An investigation into the vulnerability of UK butterflies to extreme climatic events associated with increasing climate change

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Contents

Abstract

Climate change while associated with change a in the mean climate also presents itself as a change in the variance of climate, resulting in an increase in the number of extreme climatic events (ECEs). Increased numbers of hot days, droughts and extreme precipitation events are all predicted under future climate scenarios. To date, there is very little understanding as to the potential effects that this may have on biodiversity. In order to model the future impacts of ECEs on biodiversity and to inform conservationists about the most appropriate mitigation strategies, we need to understand how ECEs have impacted species in the past, which species are sensitive and why? Finally, can factors such as habitat and topography play a role in reducing the impact of ECEs? This thesis aims to advance the knowledge relating to the above questions by examining their impact on UK butterflies, a bioindicator group.

This study developed a novel approach to identifying statistically identified, biologically relevant ECEs (heat, cold, precipitation and drought). Research into the impact of ECEs on yearly population change, localised declines and widespread decline events, identified that UK butterflies are particularly vulnerable to extreme heat during the overwintering phase, while tUK butterflies find extreme heat beneficial during their adult phase and finally are negatively impacted upon by precipitation extremes during their adult life stage. Chapter 4 of this thesis found that increasing slope heterogeneity in association with increased habitat diversity buffered butterflies against widespread declines associated with ECEs. Finally, chapter 5 of this thesis found that butterfly families respond differently when accounting for all extremes across all life stages, but that life history traits such as dispersal and number of larval host plants can be used to predict a species sensitivity to various ECEs.

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I am finding this a very difficult piece to write, not because there is nothing to write about but because there are so many people that I need to acknowledge. I think maybe the best approach is to break people into chunks. The first chunk I'd like to talk about is home. By home I mean my home in Norwich. Rich and Barney you are the reason I can call it this. We have shared our highs and lows throughout the PhD and you guys have always helped me through the lows and helped me celebrate the highs. I have been so fortunate to find two mates to go through the process with and while we are all such different characters I think we have gelled and I hope will continue to gel and see each other for years to come. Please never be a stranger either of you.

So I have acknowledged "home" so now I better acknowledge HOME. Firstly, everyone that knows me, will know I am blessed with a family that is hugely involved and supportive. Without sounding too sickening, my parents are my best friends. My parents have always been here to offer me advice and knock me straight when I need it and believe me the perspective they have offered me throughout the PhD is the reason I am able to sit here writing this. Dad, I hope you realise how important those evenings in "the Moroccan place" have been. Mum, I always love our rambling phone calls that allow me to forget whatever issues are going on at my end. You guys have been extremely busy moving home, working and travelling during my PhD but you have always made time for me and I hope you know it is appreciated. Muzz, Finn the last 4 years have seen massive change for all three of us. I now have a sister, touring Europe with her band and giving me goose bumps every time I hear her sing. I'm incredible proud of what you do and think you're incredibly talented. Finn, bloody hell, your about to start graduate medicine and in my mind your still 12. I am so happy with how close I feel we have grown in the past few years and I hope you feel it too. You two, what inspires me most about you both is your generosity with your time and your emotions, both of which you have given me in spades so thank you.

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Introduction

Today there is increasingly strong evidence that climate change is causing direct and substantial changes to our natural environment (Parmesan 2006; Morán-Ordóñez et al. 2017; Ameca y Juárez et al. 2013; Wernberg et al. 2012; Smale & Wernberg 2013), and unless effective mitigation and conservation actions can be identified an ever increasing number of species are at risk of extinction (Cahill et al. 2012; Urban 2015; Thomas et al. 2004; Foden et al. 2013). For effective mitigation and conservation actions to be carried out there is need to obtain accurate predictions of how species will respond to future predicted changes in our climate (Guisan et al. 2013). To date, the majority of studies have focused on how species respond to mean changes in climate (Morán-Ordóñez et al. 2017), with far less attention paid to the effects of extreme events. Extreme climatic events play an important and increasingly recognised role in biological change (Wernberg et al. 2012). They can impact a species population dynamics, constraining their geographic distribution and defining their climatic envelope (Lynch et al. 2014; Smale & Wernberg 2013; Kittel 2013). Extremes of climate can impinge on species directly, e.g. through thermal intolerance or indirectly by affecting their food source and/or habitat availability. This study will address how butterflies respond to extreme climatic events, using butterflies as a bioindicators of the potential responses of other taxa.

Extreme climatic events are increasing in frequency

At present, there is a dearth in the quantity of research available on the potential biological impacts of ECEs on species' geographical distributions and also on their phenology and survival (McDermott Long et al. 2017). The characteristics of extreme climatic events are also changing, making it hard to predict their impacts, the distributions of various extremes such as drought, heat wave, precipitation events are set to be altered in the future (Seneviratne et al. 2012).

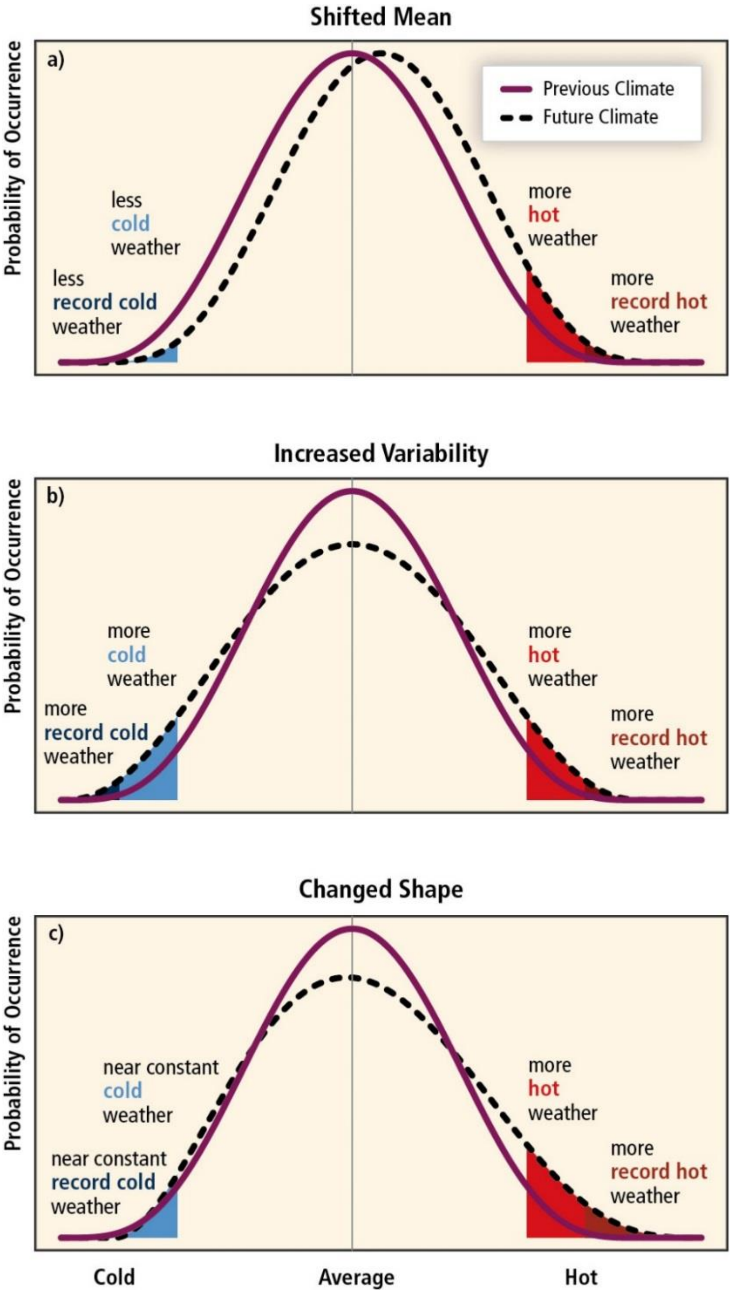

Figure 1 the effect of changes in temperature distribution on extremes. Different changes in temperature distributions between present and future climate and their effects on extreme values of the distributions: a) effects of a simple shift of the entire distribution toward a warmer climate; b) effects of an increased temperature variability with no shift of the mean; and c) effects of an altered shape of the distribution, in this example an increased asymmetry toward the hotter part of the distribution. (IPCC 2012)

Recent summary reports have summarised the evidence and highlighted that Extreme climatic events (ECEs) are increasing in intensity, frequency and duration (IPCC 2013; IPCC 2012; NAS 2016). Anthropogenic climate change is characterised by changes in the mean global climate but also changes in the intra- and inter-annual climatic variability (Bailey & van de Pol 2016; IPCC 2012). Fig. 1 graphically represents the predicted changes in global climate. Graph a) in Fig. 1 represents the shift to the right in global climate which will be associated with more frequent hot weather events. Graph b) shows the change in the distribution and variability of climatic variables associated with climate change. We can see an increase in the number of hot and cold weather events. It is important that we do not consider a) and b) separately since they occur synchronously with one another. Graph c) Fig. 1 represents this synchronous projection and we can see that depending on your global location we can expect far more hot weather events and potentially just as many cold weather events. In addition to this, change in climate variability will change the skewness of precipitation, resulting in an increase in the number of precipitation events.

ECEs are described by the IPCC (2012) as “the occurrence of a value of a weather or climate variable above or below a threshold value near the upper or lower ends of the distribution range of observed values of the variable”. This threshold value used in the IPCC has tended to vary from study to study but usually encapsulates an event that is likely to happen between a range of values with a 10-1% rate of occurrence for a given time period whether it be a day, month or a year i.e. during a specified “reference” period (IPCC 2012). If adequate long-term data of a climate variable is observed, it is then possible to analyse its statistical distribution and estimate the probability of being subjected to an event above or below a set threshold given climate variable's distribution.

The IPCC report (IPCC 2012) highlights an important problem relating to modelling extreme events as it claims that "the data for temperature and precipitation are widely available, but some associated variables, such as soil moisture, are poorly monitored, or, like extreme wind speeds and other low frequency occurrences, not monitored with sufficient spatial resolution or temporal continuity". This makes it very difficult to accurately predict extreme weather at finer scales as it is not possible to know enough about the confounding factors that influence the chance of an extreme event. ECEs may become more prominent, or rarer, under future climate conditions at any given location as climate change is likely to change the distribution of the climate variables (IPCC 2012). There is plenty of evidence to suggest that ECEs at both end of the scale, e.g. cold vs hot , drought vs heavy precipitation, are increasing in frequency and magnitude overall and will continue to do so over the next decade (Thibault & Brown 2008; Welbergen et al. 2008; Wernberg et al. 2012; Grilo et al. 2011; Sears & Angilletta 2011; Archaux & Wolters 2006; Diez et al. 2012; Hagger et al. 2013; Ummenhofer & Meehl 2017).

It is important to draw attention to the distinction between extreme weather events and extreme climate events:

- "An extreme weather event is typically associated with changing weather patterns, that is, within time frames of less than a day to a few weeks.

- An extreme climate event happens on longer time scales. It can be the accumulation of several (extreme or non-extreme) weather events (e.g., the accumulation of moderately below-average rainy days over a season leading to substantially below-average cumulated rainfall and drought conditions)"(IPCC 2012).

As in the in the IPCC report (IPCC 2012), throughout the rest of this study, both an extreme weather event and an extreme climatic event will be referred to as an Extreme Climate Event (ECE). ECEs come under many guises; e.g droughts, flash floods, strong winds and storms, torrential rain, extreme cold spells, or extreme heat waves. Research regarding the potential biological impacts of these ECEs is currently lacking (Suggitt et al. 2017).

The first and most basic problem associated with studying extremes is analysing how they have changed in the past. There are critical issues with data availability as, given the very nature of ECEs, it is difficult to quantify the impact of rare events due to data scarcity (IPCC 2012). The limited data available makes it harder to analyse trends and patterns especially in less comprehensively monitored areas of the world. The IPCC report (2012) pinpoints another key aspect impeding data availability for ECEs, it involves the timescale at which to address an ECE. Determining the appropriate temporal resolution (e.g. hourly/daily precipitation as opposed yearly drought) is key in studies investigating the impacts of ECEs. While longer period resolution data for variables such as temperature and precipitation are available globally since the early 20th century, analysing the same variables using a higher resolution i.e. daily or hourly is more difficult as the data are not generally available and if they are, only since the mid-20th century (IPCC 2012). The lack of data in many parts of the world results in limitations in the evaluation of observed changes in ECEs for many regions. Fortunately for this study, we have access to a fine scale temporal and spatial observational climate data set (Haylock et al. 2008) running in Europe for a long period of time and as such are not subjected to the same limitations involving examining ECE impacts.

ECEs are predicted to become one of the major causes of species extinction during this century (Canale & Henry 2010).The question then is, how will ECEs that have been predicted to occur more frequently in the future affect species distribution and what are the variables both in relation to species traits but also geographic variables that may make a species more or less vulnerable to increases in ECEs? For some species the climate extremes and not the mean of climate determine the extent of their geographic range or climatic envelope (Lynch et al. 2014).

Importance of life history traits in determining species' sensitivity to ECEs

Many species are experiencing pressures/ perturbations caused by continuous environmental change mainly as a result of anthropogenic activities (McDermott Long et al. 2017; Foden et al. 2013; Palmer et al. 2017). The unusual rate and extent of these anthropogenic alterations may go beyond the capacity a given population to evolve developmental, genetic, and demographic mechanisms affecting their ability to cope with environmental change, particularly ECEs (Chevin et al. 2010).

Life history traits, essentially, traits affecting a species' fitness within its habitat, optimising the species' fecundity and survival levels, evolve over a long period of exposure (Fabian & Flatt 2012). Species traits or functional traits, which fall here under life history traits, are a method of describing species in terms of their ecological roles and how they interacting with their environment or with other species. These traits, for which species groupings may be formulated, result from consistent responses to external pressures among different species (Chevin et al. 2010). In order to be able to fully understand the impacts that ECEs are having on a given population it is necessary to understand the aspects that regulate an organism's ability to cope with the fast rate of environmental change (Chevin et al. 2010). Ecologists need to be able to predict how ECEs could potentially result in differing responses depending on factors such as life history traits and habitat, influencing the level of exposure and sensitivity of a population. This is a difficult task to undertake. Williams et al. (2010) highlight that for many species, there is limited knowledge as to their critical population dynamic variables, physiological tolerances, ecological constraints, or long-term and indirect effects. It has been emphasised that in order to overcome this confusion and model how species respond to anthropogenic perturbations, it would be necessary to incorporate readily available biological information and look for consistent responses within groups that share traits (Ameca y Juárez et al. 2013; Murray et al. 2011; Foden et al. 2013; Williams et al. 2010). This will benefit models and management plans about critical thresholds affecting the potential survival of particular species or ecological communities.

Species' vulnerability?

A species' vulnerability is fundamentally based on three important characteristics (Dawson et al. 2011; Ameca y Juárez et al. 2013; Foden et al. 2013; Chevin et al. 2010; Tingley et al. 2013; Ameca Y Juárez et al. 2012):

1. **Exposure** is defined by (Ameca y Juárez et al. 2013) as "the nature and degree to which a system is exposed to significant climatic variations". In other words a species' exposure to ECEs can be described as the level of intersection between the geographic area in which a species occurs and the spatial extent of the ECE over a given length of time. It is however, important to note that exposure by itself does not equate to risk. The overall risk of a species experiencing ECEs relies not only on exposure but also the species' sensitivity and adaptability to the perturbation as highlighted below.

2. **Sensitivity** is dependent on its life history traits which may or may not make a population susceptible to an ECE due to key biological traits.

3. **Adaptive capacity** refers to species' phenotypic plasticity. It is dependent on whether behavioural and/or physiological processes exhibit enough flexibility to allow a given population to avoid or withstand the impact of an ECE. Adaptability could perhaps be placed under sensitivity as plasticity is an evolved trait (Chevin et al. 2010).

“A species’ individual susceptibility to climate change depends on a variety of biological traits, including its life history, ecology, behaviour, physiology and genetic makeup” (Foden et al. 2009). Chevin et al. (2010) highlight the lack of work that has been done in regards to identifying traits that are susceptible to climate change but especially ECEs.

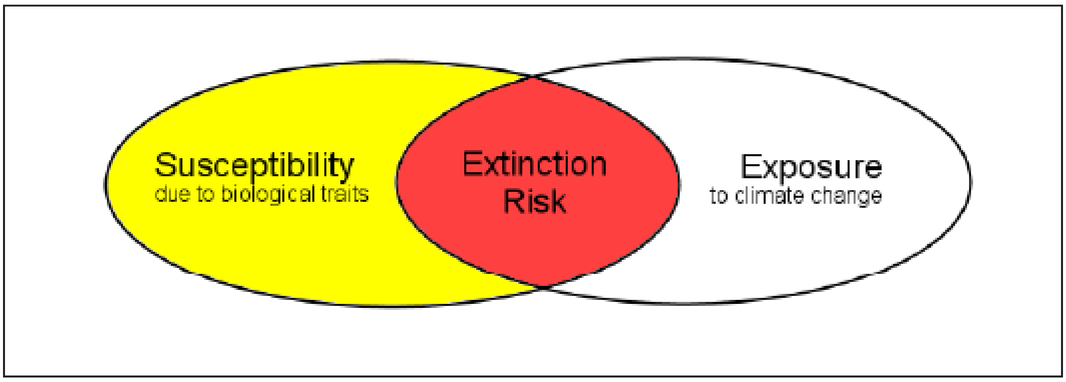

Figure 2 (Foden et al. 2009) Species highly exposed with intrinsic susceptibility are at greatest risk of extinction due to climate change

It is expected, and perhaps intuitive, that exposed species whose phenotypic traits make them more susceptible and/or unable to adapt quickly to changes in the frequency and intensity of ECEs will be those most vulnerable to this source of disturbance (Ameca y Juárez et al. 2013). ”The historical exposure of a species to a given disturbance over evolutionary time is expected to shape its intrinsic adaptability to that disturbance, reducing its likelihood of extinction from this source” (Ameca y Juárez et al. 2013). This indicates that species experiencing climate change and especially ECEs are likely to be vulnerable as they will be experiencing climate that they have not been historically exposed to.

Foden et al. (2009) through their work with the International Union for Conservation of Nature (ICUN) Red List indicate that some species are more vulnerable to ECEs than others due to intrinsic biological traits related to their life history, ecology, behaviour, physiology and genetics. Large-bodied species may also be particularly vulnerable to anthropogenic threats due to their typically slow recovery from rapid environmental perturbations (Tingley et al. 2013). These authors also indicate that specialist species may be less capable of dealing with novel environmental challenges such as ECEs because they are unable to survive outside of their climatic envelope. In addition to this, these species are more susceptible as even if they possess the phenotypic response capabilities to counteract the ECE, by being a specialist they are very often reliant on other species' survival that may not be able to cope with the extreme perturbations. This would eventually lead to the demise of the specialist species despite its ability to cope with the ECE. Species with small geographic ranges are usually subject to increased levels of risk of extinction from ECEs due to issues such as, small population sizes, increasing the likelihood of passing the minimum population threshold for no recovery.

How have species' traits been used in the past?

Progress is being made, as incorporating the species traits that increase their vulnerability has been highlighted as an issue in many studies (Chevin et al. 2010; Syphard et al. 2013; Williams et al. 2010; Ameca Y Juárez et al. 2012; Foden et al. 2013) while studies such as Van Allen *et al.*, 2012; Santini *et al.*, 2016 have begun to tackle this issue. Ameca Y Juárez *et al.*, 2012; Foden *et al.*, 2013 both stress that those traits that have prevented species extinction due to persistent exposure to continuous mean shifts in climate, might not be the same traits that prevent them from experiencing mass-mortality events as a result of ECEs. This emphasises that only accounting for traits identified as being vulnerable by (Foden et al. 2013) when assessing the potential sensitivity of species to climate change does not account for how a species may respond to ECEs. The existing IUCN criteria have a wide range of mechanisms for calibrating threat levels across different life history and threat contexts, and this approach could be extended to deal with climate change impacts (Foden et al. 2013) including ECEs. It is important to note that currently, risk assessments for mammals in the IUCN Red List are based on a categorization that incorporates continuing, expected or anticipated threats, but does not reflect ECEs in any systematic way (Ameca y Juárez et al. 2013).

Other studies (Chessman 2013; Tingley et al. 2013; Krab et al. 2013; Frederiksen & Daunt 2008; Oliver et al. 2013) have analysed the impact of specific events on the populations of specific species. In many of these studies correlative analysis was used in order to assess the traits that were most vulnerable to extirpation. Studies such as Tingley, Hitchmough and Chapple, (2013) found that intrinsic traits, that render species prone to extinction, appear largely consistent across vertebrate taxa but also put emphasis on the issue of incorporating extrinsic threats such as habitat loss and invasive species. (Murray et al. 2011) questions on-going efforts to identify species traits that best captures overall variation in vegetation response to ECEs, as species face multiple, simultaneous threats. It is important to note that a far greater number of studies underline the importance of incorporating trait specific projections into species distribution models.

So, how might species' traits be useful to help predict the impacts of ECEs on species' distribution in the future?

How might species' traits be used in future research of species' vulnerability?

Murray et al. (2011) make a fundamental point regarding the use of species traits as a future predictor. If species traits predispose them to extinction by certain stressors, then grouping species that share attributes can facilitate the prediction and management of global change impacts. This one sentence underscores why species traits are becoming more important in highlighting the impacts of climate change and ECEs on distributions and extirpations. Tingley et al. (2013) and Murray et al. (2011) both emphasise that the identification of the mechanisms/ traits that mark a species being as vulnerable to various ECEs will help to identify species at greatest risk and hence lead to more strategic management approaches for dealing with such stressors.

Few studies have considered both extrinsic and intrinsic threats simultaneously (Tingley et al. 2013; Ameca y Juárez et al. 2013). A surprising omission as the extrinsic impact heavily depends on the species intrinsic capabilities as well as location and exposure. Assessing both in combination may expose spatial eventualities in extinction risk that are not apparent when either type of variable is considered in isolation. Both studies highlight a considerable lack of knowledge on the mechanisms by which

ECEs impact upon biodiversity in terms of populations, species and ecosystems.

One method of analysing which traits are an important predictor of species vulnerability would be to identify zones where species have been exposed to ECEs. If the population data set is big enough for multiple species within the impacted zone it may be possible to run correlative analysis to demonstrate any traits that are a good predictor of the population die-off or continuity that would have been captured in the population data. This method can help target species that possess a combination of traits that makes them highly vulnerable to such ECEs while being associated with a degree of exposure for which such traits may become critical in shaping survival (Ameca y Juárez et al. 2013). Data sets such as the UK Butterfly Monitoring Scheme data set may be appropriate for studies like this. Assessing vulnerable species traits would enable the important division to be drawn between populations that are facing and might experience population die-off (and thus are in need of response conservation strategies) and those that are less vulnerable (Ameca Y Juárez et al. 2012). There is currently a large gap in identifying species which could benefit from conservation actions to mitigate impacts from such extreme phenomena (Ameca y Juárez et al. 2013). This gap in knowledge is primarily due to the lack of identified species traits that are associated with species vulnerability. Even the IUCN Red List does not, for example, include any clear concern as to the impacts of ECEs (Ameca y Juárez et al. 2013). Identification of multiple sensitive traits as opposed to a single trait is very important as species vulnerabilities will often depend not on individual traits but on combinations of traits (Díaz et al. 2013).

The importance of Habitat in limiting exposure to ECEs

Species can reduce their sensitivity and increase their adaptive capacity to extremes using their evolved life history traits. As already mentioned, there is a third element which determines how vulnerable a species will be to ECEs, exposure. When subjected to an ECE, the survival of an organism, sensitive to the ECE, will depend on whether that organism can find a refuge that buffers against the extreme conditions it is experiencing (Scheffers et al. 2014). Microhabitats, can offer a species different microclimates to those it experiences in the wider community in which it resides. The question then is, what is the capability of these microclimates in buffering against the predicted increase in frequency and intensity of ECEs that the UK expects to be subjected in the future? Again due to the increased awareness of scientists about the dangers ECEs pose to our biodiversity there has been a considerable increase in the attention that habitat may play in terms of buffering against ECEs.

Studies such as Oliver et al. 2010; Scheffers et al. 2014; Newson et al. 2014; Hylander et al. 2015; Ameca y Juárez et al. 2013 have begun addressing the importance that habitat might play as a buffer against ECEs and not just mean climate change. Indeed, Oliver et al. 2010; Oliver et al. 2015 have begun addressing the response of UK butterflies to extremes and has identified very interesting findings regarding the importance of habitat in maintaining population stability under extreme condition and also addressing the vulnerability of drought vulnerable species to a single drought event in 1995. This analysis has pushed this study to investigate the topic even further. Rather than looking at population stability, this study addresses the importance of habitat in buffering against ECEs in a year in which a large proportion of the population of a species has been directly impacted. It allows us to examine the impact of decline event years attributed to ECEs while also allowing us a longer temporal scale that studies that just looking at the impacts of one event year.

Habitat has been shown to be an important buffer to ECEs (Kindvall 1996; Oliver & Morecroft 2014), but there are many complex aspects of habitat to consider when addressing this buffering capabilities. For example, habitat patch size if too small may create issues for species when considering minimum patch requirements, but at the same time a broad range of microclimates in confined area, for which mobile organisms can move between, can allow them to maintain themselves closer to their optimum environmental conditions (Oliver & Morecroft 2014).

Land use in the UK has changed and evolved gradually for centuries and until the 19th century butterflies had thrived in habitats that had been created by forestry and farming practices (Asher et al. 2001). However, during the 20th century the rate of habitat change increased dramatically resulting in large areas that were previously suitable for UK butterflies being not so. The loss of large swaths of breeding habitats has dramatically affected UK butterflies and their distributions. Our interest in addressing the impacts of habitat on buffering extreme weather is hence two-fold. By understanding their potential buffering capabilities, it may add to their importance as an ecosystem service in the eyes of policy makers. Without understanding the importance of habitat heterogeneity in terms of dealing with ECEs, the loss of diversity in habitat that we have seen throughout the 20th century and the 21st century so far could leave UK biodiversity extremely vulnerable and exposed to future extreme events which have been predicted to occur more frequently. This may result in the constriction of range of some species but also extinction events for others.

Why study butterflies?

Butterflies are a taxonomic group that are well known to be sensitive to changes in their habitat and climate (Essens et al. 2017; Fox et al. 2015). As poikilothermic organisms and their short and complex life cycles they are predicted to respond readily to climate changes, in this case ECEs, and act as a good indicator of how other species may respond to future changes (Thomas 2005). Research in the UK on butterflies is fortunate to be able to use the exemplar data set on site level abundance provided by the UK Butterfly Monitoring Scheme (UKBMS) (M. Botham et al. 2016).

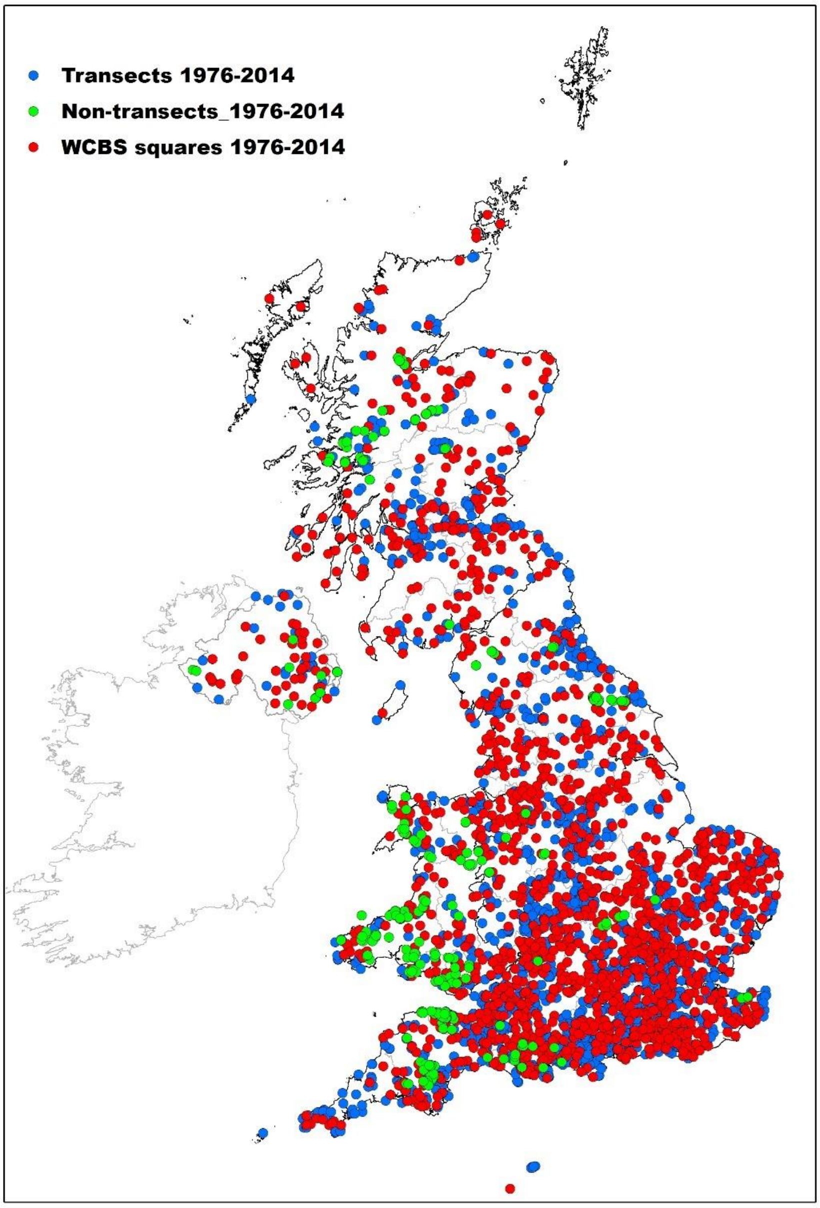

Figure 3 Identifies UKBMS transect sites used in this thesis throughout the UK

However, analysis of this data set has shown that 57% of species have decreased in abundance since 1976 (Fox et al. 2015). Trends like this emphasise the importance and urgency in understanding factors which may be driving many species to extinction in the UK. Another huge advantage of studying UK butterflies is that they are a taxonomic group that have been extensively studied in relation to the impacts of climate change. Northern range shifts (Parmesan 2006; Parmesan et al. 1999; Franco et al. 2006;

Thomas et al. 2006; Pateman et al. 2012), changes in phenology (Roy & Sparks 2000; Sparks et al. 2006), population changes (Dennis & Sparks 2007; Roy et al. 2001; Mair et al. 2014; Mason et al. 2017) and life history traits (Diamond et al. 2011) have all been extensively studied in relation to mean changes in UK climate, however fewer studies have looked at the impacts of ECEs and when they have, have only addressed short term extreme events e.g. (Morecroft et al. 2002; Oliver et al. 2015) although studies such as (McDermott Long et al. 2017; Palmer et al. 2017) have begun addressing extremes over longer term datasets.

Objectives of the thesis

The main aims of my thesis were to address the following four issues:

1. Identify the importance of ECEs in driving year to year population change at the site level for UK butterflies, chapter 2. This was carried out to understand the extent to which ECEs can explain the yearly fluctuations in butterfly populations and identify vulnerable life stages.

2. Investigate the importance of ECEs in explaining decline events, for butterflies at the site level, 50% decline in population from preceding year, and at a widespread scale, 50% decline in population across 50% of the site at which a species occurs (Fig. 3), chapter 3. This was carried out to identify whether decline events are driven by climate but also to identify the most appropriate scale at which the impacts of ECEs should be addressed.

3. Investigate the importance of habitat diversity (both topographic and biological) in buffering butterflies against ECEs, chapter 4. This will allow us to understand the potential importance of conservation efforts in dealing with

future climate change by managing habitat or whether the impact of ECEs make these efforts futile.

4. Lastly, this study aimed to identify life history traits that can indicate a butterfly’s sensitivity to ECE, allowing us to assess the potential vulnerability of other butterfly species that were not addressed in this study, chapter 5.

Thesis structure

This thesis contains 6 chapters. Chapter 1 consists of a general introduction and introducing the context and reasoning for the topic addressed throughout the rest of the thesis. Chapters 2-5 are written in the form of scientific papers. At the time of submission chapter 2 is published (McDermott Long et al. 2017) and chapters 3-5 are presented as manuscripts in preparation.

The chapters are as follows:

Chapter 2: Sensitivity of UK Butterflies to local climatic extremes: Which life stages are most at risk?

Chapter 3: The impact of extreme climatic events on butterfly population declines in the UK: a long-term analysis.

Chapter 4: Can habitat characteristics buffer butterflies against the detrimental impacts of extreme climatic events?

Chapter 5: Which life history traits explain the sensitivity of UK butterflies to extreme climatic events?

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Chapter 2: Sensitivity of UK butterflies to local climatic extremes: Which life stages are most at risk?

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Abstract

1. There is growing recognition as to the importance of extreme climatic events (ECEs) in determining changes in species populations. In fact, it is often the extent of climate variability that determines a population’s ability to persist at a given site.
2. This study examined the impact of ECEs on resident UK butterfly species (n=41) over a 37-year period. The study investigated the sensitivity of butterflies to four extremes (Drought, Extreme Precipitation, Extreme Heat, Extreme Cold), identified at the site level, across each species’ life stages. Variations in the vulnerability of butterflies at the site level were also compared based on three life history traits (voltinism, habitat requirement, and range).
3. This is the first study to examine the effects of ECEs at the site level across all life stages of a butterfly, identifying sensitive life stages and unravelling the role life history traits play in species sensitivity to ECEs.

4. Butterfly population changes were found to be primarily driven by temperature extremes. Extreme heat was detrimental during overwintering periods and beneficial during adult periods and extreme cold had opposite impacts on both life stages. Previously undocumented detrimental effects were identified for extreme precipitation during the pupal life stage for univoltine species. Generalists were found to have significantly more negative associations with ECEs than specialists.

5. With future projections of warmer, wetter winters and more severe weather events, UK butterflies could come under severe pressure given the findings of this study.

Key-words Butterfly population changes, climate change, life history traits, linear mixed effects model, and sensitivity

Introduction

Climate change is causing direct and substantial changes to biodiversity and to entire ecosystems (Cramer et al. 2014); species have been altering their growth, phenology, and distribution (Root et al. 2003; Møller et al. 2008; Chen et al. 2011). While species are changing their distribution in an attempt to track the climatic conditions optimal for their survival, i.e. their climatic niche, their ability to do so is often limited. Some species are lagging behind the high velocity of climate change (Bertrand et al. 2011; Loarie et al. 2009; Devictor et al. 2012) resulting in range contractions (Foden et al. 2007). Both widespread and range restricted species are projected to have range losses and/or increased extinction risks as a result of changes in mean climate (IPCC 2007; Warren 2011; Warren et al. 2013; Foden et al. 2013).

Most attribution of climate change impacts on biodiversity (Parmesan et al. 2000; Doney et al. 2012; Chen et al. 2011; Root et al. 2003), and the projection of future impacts (Bellard et al. 2012; Pereira et al. 2010; Pacifici et al. 2015), is based upon the observed or projected change in mean climate, however the impacts of climatic extremes, such as heatwaves, heavy rainfall, and droughts are much less frequently studies and the rate and magnitude of these events is likely to increase in the future (IPCC 2012; Jones et al. 2014).

Extreme climate events (ECEs) have been shown to directly affect species populations by influencing reproductive and mortality rates (Jiguet et al. 2011). Changes in climate variability, as a result of climate change, leading to changes in the magnitude and frequency of ECEs may be more important for determining whether a species can persist in a given location, than are modest increases in average temperature (Bauerfeind & Fischer 2014; Parmesan et al. 2000).

Butterflies have been used to demonstrate ecological examples of species' responses to climate change (Parmesan et al. 1999; Warren et al. 2001; Franco et al. 2006; Thomas et al. 2006; Diamond et al. 2011; Pöyry et al. 2009; Wilson et al. 2005) and due to their ectothermic characteristics are a good taxonomic group to look at effects of extreme climatic events. ECEs, such as drought and heavy precipitation events, have been shown to be detrimental to the survival of butterflies, causing local extinction events (McLaughlin et al. 2002; Oliver et al. 2015) which highlights the importance of incorporating these ECEs in ecological studies (Easterling et al. 2000; Jentsch & Beierkuhnlein 2008; Fischer et al. 2014; Smith 2011a). Warmer, wetter winters have been negatively associated with changes in population growth rates as has heavy rainfall (Pollard 1988; WallisDeVries, Baxter & Van Vliet 2011).

Univoltine and multivoltine species are under different selective pressures due to differing numbers and timings of life stages. Life stage can be incorporated into the analysis to allow identification of sensitive stages within a butterfly's lifecycle to particular extremes (Radchuk et al. 2013; WallisDeVries et al. 2011).

Impacts of ECEs can be examined at a large scale (Roy et al. 2001; Pollard 1988; WallisDeVries et al. 2011) or take into account site specific information to avoid hiding population losses in one area due to gains in another (Wilbanks & Kates 1999). By analysing the impacts of ECEs at site level these losses and gains can be unmasked, allowing for attributions to be identified that may not have been in a broader scale study (Pearce-Higgins 2011; Newson *et al.* 2014). Site specific differences may be a function of a species' local site adaption to regional climate variables (Ayres & Scriber 1994) and habitat availability and characteristics also affect species responses to ECEs. Oliver *et al.* (2015) showed that reducing habitat fragmentation was effective at countering negative drought effects on butterfly populations and reducing landscape-scale habitat fragmentation may influence a species ability to withstand weather-mediated population declines (Newson et al. 2014).

ECEs have been defined using specific arbitrary thresholds (WallisDeVries et al. 2011), such as extreme heat being anything above 30°C. This only identifies heat as an issue during the summer, excluding the possibility that heat may also play a role during other periods of the year and other stages of a species' life cycle.

This study takes a new approach to identifying species responses to extremes, accounting for both the life stage and site specific effects thus providing a more dynamic and biologically relevant approach in identifying climatic extremes for an organism. This study aims to assess the impacts of ECEs on UK species over the 37 year period from 1976- 2012. This study will (i) examine the influence of ECEs on butterfly population change over a

37 year period; (ii) determine which butterfly life stages are sensitive to which ECEs and (iii) determine whether butterfly population changes are more associated with extremes of temperature or precipitation?

Materials and Methods

The Datasets

The butterfly dataset – UKBMS

Site level butterfly population indices were obtained from The UK Butterfly Monitoring Scheme (UKBMS), a comprehensive dataset for UK Butterflies consisting of records from thousands of volunteers across the UK. These data covers a period from 1976 (38 monitored sites) to 2012 (878 monitored sites). In total over the 37 year period there have been 1,802 different recording sites. At monitored sites, weekly counts of adult butterflies were made over a 26 week period between the beginning of April and the end of September on fixed routes provided the weather conditions were favourable for butterfly activity (Pollard & Yates 1993). This procedure is repeated yearly allowing for comparisons between years at that particular site but also between sites. Full details of the sampling methodology can be found in (Pollard et al. 1986). Population indices are based upon all generations that fall within the recording period, the indices are not split by generation. Species with fewer than 10 sites and/or less than 15 years of continuous data were removed from the analysis as in (WallisDeVries et al. 2011) limiting the number of species included in the analyses to 41 of the 59 regularly occurring UK butterflies. A separate model was created for each species to account for different lifecycle timings, numbers of generations and overwintering strategies.

Information on life history traits (voltinism: univoltine / multivoltine, species range: Northern range limited / widespread species, habitat generalist / habitat specialist species) were collated using (Asher et al. 2001).

The weather observations dataset

Daily maximum, minimum temperature and precipitation data on a 0.25 degree regular lat/long grid were obtained from the E-OBS dataset for the UK between 1950 and 2012 (Haylock et al. 2008). Site specific daily data was extracted using the latitude and longitude of the survey sites from the UKBMS dataset. For more information on how the data is interpolated into its gridded format see (Haylock *et al.* 2008).

Identification of Extreme Climatic Events and their biological relevance

Calendar dates were identified for all life stages of each butterfly (Ovum, Larvae, Pupae, Adult and Overwintering) according to their phenology (Eeles 2014) (Annex 1 Table 1). Overwintering period was set as a fixed period for all species (WallisDeVries et al. 2011), starting on the 1st of November and finishing on the 28th of February. The phenology of each species can vary from year to year in addition to the site to site variation (Van Strien et al. 2008; WallisDeVries et al. 2011). However, In this study we use fixed phenology dates for the butterflies to identify the start and end of each lifecycle for 37 years of data which the UKBMS covers. This is a caveat to be aware of in this study.

Once the phenologies of each life stage for each species were identified, the climate data set was used to detect and extract any extreme climate events occurring during each life stage for each species at each site based on all 63 years covered by the climate data. Four types of ECEs were defined using site and species-specific thresholds, and the number of days exceeding that threshold was calculated (WallisDeVries et al. 2011), Table 1.Two standard deviations was chosen to set the extremes for temperature (Beaumont et al. 2011) and the 97.5 percentile to set extremes for precipitation as they were hypothesised to identify temperatures and precipitation beyond the climatic norm for species in each area. This was carried out at the site level over the 63 year period covered by the E-OBS dataset. All extremes were defined as the number of days exceeding the threshold criteria identified by the above methods for a given butterfly’s life cycle stage.

Table 1 Extreme Climatic Events (ECEs) included in this study and their definitions (Beaumont et al. 2011; Diaz & Murnane 2008)

Extreme	Definition
Extreme Heat	Number of days above 2 standard deviations above the mean daily maximum temperature for the life cycle period of the species in question at a particular site
Extreme Cold	As for extreme heat but 2 standard deviations below the mean of the minimum daily temperature
Drought	15 days with a combined total of less than 0.02 mm of rain with each day on top of this being counted as an extra day of drought. 15 days of 0.02mm of rain is considered as 1 day of drought.
Extreme Precipitation	Number of days above the 97.5 percentile for rainfall during the life cycle period in question for a particular species at that particular site. 2 standard deviations were not used in this case due to the shape of precipitation data (non-normal).

The ECE definitions adopted give more flexibility, biological application and meaning in relation to time of the year and location of the extreme impacts than arbitrary thresholds. Each extreme is tailored specifically to each individual species. In addition to this it accounts for the historical climate a species has experienced at a given site for a given life stage. Arbitrary thresholds of temperature, such as 30°C used in previous studies, limit our capacity to understand how temperature may affect life stages that do not fall during the hottest periods of the year. This study uses site and species specific life stage climatic extremes enabling an understanding of how extremes occurring in different stages of the life cycle may impact on population change.

Statistical Analysis

Species-specific models

Species-specific linear mixed models were built which relate the annual adult butterfly abundance of a particular species to the ECEs previously identified for the different stages of that butterfly species' life cycle: ovum, larva, pupa, adult, (repeating in multivoltine species) and overwintering period. These models assess the impacts that identified extremes during each butterfly's life stages had on the butterfly's adult population across the UK. The dependent variable was chosen as the log of the indices of adult abundance from one year to the next and was used rather than just the indices for adult abundance in order to satisfy model assumptions of normality. The log transformation has been used as in similar studies (Roy et al. 2001; WallisDeVries et al. 2011) to account for the varying numbers of butterflies present at a site (Freeman 2009).Density dependence was accounted for by including the population of a species at that site in the preceding year. Site was included as a random variable (Mair et al. 2014) to account for site specific adaptation between different populations of the same species due to issues such as habitat differences amongst sites. Counts of the number of ECEs identified for the different stages of that butterfly species' life cycle: ovum, larva, pupa, adult, and overwintering period were incorporated as fixed explanatory variables. Backwards stepwise selection using Akaike's

Information Criterion (AIC) as recommended by (Thiele 2012) was used to remove variables that don't explain the variation in butterfly populations. Due to the possibility that several models may fit our data suitably well, the Pdredge function in the *MuMIn* package in R statistical software was used (Bartoń 2015) to dredge for all the possible model options using the variables selected for by the backwards stepwise selection. Any model with a Δ AIC of less that 4 was deemed similar to the best fit model and was incorporated in the model averaging which has been increasingly backed and applied in similar studies and is recommended for prediction and forecasting (Thiele 2012).

Combined univoltine and multivoltine models

Linear models were created by separating univoltine from multivoltine species and combining all species in each group to run a combined model for univoltine and multivoltine species. It displays the differences in response of the butterflies based on their voltinism. It also helps to understand the relative importance of variables found as being significant in the individual species models when looking at them from a univoltine and multivoltine perspective. The relative importance of each variable within the combined models was assessed using the package *relaimpo* (Grömping 2006) in R and defined as the percentage contribution of each predictor to the R^2 of the model. It allows us to give statistical support relevance to counts of variables gained from species-specific models. Mixed models using species as a random variable were carried out but did not improve the performance of the models and hence were not included. Spatial autocorrelation was not evident in the residuals of the combined models (See Annex 1, Fig. 1 & 2).

Life history traits sensitivity to ECEs comparison: Welch t tests.

Welch t tests were used to make comparisons between species with different life history traits and their response to ECEs. Comparisons were based on the mean percentage of negative responses in relation to total number of possible variables from the individual species models when divided and grouped based on their life history traits.

Results

Which life stages are affected by which ECEs?

The percentage of species for which an extreme affected a certain life stage varied depending on voltinism. Thus results are presented for univoltine and multivoltine species separately. All quoted percentages in the results for species affected are based on significant effects in the individual species models.

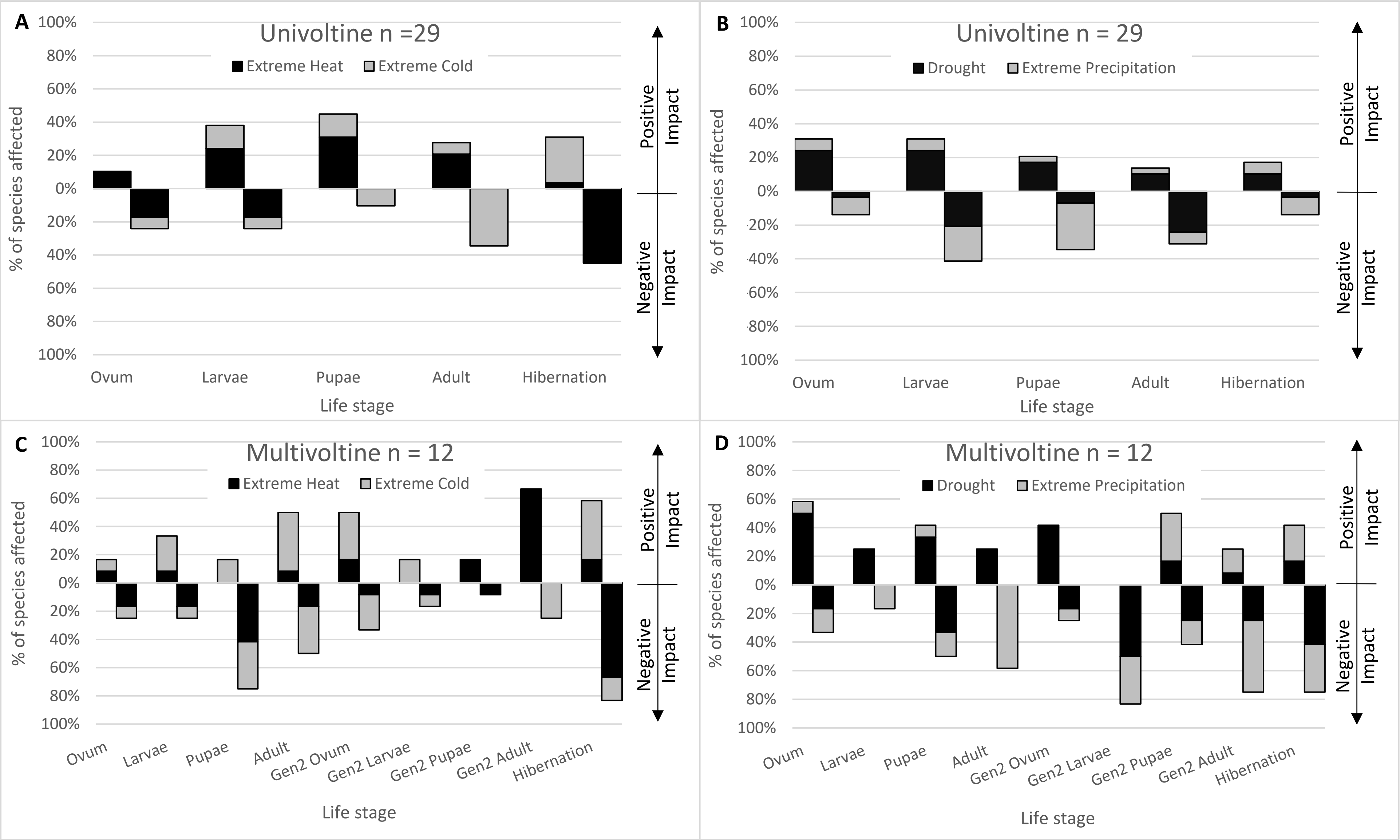
A
Univoltine n =29
■ Extreme Heat
▨ Extreme Cold
100%
80%
60%
40%
20%
0%
20%
40%
60%
80%
100%
% of species affected
Ovum
Larvae
Pupae
Adult
Hibernation
Life stage
Positive Impact
Negative Impact
B
Univoltine n = 29
■ Drought
▨ Extreme Precipitation
100%
80%
60%
40%
20%
0%
20%
40%
60%
80%
100%
% of species affected
Ovum
Larvae
Pupae
Adult
Hibernation
Life stage
Positive Impact
Negative Impact
C
Multivoltine n = 12
■ Extreme Heat
▨ Extreme Cold
100%
80%
60%
40%
20%
0%
20%
40%
60%
80%
100%
% of species affected
Ovum
Larvae
Pupae
Adult
Gen2 Ovum
Gen2 Larvae
Gen2 Pupae
Gen2 Adult
Hibernation
Life stage
Positive Impact
Negative Impact
D
Multivoltine n = 12
■ Drought
▨ Extreme Precipitation
100%
80%
60%
40%
20%
0%
20%
40%
60%
80%
100%
% of species affected
Ovum
Larvae
Pupae
Adult
Gen2 Ovum
Gen2 Larvae
Gen2 Pupae
Gen2 Adult
Hibernation
Life stage
Positive Impact
Negative Impact

Figure 1 Percentage of species, from the species specific models, for each life stage which there was a significant (p<0.05) positive or negative relationship with an Extreme Climatic Event (ECE) related to temperature or precipitation. Univoltine (A and B) and multivoltine (C and D) species are shown separately. Impact of temperature extremes (A and C) and precipitation extremes (B and D) on univoltine and multivoltine species are also shown separately. Columns above the 0 line in the y axis indicate the % of species positively impacted by ECEs while below indicates the % of species positively impacted by ECEs.

Univoltine Species

The adult and overwintering life stages are the most sensitive for 29 univoltine species (Fig 1.). Extreme heat during the overwintering life stage and extreme cold during the adult life stage are the most frequently occurring negative extreme variables both causing population declines (affecting 45% and 35% of species respectively). Adult and overwintering life stages have opposing population responses to temperature extremes, extreme heat during the adult life stage causes positive population change for 21% of species, while during overwintering it is associated with negative population change in 45% of species. Another extremely important variable to which univoltine species are vulnerable to is extreme precipitation during the pupal life stage affecting 28% of species. Drought appears to impact on the adult stage most negatively, 24% of the species, but appears to be beneficial during the ovum life stage also for 24% of species which is shown in the combined species model to be more importance for univoltine butterfly population change than its negative impacts, Table. 2. The combined model, including all univoltine species, identifies which of the variables from the species specific models to focus on when considering response of univoltine species. The first 5 variables account for 73.6% of the predictive power of the combined model (Table. 2). Extreme heat in the overwintering stage and precipitation in the pupal stage have strong negative effects on univoltine butterfly population trends. Extreme heat in the adult and pupal life stage drive positive population change in univoltine species. In summary, univoltine species seem particularly sensitive to temperature extremes at both ends of the scale (Heat or Cold) and it is the adult and overwintering phases that are

Table 2 Significant variables obtained from the combined univoltine species linear model. Bonferroni corrections applied to account for significance based on the number of variables and variables ordered by relative importance in the model using the relaimpo package. Variables bolded show a negative relationship with univoltine populations.

Univoltine Species							
Variable			Estimate	Std. Error	t value	p-value	Relative Importance
Extr. Heat	**during**	**Overwintering**	**-0.064**	**0.004**	**-17.681**	**<0.0001**	**19.93%**
Extr. Heat	during	Adult stage	0.052	0.005	11.068	<0.0001	17.54%
Extr. Heat	during	Pupal stage	0.040	0.005	8.309	<0.0001	14.24%
Extr. Precipitation	**during**	**Pupal stage**	**-0.051**	**0.004**	**-12.915**	**<0.0001**	**12.74%**
Drought	during	Ovum stage	0.044	0.004	11.365	<0.0001	9.14%
Extr. Cold	**during**	**Adult stage**	**-0.040**	**0.004**	**-10.593**	**<0.0001**	**4.93%**
Extr. Precipitation	**during**	**Larval stage**	**-0.026**	**0.004**	**-6.476**	**<0.0001**	**3.99%**
Drought	during	Pupal stage	0.031	0.004	7.259	<0.0001	3.96%
Extr. Cold	during	Overwintering	0.030	0.004	8.104	<0.0001	3.96%
Extr. Heat	**during**	**Ovum stage**	**-0.023**	**0.005**	**-4.560**	**<0.0001**	**2.79%**
Extr. Precipitation	**during**	**Adult stage**	**-0.009**	**0.004**	**-2.399**	**0.0165**	**2.01%**
Extr. Precipitation	**during**	**Ovum stage**	**-0.019**	**0.004**	**-5.031**	**<0.0001**	**1.98%**
Extr. Heat	**during**	**Larval stage**	**-0.017**	**0.005**	**-3.308**	**0.0009**	**1.38%**
Drought	**during**	**Adult stage**	**-0.011**	**0.004**	**-2.663**	**0.0077**	**0.74%**
Extr. Precipitation	**during**	**Overwintering**	**-0.015**	**0.004**	**-3.954**	**0.0001**	**0.69%**

vulnerable to these extremes. In addition to this, extreme precipitation during the pupal life stage is a detrimental driver of population change in a number of univoltine species.

Multivoltine Species

Extreme heat during overwintering and extreme precipitation during 1st and 2nd generation adult life stages are the most frequently occurring extreme variables causing population declines in multivoltine species (67%, 58% and 50% of all multivoltine species affected respectively, Fig. 1). As in univoltine species, adult and overwintering life stages have opposite population responses to temperature extremes. Extreme heat during the adult life stage is associated with positive population change in 42% of species. Drought plays a much more important role in multivoltine species than univoltine species. Drought negatively affects 50% of species during their 2nd larval life stage but has a positive impact on 25% of the species during their 1st ovum life stage. In the model combining all multivoltine species, the 9 most important variables account for 73% of the predictive power of the combined multivoltine model (Table 3). The multivoltine model is clearly driven by extremes of temperature, five were extremes in heat and one a cold extreme. Unlike univoltine species however, multivoltine seem to be susceptible across all life stages with ovum, larvae, pupae, adult and overwintering all being represented in the nine most important variables in the combined model. Species' vulnerability to extremes appears to be most prominent in the 1st generation and is primarily driven by exposure to extreme heat with the exception of the negative impacts of precipitation during the adult stage. Multivoltine species have a significantly higher

Table 3 Significant variables obtained from the combined multivoltine species linear model. Bonferroni corrections applied and variables ordered by relative importance in the model using the relaimpo package. Variables bolded show a negative relationship with univoltine populations.

Multivoltine Species							
Variable			Estimate	Std. Error	*t* value	Pr(>|t|)	Relative Importance
Extr. Heat	during 2nd generation	Adult stage	0.105	0.006	17.921	<0.001	14.81%
Drought	during 1st generation	Adult stage	0.076	0.006	13.599	<0.001	8.45%
Extr. Cold	during 2nd generation	Larval stage	0.083	0.005	15.740	<0.001	8.31%
Extr. Heat	**during**	**Overwintering**	**-0.100**	**0.007**	**-14.427**	**<0.001**	**8.22%**
Extr. Heat	during 2nd generation	Ovum stage	0.064	0.006	11.262	<0.001	7.82%
Drought	during 1st generation	Ovum stage	0.086	0.005	16.283	<0.001	7.12%
Extr. Heat	**during 1st generation**	**Pupal stage**	**-0.066**	**0.006**	**-10.533**	**<0.001**	**6.59%**
Extr. Heat	**during 1st generation**	**Ovum stage**	**-0.034**	**0.006**	**-5.253**	**<0.001**	**6.33%**
Extr. Precipitation	**during 1st generation**	**Adult stage**	**-0.050**	**0.006**	**-8.701**	**<0.001**	**5.48%**
Extr. Cold	during	Overwintering	0.080	0.006	13.284	<0.001	4.25%
Extr. Precipitation	**during 2nd generation**	**Ovum stage**	**-0.018**	**0.006**	**-2.849**	**0.004**	**2.98%**
Extr. Precipitation	**during 2nd generation**	**Larval stage**	**-0.027**	**0.007**	**-3.813**	**0.000**	**2.88%**
Extr. Cold	**during 2nd generation**	**Ovum stage**	**-0.042**	**0.005**	**-7.846**	**<0.001**	**2.28%**
Drought	**during 2nd generation**	**Larval stage**	**-0.053**	**0.007**	**-7.992**	**<0.001**	**1.80%**
Drought	during 2nd generation	Ovum stage	0.016	0.006	2.400	0.016	1.69%
Drought	**during**	**Overwintering**	**-0.031**	**0.005**	**-5.700**	**<0.001**	**1.61%**
Extr. Cold	**during 1st generation**	**Pupal stage**	**-0.052**	**0.005**	**-9.946**	**<0.001**	**1.44%**
Extr. Heat	**during 1st generation**	**Adult stage**	**-0.021**	**0.006**	**-3.468**	**0.001**	**1.38%**
Extr. Precipitation	**during 1st generation**	**Pupal stage**	**-0.036**	**0.006**	**-6.144**	**<0.001**	**1.37%**
Extr. Precipitation	**during 1st generation**	**Larval stage**	**-0.032**	**0.005**	**-6.089**	**<0.001**	**1.37%**
Extr. Cold	**during 2nd generation**	**Adult stage**	**-0.023**	**0.005**	**-4.526**	**<0.001**	**1.29%**
Extr. Cold	**during 1st generation**	**Adult stage**	**-0.031**	**0.005**	**-5.788**	**<0.001**	**0.62%**
Extr. Precipitation	during 2nd generation	Pupal stage	0.027	0.006	4.280	<0.001	0.61%
Drought	**during 2nd generation**	**Adult stage**	**-0.027**	**0.006**	**-4.370**	**<0.001**	**0.51%**
Extr. Precipitation	during	Overwintering	0.012	0.006	2.183	0.029	0.32%
Drought	during 2nd generation	Pupal stage	0.014	0.007	2.106	0.035	0.25%

Table 4 Welch T tests results comparing the mean percentage of negative responses in relation to total number of possible variables from the individual species models when divided based on their life history traits.

Life history Group (Traits being tested tested)	t Statistic	Degrees of freedom	Means (% vs %)	*p-value*
Voltinism (Univoltine versus Multivoltine)	-2.86	25.66	(13.62 vs 22.22)	0.008
Requirement (Specialist versus Generalist)	-3.00	35.99	(10.95 vs 19.81)	0.004
Within Univoltine Species (Widespread versus Northern Range limited)	1.69	25.57	(17.5, 11.25)	0.102
Within Multivoltine Species (Widespread versus Northern Range limited)	3.76	8.77	(26.98 vs 15.56)	0.005

proportion of negative responses to ECEs across their life stages than univoltine species ($t_{(25)}$=-2.86, *p*=0.008), Table 4. The results suggest that multivoltine species are more sensitive to extremes than univoltine species or potentially due to greater error in assessing the correct life history periods in univoltine species.

Within univoltine species there is no significant difference in the number of negative responses when comparing specialist with generalist species ($t_{(20)}$=-1.6, *p*=0.122) Table 4.

There is no significant difference between widespread and northern range limited species nested in univoltine species, ($t_{(20)}$= 1.69, *p*=0.102) Table 4. However when nested in multivoltine species, widespread species show more responses to extremes across their life stage than northern range limited species ($t_{(8)}$=3.76, *p*=0.004) Table 4.

Discussion

UK butterfly populations are influenced by extreme climatic events. Extreme temperature events play a significant role in determining the population changes in species from year to year in both multivoltine and univoltine species. Previous studies found that cold weather during the adult phase negatively affect population change, while warm weather has positive associations to population (Roy et al. 2001; WallisDeVries et al. 2011; Warren et al. 2001; Calvert et al. 1983). The benefit of heat on butterfly populations is to be expected given their poikilothermic nature. This study examined the effects of extreme temperature and precipitation variables on all butterfly life stages, for both univoltine and multivoltine species. For UK butterflies the overwintering stage was found to be particularly sensitive to extremes. Butterfly populations are negatively affected by hotter temperatures while overwintering and benefit from colder winters. This concurs with previous studies such as (Radchuk et al. 2013; Oliver et al. 2015) who found in their laboratory experiments that the overwintering larval stage was extremely sensitive to increases in temperature. This study identified negative associations of high temperatures during the overwintering stage but did not find that this sensitivity was confined to species overwintering in their larval stage. Radchuk *et al.* (2013) argue that elevated temperatures during the overwintering period increase rates of mortality due to increased incidences of disease and fungi both of which are more abundant in milder winters (Harvell 2002). Whilst this may be the case, we hypothesise that in the case of butterflies overwintering as larvae or adults it may be due to extreme hot temperatures acting as a cue for butterflies or their larvae to come out from overwintering too early, decoupling from photoperiod cues, (Wiklund et al. 1996) and subsequently killed off by temperatures returning to colder conditions or potentially the destruction of their food plant due to similar mechanisms (McLaughlin et al. 2002).

This study did not account for annual variation in butterfly phenology (Van Strien et al. 2008), the life stage periods were fixed based on the average of the last 37 years thus life stage exposure to extremes may have been less well quantified in years or sites with advanced or delayed phenology. Overall our approach is likely to be robust since it accounts site variability (by including the effects of climatic extremes at the site level), and includes a long-term data set (37 years) to quantify country wide species population responses to ECEs. These results should not be extrapolated beyond the UK due to issues such as local adaptation, it is prudent to expect potential differences in the responses of continental European populations of the same butterflies.

Single generation vs multi-generation species

All life stages for univoltine species showed sensitivity to ECEs during the overwintering stage, with extreme cold events being beneficial and extreme heat detrimental on butterfly populations. One of the more prominent and consistent negative contributors to univoltine species' population change is precipitation events during the pupal and larval periods. This is an important finding as it has not been identified in previous studies but would be expected from heavy rainfall events (Pollard 1988). Indeed, Hill *et al.* (2003) have previously hypothesised the potential importance of precipitation having a detrimental impact on both the larval and pupal stage, which is clearly supported by our analysis of univoltine species. The impacts of drought are difficult to interpret in this study as species do not seem to respond as uniformly to this extreme as the other extremes. However, during the ovum life stage our combined species models have indicated it plays an important and significant role in determining increases in population size.

It would appear that univoltine species prefer warmer, drier climates outside of winter periods. Current predictions forecast that the UK will have a warmer climate with drier summers (Jenkins et al. 2009) which on the face of it would seem to benefit most univoltine species however this may not be the case as warmer, wetter winters could potentially be a driving force behind many population changes as in (Radchuk et al. 2013).

Temperature extremes are the primary driving factor when analysing the impact of ECEs on multivoltine butterfly populations. As in the univoltine species, hot weather during overwintering period is negative with extreme cold being beneficial. The adult stage is extremely sensitive to extremes in temperature but primarily the second generation stage, Table 3. This is probably due to the timing of the second generation for most multivoltine species, which have their flight period during summer. Temperature has been shown to be extremely important during these summer periods (Roy et al. 2001). Similar to the univoltine species, multivoltine appear to be positively impacted by drought conditions during the 1st generation ovum and adult stages. This apparent benefit of drought may indicate that the levels of drought identified in this study are not at a level that is detrimental to butterflies.

Our analysis shows that univoltine species are less sensitive to ECEs than multivoltine species. These results need to be interpreted with caution taking into account the small number of multivoltine (n=12) species included in the analysis. This may be a due to exposure to extremes during more life stages, more generations in a year may put more selection pressures on a species. (Radchuk et al. 2013) emphasise the importance of a resource based habitat approach and it is clear that more life stages would put more selection pressures on the species or potentially due to the fact that an extreme in one year can affect two consecutive generations when life stages overlap.

Generalists vs specialists

Generalist species have more significant negative associations with ECEs than specialist species. This suggest that ECEs may affect population change in generalist species, especially in populations on the edge of their climatic range (Hellmann et al. 2008), while population change of habitat specialists species is controlled by other factors (e.g. habitat loss and degradation) (Warren et al. 2001). We hypothesise that generalist species are more vulnerable as they are filling their climatic niche and hence many populations within the species range may be situated on the climatic range edge and be more vulnerable to increased climate variability outside of their comfort zone. In contrast specialist species are confined to particular host plants which may not ubiquitous across the specialist species' climatic niche, hence those specialist species are not filling their climatic niche and are effectively in or close to their core range and are not subjected to ECEs that are outside their ability to adapt and cope. It is also possible that specialist species are being buffered by their habitats where they have been able to persist (Oliver et al. 2013).

Widespread vs Northern range limited species

No significant difference in the number of negative associations between widespread and northern range limited species was found when nested within univoltine species. The opposite was found for multivoltine species with widespread species having significantly more negative associations when nested in multivoltine species. These results need to be interpreted with caution as mentioned previously. If validated this result may indicate that widespread species may be subjected to a much higher variation in climatic conditions than northern range limited species and as such may be subject to temperatures and precipitation levels that are detrimental.

Conclusion

This study has identified a hitherto unknown sensitivity of univoltine species to extreme precipitation during their pupal life stage. In addition, this study although using novel ECE definitions, found an agreement with previous studies, indicating that warm and even climatically extreme hot summers are beneficial to butterfly populations, while extremely wet cold summers are detrimental to their populations. The detrimental effect of extreme heat during overwintering has been evidenced previously but fewer studies have shown the sensitivity of the pupal stage to extreme precipitation events and warrants further attention. Interestingly the perceived sensitivity of butterflies to drought (Oliver et al. 2015) was not evidenced in our analysis but this could be due to limitations in our definition of drought.

Sensitivity to ECEs in butterflies was primarily dominated by temperature extremes which would support our hypothesis that butterfly population changes are more dependent on heat extremes as shown by both the combined species models and the proportion of species affected in the species specific models. This study has identified scope for future work. An interesting augmentation of this study would be to identify dramatic species decline events and examine the extent to which they are associated with ECEs. Finally, building on the work of (Oliver et al. 2015), further analysis is warranted on the ability of habitats to buffer extremes other than drought that have been identified as being detrimental by this study. Extreme wind could be factored into future studies also. Unfortunately, the appropriate data was not available through the weather sources used in this paper.

The novel identification of the sensitivity of the pupal life stage to extreme precipitation supports our decision to address the impacts of extremes at a finer scale than previous studies and has also shown the importance of looking at ECEs across all life stages given these relatively new findings. This study has shown that butterflies could potentially benefit from increasing temperatures in the UK in the future but warmer and wetter winters and increases in severe weather events that have also been predicted (Jenkins et al. 2009; Defra 2009) could be detrimental to the survival of many of its butterfly species and further research is needed regarding the balance of importance that these variables could have and whether the benefits of warmer summers will be outweighed by the detrimental winter effects. Based on the results of this study, future conservation efforts hoping to mitigate against ECEs in the future should focus their efforts on the adult and overwintering life stages of UK butterflies.

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Data accessibility

Weather data (E-OBS dataset) available from http://www.ecad.eu/download/ensembles/download.php (Haylock et al. 2008).

The UKBMS (Butterfly) database is managed and maintained by the Biological Records Centre, based at the Centre for Ecology & Hydrology (CEH). Access to population indices available from the CEH Data catalogue http://doi.org/10.5285/378f0f77-1842-4789-ba15-6fbdf7d02299 (Marc Botham et al. 2016).

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Chapter 3: Extreme climatic events explain widespread butterfly population declines

Introduction

Species and ecosystems around the world are being forced to respond to dramatic climate change and changes in climate variability. The global average temperature has warmed by 0.85 [0.65 to 1.06] °C, over the period 1880 to 2012 (IPCC 2013), affecting species, communities and ecosystems with ramifications for the delivery of ecosystem goods and services (Wernberg et al. 2012). Biodiversity is responding to these changes, worldwide there is evidence of changing distributions and changing timing of the life cycle of organisms (Parmesan 2006; Foden et al. 2013; Stefanescu et al. 2003; Parmesan et al. 2000; Kittel 2013). Not all organisms can adapt to the fast changes (Velocity 2011; Burrows et al. 2014), hence there is growing evidence of detrimental impacts, climate change is now considered as a major threat to biodiversity (Cahill et al. 2012; IPCC 2014; Hampe & Petit 2005; McKechnie & Wolf 2010; Thomas et al. 2004). Lynch et al. 2014; Buckley & Huey 2016 have emphasised the need to address the impacts of extreme climatic events (ECEs) as they may be important in driving species populations especially at the extremities of their climatic range. Currently there is a lack of research regarding the impact that ECEs do have on species' population (Suggitt et al. 2017).

The majority of the evidence of climate change effects on biodiversity focuses on the impacts of gradual changes in climate or a gradual increase in mean temperature. However, the frequency, intensity, spatial extent, duration and timing of ECEs are also expected to increase (Ummenhofer & Meehl 2017; IPCC 2012; Rahmstorf & Coumou 2011; Maraun et al. 2008). Although the impacts of ECEs on biodiversity are poorly quantified they have the potential to limit the geographical extent of a species and can determine the survival and abundance of a species at a given site (McDermott Long et al. 2017; Thibault & Brown 2008; Wernberg et al. 2012; Parmesan et al. 2000), impacting the physiological performance of a species, their relative abundance, their geographic patterns and causing local to regional extinction events (Krab et al. 2013; WallisDeVries et al. 2011; McDermott Long et al. 2017; Smith 2011b; Easterling et al. 2000).

Indeed studies such as Suggitt et al. 2015; Maclean et al. 2015; Maclean et al. 2016 emphasise the importance of addressing extremes at a finer scale as microclimates may drastically alter how they impact upon species presence distributions. Microclimates, caused by variation in topography and habitat, have been identified as being a significant modifier of broader scale macroclimate for quite a while (Suggitt et al. 2015). To date very few studies have directly examined how this variation in topography and habitat may buffer against ECEs. McDermott Long et al. 2017 highlighted potential limitations of looking at population changes with rare extreme events but emphasised the potential importance ECEs may have in driving population decline events. While Zeigler 2013; Radchuk et al. 2013 emphasise another important aspect that is tackled by this study. That is, if you are to examine the vulnerability of a species to climate change and ECEs you need to examine their impact across all the life stages of that species as each life stage may have different sensitivities and exposure.

Although the climate system is dynamic and extremes are hard to predict, the frequency of ECEs such as extreme heat, drought and heavy precipitation events are increasing and becoming more extreme in intensity (IPCC 2012). The impacts of ECEs on terrestrial and marine species have focused on singular ECE events (Wernberg et al. 2012; Oliver et al. 2013), and studies using long term datasets are lacking despite a recent increase in research in the area (Palmer et al. 2017; McDermott Long et al. 2017). This is due to difficulties in obtaining good quality long term climate and biological data for the same sites, which is essential to examine the consequences of rare extreme climate events. This chapter examines the role of ECEs in driving dramatic butterfly population declines over a long period using a high temporal and spatial resolution dataset (from 1976 to 2015). Many studies addressing the impacts of ECEs identify an ECE event and look for associated impacts on population. This chapter identifies ECEs and population decline events independently of one another allowing us to test the likelihood of a decline being due to an ECE or another confounding factor. Previous studies have addressed the impacts of ECEs on butterfly population changes at the site level (McDermott Long et al. 2017) and regional level (WallisDeVries et al. 2011). This chapter examines the vulnerability of butterflies to ECEs across all their life stages examining their ability to explain localised and widespread butterfly decline events. It also investigates the role of scale as, while ECEs act at a regional scale, local conditions at a site can result in unique responses to such an extent that regional climate predictions could be irrelevant (Wiens & Bachelet 2010). We predict that if species are locally adapted to habitat and landscape features and ECEs are the main cause of population decline then the local scale model (see methods) will perform best, while if other processes operating at the site level (e.g. disease, predation, habitat management, stochastic events) also cause dramatic population declines independently from ECEs then the regional model (see methods) will be better.

Materials and Methods

The butterfly dataset – UKBMS

Annual adult butterfly population indices from the UK Butterfly Monitoring Scheme (UKBMS) were used. This is a comprehensive long-term dataset, from 1976 until the present year, assembled using citizen science, involving thousands of volunteers throughout the UK. More than 1800 sites have been surveyed, although the number of sites varies from year to year. Annual site level population indices are based on transect counts that are taken weekly during a 26 week period from the start of April until the end of September. The routes are fixed at each site and counts are only taken if the weather is favourable for butterfly movement. A more detailed and informative description of the sampling methodology can be found in (Pollard et al. 1986).

These weekly transect counts are used to create the population indices used in this study. The population indices are created using log-linear models executed using the statistical software package, TRIM (Pannekoek & Van Strien 2001). This gives a single population value for each butterfly at each site. This value encompasses all generations of that species whether it has more than one generation per year or not. Only years with 10 or more sites with an abundance of 9 or more for a species are considered when assessing species declines in order to only include species with enough data and large enough populations for a robust model (McDermott Long et al. 2017).

The weather observations dataset

The UK has been warming since the 1960 and under A1B emissions (a balanced approach to energy sourcing across fossil fuels and non- fossil fuels) scenario the UK is projected to experience average temperature increases of up to 3 °C(Gosling et al. 2011). In addition to this the UK has been subjected to increases in the frequency and magnitude of heavy precipitation events during winter (Maraun et al. 2008). Daily gridded data for maximum, minimum temperature and precipitation on a 0.25 degree regular lat/long grid was obtained for the UK from the E-OBS dataset (Haylock et al. 2008). Weather data for each site used in the butterfly transects was extracted from this gridded dataset based on site latitude and longitude. For more information on how the data are interpolated into its gridded format see (Haylock *et al.* 2008).

Identification of Extreme Weather Events

Each ECE used in this study was identified for a given life stage of each butterfly. In order to identify the ECEs, fixed phenological dates for each life stage (ovum, larvae, pupae, adult and overwintering), for each species, were identified (Eeles 2014) (Annex 1 Table 1). Overwintering is set as a fixed period for all species (WallisDeVries et al. 2011; McDermott Long et al. 2017), spanning the 1st of November until the 28th of February each year. The phenology of each butterfly will vary from year to year and from site to site (WallisDeVries et al. 2011; Van Strien et al. 2008). As a result, fixed phenologies have been chosen to represent life cycle timings in the hope that much of the 37-year variation is captured by these fixed periods (McDermott Long et al. 2017). We use population data that are based upon observations of adult life stage but we backdate life stages so an extreme impacting, for example, the ovum life stage during the winter before is included in the models by its potential impacts on the proceeding adult stage.

ECE thresholds are identified using the phenological dates to extract the daily weather data at a specific site for a specific species which match its life stage timings. For example, the ECE for the ovum phase of a particular species is based on the daily data of the timing of that life stage each year from 1961 until 1990. This study has defined four different ECEs, specific to each specie's life stages (Heat, Cold, Drought and Precipitation) (Chpt. 1, Table 1). A site specific threshold was identified for each ECE at each site for each butterfly and the number of extreme days above the extreme threshold is counted for each extreme variable. Two standard deviations above the average for that period has been used previously in order to define ECE thresholds (Beaumont et al. 2011) and is used here to define temperature extremes. Precipitation extremes are defined as any event which exceeds the 95% of the precipitation data for a given period (IPCC 2013; Zhang et al. 2011). It is defined differently due to the non-normal distribution of precipitation data. Drought is defined as a period of 15 days with less than 0.02mm of rain, with each day beyond this counting as an extra day of extreme (Matthews 2013) (Chpt. 1, Table 1). All ECEs are characterised as the number of days in which the extreme threshold is exceeded for a given stage of a butterfly lifecycle at a given site, hence the duration of the extreme event is our metric of severity (Chpt. 1, Table 1).

For species with more than one generation per year, the extreme threshold identified for each ECE is fixed as the threshold for the generation that is subjected to the most severe extreme. This method allows for the combination of multigenerational life stages as the same life stage across different generations should have similar adaptive capacities.

The definition of ECEs in this study allows for extremes to be tailored specifically to species and sites, accounting for the historical climate conditions they have previously faced, allowing for better biological application and meaning in relation to time of year. It overcomes issues associated with other studies (Ma et al. 2014; WallisDeVries et al. 2011) that have set arbitrary thresholds which for example can only examine the impacts of heat during the summer period and cold during winter periods. Definitions used in this study allow us to understand how variations in temperature and precipitation can affect all life stages.

Localised and widespread butterfly population declines

Population declines were identified for each species at the site level. A local population decline, recorded as a binary variable, occurred when there was a 50% population decline, at a site, from one year to the next year. Widespread population declines were determined for each species and occurred when there were localised population declines across at least 50% of the sites where a given species was recorded in a year.

The two definitions of decline were used to calculate two distinct response variables which were used in two separate models. The variables are represented in binary format, 1 if a decline occurred and 0 if no decline occurred. Widespread butterfly decline events are deemed to have occurred if 50% or more of sites suffered at least 50% population decline for a given year compared to the previous year, if this condition is not met then sites with local declines are ignored and (0) no decline is used. Only sites with a 50% decline for a given species in a widespread decline year are denoted by 1. This approach will enable us to examine if ECEs can predict local site population declines or are better at predicting widespread population declines. If local site declines are not well explained by the ECEs than other factors (e.g. biotic factors, habitat management or stochastic factors) may be driving local population declines in years when widespread decline does not happen.

Statistical Analysis

Species-specific models

Species specific generalised linear mixed models with a binomial link function were built to analyse the importance of ECEs in determining severe population declines at the localised site level and at the widespread national scale. Two separate models were created for each of the 36 species included in this study.

Name	Dependent Variable	Explanatory variables
Localised declines model	50% decline at the site level (binomial response variable)	Fixed: ECEs in association with each butterfly life stage, Population of butterfly from year previous (4 ECEs x 5 life stages) Random: Species, Site and Year
Widespread declines model	50% decline occurring at ≥50% of sites (binomial response variable	Fixed: ECEs in association with each butterfly life stage, Population of butterfly from year previous (4 ECEs x 5 life stages) Random: Species, Site and Year

The localised declines model (LDM) uses local weather conditions and aims to examine the importance of different ECEs during butterfly life stages in driving local population declines at the site level. Site specific adaptation by species is accounted for by incorporating site as a random variable in the models (Mair et al. 2014). The LDM approach examines how ECEs explain local population declines. If ECEs were to outweigh habitat characteristics, disease and other potential local perturbations in terms of their influence on localised declines then we would expect the LDM model to be a powerful predictor of localised decline. The WDM is more useful for identifying those extremes with the potential to cause widespread decline. This is because there are very few drivers of population that can act on this scale. Therefore, widespread decline events are likely to be driven by extremes that affect a population at a regional to national scale. The importance of examining two different models is displayed in Fig. 1. While the peak years of widespread species declines are captured in the localised variables it also incorporates a lot of further declines that are potentially associated with site level attributes.

If the WDM is far more powerful than the LDM model it indicates that there are ECEs for which UK butterflies drive wide- scale population crashes but that, generally, localised declines are likely to be driven by biotic and abiotic factors other than ECEs.

Backwards stepwise model selection based on Akaike's Information Criterion (AIC) (Thiele 2012) was used to select for the best fit models. Important variables are those variables that contribute most to the predictive power of the model and this is assessed by examining the AIC of the simplistic model only incorporating each dependent variable.

Combined species widespread and localised declines models

Two separate combined species models were created to analyse the importance of ECEs driving population declines across all species. All species data were combined and two models were run, one model addressing the localised decline events for species and one addressing widespread decline events, with ECEs across all life stages as the explanatory variables. The potential for density dependence was accounted for by including the population at the end of the previous year as a fixed effect. Species, Site and year were all included in both models as random effects. Running these models may identify the differences in species declines and the importance of the scale at which we look at ECEs. They elucidate whether localised declines across species may be as a result ECEs, or whether other factors drive local declines and whether ECEs are driving widespread declines across species. These models allow us to understand further the scale at which investigations into the impacts of extremes should be addressed. They also enable an increased understanding of the relative importance of variables found as being significant in the single species models, Fig. 1. Spatial autocorrelation was checked for and found not to be an issue in the residuals of the combined localised and widespread models (Annex 1, Fig.3 & 4).

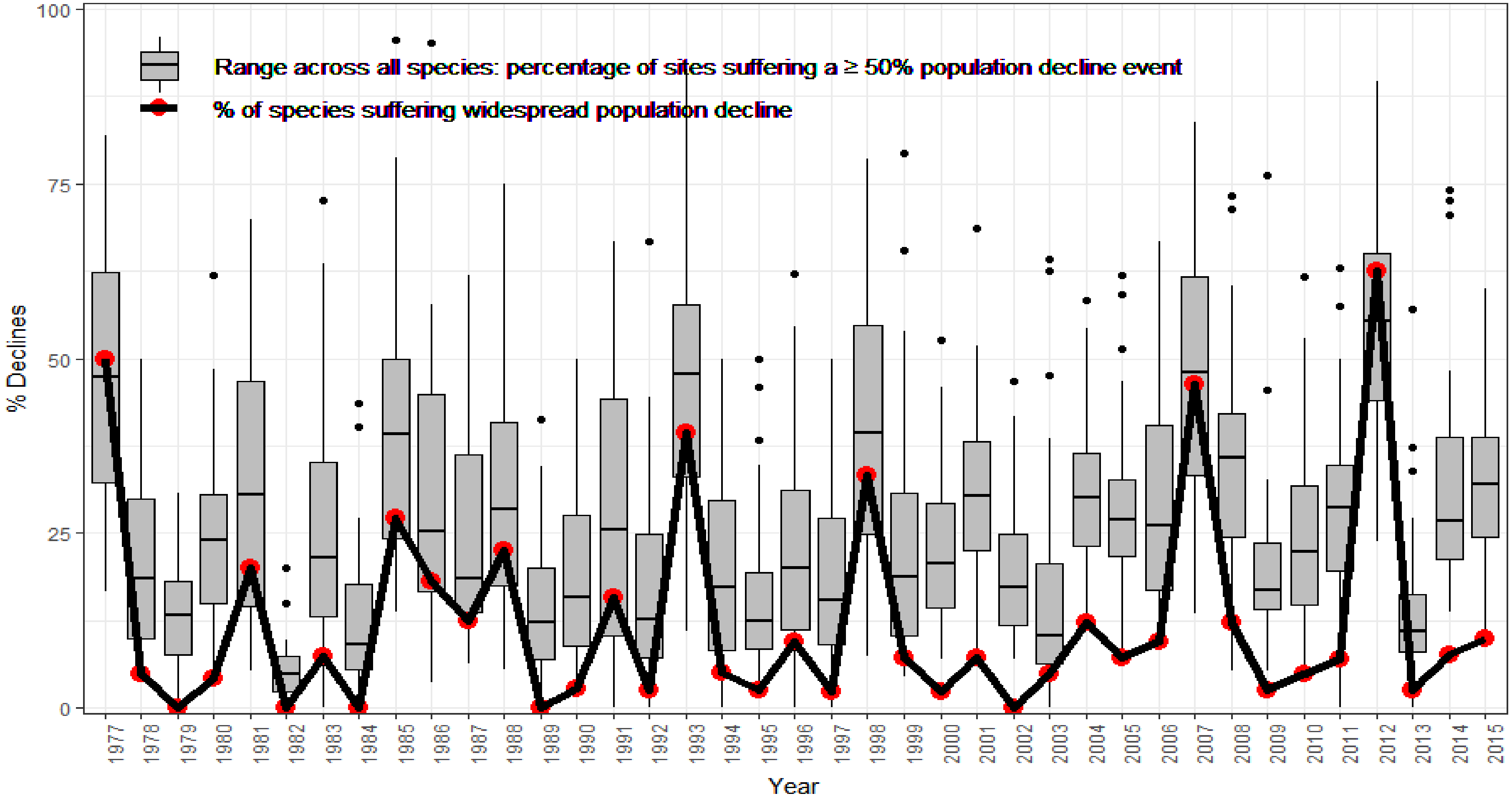
Range across all species: percentage of sites suffering a ≥ 50% population decline event
% of species suffering widespread population decline
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Figure 1 Graph exploring the differences between the dependent variables of the Localised declines model (LDM) and the Widespread declines model (WDM). The dependent variable of the LDM is represented by the boxplot showing the range of localised site declines across species. WDM dependent variable is shown by the line and points which shows the percentage of species experiencing widespread decline in a year. The y axis represents the percentage decline of species suffering from a decline.

Results

Our new approach to identify widespread population declines enabled us to determine that a large number of UK butterflies suffered widespread population declines in 1977, 1993, 1998, 2007, and 2012 (Fig 1.). These distinct years of mass population decline amongst species show the importance of carrying out multiple species models to identifying if the variables correlated with population decline are similar across species. Within year there is large variation between species in the number of sites that suffer population declines and large variation from year to year. This demonstrates that there may be several factors affecting population declines at the site level and species may respond in different ways to environmental variation, hence single species models are needed to identify species specific responses.

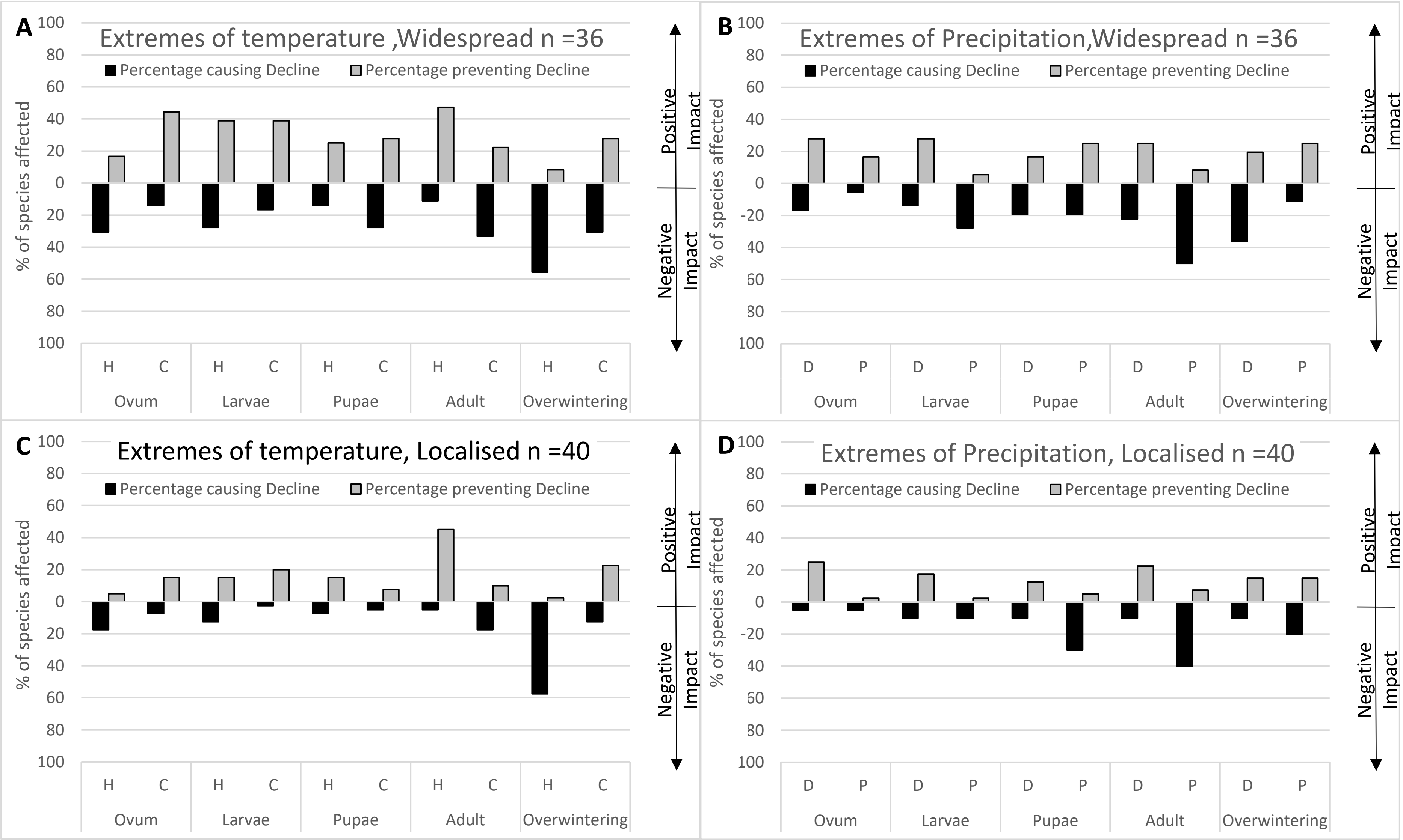
Individual species models: localised and widespread declines

The individual species models show that heat extremes during overwintering period and precipitation extremes during the adult life stage are the primary drivers of decline events in UK butterflies while extreme heat during the adult life stage appears highly beneficial in avoiding population decline events, in both the localised and widespread decline species models Fig. 2, Table 1. Indeed, these variables are included in over 45% of species in the individual widespread decline models. Extreme heat during the overwintering period significantly increases the likelihood of widespread decline for 55% of species, while 47% of species subjected to extreme heat during the adult stage are less likely to suffer widespread decline, Fig. 2. 50% of species are significantly more likely to suffer a widespread decline due to increased

Table 1 Direction of the significant coefficients of widespread declines across the individual species models across all life stages. D = Drought, P = Precipitation extreme, H = Heat extreme, C = Cold extreme. Sensitivity is identified here by the number of variables that show a significant response bot positive and negative. ++/-- indicates p value of less that 0.001, +/- indicates p value of less than 0.05.

	Ovum				Larvae				Pupae				Adult				Overwintering				Sensitivity	
Species	**D**	**P**	**H**	**C**	**D**	**P**	**H**	**C**	**D**	**P**	**H**	**C**	**D**	**P**	**H**	**C**	**D**	**P**	**H**	**C**	**Total**	**Ratio Pos:Neg**
Orange-tip	--	++	--		++		++	--		++	++	++	++	--	++	--	++	--	--	++	17	1.4
Common Blue	++		--	++	--	--			-	++		--	--	--	++	++	-	++	--	--	16	0.6
Small White				--	++	--	--	++	--	++		++	++	--	++	++	--	++	--	--	16	1.0
Comma	--		-	++	++			++			--	--	--	--	++	--	--	--		++	14	0.6
Large White		--		--		++	++	++	--			++	++		++	++	--	++	++	--	14	1.8
Small Tortoiseshell	++		++	++				--	--	--	--	++	++		++	--	--		--	++	14	1.0
Dark Green Fritillary	++				+	--	--	--		++	++	+			++		--	+		++	12	2.0
Holly Blue		++		++	++	--	++			++		++		--		--	++	--	++		12	2.0
Small Skipper	++		--	++	--		++	++		++		++		--	++	--				++	12	2.0
Speckled Wood	--			++	++					++		++	++	--		--	++	+	--	--	12	1.4
Adonis Blue		++	-	++		--	++			++			--	--	+				--	--	11	0.8
Green-veined White					++	--	++	--	+			++		--			--	++	++	+	11	1.8
Meadow Brown	--				++		--		--			--	++		++	++	-	--		--	11	0.6
Wall Brown	--	+	++	--			--	++			++	--				++	++			--	11	1.2
White Admiral		+				--	++		--		++		+		++	++	++	++	--		11	2.7
Brimstone		--	++	++	++	++	++	--						--					--	--	10	1.0
Brown Argus	++		--			--	++	++	++				--	--					--	--	10	0.7
Dingy Skipper	--			--				++	++	-		--	--				++		--	--	10	0.4
Grizzled Skipper	++		-				++		++		--			-	--	-	-		--		10	0.4
High Brown Fritillary		+	--	+			++	++		-		-			++		-			++	10	1.5
Peacock			++	++		-	++					--	-		++	-	--		--		10	0.7
Small Copper	++				--			++	+		++			--			-	++	--	+	10	1.5
Essex Skipper	+		+	--			-				++	++	-			--			--		9	0.8
Silver-washed Fritillary	+			+	--		--		++					+	++	++	--				9	2.0
Small Pearl-bordered Fritillary				+	++	--	--	+			--	--		--					--		9	0.5
Marsh Fritillary			+	+				++		--	-	--			-				-		8	0.6
Purple Hairstreak				++	--			--		--	+		++	++	--						8	1.0
Small Heath				++			++	++			++		--	--		--			--		8	1.0
Small Blue							--	++						--	--	--	+	++			7	0.8
Grayling	+		--							--		--			++	++					6	1.0

Green Hairstreak							-		--				++	--		--			--		6	0.2
Pearl-bordered Fritillary										++	++			--	++					++	5	4.0
Northern Brown Argus							--			-					+				--		4	0.3
Silver-spotted Skipper			--				++							+						+	4	3.0
Large Skipper								+											-	-	3	0.5
Silver-studded Blue			-	+																	2	1.0
Ratio Pos:Neg	1.7	3.0	0.5	3.2	2.0	0.2	1.4	2.3	0.9	1.3	1.8	1.0	1.1	0.2	4.3	0.7	0.5	2.3	0.2	0.9		


A
Extremes of temperature ,Widespread n =36
■ Percentage causing Decline
▨ Percentage preventing Decline
% of species affected
100
80
60
40
20
0
20
40
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80
100
H
C
Ovum
Larvae
Pupae
Adult
Overwintering
Positive Impact
Negative Impact
B
Extremes of Precipitation,Widespread n =36
■ Percentage causing Decline
▨ Percentage preventing Decline
% of species affected
100
80
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Ovum
Larvae
Pupae
Adult
Overwintering
Positive Impact
Negative Impact
C
Extremes of temperature, Localised n =40
■ Percentage causing Decline
▨ Percentage preventing Decline
% of species affected
100
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Overwintering
Positive Impact
Negative Impact
D
Extremes of Precipitation, Localised n =40
■ Percentage causing Decline
▨ Percentage preventing Decline
% of species affected
100
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-20
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D
P
Ovum
Larvae
Pupae
Adult
Overwintering
Positive Impact
Negative Impact

Figure 2 Percentage of species in each life stage for which there was a significant ($p<0.05$) positive or negative relationship with an Extreme Climatic Event (ECE) related to temperature or precipitation. Widespread declines models (A and B) and localised declines models (C and D) species are shown separately. Impact of temperature extremes (A and C) and precipitation extremes (B and D) in widespread declines models and localised declines models are also shown separately. Columns above the 0 line in the y axis indicate the % of species for which the specified ECE will decrease the likelihood of a decline event while below indicates the % of species for which the specified ECE increases the likelihood of a decline event. D = Drought, P = Precipitation Event, H = Extreme heat, C = Extreme cold extreme precipitation during their adult life stage. The importance of these variables is further supported by their explanatory power in the individual localised decline models, Fig. 2. These three variables were included in the models of more than 25% of the species. 57% of species are detrimentally affected by extreme heat during the overwintering life stage, 45% benefit from extreme heat during the adult life stage and 40% of the individual species models include a negative effect of extreme precipitation during the adult life stage.

In both localised and widespread species models both precipitation temperature extremes are important and contribute to butterfly population decline events, however extreme temperatures play a more important role than extremes of precipitation in preventing declines Fig. 2. Despite most variables occurring more frequently in the widespread models, the ratio of whether a variable causes or prevents a decline seems to be relatively similar when comparing the widespread and localised decline models.

Combined species models: Localised and widespread declines

The combined LDM (Table 2) has a conditional r squared value of 0.193, indicating ECEs can explain 19% of the variation in species decline events from site to site. The combined WDM (Table 3) has a conditional r squared value of 0.71188 when abundance is included in the model and 0.71167 when abundance is not included indicating that ECEs combined with the random effects included in the model explain more than 71% of the variation in the data is explained by ECEs in the widespread declines model for UK Butterflies.

Table 2 Significant variables obtained from the localised declines model. Variables in bold indicate a variable increases the likelihood of a widespread decline in UK butterflies

Variable names	Estimate	Standard Error	Z value	P value
Adult Drought	-0.275714226	0.017674098	-15.59990346	<0.001
Pupal Precipitation	-0.239159292	0.017176167	-13.9239036	<0.001
Larval Temperature Min	-0.279166261	0.022548595	-12.3806497	<0.001
Pupal Drought	**0.164374665**	**0.015539529**	**10.57784083**	**<0.001**
Adult Precipitation	**0.154349025**	**0.014652944**	**10.53365318**	**<0.001**
Hibernation Drought	**0.120847175**	**0.012152146**	**9.944513481**	**<0.001**
Hibernation Temperature Min	**0.143741555**	**0.016020208**	**8.972514729**	**<0.001**
Pupal Temperature Min	-0.156168714	0.018369487	-8.501528492	<0.001
Ovum Temperature Max	-0.173817229	0.021286984	-8.165423009	<0.001
Ovum Temperature Min	**0.111488848**	**0.0138053**	**8.075800431**	**<0.001**
Adult Temperature Max	-0.235034569	0.029499193	-7.967491534	<0.001
Hibernation Precipitation	-0.130294154	0.017195462	-7.577240491	<0.001
Larval Temperature Min	-0.161863841	0.021506567	-7.526252	<0.001
Hibernation Temperature Max	**0.066584588**	**0.013610384**	**4.892190152**	**0.002**
Pupal Temperature Max	**0.068846144**	**0.02210696**	**3.114229324**	**0.002**
Larval Precipitation	-0.055534182	0.018218005	-3.048313046	0.002

Table 3 Significant variables obtained from the widespread declines model. Variables ordered by simple AIC weighting when added to the model. Variables in bold indicate a variable increases the likelihood of a localised decline in UK butterflies

Variable Name	Estimate	Standard Error	Z value	P value
Adult Temperature Max	-0.108418004	0.011328199	-9.570630204	<0.001
Hibernation Temperature Max	**0.067000641**	**0.007449482**	**8.994000373**	**<0.001**
Ovum Temperature Max	-0.068587346	0.008559006	-8.013470991	<0.001
Ovum Precipitation	**0.040687671**	**0.006537297**	**6.223929067**	**<0.001**
Pupal Temperature Max	-0.038985887	0.009186221	-4.243952819	<0.001
Hibernation Drought	**0.027958054**	**0.00723734**	**3.863028857**	**<0.001**
Adult Drought	-0.026479363	0.007427617	-3.564987522	<0.001
Larval Drought	**0.025692531**	**0.00739788**	**3.472958844**	**<0.001**
Larval Temperature Min	-0.027520416	0.008130378	-3.384887624	<0.001
Adult Temperature Min	**0.023606792**	**0.007204369**	**3.276732578**	**<0.01**
Hibernation Precipitation	-0.021852235	0.007814399	-2.796406495	<0.01
Ovum Temperature Min	**0.018030106**	**0.006632468**	**2.718461258**	**<0.01**

The widespread decline model appears to be primarily driven by extremes of temperature. The adult life stage appears to be a sensitive life stage and is significantly linked to annual population declines due to ECEs, Table 3. Both models show that warm weather extremes significantly reduce the likelihood of population crashes of UK butterflies if experienced during the adult life state while extreme precipitation significantly increases the likelihood of occurrence of 50% population declines, Table 2. Extremely hot weather during the overwintering period is a strong predictor of population decline events in the WDM model , Table 3 and is also a significant driver of declines in the LDM, Table 2. The WDM indicates that drought has a detrimental impact on UK butterflies. A number of different extremes appear to affect the LDM while the WDM to be primarily driven by 4 variables.

Discussion

Individual species models

Individual species models go a long way to backing up the findings of the combined species models (Fig. 2)., These models are dominated by the presence of three variables as being an important significant explanatory variables. These are extreme heat during the adult life stage and overwintering period and precipitation during the adult life stage. Precipitation during the adult life stage detrimentally impacts butterfly populations and causes dramatic population declines potentially by causing a decrease in foraging times as a result of the need to shelter to avoid direct damage (Gibbs et al. 2011). This in turn may impact on the reproductive fitness of the adult butterfly resulting in a decrease in the fecundity, egg composition and egg hatching success of butterflies (Geister et al. 2008). It may also be as a result of reduced recording of butterflies in periods of rain.

Of the 3 species that benefit from warmer winter temperatures all three overwinter as pupae, accounting for 43% of the species that overwinter as pupae. Of the species that were negatively impacted by warmer winters 4 overwintered as pupae (57 % of species that overwinter as pupae), 1 as ovum (20% of all the species that overwinter as ovum), 12 as larvae (60% of all the species that overwinter as larvae), and 3 as adults (75% of the species that overwinter as adults). In total, of the species included in this model, 4 species overwinter as adults, 20 as larvae, 5 as ovum and 7 as pupae. The beneficial effects of warm winter solely being felt by species overwintering as pupae is interesting, it perhaps makes the suggested hypothesis of photoperiod cue mistiming, caused by excessive heat, being a more plausible explanation for what is impacting upon butterflies overwintering as larval or adults. Or potentially those butterflies in their pupal state that benefit from warmer winters may not be as vulnerable to the harmful effects of disease and fungal attacks and therefore benefit from an increased growth rate due to warmer temperatures. The winter period has been shown in other studies as a major period of pathogen mortality. Warmer winter that increase the overwintering success of pathogens are likely to exacerbate disease severity (Harvell 2002).

Cold extremes appear to be beneficial in preventing butterfly declines during the ovum and larval life stage, Fig. 2. However, when comparing the individual species models with the combined species models it would appear the significant preventative association with cold and the larval life stage is much more important than the association with the ovum life stage. It may be that these cold weather extremes are not enough to impact upon or kill off the larvae of the butterflies but it could perhaps reduce incidences of disease, fungi or parasites.

The final variable that appears prominent in the widespread individual species' models is the detrimental effect of drought during the overwintering period. Drought can affect butterfly communities impacting on the basic biological parameters of an individual species, affecting essential functions such as reproductive rates and increasing mortality rates (Jiguet et al. 2011). However, in this case, drought may not be directly affecting the butterfly species but could perhaps be an indirect impact on the butterflies' host plants.

An interesting contrast when comparing the output from this study and that of (McDermott Long et al. 2017) is the importance of cold weather during the overwintering period. In the site level analysis of population change carried out in the previous study, cold weather was shown to have a predominantly beneficial effect on UK butterflies. However, in this study the link is not so clear. The response of British butterflies to cold winters appears to be very species dependent. It is included in roughly 60% of the species models with an even split of 30% of butterflies associating it with widespread decline and 30% with reducing the likelihood of widespread declines. Interestingly of the 11 species that showed detrimental impacts of cold weather during the overwintering period. 8 of these overwintered as a larvae (40% of all species that overwinter as a larvae), 2 as an ovum (40% of species that overwinter as an ovum) and 1 as an adult (25% of all species overwintering as an adult). Of the 10 species that cold weather was beneficial for, 4 overwinter as a larvae (20 % of species that overwinter as a larvae), 2 as a pupae (29% of species overwintering as a pupae) , 2 as a ovum (40% of species overwintering as an ovum) and 2 as an adult (50% of species overwintering as an adult) . It is quite evident the ovum and larval life stages are the most vulnerable to extreme cold while the pupal life stage seems to be resistant to cold weather. Previous research have emphasised the cold tolerance of butterflies overwintering as pupae such as the Swallowtail butterfly which has been shown to withstand freezing at temperatures below -35°C (Kukal et al. 1991).

The Importance of scale: Combined species localised versus widespread decline models

This study has shown that widespread declines are better predicted by ECEs than localised site level declines. In fact, 71% of the variation in the data is captured by the widespread declines model indicating that climate extremes play an important role in determing the widespread declines we see in UK butterflies in a given year. ECEs are better at predicting widespread butterfly population declines than declines at the local scale. The results of this study indicate that while ECEs have a role to play in driving population decline events at the site level many other biotic and abiotic factors play a role in determining if a species will suffer a localised decline in a year. The fact that we have shown such a high percentage of variation explained when looking at widespread declines resulting from ECEs shows that ECEs are the main drive factor driving decline events at this scale. It shows that when there is an ECE of enough magnitude it will impact on all non-buffered populations that are exposed to it.

The importance of scale is often overlooked when addressing the issues of climate change. ECEs strongly influence widespread population declines across all species of butterflies, hence when addressing impacts of climate, it is important to think about the scale at which the climate process is acting upon. At the site level there could be numerous factors influencing mass population decline and this may vary from site to site and from species to species (e.g. habitat change, agricultural pesticide use, disease, fire). However, there are fewer perturbations that can impact populations at the widespread scale and ECEs seem to be one of the most important factors. It would take wide scale changes in habitat or agricultural behaviour to bring about a year to year widespread decline event in a species. The difference in r square between the localised and widespread models indicates that there are other factors leading to population decline at the local scale that cannot be explained by the climatic variables whereas the high r-squared obtained for the widespread model indicates that ECEs strongly contribute to explain widespread population declines. The r squared value of 0.71 for the widespread decline is considered to be a model with quite high explanatory power in ecology today (Møller & Jennions 2002; Low-Dećarie et al. 2014).

Which ECEs drive butterfly decline events and which life stages are most at risk?

Extremes associated with temperature, from this analyses, are a strong driving force of the butterfly population declines corroborating previous research done on population change (McDermott Long et al. 2017).

Extreme heat during the overwintering life stage is shown to be detrimental, while it is beneficial during the adult life stage of butterflies. Precipitation during the adult life stage, has detrimental impacts on UK butterfly populations. This study shows it as an important indicator of whether UK butterflies are likely to face widespread or also local population declines, Fig. 2. Elevated warmer winters cause higher rates of mortality due to increased prevalence of pathogens and fungi (Radchuk et al. 2013), which have been shown to be more abundant in milder winters (Harvell 2002). It is also possible that, in the case of butterflies overwintering as larvae or adults, extreme hot temperatures may decouple them from important photoperiod cues as suggested by (McDermott Long et al. 2017) or cause a mismatch with the availability of the food plant (McLaughlin et al. 2002). The beneficial effects of extremely warm summers may be a function of the poikilothermic nature of butterflies, hence they require heat to survive and thrive and the ECEs identified are within the physical tolerance for adult butterflies and are actually beneficial rather than detrimental to their survival. Or potentially it may be because there are more butterflies flying during warmer periods and can be better counted in warm weather. Warm weather is shown to reduce the likelihood of decline if experienced outside the overwintering period.

Drought plays a prominent role in determining widespread species decline, Table 3. The negative impacts of drought during the overwintering period are mirrored in the localised model. One explanation for the detrimental impacts of drought during the wintering period on butterflies could be the importance of the winter rainfall in determining spring growth in feeding plants. (Ehrlich et al. 1980) highlighted this as being an important factor carried out in California and while the UK has a very different climate, the detrimental impacts that we see caused by drought could indicate that there is a similar mechanism at play in the UK. Drought also clearly has a beneficial impact on the ovum life stage of UK butterflies. This could be due to it providing ideal conditions for the rapid growth during the ovum phase allowing for a stronger and better developed larval stage increasing the chances of survival and decreasing the butterflies' sensitivity to a crash.

Far fewer variables have a significant impact on the likelihood of decline in the widespread declines model than the localised declines ,Table 2 & 3. This disparity is likely to be caused by the nature of the dependent variable. Localised declines are much more likely to occur than widespread declines and are much more likely to be caused by a complex suite of things dependent on site characteristics. The power of the LDM intimates that at the local scale ECEs are not the driver of population decline but do play a significant role in contributing to decline events. However, the widespread declines by their very formation are much harder to achieve and as a result of the infrequency of these events, they are much easier to attribute to extremes that occur in concurrence with them. The widespread decline is less likely to have a complex suite of explanatory.. The attribution of an extreme event is not masked at the widespread scale by more complex issues that happen at the local scale as by their nature they are site specific while widespread decline is likely to be due to climatic forcings.

The general agreement between the two models in terms of the magnitude and direction that the ECEs have on a butterfly population's likelihood of a decline event, whether it be a local or widespread decline, gives confidence in the robustness of the models and their ability to predict decline events, Table 4.

Table 4 compares the agreement between the model output of the combined widespread model and the combined localised model. Variables are sorted based on Extreme type (temperature or precipitation related).. (+++/--- indicates a p value < 0.001, ++/-- indicates a p value < 0.01, +/- indicates a p value < 0.05)

Extreme type	Variable	Agreement (Direction Widespread/Direction localised)
Temperature	Heat during Ovum life stage	Yes (+++/+++)
	Cold during Ovum life stage	Yes (-/---)
	Heat during Larval life stage	NA (NA/+++)
	Cold during Larval life stage	Yes (+++/+++)
	Heat during Pupal life stage	No (+++/---)
	Cold during Pupal life stage	NA (NA/+++)
	Heat during Adult life stage	Yes (+++/+++)
	Cold during Adult life stage	NA (-/NA)
	Heat during Overwintering	Yes (---/---)
	Cold during Overwintering	NA (NA/---)
Precipitation	Precipitation during Ovum life stage	NA (---/NA)
	Drought during Ovum life stage	NA (NA/---)
	Precipitation during Larval life stage	NA (NA/+++)
	Drought during Larval life stage	NA (---/NA)
	Precipitation during Pupal life stage	NA (NA/+++)
	Drought during Pupal life stage	NA (NA/---)
	Precipitation during Adult life stage	NA (NA/---)
	Drought during Adult life stage	Yes (+++/+++)
	Precipitation during Overwintering	Yes (+++/+++)
	Drought during Overwintering	Yes (---/---)

Conclusion

This is the first study to look at population decline events of UK butterflies using a large dataset with excellent spatial and temporal resolution. Previous studies have addressed individual year decline events and their causes, but only Palmer et al. (2017) have looked at decline events in UK butterflies over a long period of time, 1976-2015. Four of the five years with greater than 30% of species experiencing dramatic population declines occurred in the last 25 years, emphasising potentially increasingly detrimental role that ECEs are having on UK butterflies, Fig. 1.

This study uses a pioneering approach for quantifying UK butterfly decline (events) and for identifying ECEs associated to each life stage of the butterflies' life cycle. It provides a high temporal resolution approach that enables us to explore the mechanisms underlying dramatic population decline events associated with extreme weather. By examining local and widespread decline models we have also addressed the importance of scale and the role of other factors at the site level. We found ECEs explain a small proportion of the variation at the local level possibly because localised population decline can be due to numerous other factors that can cause decline at this scale. However, the Widespread Declines Model has been shown to be very important in identifying the likelihood of widespread UK butterfly decline events emphasising the importance of ECEs in driving population declines. Both models provide an important but different function however, the most important finding is that ECEs are better at predicting widespread than localised declines likely due to other biotic and abiotic factors contributing to decline at the local level. This study argues that it is also more appropriate to look at decline events when addressing the impacts of ECE rather that year to year population changes as in (McDermott Long et al. 2017). Due to the sporadic nature of ECEs it makes much more sense to look at whether they cause dramatic decline events in UK butterflies when they occur.

Our results corroborate previous studies but also identify ECEs that are important drivers of butterfly declines. Warmer winters are shown to be extremely important in determining the likelihood of population declines in many UK butterfly species, while warm summers decrease the likelihood of decline events. Precipitation events are shown to increase the likelihood of decline events in UK butterflies and as in Oliver et al. (2015), UK butterflies were identified as being vulnerable to drought events. The UK is predicted to have warmer drier summers and warmer wetter winters in the future (Defra 2009). This has the potential, based on the results of this study, to have both positive and negative impacts on UK butterflies. The balance of direction this would have on butterfly survival is yet to be addressed and is an urgent topic to be considered especially in light of the increasing number of decline of UK butterflies(Palmer et al. 2017).

This study found strong explanatory evidence for butterfly decline events in the UK. The next steps should examine life history traits and whether they are associated with butterfly sensitivity to ECEs and the importance of habitat in reducing the exposure of butterflies to ECEs. This information is fundamental to understand biodiversity responses to ECEs given their predicted increase in frequency and intensity (IPCC 2012).

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Chapter 4: What role does habitat and topographic heterogeneity play in buffering UK butterflies against ECEs?

Introduction

Climate change is now established as a factor with major consequences for biodiversity across the globe (McLaughlin et al. 2002; Araújo & Rahbek 2006; Pacifici et al. 2015; Dawson et al. 2011; Doney et al. 2012; Summers et al. 2012; Lindner et al. 2010; Foden et al. 2009; Garcia et al. 2014). Evidence shows species are shifting their ranges poleward and to higher elevations tracking their suitable climatic conditions (Parmesan et al. 1999; Hickling et al. 2006; Diamond et al. 2011; Franco et al. 2006; Pearce-Higgins et al. 2015), colonising hypothesised suitable habitats (Iverson et al. 2011) that had been previously unattainable due to climatic conditions (Chen et al. 2011; Parmesan et al. 2000; Foden et al. 2009). While most research focuses on the impact of change in average climatic conditions, species ranges will also be influenced by extreme climatic events (ECEs) (McDermott Long et al. 2017; Bauerfeind & Fischer 2014). It is essential that we address the responses of our biodiversity to extremes, furthering our understanding of site characteristics that may increase the robustness of communities that reside there. Species capacity to cope with changing environmental conditions and climatic extremes will depend on their adaptive capacity (Summers et al. 2012) and on the characteristics of the sites. Sites with increased habitat and topographic heterogeneity have previously been shown to increase community parameters such as population stability (Oliver et al. 2010) and faster population recovery after individual perturbations like drought (Oliver et al. 2013). Heterogeneity may enhance resilience to extreme climate events (Oliver et al. 2013; Lloret et al. 2012), species which actively thermoregulate may identify microhabitats that are buffered from extreme conditions (Moritz & Agudo 2013). Further understanding is needed to know the role habitat and topography can play in reducing the initial impact of ECEs over a long time period (Suggitt et al. 2017). Sites with increased community resilience may indicate sites likely to act as microclimatic refugia allowing species to persist under future climate change scenarios (Keppel et al. 2012; Suggitt et al. 2015; Maclean et al. 2015) and will facilitate the colonization of adjacent areas (Spalding 2005; Piessens et al. 2009).

The size and speed of changes in species' distributions will depend on the severity of changes in the climate and the physiological capacity of the affected species to tolerate the change (Scheffers et al. 2013). This effectively can be considered the sensitivity, exposure and recovery capacity of a species. While habitat cannot influence the sensitivity of a species to a given ECE it can increase or decrease the exposure and facilitate or impede the species' capacity to recover after experiencing such an extreme. If a species is vulnerable to an ECE its survival depends on whether it can find locally abundant climate refuges that buffer against ECEs by reducing a species' exposure. It is often assumed that increases in topographic and habitat heterogeneity increases the number of ecological niches (Luoto & Heikkinen 2008) and hence the potential for microhabitats and their associated microclimates to occur. Analyses of macroclimates alone can produce overly pessimistic findings that assume uniform changes in microclimates (Scheffers et al. 2014). The presence of different microclimates can buffer against extremes. For example, ambient temperatures outside and within upper forest canopy in primary rainforests were found to differ by 1–2 °C and decreased the length of exposure to extreme by 14–31 times (Scheffers et al. 2014), reducing temperatures below the critical thermal maxima for the inhabitant frogs and lizards. Heterogeneous landscapes, containing a variety of suitable habitat types, are associated with more stable population dynamics (Oliver et al. 2010), but the role of habitat heterogeneity in the event of acute exposure to ECEs is poorly known. This will be linked to species specific physiological sensitivities and tolerances to ECEs and their ability to find microclimates in wider landscapes.

Habitats can be manipulated (e.g. by increasing particular habitat type patches), while prioritisation of landscapes with high topographic or soil diversity can be emphasised (Hopkins et al. 2007). The malleability of habitats suggests that there is a potential widespread beneficial role of habitat heterogeneity in regards to limiting the detrimental effects of climate change on a variety of different organisms but the reality is that currently there is a lack of evidence that can show the relationship between habitat heterogeneity and population stability explicitly (Oliver et al. 2010).

This study assesses the influence of habitat and landscape characteristics on the likelihood of species suffering severe population declines due to ECEs. By taking advantage of a high quality long-term dataset, with population change data for many species, it will be possible to examine if habitat and topographic heterogeneity can increase species resilience against extremes climatic events. Does habitat heterogeneity provide increased resources and cover for a species, reducing their exposure or does it increase the level of habitat fragmentation at a site effectively increasing the exposure of a species due to issues such as smaller patch size? This study uses a novel approach and takes advantage of a long-term dataset to identify years of widespread butterfly population decline and compares the site characteristics of locations that experienced an extreme population decline with those that did not. The fundamental aim of this study is to explore which habitat characteristics, including habitat heterogeneity, may buffer UK butterflies against the impact of ECEs.

Methods

Data collection

Butterfly data

Data on butterfly abundance were used with permission from The UK Butterfly Monitoring scheme (UKBMS). A detailed description of how this information is collected is given in (Pollard & Yates 1993). In summation annual adult butterfly population indices are created at each transect site. Transects are walked weekly over a 26 week period from the start of April until the end of September. The routes are established at each site and counts carried out if the weather is suitable for butterfly movement. The weekly transect counts ultimately are used to create the population indices for butterflies that have been identified at that site. Population indices are created using log-linear models executed using the statistical software package, TRIM (Pannekoek & Van Strien 2001). A single index value for population is created for each species at each site every year. This value accounts for all the generations of that butterfly species should it have more than one generation in a year. The whole dataset was used in this study spanning from 1976-2015. It is a comprehensive dataset assembled using citizen science, thousands of volunteers throughout the UK. During this period there have been more than 2000 sites at which transect counts have occurred, although the number of sites varies from year to year.

The response variable in this study is binary, whether a species suffered a decline event at a site in a year where a widespread decline occurred for that species. Species declines were identified as in chapter 3, population change is quantified from one year to the next and a decline event at a site is characterised as a 50% drop in population. Widespread species declines occur in years when at least 50% of the sites where a species occurs suffered a 50% or higher population decline. These widespread declines have been attributed to ECEs (Palmer et al., 2017, Chapter 3). Time series with many zero counts and low means can affect measures of population variability (Oliver et al. 2010), hence only sites with 10 or more years of data and a mean population count of 9 were included in the model. The dataset for a species was then subsampled for years in which a widespread decline occurred.

Habitat data

Identification of habitat heterogeneity at site in which a species was present was carried out as in (Oliver et al. 2010). The Shannon-Wiener H’ Index was calculated to assess habitat diversity at each site. Habitat diversity is used as a metric of habitat heterogeneity in this study. The Landcover Map 2000 (Fuller et al. 2002), was used to identify and classify 12 different broad habitat categories (Appendix 1, Table 2) and their area in a variety of buffers around the butterfly transect sites. The habitat information, while calculated in the above manner, was provided by Dr. Tom Oliver (Oliver et al. 2010). Our metric of habitat heterogeneity included all habitats, even those that were rarely used. This approach was preferred since there is little information as to the behaviour of butterflies during extreme weather and rare habitats may be used in the event of occurrence of ECEs and may buffer against extreme weather. Buffers of habitat were 500m, 2000m, and 5000m around the geographic centroid of the butterfly transects. Habitat heterogeneity in smaller buffers is associated with site characteristics at the level of the butterfly transect sites while the larger buffers are representative of habitat heterogeneity at the wider countryside level (Oliver et al. 2010).

Topographic heterogeneity data was also included and identified as the standard deviation of slope and aspect in the respective buffers around the butterfly transect sites. Slope and aspect were identified using a 50m resolution digital elevation map (Morris & Flavin 1990). For a more detailed description of how standard deviation of slope and aspect were calculated for sites see (Oliver et al. 2010). Slope is defined as degrees from horizontal so that 0 defines a flat surface while 90 defines a vertical surface. Aspect is this study is identified as Northness which is cos ((aspectxPI)/180) so that 1 indicates due north and -1 due south. The standard deviation of both slope and aspect was used in this study as a measure of their variability at a site or landscape.

Statistical analysis

Models of individual's decline potential

Species specific binomial generalised linear models were created to identify whether a decline occurred at a site in a year of widespread decline for that species as the response variable and habitat diversity/heterogeneity, topographic heterogeneity referring to aspect and slope and habitat edginess were used as our explanatory variables (as in equation 1). Edginess is the area of a patch divided by the minimum possible perimeter. Pairwise interactions between diversity and slope and diversity and edginess were included in the model. To control for the potential importance of population size in influencing the likelihood of a species' decline, the initial population of each species at each site was included in the model. Location of butterfly transect sites have been included as a random factor in the model to account for declines occurring in particular regions of the UK. This was done by identifying what which 100km^2 grid square the transect site was located in the UK National Grid Map Reference.

$$DE(WDY) = \alpha_1 + \beta_1 Hab + \beta_2 Asp + \beta_3 Slp + \beta_4 Edg + \beta_5 Hab * Edg + \beta_6 Hab * Slp + \beta_7 Abun + \text{Random effects (Location of site in UK 100km}^2\text{ grid squares + SITENO + Year)}$$

(1)

DE(WDY) = Decline event (Widespread decline year), Hab = Habitat heterogeneity, Slp = Slope, Edg = Edginess of habitats, Abun = initial species population. α represents the model constant, β represents the slope for each explanatory variable respectively.

Highly correlated variables (> 0.7) were removed from the model using the *caret* package (Wing et al. 2015). Generalised linear mixed models of decline events with habitat diversity, topographic heterogeneity and area of preferred habitat, equation 1, were carried out at three different spatial scales (500m, 2km, and 5km) in order to identify any potential importance of buffer size in relation to habitat and topography around a site.

Multi-species analysis

The overall effect of the 4 explanatory variables; habitat heterogeneity, topographic heterogeneity (slope and aspect) and habitat edginess and the 2 interactions were examined across all species included in the study, for the three different measures of scale, (Fig. 1, below). The individual species coefficients for each explanatory variable mentioned above indicated the direction and magnitude of the effect on the likelihood of a population decline at a site for a species. The explanatory variables of interest for all species were pooled and tested as to whether the median value of the pooled coefficients was significantly different from zero using a one sample Wilcoxon signed ranks test following the approach described in (Oliver et al. 2010). This was carried out for all models run, those including abundance and those not and at each buffer scale.

Landscape scale analysis

To identify the landscape scale at which habitat heterogeneity has the best potential to buffer against declines caused by ECEs, for each species, we compared generalised linear models created at the three before mentioned buffer scales (500m, 2km, and 5km). Assessing which models were more sensitive to the effects of habitat heterogeneity when it was included, Table 5. For each species the following equation was fitted:

$$De(WDY) = \alpha_1 + \beta_1 Hab + \beta_5 Abun \text{ (3)}$$

This was carried out using data from each landscape scale. The model with the highest r^2 value when compared across each landscape scale for each species was used to identify the scale at which habitat has the largest potential to prevent declines. A fisher's exact test was then carried out in order to examine whether the most appropriate landscape scale differed when comparing generalist species and specialist species (Asher et al. 2001).

Results

Topographic heterogeneity increases site resilience to ECEs

Increased topographic heterogeneity is shown to buffer species against the negative impacts of ECEs in the individual species models, Fig. 1, Table 1. Significantly more species,75% of species at 5km, are buffered against ECEs by increased variety of slope in a 5km buffer at a site than those that are negatively affected, (Table 1, Proportions test, Table 2). In the multiple species analysis, increased diversity of slope tended towards reducing and significantly reduces at the 5km scale, the likelihood of a species suffering an extreme population decline, Fig. 1, Table 1.

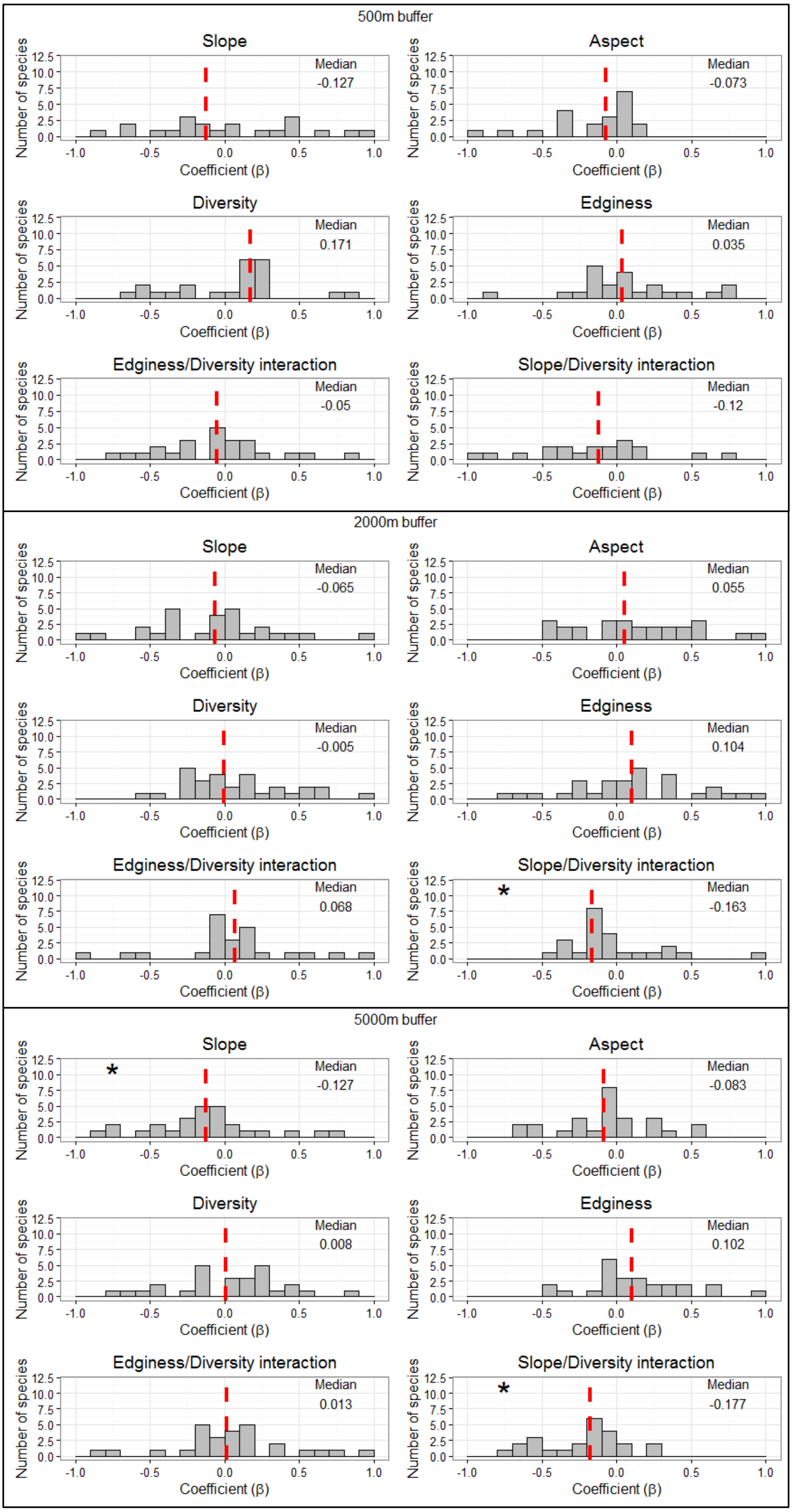
500m buffer
Slope
Median
-0.127
Aspect
Median
-0.073
Diversity
Median
0.171
Edginess
Median
0.035
Edginess/Diversity interaction
Median
-0.05
Slope/Diversity interaction
Median
-0.12
2000m buffer
Slope
Median
-0.065
Aspect
Median
0.055
Diversity
Median
-0.005
Edginess
Median
0.104
Edginess/Diversity interaction
Median
0.068
Slope/Diversity interaction
*
Median
-0.163
5000m buffer
Slope
*
Median
-0.127
Aspect
Median
-0.083
Diversity
Median
0.008
Edginess
Median
0.102
Edginess/Diversity interaction
Median
0.013
Slope/Diversity interaction
*
Median
-0.177
Number of species
0.0
2.5
5.0
7.5
10.0
12.5
Coefficient (β)
-1.0
-0.5
0.0
0.5
1.0

Figure 1 Relationship between likelihood of decline event at a site in a year of widespread decline and the habitat and topographic diversity at various landscape scales around the study sites. All panels show coefficients from 41 regression models which include initial yearly population as a fixed factor. Negative coefficients indicate that the variable in question reduces the likelihood of a decline event, buffering the species. Positive coefficients indicate the variable increases the likelihood of a decline event. Three different landscapes scales are represented: A = 500m buffer, B = 2km buffer and C = 5km buffer. For each landscape scale there are 6 explanatory variables displayed: slope, aspect, habitat diversity (Diversity), Edginess (Perimeter to area ratio of habitat), slope and diversity interaction, and edginess and diversity interaction. Asterisks indicate whether the species' coefficient for a variable at a particular landscape scale is significantly different from zero ($P < 0.05$). The median coefficient value of each explanatory variable is also displayed.

Table 1 Species' specific coefficients from generalised linear models assessing the potential buffering capabilities of habitat and topographic heterogeneity against widespread declines associated with ECEs at 3 different landscape scales (500m, 2km, and 5km. Caption continues below.

Species	500m						2km						5km						R	BLS
	S	A	D	E	D*E	S*D	S	A	D	E	D*E	S*D	S	A	D	E	D*E	S*D		
Adonis Blue	-0.2	-0.8	0.9	**1.3**	0.0	0.5	-1.5	0.3	-1.0	0.6	2.6	-3.9	0.7	1.2	-0.7	0.3	-0.5	-1.0	S	2
Brimstone	0.4	-0.6	-0.3	**-0.8**	-0.6	-0.3	0.3	-0.5	0.0	-0.2	0.1	-0.4	0.0	0.3	0.3	0.5	0.4	-0.2	G	2
Brown Argus	5.6	-0.1	0.2	**0.8**	-0.2	-0.4	0.3	-0.2	-0.2	-0.3	-0.9	0.6	-0.3	-0.1	-0.1	**0.9**	0.1	**-0.5**	G	3
Chalkhill Blue	NA	NA	NA	NA	NA	NA	0.7	-1.2	-3.6	0.8	-5.1	4.5	NA	NA	NA	NA	NA	NA	S	3
Comma	-0.2	-0.2	**-0.5**	-0.4	-0.3	0.0	0.1	-0.3	-0.2	0.3	-0.1	-0.2	-0.1	-0.1	-0.1	0.3	0.1	**-0.4**	G	1
Common Blue	-0.6	-0.1	0.2	0.2	0.2	-0.4	**-0.2**	0.1	0.0	0.2	0.0	0.0	-0.2	-0.1	0.0	-0.1	-0.1	0.0	G	3
Dark Green Fritillary	-0.1	0.2	0.3	0.3	0.0	0.1	-0.5	0.3	0.6	0.1	0.2	-0.4	-0.2	-0.1	0.1	0.0	-0.2	-0.1	S	2
Dingy Skipper	0.4	-0.4	0.2	-0.2	-0.1	0.2	0.5	**-1.1**	0.3	-0.7	-0.1	-1.2	0.2	-0.3	0.3	0.7	-0.2	**-1.3**	S	1
Essex Skipper	-0.5	0.0	-0.6	0.5	-0.5	0.2	-0.4	0.0	0.0	0.9	**4.8**	0.4	-0.2	-0.5	0.5	0.2	-0.1	-0.1	G	1
Grayling	0.3	0.0	0.3	-0.1	-0.8	-0.3	0.0	0.1	-0.1	-0.2	1.0	-1.3	**-1.3**	0.0	-1.3	**1.6**	0.6	-2.0	S	3
Green Hairstreak	0.1	0.1	0.3	0.1	-0.5	0.0	-0.1	0.2	0.5	0.1	0.1	-0.1	-0.5	0.6	0.3	0.1	-0.2	-0.1	S	3
Grizzled Skipper	0.8	3.3	1.6	-2.8	3.1	-0.6	-0.9	-1.3	-0.5	**-4.4**	5.0	0.4	0.3	-0.1	-0.8	1.4	1.3	1.8	S	3
Holly Blue	-0.2	-0.3	0.1	-0.1	-0.4	-0.1	**-0.5**	-0.2	0.3	0.2	-0.2	0.0	**-0.8**	0.0	0.3	0.6	0.1	-0.4	G	3
Large White	0.1	0.0	0.1	0.0	0.0	-0.9	0.0	0.1	0.0	-0.1	0.1	0.0	0.0	0.0	0.0	0.1	-0.1	-0.2	G	3
Meadow Brown	-2.4	0.1	0.2	-0.1	0.5	-3.4	-0.4	**0.6**	-0.2	0.4	0.2	-0.4	-0.1	0.0	-0.2	-0.1	0.2	-0.1	G	2
Peacock	0.7	-21.6	0.1	-0.1	-0.1	-3.9	3.5	118.0	0.2	0.0	-0.6	**-6.5**	0.1	0.2	-0.3	0.1	0.3	**-0.4**	G	3
Silver-washed Fritillary	-0.8	-0.3	0.8	0.6	0.8	0.8	0.1	0.9	0.7	2.3	-1.1	-0.2	0.5	-0.3	-0.5	-3.2	3.9	-0.6	S	1
Small Blue	0.3	2.7	-0.6	-0.3	0.5	1.0	-3.0	4.3	0.4	-0.6	4.9	-3.4	-0.8	-1.1	-1.7	-0.1	0.6	0.0	G	2
Small Copper	-0.4	-0.1	0.1	0.1	0.0	-0.9	-0.1	0.1	-0.2	0.1	0.1	0.0	-0.1	0.0	-0.1	0.1	0.0	-0.1	G	2
Small Heath	-0.2	0.1	0.2	0.0	0.1	-0.1	**-0.4**	0.0	0.2	0.4	0.2	-0.2	**-0.5**	0.3	0.3	-0.1	-0.3	0.0	G	3
Small Pearl-bordered Fritillary	NA	NA	NA	NA	NA	NA	-0.8	-1.0	-0.2	0.8	0.4	-0.4	-1.7	-2.1	-0.4	1.1	0.1	-2.8	S	3
Small Tortoiseshell	-0.6	9.0	0.2	0.1	0.0	**-2.3**	-0.1	18.2	0.2	0.1	-0.1	-1.1	-0.1	0.1	0.0	**0.3**	0.0	**-0.2**	G	2
Small White	-0.3	0.1	-0.2	0.2	-0.1	0.1	0.1	0.0	0.0	-0.1	0.1	-0.1	-0.1	-0.1	0.2	0.0	-0.1	-0.2	G	3

Speckled Wood	0.5	-0.4	-0.3	0.3	0.3	0.1	0.2	-0.5	0.0	0.0	0.1	0.2	NA	NA	NA	NA	NA	NA	G	3
Wall Brown	**7.0**	0.0	-0.1	-0.1	-0.2	4.1	-0.4	0.4	-0.5	-0.3	0.8	0.3	-0.6	-0.3	0.1	0.1	0.1	0.2	G	2
White Admiral	0.9	**-1.0**	-0.7	0.8	0.1	-1.3	1.2	-0.3	-2.1	0.7	0.5	-3.0	-0.1	-0.6	-0.2	0.6	-1.3	**1.5**	S	1

Significant P-values (P >0.5) are shaded in grey and are bolded. This table also includes the landscape scale for each species for which habitat heterogeneity best predicts the likelihood of a population decline event (BLS). Best fit model for each species was chosen as the model with the largest r2 value. Variables in table are as follows; S = slope, E = edginess, D = diversity, A = aspect, D*E = diversity and edginess interaction, D*S = diversity and slope interaction, R= habitat requirement (G = Generalist, S = Specialist), and BLS = Best Landscape scale. Negative values indicate that a variable is reducing the likelihood of a decline event, positive increasing.

Table 2 displays the Wilcoxon ranks test across 3 different buffers for each explanatory variable testing whether the median coefficient across species was significantly different to zero. It also displays the proportions test, assessing whether there are significantly more negative to positive values. Negative values in this table indicate a variable buffers against an extreme causing decline.

Variable	Buffer (m)	Wilcoxon Test		Proportions Test		
		V	p value	Number of species	Percentage Negative	p value
Slope	500	122	0.899	24	50%	1.000
	2000	112	0.182	26	58%	0.556
	5000	68	0.018	24	75%	0.025
Aspect	500	78	0.121	24	50%	1.000
	2000	112	0.445	26	42%	0.556
	5000	106	0.218	24	58%	0.540
Diversity	500	204	0.275	24	33%	0.153
	2000	160	0.958	26	50%	1.000
	5000	119	0.390	24	58%	0.540
Edginess	500	171	0.565	24	46%	0.838
	2000	221	0.120	26	38%	0.327
	5000	265	0.000	24	29%	0.066
Edginess*Diversity	500	117	0.360	24	54%	0.838
	2000	168	0.187	26	31%	0.078
	5000	156	0.601	24	42%	0.540
Slope*Diversity	500	81	0.147	24	63%	0.307
	2000	69	0.111	26	73%	0.031
	5000	71	0.012	24	79%	0.008

Aspect does not appear to play an important role in buffering species against ECEs at any of the scales addressed in this study. The median for aspect is not significantly different from zero when considered across all species and there is no significant difference in the number of species, ranging from 42% of species at 2km to 58% at 5km, which are buffered against ECEs by increased aspect heterogeneity (Fig. 1 and Table 2).

Habitat heterogeneity

Increasing habitat heterogeneity, in this case indicating increased habitat fragmentation, at a site has no significant impact on the likelihood of butterflies suffering population declines from ECEs at any of the habitat buffers used in this study(Fig 1, Table 2).

There is no significant effect of increased habitat edginess in relation to the likelihood of a population decline at any scale in this study, Fig 1, Table 2. This is also the case, when increased edginess interacts with increased habitat heterogeneity, there is no significant change the likelihood of a species suffering a decline event at a site at any scale, Fig 1, Table 2.

If increased slope heterogeneity occurs in conjunction with increased habitat heterogeneity there is significantly less likelihood of species suffering a decline event in years of widespread decline at 2000m and 5000m landscape buffers, Fig 1, Table 2. Significantly higher proportion of species are buffered against ECEs by this interaction, (Proportions test, Table 2)

Identifying the ideal scale at which habitat best accounts for attribution of decline

To assess if differences in scale at which habitat is important to species in its influence on population level responses to ECEs at the site level, we split species into wider countryside generalists and habitat specialists. We compared the landscape scale at which our models best fit when grouped by habitat requirement. Wider countryside species use a variety of habitats and heterogeneity at 5km was the best scale at which to assess the buffering capacity against extreme population decline events (Fig. 2). The majority of specialist species are better also best represented by models addressing heterogeneity 5km. There is no significant difference between generalist and specialist species, both appear to be best represented by models at a broader buffer scales, Fig. 2 (Fischer's exact test: $n = 41$, $P = 0.9193$. This indicates that conservation efforts to address extremes may need to tackle larger habitat areas around priority sites as species respond best to habitat changes at this scale.

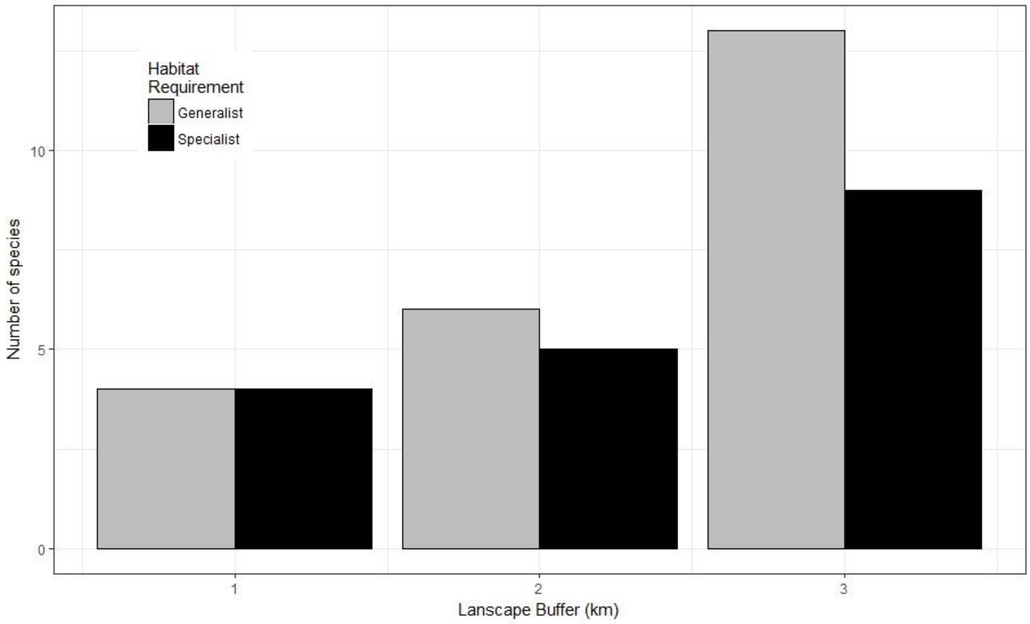

Figure 2 the landscape scales for which habitat heterogeneity best predicts a species' likelihood of decline for wider countryside versus specialist species. For each species a landscape was selected based on the highest r2 for the model looking at the relationship between habitat heterogeneity and population decline events.

Discussion

The previous two chapters have identified that, when attributing the impacts of ECEs, it is much more prudent to do so at a widespread scale. (Oliver et al. 2010) address population stability at the local site level which we have argued could be attributed to a multitude of biotic and abiotic factors, not just ECEs. Hence there is scope for looking at the potential buffering capacity of habitat and topographic characteristics at the site level when declines are attributable to ECEs, as is the aim of this study. In addition to the potential buffering effects of habitat shown in (Scheffers et al. 2014; Oliver et al. 2010) other studies such as Kindvall (1996) have contributed to furthering our understanding as to the importance of habitat. Kindvall (1996) evidenced that the bush cricket, *Metrioptera bicolor,* was more likely to suffer population extinction events on homogenous grassland patches while more heterogeneous grassland patches allowed increased survivability of local populations.

Buffering capacity of increased habitat and topographic heterogeneity

This study provides evidence that habitat heterogeneity has limited capacity to buffer the effects of ECEs on butterfly extreme population declines. However, the study does show evidence that topographic heterogeneity in association with increased habitat diversity, especially at broader scales around a site, can significantly reduce the likelihood of severe population decline events due to the impact of extreme climatic events (ECEs).

Increased topographic heterogeneity buffered sites against the impact of ECEs on species population declines at 5km. Previous studies have shown that topography shaped by factors such as slope may create significant environmental variation at fine scales (Oldfather et al. 2016) leading to ecological diversity and acting as a buffer to organisms responding to climate change. This is a potential explanation for the results of this study. Sites with fewer decline events are associated with increased variation in slope at 5km which may be a result of slope creating microrefugia which reduces a species exposure to the negative impacts of ECEs. Microrefugia are sites that support populations of species when their ranges contract during unfavourable climate episodes (Hylander et al. 2015). Interestingly, as we have already emphasised, increased habitat diversity at a site does not significantly change the likelihood of decline events for UK butterflies. However, when in conjunction with increased slope variation, increased diversity significantly to buffer against butterfly declines at 2 and 5km. This may be in due to microrefugia. Increased habitat variation at already buffered site (due to slope) is likely to increase a species persistence. Butterflies are already less exposed to the effects of an ECE. Therefore by also increasing habitat diversity, further resources may increase the stability of a population in the face of diminished ECE exposure (Oliver et al. 2010).

Habitat heterogeneity as we can see in Fig. 1 has not been shown to reduce the likelihood of decline of UK butterflies caused by ECEs. This contrasts with (Oliver et al. 2010), where butterfly populations are more stable at sites that have higher habitat heterogeneity. However, the metrics of habitat heterogeneity differ between the two studies. (Oliver et al. 2010) address habitat heterogeneity of habitat used by the species whereas this studies examines all habitats, including those that are not used, present at the sites. This study only considers years with widespread population decline for a species which have been linked to ECEs (McDermott Long et al. 2017), addresses only those decline events at the site level which have some evidence as being caused by ECEs and hence we are not looking at yearly population stability values but purely at whether habitat diversity can buffer against ECEs.

It is interesting that habitat heterogeneity has little effect positively or negatively in relation to buffering butterflies against extremes. It was hypothesised that habitat heterogeneity would reduce the buffering potential as a result of a reduction of the size of patches of habitat that actually can buffer against ECEs causing the decline. Which could potentially be exacerbated by increased fragmentation of suitable buffering habitat in habitats of higher heterogeneity. The “habitat heterogeneity hypothesis” is a key theory in ecology which assumes that more diverse habitats may provide a wider variety of niches thus allowing for an increase in species diversity (Tews et al. 2004). However, it stands to reason that in finite areas that are set by the buffers used in this study, the more diverse a site is the less space that will be available for each habitat type, resulting in increased habitat fragmentation.

Ideal Landscape scale

This study shows that landscape scale management (2-5km) is needed to better understand species responses to extremes. This may be due to the scale at which extremes impact being far greater than just the site level and larger buffers being better representative of a species ability to reduce its exposure to such extremes. The ability of butterflies to shift the local distribution to more favourable ones may the key reason why larger buffers represent a better reflection of habitat’s importance in terms of predicting the likelihood of a localised decline in a decline year. More mobile butterfly display short term thermoregulation by moving between habitats in a buffer to other habitats or microrefugia which may reduce their exposure to stochastic weather events (Oliver et al. 2010). One interesting thing to note is there is no significant difference between generalist and specialist species in terms of the ideal habitat scale which best represents habitat’s likelihood to impact on decline events.

As is the case in (Oliver et al. 2010) we are identifying habitat heterogeneity based on very broad landscape classes. It may be argued then that this scale of data is underestimating the potential habitat diversity that may exist at sites meaning that the total effect of habitat heterogeneity may be underestimated in this study. Another aspect to consider is whether we are underestimating the effects of habitat by making the definition of what is a decline attributed to ECEs too stringent? This is an important aspect to consider as using the definition in this study we are only looking at the potential of habitat and landscape heterogeneity to buffer against the most severe ECEs. We may not be addressing ECEs that don't have such wide scale and detrimental impacts but provide a more accurate representation of ECEs in the future. While the ECEs we address in this study will become more common the less severe extremes may have more continuous impact. However a counter argument is that if we can identify buffering capacity against the severest ECEs the same buffering potential will be provided against the less severe extremes. In association with this issue is potentially we are limited scope of looking at buffering capabilities as there may have been more decline years included for each species were it not for the buffering capacity of habitats and perhaps we are losing this resolution in the data and the true potential for habitats to buffer.

This study highlights the importance of slope variation in conjunction with increased habitat diversity at sites in terms of buffering against ECEs by increasing available niches and microhabitats. These complex interactions are important points for conservationist to consider. Increasing habitat without considering other potential buffers may do little to counter the effects of ECEs but carried out at sites who display good variety of slope may have more success. It emphasises the importance of recommendations in the (Lawton et al. 2010) report, suggesting that we need to establish a coherent and resilient ecological network to help the UK's biodiversity cope with pressures such as ECEs. On the basis of the findings of this paper resilience needs to account for the potential dangers of non-targeted increases in habitat diversity and always consider prioritising sites with increased topographic heterogeneity when considering buffering species against ECEs.

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Chapter 5: Can life history traits be used to predict UK butterfly responses to extreme climatic events?

Introduction

Evidence is accruing rapidly that the earth's biodiversity is under increasing pressure from anthropogenically induced climate change which is resulting in the rapid decline of many species (Van Allen et al. 2012). Conservation biologists and environmental scientists monitor and aim to predict how species and communities will respond to environmental perturbations and change such as those caused by climate change. This has always been a task and ambition that is fraught with difficulties since, for many taxonomic groups, there is little knowledge of important population dynamics, and species physiological and ecological constraints (Williams et al. 2010).

Currently the earth's biodiversity is declining at an unprecedented rate. Vertebrates have an extinction rate that is 10-100 times the expected background rate (Foden et al. 2013). This has been associated largely with habitat loss, over-exploitation, invasive species and climate change. Human induced climate change is substantially increasing the likelihood of extinction across taxonomic groups (Urban 2015), highlighting the importance of understanding which species are more vulnerable, why they are vulnerable and what can be done to prevent extinctions. The identification of individual species vulnerability to climate change requires large quantities of resources hence a better approach will be to identify general covariates of extinction risk based on life-history traits for several taxonomic groups (Van Allen et al. 2012).

This study aims to identify consistent responses within groups that share life history traits. This approach, also used in other studies (Henle et al. 2004), allows the identification and prediction of general patterns that can be applied to other taxonomic groups that share traits, by providing a mechanistic link between disturbances, such as climate change, and the response of individuals and communities. At present, most research has focused on the life history traits that allow species to respond to relatively gradual changes in mean climate change, but extreme climatic events (ECEs) have been mostly ignored. Climate change is causing an increase in climatic stochasticity (IPCC 2012), and variability (Frame et al. 2017). In the UK, this represents increased warm weather extremes throughout the year and a change in the distribution and intensity of precipitation extremes. For many species, their geographic range is determined not by the mean climate but by the ECEs that limit population processes. The magnitude and frequency of ECEs are fundamental drivers of species persistence (Lynch et al. 2014). Extreme weather has been shown to influence population size and trends (McDermott Long et al. 2017; WallisDeVries & van Swaay 2006; WallisDeVries et al. 2011; Palmer et al. 2017) but there is little understanding of the species traits that are associated with these responses (Chevin et al. 2010) and it is particularly urgent to identify those that are sensitive to ECEs. An organism’s vulnerability to ECEs is fundamentally based on three characteristics; exposure, sensitivity and adaptive capacity of the organism (Summers et al. 2012; Pacifici et al. 2015; Foden et al. 2013; Ameca y Juárez et al. 2013; Dawson et al. 2011). Hence, life history traits are likely to play an important role and will be associated with behavioural or physiological responses to ECEs.

The aim of this study is to build on our understanding of the sensitivities of UK butterflies to ECEs (McDermott Long et al. 2017) and, using life history traits, identify species vulnerabilities. Butterflies are used as the taxonomic group of interest in this study for a number of reasons. Butterflies have been consistently used in scientific research to evidence ecological response to recent climate change (Diamond et al. 2011). Butterflies have long been used as critical indicators of how species will respond to changes in habitat, land use and climate change (Fleishman & Murphy 2009). In addition to this, being poikilothermic, they are an ideal taxonomic group to study the effect of climate change and in particular ECEs. Their life cycle, activity, distribution and abundance are all associated with temperature (Roy et al. 2001) and their short life cycle mean that they will respond rapidly to changes in climate. This study will take advantage of a high temporal and spatial resolution dataset provided by the UK Butterfly Monitoring Scheme (UKBMS) with butterfly trends in the UK since 1976 (Marc Botham et al. 2016). The population data was obtained for the adult life stage, but it is possible to identify exposure to ECEs in each life history stages and test whether life history traits can predict the vulnerability of a butterfly to a particular ECE.

Methods

Butterfly population declines data

This study uses the output of the widespread population declines model obtained for each species of butterfly in the UK (Chapter 3), Table 1. The influence of ECEs was determined for all butterfly species and for each stage of each species life cycle. The coefficients of those models are used to identify which traits may influence the ability of a butterfly to respond to climate change (Diamond et al. 2011) and in particular ECEs.

Table 1 displays the sensitivity of UK butterflies to ECEs during particular life stages. They are significant predictors of whether a species will suffer a widespread decline or not. Site level abundance data on each species, maintained by the U.K. Butterfly Monitoring Scheme (UKBMS), was used to create these models. The dataset runs since 1976 to present and includes more than 2000 sites that are visited weekly during the spring and summer months, providing population abundance data for every species detected, for more details on the collection of these data see (McDermott Long et al. 2017). The thresholds of population occurrences set in chapter 3 are used to carry out species specific widespread models, 32 species fulfil the criteria and have sufficient population information to be included in the analyses (for details on the thresholds see chapter 3). The individual models include site level species specific population data and the extremes were identified at the site level for each species' life stage. Species with fewer than 10 sites in a year have that year of data removed from the model and species with fewer than 15 years of data are removed altogether.

Species' traits

The species traits were obtained from a variety of resources. Length of each butterfly's flight period was estimated using information supplied by (Asher et al. 2001). Voltinism was treated as a factor, with groups consisting of species with one generation per year (univoltine) and species with two or more generations in a year (multivoltine) (Asher et al. 2001). Overwintering stage was also treated as a factor including 4 categories, overwintering as eggs, larvae, pupae or adults (Asher et al. 2001). The speckled wood overwinters in multiple stages (larvae and pupae). Analysis was repeated for each life stage but as this resulted in no quantitative difference to our results we have displayed the results from the pupal life stage. Dispersal ability is based on composite scores of mobility, as described in Diamond et al. (2011). Diet breadth was represented by estimates of the number of host plants used by larvae reported by Diamond et al. (2011) . Family and a species' habitat requirements (specialist or generalist) was included and sourced from (Asher et al. 2001). Information on species' host plant preferences and their abundance was sourced from Dennis & Shreeve (1997). Species were grouped by their host plant preference (1, monophagous; 2, oligophagous - 1 species per habitat; 3, oligophagous - >1 species per habitat; 4, polyphagous).

We included several range size covariates as in Diamond et al. (2011), the percentage of national 10-km grid cells occupied within a species' range, the latitudinal extent of each species on the British mainland by category (1- 25%; 2- 50%; 3- 75%; 4- 100% of the total latitudinal span of the United Kingdom), and the northern range edge of a given species (latitude of the farthest northern grid cell with at least two presences). Finally, evidence of species range expansion was defined as a dichotomous variable using data from Dennis & Shreeve (1997).

Statistical analysis

All statistical analyses were performed using R (R Core Team 2016).

Identification of the butterfly traits that increase vulnerability to ECEs- Multivariate analysis

The function “adonis” from the R package “vegan” (Oksanen et al. 2016) was used to partition dissimilarities of species responses to ECEs based on sources of variation and identify traits that may significantly affect the partitions by applying permutation tests to inspect the significances of those partitions. This multivariate analysis method was applied as it allows us to address species’ responses to ECEs in their full space rather than reducing the variation to an ordination space and analysing only the first couple of elements (Oksanen 2015), “adonis” is a multivariate ANOVA based on dissimilarities which can handle both continuous and factor predictors. To carry out the analysis, a dissimilarity matrix was created using the table of species and life-stages specific responses to ECEs from chapter 3, Table 1. The distance matrix was calculated using the “manhattan” method as recommended with biological data in Oksanen (2015). Most ecologically meaningful dissimilarities are of Manhattan type, and use differences rather than squared differences (Oksanen 2015).

Table 1 displays the output of the individual species models showing the sensitivity of UK butterflies to ECEs during particular life stages and their likelihood of causing widespread decline in UK butterflies in chapter 3. The positive and negative values in the table indicate whether a ECE increases the likelihood of decline (positive values) or reduces the likelihood of decline (negative values). IF no value is given then no significant association with likelihood of causing a widespread decline event for a given species is identified for that ECE.

Species	Ovum				Larvae				Pupae				Adult				Overwintering			
	D	P	H	C	D	P	H	C	D	P	H	C	D	P	H	C	D	P	H	C
Adonis Blue		-0.5	0.5	-0.5		1.1	-1.1			-0.8			0.7	0.8	-0.4				0.5	0.5
Brimstone		0.7	-1.0	-2.7	-3.6	-1.3	-1.6	0.9						0.6					1.4	0.9
Brown Argus	-0.6		0.7			0.6	-0.8	-0.9	-0.5				0.6	0.4					1.1	0.4
Comma	0.6		0.2	-1.0	-0.5			-0.5			0.9	0.5	0.3	0.8	-1.4	0.6	0.4	0.3		-1.5
Common Blue	-1.0		0.3	-0.6	0.6	0.7			0.2	-0.4		0.3	0.2	0.2	-2.7	-0.5	0.1	-0.3	0.9	0.4
Dark Green Fritillary	-1.6				-0.8	0.9	0.9	1.3		-0.9	-3.0	-1.0			-2.0		0.6	-0.6		-6.6
Dingy Skipper	0.7			0.8				-5.7	-3.6	0.4		0.9	1.2				-3.2		0.6	1.4
Essex Skipper	-0.4		-0.4	0.5			0.3				-0.6	-1.4	0.3			1.0			0.4	
Grayling	-0.5		1.1							0.6		0.8			-2.3	-0.9				
Green Hairstreak							0.3		0.9				-1.7	1.0		0.7			0.5	
Green veined White					-2.1	0.6	-0.8	0.8	-0.7			-4.2		0.6			0.6	-2.8	-1.2	-0.3
Grizzled Skipper	-4.9		1.3				-1.8		-1.6		1.3			0.7	1.4	1.0	0.7		1.2	
High Brown Fritillary		-1.1	2.0	-3.0			-1.1	-2.4		0.8		1.8			-3.8		0.8			-5.2
Holly Blue		-0.3		-0.8	-0.6	0.3	-0.4			-0.4		-1.0		0.3		0.4	-0.3	0.4	-2.3	
Large Skipper								-23.2											5.9	4.8
Large White		0.4		1.1		-0.2	-0.4	-0.7	0.2			-0.4	-0.4		-0.8	-0.3	0.3	-0.8	-0.3	0.7
Marsh Fritillary			-0.9	-0.9				-1.9		0.7	0.7	0.9			0.6				0.6	
Meadow Brown	2.2				-2.6		1.2		1.7			1.1	-2.2		-4.6	-0.9	0.6	0.9		1.1
Northern Brown Argus							1.6			0.7					-2.6				1.6	
Orange tip	8.4	-3.4	9.8		-17.5		-35.7	0.6		-4.2	-4.7	-10.2	-5.7	9.0	-0.9	7.9	-9.5	1.9	7.4	-3.3
Peacock			-1.4	-2.8		0.2	-1.9					0.2	0.2		-2.2	0.4	0.9		0.8	
Pearl bordered Fritillary										-0.8	-1.4			0.9	-2.0					-4.0
Purple Hairstreak				-2.3	0.9			1.8		0.9	-2.4		-1.8	-1.3	2.0					
Silver spotted Skipper			1.8				-5.1							-1.5						-2.1
Silver studded Blue			36.9	-189.8																
Silver washed Fritillary	-2.4			-1.3	1.1		1.1		-0.7					-0.5	-3.0	-1.4	0.6			
Small Blue							0.8	-1.1						1.1	0.6	0.6	-0.8	-0.8		
Small Copper	-0.3				0.4			-0.5	-0.2		-0.4			0.2			0.1	-0.6	0.3	-0.2
Small Heath				-1.1			-0.9	-1.4			-1.4		0.5	0.6		0.4			0.5	
Small Pearl bordered Fritillary				-1.1	-1.4	0.7	0.7	-1.1			1.0	0.7		0.7					0.7	
Small Skipper	-9.5		25.1	-0.1	6.2		-4.8	-29.1		-1.0		-18.5		2.7	-29.5	2.2				-13.6
Small Tortoiseshell	-0.7		-0.4	-0.6				0.4	0.5	0.2	0.6	-0.2	-0.7		-1.1	0.5	0.4		0.7	-0.4
Small White				0.6	-0.5	0.3	0.3	-0.5	0.7	-0.4		-1.1	-1.4	0.3	-0.8	-0.4	0.7	-0.3	0.2	0.9
Speckled Wood	1.5			-0.8	-1.2					-0.7		-4.5	-1.9	0.8		1.1	-1.6	-0.5	1.2	0.8
Wall Brown	0.5	-0.3	-0.5	0.4			0.9	-0.9			-2.7	0.5				-0.8	-1.2			0.4
White Admiral		-0.4				0.8	-0.8		1.0		-0.8		-0.7		-1.0	-0.5	-0.5	-1.0	0.5	

The equation for the analysis is displayed below:

$$Y = \alpha X + \beta Z \ldots \ldots ..$$

Y, distance matrix based on the species specific responses to extremes.

X, Z – represent predictor variables listed in the life history traits section above. Family is included here as a fixed factor.

α,β – slopes for specific predictor variables

Identifying sensitive life history traits to important individual ECEs – Univariate analysis

The results of chapter 3 showed that precipitation and heat extremes during the adult life stage and heat extremes during the overwintering period, were the strongest predictors of likelihood of a extreme widespread population decline events across species. More than 40% of the species were affected by these three climatic extremes, hence these were examined in detail using univariate analyses.

There was little correlation between the three extreme climatic variables listed above confirming species independent responses. Linear models with the life history traits as explanatory variables were created for each of the three ECEs. The coefficient for the ECE in question from Table 1 was used as the response variable. Species that showed no statistical response were included in the model with a response of zero. This was carried out as a although they gave no significant response they should be included as they experience the same extreme but give it the equivalent of zero significance.

We used a model selection approach (Burnham & Anderson 1998) to identify models with strong empirical support of having similar predictive power to the best fit model (ΔAIC_c 0-4). AIC_c (AIC corrected for small sample sizes) was used rather than AIC, as the sample size divided by the number of model parameters was always less than 40. Model averaging was then used across the subset of best fit models to account for model uncertainty (Diamond et al. 2011). This analysis was carried out using the “MuMIN” package in R (Bartoń 2015). Species that had no significant response to the ECEs chosen were incorporated into the study with a coefficient of zero indicating no directional response. Phylogenetic autocorrelation was accounted for in our univariate models by including family as a random factor in the models.

Results

Table 2 Output table for the multivariate analysis. The response variable is the output of a distance matrix based on the Manhattan distance of the responses of each butterfly across all extremes in Table 1. Variables significant to the 95% confidence level are highlighted in grey.

Traits	Degrees freedom	Sum of squares	Mean squares	F value	P value
Flight period	1	165.832	165.832	2.475	0.008
Voltinism	1	120.893	120.893	1.804	0.04915
Dispersal ability	1	201.355	201.355	3.005	0.0006
Number of larval host plants	1	140.433	140.433	2.096	0.02665
Percent national 10Km grid cells occupied	1	75.188	75.188	1.122	0.34973
Latitudinal extent	3	225.139	75.046	1.120	0.35113
Family	3	408.383	136.128	2.032	0.0024
Habitat Requirement	1	53.658	53.658	0.801	0.64117
Host plant type	3	208.525	69.508	1.037	0.43243
Host plant abundance	3	232.637	77.546	1.157	0.30149

Identification of the butterfly traits that increase vulnerability to ECEs- Multivariate analysis

Numerous traits have been highlighted as being significantly important to explain species responses across a whole suite of different ECEs affecting different life stages (Table 2). This analysis does not give direction of how a variable impacts on species but rather is used to explain variables that can be used to group species in their response to ECEs. Family, as one might expect, is a significant predictor as to how species will respond to extremes (F = 2.032, *P* = 0.002). Lycaenidae responds differently to Hesperiidae while there is no clear difference between the other families (Fig. 7). The flight period of UK butterflies is a significant determinant of how species respond to ECEs (F = 2.475, *P* = 0.008). Dispersal ability is shown to be potentially the strongest indicator of how species respond to extremes, indicating potential avoidance behaviours (F= 3.005, *P* = 0.0006). The number of larval host plants, our variable for diet breadth, is also significant in determining a species response to extremes (F=2.096, *P* = 0.027). The final variable that is a significant predictor of how a species will respond to ECEs is their voltinism (F=2.475, *P* = 0.049).

Identifying sensitive life history traits to important individual ECEs – Univariate analysis

Traits associated with responses to extreme heat during adult stage.

Chapter 2 shows that 47% of species benefit from extremes of heat during the adult life stage while 11% of UK species are detrimentally affected. None of the traits examined were associated with these responses, Table 3.

Table 3 Ability of traits to predict how a species will respond to heat extremes during the adult stage. Lmg variable included in the table identifies the relative importance metrics for the linear model (R2 partitioned by averaging over orders, like in Lindemann, Merenda and Gold).

Traits	**Estimate**	**Imp. (n =29)**	**Standard Error**	**z value**	**p value**
Dispersal ability	-0.063	70.6%	0.033	1.830	0.0672
Requirement (Generalist)	1.008	33.9%	0.734	1.324	0.1855
Voltinism (Multivoltine)	0.753	24.5%	0.600	1.204	0.2286
Flight period (days)	0.005	20.7%	0.004	1.141	0.2540
Percent of national 10Km grid cells occupied	-0.011	18.2%	0.013	0.819	0.4129
Number of larval host plants	0.030	15.3%	0.045	0.636	0.5247
Range expansion	0.229	10.0%	0.575	0.382	0.7025

* Negative coefficients represent the variable reducing the likelihood of decline as its value increase

Dispersal ability was the only trait that was close to being a significant predictor (90% confidence level, $p = 0.067$) of the degree to which UK butterflies will be likely to experience a decline or not when faced with extreme heat events during their adult life stage. Species with increased dispersal ability were found to be less likely to suffer a decline event, although not significantly less likely, when exposed to extreme heat during the adult life stage ($p < 0.1$, Table 2, Fig.1). Model averaging of 29 different models, found to have strong levels of empirical support (ΔAICc 0–4), explained a moderate amount of the variation with adjusted r^2 values ranging from 0.05 to 0.27. Dispersal ability is clearly the major predictor variable accounted for in 89% of the best fit models.

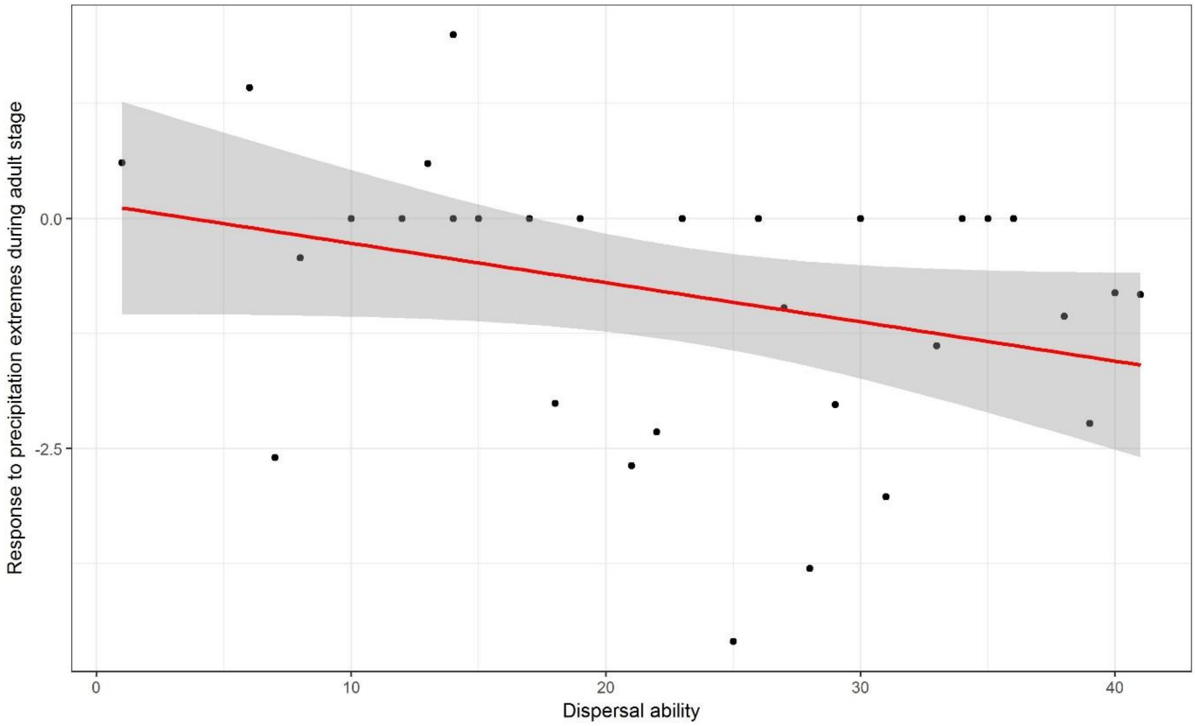

Figure 1 displays species' responses to extreme heat during the adult life stage as a function of increasing dispersal ability. Trend line is not significant at 95% confidence level ($p < 0.1$, Table 2). Responses are coefficients displayed in Table 1 and indicated the whether a species is more or less likely to suffer widespread decline as a result of the ECE. Positive coefficients indicate more likely to suffer a decline and negative coefficents indicate a species is less likely to suffer a widespread decline.

Traits associated with response to extreme precipitation during adult stage.

50% of UK species were identified as being more likely to suffer widespread decline events as a result of extreme precipitation during the adult life stage, while 8% of UK species were less likely (chapter 2). Three traits were significant predictors of these responses. Butterflies that have longer flight periods are significantly more likely to suffer from a decline event as a result of heavy precipitation during their adult life stage (Fig. 2, Table 4). Species with more larval host plants are found to be more likely to suffer a decline event as a result of extreme precipitation (Fig. 3, Table 4), and finally, increased dispersal ability decreases the likelihood of a butterfly suffering a widespread decline event as a result of extreme precipitation during the adult life stage (Fig. 4, Table 4). Sixteen models were found to have strong levels of empirical support (ΔAICc 0–4) and were averaged (Table 4). The variation of a species likelihood of decline to extreme precipitation during the adult stage ranged from 0.03 to 0.53 (adjusted r^2). Species habitat requirement is significant at the 90% confidence level (p = 0.0799, Table 4) indicating that there is a trend for habitat generalist species to be less likely to suffer a decline event as a result of extreme precipitation during the adult stage than habitat specialists, Table 4. This result seems to contradict the finding that species with more larval host plants are more vulnerable to extreme precipitation.

Table 4 Ability of traits to predict how a species will respond to precipitation extremes during the adult stage. Variables significant to the 95% confidence level are highlighted in grey. Lmg variable included in the table identifies the relative importance metrics for the linear model (R2 partitioned by averaging over orders, like in Lindemann, Merenda and Gold).

Traits	Estimate	Imp. (n=16)	Standard Error	z value	p value
Dispersal ability	-0.039	78.4%	0.013	2.912	0.0036
Flight period (days)	0.005	80.8%	0.002	2.545	0.0109
Number of larval host plants	0.050	82.8%	0.018	2.685	0.0073
Requirement (Generalist)	-0.520	48.7%	0.284	1.751	0.0799
Voltinism(Multivoltine)	0.339	35.7%	0.232	1.397	0.1624
Percent of national 10Km grid cells occupied	0.002	15.2%	0.005	0.356	0.7220
Range Expansion	-0.139	11.6%	0.249	0.540	0.5895

* Negative coefficients represent the variable reducing the likelihood of decline as its value increase.

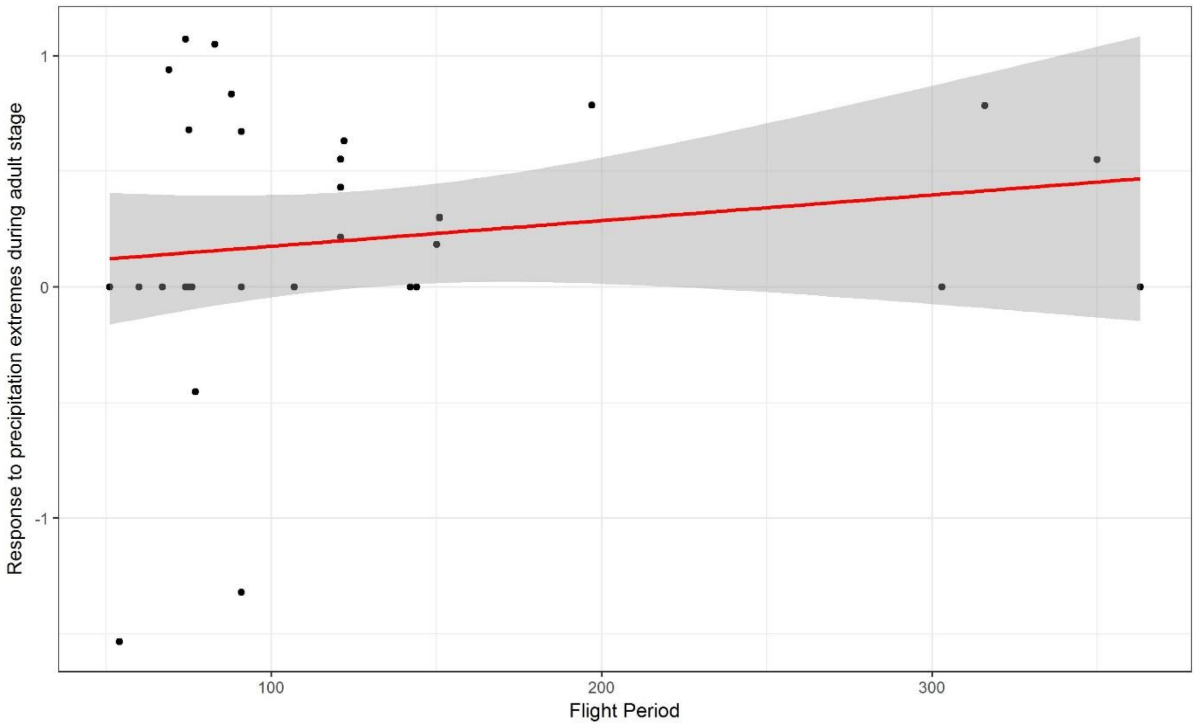

Figure 2 displays species' responses to extreme precipitation during the adult life stage as a function of increasing flight period length in days. Responses are coefficients displayed in Table 1 and indicated the whether a species is more or less likely to suffer widespread decline as a result of the ECE. Positive coefficients indicate more likely to suffer a decline and negative coefficients indicate a species is less likely to suffer a widespread decline.

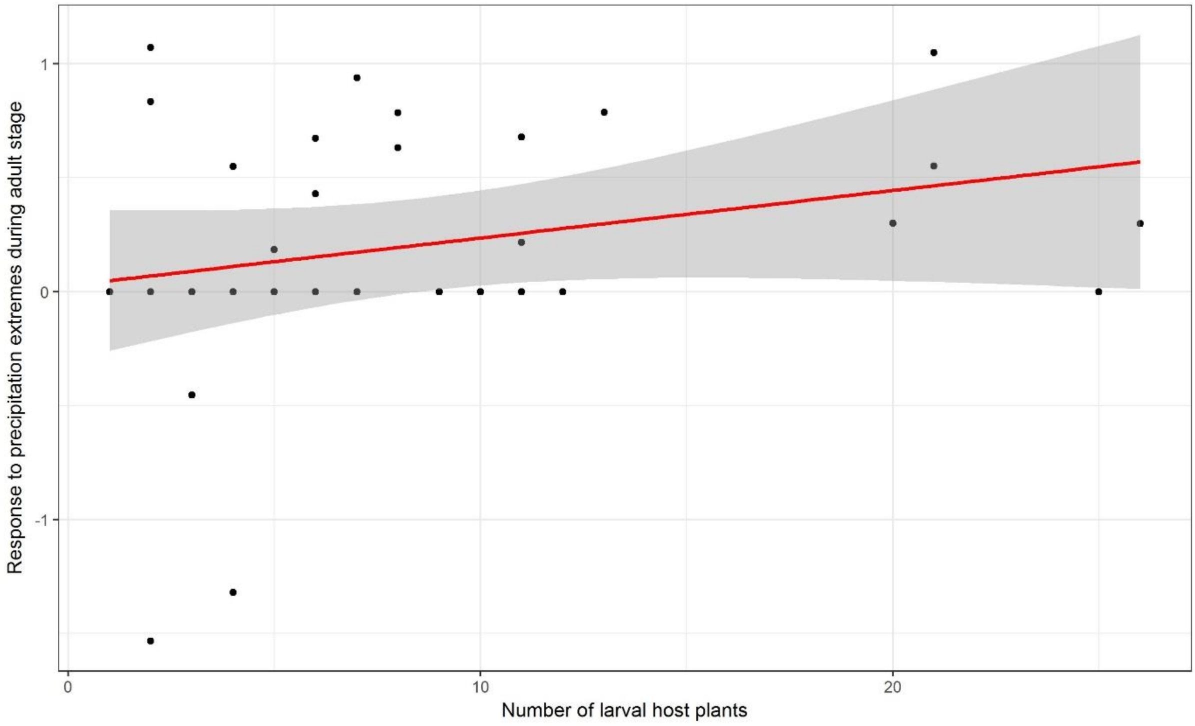

Figure 3 displays species' responses to extreme precipitation during the adult life stage as a function of increasing number of larval host plants. Responses are coefficients displayed in Table 1 and indicated the whether a species is more or less likely to suffer widespread decline as a result of the ECE.

Positive coefficients indicate more likely to suffer a decline and negative coefficients indicate a species is less likely to suffer a widespread decline.

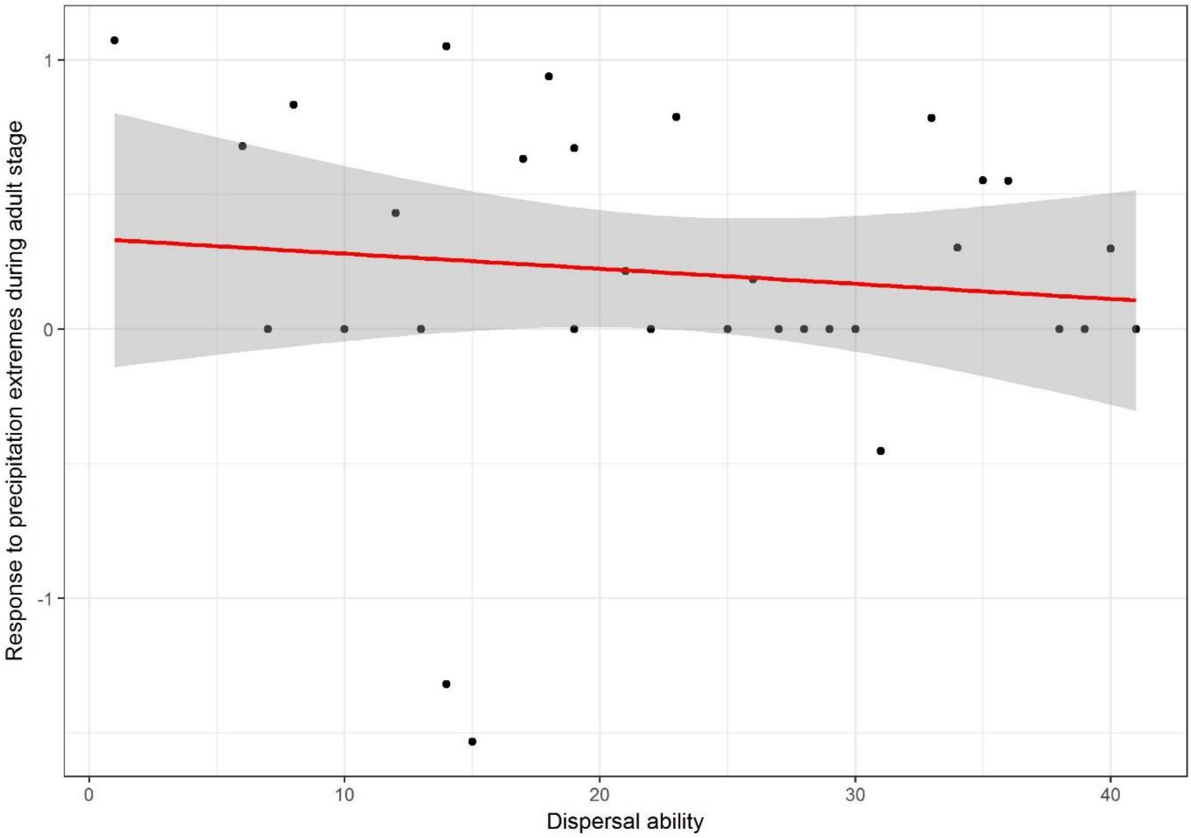

Figure 4 displays species' responses to extreme precipitation during the adult life stage as a function of increasing dispersal ability. Responses are coefficients displayed in Table 1 and indicated the whether a species is more or less likely to suffer widespread decline as a result of the ECE. Positive coefficients indicate more likely to suffer a decline and negative coefficents indicate a species is less likely to suffer a widespread decline.

Traits associated with species response to extreme heat during overwintering stage.

56% of UK butterflies included in the analysis were identified as being more vulnerable to widespread decline events as a result of being exposed to extreme heat during their overwintering period while 8 % benefited from such extremes. An increase in the number of larval host plants is associated with a species being less vulnerable to extreme heat during the overwintering period (Fig. 5, Table 5). As expected, the species life stage during the overwintering period is important, butterflies that overwinter as adults are significantly more vulnerable to extremely hot winters (Table 5). Thirteen different models, identified as having strong levels of empirical support (ΔAICc 0–4), were included in the model averaging and the variance explained ranged from 0.13 to 0.38 (adjusted r^2).

Table 5 Ability of traits to predict how a species will respond to heat extremes during the overwintering stage. Variables significant to the 95% confidence level are highlighted in grey. Lmg variable included in the table identifies the relative importance metrics for the linear model (R2 partitioned by averaging over orders, like in Lindemann, Merenda and Gold).

Traits	Estimate	Imp. (n=13)	Standard Error	z value	p value
Number of larval host plants	-0.045	83.0%	0.019	2.227	0.0260
Dispersal ability	-0.022	43.0%	0.015	1.436	0.1511
Percent of national 10Km grid cells occupied	-0.257	16.8%	0.260	0.946	0.3441
Range Expansion	0.005	19.2%	0.005	0.946	0.3440
Overwintering stage (Ovum n = 4)		6.5%			
(Larvae n = 17)	0.319		0.358	0.847	0.3972
(Pupae n = 7)	0.118		0.419	0.268	0.7885
(Adult n = 4)	1.276		0.508	2.391	0.0168
Voltinism (Multivoltine)	-0.040		0.255	0.149	0.8815
Requirement (Generalist)	0.117	9.5%	0.292	0.386	0.6997

* Negative coefficients represent the variable reducing the likelihood of decline as its value increase

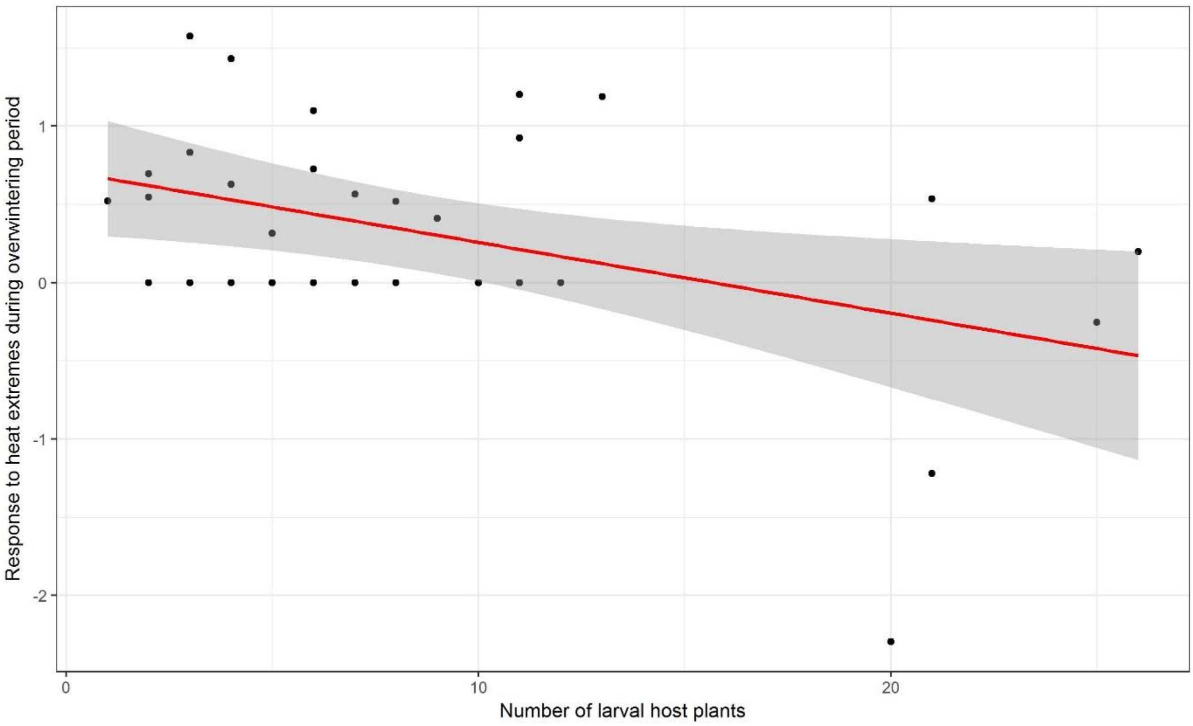

Figure 4 displays species' responses to extreme heat during the overwintering period as a function of increasing number of larval host plants. Responses are coefficients displayed in Table 1 and indicated the whether a species is more or less likely to suffer widespread decline as a result of the ECE. Positive coefficients indicate more likely to suffer a decline and negative coefficients indicate a species is less likely to suffer a widespread decline.

Discussion

Butterfly responses when considering all extremes and all life stages

The results have shown in this study that butterflies tend to respond similarly to butterflies that are part of the same butterfly family. Previous studies (Mair et al. 2012; Palmer et al. 2015; Palmer et al. 2017; Oldfather et al. 2016; Fox et al. 2015; McDermott Long et al. 2017) have found that species' responses to climate change are very individualistic and some species are more sensitive than others. (Palmer et al. 2015) argue that some species are more sensitive to climate change, as a function of their life history traits, but another potential explanation of the apparent individual responses is due to the fact that sensitivity alone cannot explain species response to climate change. As previously mentioned, vulnerability is a function of sensitivity, exposure and adaptive capacity. A species may be sensitive to several components of climate but may not be exposed to changes in those limiting climatic components. (Palmer et al. 2015) use the example of a species could be sensitive to summer precipitation, but the predominant locally occurring climatic change the species is exposed to is an increase in spring and autumn temperatures. Studies such as (Foden et al. 2013; Dickinson et al. 2014) have explained the importance of accounting for both a species' sensitivity to an extreme but also their exposure when assessing vulnerability. This could explain why this study has found that species in the same family respond more similarly when addressing the impacts of extreme weather across all life stages. This is due to the nature of the extreme events considered, the butterfly population decline events, identified for the purpose of this study, can be attributed to near synchronous, geographically widespread impacts that ECEs exhibit. Meaning all species are being exposed to the extreme and that the differences in vulnerability we are identifying are due to differences in sensitivity. While species may respond individually to particular extremes (Palmer et al. 2015), this study has shown that when looking at general trends in species response across all life stages for a number of different ECEs, different families such as Lycaenidae and Hesperiidae respond differently to ECEs (Fig. 6).

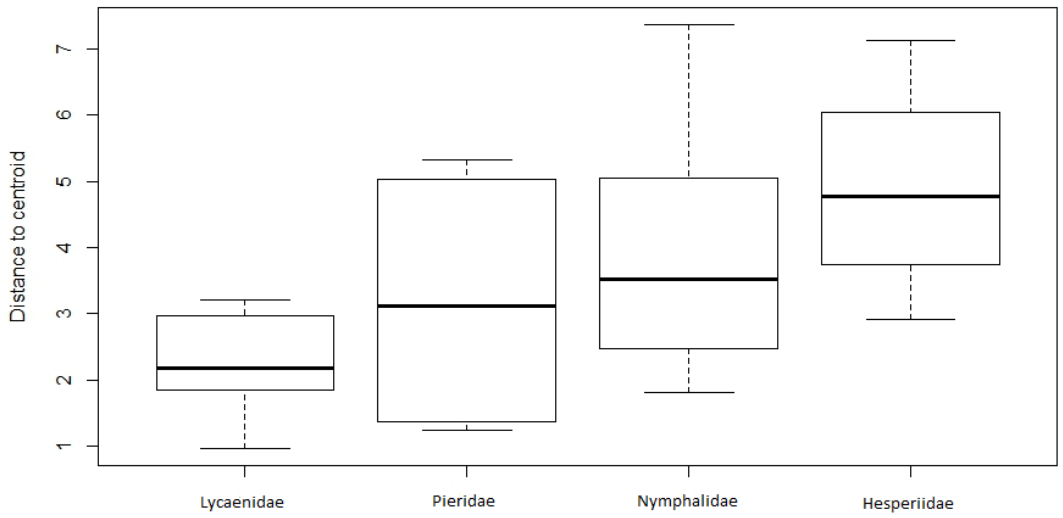

Figure 6 displays boxplot of the clustering output of the multivariate analysis showing difference in response between families to the impacts of ECEs across all life stages of a butterfly. Distances calculated across all ECEs based on coefficients in Table 1.

A number of other life history traits were indicated as being significant predictors of how species respond to ECEs. These life history traits include the flight period, voltinism, dispersal ability and the number of larval host plants. The multivariate analysis approach suggests these are significant determinants of how species will respond to the examined ECEs and it is not possible to make inferences about the direction or magnitude of the effect. Species that display similar life history traits will respond more synchronously than species displaying different values or perhaps species that are similar but due to similarities in different life history traits which are less important in determining how species will respond to ECEs.

Identifying sensitive life history traits to important individual ECEs

As well as carrying out multivariate analysis, this study addresses three ECEs which were previously identified in this thesis as being important determinants of whether a species will suffer a widespread decline event or not. These three extremes are the detrimental impacts of extreme heat during the overwintering period and of precipitation during the adult life stage and the beneficial impacts of extreme heat during the adult life stage.

Life history traits and extreme heat during the adult life period

Extreme heat during the adult life stages is considered as a beneficial impact of climate change for butterflies in the UK. When examining responses based on species' life history traits, this study has found that no life history traits are significantly associated to this specific response. However, dispersal ability of UK butterflies may play a role in how butterflies exploit the beneficial impacts of extreme heat during the adult period (Table 2 and Fig. 1). Consistent with the findings of McDermott Long et al. (2017) there was a beneficial response (at a 90% confidence limit) of UK butterflies to extreme heat during their adult life stage. Butterflies are poikilothermic organisms (Roy et al. 2001) and require heat to function. For the few species that are detrimentally impacted by extreme heat, butterflies with better dispersal ability are less likely to suffer widespread declines. Almost 50% of the butterflies in this study benefited from extreme heat during the adult life stage while only 11% did not. This roughly equates to 18 species vs 3 species which does not allow powerful inferences to be made. However, butterflies may be locally adapted, and extremes of temperatures may be detrimental for individuals, hence the butterflies with the better dispersal ability will likely be more capable of finding shade and microclimatic areas that will buffer them against the extreme heat.

Life history traits and extreme precipitation during the adult life period

The response of UK butterflies to extreme precipitation during the adult life stage was linked to several life history traits. Dispersal ability, flight period and number of larval host plants were all of similar importance across all the model subsets for which they were averaged and were all highly significant, Table 3. Species with increased mobility are less likely to suffer decline events when exposed to severe precipitation during their adult life stage, Fig. 4. When considering rainfall impacts there is need to balance the indirect beneficial impacts on factors such as the growth of their host plant and direct harmful effects on butterflies (Pollard 1988). Butterflies clearly use avoidance as a tactic in their survival when subject extreme precipitation. Species that are more mobile may be able to move themselves more rapidly out of harm's way avoiding the direct damage that the rainfall may have, reducing their exposure and hence vulnerability. Heavy precipitation poses a direct threat of injury or death for adult butterflies. Due to their size and weight heavy raindrops has the potential damage an adult. In addition to this, heavy rainfall events are often associated with a reduction in temperature. Temperatures may drop below the thermal threshold for butterfly flight meaning its ability to avoid the extreme is further diminished.

The length of a butterfly's flight period is a significant predictor of how UK butterflies will respond to extreme precipitation during their adult life stage, Table 3. This is not a surprising result if we think about this in terms of the aspects of species' vulnerability to extremes, sensitivity, exposure and recovery capacity. Butterflies with longer flight times are more likely to be subjected to periods of extreme precipitation. Butterflies with a longer flight period are more likely to be subjected to not only the wetter periods of the year but also more extreme precipitation events within a year.

Finally, species with more larval host plants appear to be more vulnerable to extreme precipitation during the adult phase, potentially, due to the trade-off of having few larval host plants to those that have many (McPeek 1996). Trade-offs are often exposed in situations where the ability to perform in one interaction comes at the expense of abilities to perform in other interaction (McPeek 1996). This may mean that a species specialised to a couple of larval host plant may be able to outperform other species even when faced with perturbations such as extreme precipitation. In this case, a butterfly may be specialised at feeding on or laying eggs in a certain plant species may also have more flexibility in dealing with the changes in climate. Species that can forage on many species or indeed lay many eggs on multiple host species which may be more sensitive to changes in conditions, such as badly protected eggs being washed away, and may potentially be outcompeted if conditions are not ideal. This may be especially important in communities of butterflies that are limited by density of population (Nowicki et al. 2009). It may be that in this case, the trade-off of having many larval host plants is that a butterfly is more vulnerable to the effects of environmental stochasticity.

Life history traits and extreme heat during the overwintering period

As with extreme precipitation during the adult life stage, extreme heat during the overwintering period has been identified as a key driver of widespread population decline in UK butterflies (See Chapter 3). This study has been able to identify certain life history traits that can significantly predict whether a species is likely to be positively or negatively affected by extreme heat during the overwintering life stage. Both the number of larval host plants and the life stage in which a species overwinters appear to be the primary determinants of vulnerability to hot winters for UK butterflies included in this study.

Butterflies that overwinter as adults are significantly more vulnerable to ECEs than butterflies that overwinter as eggs, in the UK there are 4 species that overwinter as adults and are sensitive to these extremes. However there was no significant difference found between the other life stages in terms of their sensitivities to warmer winters. We hypothesise that species vulnerability to extreme heat may be due to extreme heat drawing butterflies out of hiding in the middle of winter or that it may be due to increased incidences of disease. This study is correlative and a better understanding of the mechanistic processes behind these sharp population declines is still needed, the results provide cues to identify the processes that need further investigation. However, the results of this study may indicate that species declines associated with warm winters is as a result of species removing themselves from dormancy too early rather than increased incidence of disease which could affect more static life stages to at least a similar degree.

Species with more larval host plants are less likely to suffer decline due to extreme heat during the overwintering period. We hypothesise that this may be due to warmer winters impacting food plants differently (Hatfield & Prueger 2015). Some plants may be more vulnerable to climate stochasticity, hence having a variety of food resources will buffer butterfly populations against the detrimental impacts of ECEs on the food plants. In essence, they are not putting all their eggs in one basket.

Butterflies that had no significant responses to extremes were included in the analyses as having a coefficient value of zero. By including all species in the analyses it was possible to examine, across all species, the traits that are associated to responses to ECEs. A zero coefficient value represents the absence of a species response to the effect of the ECEs analysed, enabling the identification of traits that make species more resilient to ECEs.

Conclusion

The UK is predicted to be subjected to warmer drier summers and warmer wetter winters (Defra 2009). Based on the findings of this study this is likely to select for species that are resistant to warmer winters. Species with fewer larval host plants and those that overwinter as adults are more likely to be detrimentally affected by the future changes in the UK's climate.

This study has shown that Family grouping is an important determinant of how a species will respond to a variety of extremes across all its life stages. This study shows that Lycaenidae and Hesperiidae respond significantly differently to ECEs. A variety of traits are associated with species responses to ECEs, dispersal ability, number of larval host plants, length of the flight period and voltinism influence how UK species will respond to ECEs. Dispersal ability appears to be a predominant determinant of species' sensitivity. By understanding the general traits on which species respond we can begin to identify which species can be grouped together in conservation efforts to protect them against extremes. By further analysing the individual extremes driving declines we can identify which traits are most important to consider.

What this study also illustrates is that addressing life stage is of fundamental importance in understanding how a species will respond to an extreme. The complex life cycle of a butterfly means that different life stages are under different stressors but more importantly the life history trait of each life stage will be different and change differently between butterflies. This study has shown that having increased numbers of larval host plants can be beneficial when dealing with heat during the winter but increases a species vulnerability to precipitation during the adult phase. In is clear that traits that benefit a butterfly in dealing with an extreme in one life stage may be different to traits that benefit its response to an extreme in another life stage or it may actually mean that suddenly a butterfly is vulnerable when it wasn’t in its previous life stage.

Chapter 3 highlighted that detrimental effects of extreme heat during overwintering period and extreme precipitation during the adult life stage are driving butterfly declines. Based on the findings of this study, butterflies overwintering as adults and those with fewer larval host plants need to be protected from these predicted increases in winter temperatures. Butterflies with lower dispersal capacity, longer flight periods and more larval host plants are the species that need to be targeted when conserving and buffering adult butterflies against extreme precipitation.

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Chapter 6: Conclusion and Synthesis

Climate change has been shown to be an important determinant of species geographic range, their abundance, population change, phenology and biotic interactions (Palmer et al. 2017; Thomas et al. 2004; Warren et al. 2001; McDermott Long et al. 2017). Research into the impacts of extremes tends to receive far less research effort in ecology (Jentsch 2007; Suggitt et al. 2017). This is a concerning given the knowledge that we have, however limited, of the number of species that are sensitive to the effects of ECEs (Ameca y Juárez et al. 2013).

Improving our knowledge of how species respond to ECEs is vital for future conservation efforts especially with their predicted increases in frequency and magnitude under future climate change scenarios (IPCC 2012; IPCC 2014). It is important to know more information about how species respond to a variety of different ECEs, how aspects such as habitat and topography may reduce or exacerbate the effects of these extremes and to understand what life history traits may be a good indicator of species vulnerability to various extremes. This information will be crucial in modelling future ecological responses to climate change and climate variability in the UK and will improve our capacity to protect vulnerable species by understanding what habitat management action may help buffer them against ECEs. This thesis targeted five key questions in order to improve our understanding of how ECEs have impacted on UK butterflies; 1) Do ECEs drive year to year population changes in butterflies at the site level and which life stages are most vulnerable? (Chapter 2) 2) Do ECEs drive severe localised (50% drop in population from previous year) and widespread (localised decline event across 50% of sites in which a species is recorded in the same year) decline events? (Chapter 3) 3) What scale is best to predict the impacts of ECEs on UK butterflies? (Chapter 3) 4) Can habitat and topographic heterogeneity buffer UK butterflies against ECEs? (Chapter4) 5) Which life history traits are good predictors of how UK butterflies will respond to ECEs? (Chapter 5)

Key findings

Sensitivity of UK butterflies to extreme climatic events

This study was the first study to address the impacts of ECEs at the site level across all life stages of a butterfly. Novel techniques were developed to create statistically relevant, biologically driven extremes allowing us to tailor our model and extremes to each individual species. Chapter 2, allowed us to examine the effects of differing extremes with different thresholds depending on the life stage it was affecting. What we found was that the ECEs that had the most significant effect on yearly population change in UK butterflies were associated with temperature. The most consistent detrimental climatic extreme, across all species, was extreme heat during the overwintering period of UK butterflies. This was consistent with similar studies addressing warmer than average winters but this robust study confirmed the results of previous studies, I am particularly confident in the robustness of our models. Previous studies hypothesised that sensitivity to ECEs could be due to a number of reasons such as increased pathogen presence or indeed the early emergence of adults and larvae. Chapter 2 identified novel sensitivities of UK butterflies to extreme precipitation events during their pupal life stage. This finding was important, as while it has been suggested in previous studies, this was the first to display evidence of such a mechanism.

Univoltine species were shown to be less sensitive to ECEs than multivoltine species. Potentially due to the increased number of life stages increasing the exposure during sensitive life stages, more generations in a year may put more selection pressures on a species. It was also found, in chapter 2, that generalist species were generally more sensitive to extremes than habitat specialist species. This is counterintuitive to what we might expect but we hypothesised that generalist species were filling their climatic niche and therefore exposed to detrimental ECEs on their climatic range edge while specialist species limited in their range by their host plants do not fill the climatic range and therefore are not subjected to detrimental ECEs as often.

Chapter 3 took a different approach to identifying species sensitivities. It is the first study to look at population decline events of UK butterflies using a large dataset with excellent spatial and temporal resolution. It examines whether mass declines of butterflies are driven by our extremes. This study took a two-pronged approach addressing localised and widespread decline events. It identified 3 primary determinants of whether an extreme decline will occur for UK butterflies. Again it found that warmer winters are extremely detrimental to UK butterflies but also found that extreme heat during the adult stage proved to be beneficial for adult butterflies and reduced the likelihood of a decline event. This is likely driven by the poikilothermic and heat loving nature of butterflies, temperatures in the UK during their adult life period do not tend to reach temperatures that are likely to cause declines at the localised or widespread scale. The final variable which featured prominently in both the widespread and localised declines models was the negative impact of extreme precipitation during the adult life stage increasing the likelihood of a decline event across UK butterflies. It has been suggested that this could reduce the fecundity of adult butterflies through a number of mechanisms. The findings of these studies are largely in line with the results we would expect given previous studies. Studies such as (Palmer et al. 2015; Pateman et al. 2012) have shown the beneficial response of butterflies to warm summers while there have been others studies that have suggested that warmer winters are detrimental to butterflies (Roland & Matter 2013).

In summary from the two studies that have been carried out addressing sensitivity of butterflies to extremes, we can say that the warmer, wetter winters predicted for the UK are likely to have hugely detrimental effects on our UK butterfly populations. However, the UK will also be subjected to warmer, drier summers and the balance between this beneficial and detrimental increase in temperatures has yet to be investigated.

The importance of scale when addressing the impacts of ECEs

In addition to analysing the sensitivity of UK butterflies to ECEs, chapter 3 also addresses the most appropriate scale at which we can attribute their impact. It is a topic that is frequently overlooked in research and attributions are examined at a scales that may not be the most appropriate scale for which an extreme is impacting upon.

By examining local and widespread decline models we have identified that ECEs explain a small proportion of the variation in decline events at the local level possibly because localised population decline can be due to numerous other factors that can cause decline at this scale. However, the widespread declines in UK butterflies have had as much as 71% of their variation explained by ECEs. This is an incredibly strong result which does not occur often in biological research and emphasises the importance of ECEs in determining the widespread declines of UK butterflies. ECEs are better at predicting widespread than localised declines, likely due to other biotic and abiotic factors contributing to decline at the local level while no other drivers act at the widespread levels to influence widespread decline. This study argues that it is also more appropriate to look at decline events when attributing ECE impacts rather that year to year population changes as in (McDermott Long et al. 2017).

What role does habitat and topographic heterogeneity play in buffering UK butterflies against ECEs?

ECEs and their impact on biodiversity is a relatively understudied field in conservation science but the role that habitat and topography can play in buffering against their detrimental impacts is even more understudied. It has come under more scrutiny recently mainly due to research been carried out in order to identify microrefugia for species responding to climate change. This is the first study to address the importance of habitat and topographic heterogeneity in buffering UK butterflies against numerous ECEs occurring over a long temporal time scale. It has identified that increased heterogeneity of slope and diversity of habitat in conjunction with each other reduces the likelihood of a species suffering a decline when subjected to a variety of ECEs. This is likely due to the increased number of niches created by the topographic heterogeneity which can shelter a species in periods of stress related to ECEs.

Can species life history traits predict how a species will respond to ECEs?

Again as in previous chapters, chapter 5 took a twofold approach to addressing how life history traits can be used to explain patterns in the responses of butterflies to the ECEs they experience. The first approach involved grouping species based on their life history traits and investigating how those life history traits predicted their likelihood of suffering a decline across all ECEs affecting all life stages. Some very interesting and important results came from this study the first being that butterflies are more likely to respond similarly to species of the same family. This is an important finding as studies such as (Palmer et al. 2015) cite the individualistic nature of how species respond to extremes. This study doesn't refute that species respond in a very individualistic manner but when we look at patterns across all species there are similarities in how families respond across ECEs. A species voltinism, dispersal ability, flight period and number of larval host plants were all also significant predictors of how ECEs will affect species across their life stages.

Chapter 5 also addressed the three ECEs that were found to be significant drivers of widespread species declines in chapter 3. Only dispersal ability was close to being a significant predictor of how heat was beneficial during the adult life stage. This may be due the uniform beneficial impacts of extreme heat across all butterflies given their poikilothermic nature. Adult butterflies with higher dispersal ability were found to be less vulnerable to extreme precipitation indicating that avoidance is a key behavioural mechanism to deal with extremes. In addition to this adults with longer flight periods were found to be more exposed to extremes of precipitation, perhaps due to their flight period extending into more volatile periods of the year. The final extreme examined was the detrimental impact of extreme heat during overwintering. Butterflies overwintering as adults were found to be significantly more vulnerable than the pupal life stage indicating that the detrimental mechanism of extreme heat during the winter may be the mismatch of photoperiod ques and species emerging early due to hotter periods.

General summary

The UK is expected to experience warmer wetter winters and warmer drier summers. This research has shown that there could be contrasting effects of both these findings however there is no knowledge available about the overall effects the balance between positives and negatives will have on butterfly populations in the UK. Will butterflies be driven to extinction by the increasing frequency and magnitude of warmer winters or will the beneficial effects of warmer summers allow for population sizes that buffer species against the negative impacts of warm winters. Should the detrimental effects outweigh the beneficial effects there is a need to understand how we can tackle the issue. This study has highlighted that topographic heterogeneity is an important variable to consider when considering which sites to prioritise. There needs also to be targeted increase of habitat heterogeneity in order to buffer species as increasing useless habitat to the butterflies is likely to increase fragmentation of their habitat resulting in increased exposure.

Limitations

One of the major limitations of this study was the distribution of the UKBMS dataset. There is a much greater density of sites in the south and south east and areas such as Scotland have a much more sparse and sporadic spread of their butterfly transect sites. While all the models were checked for issues in spatial autocorrelation it is still an issue that needs to be factored in. The majority of the information regarding butterfly populations and extremes will be in relation to those happening in the south of the UK. Therefore, extremes associated with the north, such as precipitation or cold extremes, may be underestimated. In addition to this, we imposed limitation on the dataset to only use data that is of sufficient temporal length and abundance level that we can make robust prediction based on it. This in essence means that the results of this study are primarily based on species that are more common within the UK and more scarce species, especially those confined to Scotland, e.g. the Scotch Argus did not provide enough information to be incorporated into the study.

We have talked in chapter 4 about the importance of habitat that is useful to butterflies in order to buffer themselves from extremes. However, in this study habitat heterogeneity is a descriptor of habitat fragmentation. As mentioned previously increasing habitat diversity without understanding which habitats are important to a species may only serve to increase their exposure to ECEs. We do not have information about the behaviour of butterflies subjected to extremes and therefore do not have information on habitats that are useful to them in regards buffering themselves from an extreme.

Future work

This study has applied a very novel approach to identifying its extremes but also in how it has identified widespread decline events. For this reason and to understand the implications of ECEs for biodiversity in general, it would be important to apply this to other taxonomic groups. It would be interesting so apply the novel biological approach to ECEs for species with different life cycles. It would be useful to not only identify if they are vulnerable to similar extremes but would be important to understand whether similar life history traits have been involved for them to deal with ECEs. There is the opportunity with datasets provided through organisation like the BTO to carry out this sort of work, providing unique opportunity for any future work to make comparisons between species responses to ECEs and begin building a database of sensitive life history traits for diffing taxonomic groups.

Further understanding as to the behaviour of butterflies during ECEs would allow for a much more focused and applicable study as to the ability of habitat to buffer extremes. This is a difficult task to undertake due to the sporadic nature of ECEs. However, if we increased our understanding of how they responded during these periods it would allow us to look at the buffering effects of habitat that are specific to each individual species and potentially coax out those species whose habitat offers little buffering ability meaning they are likely to be more exposed to future extremes.

There is an opportunity arising from the outputs of this study to carry out a version of ground truthing. The vulnerable life stages that have been identified to particular extreme for individual species provides the opportunity for lab based experiments to validify these results and to also set thresholds for species regarding their thermal tolerance for different life stages. The lab based experiments could also look into the potential for site specific adaptation by carrying out the above laboratory experiments on the same species but from populations at either end of that species realised range.

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Annex 1

Table 1 shows the life stage timing of UK butterfly species which are used throughout this thesis (Eeles 2014).

Species	Generation timing	Ovum.1	Ovum.2	Ovum.3	Larvae.1	Larvae.2	Larvae.3	Pupal.1	Pupal.2	Pupal.3	Adult.1	Adult.2	Adult.3
Adonis Blue	Start	22-Aug	22-May		08-Sep	08-Jun		15-Apr	22-Jul		08-May	08-Aug	
	End	07-Oct	07-Jul		30-Apr	07-Aug		07-Jun	31-Aug		21-Jun	21-Sep	
Black Hairstreak	Start	15-May			15-Mar			22-May			01-Jun		
	End	14-Apr			07-Jun			21-Jun			30-Jun		
Brimstone	Start	08-May			22-May			15-Jul			22-Jul		
	End	21-Jun			31-Jul			21-Aug			07-Jul		
Brown Argus	Start	08-Aug	22-May		15-Aug	01-Jun		08-Apr	01-Jul		01-May	15-Jul	
	End	21-Sep	07-Jul		21-Apr	31-Jul		21-May	21-Aug		30-Jun	14-Sep	
Brown Hairstreak	Start	15-Aug			01-May			15-Jun			22-Jul		
	End	07-May			30-Jun			08-Aug			14-Sep		
Chalkhill Blue	Start	01-Aug			01-Apr			08-Jun			08-Jul		
	End	14-Apr			21-Jun			07-Aug			07-Sep		
Chequered Skipper	Start	01-Jun			15-Jun			15-Apr			15-May		
	End	07-Jul			21-Apr			21-May			30-Jun		
Comma	Start	01-Jul	01-Apr		15-Jul	21-Apr		08-Aug	08-Jun		15-Aug	22-Jun	
	End	07-Aug	14-May		21-Aug	14-Jun		07-Sep	07-Jul		21-Jun	15-Aug	
Common Blue	Start	01-Aug	22-May		08-Aug	01-Jun		01-Apr	08-Jul		08-May	15-Jul	
	End	30-Sep	14-Jul		30-Apr	21-Jul		31-May	21-Aug		30-Jun	21-Sep	
Dark Green Fritillary	Start	01-Jul			22-Jul			08-May			08-Jun		

	End	07-Sep			21-May			14-Jul			07-Sep		
Dingy Skipper	Start	15-May			15-Jun			08-Apr			01-May		
	End	07-Jul			21-Apr			31-May			21-Jun		
Duke of Burgundy	Start	22-May			01-Jun			15-Jul			22-Apr		
	End	07-Jul			07-Aug			31-May			21-Jun		
Essex Skipper	Start	15-Jul			22-Mar			08-Jun			15-Jun		
	End	07-Apr			21-Jun			21-Aug			21-Aug		
Gatekeeper	Start	22-Jul			15-Aug			08-Jun			15-Jul		
	End	14-Sep			21-Jun			07-Aug			31-Aug		
Glanville Fritillary	Start	22-May			01-Jul			15-Apr			01-May		
	End	14-Jul			30-Apr			31-May			30-Jun		
Grayling	Start	15-Jul			01-Aug			08-Jun			01-Jul		
	End	21-Sep			21-Jun			08-Aug			14-Sep		
Green Hairstreak	Start	08-May			15-May			22-Jul			15-Apr		
	End	07-Jul			07-Aug			14-May			07-Jul		
Green veined White	Start	22-Jul	01-May		01-Aug	15-May		08-Sep	22-Jun		22-Apr	01-Jul	
	End	14-Sep	21-Jun		21-Sep	07-Jul		07-May	31-Jul		21-Jun	31-Aug	
Grizzled Skipper	Start	08-May			01-Jun			15-Jul			08-Apr		
	End	07-Jul			31-Jul			22-May			22-Jun		
Heath Fritillary	Start	15-Jun			08-Jul			01-May			22-May		
	End	07-Aug			07-Jun			07-Jul			21-Jul		
High Brown Fritillary	Start	08-Jul			08-Mar			15-May			15-Jun		
	End	21-Mar			31-May			21-Jul			14-Aug		
Holly Blue	Start	22-Jul	22-Apr		01-Aug	01-May		08-Sep	22-Jun		01-Apr	08-Jul	
	End	31-Aug	07-Jun		21-Sep	07-Jul		30-Apr	07-Aug		07-Jul	31-Aug	
Large Blue	Start	22-Jun			08-Jul			08-May			01-Jun		

	End	07-Aug			31-May			07-Jul			21-Jul		
Large Heath	Start	08-Jul			22-Jul			08-May			08-Jun		
	End	21-Aug			21-May			07-Jul			31-Jul		
Large Skipper	Start	01-Jul			15-Jul			15-May			01-Jun		
	End	31-Aug			21-May			21-Jun			14-Aug		
Large White	Start	22-Jul	01-May		08-Aug	22-May		22-Aug	15-Jun		15-Apr	01-Jul	
	End	14-Sep	30-Jun		30-Sep	14-Jul		07-May	31-Jul		30-Jun	07-Sep	
Lulworth Skipper	Start	22-Jun			15-Aug			08-May			15-May		
	End	21-Sep			31-May			21-Jul			07-Sep		
Marbled White	Start	08-Jul			22-Jul			01-Jun			15-Jun		
	End	21-Aug			14-Jun			14-Jul			21-Aug		
Marsh Fritillary	Start	01-Jun			22-Jun			15-Apr			22-Apr		
	End	14-Jul			30-Apr			14-Jun			07-Jul		
Meadow Brown	Start	01-Jul			15-Jul			22-May			15-Jun		
	End	07-Oct			14-Jun			31-Aug			30-Sep		
Mountain Ringlet	Start	08-Jul			01-Aug			22-Apr			01-Jun		
	End	14-Aug			22-May			07-Jul			21-Jul		
Northern Brown Argus	Start	01-Jul			08-Jul			15-May			01-Jun		
	End	14-Aug			31-May			14-Jul			14-Aug		
Orange tip	Start	01-May			15-May			08-Jul			01-Apr		
	End	07-Jul			21-Jul			14-May			07-Jul		
Peacock	Start	01-May			15-May			22-Jun			15-Jul		
	End	07-Jun			07-Jul			07-Aug			14-May		
Pearl bordered Fritillary	Start	15-May			01-Jun			15-Apr			22-Apr		
	End	30-Jun			30-Apr			21-May			30-Jun		
Purple Emperor	Start	22-Jul			08-Aug			08-Jun			22-Jun		

	End	07-Sep			30-Jun			21-Jul			14-Aug		
Purple Hairstreak	Start	22-Jun			15-Mar			01-Jun			22-Jun		
	End	07-Apr			14-Jun			21-Jul			21-Sep		
Ringlet	Start	01-Jul			22-Jul			08-Jun			15-Jun		
	End	31-Aug			21-Jun			21-Jul			14-Aug		
Scotch Argus	Start	08-Aug			22-Aug			15-Jun			15-Jul		
	End	14-Sep			30-Jun			14-Aug			07-Sep		
Silver spotted Skipper	Start	15-Aug			08-Mar			15-Jul			22-Jul		
	End	21-Mar			21-Jul			21-Aug			14-Sep		
Silver studded Blue	Start	22-Jun			15-Feb			15-May			01-Jun		
	End	14-Mar			31-May			30-Jun			07-Aug		
Silver washed Fritillary	Start	22-Jul			15-Aug			15-May			15-Jun		
	End	21-Sep			07-Jun			21-Jul			31-Aug		
Small Blue	Start	22-May			08-Jun			08-Apr			01-May		
	End	07-Jul			30-Apr			31-May			14-Jul		
Small Copper	Start	22-Sep	22-Jul	22-Sep	08-Oct	22-May	01-Aug	01-Apr	15-Jun	22-Aug	22-Apr	15-Jul	08-Sep
	End	31-Oct	07-Sep	31-Oct	14-Apr	14-Jul	30-Sep	14-May	31-Jul	07-Oct	21-Jun	31-Aug	21-Oct
Small Heath	Start	01-Jun			15-Jun			15-Apr			15-May		
	End	30-Sep			30-Apr			08-Sep			14-Sep		
Small Pearl bordered Fritillary	Start	01-Jun			15-Jun			15-Apr			01-May		
	End	07-Jul			14-May			07-Jun			31-Jul		
Small Skipper	Start	08-Jul			01-Aug			08-Jun			22-Jun		
	End	21-Aug			14-Jun			14-Jul			07-Aug		
Small Tortoiseshell	Start	01-Jul	22-Apr		08-Jul	08-May		08-Aug	01-Jun		08-Aug	15-Jun	
	End	14-Aug	31-May		21-Aug	14-Jun		14-Sep	07-Jul		14-Jun	14-Aug	
Small White	Start	22-Jul	08-May		08-Aug	01-Jun		01-Sep	22-Jun		15-Apr	08-Jul	

	End	14-Sep	07-Jul		07-Oct	14-Jul		14-May	31-Jul		21-Jun	30-Sep	
Speckled Wood	Start	01-Aug	22-Apr	01-Jun	15-Aug	08-May	22-Jun	08-Sep	15-May	08-Jul	22-Mar	15-Jun	08-Aug
	End	14-Oct	21-May	14-Jul	31-Mar	14-Jun	31-Jul	21-Apr	21-Jun	21-Aug	14-Jun	07-Aug	07-Oct
Swallowtail	Start	01-Jun			15-Jun			22-Jul			15-May		
	End	14-Jul			31-Jul			07-Jun			07-Jul		
Wall Brown	Start	01-Aug	15-May		15-Aug	01-Jun		08-Apr	01-Jul		01-May	15-Jul	
	End	21-Sep	21-Jun		21-Apr	14-Jul		14-May	14-Aug		14-Jul	21-Sep	
White Admiral	Start	08-Jul			22-Jul			22-May			01-Jun		
	End	31-Aug			14-Jun			07-Jul			14-Aug		
White letter Hairstreak	Start	15-Jul			01-Apr			22-May			22-Jun		
	End	14-Apr			31-May			07-Jul			14-Aug		
Wood White	Start	01-Jun			15-Jun			15-Jul			08-May		
	End	31-Jul			14-Aug			31-May			14-Aug		

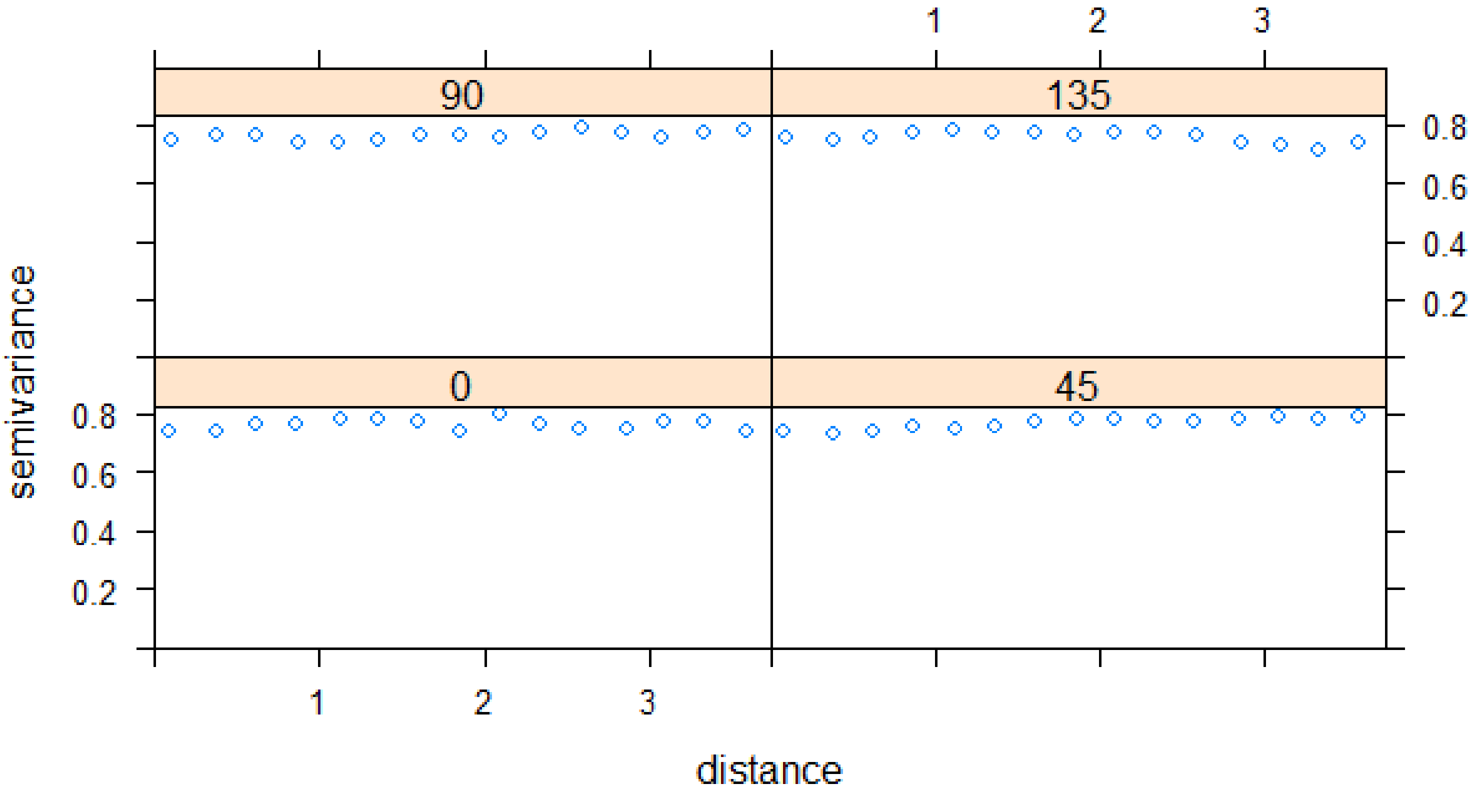

Figure 1 Variogram checking for spatial autocorrelation in the combined univoltine model in chapter 2. It shows little evident of spatial autocorrelation within the dataset.

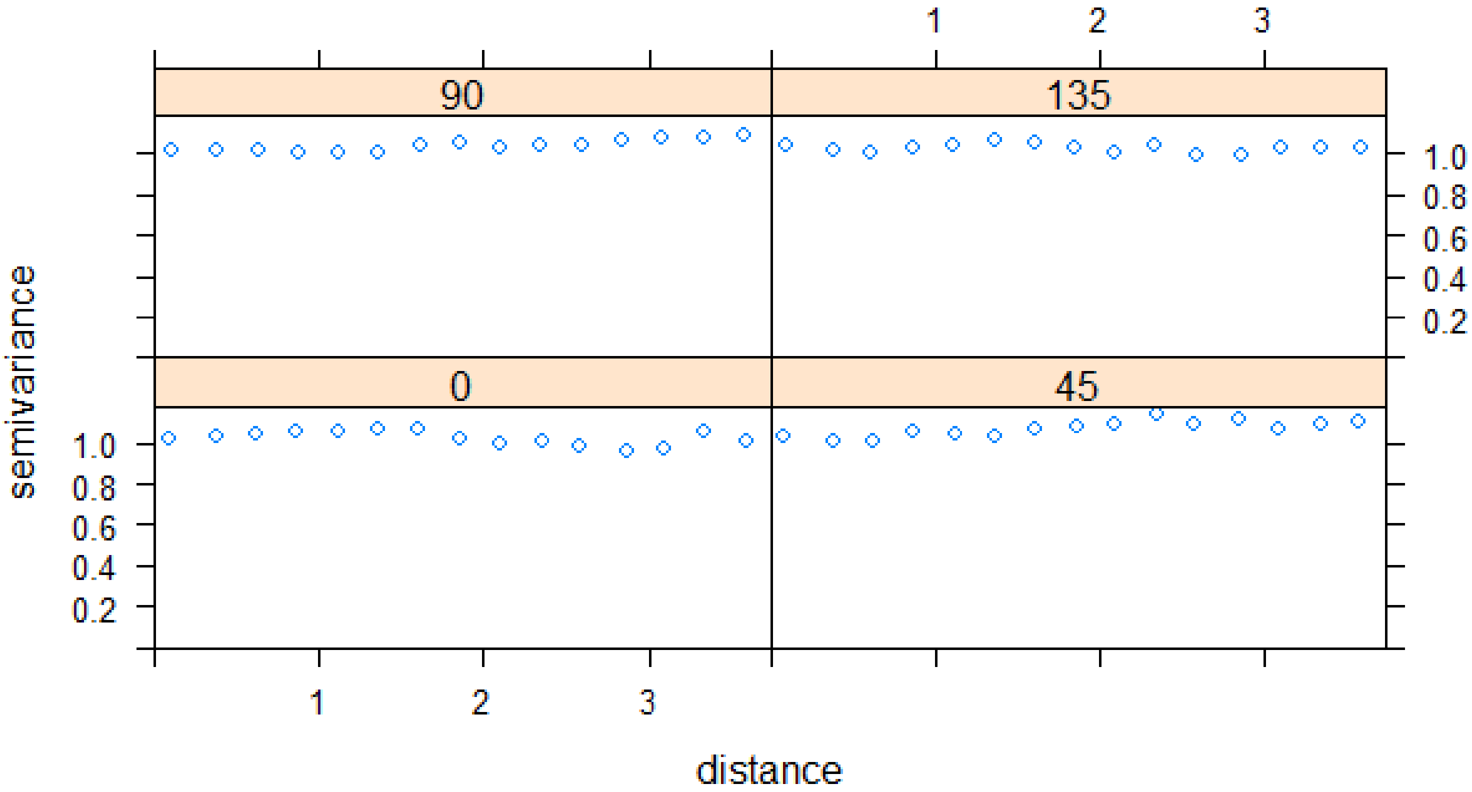

Figure 2 Variogram checking for spatial autocorrelation in the combined multivoltine model in chapter 2. It shows little evident of spatial autocorrelation within the dataset.

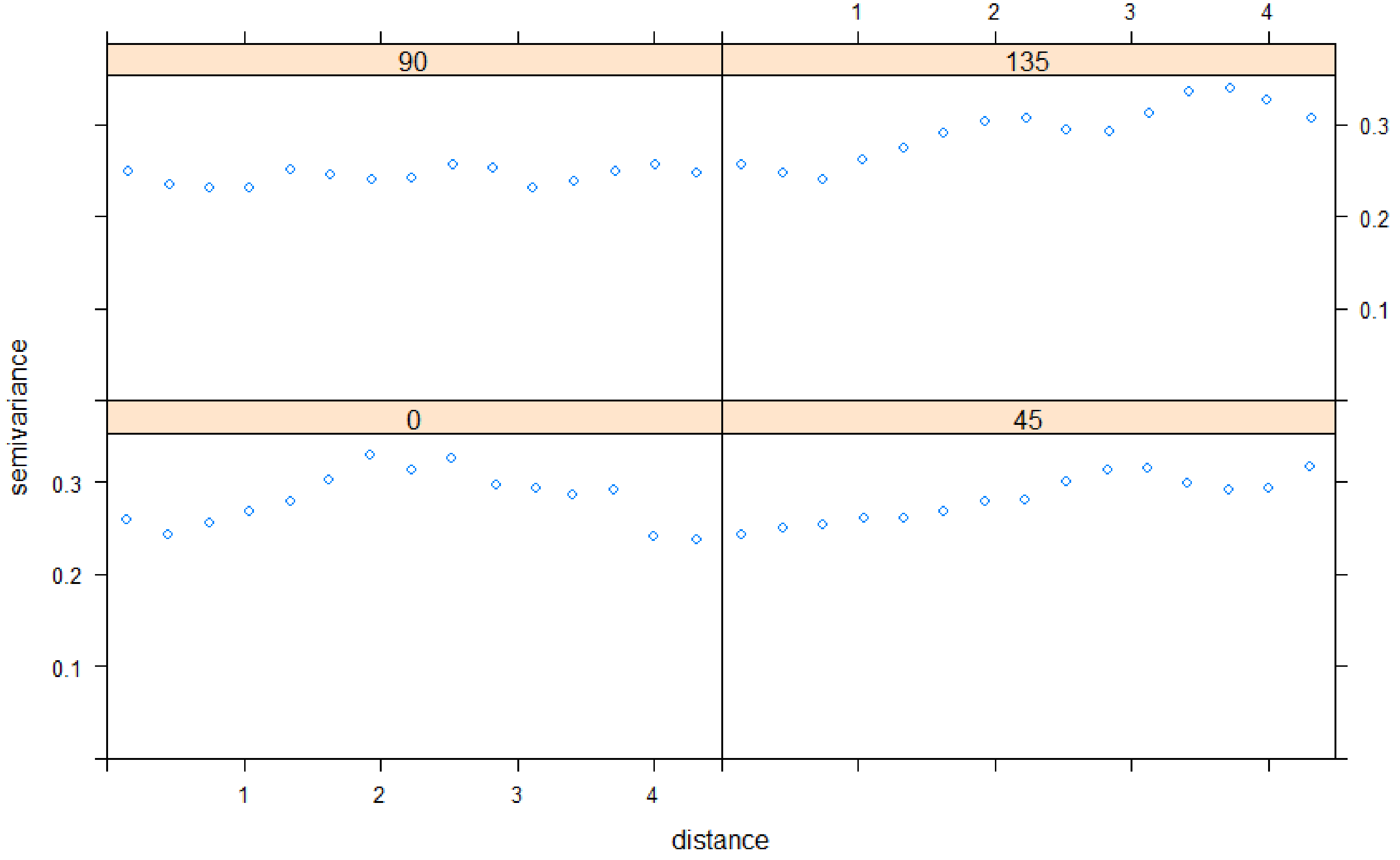

Figure 3 Variogram checking for spatial autocorrelation in the localise declines model in chapter 3. It shows little evident of spatial autocorrelation within the dataset.

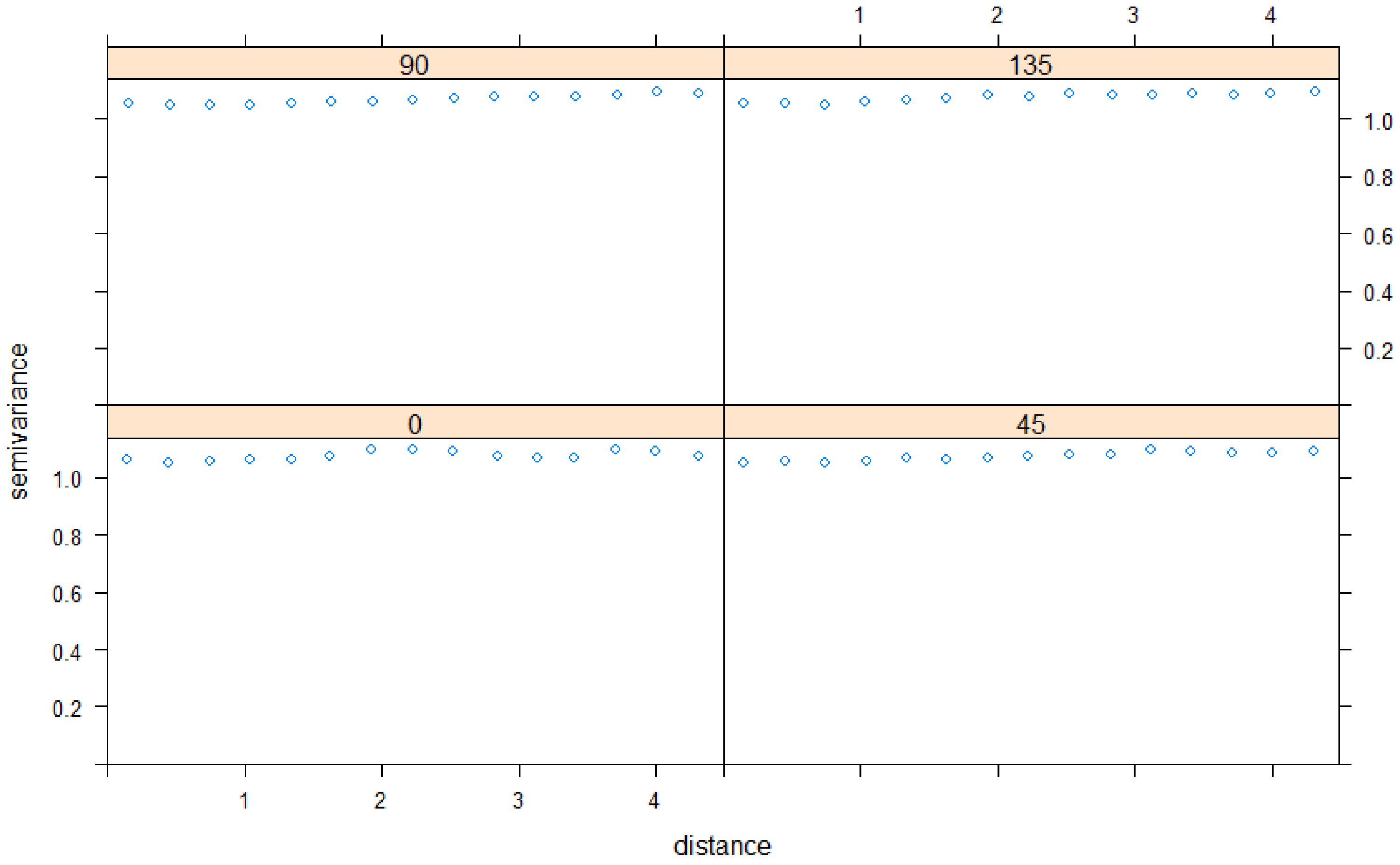

Figure 5 Variogram checking for spatial autocorrelation in the widespread declines model in chapter 3. It shows little evident of spatial autocorrelation within the dataset.

Table 2 identifying the 12 different habitat categories used in chapter 4.

Habitat identifier	Description of habitat variable
A	area of arable land in landscape
BgRo	area of bareground/rock in landscape
BR	area of bracken in the landscape
BW	area of broadleaved woodland in landscape
C	area of coastal region in landscape
CW	area of coniferous woodland in landscape
F	area of fen/bog in landscape
G	area of all grassland types in landscape
H	area of heathland in landscape
M	area of montane region in landscape
S	area of sea in landscape
R	area of river or other inland water in landscape
UG	area of urban/suburban/gardens in landscape