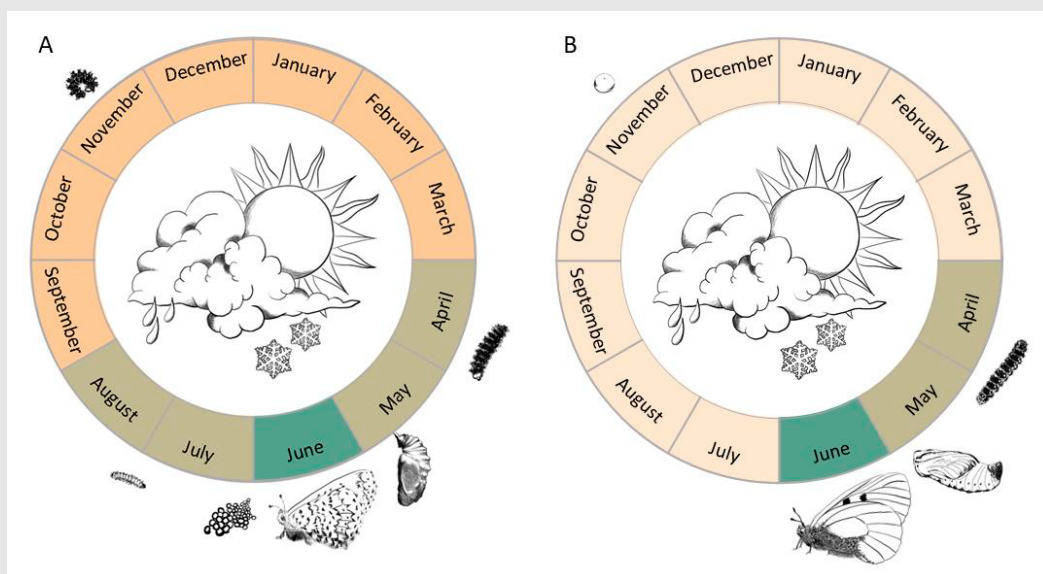


Figure 2. Life cycles of (A) the Glanville fritillary and (B) the Clouded Apollo. Adult flight season of both species is in June and different life stages are exposed to differing seasonal weather conditions. (A) In Glanville fritillary, pre-diapause larval stage takes place in July-August, diapause from September to March, and post-diapause larval stage in April-May. Long larval period makes this species susceptible to drought that may desiccate the host plants both before and after diapause. Larvae are gregarious, which boosts behavioural thermoregulation, and may cause resource competition. Short egg and pupal periods are in June-July and May-June, respectively. They partly overlap with the larval and adult periods. (B) Egg stage covers the majority of the Clouded Apollo life cycle, lasting from June to April. The short larval stage is phenologically specialised to match the growth of the host plant, fumewort, from late April to early May. Solitary larvae hide within vegetation. Pupal period takes place from late May to early June.

well as the interactions with other trophic levels adding complexity to the big picture (Walther 2010, Laws 2017, Ferguson & Sinclair 2020). Phenologically, for example, it is advantageous for a herbivore to track closely the phenological shifts of its host plant (van Asch et al. 2013, Davies 2019). Contrastingly, when it comes to predators and parasitoids, it is adaptive to increase phenological asynchrony to escape the natural enemies (Van Nouhuys & Lei 2004, Both et al. 2009).

Predation rates typically increase with temperature but decrease sharply during extreme high temperature, while the effects of climate warming and extreme heat events on herbivory seem to be more species-specific (Tylianakis et al. 2008, Lemoine et al. 2014, Schmidt et al. 2017, Stoks et al. 2017). For herbivores, the quality of host plants reared at high temperature may be poor causing reduced body mass, prolonged development, increased food intake and reduced food conversion efficiency (Berrigan & Charnov 1994, Bauerfeind & Fischer 2013). Microhabitat management that considers sufficient quantity, quality and developmental stage of host plants is crucial for the persistence of insect herbivore populations facing increasingly variable and even extreme weather conditions (Eskildsen et al. 2015, Walsh 2017).

Extreme weather events often have contrasting consequences for species with different life histories and ecological specialisations (De Palma et al. 2017, Forister et al. 2018). In short-lived insects, the severe immediate crashes after adverse climatic extremes have so far been mostly followed by fast recovery (Palmer et al. 2017), but there are already examples of local extinc-

tions attributed to increased variability in weather and its effects on food availability (McLaughlin et al. 2002). Drought, for example, can cause host-mediated crashes of insect populations over varying taxa and outbreaks over others (Mattson & Haack 1987, Hawkins & Holyoak 1998, De Palma et al. 2017, Cayton & Haddad 2018, Forister et al. 2018, van Bergen et al. 2020).

2 AIMS OF THE THESIS

The general aim of this thesis is to improve the understanding on the effects of changing weather conditions on the metapopulation dynamic processes, namely local population growth rates, dispersal, and correlation among local population dynamics, of insects (Fig. 3). A further aim is to find out how the metapopulation dynamic consequences of changing weather may affect insect conservation planning. I utilised available long-term and large-scale field data sets (I-IV) on two butterfly species, the Glanville fritillary (*Melitaea cinxia*, I,II) and the Clouded Apollo (*Parnassius mnemosyne*, III,IV), and complemented them with more detailed experimental (I) and monitoring (II) data to address the following research questions:

1. How do snow cover and spring onset timing affect overwintering survival, post-diapause larval survival, developmental time, pupal weight or sex ratio (I, II)?
2. How does food deprivation at the pre-diapause stage affect overwintering survival under snowy and snowless conditions and at different spring onset timings (I)?



Figure 3. Schematic overview of the thesis highlighting direct and indirect ecological effects of different weather conditions during several butterfly life stages. Roman numerals refer to chapters in which each effect was addressed.

Box 3. Translocation as a conservation tool

Conservation translocation means intentional movement of living organisms from one area to another, and it has been proposed to be the only feasible means to save species that are affected most negatively by the rapid anthropogenic changes such as climate change and habitat loss (Seddon 2010, Thomas 2011, Seddon et al. 2014). Traditionally, the introduction of species outside their current distribution or particularly outside their historical range (i.e. assisted colonisation or assisted migration) has been considered risky and unnatural, but what actually is natural in today's world where human impact reaches every ecosystem (Thomas 2011)? Climate change plays an important part in shaping conservationists' views on the necessity of translocations, as more and more species are unable to track their climatic niche in highly fragmented habitats (Seddon 2010, Widhalm et al. 2020).

Translocations are expensive and often fail, which has increased the interest in identifying the predictors of success or failure of a translocation project (Bellis et al. 2019, 2020, Berger-Tal et al. 2020). Common problems include difficulties in post-release monitoring because of the lack of funding (Berger-Tal et al. 2020). Climatic suitability of the release site has been identified as a key predictor of the success or failure of translocations in general (Bellis et al. 2020). For insects, suitable weather conditions following the release, high-quality release habitat, and suitable characteristics of the release landscape are important factors ensuring a successful translocation (Bellis et al. 2019, Berger-Tal et al. 2020).

Translocation has proved to be an effective conservation measure for several insects (Wynhoff et al. 2008, Thomas et al. 2009, Kuussaari et al. 2015, Dolný et al. 2018). Habitat management to provide a high-quality release site is often

needed to ensure a successful insect translocation (Fig. 4, Thomas et al. 2009, Dolný et al. 2018). Insect translocations are strongly taxonomically biased towards lepidopteran species, which may be explained by their iconic status and conservationists' expertise on them (Bellis et al. 2019). It is important, on one hand, to increase the success potential of translocations by translocating only species which can be monitored effectively and for which the habitat requirements are known. On the other hand, concentrating the translocation efforts on relatively few well-studied taxonomic groups may compromise the viability of numerous other species (Bellis et al. 2019).



Figure 4. The Large blue (*Phengaris arion*) was successfully reintroduced to the UK after national extinction and intensive habitat management projects (Thomas et al. 2009).

3. Does the increasing exposure to freezing caused by shortened snow cover duration decrease population growth rates (I)?
4. What are the impacts of spatial variation in weather and varying microclimates on larval development and survival (II)?
5. Do the local effects of weather and microclimate on larval development translate into metapopulation-level variations in population growth rates (II)?
6. How do the larval body surface temperatures deviate from concurrent ambient temperatures and how does this affect larval feeding activity (II)?
7. How do the weather conditions of the flight season alter the emigration and colonisation rates, residence times and dispersal distances within a metapopulation (III, IV)?
8. Is it possible to predict the spatial expansion of a translocated population in a novel landscape based on prior knowledge of the species' movement rate? How does the annually varying flight season weather affect the accuracy of the predictions (IV)?

3 MATERIAL AND METHODS

3.1 Study systems

In this thesis, I utilised long-term data from two study systems (the Glanville fritillary, I, II, and the Clouded Apollo, III, IV) to cover multiple life stages of butterflies. Direct data covering the whole life cycle would be optimal to study the multiple effects of changing weather conditions on insects, but long time series of such data are rarely if ever available. Thus, combining different types of observational data from separate study systems was a useful way to cover a bigger proportion of the butterfly life cycle.

3.1.1 The Glanville fritillary

The distribution of the Glanville fritillary spans over Eurasia. Habitat deterioration and possibly microhabitat cooling caused by climate change have led to declining population trends in many parts of its northern European distribution area (WallisDeVries 2006). In Finland, the distribution is limited to a well-studied metapopulation in the Åland Islands (Fig. 5A), and the species is classified nationally endangered due to its strong population fluctuations (Nupponen et al. 2019). In the Åland Islands, the Glanville fritillary inhabits a network of approximately 4 500 dry meadows with one or both of the larval host plants, the ribwort plantain (*Plantago lanceolata*) and the spiked speedwell (*Veronica spicata*) (Fig. 6, Ojanen et al. 2013, Hanski et al. 2017).

Flight season is in June and females lay their eggs as large groups on the leaves of the host plants (Kuussaari & Singer 2017). The gregarious larvae hatch in July, and

live and overwinter in large family groups (Fountain et al. 2018) in silk nests they spin around a host plant (Ojanen et al. 2013, Kuussaari & Singer 2017). They enter the diapause usually in August (Kuussaari & Singer 2017). After the end of their diapause in late March or early April, the black and hairy larvae remain in groups basking to warm up and feeding on the first emerging leaves of the host plants (Fig. 6, Kuussaari & Singer 2017). The resources acquired during the post-diapause larval stage are critical for the lifespan and reproductive rate of the adult butterfly (Saastamoinen et al. 2013a). In late April or early May, larvae reach the last instar and spread out to find a pupation site (Kuussaari & Singer 2017). Larval nests are easy to observe in the low and sparse vegetation typical to the breeding habitat (Fig. 7). Post-diapause larvae can be monitored in the field until they moult to the last instar and become solitary and more mobile.

3.1.2 The Clouded Apollo

The Clouded Apollo is a Palearctic butterfly that has declined severely in many parts of Europe due to forestation and agricultural intensification of breeding habitat (Van Swaay et al. 2010, Cousins et al. 2015, Johansson et al. 2017). It has been listed on the EU Habitats Directive Annex 4 and Bern Convention Annex 2 (van Swaay et al. 2010). In Finland, it has been classified vulnerable and protected by law (Nupponen et al. 2019). Larvae of the Clouded Apollo feed on *Corydalis* spp., and the only host plant available in Finland is the fumewort (*Corydalis solida*). Therefore, the scarcity and overgrowth of fumewort-rich meadows threatens the persistence of the butterfly in Finland (Nupponen et al. 2019). The flight season of the Clouded Apollo in

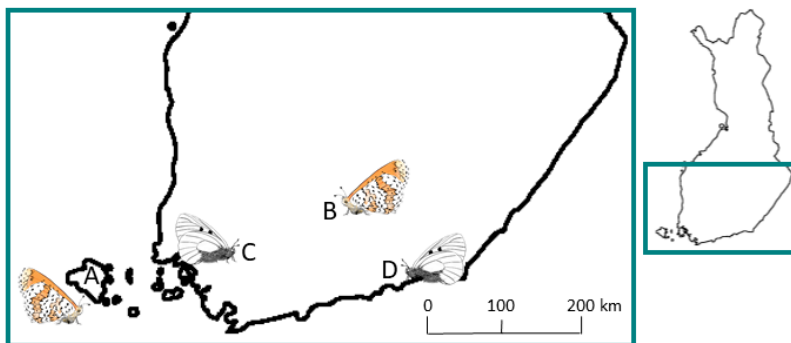


Figure 5. Locations of the study sites in southern Finland. The Finnish distribution of the Glanville fritillary is limited to Åland Islands (A). I studied Glanville fritillary overwintering under semi-natural field conditions at Lammi Biological Station (B). The largest remaining Finnish Clouded Apollo metapopulation is located in Somero (C). I studied Clouded Apollo dispersal and colonisation in a translocated population in Porvoo (D).



Figure 6. Glanville fritillary habitats are shallow-soiled dry meadows (left). Penultimate-instar larvae exploit the small host plants efficiently to the last bite in the spring (right).

Finland is mainly in June. Females lay their eggs in the litter near the already senesced host plants (Konvicka & Kuras 1999, Bergström 2005). The egg stage lasts over the rest of the summer, autumn and winter. Larvae hatch in the spring, and larval and pupal stages last on average from April to May. While adult butterflies are easy to observe and study, the other life stages are cryptic and single larvae are found only infrequently.

The largest remaining Clouded Apollo metapopulation in Finland is situated in Somero (Fig. 5C). The landscape inhabited by some 10 000 Clouded Apollos (Kuussaari et al. 2013) is dominated by open agricultural landscape, with relatively large and well-connected riparian meadows that hold high densities of the fumewort (Luoto et al. 2001). In 2000, 20 mated female Clouded Apollos were translocated from Somero to a release site in Porvoo (Fig. 5D; Kuussaari et al. 2015). The release site is a four-hectare meadow in a spruce forest dominated seashore landscape. There are several smaller habitat patches within a two-kilometre radius from the release site.

3.2 Data

I used a combination of different types of methods to address my research questions. In chapter I, I combined individual-level experimental data on the effects of overwintering weather conditions on survival and development to long-term field data describing metapopulation growth rates in relation to variations of weather. In chapter II, I monitored closely the effects of spring weather and microclimate on post-diapause larvae in the wild, and utilised large-scale survey data to see whether metapopulation-level population growth rates reflect the results of the detailed monitor-

ing data. In chapter III, I used long-term mark-recapture data to explain the impacts of flight season weather on butterfly dispersal in a metapopulation. Finally, in chapter IV, I adopted a simulation approach based on a spatially explicit movement model to predict the spatial expansion of a translocated butterfly population in a novel landscape.

3.2.1 Survey and monitoring data on the Glanville fritillary

The large-scale field surveys on the metapopulation of the Glanville fritillary in the Åland Islands have been conducted biannually since 1993 (Ojanen et al. 2013). These long-term data contain information on annually varying local population sizes and overwintering survival, as the conspicuous larval winter nests are surveyed throughout the 50 km x 70 km study area in September and the number of post-diapause larvae of the respective nests in the following April (Ojanen et al. 2013).

I utilised the long-term fall survey data from 1993-2018 in chapter I to analyse the effects of snow cover on the population growth rates. The spring survey data of 2016 and 2017 were complemented with microhabitat data for each larval group, and I used these data in chapter II to find out how the spatial variations in weather and microclimate affected local population growth rates in 406 populations from autumn 2015 to autumn 2016 and in 342 populations from autumn 2016 to autumn 2017. The main focus in chapter II was in detailed monitoring data on post-diapause larval weight gain, survival and temperature, and host plant growth in the spring. I collected the larval temperature data set on seven habitat patches across the main

island of Åland in April 2016 and the growth and survival data set on 13 habitat patches from March-May 2017. I used weather and microhabitat data to explain larval temperature, weight gain and survival, as well as host plant growth in the absence of larvae.

3.2.2 Overwintering experiment on the Glanville fritillary

I did a larval overwintering experiment at Lammi Biological Station (Fig. 5B) under semi-natural field conditions during winter 2017-2018 to gain precise information of the direct and indirect effects of snow cover and spring onset timing on the survival and other life-history traits of the Glanville fritillary (I). Furthermore, I tested whether pre-diapause food stress affects overwintering survival under different snow conditions and spring onset timings. I reared 43 larval clutches on petri dishes in laboratory (28:15 °C; 12:12 h light:dark). As the larvae moulted into third instar, 13 clutches went through a food deprivation treatment for five consecutive days. This treatment did not cause direct mortality. In the wild, pre-diapause larvae may undergo severe food deprivation due to drought that desiccates the host plants (Salgado et al. 2020, van Bergen et al. 2020). I moved the third-instar larvae onto spiked speedwells growing in pots in order to enable the larvae to construct winter nests around host plants as they do in nature (Fig. 7). I divided the larvae of each family into four groups that went through a different combination of overwintering treatments: snowy winter and early spring, snowless winter and early spring, snowy winter and late spring, or snowless winter and late spring. In early November, I took the larvae outside on a field. Half of the pots were covered

with boxes made of mosquito net fabric that prevented the snow from falling on the pots but did not otherwise alter the microclimate (Fig. 7). The rest of the pots were naturally covered by snow (Fig. 7). I used data loggers to keep track of the changes in microclimatic temperature through the winter.

I brought the first half of both snowy and snowless pots back to the laboratory (28:15 °C; 12:12 h light:dark) in mid-March after a two-hour acclimation period at an intermediate temperature. In Åland, I have observed the first post-diapause larvae outside their winter nests during the second half of March in exceptionally early springs. I chose a warm day with above-zero temperature to avoid too rapid a temperature change for the larvae. The last half of larvae continued diapause four weeks longer – matching the end of the diapause in Åland in late springs – prior to being brought back to the laboratory. After two days in the laboratory, the numbers of living and dead larvae were counted. A subset of ten larvae per each of the four treatment combinations out of eight families were raised to adults to measure the post-diapause effects of snow cover and diapause duration. I measured post-diapause survival, sex ratio, developmental time and pupal weight of the butterflies. Food-deprived larvae were not raised, as their overwintering survival was too low to allow sufficient sample sizes.

3.2.3 Mark-recapture data on the Clouded Apollo

Mark-recapture (MR) method (Nowicki et al. 2005) was used to study the characteristics of the Clouded Apollo source population in Somero in 1999 (Luoto et al. 2001,



Figure 7. Glanville fritillary larvae overwinter as a group in a nest spun around a host plant at ground level (left). In my overwintering experiment, half of the nests overwintered under snow (middle of the picture on the right; photo © Suvi Ikonen) and half of the nests overwintered without snow under mesh fabric boxes.

Ovaskainen et al. 2008b). The same approach has been used in the release area in Porvoo to evaluate the success of the translocation and the spatial expansion of the translocated population every year since 2000 (Fig. 8, Kuussaari et al. 2015), and I utilised these data in chapters III and IV. MR method is based on capturing an individual, marking it uniquely, and immediately releasing it. This is repeated for each individual encountered in the study area, and the exact capture times and places (at the resolution of 50 m x 50 m) are recorded. When a marked individual is recaptured, similar record is kept of its locality, thus gaining information on its movements. The capturing is repeated through the study season as often as the weather conditions and monitoring resources permit. This approach allows the estimation of population size and dispersal rate (Kuussaari et al. 2015).

In chapter III, the annual variations in emigration rates, residence times in a natal patch, and movement distances in 2004-2015 were explained using measures of the flight season weather, butterfly density and study effort as explanatory variables. During the 12 years, a total of 1 308 of the marked butterflies were recaptured at least once with the annual number of recaptured individuals varying between 33 and 250 (average

109). In chapter IV, I used the parameter values of a mechanistic movement model of Ovaskainen et al. (2008a) parameterised with the MR data from the source population in Somero (Luoto et al. 2001, Ovaskainen et al. 2008b) for a simulation study to predict the expansion of the translocated population in the novel release landscape during 2000-2016. The spatially explicit movement model can be used to evaluate the functional connectivity of a given landscape, as it contains habitat-specific parameters for movement, edge-mediated behaviour, mortality, and capture probability (Ovaskainen et al. 2008a, 2008b). I did not model the population sizes, but obtained them from the MR data collected in Porvoo (see Kuussaari et al. 2015 for the calculation of the conservative minimum estimate of the population size used here).

3.3 Statistical analyses

I used different variations of regression models and statistical software R (R Core Team 2019) in all chapters to analyse the data. For most response variables, such as post-diapause developmental time of larvae (I), host plant availability (II), and butterfly dispersal distance (III), I used linear models (LM). For binomial response variables, such as larval survival (I, II) and adult emigra-



Figure 8. Every Clouded Apollo the researchers have encountered in the release area after year 2000 has received an ID number on its hind wing. Marking and recapturing gives estimates of population size and movements of individuals.

tion rate (III), I used generalised linear models (GLM) with a binomial error distribution and a logit link function. I used a Bayesian approach to analyse the spatial field data from Åland (I, II) and fitted models using R packages brms (Bürkner 2017, 2018) and RStan (Stan Development Team 2020) (I), and R-INLA (Rue et al. 2009, Lindgren et al. 2011, <http://www.r-inla.org>) (II). For the experimental data (I), I fitted mixed models (LMM and GLMM) with larval family as a random intercept to take into account the possible differences between families. In chapter IV, I predicted the butterfly occupancy times in different habitat patches by running a simulation study using software Disperse (Ovaskainen et al. 2008a). The occupancy times could be predicted based on habitat-specific parameters for movement, edge-mediated behaviour, mortality, and capture probability obtained from the source population based on MR data from the flight season preceding the translocation (Ovaskainen et al. 2008b).

4 RESULTS AND DISCUSSION

In this thesis, I found that changes in weather conditions generally attributed to climate change may decrease the stability of butterfly populations. Furthermore, increasing annual variability of weather increases the uncertainty of conservation planning and may compromise the effectiveness of conservation measures. Snowless overwintering conditions and advanced spring onset timing decreased overwintering survival under experimental conditions (I). This effect was further amplified by pre-diapause food stress. However, the effects of snowless overwintering conditions were not reflected by the metapopulation growth rates (I). In the wild, exceptionally early spring onset led to increased post-diapause mortality caused by a phenological asynchrony between larvae and host plants (II). Microclimatic variability buffered populations against the phenological asynchrony, as survival was highest in shaded microhabitats only infrequently used for oviposition by the thermophilous butterfly. The dispersal and colonisation of adult butterflies was enhanced by warm and sunny flight season weather (III, IV). Annually variable flight season weather conditions cause fluctuations in butterfly residence times, emigration rates and dispersal distances with potential implications on metapopulation persistence and range shifts, as well as on conservation planning.

4.1 How do snow cover and spring onset timing affect overwintering survival, post-dia-

pause larval survival, developmental time, pupal weight or sex ratio?

In chapter I, the presence of snow cover increased larval overwintering survival. Later spring onset and thus a longer diapause duration also enhanced overwintering survival. We did not detect any effect of snow cover on the subsequent post-diapause development. Contrastingly, the timing of the spring onset affected post-diapause larvae in multiple ways: post-diapause survival of both sexes and the pupal time of females increased with a lengthening diapause duration whereas the post-diapause larval developmental time of both sexes decreased when the diapause lasted longer. The sex ratio of adults was female-dominated in the early spring group with 56 % of the 132 butterflies being females, and male-dominated in the late spring group with 45 % of the 148 butterflies being females. Males of the late spring group had a lower pupal weight than the ones of the early spring group. In females, the diapause duration did not affect pupal weight. Detailed monitoring of wild larvae in the field in chapter II showed an indirect, host plant mediated, effect of the exceptionally early spring onset on larval post-diapause survival. Survival was decreased due to a phenological asynchrony between larvae and host plants particularly in the warm microclimates favoured for oviposition by the thermophilous butterfly (for further discussion, see sections 4.4 and 4.5).

Insulating snow cover greatly increased the stability of overwintering microclimate (Fig. 9) in my experiment enhancing the diapause survival of larvae (Fig. 10). The conditions were indeed severe without the snow cover, as the minimum temperature was -28 °C and there were several fluctuations of more than 20 °C within a day (Fig. 9A). It is noteworthy, however, that in the wild such cold temperatures are encountered only infrequently, as the climate at the study site is more continental than that of the Åland Islands. My results indicate that – at least under cold, continental winter conditions – the stable subnivean microclimate is more favourable for overwintering larvae than the more variable snowless microclimate. Similar beneficial buffering effect of snow cover against extreme temperatures has been thoroughly documented in the Rocky Mountain Apollo (*Parnassius smintheus*) butterfly diapausing as an egg (Roland & Matter 2016). These results support the idea of Marshall and Sinclair (2015), who stated that the increased frequency of cold stress events reduces the survival of insects.

Extending the diapause duration from 7.5 months to 8.5 months – and thus the time spent outside in winter

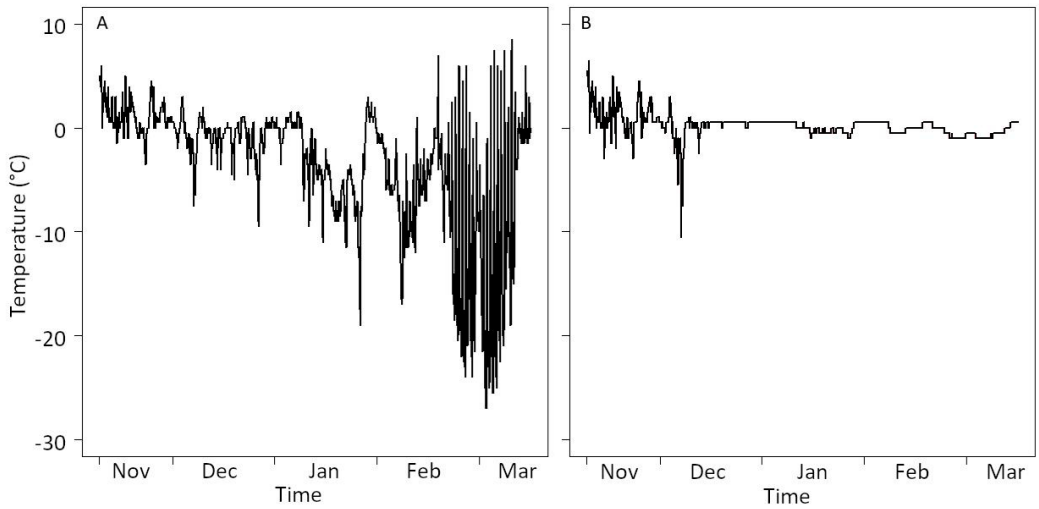


Figure 9. Insulating snow cover importantly decreased microhabitat temperature variability in the overwintering experiment under semi-natural field conditions. (A) Temperature measured with a data logger in snowless microhabitat varies greatly while (B) the temperature under snow is more stable. Snow cover period started in early December and lasted until the end of the experiment.

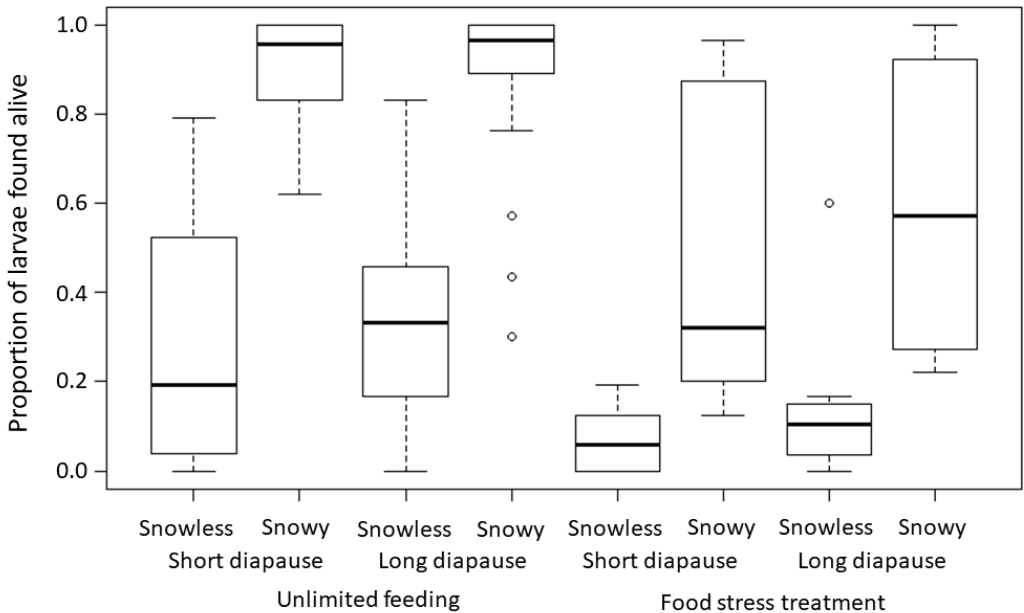


Figure 10. Overwintering survival of *Glanville fritillaria* larvae was highest under snowy conditions. Long diapause duration due to late spring onset further improved survival. Contrastingly, pre-diapause food stress reduced survival.

conditions from four to five months – enhanced both diapause and post-diapause survival regardless the snow conditions (Fig. 10). In Åland Islands, the diapause duration varies roughly from seven to nine months with some variation in the onset timing in autumn, but particularly in the offset timing in spring, which is determined largely by the early spring temperature and snowmelt timing in snowy winters (personal observations, Ojanen et al. 2013). Larvae end the diapause as soon as the first sunny spring days enable basking, and thus the advancing spring onset timing likely shortens diapause duration with possible adverse effects for survival. By the period 2040–2069, the average length of the thermal winter in northern Europe is expected to shorten by 30–60 days relative to 1971–2000 (Ruosteenoja et al. 2020). Ruosteenoja et al. (2020) modelled the annual probability of the absence of thermal winter to rise from 10–20 % in the period 1971–2000 to 60–70 % in 2040–2069 in Åland Islands.

Increased diapause mortality and phenological delays of butterflies have been attributed to winter warming and advancing spring onset in species diapausing as pupae (Posledovich et al. 2015, Stålhandske et al. 2017). In agreement with the previous studies, larval development was delayed with shorter diapause duration in my experiment. However, I cannot distinguish whether this was caused by adverse effects of the short diapause on early spring groups or by the late spring groups accelerating their phenology to compensate for the time they had lost because of the later end of diapause. Early eclosion is critical especially for male fitness in protandrous animals such as my focal species (Forsberg & Wiklund 1988, Saastamoinen et al. 2013b). In accordance with this idea, the late spring males in my experiment advanced their eclosion by faster post-diapause development compared to the early spring males, with the cost of reduced pupal weight. For female fecundity, sufficient body size is more important than for male fecundity, as indicated by the equal pupal weights of both early and late spring females in my experiment (Blanckenhorn 2000, Saastamoinen 2007). Despite growing as heavy as the early spring females, the late spring females accelerated their post-diapause larval development. Contrastingly, their pupal time was prolonged.

4.2 How does food deprivation at the pre-diapause stage affect overwintering survival under snowy and snowless conditions and at different spring onset timings?

Pre-diapause food deprivation decreased larval overwintering survival under both snowy and snowless conditions (I, Fig. 10). The diapause survival of food-deprived larvae was increased by longer diapause, which indicates that their decreased overall diapause survival was not caused primarily by the energy reserve depletion during the overwintering, a mechanism frequently associated with high diapause mortality (Williams et al. 2015). Rather, their response to changes in conditions, such as variations in temperature and humidity, was possibly less effective than that of the larvae fed *ad libitum* through the pre-diapause stage. Lower survival without the insulating snow cover supports this idea, because the snowless larvae were exposed to much larger and steeper changes in microclimatic conditions compared to the snowy ones.

Lavy et al. (1997) suggested that producing the substances needed to become cold tolerant is costly and that starved animals do not have enough resources to produce them. Our results highlight that the stress caused by pre-diapause food deprivation may lower diapause survival severely even with the opportunity to compensate by feeding *ad libitum* between the food deprivation and the diapause onset. The most drastic reductions of survival took place when the pre-diapause food stress was coupled with the lack of insulating snow cover and a shortening diapause duration. This may be particularly relevant in the face of climate change, as organisms are exposed to more extreme conditions during both the growing season and the winter with increasing probability of having to endure the harsh winter weather when already stressed by adverse growing season weather and its consequences for individual condition.

4.3 Does the increasing exposure to freezing caused by shortened snow cover duration decrease metapopulation growth rates?

Increase in the larval exposure to freezing during overwintering did not alter metapopulation growth rates, which were instead driven by growing season precipitation (I). In addition, metapopulation growth rates had a clear negative temporal autocorrelation typical for systems exhibiting density dependent fluctuations in population trends. These results are in line with the findings of several recent studies showing that the adverse effects of drought, which desiccates the host plants leading to larval food deprivation, are a key driver of the Glanville fritillary population declines (Tack et al. 2015, Kahilainen et al. 2018, van Bergen et al. 2020). It is possible that the drastic impacts of summer drought on population growth rates overrun

the more subtle effects of other weather conditions throughout the butterfly life cycle (van Bergen et al. 2020).

This result highlights that some ecological relationships found on individual level under experimental settings may not hold much relevance under natural conditions on the level of metapopulation growth. In the wild, multiple stressors operate during an insect life cycle, and their potentially complex interactions make it difficult to tease apart the independent effects of every stressor (Kaunisto et al. 2016). Without further analyses, I do not know whether the overwintering survival is lowered by the exposure to freezing as can be expected in the light of my experimental results. Decreasing exposure to freezing has been shown to increase the population growth of the specialist pathogen of the ribwort plantain, *Podosphaera plantaginis*, in Åland Islands (Penczykowski et al. 2015).

Decreased overwintering survival might not be translated into decreasing population growth rates for several reasons, but I speculate that one probable reason is the complexity of implications of the larval gregariousness. Larval performance under both natural and common garden conditions is improved by large group size (Kuussaari & Singer 2017, Rosa et al. 2017). The positive impact of a large group for the survival on both group and individual level is most pronounced during the diapause (Kuussaari & Singer 2017). At the post-diapause stage, the scarcity of the available food resources may increase within- and between-group competition decreasing individual and group survival particularly in the largest groups (II, Nieminen et al. 2004). Assuming that the increased exposure to freezing lowers individual but not group overwintering survival leads to relaxed competition at the post-diapause stage, which may, in turn, contribute to increasing population size. This would buffer the population growth against the increased winter mortality (for a similar buffering effect, see Reed et al. 2013). Strong negative temporal autocorrelation in metapopulation growth rates further suggests that intraspecific competition may be an important driver of strong population fluctuations of the Glanville fritillary. I argue that competition most probably takes place during the post-diapause larval stage when the food resources may be scarce (II).

4.4 What are the impacts of spatial variation in weather and varying microclimates on larval development and survival, and host plant growth?

In chapter II, I demonstrate how shaded microclimatic conditions can, under specific macroclimatic conditions, enhance the larval survival of a thermophilous butterfly. My data from a detailed field monitoring study suggests that exceptionally warm weather early in the spring 2017 led to phenological asynchrony between larvae and their host plants. This asynchrony was buffered by microhabitat heterogeneity, as larval survival was highest in shaded microhabitats that normally are suboptimal for the development of thermophilous larvae. Consequently, local population growth rates were increased in habitat patches with more shaded microhabitats. Larval survival and weight gain were both highest under warm weather conditions, but were affected contrastingly by microhabitat and climate, with survival increasing in shaded and northward microhabitats but weight gain increasing in sunny and southward microhabitats. Host plants grew poorly under predominantly cool weather conditions of April, and big larval groups decreased host plant availability towards the end of the month by eating out all the plants within their movement distance. Generally, in habitat patches with highest larval growth rate, the change in the host plant availability was negative during the penultimate larval instar that requires most food, which probably led to starvation and increased mortality (Fig. 11).

Warm weather is generally beneficial for the survival and weight gain of insects at their high latitude or altitude range margin (Chen et al. 2011b, Hodgson et al. 2015), which I also observed in my monitoring study. I did not find the subtle spatial variation in the precipitation of the study season to affect larval survival and weight gain. Ambient temperatures at the high latitude range margin are prone to be far below the optimal larval body temperature for development (Porter 1982, Bryant et al. 2000, WallisDeVries 2006), and I therefore expected warm microclimatic conditions to increase weight gain and survival (Weiss et al. 1988). Consistent with expectations, I recorded accelerated growth rates in sunny and southward microhabitats for as long as the larvae found host plants. However, many larval groups, especially in warm microhabitats, starved after consuming all the food within a few metre radius from the winter nest, which led to the finding that larval survival was enhanced by increasing shadiness of the microhabitat and northward slope. The reduced ability of larvae for basking in shaded conditions synchronised their phenology with that of the host plants leading to slower growth but higher survival.

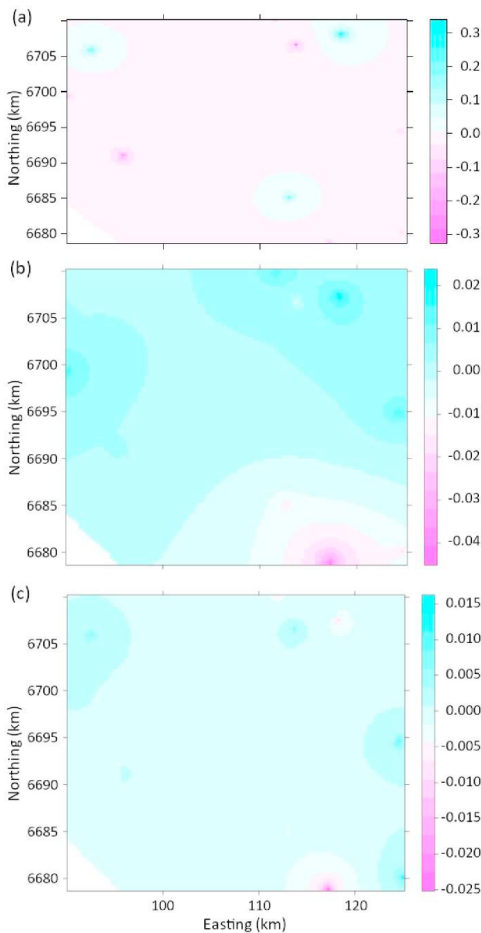


Figure 11. Posterior mean spatial random fields for the full models of (a) larval weight gain, (b) the change of host plant availability in the first half of April and (c) the change of host plant availability in the second half of April. In patches with the highest larval weight gain, host plant availability changed positively during the first half of the study season, but turned mainly negative during the second half. In patches with lower larval growth rate, the change of the host plant availability became mainly more positive towards the end of the study season. The inability of the fastest-growing larvae to find food during the penultimate instar probably lowered their survival.

The impact of microclimatic factors on larval survival is probably highly context-dependent. The females typically lay their eggs in the warmest and driest microhabitats within the breeding habitat patches, which generally enhances the survival of the offspring until spring (Salgado et al. 2020). In an average spring, when the lag between the end of larval diapause and the beginning of the plant growing season is shorter, the

thermophilous larvae can exploit host plant resources most efficiently in the warmest microclimates. Amplified variability of weather conditions coupled with up-scaled spatial synchrony of weather and increased occurrence of extreme weather events is expected to become more common in the future (Easterling et al. 2000, Kovats et al. 2014). These changes in weather conditions are likely to induce phenological asynchrony between larvae and host plants more frequently in the future in this and other herbivore insect systems (Parmesan 2007, Thackeray et al. 2016). On the other hand, climate change may cause microclimatic cooling in the spring by increasing vegetation growth and shading, which may also threaten thermophilous insects including the Glanville fritillary in other parts of its distribution range (WallisDeVries 2006, WallisDeVries & Van Swaay 2006).

In the face of climate change, it is adaptive for plants to lag the phenological phases slightly behind the warming spring temperatures, because there are still late frosts that are more harmful for plants at later phenological phases (Scheifinger et al. 2003). This would be adaptive for herbivores as well to avoid both the phenological asynchrony with the host plants and potential direct adverse effects of frosts. My data, however, suggest that butterfly larvae at the high latitude range edge react strongly to the warming of early spring by ending the diapause as early as possible. Parmesan (2007) reported similar trend of butterflies advancing their emergence more than threefold compared to the advancement in the flowering of herbs and grasses, but direct observational studies showing that warming springs induce phenological asynchronies between specialist herbivores and their host plants have been largely lacking (Renner & Zohner 2018, for an exception, see Visser & Holleman 2001).

4.5 Do the local effects of weather and microclimate on larval development translate into metapopulation-level variations in population growth rates?

In chapter II, I also show that the local population growth rates are increased by higher variation in larval shading conditions in a metapopulation where most larvae are restricted to open habitat without any shading. The local population growth rates were affected contrastingly by the spatial variations in weather of May in two consecutive springs, with warm weather increasing population growth in May 2016, but cool, rainy weather in May 2017. These results indicate that the impacts of spatial variation of weather on local population growth rates are highly context-dependent,

which highlights the importance of long-term data when studying the impacts of weather on biological systems. Previous work has shown the metapopulation growth rate to be largely determined by the annual variation in the precipitation from spring to late summer, as drought desiccates the host plants, which may be fatal for the larvae (I, Tack et al. 2015, Kahilainen et al. 2018, van Bergen et al. 2020).

Local population growth rates were increased by nest sites situated at slopes with on average more south than northward aspect in both years. In the light of the small-scale results, the fast larval weight gain and development enabled by warm southward microclimates enhanced population growth. Interestingly, the population growth rate from 2015 to 2016 was increased also by variable shading conditions at the nest sites, and the population growth rate from 2016 to 2017 by increasing average shadiness of the nest sites. This indicates the importance of at least partly shaded microhabitats to buffer the relatively immobile life stages of the thermophilous butterfly against adverse weather conditions. The desiccation of host plants in dry summers may be less severe in shaded microhabitats, as well as the phenological asynchrony with the host plants in spring demonstrated by my monitoring study.

Previously, Weiss et al. (1988) found that topographic diversity is a key predictor of long-term population persistence for the Bay checkerspot (*Euphydryas editha bayensis*). However, the mechanisms related to the enhanced performance under variable microhabitats are somewhat different between their case study and mine: the Bay checkerspot lives under Mediterranean climatic conditions and diapauses during the hot and dry season. Its pre-diapause larvae are threatened by phenological asynchrony and thus starvation due to early senescence of host plants especially in the warmest microhabitats (Weiss et al. 1988). The post-diapause larvae of the Bay checkerspot are more mobile than those of the Glanville fritillary, and may hence be able to move between different microhabitats to optimise food gain (Weiss et al. 1988). The movement of the Glanville fritillary larvae until the moulting to ultimate instar is limited to < 5 m, making the larval development and survival largely dependent on their mothers' oviposition site choice (Nieminen et al. 2004; S. Rytteri, unpublished data).

Increased plasticity in oviposition site selection is a prerequisite for the adaptation of insects to more variable and rapidly changing weather conditions (Ehrlich et al. 1980, Salgado et al. 2020). As adults, butterflies and

other flying insects are capable of choosing the microhabitat that enhances their performance under the prevailing weather conditions, given that there are diverse microhabitats within the dispersal distance (Suggitt et al. 2012). Immobile juvenile life stages are closely tied to the microhabitat their mother has chosen for oviposition, and thus ovipositing in a wide range of microhabitats is the best way to secure the survival of at least some offspring until adults in unpredictable climatic conditions (Starrfelt & Kokko 2012). From the conservation point of view, increasing the heterogeneity of insect breeding habitats is crucial to buffer populations against adverse climatic conditions (Benton et al. 2003). Diverse habitats at spatial scales from centimetres to several kilometres have been reported to act as an important indicator of long-term population persistence for numerous taxa (Kindvall 1996, Benton et al. 2003, Oliver et al. 2010, Suggitt et al. 2011, Merckx et al. 2019). Microhabitat variability also shapes the responses of populations to climate change and other environmental changes (Suggitt et al. 2012, Scheffers et al. 2014, Bennett et al. 2015, Pincebourde et al. 2016).

4.6 How do the larval body surface temperatures deviate from concurrent ambient temperatures and how does this affect larval feeding activity?

My search for a mechanism behind the larval activity in warmest microhabitats early in the spring, while host plants did not grow yet, led me to the finding that larval body surface temperatures were highly variable depending on whether direct sunlight reached the larvae (II). At the warmest, larval temperature was 26°C warmer than the concurrent ambient temperature. On average, it was 10°C warmer and at the coldest 11°C cooler than the ambient temperature. Larval activity levels (proportion of day spent by resting, basking and feeding) were dependent on larval and ambient temperature, larval group size and the sunshine reaching the larvae. Larval temperature was explained by all variables tested: ambient temperature, sunshine reaching the larvae and larval group size.

Effective behavioural thermoregulation of the larvae led their body temperature to exceed the ambient temperature considerably especially in sunny microhabitats, which consequently increased larval activity. Insects have a variety of behavioural (e.g. movement between microclimates, basking and gregarious behaviour) and morphological (e.g. colouration) adaptations for effective thermoregulation (Bryant et al. 2000, Pincebourde et al. 2016). In the light of gregarious

basking behaviour and the black colour of the larvae in my study species (Kuussaari & Singer 2017), high larval temperatures during cool but sunny days were expected. Similar results were reported by Van Nouhuys and Lei (2004) and WallisDeVries (2006). High body surface temperature and large group size of larvae were important factors in explaining larval activity, which was expected as sufficient body temperature is required for feeding and a big group of larvae warms up more effectively than a small one (Porter 1982, Bryant et al. 2000). Larval temperatures in shaded microhabitats were often cooler than ambient temperature, indicating the importance of sunshine for the effective behavioural thermoregulation. The range of body temperatures under which I observed larvae feeding was narrower than the full range of body temperatures with a median of 28.6 °C. Experience from laboratory experiments has also indicated that optimal larval growth is obtained under temperature of 28 °C (e.g. Saastamoinen et al. 2013a, 2013b). Host plants do not warm up similarly as the larvae due to evaporation (WallisDeVries 2006), which amplifies the difference between the effects of microclimate on the interacting species.

4.7 How do the weather conditions of the flight season alter the emigration and colonisation rates, residence times and dispersal distances within a metapopulation?

Butterfly emigration rate was affected positively and residence time in the natal patch negatively by warm, sunny weather of the flight season and high population density in chapter III (Fig. 12). Movement distance increased with increasing flight season temperature and number of occupied habitat patches in the metapopulation. More than 75 % of the variation in all three dispersal measures was explained by the combination of weather and intrinsic population variables. Colonisation rates in the newly translocated population were enhanced by the high proportion of exceptionally warm days during a flight season in chapter IV.

The importance of flight season weather conditions for butterfly dispersal may seem obvious, but it has not been previously thoroughly documented in a long-term study under natural conditions. A probable reason for this is the general lack of comprehensive time series of butterfly movement data that could be combined with representative weather data. In previous studies, considerable annual variation in butterfly dispersal have been reported, but it has not been attributable to varying weather conditions (Matter et al. 2011, Schtickzelle et al. 2012). In accordance with my results, several

short-term field studies and experiments have suggested that weather importantly alters lepidopteran movement (Cormont et al. 2011, Franzén & Nilsson 2012, Delattre et al. 2013, Legrand et al. 2015).

Variable weather conditions may induce annual variations in dispersal and colonisation of many other insects as well, affecting e.g. range shifts taking place due to climate change (Nève et al. 1996, Mitikka et al. 2008, Cormont et al. 2011, Bennie et al. 2013). Extreme weather events may have a disproportionately high effect on dispersal and colonisation as pointed out by Nève et al. (1996), who reported modest colonisation rates and distances for a translocated population of *Proclissiana eunomia* in the first years after release, when the flight season weather was cool and cloudy. During the first hot and sunny flight season in the release area, the butterfly population showed great increase in colonisation rates and distances. Bennie et al. (2013) showed that fine-scale variation in thermal conditions drives the variations in the range expansion rate of *Hesperia comma*. The species showed increased colonisation rates in periods with exceptionally hot flight seasons, but they were offset by retractions to localities with exceptionally warm microhabitats during periods with cooler flight seasons.

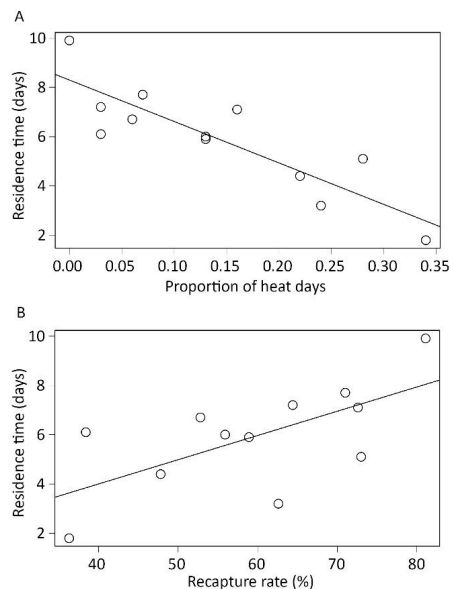


Figure 12. Clouded Apollo residence time in a natal patch was (A) reduced by increasing proportion of heat days (max. temperature ≥ 25 °C) during the flight season and (B) prolonged by increasing recapture rate, which indicates smaller butterfly density, as bigger proportion of butterflies was recaptured in years with small population size.

Dispersal rates of insects near their high-latitude and -altitude range margins may be importantly increased assuming that climate change causes the flight seasons to become warmer, on average (Cormont et al. 2011). This would also enhance range expansions. There is no certainty, however, on the precise effects of climate change on the weather conditions relevant for insect dispersal. If the rising average temperature is primarily caused by increasing nocturnal temperatures (Vose et al. 2005, Sun et al. 2019), or accompanied by increasing cloudiness (Croke et al. 1999, Sanchez-Lorenzo et al. 2012, Komarov et al. 2015, An et al. 2017), the dispersal of diurnal, heliothermic insects may not be enhanced.

4.8 Is it possible to predict the spatial expansion of a translocated population in a novel landscape based on prior knowledge of the species' movement rate? How does the annually varying flight season weather affect the accuracy of the predictions?

I predicted colonisation rates in the release landscape by a simulation approach using parameter estimates of

a mechanistic movement model from the source population in chapter IV. The MR data for parameter estimation was collected during an exceptionally warm flight season with the proportion of days with maximum temperature $\geq 25^\circ\text{C}$ being 0.50, while it varied between 0.00 and 0.34 in the release site from 2001-2016. The predictions were qualitatively correct, but the model overestimated short-distance colonisation rates (Fig. 13). Further search for the reason of the overestimation revealed that the predicted colonisation rates were most correct in predominantly warm and sunny flight seasons. While the average weather conditions (average solar radiation and average temperature) of a flight season did not explain the residuals of the predicted annual colonisation numbers, the measure of exceptionally high maximum temperature (the proportion of days with maximum temperature $\geq 25^\circ\text{C}$) did. This result is in line with the findings in chapter III, showing that the high proportion of exceptionally warm days importantly decreased butterfly residence times in a natal patch.

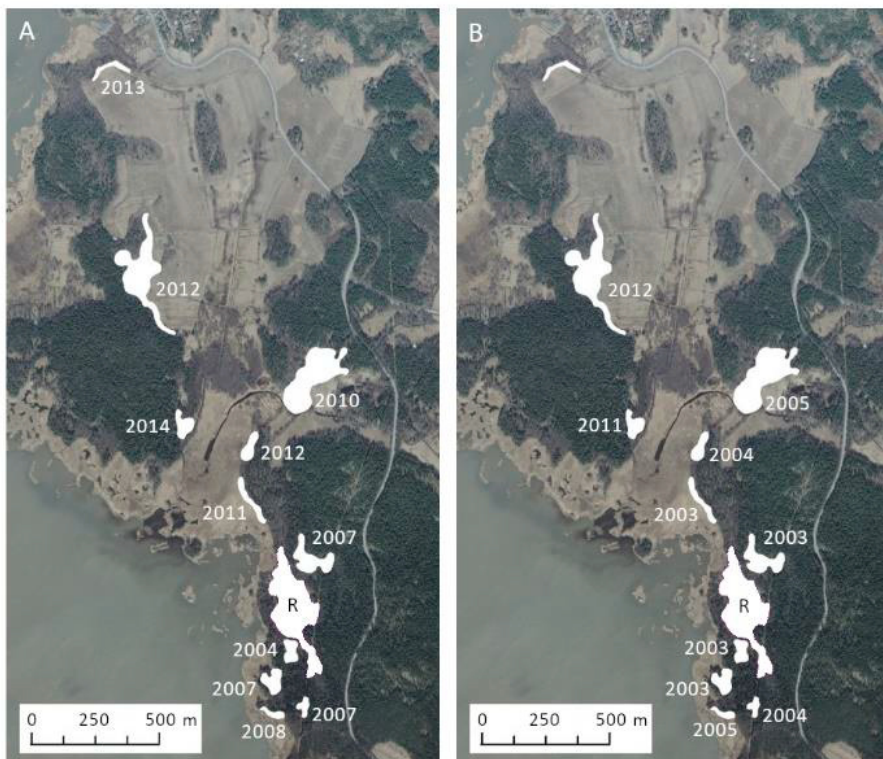


Figure 13. Observed (A) and predicted (B) colonisation years of habitat patches in the Clouded Apollo release area in Porvoo. The patch with R is the release site where 20 mated female butterflies were released in 2000. Movement model parameterised in the source population in a flight season with exceptionally many heat days overestimated colonisation rates in the release area especially in predominantly cold flight seasons.

In addition to weather conditions, several other factors not tested may have induced the overestimation of colonisation rates. Firstly, during the first years after translocation, the population in the release area was small and butterfly density was importantly decreased compared to the source population used for model parameterisation. As shown in chapter III and several other studies on butterflies, emigration is often density-dependent (Roland et al. 2000, Schtickzelle et al. 2012). Secondly, in the habitat type classification needed for the movement analyses, I treated the open fields in the source landscape similarly to the closed forests in the release landscape, because the Clouded Apollo generally avoids crossing either. It is possible, though, that open field areas are more permeable for the focal species because of their structural similarity to meadows (Luoto et al. 2001, Kuussaari et al. 2015). Thirdly, variable habitat quality may have shaped the emigration and immigration decisions of butterflies (Dover & Settele 2009), but was not assessed in the colonisation predictions.

Incorporating variable weather conditions in a predictive model is an inevitable challenge, because the annual variations of weather are unpredictable and expected to become even more so in the future. Nevertheless, recent technical advances, such as the mechanistic modelling approach of Maclean (2020), may importantly improve the ability to predict future climatic conditions at biologically relevant scales. Including average climatic suitability of the release area in translocation planning may importantly improve the probability of success (Bellis et al. 2020), but especially with short-lived insects, the weather conditions over a few years following the release may dictate the success or failure of the translocation (Kuussaari et al. 2015, Bellis et al. 2019, Berger-Tal et al. 2020). The colonisation simulation approach presented in chapter IV does not help to overcome the problems related to forecasting optimal weather for a translocation project, but it helps to decide how to manage the release area to enable the spatial expansion of the translocated population to enhance its long-term persistence. It also helps to choose among several potential release areas the ones with the best functional connectivity to support a large and persisting translocated population. A recent effort of L. C. Evans et al. (2019) to integrate the effects of weather in an individual-based movement model is a step towards predictive ability of the consequences of variable weather on butterfly dispersal. However, their rather simplistic way to handle movement through only two parameters – the duration of flights and of inactive periods between flights – may

not be sufficient to predict dispersal rates in variable landscapes.

5 CONCLUSIONS

In this thesis, I found that several changes in weather conditions generally attributed to climate change threaten butterfly populations through both direct and host plant mediated adverse effects. Furthermore, I found that warming flight seasons may potentially enhance the dispersal and colonisations of butterflies with positive impacts on range expansions on high-latitude and -altitude range edges. Increasing variability of weather conditions compromises the effectiveness of conservation planning especially for short-lived insects. Therefore, the results of my thesis highlight that the priority in conservation management should be given to the creation and preservation of heterogeneous micro- and macrohabitats to buffer populations against unpredictable weather conditions.

Winter and early spring are the seasons warming most prominently in the Northern Hemisphere (Pauli et al. 2013, IPCC 2014). Reductions in the snow cover duration lead to functional cooling of the ground level microhabitats despite of climatic warming (Zhu et al. 2019). For insects overwintering at the ground level, the insulating snow cover offers important shelter from the variable winter temperatures and humidity conditions, as shown experimentally in chapter I. Snowless overwintering conditions, especially coupled with stressful pre-diapause conditions, can drastically reduce the overwintering survival of butterflies. Nevertheless, the growth rates of natural populations may be buffered against the adverse effects of weather on survival. Further understanding of the potentially interacting effects of the weather conditions through the insect life cycle is required for an improved ability to predict the risks that climate change causes to population persistence.

Advancing spring onset timing may cause direct adverse effects on insects, e.g. by reducing their post-diapause developmental rate (Posledovich et al. 2015, Stålhandske et al. 2017). In chapter I, I showed experimentally that both diapause and post-diapause mortality increased and post-diapause development became slower due to the advancing of spring onset. Under natural conditions in chapter II, I found that exceptionally early spring onset was indirectly harmful for post-diapause larvae, as it caused a phenological asynchrony between them and their host plants. The phenologies of the interacting species were more synchronous in

shaded microhabitats, and local population growth rates were enhanced by within-population microhabitat heterogeneity. Time shifts in trophic interactions in response to advancing spring onset are common, but whether interacting species are becoming more or less synchronous varies greatly (Kharouba et al. 2018). The phenological shifts at earlier life stages may not be apparent based on the adult emergence timing. Hence, in future studies, it would be important to consider the phenological shifts throughout the life cycle with direct data on the life stages that may be most vulnerable to trophic mismatch in phenology (Post et al. 2008).

Dispersal and colonisation of new habitats is importantly enhanced by warm and sunny flight season weather at the poleward range margin, as shown in chapters III and IV. Residence times in a natal patch were decreased and colonisation rates were increased by high proportion of especially warm days, indicating that exceptional weather conditions may be important for the spatial expansion of butterfly populations, as suggested also by Bennie et al. (2013). Increasing inter-annual variability of weather conditions due to climate change may cause favourable periods of fast expansion followed by unfavourable periods of retraction back to the sites of highest habitat quality and particularly suitable microclimate (Bennie et al. 2013). Furthermore, increasing variations in weather conditions make conservation translocations for short-lived insects more difficult, as even a well-planned and -executed project may fail because of adverse weather following the release (Kuussaari et al. 2015, Bellis et al. 2019, Berger-Tal et al. 2020). The short-term effectiveness of other conservation measures may also be hindered by adverse weather conditions: for example, habitat management may not result in the increase of population growth rates during generations exposed to detrimental weather at some life stage.

In future, studies that quantify the direct and indirect key effects of weather conditions throughout the insect life cycle are required to gain a better understanding on the multiple interacting impacts during different life stages. Phenological studies with direct observations through the life cycle would also be valuable for identifying the exact life stages that undergo greatest phenological shifts or are most vulnerable to trophic mismatches. This would also allow identifying the climatic cues to which the insects respond by shifting phenology. In general, further research is needed on the multifaceted environmental stress faced by insects in the era of anthropogenic environmental change. The effects of extreme weather on insect dispersal and range expansions require further attention. Spatially

explicit movement models, such as the one presented in this thesis, could be utilised to improve the success potential of conservation management. Such models may enhance the evaluation of the functional connectivity of a landscape and help to plan the measures needed to increase it. Integrating the effects of weather variables into individual-based, spatially explicit movement models could increase their predictive ability.

6 ACKNOWLEDGEMENTS

First of all, I am grateful to my supervisors Marjo and Mikko for all the help, support and patience through the years of this project. Marjo always had the greatest and sometimes craziest ideas for study design and questions, while Mikko balanced the planning of the research with all his experience and realism. Thank you for always finding time to reply my emails and to comment on my texts. Thank you for the freedom to work in my own way and the responsibility to plan and run things on my own, which has taught me a great deal about independent research work. During manuscript preparation, your different insights complemented the work perfectly.

I would like to thank my co-authors. Otso, with his amazing ability to make mathematics understandable, made the process of producing my very first first-author manuscript a relatively painless one. Aapo's contribution for the statistics, helpful discussions, and thoughtful insights importantly improved the *cinxia* studies. The work with Mikko, Janne and Risto at SYKE before actually starting my PhD project was a nice first touch on the research world and encouraged me to begin my doctoral studies. I always enjoyed the discussions with Peter in the middle of the field work and he also had the best butterfly travel tips. I still would not have observed the Apollo nor the Large blue in Finnish nature if I had not followed his tips.

I want to thank Robert Wilson and Nicolas Schtickzelle for agreeing to be the preliminary examiners of my thesis and giving me valuable feedback. I am grateful to Toke Høye for agreeing to be my opponent. Warm thanks to my advisory committee, Jon Brommer, Mar Cabeza and Johan Ekroos, for the great support and good ideas that helped to keep the goals of this project clear in my mind even during the times when I was otherwise confused.

This thesis was made possible by the people helping to collect the data through the years. The Glanville fritillary research started in 1991, so there are too many

people involved to thank by name. Thanks to all of them. Big thanks especially to Sami who helped to design the microclimate data collection and coordinated it at the metapopulation survey level, and to Suvi who is irreplaceable at the Lammi Biological Station knowing exactly what to do with the larvae. Henna was a reliable and great help who ensured that the larvae were doing well while growing and spinning winter nests for my overwintering experiment. Alma and Heini helped importantly in rearing the larvae. Several people also participated in the Clouded Apollo mark-recapture study: thank you Hanna Aho, Aki Aintila, Peter von Bagh, Tea von Bonsdorff, Annika Harlio, Markus Haveri, Soili Huttunen, Elina Karhu, Marika Kuokkanen, Marianne Mayer, Juha Pöyry, Marko Saarela and Elina Uotila. Without Aki, most of the work in this thesis would not have been possible. Thank you for the numerous 16-hour field and lab days, support when I was most hopeless, and the hilarious moments in between the hopeless ones.

Many people helped to make the bureaucracy and practical issues at the university easier: firstly, Juhis was of great help during my years at MRC. It was also fun to share the office with you and good to have someone reminding me of lunch breaks and meetings when I was too deep in my own stuff to notice what happened around me. Sami, Viia, Kaisa, Krista and Pauliina have also been great at organising everything at the MRC and REC office.

It has been a privilege to conduct a PhD in the community composed by the Life-History Evolution research group, all *cinxia* people, and MRC and REC. It has taught me a lot to work with all of you people. Elena as an office mate provided support during the early stages of my PhD. Torsti patiently answered all my stupid questions on statistics. It was nice to collaborate with Anne on the overwintering: your personality brightened up the dark November days in Lammi. It was always a pleasure to have a chat with Luisa, Ana, Michelle, and Anniina.

I would also like to thank my fellow PhD students and other friends with whom I shared highs and lows during the project: Sanja, thank you for making lunches and Cultural Foundation parties much more fun. Mikko T., Mikko A., Kati, Virve, Kristiina, Hanna, and Teemu, thank you for the friendship and being there for me.

The biggest thanks go to all my and Taneli's relatives, who have helped critically in finishing the project by babysitting (mostly the baby, sometimes also dogs or butterfly larvae). Kiitos äiti ja isä. Kiitos isovanhemmat

(erityiskiitos Arjalle ja Arille toukkahotellin pitämisestä). Kiitos Anneli, kun järjestit minulle kirjoitusretiriitin kriittisellä hetkellä. Kiitos Aate avusta toukkakokeessa ja siitä, kun pelastit minut lahtelaiselta parkkipaikalta. Kiitos myös siitä, että pakotit minut osallistumaan perhosharrastukseeni pari vuosikymmentä sitten. Muuten minusta tuskin olisi tullut biologia.

Last but not least: thank you to my family: Taneli, Aarni, and the baby. Thank you for being there for me and persisting through the stressful times. I want to thank Taneli particularly for the help with graphics, and also for the early mornings and long days waking up the larvae in Lammi. The two (soon three) of you mean everything to me.

7 REFERENCES

- Aalto, J., Pirinen, P., & Jylhä, K. (2016). New gridded daily climatology of Finland: permutation-based uncertainty estimates and temporal trends in climate. *Journal of Geophysical Research: Atmospheres*, 121(8), 3807-3823.
- Allen, M. J., & Sheridan, S. C. (2016). Evaluating changes in season length, onset, and end dates across the United States (1948–2012). *International Journal of Climatology*, 36(3), 1268-1277.
- Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, 277(1685), 1281-1287.
- An, N., Wang, K., Zhou, C., & Pinker, R. T. (2017). Observed variability of cloud frequency and cloud-base height within 3600 m above the surface over the contiguous United States. *Journal of Climate*, 30(10), 3725-3742.
- Banks, S. C., Cary, G. J., Smith, A. L., Davies, I. D., Driscoll, D. A., Gill, A. M., Lindenmayer, D. B., & Peakall, R. (2013). How does ecological disturbance influence genetic diversity? *Trends in Ecology & Evolution*, 28(11), 670-679.
- Bauerfeind, S. S., & Fischer, K. (2013). Increased temperature reduces herbivore host-plant quality. *Global Change Biology*, 19(11), 3272-3282.
- Bellis, J., Bourke, D., Williams, C., & Dalrymple, S. (2019). Identifying factors associated with the success and failure of terrestrial insect translocations. *Biological Conservation*, 236, 29-36.
- Bellis, J., Bourke, D., Maschinski, J., Heineman, K., & Dalrymple, S. (2020). Climate suitability as a predictor of conservation translocation failure. *Conservation Biology*. doi: 10.1111/cobi.13518
- Bennett, N. L., Severns, P. M., Parmesan, C., & Singer, M. C. (2015). Geographic mosaics of phenology, host preference, adult size and microhabitat choice predict butterfly resilience to climate warming. *Oikos*, 124(1), 41-53.
- Bennie, J., Hodgson, J. A., Lawson, C. R., Holloway, C. T., Roy, D. B., Brereton, T., Thomas, C. D., & Wilson, R. J. (2013). Range expansion through fragmented landscapes under a variable climate. *Ecology Letters*, 16(7), 921-929.
- Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, 18(4), 182-188.
- Berger-Tal, O., Blumstein, D. T., & Swaisgood, R. R. (2020). Conservation translocations: a review of common difficulties and promising directions. *Animal Conservation*, 23(2), 121-131.
- Bergström, A. (2005). Oviposition site preferences of the threatened butterfly *Parnassius mnemosyne*—implications for conservation. *Journal of Insect Conservation*, 9(1), 21-27.

- Bewick, S., Cantrell, R. S., Cosner, C., & Fagan, W. F. (2016). How resource phenology affects consumer population dynamics. *The American Naturalist*, 187(2), 151-166.
- Berrigan, D., & Charnov, E. L. (1994). Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos*, 474-478.
- Bintanja, R., & Andry, O. (2017). Towards a rain-dominated Arctic. *Nature Climate Change*, 7(4), 263-267.
- Blanckenhorn, W. U. (2000). The evolution of body size: what keeps organisms small? *The Quarterly Review of Biology*, 75(4), 385-407.
- Bosch, J., & Kemp, W. P. (2003). Effect of wintering duration and temperature on survival and emergence time in males of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). *Environmental Entomology*, 32(4), 711-716.
- Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B., & Visser, M. E. (2009). Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*, 78(1), 73-83.
- Bowden, J. J., Hansen, R. R., Olsen, K., & Høye, T. T. (2015a). Habitat-specific effects of climate change on a low-mobility Arctic spider species. *Polar Biology*, 38(4), 559-568.
- Bowden, J. J., Eskildsen, A., Hansen, R. R., Olsen, K., Kurlle, C. M., & Høye, T. T. (2015b). High-Arctic butterflies become smaller with rising temperatures. *Biology Letters*, 11(10), 20150574.
- Bramer, I., Anderson, B. J., Bennie, J., Bladon, A. J., De Frenne, P., Hemming, D., Hill, R. A., Kearney, M. R., Körner, C., Korstjens, A. H., Lenoir, J., Maclean, I. M. D., Marsh, C. D., Morecroft, M. D., Ohlemüller, R., Slater, H. D., Suggitt, A. J., Zellweger, F., & Gillingham, P. K. (2018). Advances in monitoring and modelling climate at ecologically relevant scales. *Advances in Ecological Research*, 58, 101-161.
- Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, 23(8), 453-460.
- Brown, R. D., & Mote, P. W. (2009). The response of Northern Hemisphere snow cover to a changing climate. *Journal of Climate*, 22(8), 2124-2145.
- Brown, R. D., & Robinson, D. A. (2011). Northern Hemisphere spring snow cover variability and change over 1922-2010 including an assessment of uncertainty. *The Cryosphere*, 5(1), 219-229.
- Bryant, S. R., Thomas, C. D., & Bale, J. S. (2000). Thermal ecology of gregarious and solitary nettle-feeding nymphalid butterfly larvae. *Oecologia*, 122(1), 1-10.
- Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80(1), 1-28.
- Bürkner, P.-C. (2018). Advanced Bayesian Multilevel Modeling with the R Package brms. *The R Journal*, 10(1), 395-411.
- Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., Warsi, O., & Wiens, J. J. (2013). How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, 280(1750), 20121890.
- Caplins, S. A., Gilbert, K. J., Ciotir, C., Roland, J., Matter, S. F., & Keyghobadi, N. (2014). Landscape structure and the genetic effects of a population collapse. *Proceedings of the Royal Society B: Biological Sciences*, 281(1796), 20141798.
- Cayton, H. L., & Haddad, N. M. (2018). Water availability coincides with population declines for an endangered butterfly. *Diversity*, 10(3), 94.
- Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011a). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(6045), 1024-1026.
- Chen, I. C., Hill, J. K., Shiu, H. J., Holloway, J. D., Benedick, S., Chey, V. K., Barlow, H. S., & Thomas, C. D. (2011b). Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Global Ecology and Biogeography*, 20(1), 34-45.
- Chmura, H. E., Kharouba, H. M., Ashander, J., Ehlman, S. M., Rivest, E. B., & Yang, L. H. (2019). The mechanisms of phenology: the patterns and processes of phenological shifts. *Ecological Monographs*, 89(1), e01337.
- Choi, G., Robinson, D. A., & Kang, S. (2010). Changing northern hemisphere snow seasons. *Journal of Climate*, 23(19), 5305-5310.
- Cook, B. I., Wolkovich, E. M., & Parmesan, C. (2012). Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences*, 109(23), 9000-9005.
- Cook, B. I., Mankin, J. S., & Anchukaitis, K. J. (2018). Climate change and drought: From past to future. *Current Climate Change Reports*, 4(2), 164-179.
- Cormont, A., Malinowska, A. H., Kostenko, O., Radchuk, V., Hemerik, L., WallisDeVries, M. F., & Verboom, J. (2011). Effect of local weather on butterfly flight behaviour, movement, and colonization: significance for dispersal under climate change. *Biodiversity and Conservation*, 20(3), 483-503.
- Coumou, D., & Rahmstorf, S. (2012). A decade of weather extremes. *Nature climate change*, 2(7), 491-496.
- Cousins, S. A., Auffret, A. G., Lindgren, J., & Tränkle, L. (2015). Regional-scale land-cover change during the 20th century and its consequences for biodiversity. *Ambio*, 44(1), 17-27.
- Croke, M. S., Cess, R. D., & Hameed, S. (1999). Regional cloud cover change associated with global climate change: Case studies for three regions of the United States. *Journal of Climate*, 12(7), 2128-2134.
- Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature climate change*, 3(1), 52-58.
- Davies, W. J. (2019). Multiple temperature effects on phenology and body size in wild butterflies predict a complex response to climate change. *Ecology*, 100(4), e02612.
- De Palma, A., Dennis, R. L., Brereton, T., Leather, S. R., & Oliver, T. H. (2017). Large reorganizations in butterfly communities during an extreme weather event. *Ecography*, 40(5), 577-585.
- Deacy, W. W., Armstrong, J. B., Leacock, W. B., Robbins, C. T., Gustine, D. D., Ward, E. J., Erlenbach, J. A., & Stanford, J. A. (2017). Phenological synchronization disrupts trophic interactions between Kodiak brown bears and salmon. *Proceedings of the National Academy of Sciences*, 114(39), 10432-10437.
- Delattre, T., Baguette, M., Burel, F., Stevens, V. M., Quénol, H., & Vernon, P. (2013). Interactive effects of landscape and weather on dispersal. *Oikos*, 122(11), 1576-1585.
- Doi, H., Gordo, O., & Katano, I. (2008). Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. *Climate Research*, 36(3), 181-190.
- Doiron, M., Gauthier, G., & Lévesque, E. (2015). Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Global Change Biology*, 21(12), 4364-4376.
- Dolný, A., Šigutová, H., Ožana, S., & Choleva, L. (2018). How difficult is it to reintroduce a dragonfly? Fifteen years monitoring *Leucorhinia dubia* at the receiving site. *Biological Conservation*, 218, 110-117.
- Dover, J., & Settle, J. (2009). The influences of landscape structure on butterfly distribution and movement: a review. *Journal of Insect Conservation*, 13(1), 3-27.
- Durant, J. M., Hjermand, D. Ø., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate research*, 33(3), 271-283.
- Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: observations, modeling, and impacts. *Science*, 289(5487), 2068-2074.
- Ehrlich, P. R., Murphy, D. D., Singer, M. C., Sherwood, C. B., White, R. R., & Brown, I. L. (1980). Extinction, reduction, stability and increase: the responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. *Oecologia*, 46(1), 101-105.
- Eskildsen, A., Carvalheiro, L. G., Kissling, W. D., Biesmeijer, J. C., Schweiger, O., & Høye, T. T. (2015). Ecological specialization matters: long-term trends in butterfly species richness and

- assemblage composition depend on multiple functional traits. *Diversity and Distributions*, 21(7), 792-802.
- Evans, L. C., Sibly, R. M., Thorbek, P., Sims, I., Oliver, T. H., & Walters, R. J. (2019). Integrating the influence of weather into mechanistic models of butterfly movement. *Movement Ecology*, 7(1), 1-10.
- Evans, T. R., Salvatore, D., van de Pol, M., & Musters, C. J. M. (2019). Adult firefly abundance is linked to weather during the larval stage in the previous year. *Ecological Entomology*, 44(2), 265-273.
- Ferguson, L. V., & Sinclair, B. J. (2020). Thermal variability and plasticity drive the outcome of a host-pathogen interaction. *The American Naturalist*, 195(4), 603-615.
- Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., Thomas, C. D., Wheatley, C. J., Bickford, D., Carr, J. A., Hole, D. G., Martin, T. G., Pacifici, M., Pearce-Higgins, J. W., Platts, P. J., Visconti, P., Watson, J. E. M. & Huntley, B. (2019). Climate change vulnerability assessment of species. *Wiley Interdisciplinary Reviews: Climate Change*, 10(1), e551.
- Forister, M. L., Fordyce, J. A., Nice, C. C., Thorne, J. H., Waetjen, D. P., & Shapiro, A. M. (2018). Impacts of a millennium drought on butterfly faunal dynamics. *Climate Change Responses*, 5(1), 1-9.
- Forsberg, J., & Wiklund, C. (1988). Protandry in the green-veined white butterfly, *Pieris napi* L. (Lepidoptera; Pieridae). *Functional Ecology*, 81-88.
- Fountain, T., Husby, A., Nonaka, E., DiLeo, M. F., Korhonen, J. H., Rastas, P., Schulz, T., Saastamoinen, M. & Hanski, I. (2018). Inferring dispersal across a fragmented landscape using reconstructed families in the Glanville fritillary butterfly. *Evolutionary Applications*, 11(3), 287-297.
- Fox, R., Oliver, T. H., Harrower, C., Parsons, M. S., Thomas, C. D., & Roy, D. B. (2014). Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology*, 51(4), 949-957.
- Franzén, M., & Nilsson, S. G. (2012). Climate-dependent dispersal rates in metapopulations of burnet moths. *Journal of Insect Conservation*, 16(6), 941-947.
- Greenwood, O., Mossman, H. L., Suggitt, A. J., Curtis, R. J., & Maclean, I. M. (2016). Using in situ management to conserve biodiversity under climate change. *Journal of Applied Ecology*, 53(3), 885-894.
- Halsch, C. A., Shapiro, A. M., Fordyce, J. A., Nice, C. C., Thorne, J. H., Waetjen, D. P., & Forister, M. L. (2021). Insects and recent climate change. *Proceedings of the National Academy of Sciences*, 118(2), e2002543117.
- Hansen, B. B., Grøtan, V., Herfndal, I., & Lee, A. M. (2020). The Moran effect revisited: spatial population synchrony under global warming. *Ecography*, 43(11), 1591-1602.
- Hanski, I., Pakkala, T., Kuussaari, M., & Lei, G. (1995). Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos*, 72(1), 21-28.
- Hanski, I., Schulz, T., Wong, S. C., Ahola, V., Ruokolainen, A., & Ojanen, S. P. (2017). Ecological and genetic basis of metapopulation persistence of the Glanville fritillary butterfly in fragmented landscapes. *Nature Communications*, 8(1), 1-11.
- Harris, J. E., Rodenhouse, N. L., & Holmes, R. T. (2019). Decline in beetle abundance and diversity in an intact temperate forest linked to climate warming. *Biological Conservation*, 240, 108219.
- Hawkins, B. A., & Holyoak, M. (1998). Transcontinental crashes of insect populations? *The American Naturalist*, 152(3), 480-484.
- Hodgson, J. A., Bennie, J. J., Dale, G., Longley, N., Wilson, R. J., & Thomas, C. D. (2015). Predicting microscale shifts in the distribution of the butterfly *Plebejus argus* at the northern edge of its range. *Ecography*, 38(10), 998-1005.
- Høye, T. T. (2020). Arthropods and climate change—Arctic challenges and opportunities. *Current Opinion in Insect Science*, 41, 40-45.
- IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, Pachauri, R. K., & Meyer, L. A. (Eds.)]. IPCC, Geneva, Switzerland, 151 pp.
- Johansson, J., & Jönzén, N. (2012). Game theory sheds new light on ecological responses to current climate change when phenology is historically mismatched. *Ecology Letters*, 15(8), 881-888.
- Johansson, V., Knape, J., & Franzén, M. (2017). Population dynamics and future persistence of the clouded Apollo butterfly in southern Scandinavia: The importance of low intensity grazing and creation of habitat patches. *Biological Conservation*, 206, 120-131.
- Kahilainen, A., van Nouhuys, S., Schulz, T., & Saastamoinen, M. (2018). Metapopulation dynamics in a changing climate: Increasing spatial synchrony in weather conditions drives metapopulation synchrony of a butterfly inhabiting a fragmented landscape. *Global Change Biology*, 24(9), 4316-4329.
- Kankaanpää, T., Skov, K., Abrego, N., Lund, M., Schmidt, N. M., & Roslin, T. (2018). Spatiotemporal snowmelt patterns within a high Arctic landscape, with implications for flora and fauna. *Arctic, Antarctic, and Alpine Research*, 50(1), e1415624.
- Kaunisto, S., Ferguson, L. V., & Sinclair, B. J. (2016). Can we predict the effects of multiple stressors on insects in a changing climate? *Current Opinion in Insect Science*, 17, 55-61.
- Kerr, N. Z., Wepprich, T., Grevstad, F. S., Dopman, E. B., Chew, F. S., & Crone, E. E. (2020). Developmental trap or demographic bonanza? Opposing consequences of earlier phenology in a changing climate for a multivoltine butterfly. *Global Change Biology*, 26(4), 2014-2027.
- Kharoubia, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J. M., Travers, S. E., & Wolkovich, E. M. (2018). Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences*, 115(20), 5211-5216.
- Kindvall, O. (1996). Habitat heterogeneity and survival in a bush cricket metapopulation. *Ecology*, 77(1), 207-214.
- Kingsolver, J. G., Woods, H. A., Buckley, L. B., Potter, K. A., MacLean, H. J., & Higgins, J. K. (2011). Complex life cycles and the responses of insects to climate change. *Integrative and Comparative Biology*, 51, 719-732.
- Koltz, A. M., Schmidt, N. M., & Høye, T. T. (2018). Differential arthropod responses to warming are altering the structure of Arctic communities. *Royal Society Open Science*, 5(4), 171503.
- Komarov, V. S., Matvienko, G. G., Il'in, S. N., & Lomakina, N. Y. (2015). Regional features of long-term changes in cloud cover in Siberian sector of Northern hemisphere for the last 45 years (1969–2013). *Atmospheric and Oceanic Optics*, 28(2), 175-179.
- Konvička, M., & Kuras, T. (1999). Population structure, behaviour and selection of oviposition sites of an endangered butterfly, *Parnassius mnemosyne*, in Litovelské Pomoraví, Czech Republic. *Journal of Insect Conservation*, 3(3), 211-223.
- Kovats, R. S., Valentini, R., Bouwer, L. M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M., Soussana, J.-F., 2014. Europe. In: Barros, V. R., Field, C. B., Dokken, D. J. (Eds.): *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* Cambridge University Press, Cambridge and New York, pp. 1267–1326.
- Kuussaari, M., & Singer, M. C. (2017). Group size, and egg and larval survival in the social butterfly *Melitaea cinxia*. *Annales Zoologici Fennici* 54(1–4), 213-223.
- Kuussaari, M., Luoto, M., Heikkinen, R. K., Lehtomäki, J., Mayer, M., Salminen, J. & von Bonsdorff, T. (2013). Occurrence of the Clouded Apollo along the inland river valleys in southwestern Finland. *Baptria*, 38, 70–83.
- Kuussaari, M., Heikkinen, R. K., Heliölä, J., Luoto, M., Mayer, M., Rytteri, S., & von Bagh, P. (2015). Successful translocation of the threatened Clouded Apollo butterfly (*Parnassius mnemosyne*)

- and metapopulation establishment in southern Finland. *Biological Conservation*, 190, 51-59.
- Lavy, D., Nedved, O., & Verhoef, H. A. (1997). Effects of starvation on body composition and cold tolerance in the collembolan *Orchesella cincta* and the isopod *Porcellio scaber*. *Journal of Insect Physiology*, 43(10), 973-978.
- Laws, A. N. (2017). Climate change effects on predator-prey interactions. *Current Opinion in Insect Science*, 23, 28-34.
- Legrand, D., Trochet, A., Moulherat, S., Calvez, O., Stevens, V. M., Ducatez, S., Clobert, J., & Baguette, M. (2015). Ranking the ecological causes of dispersal in a butterfly. *Ecography*, 38(8), 822-831.
- Lemoine, N. P., Burkepile, D. E., & Parker, J. D. (2014). Variable effects of temperature on insect herbivory. *PeerJ*, 2, e376.
- Lindgren, F., Rue, H., & Lindström, J. (2011). An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73(4), 423-498.
- Loboda, S., Savage, J., Buddle, C. M., Schmidt, N. M., & Høye, T. T. (2018). Declining diversity and abundance of High Arctic fly assemblages over two decades of rapid climate warming. *Ecography*, 41(2), 265-277.
- Luomaranta, A., Aalto, J., & Jylhä, K. (2019). Snow cover trends in Finland over 1961–2014 based on gridded snow depth observations. *International Journal of Climatology*, 39(7), 3147-3159.
- Luoto, M., Kuussaari, M., Rita, H., Salminen, J., & Bonsdorff, T. V. (2001). Determinants of distribution and abundance in the clouded apollo butterfly: a landscape ecological approach. *Ecography*, 24(5), 601-617.
- Maclean, I. M. D. (2020). Predicting future climate at high spatial and temporal resolution. *Global Change Biology*, 26(2), 1003-1011.
- Marshall, K. E., & Sinclair, B. J. (2015). The relative importance of number, duration and intensity of cold stress events in determining survival and energetics of an overwintering insect. *Functional Ecology*, 29(3), 357-366.
- Marshall, K. E., Gotthard, K., & Williams, C. M. (2020). Evolutionary impacts of winter climate change on insects. *Current Opinion in Insect Science* 41, 54-62.
- Matter, S. F., & Roland, J. (2017). Climate and extreme weather independently affect population growth, but neither is a consistently good predictor. *Ecosphere*, 8(5), e01816.
- Matter, S. F., Doyle, A., Illerbrun, K., Wheeler, J., & Roland, J. (2011). An assessment of direct and indirect effects of climate change for populations of the Rocky Mountain Apollo butterfly (*Parnassius smintheus* Doubleday). *Insect Science*, 18(4), 385-392.
- Mattson, W. J., & Haack, R. A. (1987). The role of drought in outbreaks of plant-eating insects. *Bioscience*, 37(2), 110-118.
- McDermott Long, O., Warren, R., Price, J., Brereton, T. M., Botham, M. S., & Franco, A. M. (2017). Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? *Journal of Animal Ecology*, 86(1), 108-116.
- McLaughlin, J. F., Hellmann, J. J., Boggs, C. L., & Ehrlich, P. R. (2002). Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences*, 99(9), 6070-6074.
- Merckx, T., Dantas de Miranda, M., & Pereira, H. M. (2019). Habitat amount, not patch size and isolation, drives species richness of macro-moth communities in countryside landscapes. *Journal of Biogeography*, 46(5), 956-967.
- Mitikka, V., Heikkinen, R. K., Luoto, M., Araújo, M. B., Saarinen, K., Pöyry, J., & Fronzek, S. (2008). Predicting range expansion of the map butterfly in Northern Europe using bioclimatic models. *Biodiversity and Conservation*, 17(3), 623-641.
- Morris, W. F., Pfister, C. A., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. S., Bruna, E. M., Church, D. R., Coulson, T., Doak, D. F., Forsyth, S., Gaillard, J.-M., Horvitz, C. C., Kalisz, S., Kendall, B. E., Knight, T. M., Lee, C. T. & Menges, E. S. (2008). Longevity can buffer plant and animal populations against changing climatic variability. *Ecology*, 89(1), 19-25.
- Møller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences*, 105(42), 16195-16200.
- Nève, G., Barascud, B., Hughes, R., Aubert, J., Descimon, H., Lebrun, P., & Baguette, M. (1996). Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). *Journal of Applied Ecology*, 14-22.
- Nice, C. C., Forister, M. L., Harrison, J. G., Gompert, Z., Fordyce, J. A., Thorne, J. H., Waetjen, D. P. & Shapiro, A. M. (2019). Extreme heterogeneity of population response to climatic variation and the limits of prediction. *Global Change Biology*, 25(6), 2127-2136.
- Nieminen, M., Siljander, M., & Hanski, I. (2004). Structure and dynamics of *Melitaea cinxia* metapopulations. In: Ehrlich, P. R. & Hanski, I. (Eds.). *On the wings of checkerspot: a model system for population biology*. Oxford University Press. New York. Pp. 63-91.
- Nowicki, P., Witek, M., Skórka, P., Settele, J., & Woyciechowski, M. (2005). Population ecology of the endangered butterflies *Maculinea teleius* and *M. nausithous* and the implications for conservation. *Population Ecology*, 47(3), 193-202.
- Nupponen, K., Nieminen, M., Kaitila, J.-P., Hirvonen, P., Leinonen, R., Koski, H., Kullberg, J., Laasonen, E., Pöyry, J., Sallinen, T. & Välimäki, P. (2019). Butterflies. In: Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A. & Liukko, U.-M. (Eds.). *The 2019 Red List of Finnish Species*. Ministry of the Environment & Finnish Environment Institute. Helsinki. Pp. 263-312.
- Ojanen, S. P., Nieminen, M., Meyke, E., Pöyry, J., & Hanski, I. (2013). Long-term metapopulation study of the Glanville fritillary butterfly (*Melitaea cinxia*): survey methods, data management, and long-term population trends. *Ecology and evolution*, 3(11), 3713-3737.
- Oliver, T., Roy, D. B., Hill, J. K., Brereton, T., & Thomas, C. D. (2010). Heterogeneous landscapes promote population stability. *Ecology Letters*, 13(4), 473-484.
- Oliver, T. H., Marshall, H. H., Morecroft, M. D., Brereton, T., Prudhomme, C., & Huntingford, C. (2015). Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change*, 5(10), 941-945.
- Ovaskainen, O., Rekola, H., Meyke, E., & Arjas, E. (2008a). Bayesian methods for analyzing movements in heterogeneous landscapes from mark-recapture data. *Ecology*, 89(2), 542-554.
- Ovaskainen, O., Luoto, M., Ikonen, I., Rekola, H., Meyke, E., & Kuussaari, M. (2008b). An empirical test of a diffusion model: predicting clouded apollo movements in a novel environment. *The American Naturalist*, 171(5), 610-619.
- Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A., Meyke, E. & del Mar Delgado, M. (2013). Community-level phenological response to climate change. *Proceedings of the National Academy of Sciences*, 110(33), 13434-13439.
- Palmer, G., Platts, P. J., Brereton, T., Chapman, J. W., Dytham, C., Fox, R., Pearce-Higgins, J. W., Roy, D. B., Hill, J. K. & Thomas, C. D. (2017). Climate change, climatic variation and extreme biological responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1723), 20160144.
- Park, B. J., Kim, Y. H., Min, S. K., & Lim, E. P. (2018). Anthropogenic and natural contributions to the lengthening of the summer season in the Northern Hemisphere. *Journal of Climate*, 31(17), 6803-6819.
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637-669.
- Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, 13(9), 1860-1872.

- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37-42.
- Parmesan, C., Root, T. L., & Willig, M. R. (2000). Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, 81(3), 443-450.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A. & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399(6736), 579-583.
- Pauli, J. N., Zuckerberg, B., Whiteman, J. P., & Porter, W. (2013). The subnivium: a deteriorating seasonal refugium. *Frontiers in Ecology and the Environment*, 11(5), 260-267.
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M. & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25(6), 1922-1940.
- Pincebourde, S., & Casas, J. (2019). Narrow safety margin in the phyllosphere during thermal extremes. *Proceedings of the National Academy of Sciences*, 116(12), 5588-5596.
- Pincebourde, S., Murdock, C. C., Vickers, M., & Sears, M. W. (2016). Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integrative and Comparative Biology*, 56(1), 45-61.
- Platts, P. J., Mason, S. C., Palmer, G., Hill, J. K., Oliver, T. H., Powney, G. D., Fox, R. & Thomas, C. D. (2019). Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. *Scientific Reports*, 9(1), 1-10.
- Porter, K. (1982). Basking behaviour in larvae of the butterfly *Euphydryas aurinia*. *Oikos*, 38, 308-312.
- Posledovich, D., Toftegaard, T., Wiklund, C., Ehrlén, J., & Gotthard, K. (2015). Latitudinal variation in diapause duration and post-winter development in two pierid butterflies in relation to phenological specialization. *Oecologia*, 177(1), 181-190.
- Post, E., & Forchhammer, M. C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1501), 2367-2373.
- Post, E., Forchhammer, M. C., Stenseth, N. C., & Callaghan, T. V. (2001). The timing of life-history events in a changing climate. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1462), 15-23.
- Post, E. S., Pedersen, C., Wilmers, C. C., & Forchhammer, M. C. (2008). Phenological sequences reveal aggregate life history response to climatic warming. *Ecology*, 89(2), 363-370.
- R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Radchuk, V., Turlure, C., & Schtickzelle, N. (2013). Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, 82(1), 275-285.
- Reed, T. E., Grøtan, V., Jenouvrier, S., Sæther, B. E., & Visser, M. E. (2013). Population growth in a wild bird is buffered against phenological mismatch. *Science*, 340(6131), 488-491.
- Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, 49, 165-182.
- Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142(6), 1141-1153.
- Roland, J., & Matter, S. F. (2016). Pivotal effect of early-winter temperatures and snowfall on population growth of alpine *Parnassius smintheus* butterflies. *Ecological Monographs*, 86(4), 412-428.
- Roland, J., Keyghobadi, N., & Fownes, S. (2000). *Alpine Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology*, 81(6), 1642-1653.
- Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences*, 117(8), 4211-4217.
- Rosa, E., van Nouhuys, S., & Saastamoinen, M. (2017). The more the merrier: conspecific density improves performance of gregarious larvae and reduces susceptibility to a pupal parasitoid. *Ecology and Evolution*, 7(24), 10710-10720.
- Rue, H., Martino, S., & Chopin, N. (2009). Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 71(2), 319-392.
- Ruosteenoja, K., Markkanen, T., & Räsänen, J. (2020). Thermal seasons in northern Europe in projected future climate. *International Journal of Climatology*, 40, 4444-4462.
- Saastamoinen, M. (2007). Life-history, genotypic, and environmental correlates of clutch size in the Glanville fritillary butterfly. *Ecological Entomology*, 32(2), 235-242.
- Saastamoinen, M., Hirai, N., & van Nouhuys, S. (2013a). Direct and trans-generational responses to food deprivation during development in the Glanville fritillary butterfly. *Oecologia*, 171(1), 93-104.
- Saastamoinen, M., Ikonen, S., Wong, S. C., Lehtonen, R., & Hanski, I. (2013b). Plastic larval development in a butterfly has complex environmental and genetic causes and consequences for population dynamics. *Journal of Animal Ecology*, 82(3), 529-539.
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., Hüppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M. & Sokolov, L. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, 278(1707), 835-842.
- Salgado, A. L., DiLeo, M. F., & Saastamoinen, M. (2020). Narrow oviposition preference of an insect herbivore risks survival under conditions of severe drought. *Functional Ecology*, 34, 1358-1369.
- Sanchez-Lorenzo, A., Calbó, J., & Wild, M. (2012). Increasing cloud cover in the 20th century: review and new findings in Spain. *Climate of the Past*, 8(4), 1199-1212.
- Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., & Evans, T. A. (2014). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, 20(2), 495-503.
- Scheffinger, H., Menzel, A., Koch, E., & Peter, C. (2003). Trends of spring time frost events and phenological dates in Central Europe. *Theoretical and Applied Climatology*, 74(1-2), 41-51.
- Schmidt, N. M., Hardwick, B., Gilg, O., Høye, T. T., Krogh, P. H., Meltofte, H., Michelsen, A., Mosbacher, J. B., Raundrup, K., Reneerkens, J., Stewart, L., Wirta, H. & Roslin, T. (2017). Interaction webs in arctic ecosystems: Determinants of arctic change? *Ambio*, 46(1), 12-25.
- Schmitz, O. J., Rosenblatt, A. E., & Smylie, M. (2016). Temperature dependence of predation stress and the nutritional ecology of a generalist herbivore. *Ecology*, 97(11), 3119-3130.
- Schtickzelle, N., Turlure, C., & Baguette, M., (2012). Temporal variation in dispersal kernels in a metapopulation of the bog fritillary butterfly (*Boloria eunomia*). In: Clobert, J., Baguette, M., Benton, T. G., Bullock, J. M. (Eds.), *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, pp. 231-239.
- Seddon, P. J. (2010). From reintroduction to assisted colonization: moving along the conservation translocation spectrum. *Restoration Ecology*, 18(6), 796-802.
- Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: restoring species in a changing world. *Science*, 345(6195), 406-412.
- Singer, M. C., & Parmesan, C. (2010). Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transac-*

- tions of the Royal Society B: Biological Sciences, 365(1555), 3161-3176.
- Soroye, P., Newbold, T., & Kerr, J. (2020). Climate change contributes to widespread declines among bumble bees across continents. *Science*, 367(6478), 685-688.
- Stan Development Team (2020). RStan: the R interface to Stan. R package version 2.21.2. <http://mc-stan.org/>
- Starrfelt, J., & Kokko, H. (2012). Bet-hedging—a triple trade-off between means, variances and correlations. *Biological Reviews*, 87, 742-755.
- Stewart, J. E., Illán, J. G., Richards, S. A., Gutiérrez, D., & Wilson, R. J. (2020). Linking inter-annual variation in environment, phenology, and abundance for a montane butterfly community. *Ecology*, 101(1), e02906.
- Stoks, R., Verheyen, J., Van Dievel, M., & Tüzün, N. (2017). Daily temperature variation and extreme high temperatures drive performance and biotic interactions in a warming world. *Current Opinion in Insect Science*, 23, 35-42.
- Stålhandske, S., Gotthard, K., & Leimar, O. (2017). Winter chilling speeds spring development of temperate butterflies. *Journal of Animal Ecology*, 86(4), 718-729.
- Suggitt, A. J., Gillingham, P. K., Hill, J. K., Huntley, B., Kunin, W. E., Roy, D. B., & Thomas, C. D. (2011). Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, 120(1), 1-8.
- Suggitt, A. J., Stefanescu, C., Páramo, F., Oliver, T., Anderson, B. J., Hill, J. K., Roy, D. B., Brereton, T. & Thomas, C. D. (2012). Habitat associations of species show consistent but weak responses to climate. *Biology Letters*, 8(4), 590-593.
- Suggitt, A. J., Wilson, R. J., Isaac, N. J., Beale, C. M., Auffret, A. G., August, T., Bennie, J. J., Crick, H. Q. P., Duffield, S., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft, M. D., Walker, K. J. & Maclean, I. M. D. (2018). Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, 8(8), 713-717.
- Sun, X., Ren, G., You, Q., Ren, Y., Xu, W., Xue, X., Zhan, Y., Zhang, S., & Zhang, P. (2019). Global diurnal temperature range (DTR) changes since 1901. *Climate Dynamics*, 52(5-6), 3343-3356.
- Tack, A. J., Mononen, T., & Hanski, I. (2015). Increasing frequency of low summer precipitation synchronizes dynamics and compromises metapopulation stability in the Glanville fritillary butterfly. *Proceedings of the Royal Society B: Biological Sciences*, 282(1806), 20150173.
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., Elliott, J. M., Hall, S. J. G., Harrington, R., Pearce-Higgins, J. W., Høye, T. T., Kruuk, L. E. B., Pemberton, J. M., Sparks, T. H., Thompson, P. M., White, I., Winfield, I. J. & Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), 241-245.
- Thomas, C. D. (2011). Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology & Evolution*, 26(5), 216-221.
- Thomas, J. A., Simcox, D. J., & Clarke, R. T. (2009). Successful conservation of a threatened *Maculinea* butterfly. *Science*, 325(5936), 80-83.
- Tscharntke, T., & Brandl, R. (2004). Plant-insect interactions in fragmented landscapes. *Annual Reviews in Entomology*, 49(1), 405-430.
- Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology letters*, 11(12), 1351-1363.
- Van Asch, M., Salis, L., Holleman, L. J., Van Lith, B., & Visser, M. E. (2013). Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Climate Change*, 3(3), 244-248.
- van Bergen, E., Dallas, T., DiLeo, M. F., Kahilainen, A., Mattila, A. L., Luoto, M., & Saastamoinen, M. (2020). The effect of summer drought on the predictability of local extinctions in a butterfly metapopulation. *Conservation Biology*. doi: 10.1111/cobi.13515
- Van Dievel, M., Stoks, R., & Janssens, L. (2017). Beneficial effects of a heat wave: higher growth and immune components driven by a higher food intake. *Journal of Experimental Biology*, 220(21), 3908-3915.
- Van Dyck, H., Bonte, D., Puls, R., Gotthard, K., & Maes, D. (2015). The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? *Oikos*, 124(1), 54-61.
- Van Nouhuys, S., & Lei, G. (2004). Parasitoid-host metapopulation dynamics: the causes and consequences of phenological asynchrony. *Journal of Animal Ecology*, 526-535.
- Van Swaay, C., Wynhoff, I., Verovnik, R., Wiemers, L. M., Maes, D., Sasic, M., Verstrael, T., Warren, M. & Settele, J. (2010). *Parnassius mnemosyne*. In: The IUCN Red List of Threatened Species 2010: e.T174210A7029050.
- Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D., McCann, K. S., Savage, V., Tunney, T. D. & O'Connor, M. I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences*, 281(1779), 20132612.
- Vázquez, D. P., Gianoli, E., Morris, W. F., & Bozinovic, F. (2017). Ecological and evolutionary impacts of changing climatic variability. *Biological Reviews*, 92(1), 22-42.
- Verheyen, J., & Stoks, R. (2019). Temperature variation makes an ectotherm more sensitive to global warming unless thermal evolution occurs. *Journal of Animal Ecology*, 88(4), 624-636.
- Visser, M. E., & Holleman, L. J. (2001). Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1464), 289-294.
- Vose, R. S., Easterling, D. R., & Gleason, B. (2005). Maximum and minimum temperature trends for the globe: An update through 2004. *Geophysical Research Letters*, 32, L23822.
- WallisDeVries, M. (2006). Larval habitat quality and its significance for the conservation of *Melitaea cinxia* in northwestern Europe. In: Fartmann, T. & Hermann, G. (Eds.). *Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa. Abhandlungen aus dem Westfälischen Museum für Naturkunde. Heft 68 (3/4): 281-294.*
- WallisDeVries, M. F., & Van Swaay, C. A. (2006). Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biology*, 12(9), 1620-1626.
- Walsh, R. P. (2017). Microclimate and biotic interactions affect Karner blue butterfly occupancy and persistence in managed oak savanna habitats. *Journal of Insect Conservation*, 21(2), 219-230.
- Walther, G. R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1549), 2019-2024.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389-395.
- Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D., & Thomas, C. D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414(6859), 65-69.
- Weiss, S. B., Murphy, D. D., & White, R. R. (1988). Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology*, 69(5), 1486-1496.
- Widhalm, T., Fourcade, Y., Frank, T., & Öckinger, E. (2020). Population dynamics of the butterfly *Pyrgus armoricanus* after translocation beyond its northern range margin. *Insect Conservation and Diversity*. doi: 10.1111/icad.12430

- Williams, C. M., Henry, H. A., & Sinclair, B. J. (2015). Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, 90(1), 214-235.
- Wilson, R. J., Gutierrez, D., Gutierrez, J., & Monserrat, V. J. (2007). An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*, 13(9), 1873-1887.
- Wynhoff, I., Grutters, M., & Van Langevelde, F. (2008). Looking for the ants: selection of oviposition sites by two myrmecophilous butterfly species. *Animal Biology*, 58(4), 371-388.
- Zhang, X., Tarpley, D., & Sullivan, J. T. (2007). Diverse responses of vegetation phenology to a warming climate. *Geophysical Research Letters*, 34(19).
- Zhu, L., Ives, A. R., Zhang, C., Guo, Y., & Radeloff, V. C. (2019). Climate change causes functionally colder winters for snow cover-dependent organisms. *Nature Climate Change*, 9(11), 886-893.