Adapting to climate change- the impact of changing daylight regimes on range shifting insect populations

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I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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Abstract

Species are shifting their ranges to higher latitudes and elevations as a response to climate change. This expansion can cause populations to encounter novel species, as well as changing the interaction strength of pre-existing associations. The following four chapters assess the impact of range expansion using evidence synthesis, in addition to lab-based experiments and population dynamic models.

A meta-analysis consisting of 44 studies showed an overall negative effect of populations expand their ranges on species and community performance for both expanding and resident species, mediated by changes in inter-species interactions. This effect was driven by negative effects on species abundance, activity and diversity.

A tri-trophic, multi-generational climate chamber experiment showed that different daylengths bring about a change in competitive hierarchy between aphids, with *Acyrthosiphon pisum* dominant at the shorter, more southern daylength of 14.5:9.5 L:D, while the other aphid *Megoura viciae* was dominant when exposed to the longer, more northern daylength of 22:2 L:D. This change in dominance of *M. viciae* was not driven directly by daylength but indirectly through daylength's effect on *A. pisum.*

A second set of experiments showed that longer daylengths in addition to Artificial Light At Night (ALAN) increase the attack rate of the parasitoid *Aphidius megourae* both over 24 hours as well as throughout its life. I then show using a simple lokta-voltera model, that this increase in attack rate causes a drop in the stability of the system causing localised extinctions and outbreaks.

The final experiment empirically tested the predictions of the above lokta-voltera model. I show that longer days represented by increased parasitism rate result in increased variation in parasitoid abundance, causing more frequent and larger extremes of peaks and crashes, as well as reducing the stability of the system and increasing extinction events. These events were brought about by a higher parasitism rate on the aphid. These chapters display the importance of research into the changing dynamics of insects, and especially crop pests in response to a changing world.

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Author’s Declaration

I declare that the thesis has been composed by myself and that the work has not been submitted for any other degree or professional qualification. I confirm that the work submitted is my own, except where work which has formed part of jointly authored publications has been included. My contribution and those of the other authors to this work have been explicitly indicated below. I confirm that appropriate credit has been given within this thesis where reference has been made to the work of others.

The work presented in **Chapter Three** was previously published in Ecology and Evolution as “Shifting daylength regimes associated with range shifts alter aphid-parasitoid community dynamics” by myself (Rachel C Kehoe), David Cruse, Dirk Sanders, Kevin J Gaston and FJ Frank van Veen. This study was conceived by all of the authors. I carried out the conception, experiment set up and data collection, analysis and write up, with aid from the other authors.

The work presented in Chapter **Four** is published in Journal of Animal Ecology as “Light regime drives community stability” by myself (Rachel C Kehoe), David Cruse, Dirk Sanders, Kevin J Gaston, Matthew Silk, Jon Bridle and FJ Frank van Veen. This study was conceived by myself and Frank van Veen. I carried out the conception, experiment set up and data collection, analysis, and write up, with aid from the other authors.

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Chapter One

General Introduction

Thesis background

This thesis reports research into how climate change-induced range expansion affects species interactions, using crop pests and their natural enemies as a model system. Rising temperatures are causing populations to expand their ranges, both latitudinally and to higher elevations (Chen *et al.* 2011). As populations expand their range and move polewards, the daylength that they experience changes. Additionally, the last 100 years has seen a dramatic increase in artificial light at night (ALAN) with substantial impacts on light regimes. We know that many biological traits such as physiology, behaviour and species interactions in ecological communities are foremost organised by light. As such changes in light regime from both poleward range expansion and ALAN may affect individual species as well as their interactions with other species. We still lack an understanding of how light regime changes through range expansion or increased ALAN impact on species individually and on their interactions with other species. Here I will demonstrate the impact of range expansion, daylength and ALAN on species interactions and community dynamics.

Climate change

Global temperatures are increasing at a rate unprecedented in the last 50 million years (Change 2007) to an increase now of at least 0.6°C since pre-industrial times (Ekwurzel *et al.* 2017). This trend is predicted to continue, with the IPCC reporting a projected increase in the mean global surface air temperature of between 0.3 and 0.7°C within 2016 and 2035 (Houghton *et al.* 2001; Flato *et al.* 2013). Additionally, the oceans have been getting warmer, with sea surface temperatures consistently higher during the last three decades than at any other time since records began in 1880 (Agency 2016).

The impact of climate change on organisms

These changes in climate have already had a large impact on the earth's biota, marine, freshwater and terrestrial (Change 2001), with climate change having caused the local and complete extinction of many species (List 2012), through the direct impact of temperature e.g. (Sinervo *et al.* 2010) and changes in precipitation, e.g. (Epps *et al.* 2004). In aquatic organisms, increased water temperatures may lead to increased metabolic demand for oxygen while reducing the oxygen content of the water (Pörtner & Knust 2007), with declining oxygen concentrations having played a major role in at least four or five mass extinction events (Kump, Pavlov & Arthur 2005). These current high levels of extinction are bringing about debates about whether we are currently experiencing the sixth mass extinction (Barnosky *et al.* 2011).

Range expansion

In order to escape these changing environments, species are shifting their ranges both latitudinally and to higher elevations, becoming 'climate refugees'. Other species are expanding their ranges into new areas, while keeping their original range. Terrestrial species are shifting their ranges to higher latitudes at a median rate of 16.9 kilometres per decade, and to higher altitudes at a rate of 11 metres a decade, with many of these patterns correlating with warming (Chen *et al.*, 2011). Invasive insects alone cost a minimum of US$70.0 billion per year globally, while associated health costs exceed US$6.9 billion per year (Bradshaw *et al.*

2016). When expanding their ranges, populations experience novel abiotic and biotic factors. For organisms expanding towards higher elevations, they may be exposed to a change in oxygen levels (Elder & Seibel 2015), and populations expanding both latitudinally and to higher elevations could see changing landscapes and substrate, precipitation levels and type, mineral levels and type as well as levels of human disturbance. Additionally, they may experience changes in species interactions such as predation (Johnston & Smith 2018), parasitism (Menéndez *et al.* 2008), herbivory (Nooten & Hughes 2014) competitors (Marshak & Heck 2017), or disease (Katz & Ibanez 2016b), and food resources (Buckley, Butlin & Bridle 2012).

Historical Range Expansion

Climate change-induced range shifts are not unprecedented (Fields et al., 1993). The extreme cooling during the Late Ordovician caused a mass extinction event, with extinctions clustered around taxa from lower latitudes, suggesting that a lack of thermally suitable habitat was available for species to colonise (Finnegan *et al.*, 2012). Species extinctions recorded from during the end-Permian climate change induced mass extinction were clustered around taxa from higher latitudes, again, suggesting that they ran out of thermally suitable habitat (Penn *et al.*, 2018). There is also evidence for species undergoing range expansions and contractions during the Quaternary period, in response to changes in temperature (Hewitt, 1996; Taberlet *et al.*, 1998), with species extinctions more common in northern populations in cooler times (Hewitt, 1996).

Non-climatic induced range expansion

Although often linked with climate change, populations are expanding their ranges through additional routes. The urbanisation of landscapes, for example, has resulted in a winter range expansion of more than 700 km by Anna's hummingbird *Calypte anna* in North America (Greig, Wood & Bonter 2017). The successful range expansion of *C. anna* is primarily attributed to people providing supplementary food over winter, allowing the species to colonise cooler areas. In the marine environment, humans are inducing range expansions by creating artificial reefs which provide an increase in prey, encouraging predatory species to colonise the new habitat (Ross *et al.*, 2016). A controversial method of range expansion is assisted colonisation, where a species threatened with extinction is moved and released outside its indigenous range to avoid extinction of populations (List 2012).

Impact of range shifts on experienced daylength

A little-discussed result of this poleward range shift is that populations will experience a change in daylength regime, with longer summer days and conversely winter nights as an organism moves polewards. Light plays an important role in biology, as daylight regimes have been a long-constant cue, they have become a trigger for a wide range of species traits, the timing of migration for example from, insects (Walters & Dewar 1986) through to birds (Helm & Gwinner 2005), and the southern right whale (Dickeson 2018). Day length has also been shown to impact on behavioural traits. Long days have been shown, for example, to disrupt bird singing and nesting (Karplus 1952), while short days cause depression in rodents (Einat, Kronfeld-Schor & Eilam 2006; Otsuka *et al.* 2014) as well as in humans (Friborg *et al.* 2012).

Impact of light on plants

Light is an integral part of a plant's existence. From using light to photosynthesise, through to following the sun's orientation (von Erhardt-Siebold 1937) and some requiring light for germination (Milberg, Andersson & Thompson 2000), plants use light in many ways. The length of day that plants experience is both used as a cue and is a direct impact of a plant's physiology and phenology. The chemical structure of peppermint plants subjected to long or short days has been shown to change (Clark & Menary 1980). The shape of wheat leaves is dependent on daylength (Baker, Gallagher & Monteith 1980), as is the orientation of spinach leaves, which are horizontal in short days and vertical in long days. Spinach also exhibits longer stems and earlier flowering under long days (Zeevaart 1971). Plants use daylength as a cue to enter overwintering, such as potatoes which require short days to stimulate tuber growth (Chapman 1958), as well as a cue to exit their overwintering strategy, such as Norway spruce bringing forward budburst under long days (Partanen, Koski & Hänninen 1998).

Artificial light at night

Artificial Light At Night (ALAN) has become increasingly abundant, brighter and in a greater spectral range in the last 100 years (Elvidge *et al.* 2010; Gaston *et al.* 2014; Kyba *et al.* 2017), to the point that approximately 23% of global land area now experiences light-polluted skies, more than 99% of U.S. and European human populations live under light-polluted skies and the Milky Way being hidden from more than one-third of humanity (Falchi *et al.* 2016). ALAN has been shown to impact on many of the biological traits that photoperiod acts upon such as bringing forward bud burst (Miller 2006; Somers-Yeates *et al.* 2016), elongating bird song (Miller 2006), and increasing movement (Stone, Jones & Harris 2009; Patriarca & Debernardi 2010). It has also been shown to alter species interactions both in isolation (Luarte *et al.* 2016; Miller *et al.* 2017) and community dynamics (Davies *et al.* 2013; Sanders *et al.* 2015).

Species networks

Species are not isolated but exist in a complex network of, both directly and indirectly, interacting species (Thébault & Fontaine 2010). These interactions are among the most important forces structuring ecological communities, with most living organisms requiring interactions to survive. The majority of plants, for example, would become extinct without animal pollinators (Kearns, Inouye & Waser 1998). The structure of the ecological network also can buffer against extinction pressures, leading to greater stability (Sanders *et al.* 2018b).

Insects

Insects serve a variety of uses to humans, from pollination through pest control to forensic law (Tomberlin & Benbow 2015). Insects comprise the vast majority of eukaryotic species diversity with studies estimating between 2.5 million and 5.5 million species (Mora *et al.* 2011). They provide financial ecosystem services, estimated to be more than $57 billion annually in the USA (Losey & Vaughan 2006) and pollination by insects contributing to 5000 million euros within Europe (Corbet, Williams & Osborne 1991). However, they also cause agricultural destruction, with invasive insects alone costing a minimum of US$70.0 billion per year globally, and health costs associated with invasive insects exceeding US$6.9 billion per year. Globally, insect pests have been reported to reduce agricultural yields by 10–

16% before harvest and to consume a similar amount following harvest (Bebber, Ramotowski & Gurr 2013). Insects are also among the most pervasive of invasive species. For example, 87% of the 2,500 non-native terrestrial invertebrates in Europe are insects (Hulme 2009).

Aphids and parasitoids as groups of insects

One important group of insects are the aphids. This family consists of around 4000 species of soft-bodied, plant-sucking insects. Aphids experienced their major diversification in the Cretaceous period, having evolved 280 million years ago. Although predominant in temperate regions aphids have a world-wide distribution (Dixon 2012) and are an important crop pest, causing the loss of an estimated of tens of millions to billions US$ per year, (Blackman & Eastop 2000), and a loss of £120 million a year in damage to U.K. cereals alone (Tatchell 1989). Aphids consume a large amount of sap relative to their body size, with adult sycamore aphids processing their body weight in sap every day and immatures processing several times their weight (Dixon & Logan 1973).

Aphids have both a viviparous, parthenogenetic mode of life in addition to a more locomotory form, where they can reproduce and overwinter. Although the lifetime fecundity of an individual aphid female is relatively small (100 offspring being at the upper end of the range), their short generation times and their ability to ‘telescope’ their generations allows a theoretical progeny of 524 billion over a year from a single aphid (Kennedy & Stroyan 1959). The largest family of aphids is the Aphididae, many of which are important crop pests (Vickerman & Wratten 1979; Blackman & Eastop 2000). Aphids are a prey resource for many insect predators, such as ladybirds and hoverflies, as well as being hosts for many parasitoid wasps. These primary aphid parasitoid wasps are found in two families of Hymenoptera: the Aphidiinae (Braconidae) and the Aphelinidae, consisting of over 600 described species. All of these aphid parasitoids are solitary endoparasitoids (Mackauer & Stary ´, 1967) laying their eggs in a living aphid, the larva develops over the space of approximately two weeks, after which the aphid has turned into an aphid ‘mummy’ from which the parasitoid hatches. The aphid- parasitoid network is extensive (Van Veen *et al.* 2008; Elias, Fontaine & van Veen 2013), and its structure in the field depends on the presence or absence of other interacting species (Sanders et al 2010), as well as aspects of climate change such as temperature and nitrogen levels (de Sassi and Tylianakis 2012). Aphids and parasitoids are a useful model system due to their short generation times, and will be used as such in this thesis in order to study the general principles of range expansion.

Light effect on insects

Daylength has a substantial impact on many insects, from growth and development eg. (Leimar 1996), through predation rates of aphids (Perdikis, Lykouressis & Economou 1999) to parasitoid lifetime fecundity (Sagarra *et al.* 2000), with the duration of the scotophase or dark component of the daily photocycle more important than the duration of the photophase or light phase (Dickson 1949; Barker & Cohen 1965). Insects, indeed most organisms, have adapted to use light to influence circadian rhythms. These rhythms can be split into diurnal (active in light phases), nocturnal (active in dark phases) and crepuscular (active predominantly at twilight). These adaptations can be due to availability of resources, e.g. prey or mating opportunities, predator avoidance, the requirement of light for vision, or avoiding extremes of temperature. In the laboratory, it is possible to change the rhythm of daylight, yet many species remain entrained to activity levels at certain times of the day. For example, the common house cricket becomes active shortly after the onset of darkness, even when exposed to a reversed photoperiod, whereby the beginning of the dark cycle was at noon (Lutz 1932). This is also seen in the mating behaviour of Mexican fruit flies, which predominantly mate in the late afternoon/ early evening. When the photoperiod was reversed, with twilight around noon, they still mated in the new late afternoon/ early evening (Flitters 1964). (Haddow & Gillett 1957) describe a very specific photoperiod timing, with *Aedes aegypti* only ovipositing between the hours of 2 and 3 pm. As with many visual predators, the parasitoid *Aphidius megourae* will only parasitise its host the aphid *Megoura viciae* during light hours (Sanders *et al.* 2018b), and responds attacks with changing frequency dependent on the spectra of light (Sanders *et al* unpublished data).

Light as a seasonal cue

Another way in which daylength impacts insects is through seasonal cues. Photoperiodic regulation of insect overwintering, for example, is widespread, especially among insects in the temperate zone (Saunders 2002) as by appropriate entry into and exit of overwintering, insects can synchronise the time of growth and breeding with the favourable season of the year. Most diapausing insects such as aphids and parasitoids are univoltine, only entering diapause once (Masaki 1961). However, there are some species such as the grasshopper *Pardalophora apiculata* or the saturniid moth *Pseudohazis eglanterina* that respond to exceptionally short growing seasons by entering diapause twice in their lifetime, over two winters

(Pickford 1953; Evans 1958). The photoperiodic control of diapause often interacts with temperature, with diapause able to be aborted in the case of high temperatures (Beck 1962).

Knowledge Gaps and thesis aims

The impact of climate change on pest species, and aphids and their natural enemies, in particular, is not well understood. One element, in particular, that warrants further investigation is the effects of range expansion, and thus changes in daylength, in addition to the rapid increase in ALAN, on these crop pests. The aphid-parasitoid study system is representative of a wide range of insect host-parasitoid systems, many of which are expanding their ranges (Bebber *et al.* 2015). This system allows me to study the general principles of range expansion. As such, this thesis will investigate the impact of range expansion, and in particular, light regime on species interactions, using experimental analyses, population dynamic models and evidence synthesis.

Thesis Structure

The remaining chapters presented in this thesis are written as discrete units of study, one of which has been published in a peer-reviewed journal, and one is in revision. The data chapters are presented in the format of manuscripts, as they were submitted for publication. As a result, there is some repetition between chapters, particularly in the methods sections and literature cited.

Chapter Two of the thesis comprises of a meta-analysis extracting the impact of climate change-induced range expansion on performance traits mediated through species interactions from 45 studies. We expect that species in their expanded range by interacting with resident species, will cause 1) an overall negative effect on life-history traits and community structure in all studies included. We expect this both overall and within some of the relevant categories detailed above. We further predict 2) an overall negative effect on resident species, which will be more impacted by novel competitors and enemies while expecting no overall effect on expanding species, which, despite new challenges, may also be able to exploit new resources, or be released from enemy control.

In **Chapter Three** I investigate the impact of different daylengths on the community dynamics of a multitrophic insect community using a multi-generational climate chamber experiment, allowing for competition between aphids to assess both the direct and indirect impacts of daylength. I hypothesise that longer daylengths would increase the attack rate by the diurnal parasitoid and that this would (a) negatively affect the host aphid population and, through reduced interspecific competition, (b) positively affect the other aphid species.

Chapter Four explores the impact of photoperiod, ALAN and a drop in night temperature, all separately and interacting, on the attack rate of a parasitoid wasp. I then model the changes in attack rate on the population dynamics and stability of the parasitoid and its aphid host. I hypothesise that 1) Longer daylengths lead to higher parasitism rates of parasitoids on aphids; 2) Artificial light at night exposure is associated with higher parasitism rates; 3) A drop in night temperature reduces the effect of ALAN on parasitism rates. 4.) Daylength and ALAN exposure interact in driving parasitism rate, with a more substantial ALAN impact under short days. Additionally, I test the effects of daylength on the lifetime fecundity of a parasitoid.

Chapter Five experimentally investigates the effect of photoperiod on the community dynamics and stability seen from the model in **Chapter Four** using a multi-generational climate chamber experiment. I hypothesise 1) greater variability in population size under long day treatments 2) that longer daylength destabilises an aphid-parasitoid system.

Chapter Two

Novel species interactions through range expansion impact species life-history traits

- a meta-analysis

Photo Credit Ben Andrew

2.1 Abstract

Climate change allows many species to expand their natural ranges leading to encounters with resident species in the new ranges. While this process has been reported for many species, we still lack general knowledge on how range expansion changes the way species interact and how this impacts species life-history traits. Here we use a systematic review of published studies and a meta-analysis of 44 studies to explore how novel encounters between species through range expansion impacts on the expanders' and resident's performance. We found an overall negative effect on species life-history traits, with this effect consistent for both the expander and resident species both together and separately. This negative effect indicates that although range expansion is seen as beneficial for the expanding species, it imposes costs to both the expanders and residents. When divided into life-history trait and community structure categories, combining both resident and expanding species we find a significant reduction in abundance, species diversity and activity, with negative trends for survival, feeding, body size, defence and fecundity. Our data set included a variety of different interactions types such as trophic interactions (50%), competition (36%), disease (7%), parasitism (5%), and facilitation (2%). Therefore, range expansion puts pressure on both the resident and expanding species, particularly through a negative impact on abundance with potential consequences for ecosystem stability.

2.2 Introduction

The global climate is warming with a significant increase over the last decades (Pachauri *et al.* 2014), with a further projected increase of at least 1.5°C by the end of the 21st century (Mbow *et al.* 2017). Studies have shown that this increase in temperature has a marked impact on ecological communities and their functions (Tylianakis *et al.* 2008; Yang & Rudolf 2010). For instance, climate warming allows for the survival of species in new ranges and is driving the latitudinal and elevational range expansion of populations (Hoegh-Guldberg *et al.* 2008). Terrestrial species are shifting their ranges to higher latitudes at a median rate of 16.9 kilometres per decade, and to higher altitudes at a rate of 11 metres a decade, with many of these movement patterns correlating with climate warming (Chen *et al.* 2011). By expanding their rages, these species are experiencing novel abiotic and biotic factors. For example, organisms expanding to higher elevations experience a change in oxygen levels (Elder & Seibel 2015). Populations expanding both latitudinally and to higher elevations may experience changes in landscape, substrate, precipitation, and minerals as well as levels of human disturbance, and day: night regime (Kehoe *et al.* 2018, Kehoe *et al.* in revision (Chapter three). Climate change-induced range shifts are not unprecedented (Fields *et al.* 1993; Chen *et al.* 2011), although the current rate of climate change is faster than in both recent history (Change 2001) and at any point during the past 50 million years (Change 2007). Species extinctions recorded from during the end-Permian climate change induces mass extinction, were clustered around taxa from higher latitudes, again, suggesting that they ran out of thermally suitable habitat (Penn et al. 2018). There is also evidence for species undergoing range expansions and contractions during the Quaternary period, in response to changes in temperature (Taberlet et al.

1998; Hewitt et al. 2016), with species extinctions more common in northern populations in colder times, and poleward range expansions response to climate warming (Hewitt *et al.* 2016).

Probably one of the most critical challenges a range-expanding species will face is the encounter with novel biotic factors, including interactions with other species. Interactions between species deserve particular attention because they are critical for many evolutionary and ecological processes (Thompson 1999). Expanding species may experience new interactions with other species including predation (Johnston & Smith 2018), parasitism (Menéndez *et al.* 2008), herbivory (Nooten & Hughes 2014) competitors (Marshak & Heck 2017), disease (Katz & Ibanez 2016), and food resources (Buckley *et al.* 2012). At the same time, however, resident species may be impacted by the arrival of expanding ones. Species interactions are fundamental for our understanding of ecological communities, as organisms are linked through complex interaction networks with other species, the impact of one novel interaction can thus spread through a whole ecological network with important consequences for the ecosystem services these communities provide. A previous meta-analysis limited to marine species showed a change in species interactions in eight expanding and 46 introduced species, noting changes in competition, disease herbivory and predation. While range expanding and introduced species have some similarities they should be considered separately. The spread rate for example of introduced species is twice as fast as range expanding species (Sorte *et al.* 2010), which may be due to release from predators or competition (Liu & Stiling 2006).

Further, because the data for the expanding species is limited in this study we don’t know how range expansion impacts on the life-history traits of expanding species through their range expansion.

Species interactions can impact life-history traits such as body size, fecundity, and predation rate in many ways, both through direct and indirect interactions with the latter including at least a third intermediated species that transmits the impact (Wootton 1994). One common form of direct interaction is a trophic interaction where the presence of a species usually reduces the performance of another species in the food web. Facilitation, an interaction in which the presence of one species alters the environment in a way that enhances growth, survival or reproduction of a second, neighbouring species is another important direct interaction, via mutualistic interactions like those established between plants and microorganisms or the shading effect of larger plants supporting growth in another species e.g. (Weltzin & Coughenour 1990). Many species further directly compete for resources such as food or light (e.g. Brian 1956; Hautier *et al.* 2009). Studies have shown that indirect effects of species interactions are at least equally ubiquitous and important (Frank van Veen *et al.* 2006; Ohgushi *et al.* 2012), such as the presence of a species stabilising a community leading to reduced extinction events (Sanders *et al.* 2015; Sanders *et al.* 2018) or disrupting host-finding (Kehoe *et al.* 2016). Currently we lack knowledge of how range expansion impacts on the way species interact with each other, and through these interactions on species’ life-history traits. This is so far mainly limited to individual empirical studies e.g. (IMBERT *et al.* 2012; Carrasco *et al.* 2017; Wilschut *et al.* 2017), though see (Sorte *et al.* 2010).

To assess how climate change-induced range expansion impacts on expanding and resident species, we conducted a systematic review of published studies followed by a meta-analysis. We first evaluated the impact of range expansion on overall, resident and expander life-history traits and community structure, then we assessed the differences within eight categories, namely abundance, survival, feeding, size, defence, fecundity diversity and activity. These categories represented the extracted measures from the systematic review and contained enough data to be meaningful for analysis. We further assessed the impact of range expansion on species interactions themselves.

We expect that species in their expanded range by interacting with resident species, will cause 1) an overall negative effect on life-history traits and community structure in all studies included. We expect this both overall and within some of the relevant categories detailed above. We further predict 2) an overall negative effect on resident species, which will be more impacted by novel competitors and enemies while expecting no overall effect on expanding species, which, despite new challenges, may also be able to exploit new resources, or be released from enemy control.

2.3 Methods

We first completed a systematic review searching for the following terms: TS=(“Range Expansion” AND “Climate Change” AND (“species interaction” OR pollination OR predation OR consumption OR parasitism OR herbivory OR competition)) in Web of Science (all databases) and Scopus, resulting in 434 results. The remaining results were screened to ensure that they were primary research articles and referred to the search terms. They were then assessed for the following inclusion criteria: (1) the study needs to have a true control treatment that tests for the absence of a species or a group of species that studied in the novel interaction treatment group (expander or resident); this control treatment could either be an experimental exclusion or based on different locations. (2) a replication level of at least two per treatment and (3) data needed to be available to extract the mean and variation for treatment groups (and provide information about true replicates). We extracted effect sizes that described the impact of a new species or group of species arriving in a new area or in an experimental setting leading to novel interactions and the impact of these interactions on the expanding species and the resident one. This screening gave a total of 44 studies that were included in the meta-analysis. From these studies the data for treatment and control were extracted, either directly from the publication, computed from original data or extracted from plots using Plot Digitizer (Huwaldt & Steinhorst 2005). We further excluded 4 data points from the analysis of categories because the data they contained would not fit into any category which with them included had at least two articles making up the data.

The response to novel interactions between expanding and resident species was categorised into the following eight categories: ‘abundance’, ‘survival’, ‘feeding’, ‘body size’, ‘defence’, ‘fecundity, ‘diversity’, and ‘activity’ (see Figure 2.1). **Abundance** describes the number or biomass of one species or functional group. **Survival** contained data about both the survival and mortality of at least one species. As mortality and survival are inversely related, the effect sizes of mortality were inversed to keep the effect sizes relatable. **Feeding** consisted of herbivory and predation (including risk of predation), of one focal species. **Size included** body size in part or whole, and individual biomass, as body size is linked to biomass, e.g. (17, 18). **Defence** contained data consisting of a species’ response to predation, herbivory or parasitism. This category included only two studies, with 12 effect sizes, all investigating the defence of trees to the mountain pine beetle (*Dendroctonus ponderosae*). As such, all effect sizes in the group correspond to impacts on local species. **Fecundity** described the number of offspring in a given time. **Diversity** covers both species richness and the Shannon diversity index. These effect sizes are only of resident communities experiencing a novel expanding species. **Activity.** This category included direct individual activity within a period of time, as well as inversely, amount of time inactive, which was inversed. We also included dispersal ability in this category.

2.4 Statistics

Data analysis. The meta-analysis was conducted in R version 3.6.0 (R Core Team 2013). We used the “escalc(measure= "SMDH")” command in the package metaphor (Viechtbauer 2010) to calculate effect sizes using the Hedges’ d metric. Hedges’ d compares measures of the variables between treatment and controls. To test for the impact of novel species interactions on species performance, we run a mixed effects meta-analysis using the package MCMCglmm (Hadfield 2010). To account for the potential non-independence of effect sizes obtained from the same study, “Study ID” was included in the model as a random effect. The random term idh(SE):units was fixed to one in the prior, which ensures that all measurement errors are independent of each other. The MCMC chain ran for 150.000 iterations, although the first 50.000 were removed as burn-in. The chain was sampled every 50 iterations leading to a total of 2000 samples. Autocorrelation between consecutive samples was always lower than 0.1, and convergence of the chains was inspected visually to ensure that there were no trends in the chain and that posterior distributions were not skewed. Significance is reported as the pMCMC statistic (Hadfield & Nakagawa 2010; Hadfield 2010). As we did not have any a priori knowledge on the distribution of our data, we used a flat prior: the inverse-Gamma prior (V = 1, nu = 0.002). We present the mean effect size and 95% credible intervals around the mean; the mean effect size was considered significantly different from 0 if its 95% CI did not include 0, a measure that is also expressed by the pMCMC metric.

First, we analysed how the novel interactions between residents and expanders affected overall species performance. Then we included the eight categories as a moderator in three separate models to test for (a) the overall impact within each category and for (b) resident and (c) expanding species separately. Categories were only included in the overall category analysis if they contained data on both expanding and resident species.

2.5 Results

The dataset was dominated by measures on abundance (81 effect sizes from 22 studies), survival (39 effect sizes from 8 studies), and feeding (35 effect sizes from 10 studies). The other categories in order of the number of studies were body size (26 effect sizes from 6 studies), defence (12 effect sizes from 2 studies), fecundity (8 effect sizes from 2 studies), diversity (6 effect sizes from 3 studies) and activity (4 effect sizes from 2 studies) (Figure 2.1 A). Only one article contained data on changes in photosynthetic ability, which was excluded from the analysis. Effect size measures span from negative to positive effects (Figure 2.1 A), with data coming from both the laboratory and field studies, focussing on species expanding latitudinally and to higher elevations, and studying freshwater, marine, saltmarsh and terrestrial species.

The results from the meta-analysis support hypothesis 1), with a marked negative effect of interactions between expander and resident species on overall species life-history traits (Figure 2.1 B), posterior mean (lower and upper 95% Credible Interval): -1.15 (-2.04, -0.18), pMCMC = 0.019). The overall impact on effect size measures in all main categories points to a negative impact of range expansion on species' life-history traits. When split into the eight main categories, this effect was particularly marked for abundance: -1.48 (-2.55, -0.22), activity: -5.81 (-8.82 -2.87) and diversity: -3.07, (-5.07, -1.02) (Figure 2.1B). Data in the category abundance come from both laboratory and field studies as well as from a variety of trophic groups, from soil microorganisms to carnivores. The category diversity included studies report of impact on species diversity and richness in both marine and terrestrial systems, with range expanders bringing about reduced diversity in five out of six measures. The category activity consisted of two lab-based studies that measured the impact of a range expanding competitor and predator on a resident's dispersal ability, and activity.

Species survival was not negatively affected by novel species interactions with a non-significant increase in survival in resident species (Figure 2.1B). There was also a non-significant trend towards decreased feeding in systems exposed to an expanded species, with studies focusing on herbivory (six) and predation (four). The data set included measures for expanding (arriving) species in addition to residents that are exposed to expanders. We next considered these two types of interactions as independent datasets, finding an overall negative effect of these novel interactions on both resident (mean= -1.05 (-2.06, 0.019), pMCMC = 0.051) and expanding (mean= -1.29 (-2.48, -0.18), pMCMC = 0.026) species. At the level of individual categories, resident species were affected by decreased abundance and activity when exposed to an expanding species (Figure 2.2 A). The negative trend for abundance was non-significant in expanding species. This large negative impact on activity includes increased activity as an antipredator response, potentially costly for the species.

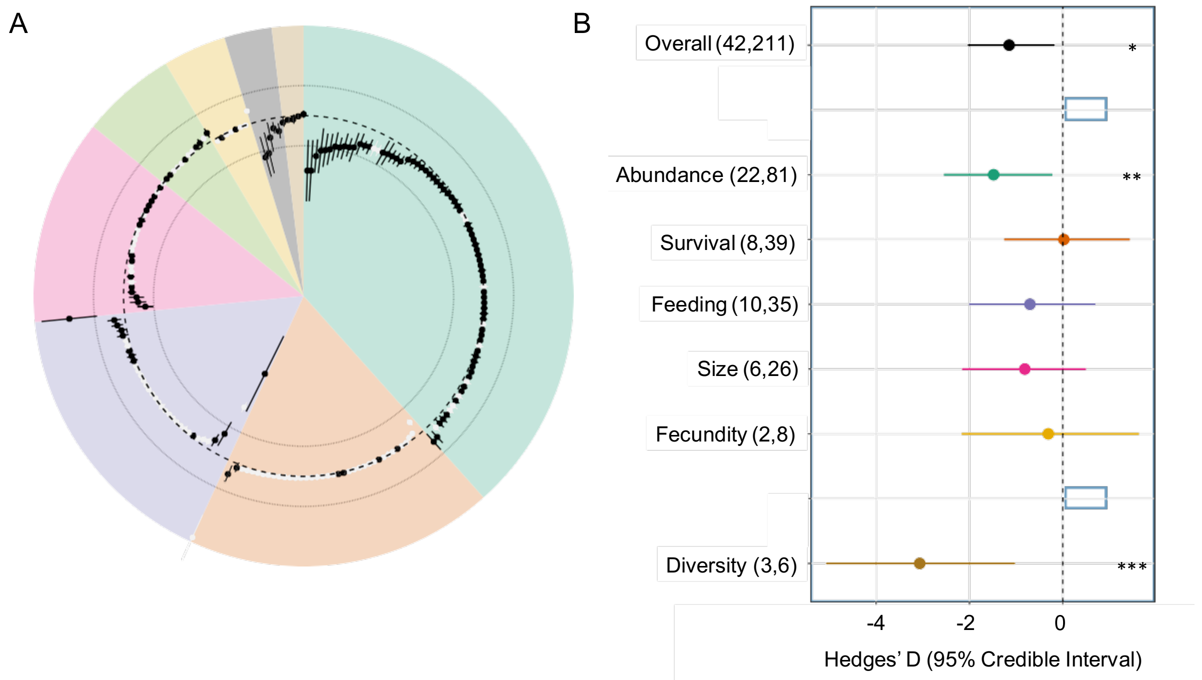

Figure 2.1. (A) Single effect sizes for the eight categories: abundance, survival, feeding, size, defence, fecundity, diversity, and activity. Single effect size measures are presented as Hedges' d with 95 % CI, of expanding (black) and resident (white) species, within each of eight categories. Coloured sections; organismal abundance (teal), survival (orange), feeding (purple), body size (pink), defence (green), fecundity (yellow), diversity (brown), and activity (grey), and arranged in sequence according to increasing effect size (negative to positive). Circle line indicates zero effect size and small dotted lines show an effect size of 10 in either direction. (B) Effect sizes for the measures from the main categories. Effect sizes (Hedges' d) with post mean and 95% credible intervals based on results from a single MCMCglmm with each of the eight main categories (abundance, survival, feeding, size, defence, fecundity, activity, and diversity) as subcategories. Numbers in

brackets indicate the sample size (datapoints and number of studies) and * the significance level for pMCMC, with ***<0.001, **<0.01, *<0.05).

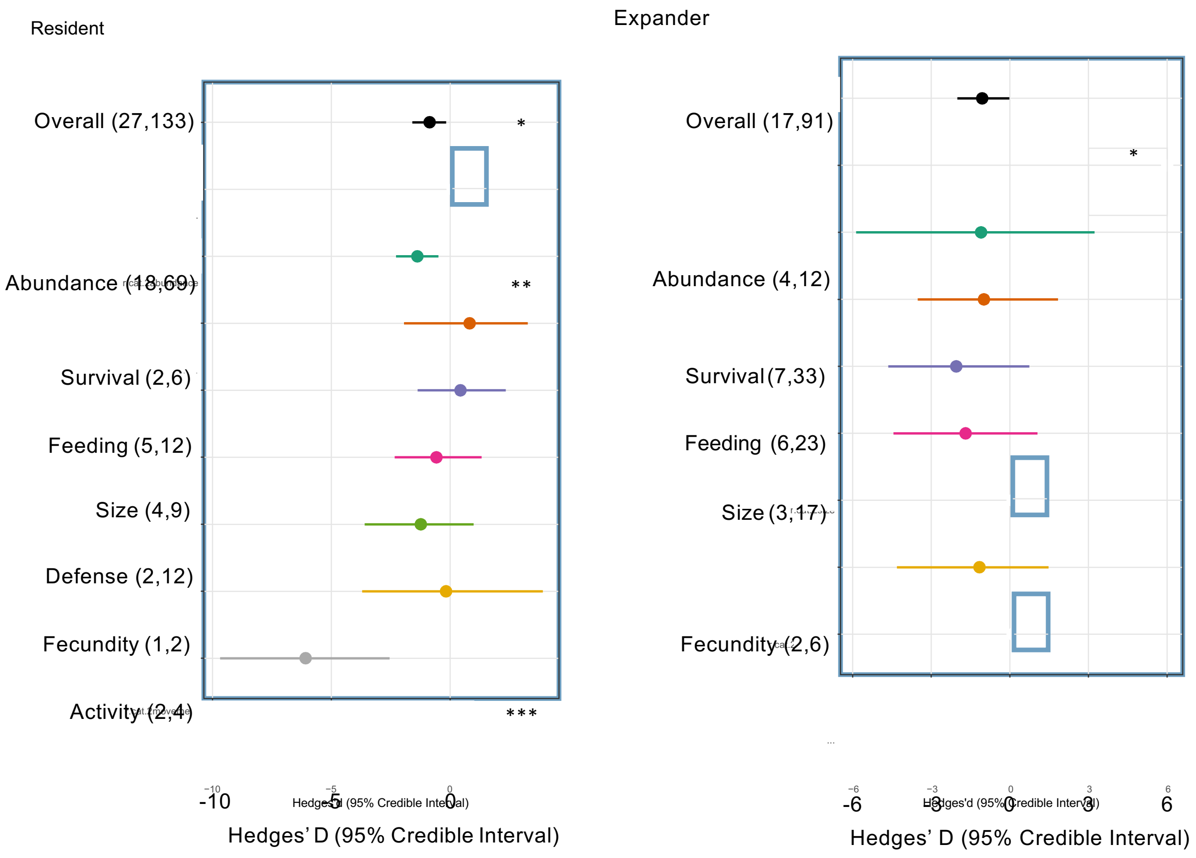

Figure 2.2. Effect sizes for the measures from the main categories in (A) resident species and (B) expanding species. Effect sizes (Hedges' d) with post mean and 95% credible intervals based on results from MCMCglmm's for each variable from the eight main categories (Coloured sections; organismal abundance (teal), survival (orange), feeding (purple), body size (pink), defence (green), fecundity (yellow), activity (grey), and diversity (brown)). Numbers in brackets indicate the sample size and * the significance level for pMCMC, with ***<0.001, **<0.01, *<0.05).

2.6 Discussion

In this meta-analysis we tested for the response of resident and expanding species to novel interactions between the two groups of species. The 44 studies included in this analysis mainly investigated the impact of trophic interactions (50%) and competition (36%). The dataset shows an overall negative impact of expander-resident interactions on species life-history traits, primarily through a marked drop in abundance. Interestingly, both residents and expanders demonstrated negative effects, indicating that expanders suffer costs associated with range expansion in addition to residents. However, when considering single life-history traits, the impact on residents was more profound than on expanders. We also found evidence that range expansion impacts whole communities by reducing diversity.

Regarding resident species, when split into performance categories, there was a significant negative effect of novel species interactions on abundance, and activity. Changes in abundance was the most often used measure of response to range expansion in our dataset. A better database for some of the other traits, would increase the power of the analysis and potentially change the outcome. The overall reduction in abundance due to range expansion altering species interactions come in many forms, from novel predators reducing invertebrate numbers through both direct predation, and avoidance behaviours in prey (Khamis *et al.* 2014), through novel herbivores reducing plant abundance *(Zarco*-Perello *et al. 2017)* or the arrival of a novel plant reducing the abundance of natives through competition (Molina-Montenegro *et al.* 2012). The overall negative effect on abundance was dominated by resident species, which experienced a significant drop in abundance, while expanders had a large degree of variation, including both positive and negative effect sizes (see figure 2.1 B). The majority of data points for the resident responses assessed the impact of novel consumers or competitors on resident species. A novel competitor expanding into a range may limit the amount of resources available to the resident species. Novel consumers may also, in the short term at least, reduce the abundance of a resident species on which it feeds. Alternatively, expanding species have a positive effect on the density of resident ones. For example, the range expansion of a shrub increased arthropod abundance (Rich *et al.* 2013). This may be due to the shrub providing a new habitat for arthropods (ecosystem engineering) or refugia from predators (Finke & Denno 2006). The long-term effect of these mechanisms on abundance may be different from the short term, as these systems may experience transient dynamics until they reach a state of equilibrium within the metapopulation. Our results also demonstrate that a range expanding species can negatively affect resident species indirectly, by changing their activity levels, such as a novel predator causing its prey to spend a more extended period in sheltered areas, thus reducing the amount of time it can forage or look for mates (McMahan & Grabowski 2019). There was no activity data for expanding species. Indirect effects that are mediated via changes in behaviour are known as trait-mediated indirect effects. Such trait-mediated indirect effects have substantial attention in community ecology, and reviews indicate that these interactions are as ubiquitous as direct trophic interactions with important consequences for communities including the functions they perform and their stability (Werner & Peacor 2003; Ohgushi *et al.* 2012). Even if the overall analysis point to a negative impact on both the expander and the resident, abundance and activity data show that the impact on the resident species is more marked through direct effects on abundance and indirect trait-mediate interactions.

We expected a positive effect of range expansion on the expander population's survival as organisms escape from consumers or disease, according to the Enemy Release Hypothesis (Williamson & Griffiths 1996). Our results don't show this overall positive impact on survival, as although we see it in effect in some studies in this meta-analysis, e.g. (Lakeman-Fraser & Ewers 2013), we find a similar number of negative effect sizes (16 negative compared to 15 positive). As such, any occasions of this occurring must be clouded by the adverse effects of novel competitors or consumers that expanders find in their new range, or the expanded population is in the earlier stages of its new range. The great majority of data in this category are concerned with changes in consumption and competition, with disease and parasitism also affecting survival. Surviving expanders contribute to the new range, whilst their expansion causing a decrease in survival of species with which they depend may have negative consequences for their future survival if they overexploit the population (Schöps 2002).

Expanding species can impact whole ecological communities in their new ranges e.g. (Gompper 2002; Le Roux & Mcgeoch 2008). Our data show an overall reduction in species richness following the appearance of expanding species, through increasing predation or competition pressure. This data covers both terrestrial and marine environments, though is limited to only three studies, but with very strong effects. These studies include, for example, both the arrival of tropical rabbitfish in the marine environment, which turned algal forests into 'barrens' dominated by urchins and coralline algae (Verges et al. 2014), and the expansion of shrubs into arctic tundra markedly reducing species diversity (Rich, Gough & Boelman 2013). A study by Collins *et al.* (2016), however, shows the opposite effect, with the range expanding sagebrush increasing soil microbial richness and diversity. A previous meta-analysis on the effect of range expansion on marine species interactions had a minimal dataset (all interaction types excluding herbivory had a sample size of one) but support the results of this study showing that range expanding species alter the interaction strength of competition, herbivory, predation, and disease (Sorte, Williams & Carlton 2010). Therefore, considering the limited data basis evidence so far points to a very negative impact on those communities that have been studied, this topic warrants further research to assess the implications and exasperations of range expansions on the current extinction crisis.

We expected only resident populations to experience an overall negative effect on life-history traits mediated by changing interactions through range expansion. Instead, we found that both resident and expanding species we negatively affected, although in different ways. The number of articles focussing on the impact on expanding species was lower than residents (17 compared to 27), with higher numbers addressing residents' abundance and expanders' survival. The drop in abundance of resident species due to the arrival of a novel species suggests that expanding species are negative for residents. The lack of this negative effect on expanding species suggests no detrimental effect of novel interactions on range expansion, whilst they are not becoming invasive, as they do not have negative ecological or economic effects. With more studies investigating a larger number of traits, it would be possible to have a deeper understanding of the impact on residents and expanders, both separately and together.

The taxa in this analysis are primarily focused on plants, insects and marine fish. Although there were a number of articles investigating the impact of range expansion on birds, there were none that discussed its impact on or through their interactions with other species or had clear controls. Our dataset, therefore, although able to provide clear insights into the impacts of novel interactions on life-history traits, would benefit from a larger number of articles discussing mammals and birds and freshwater fish amongst others. We did not include data investigating the impact of introduced species. As these species may respond in different ways to range expanding species (Sorte *et al.* 2010), we considered this a separate topic, but one that warrants undertaking, and comparison with our results.

Predicting the change in the dynamics of species due to climate change now becomes of utmost importance for effective management and conservation of biodiversity (Hannah, Midgley & Millar 2002). Here we show that species escaping thermal pressures both experience and cause novel pressures, through interactions with other species. To get a predictive understanding of these impacts we need to have experimental studies that can tease apart the mechanisms that underly the patters we see in nature, for examples see (Guo *et al.* 2013). While species may accommodate or adapt to the presence of a single novel species, the expansion of many species into the same system may cause large pressures on natives (Lau 2006). Therefore we need a combination of community ecology (ecological networks) and macroecology (large scale patterns) to fully understand the impact of range expansion of ecological communities and their functions.

Chapter Three

Shifting daylength regimes associated with range shifts alter aphid- parasitoid community dynamics

3.1 Abstract

1. With climate change leading to poleward range expansion of species, populations are exposed to new daylength regimes along latitudinal gradients. Daylength is a major factor affecting insect life cycles and activity patterns, so a range shift leading to new daylength regimes is likely to affect population 915 dynamics and species interactions, however the impact of daylength in isolation on ecological communities has not been studied so far.

2. Here we tested for the direct and indirect effects of two different daylengths on the dynamics of experimental multi-trophic insect communities. We compared the community dynamics under ‘southern’ summer conditions of 14.5 hours day light to ‘northern’ summer conditions of 22 hours daylight.

3. We show that food web dynamics indeed respond to daylength with one aphid species (*Acyrthosiphon pisum*) reaching much lower population sizes at the northern day-length regime compared to under southern conditions. In contrast, in the same communities, a competing aphid species (*Megoura viciae*) reached higher population densities under northern conditions.

4. This effect at the aphid level was driven by an indirect effect of daylength causing a change in competitive interaction strengths, with each aphid species being more competitive at different daylength regimes. Additionally, increasing daylength also increased growth rates in *M. viciae* making it more competitive under summer long days. As such, the shift in daylength affected

aphid population sizes by both direct and indirect effects, propagating through species interactions. However, contrary to expectations, parasitoids were not affected by daylength.

5. Our results demonstrate that range expansion of whole communities due to climate change can indeed change interaction strengths between species within ecological communities with consequences for community dynamics. This study provides the first evidence of daylength affecting community dynamics, which could not be predicted from studying single species separately.

3.2 Introduction

Climate change has led to an increase in global temperatures (Hansen *et al.* 2016), which is predicted to continue, with a projected increase in the mean global surface air temperature of 3.0°C by the end of the 21st Century (2071 to 2100), relative to the period between 1961 and 1990 (Houghton *et al.* 2001; Flato *et al.* 2013). The increase in global temperatures is causing a change in species ranges; a meta analysis with data consisting of 1367 species from a wide variety of taxa showed poleward range shifts and expansions of between 12.2 and 91.1 km per decade (Chen *et al.* 2011).

While a poleward range shift allows populations to track climatic conditions, it also causes organisms to be exposed to other environmental conditions that do not match those within the original range. A key example of this is the day-length regime, with a poleward shift extending both summer days and winter nights and increasing the rate of daylength change in spring and autumn. Photoperiod drives many aspects of life-history and activity patterns of temperate organisms (Vaartaja 1959; Withrow 1959; Beck 2012) and thereby has the potential to affect population dynamics and species interactions.

Insects use photoperiod to a great degree as a cue to induce seasonal changes, for example in the induction of diapause (Adkisson, Bell & Wellso 1963; Ruberson, Bush & Kring 1991), as well as its termination (Tauber & Tauber 1976), with these reactions dependent on geographic location (Lankinen 1986), and in interaction with temperature (Saunders 1973; Liefting, Cosijn & Ellers 2017). Some species have been shown to use photoperiod to influence egg morphology (Wardhaugh 1977) whilst others use it to determine number of moults (Ingram & Jenner 1976). Daylength has also been shown to have an impact on insect growth rate (Kamm 1972), as well as development rate (Fisher, Higley & Foster 2015), fecundity (Nissinen *et al.* 2017) and the regulation of insect seasonal development in nature (Danilevskii 1965; Abrams *et al.* 1996). However, there is currently a lack of studies investigating how photoperiod affects communities.

All these factors are likely to affect the interactions between species that drive ecological and evolutionary processes in ecosystems (Thompson 1999) and are important for ecosystem stability (de Ruiter, Neutel & Moore 1995; Thébault & Fontaine 2010). As species are interconnected within networks of interactions (van Veen, Memmott & Godfray 2006; Bukovinszky *et al.* 2008), a perturbation affecting one single species can therefore lead to community wide impacts, see Rosenblatt & Schmitz (2016) for a conceptual framework of the direct and indirect effects of climate change on a food web. For example, the harvesting of a single parasitoid species led to a community-wide extinction cascade in a recent experiment, an effect that was transmitted indirectly via competition at the herbivore level (Sanders, Kehoe & van Veen 2015). Similarly, removing predators from an intertidal system led to extinctions of algae species through indirect interactions (Donohue *et al.* 2017). This demonstrates the importance of indirect as well as direct interactions for community stability. Intriguingly, it has also been shown that photoperiod disruption from artificial light at night can alter multi-trophic insect community dynamics (Sanders *et al.* 2015).

Aphids are sap feeding herbivorous insects. Many are major pest species, especially when acting as vectors for plant viruses, causing critical damage to agricultural crops (Dedryver, Le Ralec & Fabre 2010). Their population and community dynamics have been studied extensively, including in the context of indirect species interactions (Müller & Godfray 1999; Hassell 2000; Snyder & Ives 2001; Kaiser-Bunbury & Müller 2009; Sanders, Sutter & Veen 2013; Sanders, Kehoe & van Veen 2015) as well as climate change (Forrest 2016). Aphids and aphid parasitoids are therefore an ideal model system to study population dynamics and species interactions in a community context as the system is very tractable and the generation times are short (Sanders, Kehoe & van Veen 2015), allowing for the observation of parasitoid-host interactions across a multi-generational time frame.

Here, we study for the first time, the effects of daylength on the dynamics of multi-trophic communities, whilst keeping other factors such as temperature and the rate of change in daylength constant to test for the impact of short and long daylength in isolation. We focus in particular on the effects during summer conditions, when populations of aphids reach their greatest pest potential. In our experiments, we used a simple host-parasitoid community consisting of two aphid species that compete for a single host plant species and a parasitoid that attacks one of the aphid species. We hypothesised that longer daylength, associated with a poleward range shift, would increase the attack rate by the diurnal parasitoid and that this would 1) negatively affect the host aphid population and, through reduced interspecific competition, 2) positively affect the other aphid species. We show that while the host-parasitoid interaction was not affected by daylength, we discovered that the competitive strength of the two aphid species changed with daylength resulting in higher *M. viciae* abundance under long days.

3.3 Methods

3.3.1 *Study System*

The study system consisted of broad bean plants (*Vicia faba*, L., var. the Sutton), which supported two aphid species, *Megoura viciae* (Buckton) and *Acyrthosiphon pisum* (Haliday), and the parasitoid *Aphidius megourae* attacking the aphid *M. viciae* (Figure 3.1).

3.3.2 *Food web experiment*

We used eight climate chambers (Percival Model 1-30vl) programmed to constant 22°C and 75% humidity. The temperature was kept constant so as to enable the separation of daylength from any confounding impact of temperature, which has been shown to be linked to photoperiod, see (Fischer *et al.* 2012). To test for the effect of daylength on aphid-parasitoid communities, four chambers produced a day-night cycle of 14.5- 9.5 hours (Southern) (depicting Marseille, France, 43°N, average daylength for the 9 weeks either side of the summer solstice), while the other four units produced a 22-2 hour day-night cycle (Northern) (replicating Mosjoen, Norway, 65°N for the same time period). These locations were used to provide two distinct conditions for summer days, and daylength was kept constant in order to test for daylength per se and not the rate of daylength change. The intensity of the light within the incubators during 'daylight' hours was recorded at 4,239 lux, equivalent to a typical overcast day (Gaston *et al.* 2013). We established two different communities with the aphid *A. pisum* either included 'Competitor Present' or excluded ‘Competitor Absent’. This extended community allows for resource competition (Holt 1977) between the two aphids and the potential for indirect interactions among the insects. Within each chamber were four cages, two consisting of the ‘Competitor Absent’ community, with the other two consisting of the ‘Competitor Present’ community, thus giving four treatments, each replicated eight times (see Figure 3.1). These cages were 35cm x 24cm x 20cm, and were constructed of untreated timber and thrip net with a mesh size of 0.29mm x 0.8mm, each with four 15cm diameter pots containing a single broad bean plant in Melcourt All-purpose Peat Free Compost.

All insects used in this experiment were taken from laboratory stock cultures, reared on broad bean plants at a temperature of 18 degrees Celsius and at a 16:8 day: night regime, for a number of years, and were kept at low insect densities. We tested for a difference in the growth rate of aphids under different daylength regimes from these stock cultures to those reared for three generations at the short daylength regime and found no difference for growth under short and long days (supplementary 1). There was no impact of the origin of either species of aphids on their growth rate, (*M. viciae* GLM Offspring number~ Origin, mean = 13.371, t=0.499, P= 0.621, *A. pisum* GLM Offspring number~ Origin, mean = 18.361, t=-1.234, P= 0.226.

To establish the replicate insect communities, in week one, five parthenogenically reproducing adults of each aphid species (dependent on the treatment) were placed onto four 2-week old broad bean plants and set into the climate chambers. The different starting densities of the different communities do not provide founder effects in the experiment as the number of individuals is low enough to not give rise to competition at this stage impact each other. At week 4, once aphid numbers had grown large enough to support an additional trophic level, two female, mated parasitoids of *A. megourae* were introduced to each cage with a further two added at week 5. This double introduction allowed for continuous production of parasitoids throughout the experiment. The numbers of both aphids and parasitoid mummies, the latter depicting a successful attack on aphids, were recorded. This count was repeated weekly over a nine-week period, equivalent to 9-10 aphid generations. Plants were watered every second day through-out the experiment, with the oldest plants in each cage being replaced weekly with two-week-old plants in order to ensure a continual food source for the aphids, whilst keeping all organisms in the cage. This method has been shown in (Sanders, Sutter & Veen 2013). The cages were rotated within and between incubators of the same treatments weekly in a block design to account for a potential incubator bias.

3.3.3 Competition experiment

In order to explain the effects of the main experiment, we set up an additional competition experiment using 3 aphid combinations; *A. pisum* only, *M. viciae* only and a combination of 2 species. 2 adult aphids of each species, depending on the species combination, were placed onto a 2 week old broad bean plant over which a breathable bag was placed and secured with a rubber band. These were then placed into an incubator at photoperiods of either 14.5:9.5 or 22:2, at 22^{o}C. The number of aphids was counted weekly for 3 weeks. Each treatment was replicated ten times. The cages were again rotated within and between incubators of the same treatments weekly in a block design to account for a potential incubator bias.

3.4 Statistical Analysis

3.4.1 Food web experiment

Aspects of aphid and parasitoid population dynamics were analysed using generalized linear models (GLM) with daylength treatment and community as explanatory variables. We used the following response variables:

1. Log transformed cumulative abundance (for each species, the total number of individuals for each cage over the length of the experiment), with Gaussian error structure (Sanders *et al* 2015, 2016, 2018).

2. Peak abundance. This is an ecologically important population measure for pest insects. This was measured as the maximum population size of each species at any point during the experiment and was analysed using a GLM with Gaussian error structure. The data for *M. viciae* and *A. pisum* were normally distributed, whereas data for *A. megourae* were log transformed, to improve fit to a normal distribution.

3. Parasitism rate (proportion of hosts parasitised). This was analysed using a GLM with a quasibinomial error structure due to over dispersion of the dataset. The response variable included the parasitized and non-parasitized aphid numbers per cage (using “cbind” in R).

4. Aphid population growth rate. This was analysed using a GLM with a quasiPoisson error structure due to over dispersion of the dataset. Growth rate was calculated as daily increase in aphid number per cage between week 2 and week 4

(week 4 number - week 2 number, then divided by 14). These points were chosen as by that time there was no impact of parasitism on aphid numbers before week 4.

3.4.2 Competition experiment

The impact of treatment (4 treatments: 14.5 single, 14.5 competitor present, 22 single, 22 competitor present) on aphid cumulative numbers were tested using linear models based on generalized least squares (errors are allowed to have unequal variances) provided by the nlme package (Pinheiro *et al.* 2017). We used VarIdent to account for variance heterogeneity in effect sizes between treatment groups. This test was replicated for both *A. pisum* and *M. viciae*. A Tukey comparison was then used as a post hoc test for between treatment contrasts.

Throughout, best fitting models were chosen using AIC model selection (Akaike 1998). Models for all analyses were visually checked for homoscedasticity and normality of the residuals, and all fulfilled the assumptions. All statistical analyses were computed using R version 3.2.1 (R Core Team 2013).

3.5 Results

3.5.1 *Cumulative Aphid Abundance*

The aphid *M. viciae* was not affected by daylength in the absence of the competitor *A. pisum*, but in its presence *M. viciae* densities were 32% higher in the Northern compared to the Southern treatment with *A. pisum* present (Figure 3.2, GLM Community * Daylength t= -2.09 (1,28), P =0.0495). *A. pisum* was negatively affected by a longer daylength, with populations 50% smaller compared to the Southern treatment (t= 2.21 (1, 14), P= 0.03). Neither community nor daylength affected the abundance of the parasitoid *A. megourae* (Daylength GLM t= -0.715 (1, 30), P=0.481) (Community GLM t= 0.78 (1, 29) P= 0.44), see Figure 3.2.

3.5.2 *Peak Aphid abundance*

Peak abundances of *M. viciae* were not affected by daylength in the absence of the competitor but in the presence of the competitor, the Northern treatment lead to 56% higher abundances than the Southern Treatment with *A. pisum* present (GLM Community * Daylength t=-3.32 (1,28) P= 0.003). The peak densities of both the aphid *A. pisum* (Treatment GLM t= 1.52 (1, 16), P=0.15) and the parasitoid *A. megourae* (Treatment t= -0.53 (1, 30), P= 0.6, community t= 1.12 (1, 29), P= 0.27) were not affected by daylength, see Figure 3.3.

3.5.3 *Parasitism rate*

Parasitism rate of the aphid *M. viciae* by the parasitoid *A. megourae* was not affected by daylength or presence of competitor (Treatment (Daylength, Community) GLM t= -0.56 (1,30), P= 0.6).

3.5.4 *Aphid population growth rate*

The population growth rate of *M. viciae* was reduced by 72% by the presence of the competitor, *A. pisum* (t=-2.90 (1, 29) P= 0.007), with no effect of daylength (t= -0.85 (1,30) P= 0.40), or interaction between daylength and community (t=1.352 (1,31), P= 0.187). Daylength regime did not affect the population growth rate of *A. pisum* (t= -1.51 (1, 14), P= 0.15).

3.5.5 *Competition experiment*

In an additional experiment we tested whether aphid growth would be affected by the interplay between daylength treatment and competition between aphids in the absence of parasitoids. *M. viciae* numbers were indeed reduced when competing with *A. pisum* under short daylength but not long days (see Figure 3.4). *M. viciae* abundance declined by 86% in the presence of *A. pisum* under short day conditions (z=-5.35 P<0.001). Interestingly, the opposite pattern was observed for *A. pisum*, with it's densities being strongly negatively affected with a reduction by 81% in the presence of *M. viciae* under long day condition (see Figure 3.4, z= -2.65 P= 0.036). *M. viciae* densities were also higher under 22 than 14.5 daylength indicating that in isolation *M. viciae* grows better under longer (Northern) summer days (see Figure 3.4, t=4.03 (1,10), P= 0.002).

3.6 Discussion

We expected that longer daylength would increase parasitoid attack rate, which would in turn 1) negatively affect the host aphid population and, through reduced interspecific competition, 2) positively affect the non-host aphid species. We did not observe this but instead found a decrease in cumulative abundance of the aphid *A. pisum* under Northern conditions, coupled with an increase in cumulative and peak abundances of the aphid *M. viciae*. However, *M. viciae* did not respond to daylength when it was the only aphid species present in the food web experiment. This shows that an increase in summer daylength, associated with a poleward range shift, has an indirect positive impact on one pest species due to reduced competition from another that is negatively affected by increased daylength. Interestingly, the competition experiment demonstrated that the competitive dominance between the two aphids species switched with daylength. *M. viciae* is the dominant competitor under long days while it suffers more from competition with *A. pisum* under short days. This explains the outcome in the food web experiment, with *M. viciae* profiting from longer days under Northern conditions. This effect appears to be driven by different growth rates of *M. viciae* under the different daylength regimes as shown in the competition experiment. This effect was not visible in the food web experiment, maybe due to the more complex setting of the experiment.

One might expect that the population growth of, essentially sessile, sap-feeding insects, such as aphids, will mostly be affected by changes in photosynthesis of their host plant which will determine resource availability, with aphid reproduction rate depending on the growth stage of its host plant (Watt 1979), as well as the plant’s degree of water stress (Simpson, Jackson & Grace 2012). Photosynthesis is highly dependent on photoperiod, with photosynthetic activity increasing with increasing photoperiod (Bauerle *et al.* 2012). The increase in growth rate for M. viciae in the competition experiment supports this effect in our experiments. However this evidence that longer summer days had positive effects either on the early population growth rate of aphids was not found in the food web experiment. In fact, a negative effect was observed for *A. pisum* cumulative abundance, reflecting sustained differences between the treatments over at least three generations (Figure 3.2E). Photoperiod has been shown to affect individual growth rate and body size for a number of insects, a response that may or may not be adaptive (Gotthard, Nylin & Wiklund 1999; Margraf, Gotthard & Rahier 2003; Shama & Robinson 2006) and we suggest that *A. pisum* and *M. viciae* were indeed affected by daylength but with very different outcomes, which is intriguing because the two species are ecologically and phylogenetically similar.

Our prediction that longer days would lead to increased top-down control of aphids by parasitoids due to extended activity patterns had a number of underlying assumptions. First of these is that parasitoids are time-limited rather than egg-limited, or, in other words, that the number of hosts a female parasitoid parasitises is limited by the number of hosts that she encounters (Henri & Van Veen 2011). It is not unlikely that in the confines of our experimental cages, with high densities of aphids, the female parasitoids encountered a sufficient number of hosts for all their eggs even in the shorter day. Further research is required under realistic field conditions in which host encounter rates will be lower to test the effect of changes in photoperiod on parasitoid efficiency. Our second assumption was that increased parasitoid attack rate would lead to increased parasitoid population growth and increased parasitism rate of the host aphid. It is, however, possible that higher attack rates lead to reduced parasitoid lifespan (Werner & Anholt 1993) so that there is overall little net effect on the parasitoid population growth. It should also be noted that the parasitoid populations in the experiment remained relatively low despite the abundance of hosts. This indicates that larval survival of the parasitoids may have been low due to the competitive inferiority of parasitized aphids compared to unparasitised aphids under crowded conditions (Ives & Settle 1996, Cameron *et al.* 2007). This may have further weakened the effect of a change in attack rate on the numerical response of the aphid population. Again, this effect is likely to be less important under natural conditions because of non-uniform host distributions and therefore greater variation in intraspecific competition in the population.

Another mechanism by which the parasitoid *A. megourae* might have impacted upon the community is through their reluctance to parasitise aphids in unlit periods (Sanders *et al.* 2018), as well as the disruptive effect of non-hosts in the community reducing parasitism rate (Kehoe *et al.* 2016). Both of these mechanisms however do not explain the direction of the interaction, and as such we can conclude that these effects were overwhelmed by bottom up effects.

Understanding of how ecosystems do and will respond to climate change and associated range expansion of species needs to take into account that shifts in day-night regimes can trigger significant changes in species interactions. Our study was limited to summer conditions and it is likely that a year-round perspective that includes key life-cycle stages such as diapause would reveal further effects on insect community dynamics. The responses of agricultural pests to climate change remains one of the main unknown factors in the ability to predict crop productivity under future climate scenarios (Gornall *et al.* 2010; War *et al.* 2016), though see (Gebauer, Hemerik & Meyhöfer 2015). With crop plants already grown outside of their natural range, the range expansion of any insects using them as a host plant will be instantaneous, as they do not require the expansion of their host plant range. As our study shows, species responses should not be studied in isolation but should be considered in the context of communities of interacting species, taking into account the change in abiotic factors such as photoperiod as well as evolutionary processes associated with poleward range shifts and expansions.

Figures

a

b

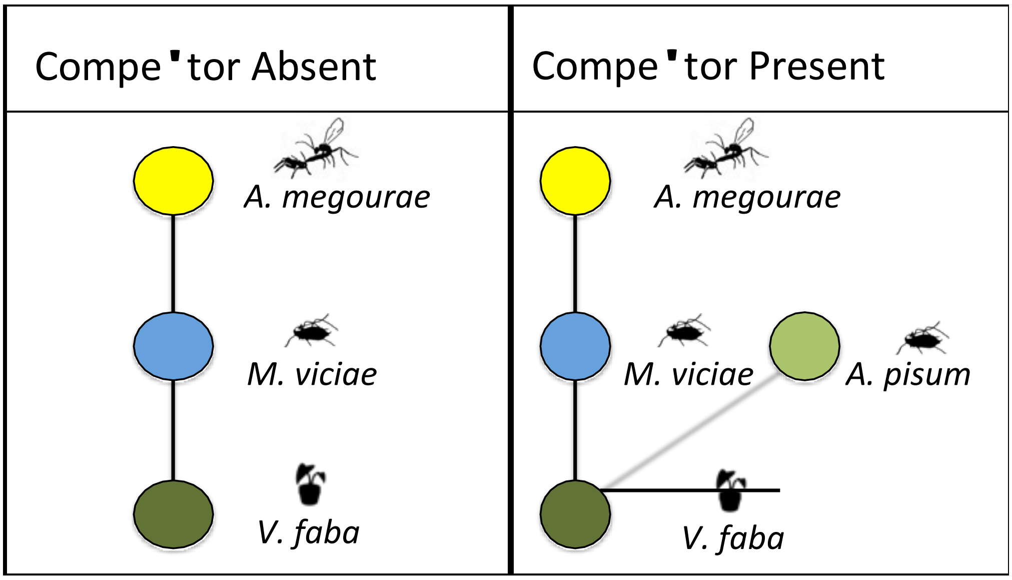

Figure 3.1: A. megourae attacking M. viciae. B. Food web structure for experimental ‘Competitor Absent’ and ‘Competitor Present’ Communities.

Figure 3.2: Population dynamics (mean and standard error) of all species. Sub plots A & B depict the parasitoid *A. megourae*, C & D the aphid *M. viciae* and E the aphid *A. pisum*. A & C show dynamics of the ‘Competitor Absent’ community, whilst B, D & E depict the ‘Competitor Present’ community. Black lines show Southern treatments, with grey lines showing Northern treatments. Error bars indicate standard error.

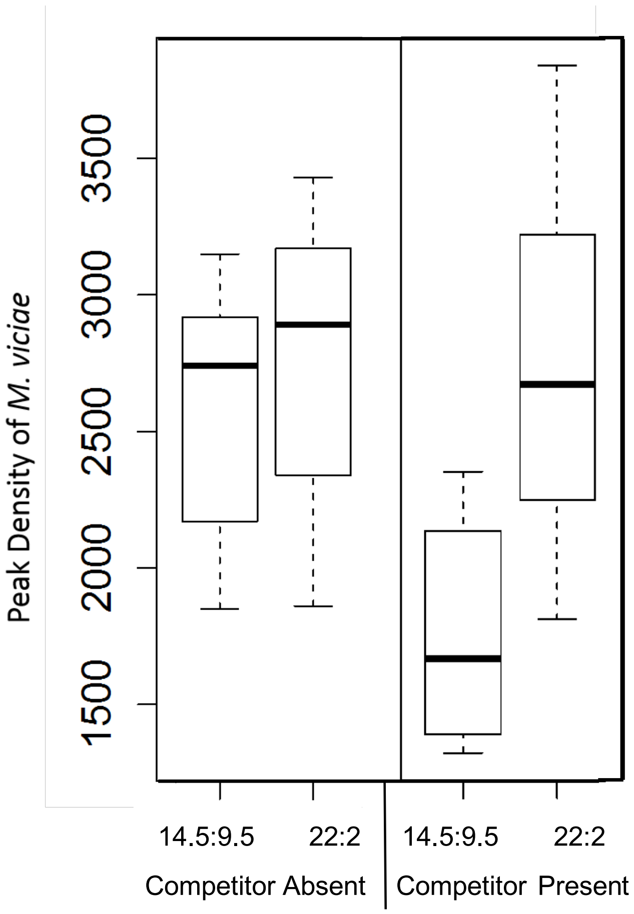

Figure 3.3: Peak density median, and quartiles of *M. viciae*, divided into ‘Competitor Absent’ community and ‘Competitor Present’ community, and then subdivided into long and short daylength treatments.

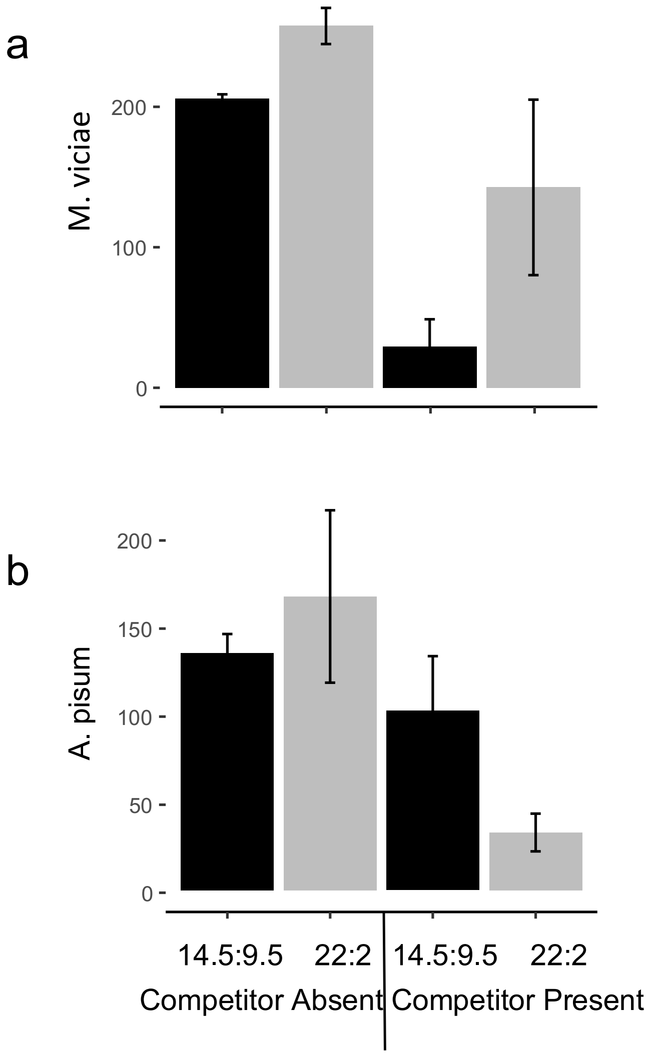

Figure 3.4: The mean cumulative density and standard error of a) *M. viciae* and b) *A. pisum* in long (22:2) and short (14.5:9.5) daylengths, with and without a competitor. Black bars depict short daylengths, and grey long daylengths.

Supplementary Information

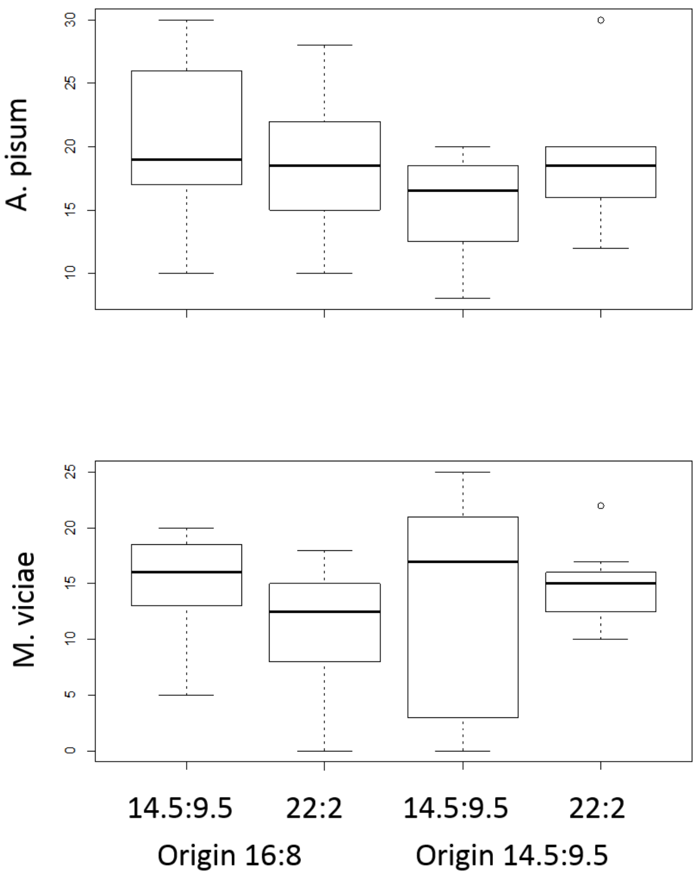

Figure S3.1. To test whether there is an effect on aphids entering the different light regimes from a photoperiod of 16:8 L:D, a growth rate experiment was undertaken. Adults of each aphid species were placed onto a single plant and placed into a mesh cage. These cages were then exposed to a photoperiod of either 16:8 or 14.5:9.5. After two days, the adults were removed and the offspring kept. This was repeated until the aphids had been in the different photoperiods for 3 generations. A single eight-day-old adult of each aphid species, and of each photoperiod treatment were placed in a petri dish, which contained one shoot of a broad bean plant, containing two leaves. They were then placed into incubators with a photoperiod of either 14.5:9.5 or 22:2. The growth rate of the aphids was measured over the course of 7 days. Each treatment- origin combination was replicated 10 times. Plot shows the median and quartiles of aphid abundance.

Chapter Four

Changes in light regime by daylength and artificial light drive host-parasitoid population dynamics

4.1 Abstract

1. Many organisms are experiencing changing daily light regimes due to latitudinal range shifts driven by climate change and increased artificial light at night (ALAN). Activity patterns are often driven by light cycles, which will have important consequences for species interactions.

2. We tested whether longer photoperiods lead to higher parasitism rates by a day-active parasitoid on its host using a laboratory experiment in which we independently varied daylength and the presence of ALAN. We then tested whether reduced nighttime temperature tempers the effect of ALAN.

3. We found that parasitism rate increased with daylength, with ALAN intensifying this effect only when the temperature was not reduced at night. The impact of ALAN was more pronounced under short daylength. Increased parasitoid activity was not compensated for by reduced lifespan, indicating that increased daylength leads to an increase in total parasitism effects on fitness.

4. To test the significance of increased parasitism rate for population dynamics, we developed a host-parasitoid model. The results of the model predicted an increase in time-to-equilibrium with increased daylength and, crucially, a threshold daylength above which interactions are unstable, leading to local extinctions.

5. Here we demonstrate that ALAN impact interacts with daylength and temperature by changing the interaction strength between a common day-active consumer species and its host in a predictable way. Our results further suggest that range expansion or ALAN induced changes in light regimes experienced by insects and their natural enemies will result in unstable dynamics beyond key tipping points in daylength

4.2 Introduction

Climate change has caused many species to shift their ranges poleward (Parmesan & Yohe 2003), altering their interactions with other species (Carrasco *et al.* 2017; Ettinger & HilleRisLambers 2017). Given that some insects can migrate 700km in 8 hours (Chapman *et al.* 2010), and thousands of kilometres over a single seasonal migration (Stefanescu *et al.* 2013), range expansions of insects can happen very quickly. However, as species track their thermal niches, and move closer to the poles, they experience longer summer days. Additionally, the light cycles they experience throughout their range are now less predictable due to the increasingly widespread introduction and increased use of Artificial Light At Night (ALAN). Much of this lighting has also become brighter and with a broader spectral range than in the 20th century (Elvidge *et al.* 2010; Gaston *et al.* 2014; Kyba *et al.* 2017). Approximately 23% of global land area now experiences light pollution (Falchi *et al.* 2016). ALAN causes a range of biological effects, such as advancing budburst timings by seven days (Partanen, Koski & Hänninen 1998), (Ffrench-Constant *et al.* 2016) and altering activity patterns, e.g. (Beier 2006; Stone, Jones & Harris 2009).

Given that daily light-cycles govern the activity patterns of many insect species, such changes in light regime are likely to affect the direct and indirect interactions among insect species. One key, and agriculturally important, species interaction is between European aphids and their parasitoids. A multi-generational experiment has shown that increasing the daylength experienced by an aphid-parasitoid community altered the relative abundance of the aphid species (Kehoe *et al.* 2018). ALAN also affects the dynamics of such systems, destabilising communities (Sanders *et al.* 2015; Sanders *et al.* 2018). A potential mechanism for these effects is an increase in parasitoid daily activity with increased photoperiod (Zilahi-Balogh *et al.* 2006; Guo, Snell & Yang 2010), leading to higher attack rates. It is, therefore, becoming clear that predicting some of the effects of global change depends on understanding the effect of altered photoperiod and ALAN on species' interactions, in concert with its direct effects on species' performance (Sanders *et al.* 2015; Urban *et al.* 2016; Sanders & Gaston 2018).

The responses of agricultural pests to climate change and how they interact with responses to other forms of anthropogenic change such as ALAN remain a key unknown in predicting crop productivity under future climates (Gornall *et al.* 2010). Aphids and their natural enemies are an important model system to address this question, given the detailed understanding of their life-history and ecology, and because many species are major agricultural pests, causing extensive damage to crops (Dedryver, Le Ralec & Fabre 2010). Parasitoid wasps are an important group of natural enemies of aphids and are widely used as biological control agents in agriculture (Van Veen *et al.* 2008; von Burg *et al.* 2011) . They are mainly active during daylight hours (Sanders *et al.* 2018). Therefore, if their host parasitism rate is time-limited (Henri *et al.* 2012), parasitism rates should increase with longer daily light exposure, whether from longer daylength or ALAN. ALAN has the potential to increase activity, but for ectothermic animals (whose activity is also reliant on temperature), this will only be possible when night-time temperatures also permit activity. However, any effect of increased attack rate on population dynamics could reduce if it is associated with a reduction in the reproductive life span (and attack rate later in life) of parasitoids, in the manner of 'live fast, die young' (Travers 2016). This effect would reduce any effect on increased lifetime fecundity of the parasitoids.

In this study, we use controlled experiments to test the following predictions of the effect of photoperiod on parasitism rate: (1) Longer daylengths lead to higher daily parasitism rates of parasitoids on aphids; (2) Exposure to ALAN is associated with higher parasitism rates; (3) Reduced night-time temperature relative to day-time reduces the effect of ALAN on parasitism rates (4); (5) ALAN impact will be stronger under shorter daylength. Increased parasitoid attacks associated with long day treatments will reduce attack frequency later in life so that life-time fecundity remains unaffected by photoperiod. Finally, we apply the effects we observe in predictions 1-5 above to a host-parasitoid population dynamic model. This model allows us to predict (6) the effects of photoperiod on the stability of host-parasitoid interactions and thereby the likelihood of light regime-driven extinctions and pest outbreaks in a range of biologically and environmentally-realistic parameters across their geographical and future ranges.

4.3 Methods

4.3.1 Study System

We used a plant-aphid-parasitoid food chain consisting of broad bean plants (*Vicia faba*, L., var. the Sutton, grown from seed) as the food resource for the vetch aphid *Megoura viciae* (Buckton). *M. vici*ae, in turn, was the host of the day-active parasitoid *Aphidius megourae* (Stary).

4.3.2 Experiment 1: Impact of Daylength, ALAN and Night Temperature on Parasitism Rate

To assess how different day-night regimes, artificial light and a reduction in night-time temperature affect the parasitism rate of the parasitoid *A. megourae*, we conducted a laboratory experiment where individual parasitoids were exposed to 100 aphids under one of 16 treatments for 24 hours. This short-term experiment recreates the first generation of a parasitoid which has recently expanded its range through range expansion or migration. Each experimental trial consisted of a two-week-old broad bean plant infected with 100 3rd instar *Megoura viciae* aphids (100 aphids is above the maximum number that can be attacked within 24hrs by *A. megourae* (Sanders *et al.* 2018a)). We then covered each plant with a ventilated, transparent plastic bag for the duration of the experiment. A freshly hatched (less than 12 hours old) mated female *A. megourae* parasitoid, from stock culture, reared at a 16:8 LD regime at 18°C was then released onto the plant, and the replicate placed into a climate chamber (Percival Model 1-30vl).

Once in the climate chambers, each plant was exposed to one of the 16 experimental treatments, in a fully cross-factored design that consisted of four different daylength treatments (12:12, 14:10, 16:8 and 18:6 hour day-night cycles). The daytime light was set to 4,239 lux, equivalent to a typical overcast day (Gaston, Bennie, Davies, and Hopkins 2013). For each daylength treatment, half of the mesocosms were exposed to either completely dark nights, while the other half experienced artificial light during the night period (20 lux, equivalent to street lighting (Stone *et al.* 2009, Gaston *et al.* 2013)). These treatments were further divided into those exposed to constant temperature (18^{o}C) or exposed to a drop in night-time temperatures (18^{o}C during the day and 12^{o}C at night) to simulate the natural drop (see Table S1 for a summary). Each treatment was replicated ten times, giving a total of 160 plant-aphid-parasitoid trials.

Each replicate was left in the climate chamber for 24 hours, after which time the parasitoid was removed, and the plants relocated to a temperature-controlled room set to 16:8 Light: Dark and 18^{o}C and were left for two weeks. The bag was then removed, and the number of aphid mummies (indicating the number of successful attacks) counted.

3.3.3 Experiment 2: Impact of Daylength on parasitoid longevity and Lifetime Fecundity

A freshly hatched (less than 12 hours old) mated female *A. megourae* parasitoid, from stock culture, reared at a 16:8 LD regime at 18^{o}C was placed in a transparent ventilated plastic bag with one two-week-old broad bean plant, and 100 3rd instar *M. viciae* aphids. This mesocosm was then placed in a climate chamber set to either 12:12 or 18:6 hrs Light: Dark and constant 18^{o}C temperature. Each day at noon the parasitoid was removed from the mesocosm and placed in a new one with 100 new aphids on a new plant. This daily transfer continued until the death of the parasitoid. Once the parasitoid was removed from each mesocosm and placed in the new one, the old mesocosms, complete with bean plant and both parasitised and unparasitised aphids, were placed in an 18°C controlled temperature room at 16:8 Light: Dark for two weeks to allow the mummies to develop. The number of mummies, signifying the number of successful attacks, was then recorded. Each treatment was replicated seven times, giving a total of 14 parasitoids.

4.4 Testing the effect of changes in parasitism rate on population dynamics models

To assess how the changes in parasitism rate of *A. megourae* with increasing light hours, observed in Experiment 1, would affect the population dynamics of its interaction with *M. viciae,* we used a variation of the Lotka-Volterra predator-prey model, specifically modified and parameterised for aphid parasitoid systems (van Veen, van Holland, and Godfray 2005). The simplicity of the model allows us to see the direct effects of increasing attack rate on community stability. The lack of time lags is not of great consequence as it descibes a population which attacks at different times, a phenomenon which we replicate in our expieriments by multiple introductions.

$$\frac{dN}{dt} = rN(1 - \propto N) - N\frac{\propto_{!} P}{1 + bN}$$

$$\frac{dP}{dt} = N\frac{s \propto_{!} P}{1 + bN + cP} - \mu P$$

The model above describes the relationship between *M. viciae* (N) and the parasitoid *A. megourae* (P). r represents the intrinsic rate of aphid increase and α the intraspecific competition coefficient between aphids (i.e. the inverse of their carrying capacity). Parasitoid handling time is represented by b, parasitism rate by α_P and parasitoid sex ratio by s. The effect of parasitoid density on its recruitment is represented by c, and parasitoids die at a density-independent rate of μ.

We randomly sampled 1000 parameters corresponding to 1000 sets of simulations where we varied the intrinsic rate of aphid increase (r), parasitoid handling time (b) and parasitoid death rate (μ). We generated these random parameters using a normal distribution around the mean of the numbers listed below, and the standard deviation of the mean divided by 20. The initial parameters used were taken from Van Veen, van Holland & Godfray (van Veen *et al.* 2005 (Van Veen, van Holland & Godfray 2005)). These have been shown to predict accurately empirical data on aphid-parasitoid population dynamics. These parameters were as follows: intrinsic rate of aphid increase (r) = 3.22, parasitoid handling time (b) = 0.0233, parasitoid sex ratio (s) = 0.5, the effect of parasitoid density on recruitment (c) = 1.26, and parasitoid death rate (μ) = 0.634. α is the intraspecific competition coefficient for the host and is the reciprocal of carrying capacity, which we arbitrarily set at 10,000 (therefore α = 0.0001). The parasitism rate was estimated empirically by van Veen *et al.* (2005) as α_p = 0.281 at 16 hrs daylight.

If we assume that daily parasitism rate is in a linear relationship with available daylight hours in time-limited parasitoids, the 12-18hrs daylight range would be represented by a range in α_p of 0.21-0.32. We tested the model predictions for this range of α_p in increments of 0.01 with host starting density at carrying capacity and the parasitoid starting density at 1. For each increment of α_p, we ran 1000 simulations with randomly drawn parameters (see above). We recorded whether the simulation reached a stable equilibrium and, if so, the aphid and parasitoid densities at equilibrium, and the time taken to reach a stable equilibrium.

4.5 Statistical Analysis

4.5.1 *Experiment 1:* To analyse the number of successful attacks by *A. megourae,* we used a generalised linear model with a Gaussian error structure. Log-transformed number of mummies (parasitism rate) was used as the response variable, and a three-way interaction between daylength, ALAN and a reduction in night temperature included into the model as the explanatory variables. Daylength was analysed as a continuous value, reflecting the nature of the data and that the model was unable to converge when set as a discrete value.

4.5.2 *Experiment 2:* The lifetime fecundity of *A. megourae* was analysed using a mixed-effects model from the package *nlme* (Pinheiro *et al.* 2017), with the number of mummies as the response variable, and daylength and day as explanatory variables. The terms “parasitoid ID” and “Day” which represents parasitoid age over the time of the experiment were used as random effects. The significance of the interaction between parasitoid age and daylength was also tested by comparing the model with and without the interaction using likelihood ratio tests. Temporal autocorrelation was negligible (all partial autocorrelations were below 0.2), and therefore not included in the model. Model assumptions were checked visually for heteroscedasticity and common distributions.

We performed all analyses using R version 3.5.1 (R Core Team 2013). Final models were chosen based on the lowest AIC values (Akaike 1998) and by using likelihood ratio tests to determine which parameters were included.

4.6 Results

4.6.1 Experiment 1: Impact of Daylength, ALAN and Night Temperature on Parasitism Rate

The duration of light hours per day had a marked impact on parasitoid performance. We found a significant three-way interaction between daylength, ALAN and a reduction in night temperature on the parasitism rate of *A. megourae* (Table 1). This interaction indicated that all three variables and their interactions were important in explaining the parasitoid's response to changes in light regime. Longer daylight hours were associated with an increased mean parasitism rate of *A. megourae* from 31.48 ± 15.58 SD successful attacks out of 100 aphids at 12-hour days to 61.26 ± 17.12 at 18-hour days (Figure 4.1C, Table 1).

Additionally, parasitoids experiencing ALAN under constant temperature increased their parasitism rate by an average of 26.5 per 100 aphids at short daylight hours (Figure 4.1A, Table 1). This effect diminished at a high number of daylight hours to an average increase of 10 per 100 aphids. However, this relationship between ALAN exposure and parasitism rate largely disappeared with a drop in night temperature (See Figure 4.1B, Table 1 for interaction between ALAN, Daylength and Temperature).

4.6.2 Experiment 2: Impact of Daylength on Lifetime Fecundity

A longer photoperiod increased the overall fecundity of *A. megourae*, from 82 ± 36.66 SD successful parasitisation events over a parasitoids lifetime to 132.67 ± 55.84 ($t_{1,28}$ =3.5, P= 0.002). In addition, parasitism rate decreased with age from 0.23 ± 0.09 (12:12) and 0.41 ± 0.01 (18:06) at the first day to 0.05 ± 0.007 (12:12) and 0.05 ± 0.008 (18:06) on day 7 ($t_{1,40}$ = -7.3, p = <0.001) (Figure 4.2). There was no interaction between photoperiod and parasitoid age ($\chi^2 = 1.6$, df = 1, p = 0.2), showing that the effect of daylength was consistent over the lifetime of the parasitoids, with no reduction in parasitism rate in longer-lived parasitoids. There was also no significant effect of daylength treatment on survival of parasitoids (Figure S4.1).

4.6.3 Impact of Parasitism Rate on Population Dynamic Models

At lower levels of parasitism rate (<0.27), representing shorter days of less than 16 hrs daylight, 55% of simulations showed damped oscillations leading to a stable equilibrium. In these scenarios, the equilibrium density of the host decreased with increasing parasitism rate, and time taken to reach equilibrium increased exponentially (Figure 4.3). However, at a parasitism rate of 0.28, representing daylengths of just longer than 16:8, only 26% of simulations reached equilibrium, reducing to 4% of simulations reaching equilibrium at a parasitism rate of 0.29. The remaining simulations did not reach equilibrium instead showing wide population size fluctuations fluctuating between hundreds of parasitoids and thousands of parasitoids. These model outputs frequently lead to population extinctions.

4.7 Discussion

Our experiments test the relationship between parasitism rate and light regime for a common diurnal consumer species and its host. The results demonstrate that the strength of the interaction between the parasitoid *A. megourae* and its host *M. viciae* depends closely on light regimes, with both increasing daylength and artificial light at night increasing the parasitism rate of *A. megourae*. There was a steep increase in parasitism rate with longer daylength, which was matched by a positive effect of ALAN on parasitism rate that was strongest under shorter daylengths. However, this increase in parasitism rates associated with ALAN was only observed when the insects experienced constant temperatures, and not when there was a nocturnal drop in temperature of 6^{o}C (i.e. cool nights and warmer days, as is typically the case in temperate regions). As such, below, we relate this to its likely effects on the demography of the aphids, and the stability of the aphid-parasitoid interaction. These results highlight how poleward range shifts are likely to alter host-parasitoid associations substantially, and that the strength and pattern of this effect will depend on the local microclimates available to (and used by) the aphids.

While we know that both an increase in temperature and the presence of artificial light can increase parasitism rate in some parasitoids (Burnett 1951; Malina & Praslicka 2008), but not in others (Heimpel & Rosenheim 1998), here we show how ALAN, night-time temperature and daylength interact in driving parasitism rate. In the absence of ALAN, a drop in night-time temperature had little or no effect on parasitism rate in our study, probably because day-active parasitoids are not active when it is dark, irrespective of temperature (Sanders *et al.* 2018a). However, under ALAN, night time temperature becomes the limiting factor determining the activity level of the parasitoid. Here, we only included two nocturnal temperature treatments, and so cannot detect any non-linearity or threshold effects in this relationship. Any such threshold could be used to manage or maintain pest control effectiveness, or to predict tipping points for the maintenance of ectotherm species interactions in ecological communities.

The interaction observed between daylength and ALAN highlights that the effect of ALAN on species and their communities depends on the season and associated day-night regimes. Our results demonstrate that ALAN will increase parasitism rates more in early spring and autumn, in situations where temperature is not a limiting factor. However, given night-time temperatures are known to be increasing at rates greater than daytime temperatures due to climate change (Davy *et al.* 2017), this impact of ALAN on populations is likely to increase with ongoing climate change.

The observation of increased parasitism under long daylengths indicates that parasitoids are time rather than egg limited. Therefore the impact of a longer activity period may not affect the total number of hosts killed by a parasitoid in its lifetime, our second experiment, however, could not detect such a trade-off. Initial parasitism rates were much higher for long daylengths, and the decline in parasitism rate with age was not statistically significantly steeper in the long daylength treatment than observed at shorter daylengths.

Furthermore, in natural habitats, parasitoid life span is likely to be much shorter than in the laboratory due to elevated extrinsic mortality rates. As such, the effects of daylength on parasitism rate in early life reported here are more representative of population-level responses than late age ones (given fewer individuals make it to late-life stages). These early life rates of parasitism and their sensitivity to daylength and night temperature are therefore likely to have a major effect on species interactions in natural populations.

Parasitism rate is a critical parameter determining host and parasitoid population dynamics and their stability. Using simulation models, we tested how the variation in parasitism rate that we observed empirically in our experimental treatments will affect host population densities and the stability of the interaction across the thermal and geographic ranges of their natural interaction. Our model results showed that with these biologically realistic increases in parasitism rate, as equilibrium host density declines, the interaction simultaneously becomes less stable (measured as the time taken to reach equilibrium). At daylengths longer than 16.8, equivalent to summer in southern England, this leads to highly fluctuating dynamics that never reach equilibrium and result in extinctions of the parasitoid or both the aphid and parasitoid from ecological communities. If the parasitism rate is time-limited (as our experimental data show) and increases linearly with the number of daylight hours, this transition occurred at a daylength of approximately 16 hrs. Importantly, this means that for crop pest insects controlled by parasitoids or similar natural enemies although equilibrium pest densities will decline with poleward range-shifts, the population fluctuations will also increase. This increased variation may result in more unpredictable and damaging pest outbreaks under conditions of ongoing climate change. While the specific thresholds will vary between species, our predictions of strong threshold effects on such interactions should hold for any consumers with a clear diurnal activity pattern. Additionally, the approach towards such a threshold (and community collapse, or a possible pest outbreak) would be characterised by a steadily decreasing prey abundance, with increasing demographic fluctuations.

Because of the minimal changes in daylength a single parasitoid generation experiences, we kept daylength constant in the lifetime fecundity experiment. However, daylength varies seasonally, and more strongly nearer to the poles, and most temperate insects are only active between the spring and autumn equinoxes (when daylengths are longer nearer the poles). Further theoretical and experimental work is required to study the effect of seasonal variation in daylength in addition to the overall effect of increased daylength with poleward range shifts and how these results extrapolate to more complex communities

The experiments and modelling in this study demonstrate the importance of including natural and artificial light regimes, as well as diurnal thermal shifts when predicting the effects of environmental change on species interactions as an important building block of any ecological community. Such understanding is especially important where food security depends on the natural control of agricultural pests. Here we show that the impacts of artificial light are strongly seasonal, as well as being strongly affected by latitudinal shifts and night temperature. Given the strong response of a diurnal host-parasitoid system reported here, there also needs to be a shift from focussing on the impact of ALAN on nocturnal species to include those that are chiefly diurnal, on which the effects of ALAN may be just as profound.

Figures and Tables

Table 4.1 Results of a generalized linear model including a three-way interaction between daylength, ALAN and a drop in night temperature on *A. megourae's* parasitism rate. Levels of significance: * P < 0.05; ** P < 0.01; *** P < 0.001.

	Estimate	Standard Error	Df	T Value	P Value
Intercept	2.68	0.42	159	6.43	<0.001 ***
Daylength	0.09	0.03	158	3.27	0.001 ***
ALAN	-1.96	0.59	157	-3.33	0.001 ***
Drop in Night Temperature	-1.04	0.59	156	-1.77	0.08
Daylength * ALAN	0.09	0.04	155	2.44	0.02 *
Daylength * Drop in Night Temperature	0.05	0.04	154	1.34	0.18
ALAN * Drop in Night Temperature	2.09	0.83	153	2.51	0.01 **
Daylength * ALAN * Drop in Night Temperature	-0.12	0.05	152	-2.24	0.03 *

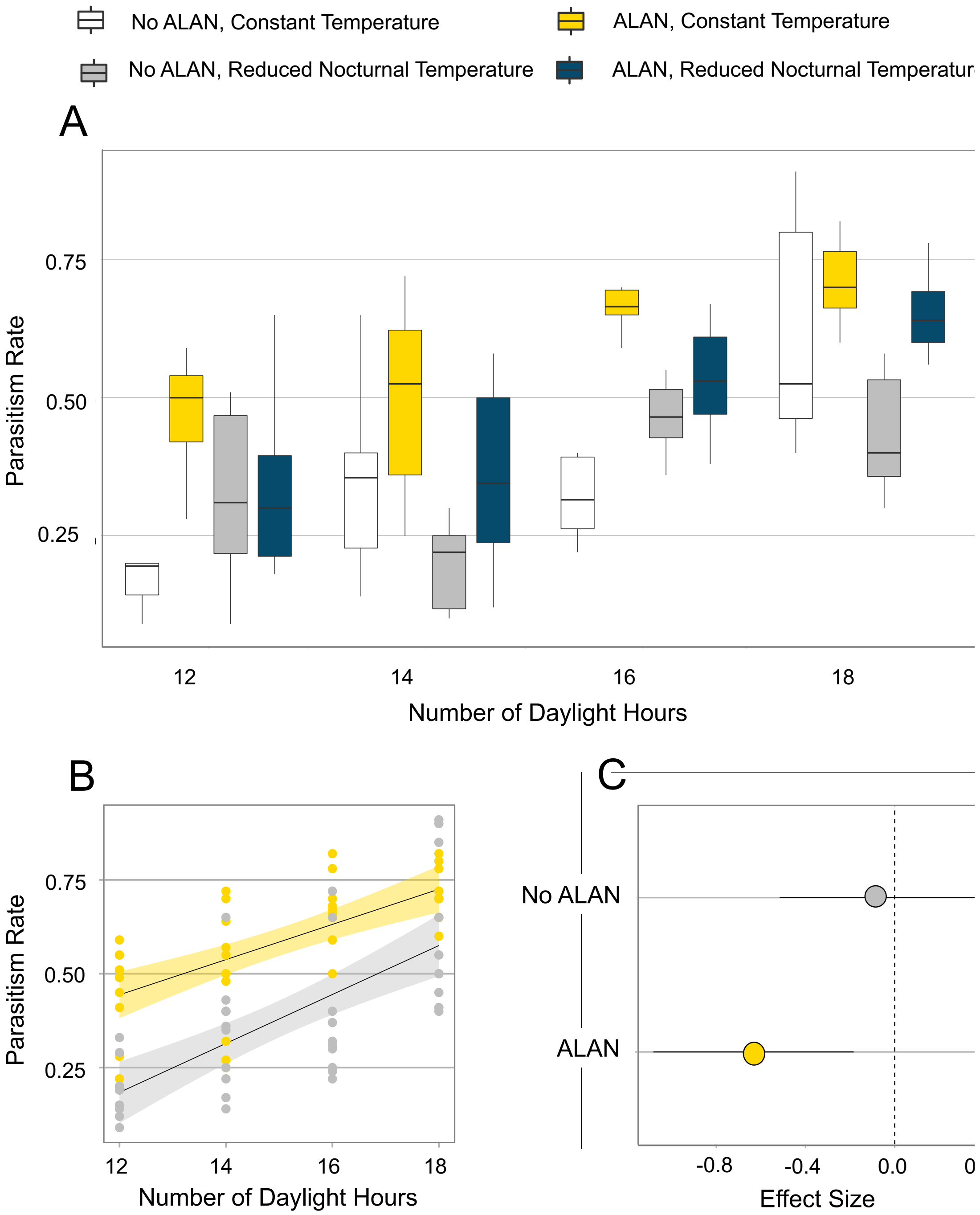

Figure 4.1 A) Line plot showing individual parasitism rate, mean and 95% CI based on a linear model for each daylength incorporating unlit and lit treatments without a drop in temperature. B) The effect size (Cohen's D) of a reduction in night vs day temperature on the parasitism rate of *A. megourae* under lit and unlit treatments. C) Boxplots with median, and quartiles showing the effect of all treatments (daylength, artificial light at night and a reduction in temperature at night) on the parasitism rate of *A. megourae* on 100 *M. viciae* aphids over a 24 hr period.

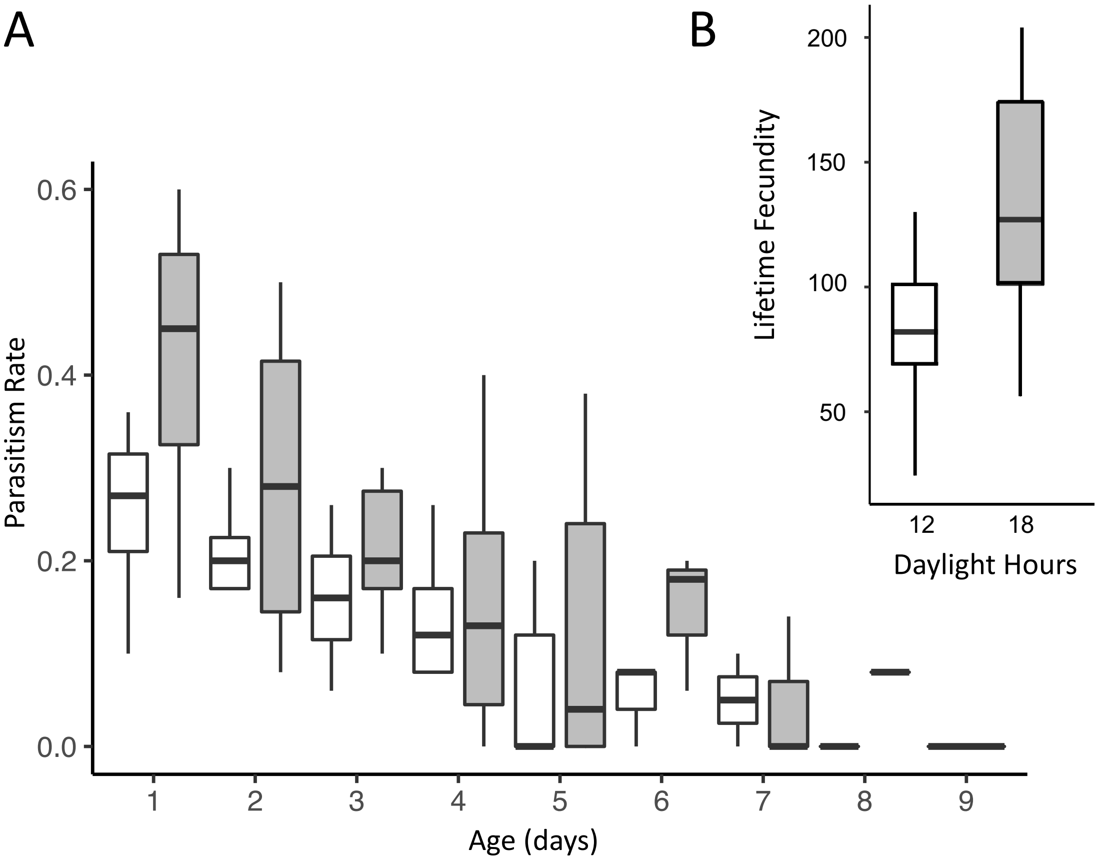

Figure 4.2 (A) Box plot and interquartile range showing the effect of daylength on the parasitism rate of *A. megourae* over the parasitoids' lifetime. White boxes display the 12-hour daylength treatment and grey boxes the 18-hour treatment. (B) shows overall lifetime fecundity as the sum of all successful attacks.

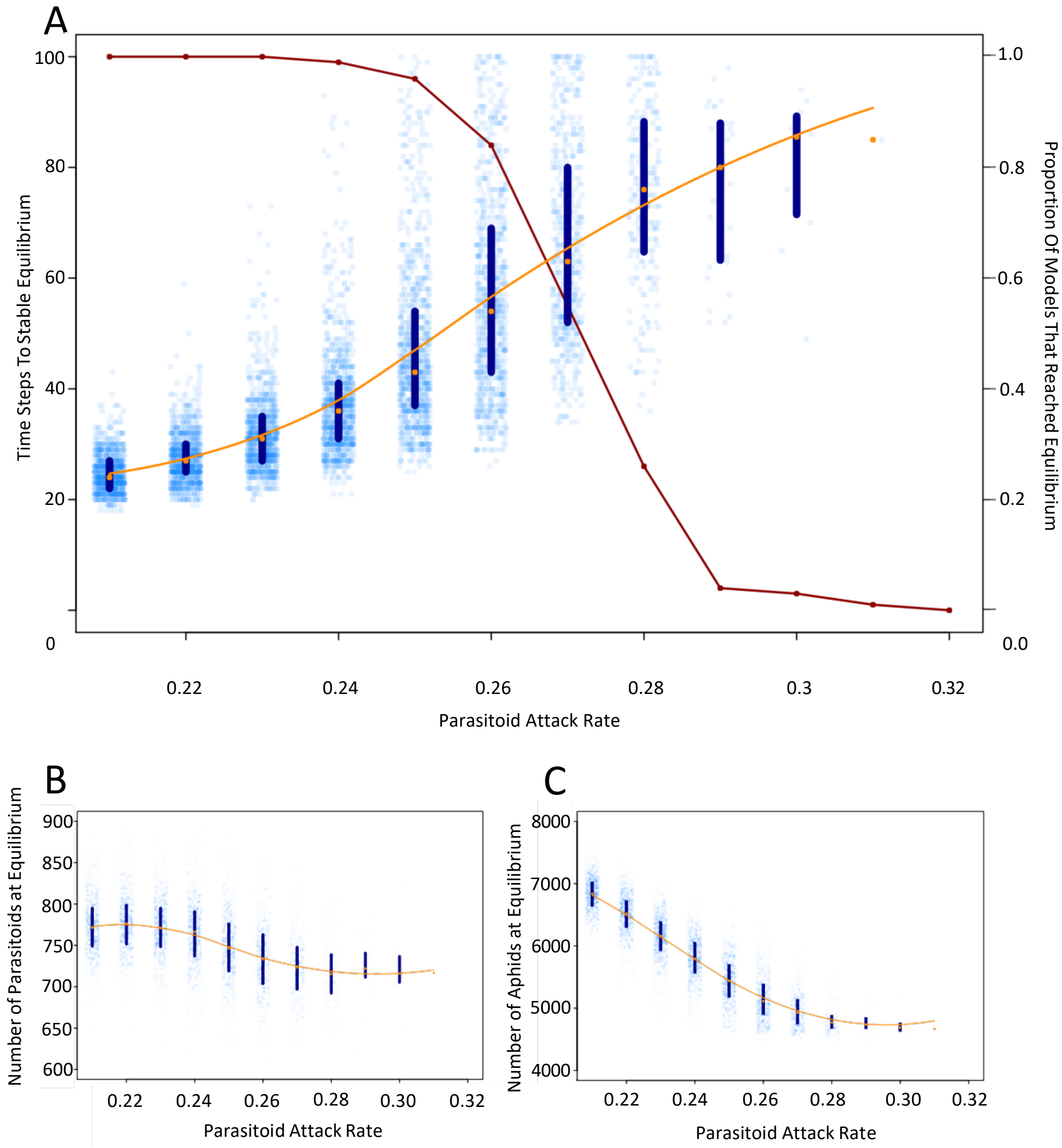

Figure 4.3 The median and interquartile range of the time for the Lotka-Volterra model to reach equilibrium, based on 1000 simulations per attack rate step, model prediction (orange line), and proportion of simulations reaching equilibrium (dark red line) (A). The median and interquartile range for population densities of parasitoids (B) and aphids (C) and at the point of equilibrium.

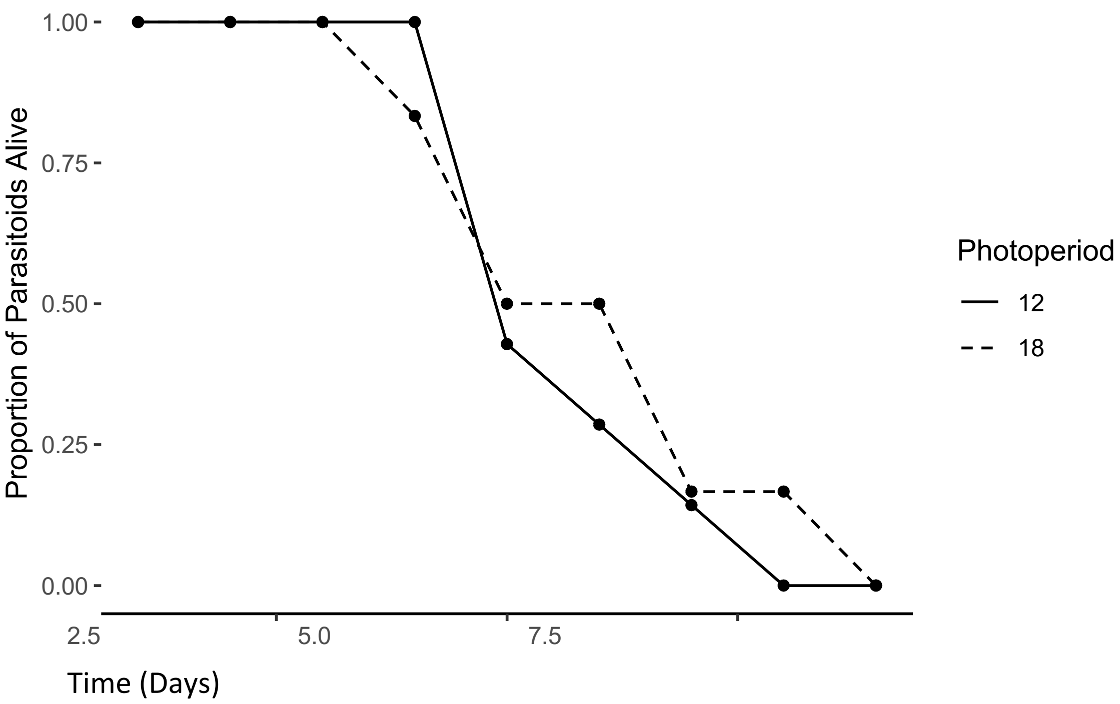

Figure S4.1 Parasitoid survival over several days under short (12h) and long (18h) photoperiods in Experiment 2: Impact of Daylength on Lifetime Fecundity.

Table S4.1: The design of the parasitism rate experiment. All treatments were replicated ten times, totalling 16,000 aphids and 160 parasitoids.

		Hours of Daylight			
		12	14	16	18
ALAN Regime	Unlit	Constant Temperature	Constant Temperature	Constant Temperature	Constant Temperature
		Drop in night temperature	Drop in night temperature	Drop in night temperature	Drop in night temperature
	Lit	Constant Temperature	Constant Temperature	Constant Temperature	Constant Temperature
		Drop in night temperature	Drop in night temperature	Drop in night temperature	Drop in night temperature

Chapter Five

Experimental evidence for destabilising effect of longer daylength on host-parasitoid population dynamics

5.1 Abstract

1. Climate change is causing the poleward expansion of many species. Populations that have expanded will experience a change in the daylength regime that they experience. A recent model predicts that communities experiencing longer daylengths will exhibit lower stability with higher extinction probabilities and increased variability of host and parasitoid abundances, but we still lack empirical evidence that daylength affects population stability.
2. We conducted a multi-generational plant-aphid-parasitoid community laboratory-based experiment, with communities experiencing either a short (14 hrs daylight) or long (18 hrs daylight treatment), assessing the abundance of both species as well as the stability of the system measured as time to extinction.
3. We found decreased community stability with longer daylengths, with six out of eight long-day communities becoming extinct within seven weeks compared to two out of eight short-day treatments. Long-day treatments also exhibited increased variation in parasitoid numbers and increased cumulative parasitoid population size.
4. Our results demonstrate that light regime can drive community stability and therefore, ecological functions. This effect highlights that climate change-driven range expansion can destabilise community dynamics with implications for conservation and agriculture.

Key Words (3-6)

Community Stability, Population Dynamics, Photoperiod, Aphid, Parasitoid.

5.2 Introduction

Ongoing climate change is altering the range of areas potentially suitable for habitation (Rosenzweig *et al.* 2007), with populations able to maintain their thermal niche by expanding their ranges both latitudinally and elevationally (Chen *et al.* 2011). Climate change is the primary driver for patterns observed in present-day species range shifts (Walther *et al.* 2002). Although past climate change-induced range expansion is historically documented, e.g. (Pandolfi & Kiessling 2014), the current rate of climate change is faster than in both recent history (Change 2001) and at any point during the past 50 million years (Change 2007).

Insects should respond quickly to climate change as they are ectothermic, with the rapid adaptation of insects in response to climate change already documented (Thomas *et al.* 2001). Insects are also of particular interest in the context of climate change-induced range expansion, as they can travel both far and fast. Some insects can migrate 700km in 8 hours (Chapman *et al.* 2010), and thousands of kilometres over a single seasonal migration (Stefanescu *et al.* 2013). In altering their ranges, populations can experience a change in species interactions with competitors (Johnson *et al.* 2011; Marshak & Heck 2017), consumers (Nooten & Hughes 2014; Katz & Ibanez 2016a), hosts (McMahan & Grabowski 2019), pollinators (Polce *et al.* 2014) as well as indirect interactions **Chapter Two**; (Sorte, Williams & Carlton 2010; Kehoe *et al.* 2016). Interactions are also changed by differential rates of range expansion, with predators not expanding at the same rate as its prey (Hopper *et al.* 2014) or experiencing novel species interactions.

When expanding their ranges latitudinally, populations experience a change in daylength regime, with poleward range-expanding populations experiencing longer summer days, these having been extensively studied as a barrier to invasion (Saikkonen *et al.* 2012). Daylength has been shown to impact directly on a large number of species traits, such as timing into and out of overwintering (Tauber & Tauber 1970) including migration (Dickeson 2018), size of both individual organisms (Mousseau & Roff 1989) and populations (Oleksyn, Tjoelker & Reich 1992), activity and feeding cycles (Spieler & Noeske 1984) and parasitism (Sanders *et al.* 2018). Changes in daylength have been shown to affect the competitive ability of aphid species, in a multi-generational experiment, with one species being competitively dominant at a short photoperiod, and a different competing aphid dominant at a long photoperiod (Kehoe *et al.* 2018).

Insects comprise the great majority of eukaryotic species diversity consisting of around 2.5 million species (Mora *et al.* 2011). They provide both financial ecosystem services, estimated to be more than $57 billion annually in the USA alone (Losey & Vaughan 2006) as well as agricultural destruction, with invasive insects alone costing a minimum of US$70.0 billion per year globally (Bradshaw *et al.* 2016). Health costs associated with invasive insects exceed US$6.9 billion per year. A well-studied group of insects is aphids and parasitoid wasps. The natural history and ecology of aphids are well known, causing extensive damage to crops (Dedryver, Le Ralec & Fabre 2010), producing an estimated loss of $28 million in Australia alone (Murray, Clarke & Ronning 2013). Parasitoid wasps are an important group of natural enemies of aphids and act as biological control agents in agriculture (Van Veen *et al.* 2008; von Burg *et al.* 2011). Both have short generation times making them ideal for multi-generational experiments.

Chapter Four showed experimentally that parasitoids experiencing longer daylengths, as happens in poleward range shifts, caused an increase in their attack rate. The implications of an increase in attack rate were then tested with a Lokta-Voltera population dynamic model, noting the time it took for the two species to reach a stable equilibrium. Increasing the daylength that the community experienced, through increasing the parasitism rate, decreased the stability of the interaction in two ways; 1) with population sizes fluctuating to a greater degree, and, 2) above certain daylengths, these interactions became unstable, leading to the extinction of the host, parasitoid or both.

To test the theoretical predictions from the above study, here we experimentally investigate using a multi-generational climate chamber experiment, how the stability of aphid parasitoid community dynamics respond to different daylength regimes. We hypothesise we expect that communities experiencing the longer daylength (18:06) will experience 1) greater population variability and 2) lower stability, and as such more extinctions than the community experiencing the shorter daylength (14:10).

5.3 Methods

5.3.1 Model system

The plant-aphid-parasitoid communities consisted of bean plants (*Vicia faba*, L., var. the Sutton) as the resource for the aphid *Megoura viciae* (Buckton), which was in turn parasitised by the parasitoid *Aphidius megourae* (Stary).

5.3.2 Experiment set up

To test the effect of daylength on the stability of a plant-aphid-parasitoids network, we conducted a multi-generational laboratory experiment. Each replicate consisted of two two-week-old bean plants, infected with five aphids between them, and contained in a 40cm^3 mesocosm, constructed of untreated timber and thrip netting. These replicates were then placed into one of four climate chambers (Percival Model 1- 30v), programmed to one of two daylight treatments: 14:10 day:night and 18:06 day:night. These daylengths have population parameters that lead to predictions of varying stability (Chapter Four). After one week (approximately one aphid generation), we released two 24hr old, mated, female parasitoid wasps into each mesocosm. The numbers of all aphids and aphid mummies in each mesocosm were counted twice-weekly and checked for extinctions (defined as no individuals of that species left in the cage. Cages with extinct species were counted and checked for a further two weeks to confirm species extinctions. If no further individuals were found within this time, this additional data was removed from further analysis. Plants were watered twice weekly, and the oldest plant replaced weekly with a new plant, leaving the foliage, and any insects in the cage. This method allows for the observation of long term population dynamics (Sanders *et al.* 2016; Kehoe *et al.* 2018; Sanders *et al.* 2018a; Sanders *et al.* 2018b). The placement of mesocosms was rotated both within and between the two climate chambers of the same treatment to avoid climate chamber effects.

5.4 Statistical Analysis

To test hypothesis 1) we compared the variation in both aphid and parasitoid densities over time dependent on different treatments. We analysed the differences using an asymptotic test from the R package cvequality, with aphid and parasitoid abundances individually used as response variables and treatment (long or short days) as an explanatory variable (Marwick 2019). We analysed the treatment effect on both aphid and parasitoid cumulative abundance using a glm, with treatment used as the explanatory variable and log transformed abundance as the response variable.

To test hypothesis 2) we compared the extinction probability of aphids and parasitoids between the different treatments, recording the number of days that each two species community persisted in each of the 16 mesocosms. We considered species extinct when numbers were zero for over two weeks. We treated species that persisted in mesocosms until the end of the experiment as censored data. We compared the survival of species for the two daylength treatments using Kaplan-Meier survival curves and a log-rank test as implemented in the R-function survdiff.

To test for an impact of daylength on aphid population size without parasitoid presence, we used data from days 1-12, conducting a mixed-effects model, with aphid population size as the response variable and treatment as the explanatory and including ‘day’ in the model as a random factor.

We used a generalized linear model with binomial error structure to test for the impact of daylength on the parasitism rate of *A. megourae*. As a response variable, the number of (1) aphid mummies and (2) live aphids for each mesocosm for each of the two parasitoid species was combined. The interaction between treatment and time was used as the explanatory variable.

5.5 Results

Our results support hypothesis 1, showing increased variation in population abundance of the parasitoid *A. megourae* (D'AD= 7.30, P=0.007) in the long day treatment throughout the experiment (Figure 5.1). *A. megourae* also displayed higher cumulative densities in the long day treatment, (617 ± 475 in the long-day treatment compared to 208 ± 96 in the short-day treatment, t_{15}=2.691, P= 0.0176). However, neither changes in variation (D'AD= 0.16, P=0.69) nor abundance (t_{15} = 0.823, P=0.425), were observed in the aphid *M. viciae*. In addition to increases in both populations numbers and variation, parasitoids under long day treatments displayed increased abundance proportional to aphid abundance compared to parasitoids experiencing short days (z= 2.044, P=0.0409), which can be used to indicate parasitism rate (Figure 5.2).

These results also support hypothesis 2, with replicates experiencing longer daylengths displaying increased extinction rates compared to those under short days (Figure. 5.3, χ^2 = 5.7, df = 1, P= 0.02). The first aphid extinctions occurred after 33 days with 75 percent extinction by day 50 in the long day treatments, with replicates in the short-day treatment experiencing the first extinctions at day 36, with 25% of aphid replicates extinct by day 50. Parasitoid extinctions happened from day 43 onwards in long day replicates, and 47 in long day replicates, with both treatments exhibiting a very similar pattern to that of the aphids (see Figure 5.3). Before the introduction of the parasitoids, there was no difference in the population size of the aphids due to treatment (t= $_{59}$ -0.78, P= 0.44).

5.6 Discussion

Chapter Four shows experimentally that longer daylengths cause an increase in the parasitism rate of a parasitoid wasp on its aphid host. It further predicts using population-dynamic models that this impact of longer daylengths would increase variation in the population size of both aphids and parasitoids, in addition to a higher extinction probability. This study tested these predictions empirically. We found that replicates in the long day (18:06) treatment exhibited higher variation, producing greater peaks and troughs, as well as an increased extinction rate, with six out of eight long day replicates going extinct within 50 days, compared to two out of eight replicates becoming extinct by day 50 in the short day (14:10) treatment.

It is possible to predict that the longer daylength itself directly caused the extinction of aphids, independent of the impact of daylength on the parasitoids. The data show no effect of daylength on either the growth rate or the total number of aphids in the first two weeks, a replication of the result from (Kehoe *et al.* 2018). This result is a logical one as aphids feed throughout both day and night (Spiller, Koenders & Tjallingii 1990). If daylength were to impact on the growth rate of the aphids in this experiment, we would expect a higher growth rate due to increased plant photosynthesis, e.g. (Bamberg, Schwarz & Tranquillini 1967). However, previous studies show that although shorter daylengths reducing fecundity and length of the aphid’s reproductive period, this, in turn, does not affect population size, as these costs are only apparent towards the end of the aphid’s life (Joschinski, Hovestadt & Krauss 2015). Daylength has also been shown to affect aphid growth rate, but only when interacting with changes in temperature (Wyatt & Brown 1977).

The model in Chapter Four predicted that longer days, represented by a higher parasitism rate, should increase parasitoid numbers, causing overexploitation of the host, which in turn would cause host, and subsequently parasitoid population crashes. This effect is shown in Figure 5.4: the long day replicates in which the aphids became extinct (six out of eight replicates) show a high peak of parasitoids, at the point that the aphid numbers crash, around days 29-36. We further expect the host crash to coincide with the parasitoid peak, rather than following it due to the time lag between the parasitism of the aphids, and their development into a parasitoid mummy. In those replicates of the short day treatment where the aphids became extinct (two out of eight replicates), there was no large peak in parasitoid densities. As such a different mechanism caused the extinctions in the short day replicates.

There is a large amount of theory about host-parasitoid dynamics (Hassell 2000). In basic models, e.g. (Nicholson & Bailey 1935), diverging host-parasitoid dynamics always lead to local extinctions. Hosts and parasitoid relationships are inherently unstable when under model assumption of random parasitism, as well as in this particular system (Sanders, Sutter & Veen 2013). However, in nature, there is a great deal of heterogeneity in the likelihood of parasitism. These may be genetic, due to protective symbionts (Sanders *et al.* 2016), non-host interference (Kehoe *et al.* 2016), spatial heterogeneity (Wiens 1989), levels of competition (Sanders, Kehoe & van Veen 2015) and the structure of the community of which the relationship is part (Sanders *et al.* 2018b). Additionally meta-population dynamics (Levins 1968) and the pattern of local extinctions and later recolonisations can maintain a regional network of inherently unstable local populations (Gurney & Nisbet 1978). Similar stabilising factors may prevent extinctions in poleward expanding host-parasitoid systems.

The increase in parasitoid rate observed in this experiment will not translate to lower crop pest numbers for agriculture. As parasitoids control the aphids to a higher degree, aphid numbers will drop. However, when aphids are in low numbers, it is hard for parasitoids to find their hosts (Kehoe *et al.* 2016), and as such, the parasitoids can go extinct. With no parasitoids providing top-down control of the aphids, they can reach higher numbers, resulting in a greater degree of crop damage. The increased variability I observed in the parasitoid populations and increased local extinction risk may lead to greater frequency of uncontrolled pest outbreaks as seen in the higher peaks. I did not observe this in the experiments as there was no effect on aphid variability, but this remains a distinct possibility that warrants further investigation.

To test whether longer days increase both variation in abundance and extinction rates of host-parasitoid interactions in the field needs further research. To assess the impact of daylength on these interacting insects in the field would require a simple community experiment replicated along a latitudinal gradient within a temperature-controlled environment to avoid the confounding effect of temperature. Once the mechanics of the system are confirmed, a larger scale community experiment along the same latitudinal gradient would give more knowledge into the impact of daylength on more ‘real world’ communities.

Figures

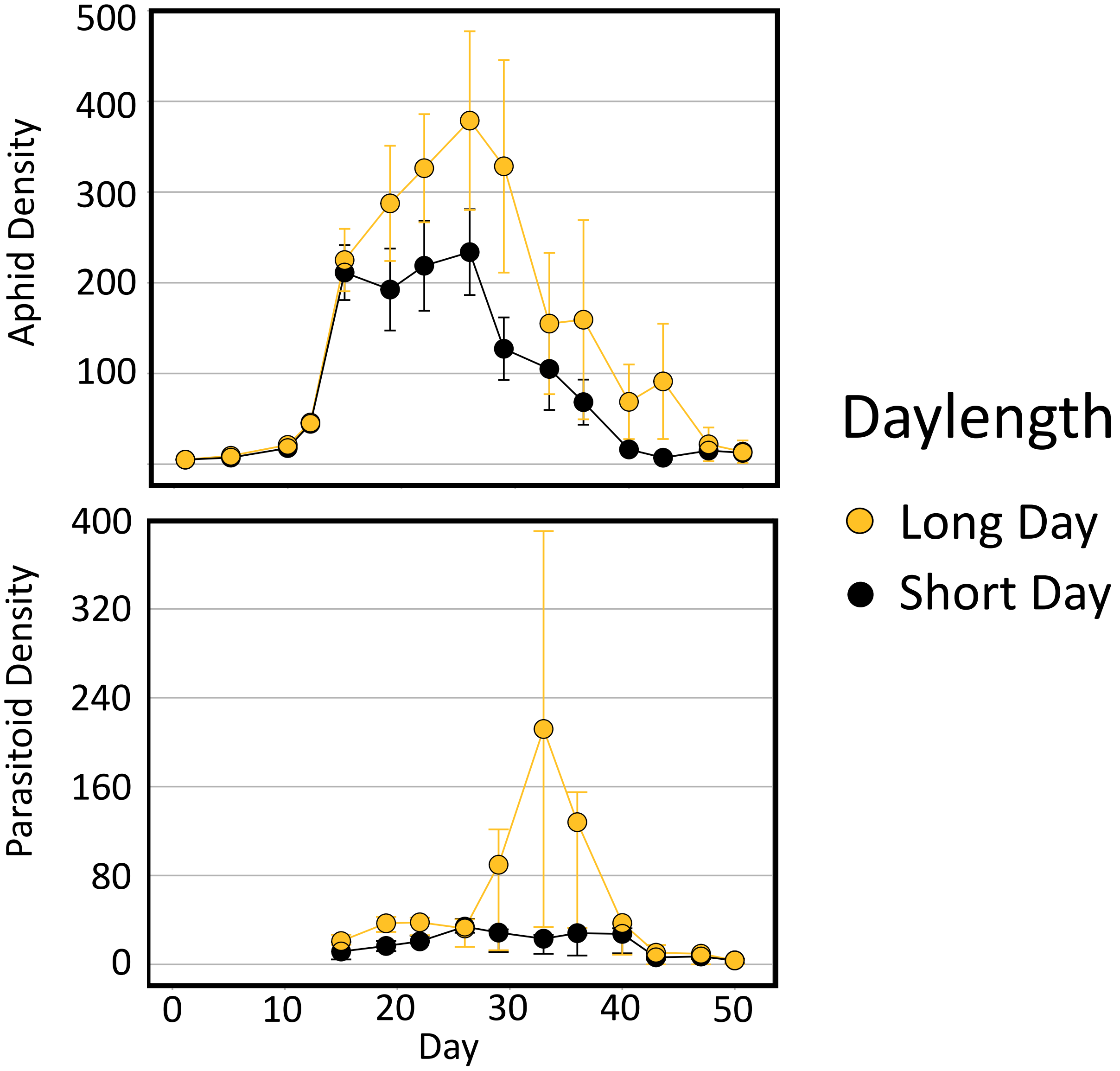

Figure 5.1: Population dynamics (means of 8 replicates + standard error) of the aphid species *Megoura viciae*, and the parasitoid *Aphidius megourae*.

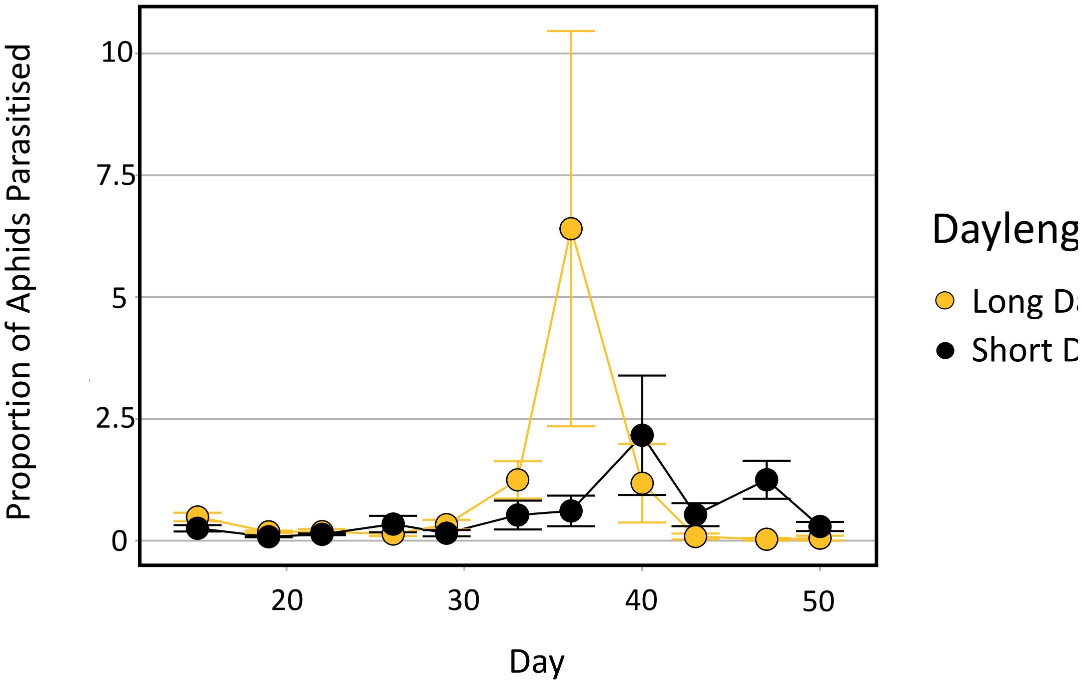

Figure 5.2: The proportional abundance of the parasitoid *Aphidius megourae* relative to the aphid *Megoura viciae* (means of 8 replicates + standard error). Short days (14:10 L:D) are shown in black, and long days (18:06 L:D) are shown in yellow.

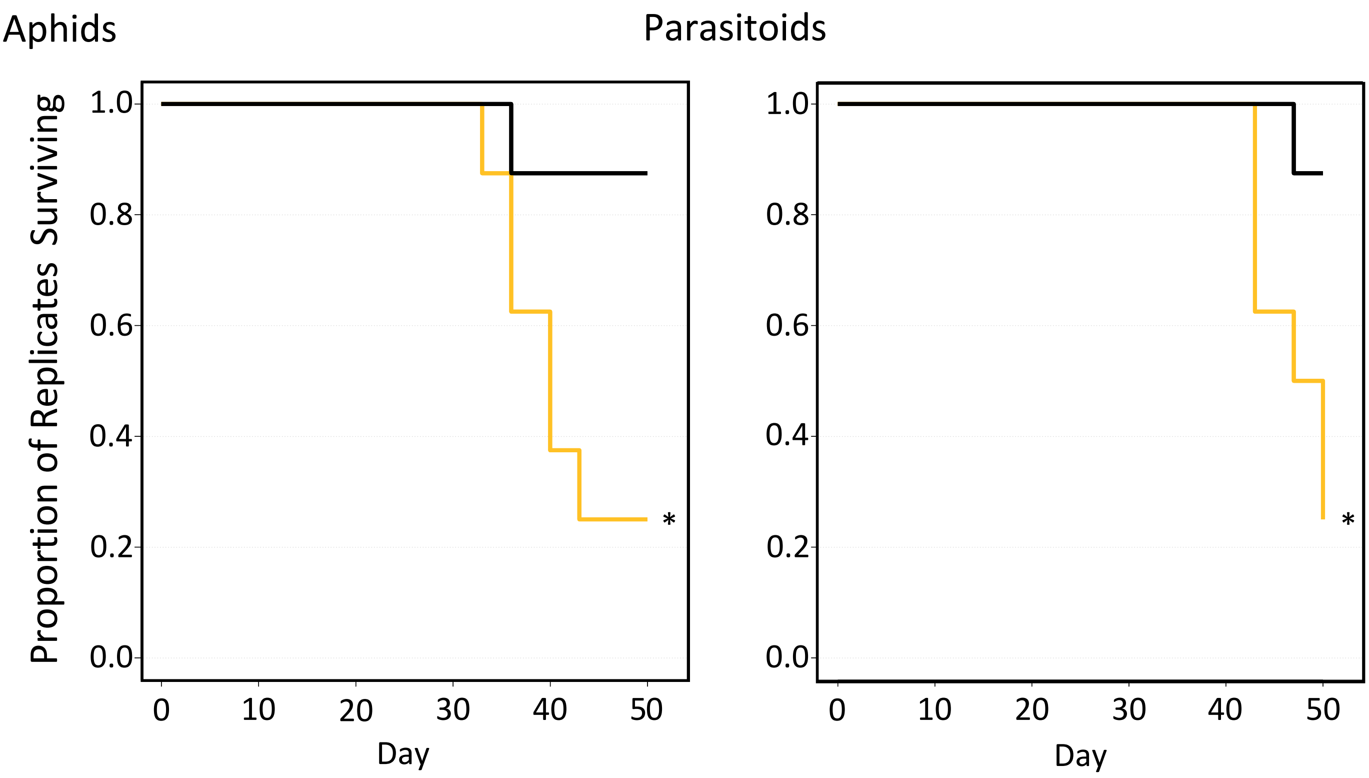

Figure 5.3: The persistence of *M. viciae* and *A. megourae* communities in long (18:06) (yellow line dots) and short (14:10) (black line) day treatments. Each treatment was replicated eight times. *P<0.05.

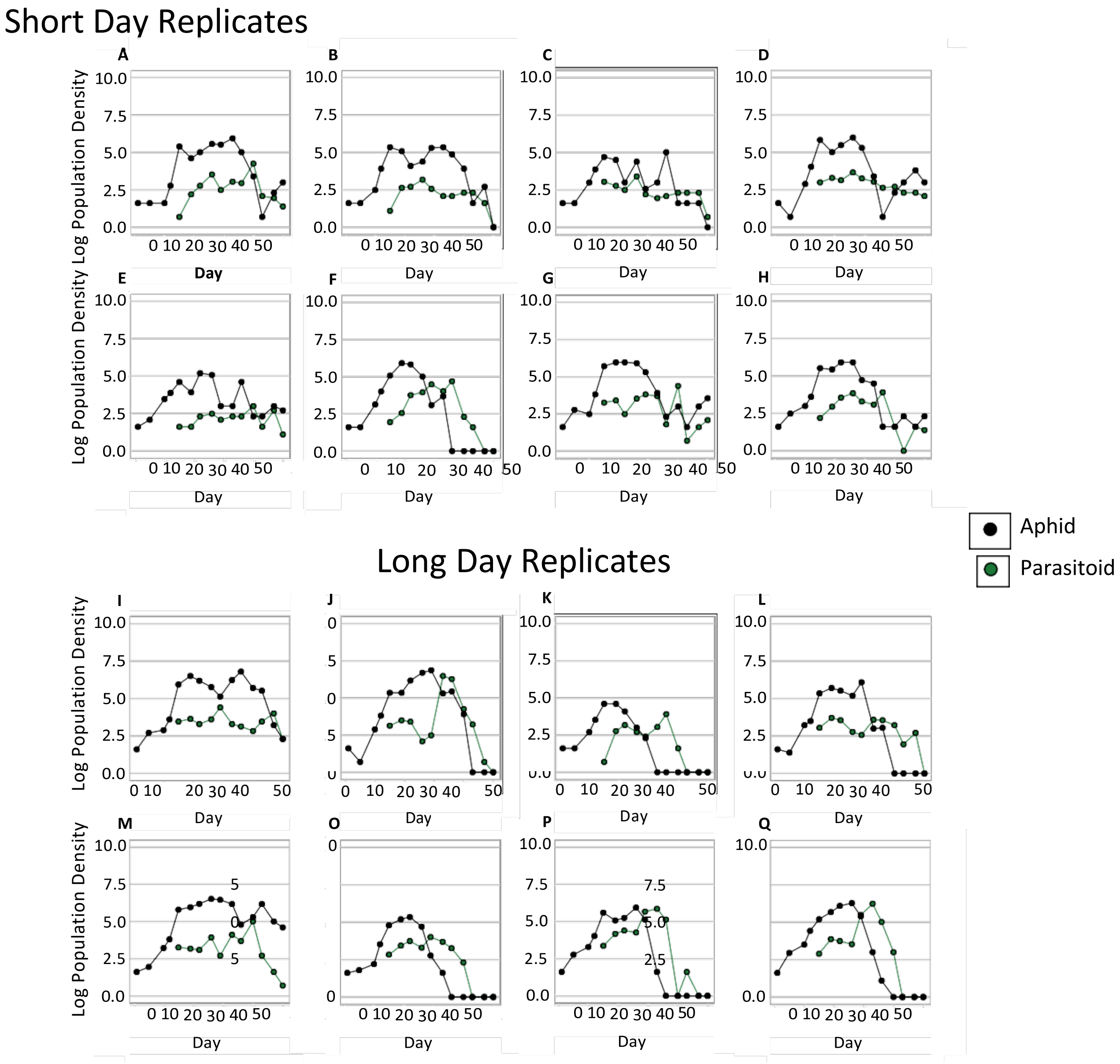

Figure 5.4: Population dynamics of the aphid species *Megoura viciae*, *and the parasitoid Aphidius megourae* over the 50 days of the experiment. Plots A-H display short day replicates while plots I-Q show long days.

Chapter Six

General Discussion

Overall summary

This thesis combines three scientific methods to explore the effect of climate change-induced range expansion on species interactions and community stability. Synthesis brings together the work of many scientists, finds general patterns and exposes the gaps that require further research. I used experiments to observe detailed mechanisms, which we can then expand using experimental parameters and modelling to explore the impacts of the mechanism on the wider community. Here I show that range expansions both directly, and as a result of changing daylengths change both species interactions and through this, life-history traits and community stability (Figure 6.1). I look in detail at one mechanism behind the changes in interactions- the impact of light regime of interspecific interactions. We find that daylength changes the competitive strength between two herbivores, as well as the top-down control of herbivore by a parasitoid wasp. We then link this change in top-down control to changes in community stability.

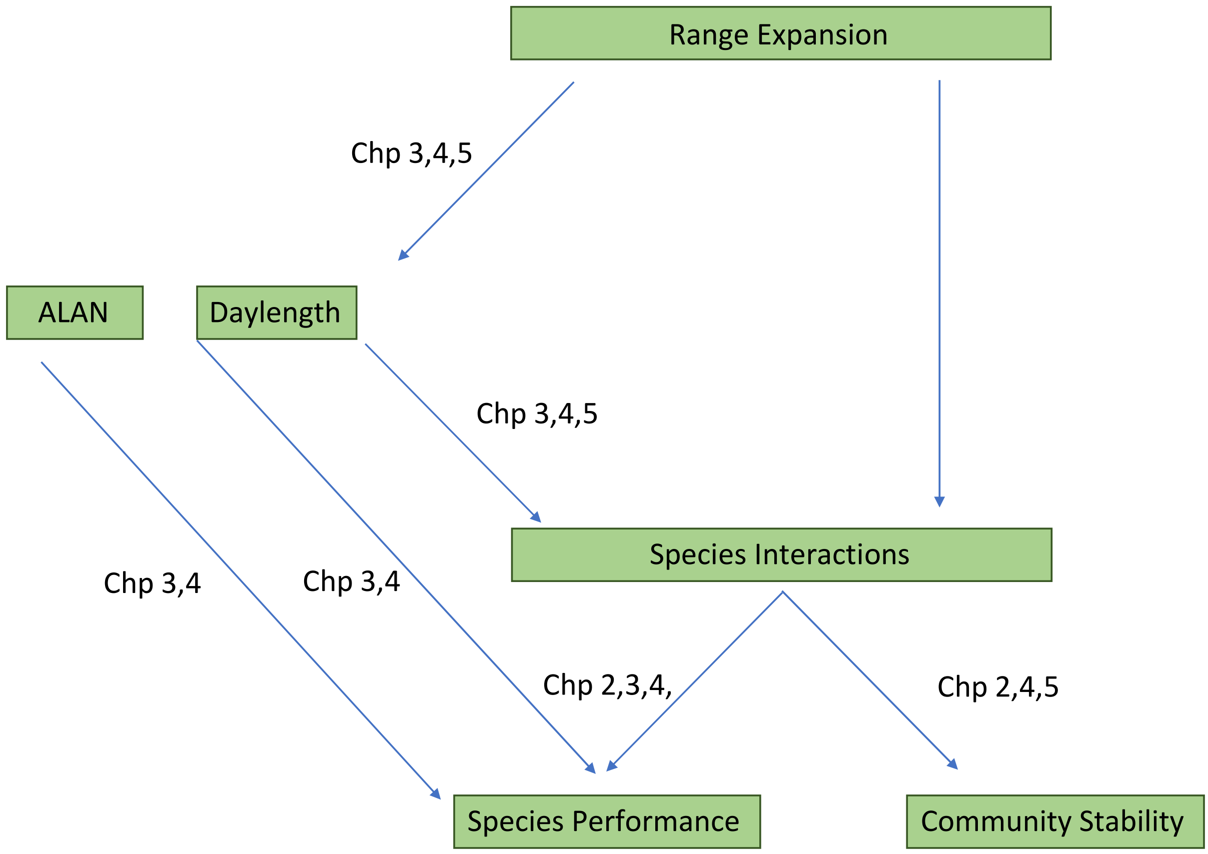

Figure 6.1: Summary of thesis. **Chapter 2**- Range expanded species alter interactions with others, and through this change both species and community performance. **Chapter 3**- More northerly summer daylengths change aphid competitive ability, impacting directly and indirectly on numbers. **Chapter 4**- More northerly summer daylengths as well as ALAN cause an increased parasitism rate of aphids by a parasitoid wasp. **Chapter 5**- More northerly summer daylengths reduce system stability due to increased parasitism rate of aphids by a parasitoid wasp.

Detailed Summary

Each data chapter of the thesis aimed to answer a different aspect, each with direct hypotheses. I initially conducted a meta-analysis, investigating how changes in species interactions caused by range expansion affect life history traits. In the final three chapters, I experimentally studied the impact of one abiotic factor impacting on populations expanding their ranges, and how it impacts of biotic interactions. I investigated how daylength impacts both population dynamics and inter-species interactions, using a plant-aphid- parasitoid model system.

Chapter Two aimed to discover the impact of climate change-induced range expansion on species and community performance driven by changing interactions between species. This was done using a systematic review of current literature and conducting a meta-analysis on the resulting data. I hypothesised that the interactions of both the expanding and native organisms will change as a population expands, but that the strength of the effect will vary between interaction types. I found that range expansion caused changes in species interactions, and as such an overall negative effect on species performance, with this effect consistent for both the expander and resident species.

In **Chapter Three,** I aimed to investigate the impact of different daylengths on the community dynamics of a multitrophic insect community. I found a decrease in cumulative abundance of the aphid *A. pisum* under Northern conditions, coupled with an increase in cumulative and peak abundances of the aphid *M.* viciae when in the two aphid community. However, *M. viciae* did not respond to daylength when it was the only aphid species present in the food web experiment, showing an indirect effect of daylength on the competitive dominance of *A. pisum.*

Chapter Four aimed to explore the impact of photoperiod, ALAN and a drop in night temperature, all separately and interacting, on the attack rate of a parasitoid wasp. I found that both increasing daylength and artificial light at night increased the parasitism rate of *A. megourae*. These results highlight how poleward range shifts are likely to substantially alter host-parasitoid associations, and that the strength and pattern of this effect will depend on the local microclimates available to (and used by) the aphids. I then used a model to test the potential impact of such increased attack rates on host-parasitoid population dynamics and found that it predicted a dramatic decrease in stability with increasing daylength.

Chapter Five aimed to experimentally test the predictions concerning the effect of photoperiod on the community dynamics and stability from the model in **Chapter Four.** I show that increased length of day corresponded with decreased stability, demonstrated by increased species extinctions and variation in parasitoid population dynamics, with this effect driven by a higher parasitism rate in the long day treatment. Therefore, a change in light regime can drive community stability by impacting on the strength of species interactions, which have the potential to cascade through food webs.

Crop pest impacts

The results of thesis predict a change in crop pest dynamics, with greater peaks and troughs of both herbivorous pests such as aphids as well as their natural enemies, as the natural enemies over exploit their hosts. There may be more occurrences of local extinctions and re-colonisations as for example seen in a study about plant hoppers and an associated egg parasitoid (Cronin 2004). These local extinctions are most likely to be more specialist species that rely on a smaller number of hosts

(Petchey *et al.* 2008). The range expansion of crop pests into novel agricultural areas have the potential to greatly decrease production. In the U.K. seed potatoes have historically been grown in Scotland to reduce the potential of aphid attack (Pickett 1989), this business could be substantially impacted by an expansion of aphids.

As daylength change is related to both the time of year as well as latitude, it is hard to make assertions about daylengths that expanding species will experience in their new range. However Bebber et al. (2013) have shown through a meta analysis, an average poleward shift of pests and pathogens of 2.7±0.8 km yr^{-1}since 1960. Over the last 60 years pest species will therefore have moved approximately 162km, roughly equal to the poleward distance between London and Lincoln, UK. The difference of daylength between these two regions is 20 minutes on the summer solstice. However, as more mobile species are able to expand their ranges both further and faster, this average effect may be dwarfed by some species. As such many species may be experiencing daylength shifts that are in the hours different to their native range, which as I have shown in the previous chapters, may have wide reaching effects on species interactions and stability to extinction.

Generality of results

Despite the findings of this thesis being primarily concerned with aphids and parasitoids, the results can be more generalised. For the effect of increased attack rate for example I would argue that this effect would be expected to occur for any consumer whose consumption of lower trophic levels is restricted by available foraging time (assuming a diurnal activity pattern). Although this may not apply to egg-limited parasitoids for example it may apply to many predator species. Additionally while I have shown an increase in attack rate here with increased daylength, the opposite may well apply to nocturnal consumers whose attack rate would be expected to decline as has been seen in (Perdikis, Lykouressis & Economou 1999).

Species Extinctions

The reduction in system stability through longer light regimes as communities move poleward hypothesised in **Chapter Four** and shown in **Chapter Five,** as well as shown directly in **Chapter Two** where range expanders invade native communities and have effects that way, may partly explain the current extinction crisis. Insects are currently declining at an exceptionally high rate, with 40% of insects threatened with extinction (Sánchez-Bayo & Wyckhuys 2019). As diversity gets eroded through the loss of species, this can lead to a reduced community stability with the potential of further extinction cascades (Sanders, Kehoe & van Veen 2015; Sanders *et al.* 2018b). The range expansion of populations has already been shown to impact the stability of native communities, causing local extinctions through changes in competition, e.g. (Vogel *et al.* 2002). Range expanding predators can have a large impact on the stability of native communities. The introduction and subsequent range expansion of the brown tree snake in Guam correlate well with the range contraction of the forest avifauna (Savidge 1987). Even when not exhibiting local extinctions, range expanding species can reduce the stability of communities, as seen in decreased species richness and higher variation in communities invaded by a range expanding shrub (Báez & Collins 2008).

As global species richness decreases the ability of communities to buffer against perturbations decreases, increasing the likelihood of cascading extinctions. The reduction of stability due to decreased species richness has been shown both experimentally (Sanders *et al.* 2018b) and theoretically (Thébault & Fontaine 2010). A species can also become functionally extinct while still existing in low numbers in a community. At this point, the species exhibiting a greatly reduced population size leads to the extinction of another species in the community. As such, it is of great importance to have a mechanistic understanding of how a change in daylength of the range expanding species impacts on both them and the community they expand into a new region.

Future work

The work herein shows that species interactions change when experiencing a range shift. I provide some mechanistic insights, demonstrating how the shift in light regime associated with range expansion changes species interactions and influences population dynamics and stability in a small community, lab-based system. The impact of light regimes on species warrants a deeper understanding.

Complex communities

It is of fundamental importance to use small communities to get a mechanistic understanding of species interactions, which we can then use to piece knowledge together. Species may respond in complex and different ways, clouding the results. However, once we have a predictive understanding, it is important to use larger communities to test the stability of these predictions in real-world scenarios. The plant-aphid-parasitoid system is highly advantageous in this setting, as the network is very large (Van Veen *et al.* 2008), consists of generalists and specialists, e.g. (Sanders *et al.* 2018) and can be put together into larger communities as knowledge increases. By introducing hyperparasitoids, the system can gain another one or even two trophic levels (Sanders *et al. in prep*).

Additionally, the patterns described in this are for a sessile aphid and a diurnal parasitoid. This effect is the opposite for a nocturnal predator, displaying an increased attack rate under shorter than longer days (Perdikis, Lykouressis & Economou 1999). It would be interesting to investigate the different population dynamics of a community consisting of diurnal species, nocturnal ones and a combination of the two.

Field experiments

Laboratory experiments are important as they reveal the mechanisms under more controlled conditions. However, it is also important to test how these communities respond in field conditions to validate results from laboratory experiments. To test how communities respond to range expansion, experimental communities ranging from individual species through to more complex species assemblages could be placed in temperature-controlled cages (to control for the confounding effect of temperature and to mimic that climate warming effect), along a latitudinal gradient. The alternative to this approach, requiring a lower number of researchers, would be to conduct the same experiment as above in one location but extending the daylength using artificial grow lights which have the correct spectra of lights for growth and reproduction. Both of these experimental approaches have advantages and disadvantages, with the latitudinal gradient experiment requiring a large number of people to conduct the experiments and potentially more confounding factor but any results being closer to reality. The artificial lights in the alternative experiment will not be able to completely replicate daylight, and as such, would address more the impact of artificial light, rather than daylength caused by range expansion on communities. Ideally both experiments would be conducted at the same time and combined with models using parameters taken from experimental systems.

Additional effects of changing daylength regime

As daylength is not consistent over the course of the year, many organisms have adapted to using the changes in daylength as a cue. The entry into and out of insect diapause, for example, is predominantly controlled by photoperiod (Nijhout 1994). An important next step in research understanding range expansion and light regime impact on ecological populations would be to investigate whether it is daylength per se or the rate of daylength change that causes the induction of this important life stage. The importance of this lies in that diapause induction would either advance or retreat temporally dependant on which way insects use daylength as a cue.

Modelling

After having completed these experiments, it would be of great value to extract parameters from the data and using these, to construct more complex population dynamic models. Through this, we can test the impact of changes in daylength, artificial light, and changes in temperature on the population dynamics and stability of these systems. This knowledge will be of great importance not only to range expansion science, but also to agriculture, allowing greater insight into predicting crop pest outbreaks, and as such can improve timings of planting and insecticide applications. In addition to modelling population dynamics of these insects, it would also be of great benefit to use to the data collected in previous experiments in Species Distribution Models (SDMs), to assess where individuals and groups of species are likely to expand into dependent on their abiotic and biotic limitations. Although many papers comparing the modelled and actual ranges of a species show that the actual range is less than that of the modelled (Bulgarella *et al.* 2014; McQuillan & Rice 2015; Stewart *et al.* 2015), regularly it is biotic rather than abiotic factors that are predicted to be the restricting force, e.g. (Engler *et al.* 2013; McQuillan & Rice 2015; Wilschut *et al.* 2016). As such, including biotic interactions will give a better prediction of future species distributions, which will be of high value to both conservation, agriculture and natural history.

Conclusion

As the climate continues to change, we can expect further range expansions, which, as I have shown will alter species interactions and traits. This can have a detrimental effect on ecological network structure and the stability and functionality of systems, as well as crop security, which is of particular importance in the current turbulent times. Despite these challenges, there are also opportunities to range expansion. Invasions have been used as large scale experiments, where we can begin to understand community assembly and changing interactions. With range shifts occurring naturally, conservationists may be able to save a species by relocating it, when there is a barrier to its natural range expansion, whilst knowing at least some of the impacts of this range change. Further the impact of range expansion will depend on the time expanders and resident species have cooccurred in the same habitats. We can expect the dynamics between species and for whole communities to chance with increased evolutionary time. Understanding how species and network structure will respond to our changing world will allow us to put systems in place to slow the detrimental effects of range expansion, safeguard species and crops.

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