Citizen science and Lepidoptera biodiversity change in Great Britain

Submitted by Richard J.P. Fox BA (Hons) University of Oxford MSc University College London

To the University of Exeter as a thesis for the degree of Doctor of Philosophy by Publication in Biological Sciences February 2020

This thesis is available for Library use on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

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

(Signature)

Citizen science and Lepidoptera biodiversity change in Great Britain



Richard Fox

Frontispiece illustrations: Buff Arches *Habrosyne pyritoides* (left) and Comma *Polygonia c-album* (right) on Bramble by Richard Lewington. © Richard Lewington, reproduced with kind permission of the artist.

Abstract

A considerable body of scientific evidence shows that the world is currently suffering a biodiversity crisis driven by anthropogenic factors such as land-use change, environmental pollution and climate change. Our knowledge of this crisis is incomplete, however, particularly when it comes to the most diverse multi-cellular organisms on the planet, the insects. Although there is evidence of decline in the abundance, distribution and biomass of many insect species, recent attempts to extrapolate these to global scales and encourage a policy response have been met with scepticism. More data are required, together with reliable methods to integrate and interpret them. In parallel, evidence-based conservation initiatives are urgently needed to address the biodiversity crisis.

Citizen science has great promise for gathering much-needed data on insect trends and for engaging the public in biodiversity conservation. Citizen science has undergone a rapid rise in popularity over the past two decades, increasing the capacity for cost-effective, spatially-extensive biodiversity monitoring, while also raising awareness and commitment to nature conservation among participating members of the public. However, citizen science approaches can also present challenges, such as reductions in data quality, constraints in sampling strategies and in the onward reuse of data.

In this thesis, citizen science monitoring of Great Britain's (GB) moths and butterflies is examined as a case study, assessing some of the benefits and limitations of increased participation and demonstrating applications of citizen science data in determining species trends, drivers of change and estimates of extinction risk.

Overall moth abundance has decreased in GB, probably mainly as a result of habitat degradation, while climate change has enabled the range expansion of some species (Chapter 2). Much remains to be learnt about other potential drivers of change, such as chemical pollution and artificial light at night (Chapter 2). I demonstrated the efficacy of citizen science by calculating GB distribution trends for 673 moth species for the first time, finding that 260 species had undergone statistically significant long-term declines compared with 160 that

had increased significantly (Chapter 3). The geographical patterns of change were consistent with expected responses to land-use, nutrient enrichment and climatic change (Chapter 3). I also utilised citizen-science derived monitoring data for 485 Lepidoptera species to investigate the impact of insect population variability on the assessment of Red List extinction risk using 10-year trends as specified by the International Union for Conservation of Nature procedure (Chapter 5). I concluded that for these taxa, strict use of 10-year trends produces Red List classifications that are unacceptably biased by the start year (Chapter 5).

In Chapter 4, I showed that mass-participation citizen science data obtained using a simple sampling protocol produced comparable estimates of butterfly species abundance to data collected through standardized monitoring undertaken by experienced volunteers. Resulting increases in participation, along with the associated benefits of public engagement and awareness raising, need not have a detrimental impact on the ability to detect abundance trends in common butterfly species. However, citizen science participation may affect the onward use of data, unless this is considered at the outset. I found that despite support in principle for open access to distribution records of butterflies and moths, most citizen scientists were much more cautious in practice, preferring to limit the spatial resolution of records, particularly of threatened species, and restrict commercial reuse of data (Chapter 6).

Overall, these results demonstrate the potential for citizen science, involving both expert volunteer naturalists and inexperienced members of the public, to address the global biodiversity knowledge gap through generating meaningful trend estimates for insect species and elucidating the drivers of change.

Contents

Abstract5
Contents7
List of figures 12
List of tables
Author's declaration and contributions16
Acknowledgements
Chapter 1: Extended Introduction
Global biodiversity change19
The insect information gap21
Insect Armageddon23
Citizen science and insect biodiversity assessment
Lepidoptera citizen science in GB25
Butterflies for the New Millennium25
National Moth Recording Scheme26
UK Butterfly Monitoring Scheme
Rothamsted Insect Survey 29
Big Butterfly Count
Lepidoptera change in GB
Drivers of Lepidoptera biodiversity change
Land use
Environmental pollution
Climate change
Interactions between drivers of change
Overview of the rationale of this thesis
Aims, results and contribution to scientific knowledge of each chapter 39
Chapter 2 The decline of moths in Great Britain: a review of possible
causes
Chapter 3 Long-term changes to the frequency of occurrence of British
moths are consistent with opposing and synergistic effects of climate
and land-use changes40
Chapter 4 Using citizen science butterfly counts to predict species
population trends 42
Chapter 5 Insect population trends and the IUCN Red List process 43

Chapter 6 Opinions of citizen scientists on open access to UK butterfly
and moth occurrence data 44
Future directions
Conclusions
References
Chapter 2: The decline of moths in Great Britain: a review of possible causes 89
Abstract
Introduction
Moth declines in GB and beyond91
Drivers of change in moth populations93
Habitat loss, degradation and fragmentation
Agricultural management94
Woodland management97
Urbanisation99
Habitat loss summary100
Chemical pollution100
Light pollution101
Climate change 102
Non-native species105
Exploitation of populations106
Synthesis: why have GB moths declined?107
Multiple drivers of change 107
Interactions and synergies108
Future perspectives108
Acknowledgments112
References 112
Chapter 3: Long-term changes to the frequency of occurrence of British moths
are consistent with opposing and synergistic effects of climate and land-use
changes132
Abstract132
Introduction
Materials and Methods135
Data sources135
Classification of southern, northern and widespread species 136
Analysis of changes in frequency of occurrence

Correlation with host plant and environmental variables
Results138
Discussion142
Acknowledgements147
References
Chapter 4: Using citizen science butterfly counts to predict species population
trends
Abstract
Introduction
Methods 158
Big Butterfly Count
UK Butterfly Monitoring Scheme 158
Comparisons of BBC and UKBMS data 159
Comparison of annual growth rates 159
Effects of phenology and effort 161
Predicting UKBMS species trends from BBC data
Results
Comparison of BBC and UKBMS data163
Comparison of annual growth rates
Effects of phenology and effort165
Predicting UKBMS species trends from BBC data
Discussion 170
Acknowledgments 174
References 175
Chapter 5: Insect population trends and the IUCN Red List process
Abstract
Introduction
Methods and results
Case study 1: UK butterflies186
Case study 2: UK macro-moths 189
Discussion
Acknowledgements196
References
Chapter 6: Opinions of citizen scientists on open access to UK butterfly and
moth occurrence data

Abstract
Introduction
Methods
Focal citizen science projects
Questionnaires
Regional co-ordinator questionnaire
Recorder questionnaire210
Analysis211
Ethics statement
Results
Regional co-ordinators
Survey coverage213
Support for open access
Spatial resolution of records214
Time lags217
Additional restrictions for species or colonies
Creative Commons licences
Recorders
Survey coverage218
Spatial resolution of open access to own records
Future support for open access recording schemes
Discussion
Citizen scientist support for open access
Concerns and alleviating factors 221
Differences between roles, countries and taxa
Wider applicability
Practical recommendations for citizen science
Conclusions
Acknowledgements228
References
ppendix 1: Richard Fox Peer-reviewed publications
ppendix 2: Affiliations of co-authors
ppendix 3: Supporting Information for Chapter 3: Long-term changes to the
equency of occurrence of British moths are consistent with opposing and
ynergistic effects of climate and land-use changes

Appendix 4: Supporting Information for Chapter 4: Using citizen science	
butterfly counts to predict species population trends	32
Appendix 5: Supporting Information for Chapter 5: Insect population trends and	t
the IUCN Red List process	77
Appendix 6: Supporting Information for Chapter 6: Opinions of citizen scientists	5
on open access to UK butterfly and moth occurrence data 28	38

List of figures

Fig. 1.1 The recording coverage of the NMRS
Fig. 1.2 The locations of all sites contributing to the UKBMS
Fig. 3.1 Change in frequency of occurrence (per year change in relative
reporting rate) 1970-1999 versus 2000-2010 for southerly distributed, northerly
distributed and geographically widespread moths140
Fig. 3.2 Change in the frequency of occurrence (per year change in relative
reporting rate) 1970-1999 versus 2000-2010 of geographically widespread moth
species in the northern and southern halves of GB140
Fig. 3.3 Change in the frequency of occurrence (per year change in relative
reporting rate) 1970-1999 versus 2000-2010 of monophagous moth species in
relation to host plant Ellenberg indicator values142
Fig. 4.1 Comparison of estimated log growth rates of populations of 18 butterfly
species from Big Butterfly Count and UK Butterfly Monitoring Scheme counts for
2011-2014
Fig. 4.2 Total counts of Gatekeeper and Large White from Big Butterfly Count
data per day in each year166
Fig. 4.3 Total counts of three butterfly species (Gatekeeper, univoltine; Large
White, bivoltine; Comma, multivoltine) from Big Butterfly Count data per day
versus the expected value from a negative-binomial model with log-link 167
Fig. 4.4 Comparison of the generalized abundance index from UK Butterfly
Monitoring Scheme data and predicted butterfly abundance indices
Fig. 4.5 Comparison of linear trends in relative butterfly abundance from the
generalized abundance index model
Fig. 6.1 Levels of general support for open access, assessed by modified NPS
categories, among regional co-ordinators from UK, England, Scotland and
Wales
Fig. 6.2 Preferred resolution of open access records of threatened species and
widespread species among regional co-ordinators from UK, England, Scotland
and Wales
Fig. A3.1 The frequency and proportion of moths in different distribution
groupings (northerly, southerly, geographically widespread) by taxonomic family

Fig. A3.2 Change in the frequency of occurrence of monophagous moth species 1970-99 versus 2000-10 in relation to change in host plant distribution between Fig. A3.3 Relationship between number of hectads (grid squares) occupied by each species in 1970-99 and 2000-10 versus the relative reporting rate 259 Fig. A3.4 Change in moth frequency of occurrence versus proportional change Fig. A4.1 Locations of UK Butterfly Monitoring Scheme (1,462 transects) and Big Butterfly Count (65,197 1km squares surveyed) counts 2011-2014...... 270 Fig. A4.2 Comparison of estimated year-to-year log growth rates from the Big Fig. A4.3 Total daily counts of nine species from Big Butterfly Count data 274 Fig. A4.4 Total counts for each butterfly species from Big Butterfly Count data Fig. A4.5 Comparison of linear trends in relative abundance from the GAI index, where 2015 is from observed data or predicted from the model with the best estimate of the index in 2015......276 Fig. A4.6 Comparison of percentage changes in relative abundance 2014-2015, where 2015 is from observed data or predicted from the model with the best estimate of the index in 2015......276 Fig. A6.1 Levels of general support for open access, assessed by modified NPS categories, among regional co-ordinators for butterflies, moths or both taxa. 296 Fig. A6.2 Preferred resolution of open access records of threatened species and widespread species among regional co-ordinators in different modified NPS

List of tables

Table 3.1 Relationships from a multiple regression and linear mixed model of
host plant Ellenberg indicator values on change in frequency of occurrence of
monophagous moth species141
Table 4.1 Estimated population trends in relative abundance for 18 UK butterfly
species
Table 5.1 Number of UK butterfly species meeting Red List threat thresholds
under IUCN Criterion A2 on basis of 10-year UKBMS population trends over
different year ranges
Table 5.2 Red List threat thresholds met by UK butterflies under IUCN Criterion
A2 on basis of 10-year UKBMS population trends over different year ranges 188
Table 5.3 Number of UK macro-moth species meeting Red List threat
thresholds under IUCN Criterion A2 on the basis of preliminary 10-year RIS
population trends
Table A3.1 Change in frequency of occurrence (measured as annual change in
relative reporting rate) 1970-99 versus 2000-10 for 673 resident GB macro-
moths
Table A4.1 Official Big Butterfly Count period for each year
Table A4.2 Common UK butterflies counted by the Big Butterfly Count
Table A4.3 Summary of Big Butterfly Count data 2011-2015
Table A4.4 Percentage of Big Butterfly Count counts recorded in different
habitat categories each year
Table A4.5 Mean and standard error of the percentage habitat types for 1km
squares sampled by the UK Butterfly Monitoring Scheme and Big Butterfly
Count 2010-2014
Table A4.6 Estimated net population change 2011-2014 (log growth rate) from
Big Butterfly Count and the UK Butterfly Monitoring Scheme
Table A4.7 Overdispersion estimated by the ratio of the Pearson Chi-squared
statistic to its degrees of freedom
Table A4.8 Residual deviance, degrees of freedom and associated ratios from
fitting a Poisson and negative-binomial GLM where the response is the total Big
Butterfly Count count per day and measures of effort and phenology as
covariates

Table A4.9 Relative importance of Big Butterfly Count and weather for each
species
Table A5.1 UK butterfly species' 10-year population trends over six overlapping
date periods, and the median, lower and upper quartile values of these trends
Table A5.2 UK macro-moth 10-year population trends for the most recent 10-
year period, and preceding 10-year periods each starting one year earlier than

Author's declaration and contributions

The work contained in this thesis is my own. Chapters 1, 5 and 6 were written under the supervision of Dr Robert Wilson and Dr Ilya Maclean. Chapter 1 Extended Introduction was drafted by myself and reviewed by my supervisors, who offered advice and made suggestions for improvement. Collaborators on other chapters are listed below. Any further assistance has been acknowledged as appropriate at the end of each chapter.

This thesis for PhD by Publication is based on the following published papers:

Chapter 2

Fox R (2013) The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity* **6**, 5-19.

I conceived the idea for this paper from an original suggestion by John Hopkins. I conducted the literature review, wrote the first draft of the manuscript and was responsible for subsequent editing.

Chapter 3

Fox R, Oliver TH, Harrower C, Parsons MS, Thomas CD & Roy DB (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology* **51**, 949-957.

I conceived the idea for this paper together with THO, CDT and DBR. I oversaw data collection and preparation, with input from MSP. Analyses were performed by THO and CH. I led the writing of the manuscript with THO. All authors contributed critically to drafts and I was responsible for subsequent editing.

Chapter 4

Dennis EB, Morgan BJT, Brereton TM, Roy DB & Fox R (2017) Using citizen science butterfly counts to predict species population trends. *Conservation Biology* **31**, 1350-1361.

I conceived the idea for this paper together with EBD and TMB. I oversaw data collection. Analyses were designed and performed by EBD and BJTM. EBD and

I led the writing of the manuscript and were responsible for subsequent editing. All authors contributed critically to drafts.

Chapter 5

Fox R, Harrower CA, Bell JR, Shortall CR, Middlebrook I & Wilson RJ (2019) Insect population trends and the IUCN Red List process. *Journal of Insect Conservation* **23**, 269–278.

I conceived the idea and designed the methodology with input from RJW. Moth population data were provided by JRB and CRS and analysed by CAH. I wrote the first draft of the manuscript and was responsible for subsequent editing, with all authors contributing significantly to revisions.

Chapter 6

Fox R, Bourn NAD, Dennis EB, Heafield RT, Maclean IMD & Wilson RJ (2019) Opinions of citizen scientists on open access to UK butterfly and moth occurrence data. *Biodiversity and Conservation* **28**, 3321–3341. I conceived the idea and designed the methodology with input from NADB and RTH. I undertook analysis of the data following statistical and software guidance from EBD. I wrote the first draft of the manuscript and was responsible for subsequent editing, with all authors contributing significantly to revisions. RJW and IMDM offered advice and made suggestions for improvement.

Acknowledgements

Many thanks are due to my supervisors Rob Wilson and Ilya Maclean for their guidance and input, and to all of my co-authors for their contributions to the papers presented in this thesis. I am hugely grateful to my colleagues at Butterfly Conservation, particularly Julie Williams and Nigel Bourn, for their encouragement, financial support, permission to use datasets and for allowing me to carry out the research for this thesis as part of my job. Emily Dennis kindly taught me the basics of R and Richard Lewington, king of Lepidoptera illustrators, generously allowed me to use two of his pictures in this thesis.

I have been very fortunate to work alongside and collaborate with many inspiring, knowledgeable and brilliant people over the past 20+ years. There are too many to list in full, but particular thanks go to Martin Warren (my line manager for many years who always encouraged the research side of my work), Mark Parsons (who lent me my first moth-trap and turned me to the dark side), Chris Thomas and Jane Hill (and their numerous talented students & post docs at Leeds and then York University), David Roy (and his team at the Biological Records Centre) and collaborators at Rothamsted Research (especially the late Kelvin Conrad).

I would like to thank all of the volunteer recorders, citizen scientists and colleagues involved in gathering, verifying and processing the UK butterfly and moth datasets on which most of the research presented in this thesis is based.

Finally, I am incredibly thankful for the patience and support of my family. My wife Tamsin has encouraged and supported me unfailingly through all the years of work for this thesis - without her I would never have started, let alone finished, my thesis. She, and our children, Kerra and Jake, have kept me sane and happy, providing a continual reminder that there are many wonderful things in life apart from Lepidoptera. My parents for all their support and for instilling an interest in nature in me at an early age and the rest of the family for their enthusiastic interest in my work on butterflies and moths.

Chapter 1: Extended Introduction

Global biodiversity change

Scientific research has provided compelling evidence of a global biodiversity crisis, sometimes characterised as the sixth mass extinction (Pimm *et al.* 1995; Barnosky *et al.* 2011; Dirzo *et al.* 2014). It is equally clear that this crisis is driven by human activities including habitat modification, overexploitation of species, nitrogen pollution, introduction of invasive species and anthropogenic climate change (Sala *et al.* 2000; Brook *et al.* 2008; Bellard *et al.* 2012; Newbold *et al.* 2015; Díaz *et al.* 2019).

The current biodiversity crisis is apparent in many demographic phenomena that can be estimated empirically. For example, the rate of species extinction in recent history is estimated to be 100-1000 times greater than the background rate measured across geological time (Pimm et al. 2014; Ceballos et al. 2015; De Vos et al. 2015). While relatively few modern extinctions have been documented (currently 872 species, comprising 750 animal species and 122 plants; IUCN 2018), a much larger number of species, estimated at c.9% (c.500,000 species) of terrestrial biodiversity (IPBES 2019), may already be destined for extinction as biotic communities transition to new equilibria following habitat loss or other environmental changes that have already occurred (Kuussaari et al. 2009; Halley et al. 2016). An overall increase in extinction risk has been shown for some vertebrate taxa using the Red List Index approach (e.g. amphibians and birds; Butchart et al. 2005), and estimated total vertebrate abundance decreased by 60% over the period 1970-2014 (WWF 2018). Approximately one third of land vertebrate species have decreased in abundance or range size (Ceballos et al. 2017). An abundance index based on studies of 452 invertebrate species (mostly insects) showed a 45% decline over 40 years (Dirzo et al. 2014), although the sample was heavily biased towards Europe and North America. Furthermore, significant decreases in biomass have been recorded in a variety of ecosystems (Shortall et al. 2009; Worm et al. 2009; Hallmann et al. 2017; Lister & Garcia 2018; Seibold et al. 2019).

However, not all species or populations are in decline (McGill et al. 2015; Dornelas et al. 2019), leading to counter-intuitive trends in some biodiversity metrics e.g. species richness. Meta-analyses of terrestrial plant and phytoplankton communities reported no net loss of local species richness despite high turnover in species identity and dominance (Vellend et al. 2013, Hillebrand et al. 2018), although these findings have been criticised (Cardinale et al. 2018). Herrera (2019) found increased flower visitation rates by insects over a 21-year study in undisturbed montane habitats in Spain, driven mainly by abundance increases of solitary bees. Even in taxa undergoing substantial overall decline in a particular region, there are species bucking the trend e.g. among bees (Powney et al. 2019) and moths (Boyes et al. 2019) in Great Britain (GB) and butterflies in the Netherlands (van Strien et al. 2019). The human impacts driving the global biodiversity crisis may also have positive effects on some species. Forest fragmentation can cause increased abundance in some vertebrates (Pfeifer et al. 2017), more intensive agricultural management benefits a minority of moths (Mangels et al. 2017), while urbanheat-island effects favour small-bodied invertebrates (Merckx et al. 2018). Anthropogenic climate change is causing regional range expansion of some species (Parmesan et al. 1999; Pearce-Higgins et al. 2017) and the introduction of non-native taxa not only increases their global distribution but also, in some cases, produces net gains in local biodiversity (Sax & Gaines 2003).

Because human environmental impacts generate winners and losers among species in a non-random way, another phenomenon of the biodiversity crisis is biotic homogenisation, whereby communities are increasingly similar and often dominated by a relatively small number of generalist species that are well-adapted to highly-modified landscapes (McKinney & Lockwood 1999; Smart *et al.* 2006; Le Viol *et al.* 2012; Carvalheiro *et al.* 2013; Gossner *et al.* 2016).

Overall, these changes threaten the resilience of ecological communities and the provision of ecosystem services upon which the human race depends (Chapin *et al.* 2000; Cardinale *et al.* 2012; Bernstein 2014; Oliver *et al.* 2015a). This holds irrespective of the ongoing debate regarding the relative importance for ecosystem functioning of high species diversity (Isbell *et al.* 2011; Tilman *et al.* 2014; but see Pillai & Gouhier 2019) versus high abundance of common species (Gaston & Fuller 2008; Kleijn *et al.* 2015), as there is ample evidence of decline in both.

Yet, despite political agreements to address global biodiversity loss (e.g. the Convention on Biological Diversity), drivers of change continue to intensify and biodiversity continues to decline (Butchart *et al.* 2010; Tittensor *et al.* 2014; Díaz *et al.* 2019). Unless radical steps are taken to address human pressures on biodiversity, projections indicate further severe losses (Pereira *et al.* 2010; Maclean & Wilson 2011; Visconti *et al.* 2016; Warren *et al.* 2018).

Insects represent a key gap in our understanding of biodiversity change. In this thesis, I focus on Lepidoptera (moths and butterflies) in GB to assess evidence of insect biodiversity change. More specifically, I seek to gauge the potential for citizen science to provide robust data on insect trends. Awareness of the problems of biodiversity loss is increasing globally (Díaz *et al.* 2019) and, in GB, volunteer time devoted to conservation organisations has increased by 46% this century (Hayhow *et al.* 2019). I investigate the scope to which this public engagement can be harnessed to document and understand change in GB Lepidoptera populations, addressing several factors that may influence the effectiveness of such an approach.

The insect information gap

Insects are the most speciose eukaryotic organisms on Earth (Mora *et al.* 2011) and are essential to the functioning of many terrestrial and freshwater ecosystems (Wilson 1987; Collen *et al.* 2012; Yang & Gratton 2014). They have numerous economically significant impacts on humans, including positive ecosystem services such as pollination (Losey & Vaughan 2006; Gallai *et al.* 2009) and negative interactions e.g. as disease vectors and crop pests (Bradshaw *et al.* 2016). Despite their ecological and economic importance, insects are poorly represented in assessments of extinction risk and biodiversity change (Dunn 2005; Stuart *et al.* 2010; Cardoso *et al.* 2011a,b). For example, global extinction risk has been assessed for 100% bird and mammal species and 67% of all vertebrate taxa, but only 0.8% of described insect species (Eisenhauer *et al.* 2019). Empirical estimates in well-studied regions suggest that proportions of threatened species and rates of decline in insects exceed or

are similar to those of vertebrate taxa (McKinney 1999; Thomas *et al.* 2004; Sánchez-Bayo & Wyckhuys 2019), suggesting that real rates of species extinction globally are much higher than previous, vertebrate-based estimates (Régnier *et al.* 2015). Indeed, given the specialized niches and co-dependence of many insect species, extinction rates may be expected to greatly exceed those of other taxa (Koh *et al.* 2004; Dunn 2005; Fonseca 2009).

The under-representation of insects in considerations of biodiversity change stems from insufficient knowledge of insect taxonomy, ecology and biogeography, reinforced by societal preferences (Diniz-Filho *et al.* 2010; Cardoso *et al.* 2011a; Troudet *et al.* 2017). Invertebrates are greatly under-represented in conservation biology research compared with vertebrates or plants (Clark & May 2002; Deikumah *et al.* 2014). Even among invertebrates, insects are under-represented relative to their species richness in scientific publications (Di Marco *et al.* 2017). For the vast majority of insect species across most of the world, occurrence and population data from which to compile trends in insect biodiversity are non-existent (IPBES 2019; Wagner 2020).

While this information gap remains a major impediment to large-scale assessment of insect biodiversity change, substantial progress has been made recently in developed nations for certain insect groups. These include continental or national-scale assessments of butterflies (van Swaay *et al.* 2011; Breed *et al.* 2013; Maes *et al.* 2019), bees (Cameron *et al.* 2011; Nieto *et al.* 2014; Kerr *et al.* 2015), moths (Conrad *et al.* 2006; Groenendijk & Ellis 2011), ladybirds (Harmon *et al.* 2007; Roy *et al.* 2012), hoverflies (Powney *et al.* 2019) and dragonflies (Kalkman *et al.* 2010; Termaat *et al.* 2019). In addition, a partial global Red List assessment has been undertaken for Odonata (Clausnitzer *et al.* 2009), using a sample of 1500 species, and the same approach has been advocated for butterflies (Lewis & Senior 2011).

Nevertheless, huge gaps remain for other insect taxa, particularly those that are species-rich or perceived to be less appealing (Sumner *et al.* 2018), and for biodiversity as a whole in many developing countries (Collen *et al.* 2008; Stephenson *et al.* 2016; Barlow *et al.* 2018).

Insect Armageddon

Despite the general paucity of data, several recent papers about insect declines have achieved a high profile in the media and stimulated vigorous debate within the scientific community. Hallmann et al. (2017) estimated a 77% reduction in the biomass of flying insects over 27 years in German nature reserves, with an even greater loss (82%) in mid-summer when biomass values peak. Lister & Garcia (2018) reported dramatic declines in biomass and abundance across all the main insect groups in a protected rainforest in Puerto Rico. For example, arthropod biomass in ground-level sticky traps decreased by 36-60 times (depending on the season) between 1976-1977 and 2011-2013. Despite many previous studies documenting insect population decline, these two studies generated major media coverage with much hyperbole and the invention of phrases such as "ecological armageddon", "insect apocalypse" and "insectageddon". A global review of insect declines (Sanchez-Bayo & Wyckhuys 2019) coincided with the media zeitgeist and also received huge publicity. This review did nothing to temper exaggerated reporting, with the authors suggesting that insects could become extinct within decades: "The conclusion is clear: unless we change our ways of producing food, insects as a whole will go down the path of extinction in a few decades" (Sanchez-Bayo & Wyckhuys 2019).

These studies and the associated media coverage provoked a considerable response from the scientific community. While the evidence for overall declines in insect biodiversity is clear (Wagner 2020) and raising public awareness vital, potential problems with the analyses and extrapolation of local results to the global scale leading to overstated claims have been widely criticised (Leather 2018; Saunders 2019; Simmons *et al.* 2019; Thomas *et al.* 2019). Researchers have called instead for investment in more rigorous and spatially extensive monitoring, greater sharing of ecological data and the deployment of new technologies to provide better estimates of global insect biodiversity change (Montgomery *et al.* 2020; Saunders *et al.* 2020). Others have pointed out that, even excluding the recent media hype, there is a sufficient scientific basis to be deeply concerned about insect declines and to start to formulate policy responses (Forister *et al.* 2019; Habel *et al.* 2019a; Harvey *et al.* 2020).

Citizen science and insect biodiversity assessment

Citizen science has huge potential to help fill the data shortfalls that hinder comprehensive biodiversity assessments of insects (Danielsen et al. 2014; Theobald et al. 2015; McKinley et al. 2017; Pocock et al. 2018). Sumner et al. (2019), for example, showed that a two-week UK citizen science project could generate comparable spatial coverage for social wasp species as four decades of recording by expert amateurs. Furthermore, participation in citizen science also engenders increased understanding of and engagement with conservation (Jordan et al. 2011; Haywood et al. 2016; Domroese & Johnson 2017; Lewandowski & Oberhauser 2017) and may benefit mental wellbeing (Coventry et al. 2019). Although 'citizen science' is a recently coined term, it is nothing new; non-professional scientists and members of the public have been involved in gathering data and undertaking research in many branches of science for centuries (Miller-Rushing et al. 2012; Kobori et al. 2016). However, there has been a rapid growth in the number of citizen science projects, participants and research publications in the past two decades, particularly in ecology (Silvertown 2009; Follett & Strezov 2015; Pocock et al. 2017).

Citizen science already makes a considerable contribution to knowledge of the status, distribution, abundance and trends of biodiversity (Dickinson *et al.* 2012; Chandler *et al.* 2017). This is particularly the case for birds (e.g. Gibbons *et al.* 2007; VanDerWal *et al.* 2013; Sullivan *et al.* 2017; Lehikoinen *et al.* 2019), but also applies to insects (e.g. Biesmeijer *et al.* 2006; van Swaay *et al.* 2008; Soroye *et al.* 2018) and other taxa.

Nowhere is this more evident than in GB. Thanks to a long tradition of citizen science (Pocock *et al.* 2015), GB biodiversity is probably the most thoroughly monitored in the world (Burns *et al.* 2018). Certain charismatic taxa (e.g. birds, butterflies) are the focus of long-term standardised monitoring schemes that utilise repeatable, distance sampling techniques and skilled volunteer observers to produce count data from which population estimates can be derived (Freeman *et al.* 2007; Roy *et al.* 2007; Dennis *et al.* 2016).

In addition to such 'gold standard' monitoring, opportunistic sightings (occurrence records) of many GB taxa are contributed by citizen scientists

through national recording schemes and local environmental records centres (Thomas 2005; Powney & Isaac 2015). However, species records made by citizen scientists and without standardised sampling protocols are subject to data quality problems (Kosmala *et al.* 2016) and bias resulting from uneven sampling (Boakes *et al.* 2010; Isaac & Pocock 2015). In order to account for sampling bias in estimates of species distribution change, a range of statistical approaches has been developed (Pardo *et al.* 2013; Bird *et al.* 2014; Isaac *et al.* 2014; Dennis *et al.* 2017a). Through the application of such techniques, long-term distribution changes have been assessed for thousands of GB taxa (Hickling *et al.* 2006; Burns *et al.* 2018; Outhwaite *et al.* 2019) and the drivers of change examined (Burns *et al.* 2016). Relatively minor adjustments to the collection of citizen science data could also yield significant improvements in the accuracy of scientific outputs (Altwegg & Nichols 2019; Callaghan *et al.* 2019; Kelling *et al.* 2019).

Lepidoptera citizen science in GB

Citizen science, broadly taken to mean the involvement of non-professionals in the generation of scientific knowledge (Strasser *et al.* 2019), encompasses both the long-standing participation of amateur (but often expert) naturalists in the recording of fauna and flora (see Asher *et al.* 2001 and Randle *et al.* 2019 for histories of GB Lepidoptera recording) and recent projects designed to engage the wider public (Pocock *et al.* 2017). The research in this thesis draws upon Lepidoptera data from five GB citizen science schemes: Butterflies for the New Millennium, the National Moth Recording Scheme, the UK Butterfly Monitoring Scheme, the Rothamsted Insect Survey and Big Butterfly Count. Other projects that collect Lepidoptera records, e.g. the Garden Moth Scheme (Wilson *et al.* 2015), Moth Night (www.mothnight.info), Garden Butterfly Survey (www.butterfly-conservation.org) and Garden BirdWatch (www.bto.org), are not considered here.

Butterflies for the New Millennium

The distribution recording scheme for butterflies, Butterflies for the New Millennium (BNM), is operated by Butterfly Conservation and collates occurrence records across the UK. Records (unique combinations of species x recorder x location x date) are opportunistic and sampling is neither

standardised nor systematic. Records can be of any life-cycle stage on any date and at any terrestrial location. The scheme began in 1995 as a five-year survey to map current species distributions and measure change over time for a butterfly atlas. This initial phase gathered 1.6 million records from an estimated 10,000 citizen scientists and covered 98.7% of the 10km x 10km grid squares across the study area. These data and historical records (mainly from Heath *et al.* 1984) were used to produce the planned atlas (Asher *et al.* 2001) and assessments of change (e.g. Warren *et al.* 2001; Thomas *et al.* 2004).

Back-to-back five-year BNM surveys have continued since then, with increasing recording effort, and the scheme currently holds 14.0 million butterfly records (13.6 million for GB), the earliest dating from 1690 (Fox *et al.* 2015). Records are gathered and verified by a network of expert volunteer 'County Recorders', prior to being collated into the BNM database.

National Moth Recording Scheme

The National Moth Recording Scheme (NMRS) was launched by Butterfly Conservation in 2007 to create a UK database of moth occurrence records to underpin conservation (Fox *et al.* 2011a). Initially focussed on c.900 species of macro-moths, the scheme amassed 25.3 million records covering the period 1741-2016 (Randle *et al.* 2019). Recently, the NMRS has widened to include micro-moths. NMRS recording is largely unstructured and opportunistic and County Recorders collate and verify local datasets, which are then merged into a single database. Most records are of nocturnal adult moths attracted to lighttraps, but sightings of any life-cycle stage at any time of day can be contributed. Thus, in contrast to the Rothamsted Insect Survey, the NMRS gathers data on all macro-moths, not just nocturnal species that are attracted to light.

Recording has increased greatly over time. For example, the NMRS contains c.680,000 pre-1970 records, representing 73% of 10km x 10km grid squares in GB, but has 17.9 million records from 97% of 10km grid squares for 2000-2016 (Fig. 1.1) (Randle *et al.* 2019). The number of participants is unknown, because of variation in the way that recorders' names are collated by County Recorders, but is estimated at 5,000-10,000.

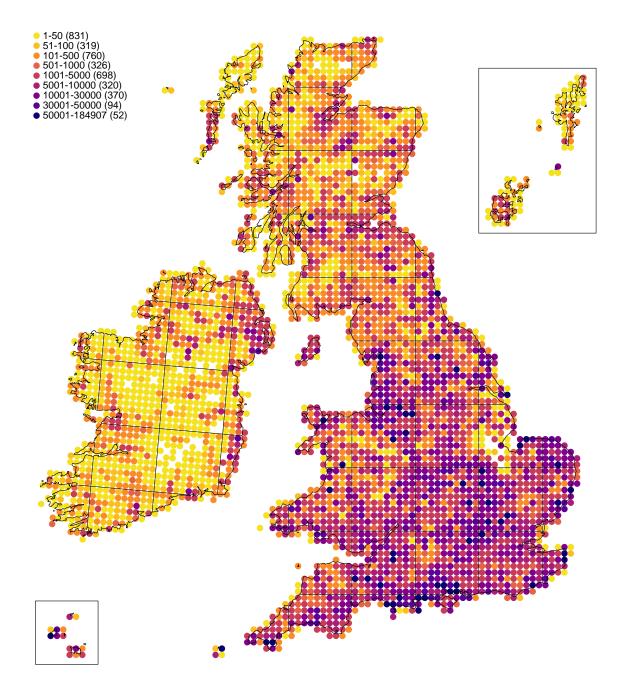


Fig. 1.1 NMRS recording coverage illustrated by the number of macro-moth records per 10km grid square (2000-2016). The data for GB, Isle of Man and Channel Islands comes from the NMRS. Data for the Republic of Ireland comes from MothsIreland. Both the NMRS and MothsIreland contain records for Northern Ireland, so the map shows data from both schemes. The number of 10km squares in each numerical banding is given in the key. This map also appears in Randle *et al.* (2019).

UK Butterfly Monitoring Scheme

A standardised method for measuring change in the relative abundance of butterflies along fixed-route, 5m wide transects (Pollard 1977) was rolled out as a UK-wide scheme in 1976 (Pollard & Yates 1993). Transect locations are selected by volunteer recorders, who then undertake weekly counts in good weather from April-September each year. Some sites have been monitored over many years, but there is turnover of locations due to volunteer availability. While the monitoring is standardised, enabling counts to be combined and compared across sites and years, transects are biased towards high biodiversity sites managed (at least partly) for nature conservation. The skewed distribution of transects ensures sufficient coverage of rare species to enable annual population indices to be produced for almost all UK butterflies, but is not representative of the wider landscape. To address this, a reduced-effort transect methodology was developed (Roy *et al.* 2007) and applied to a stratified random sample of 1km x 1km grid squares for the Wider Countryside Butterfly Survey (Brereton *et al.* 2011a).

The UK Butterfly Monitoring Scheme (UKBMS) is run by the UK Centre for Ecology & Hydrology, Butterfly Conservation and British Trust for Ornithology and incorporates data annually from >1,700 transects, c.800 Wider Countryside Butterfly Survey squares and c.300 sites where timed counts are carried out (Fig. 1.2). Thus, in 2018, approximately 2,500 UKBMS citizen scientists walked some 92,000km counting butterflies at 2,868 sites (Brereton *et al.* 2019).

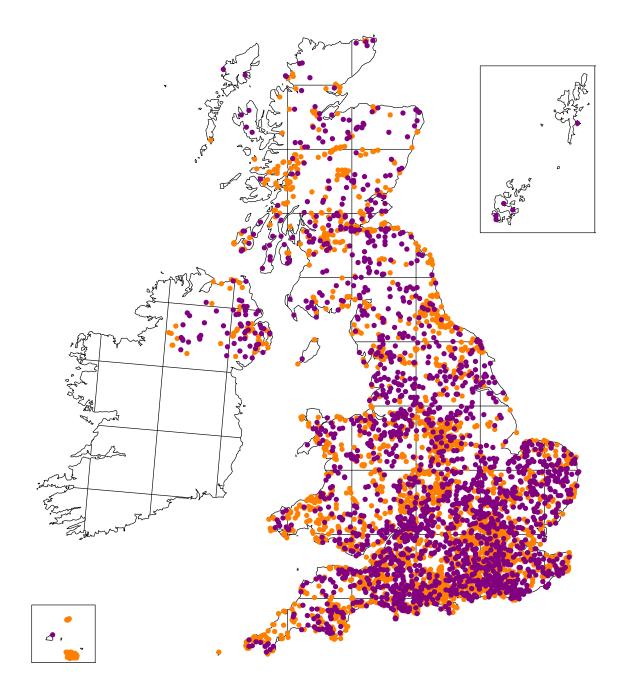


Fig. 1.2 Locations of UKBMS sites (1976-2018). Purple dots show transects, orange dots show Wider Countryside Butterfly Survey squares.

Rothamsted Insect Survey

In the 1960s, Rothamsted Research set up two separate UK networks to monitor insects, particularly those of interest to the agricultural sector. These are managed collectively as the Rothamsted Insect Survey (RIS) (Storkey *et al.* 2016). One comprises continuously-running suction-traps, used mainly to monitor aphid populations (Bell *et al.* 2015), although it has also been used to assess trends in aerial insect biomass (Shortall *et al.* 2009). The other is a network of standardised, automated light-traps, which operate nightly and are

used to monitor the relative abundance of nocturnal macro-moths (Woiwod *et al.* 2005; Conrad *et al.* 2007). RIS light-traps have operated at c.540 sites for various durations between 1968-2018, with c.80 traps active each year in recent times. The first RIS light-trap was operated at Rothamsted Research in the 1930s and 1940s and the fundamental design of the trap and light source has remained unchanged since then (Williams 1948).

The RIS light-trap network has less citizen science involvement than the other schemes detailed here. For much of its history, the catch from most traps was counted by professional entomologists, although some traps have always been monitored by volunteers and nowadays most are done by expert citizen scientists.

Big Butterfly Count

In contrast to the previously discussed schemes, which all have records extending back to at least the mid-1970s, Butterfly Conservation's Big Butterfly Count has collected count data for selected, widespread butterflies and diurnal macro-moths during a short survey window (usually three weeks) each summer since 2010 (Dennis *et al.* 2017b). Big Butterfly Count also differs from the other schemes in that an explicit aim is to engage new audiences, outside of the existing community of biological recording volunteers. To minimize barriers to participation, a simple sampling protocol is used, comprising a 15-minute count of the (currently) 19 target species. There is no other standardisation of sampling effort and no verification of records before analysis.

Participation rates are high compared to most citizen science biodiversity projects. An estimated 113,000 people carried out 116,000 counts during Big Butterfly Count 2019. Most counts take place in gardens (mean 65% p.a. 2011-2014) and are biased towards urban landscapes (Dennis *et al.* 2017b); 1km squares with Big Butterfly Counts contained a mean of 33.4% urban landcover, which contrasts with a mean of 9.8% for squares sampled by the UKBMS.

Lepidoptera change in GB

Thanks to long-term citizen science, the changing status of GB's Lepidoptera fauna is well documented.

Population and distribution trends of butterfly species have been regularly assessed since the 1970s, repeatedly demonstrating decreases for most species (Heath *et al.* 1984; Asher *et al.* 2001; Fox *et al.* 2015) and greater overall declines than equivalent trends for mammals, birds and vascular plants (Thomas *et al.* 2004; Hayhow *et al.* 2019). The most recent assessment, using UKBMS and BNM data, found that 76% of butterfly species had decreased in either abundance or occurrence or both over the period 1976-2014, while 47% increased in one or both measures (Fox *et al.* 2015). The GB Red List of butterflies categorises 31% of species as threatened (Fox *et al.* 2011b).

Multi-species population indicators using UKBMS data have been adopted by Government for environmental monitoring (Brereton *et al.* 2011b). These show long-term (1976-2018) statistically significant decreases of 68% for habitat specialist butterflies and 30% for wider countryside species (Defra 2019). Analysis of BNM distribution trends also showed habitat specialists faring worse than generalists (Warren *et al.* 2001), and this pattern has been found widely in butterflies (Öckinger *et al.* 2010; Eskildsen *et al.* 2015; Habel *et al.* 2019b) and other taxa (Clavel *et al.* 2011; MacLean & Beissinger 2017; Platts *et al.* 2019).

Declines of habitat specialist butterflies in GB are long-term, driven by land-use changes that commenced in the first half of the 20th century, such as agricultural intensification and reductions in woodland management. Severe decreases of species such as Heath Fritillary *Melitaea athalia* (Warren *et al.* 1984), Marsh Fritillary *Euphydryas aurinia* (Warren 1994) and Large Blue *Maculinea arion* (Thomas 1980) were documented decades ago and conservation programmes initiated. More recently, abundance declines of some widespread butterflies (e.g. Wall *Lasiommata megera*, Small Tortoiseshell *Aglais urticae*) have become evident in GB (Gripenberg *et al.* 2011; Fox *et al.* 2015) and neighbouring countries (Van Dyck *et al.* 2009; Van Dyck *et al.* 2015).

Data with which to evaluate biodiversity change among GB moths, while good compared to most insect taxa, are less comprehensive than for butterflies. National-scale assessments of moth biodiversity have been undertaken however, albeit based on subsets of species (Fox *et al.* 2013; Chapter 3). Sixty-five moth species were extirpated from GB over the period 1900-2009, while

112 species became established (Parsons 2010). Long-term population trends have been derived for 337 relatively widespread macro-moths using RIS count data (Conrad *et al.* 2004). Two-thirds of these had negative trends and the overall abundance of GB macro-moths decreased by 31% over 35 years (1968-2004) (Conrad *et al.* 2006). The decrease in overall abundance was even more marked in southern GB (44% decline), while there was no significant change in the northern half of GB (Conrad *et al.* 2006). A more recent analysis of macromoth abundance from RIS traps in Scotland, however, showed a significant decrease of 20% for 1975-2014 (Dennis *et al.* 2019).

RIS data for the most rapidly declining widespread moth species also contribute, with population monitoring of a small number of rare moths, to an UK Government indicator of priority species (Eaton *et al.* 2015). Of the four taxonomic groups in this indicator, moths (76 species) showed the greatest abundance decline, with a 2016 index value that was only 14% of the baseline 1970 value. Butterflies (23 species) also experienced a strong decline, with a 2016 index value that was 17% of its start value in 1976, while the bird index (104 species) showed no overall change and the mammal index (11 species) increased (Burns *et al.* 2019).

Macgregor *et al.* (2019a) recently estimated biomass change of GB moths using RIS data. While the effect size of their trend suggested a 32% decrease over the period 1983-2017, this was far less severe than the 77% decrease in flying insect biomass reported in Germany over a similar period (Hallmann *et al.* 2017). Surprisingly, however, Macgregor *et al.* (2019a) found a major increase in GB moth biomass during 1967-1982, meaning that biomass levels were still much higher in 2017 than they had been in 1967.

In addition to abundance and biomass change, some GB moth species have shown large contractions or expansions of range (Randle *et al.* 2019). In a study of NMRS data for 673 moth species, Fox *et al.* (2014; Chapter 3 of this thesis) found that 39% had significant negative trends in frequency of occurrence (1970-2010), compared with 24% that had significant positive trends. Recently, an occupancy modelling approach generated long-term (1970-

2016) trends for 390 species at a finer spatial scale (Randle *et al.* 2019); 121 species (31%) decreased significantly, while 148 (38%) increased significantly.

Drivers of Lepidoptera biodiversity change

Utilising citizen science data in GB and elsewhere (particularly in western Europe and North America e.g. Schmucki *et al.* 2016; Wepprich *et al.* 2019), as well as experimental results, considerable progress has been made in understanding the causative environmental drivers of Lepidoptera biodiversity change (discussed further in Chapters 2 and 3).

Land use

Land-use change, including both the conversion of semi-natural habitats to highly modified landscapes and major increases/decreases in management intensity, is thought to have been a key driver over recent decades (Thomas 1995; Warren *et al.* 2001; Bubová *et al.* 2015; Thomas 2016). The impact of intensive agriculture has been particularly harmful (Burns *et al.* 2016; Hayhow *et al.* 2019). Higher diversity and abundance of butterflies and moths are typically found in less intensively managed agricultural habitats (Mangels *et al.* 2017; Habel *et al.* 2019c) and reduced management (e.g. through agrienvironment schemes) often leads to increased numbers and species richness (Fuentes-Montemayor *et al.* 2011; Zingg *et al.* 2019). For example, reduced frequency and intensity of hedgerow cutting in GB agricultural landscapes benefitted Lepidoptera communities (Staley *et al.* 2016; Staley *et al.* 2018; Froidevaux *et al.* 2019).

However, reduced management can also drive Lepidoptera decline. Abandonment of low-productivity grasslands in Europe, with subsequent succession to woodland, has impacted negatively on specialist butterflies and moths of open habitats (Nilsson *et al.* 2013; Herrando *et al.* 2016; Ubach *et al.* 2019), as has the cessation of traditional woodland management (e.g. coppicing) (Warren & Key 1991; Fartmann *et al.* 2013; Thomas *et al.* 2015). On the other hand, many moth species are associated with woodland habitat and should benefit from afforestation and reduced management (Merckx 2015).

Urbanisation is linked to reductions in Lepidoptera abundance and species richness, particularly the loss of habitat specialists (Deguines *et al.* 2016; Ramírez-Restrepo & MacGregor-Fors 2017; Merckx & Van Dyck 2019). Furthermore, in an assessment of population change for GB butterfly species (1995-2014) in urban versus rural UKBMS locations, trends were more negative in urban areas for 25 of 28 species and a composite index of all species showed a significantly greater decrease for urban than for rural areas (-69% for urban compared with -45% for rural) (Dennis *et al.* 2017c).

Habitat loss decreases the size of remaining patches and increases their isolation. Both can increase the risk of local extirpation of Lepidoptera species through reduced population size (leading to greater extinction rates) and decreased dispersal (leading to lower colonisation rates) (Thomas 2000; Öckinger *et al.* 2010).

In contrast, land management to enhance biodiversity can benefit Lepidoptera populations. This is exemplified by the successful reintroduction of the Large Blue to GB (Thomas *et al.* 2009), but also in many other examples where threatened species have been the focus of conservation action e.g. New Forest Burnet *Zygaena viciae* (Young & Barbour 2004), High Brown Fritillary *Argynnis adippe* (Ellis *et al.* 2019). Although not immune from biodiversity declines, protected areas of high-quality habitat maintain higher abundance and species richness of butterflies than the surrounding landscape (Gillingham *et al.* 2015; Rada *et al.* 2018) and agri-environment schemes have benefitted some declining species (e.g. Brereton *et al.* 2008).

Environmental pollution

Disentangling the impact of pesticides from other aspects of intensive management is difficult, particularly given the lack of ecotoxicological data for insecticides on non-target Lepidoptera (Pisa *et al.* 2015; Braak *et al.* 2018) and the potential for direct (Russell & Schultz 2010; Stark *et al.* 2012) and indirect effects of herbicides via impacts on larval hostplants (Prosser *et al.* 2016; Belsky & Joshi 2018). Nevertheless, the overall impact of systemic insecticides is thought to be substantial (Chagnon *et al.* 2015), routes of exposure via nectar, pollen and tissues of wild plants have been demonstrated (Botías *et al.*

2015; Botías *et al.* 2016; Basley & Goulson 2018) and correlative studies using citizen science data suggest negative effects on butterfly populations (Gilburn *et al.* 2015; Muratet & Fontaine 2015; Forister *et al.* 2016). A short-term field experiment found negative effects of insecticide application on moth caterpillar abundance in field margins, but no effect of herbicide treatment (Hahn *et al.* 2015).

Nutrient enrichment is expected to affect insect herbivores via changes to the chemistry, structure and composition of plant communities (Nijssen *et al.* 2017; Stevens *et al.* 2018). Several studies have found positive correlations between Lepidoptera species trends and the Ellenberg nitrogen indicator values of their larval hostplants (where plants preferring fertile soils have higher Ellenberg nitrogen scores) (Öckinger *et al.* 2006; Betzholtz *et al.* 2013; Fox *et al.* 2014; Pöyry *et al.* 2017; WallisDeVries & van Swaay 2017). Kurze *et al.* (2018) recorded increased larval mortality in all six study species of grassland Lepidoptera when nitrogen fertilizer was applied to hostplants at rates typically used in agriculture. In a similar study, positive responses were found in two butterfly species to nitrogen fertilization of their nitrophilous hostplant (Kurze *et al.* 2017).

Reduced air pollution in GB may also be indirectly driving some species trends. Moths with larvae that feed on lichens, e.g. Dingy Footman *Eilema griseola* and Marbled Green *Nyctobrya muralis*, have fared well against a background of general decline (Conrad *et al.* 2004; Randle *et al.* 2019). Using citizen science data, Pescott *et al.* (2015) linked this to the recovery of lichen populations following air quality improvements, particularly reduction in sulphur dioxide pollution.

Urbanisation is accompanied by large increases in artificial light at night. The global extent and intensity of artificial light are both increasing at c.2% per year and 83% of the human population now lives under light-polluted skies (Gaston 2018). Artificial light can alter invertebrate community composition (Manfrin *et al.* 2017), drive population change (Bennie *et al.* 2018) and affect insect behaviour (Owens & Lewis 2018). As yet, there is no evidence for a direct causative link with population change in any Lepidoptera species, although

many moths are attracted to light (e.g. Somers-Yeates *et al.* 2013) and nocturnal moths that exhibit positive phototaxis decreased more over 30 years in the Netherlands than diurnal species or moths that are not attracted to light (Van Langevelde *et al.* 2018). Artificial light can disrupt pheromone production in Cabbage Moth *Mamestra brassicae* (Van Geffen *et al.* 2015a), reduce mating in Winter Moth *Operophtera brumata* (Van Geffen *et al.* 2015b), decrease larval growth in Rustic Shoulder-knot *Apamea sordens* (Grenis & Murphy 2019) and inhibit feeding in adult moths (Van Langevelde *et al.* 2017). It has also been shown to alter nocturnal pollination by moths and other insects (Knop *et al.* 2017, Macgregor *et al.* 2019b). While research has focussed on nocturnal insects, artificial light could influence populations of diurnal Lepidoptera directly (e.g. through impacts on nocturnal larvae) and indirectly via effects on the growth and phenology of hostplants (Bennie *et al.* 2016; ffrench-Constant *et al.* 2016).

Climate change

Substantial effects of climate change on Lepidoptera populations are evident in GB and elsewhere (e.g. Parmesan *et al.* 1999; Parmesan 2006; Chen *et al.* 2011; Molina-Martínez *et al.* 2016). Citizen science data from the BNM and UKBMS have shown climate-related shifts in distribution and abundance for butterflies in GB and Europe (Warren *et al.* 2001; Hill *et al.* 2002; Devictor *et al.* 2012). Drawing on BNM and NMRS data, Mason *et al.* (2015) showed that the distributions of butterflies and moths with northern range margins in GB have expanded polewards at an increasing rate since the 1960s. Risk assessments predict that 46% of 52 butterfly species and >60% of 422 moths could increase in overall extent in GB due to climate change this century (Thomas *et al.* 2011; Pearce-Higgins *et al.* 2017).

Other studies, however, have found evidence of climate-driven range contraction (e.g. Thomas *et al.* 2006; Breed *et al.* 2013), although microclimatic buffering may ameliorate these effects (Suggitt *et al.* 2018), and negative impacts on Lepidoptera population growth (Conrad *et al.* 2002; Palmer *et al.* 2017). Analysing RIS data, Martay *et al.* (2017) implicated climate change as a major driver in the population declines of some moth species and in the overall abundance decline of macro-moths. In addition, negative impacts on butterfly

abundance of extreme climatic events, which are expected to increase with climate change, have been demonstrated using UKBMS data. Oliver *et al.* (2015b) predicted substantial long-term abundance declines of six drought-sensitive butterflies in response to the increasing frequency of summer drought, while extreme winter warmth exerted detrimental population effects in 21 of 41 butterfly species (versus only two species with positive effects) (McDermott Long *et al.* 2017).

Changes to phenology are common biotic responses to climate change (Cohen *et al.* 2018), including among butterflies and moths (Roy & Sparks 2000; Stefanescu *et al.* 2003; Kearney *et al.* 2010), raising concerns about temporal mismatches in ecological interactions (Thackeray *et al.* 2016; Burgess *et al.* 2018). Using GB citizen science data for 130 Lepidoptera species, Macgregor *et al.* (2019c) showed that phenological advance was associated with increased population growth but only in multivoltine species; flight periods of univoltine species did advance significantly over a 20-year period but there was no clear relationship with abundance trends. Patterns of voltinism are also changing in response to climate change, with increased incidence of multiple broods per year (Altermatt 2010; Pöyry *et al.* 2011). The demographic consequences of such changes are not yet understood, although a third generation 'development trap' has been proposed as a cause for the decline of the Wall butterfly (Van Dyck *et al.* 2015).

Interactions between drivers of change

Drivers can act synergistically to amplify impacts on biodiversity (Brook *et al.* 2008) or in opposition to reduce responses. Interactions of land-use change and climate change have been investigated by numerous studies (Mantyka-pringle *et al.* 2012; Guo *et al.* 2018; Newbold *et al.* 2019; Northrup *et al.* 2019). In fragmented GB landscapes, the ability of species to track climate change by shifting their distributions is limited by habitat availability (Mair *et al.* 2014; Platts *et al.* 2019). The range expansion of Speckled Wood *Pararge aegeria* was slower in landscapes with less woodland (Hill *et al.* 2001), while the spread of Silver-spotted Skipper *Hesperia comma* was facilitated by conservation management of protected areas (Lawson *et al.* 2014).

Climate change and nitrogen deposition can also act in synergy to increase vegetation growth, reducing the availability of warm micro-climates for thermally-constrained species. As yet there is limited evidence for this as a driver of population change in Lepidoptera, although it has been implicated in the decline of European butterflies that overwinter in the egg or larval stage (WallisDeVries & van Swaay 2006) and specific species such as the Wall (Klop *et al.* 2015) and High Brown Fritillary (Ellis *et al.* 2019). De Sassi *et al.* (2012) found independent and synergistic effects of climate change and nitrogen deposition on Lepidoptera community composition and biomass, mediated through changes in plant species dominance and quality.

Overview of the rationale of this thesis

Although Lepidoptera biodiversity recording through citizen science is well developed in GB, many gaps in our knowledge remain. My thesis aims to address two overarching areas regarding the efficacy of citizen science in biodiversity conservation:

- 1. Increasing citizen science participation while ensuring data validity.
- 2. Application of citizen science data to biodiversity conservation.

Despite statistical improvements (Dennis et al. 2013; Isaac et al. 2014). increased citizen science recording effort is desirable to increase the quantity and guality of species trends. For example, even with the high levels of UK recording, Outhwaite et al. (2019) had to discard 51% of 10,750 species trends derived from occupancy modelling due to insufficient recording coverage. There are social reasons for increasing citizen science participation too, as it can yield benefits for the biodiversity conservation movement and wider society (Bela et al. 2016; Coventry et al. 2019). But there can be trade-offs (e.g. in the quality of sampling and data) as well as benefits to the participation of citizen scientists in biodiversity monitoring. In this thesis I explore some of these pros and cons, both of which could be magnified by increased participation. First, I review evidence from the literature for moth biodiversity trends and the potential drivers of these trends, highlighting knowledge gaps that could be addressed by increased citizen science recording (Chapters 2 and 3). Next, I consider the reliability of mass-participation citizen science engaging inexperienced contributors in comparison to standardised monitoring by expert amateur

naturalists, by comparing population changes for widespread butterfly species from the Big Butterfly Count with those from the UKBMS (Chapter 4). Finally, I examine the implications of involving citizen scientists in gathering ecological information for the reuse of data (Chapter 6).

Citizen science has played an important role historically in understanding biodiversity change and has the potential to be even more significant (Powney & Isaac 2015; Pocock *et al.* 2018). I present several new applications of citizen science data using GB butterflies and moths as examples. Utilising the NMRS, I produce the first long-term occurrence trends for macro-moths (Chapter 3) and make inferences about the drivers of change. Second, I use the Big Butterfly Count data to estimate trends for a group of widespread butterfly species (Chapter 4). Then, I use UKBMS and RIS monitoring data to explore the variability of short-term population trends and how this impacts on Red List classifications (Chapter 5). Lastly, I investigate how the opinions of citizen scientists may limit the wider use of Lepidoptera records (Chapter 6).

Aims, results and contribution to scientific knowledge of each chapter

Chapter 2 The decline of moths in Great Britain: a review of possible causes Moths are a species-rich insect taxon (with c.2,500 species recorded in GB) and play important roles in ecosystem functioning, as herbivores (Young 1997; Majerus 2002), prey for a wide range of predators (Vaughan 1997; Denerley *et al.* 2019; Rytkönen *et al.* 2019) and as pollinators (Banza *et al.* 2015; Macgregor *et al.* 2015). Previous research has shown significant decreases in GB moth abundance (Conrad *et al.* 2006; Fox *et al.* 2013) and comparable studies elsewhere have produced similar evidence of overall decline (Mattila *et al.* 2006; Groenendijk & Ellis 2011; Valtonen *et al.* 2017).

Understanding the causes of moth decline and the potential impacts on other species is of high policy relevance (Sutherland *et al.* 2006) and current knowledge gap (Burns *et al.* 2016). I summarise moth biodiversity trends, review the evidence for the potential drivers of these trends and recommend future research.

Although few scientifically documented examples exist, 20th century land-use change, converting semi-natural habitats to highly-modified landscapes, will have had major detrimental effects on many moth species. Even such overwhelmingly negative (for biodiversity) land-use changes have provided opportunities for some moths however, e.g. species that utilise conifers as larval hostplants. More evidence exists for adverse impacts of changes to the intensity of land management, particularly agricultural intensification and a shift from traditional silviculture techniques such as coppicing to high forest systems. In contrast, apparent climate change effects on moths are largely positive, reflecting the fact that many species reach their cool (northern) range margin within GB. At the time of the review, there was little evidence of population-level effects on moths caused by chemical or light pollution, non-native species or direct exploitation.

I recommend more research into the impacts of light pollution, climate change and trying to disaggregate the effects of different elements of intensive land management. A broader view of GB moth trends is also recommended, beyond the selection of widespread species for which RIS trends are available, and evidence-based habitat improvement measures need to be developed and implemented via agri-environment schemes and other policy initiatives.

Although previous studies reporting moth trends had given brief overviews of suspected causes, the review presented in Chapter 2 provided a comprehensive statement of current knowledge. Much progress has been made since it was published (summarised in section 1.6), particularly into the effects of climate change, artificial light and, to a lesser extent, nitrogen pollution. A broader assessment of GB moth trends has been achieved, first through the analysis presented in Chapter 3 and more recently in Randle *et al.* (2019).

Chapter 3 Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes

As identified in Chapter 2, it is important to assess trends of GB moths because of the taxon's species richness and significant ecological roles. Such trends identify priorities for biodiversity conservation. In addition, the patterns of change can provide insight into the causal factors. Latitudinal gradients of two major drivers implicated in moth trends exist within GB; a natural climatic gradient, with warmer temperatures in the south compared with the north, and a land-use intensity gradient, with generally higher levels of intensive agriculture and urban development in the south compared with the north. By examining moth trends across these gradients, some inferences can be drawn about the contributions of drivers.

Utilising 10.5 million NMRS distribution records, I estimate GB trends for 673 resident macro-moth species for 1970-2010. The Frescalo statistical approach was used to account for major spatiotemporal variation in recording effort (Hill 2012). Overall, moths decreased in frequency of occurrence, but individual species exhibited a wide diversity of responses with 260 species showing significant declines and 160 significant increases. Northerly distributed (coldadapted) species declined, consistent with a negative response to climate change in landscapes relatively unaffected by intensive land management, while (warm-adapted) moths restricted to southern GB showed more mixed results, consistent with expected distribution increases driven by climate change but detrimental impacts of more intensive land-use. Widespread species, which were not predicted to be as sensitive to climatic change, declined on average in southern GB but not in the north, suggesting a response to land-use change. A traits-based analysis (using Ellenberg indicator values) of the larval hostplants of monophagous moth species, found a significant positive correlation between moth distribution trend and the nitrogen requirements of hostplants and a negative association with light requirements.

This study considerably extends previous knowledge of GB moth biodiversity change by estimating long-term trends for 673 species, rather than 337 species with RIS abundance trends (Conrad *et al.* 2006; Fox *et al.* 2013). This improvement is more than simply numerical, because the new assessment includes scarcer species, which may be more likely to be at risk, than those in the RIS analysis and by including diurnal moths and species that do not exhibit positive phototaxis. The study reveals likely positive and negative responses to climate change by warm- and cold-adapted moths (respectively), mirroring those of butterflies (Hill *et al.* 2002; Franco *et al.* 2006) and opposing effects of

climatic and land-use change in southern GB. It also provides one of the first demonstrations of nitrogen enrichment impacts on Lepidoptera populations mediated via plant communities (Öckinger *et al.* 2006; de Sassi *et al.* 2012; Betzholtz *et al.* 2013).

Chapter 4 Using citizen science butterfly counts to predict species population trends

Citizen science is a nebulous discipline (Pocock *et al.* 2017), even in the limited context of biodiversity monitoring. The long-standing collation of species population and distribution data in GB falls under a broad definition of citizen science, as most data are gathered by unpaid volunteers. However, these volunteers are often skilled and experienced, capable of undertaking monitoring to comparable standards as professional scientists (Chase & Levine 2016) and the results are generally accepted by policy makers and the scientific community. In contrast, in the recent proliferation of citizen science projects, many participants have little prior experience; indeed some biodiversity projects explicitly aim to engage with new audiences (e.g. Roy *et al.* 2016).

As a consequence of inexperienced participants and simplified sampling protocols, the reliability of data gathered through mass-participation citizen science may be constrained and the credibility of scientific outputs called into question (Gardiner *et al.* 2012; Riesch & Potter 2014; Lewandowski & Specht 2015; Kosmala *et al.* 2016). There have been few attempts to compare population trends generated by mass-participation citizen science against those from systematic monitoring, and none involving terrestrial invertebrates.

I address this knowledge gap by determining whether population changes for widespread butterfly species derived from a new mass-participation scheme, the Big Butterfly Count, are comparable with those from an established, highly structured programme based on expert data, the UKBMS. Using data just for the three-week Big Butterfly Count survey period each year, I found significant correlations between Big Butterfly Count and UKBMS trends for both net population change over a four-year period (2011-2014) and inter-annual population growth rates. Furthermore, linear models using Big Butterfly Count data and weather covariates were surprisingly successful at predicting UKBMS index values in 2015.

The findings inform the debate around the ability of mass-engagement projects to produce robust scientific outputs in addition to improving scientific literacy, awareness and engagement (Chase & Levine 2016; Lakeman-Fraser et al. 2016; Turrini et al. 2018). There is also much interest in the feasibility of using simple, non-systematic sampling to generate meaningful biodiversity information (e.g. Lang et al. 2019). In addition, the validation of Big Butterfly Count trends means that the data could be used as a separate indicator of GB butterfly populations or incorporated into existing UKBMS metrics (e.g. Dennis et al. 2017c) with an integrated analysis (Pagel et al. 2014). The Big Butterfly Count samples different landscape elements than the UKBMS; the majority of Big Butterfly Counts are undertaken in private gardens (a land-use type not sampled by the UKBMS) and occur, on average, in more urban settings. Thus, Big Butterfly Count data could potentially be used as an indicator of butterfly populations in gardens and parks. This could provide a valuable tool to engage the public and managers of urban greenspace to encourage more favourable land management for biodiversity (Garbuzov et al. 2015; Gunnarsson et al. 2017), as well as contributing to increased understanding of urban ecology (Wang Wei et al. 2016) and the importance of built-up areas for insects in highly modified landscapes (Baldock et al. 2015; Hall et al. 2017).

Chapter 5 Insect population trends and the IUCN Red List process

The International Union for Conservation of Nature's (IUCN) Red List process plays a vital role in biodiversity assessment, as a set of objective standards for quantifying extinction risk (Mace *et al.* 2008), assessing change (Butchart *et al.* 2005) and catalysing conservation (Rodrigues *et al.* 2006). Despite its undoubted utility and widespread application, the Red List process is not without problems. Some stem from misunderstanding (Collen *et al.* 2016), while others arise from debate over the quantitative thresholds of certain Red List criteria. Criterion A "Reduction in population size", for example, determines extinction risk solely on the basis of population decline over the most recent 10 years or three generations, whichever is longer (IUCN 2012). Several studies have questioned the reliability of measuring trends over such a short period

(Connors *et al.* 2014; d'Eon-Eggertson *et al.* 2015; White 2019) and cautioned that long time series may be necessary to detect impacts of drivers and changes in ecosystem functioning (McCain *et al.* 2016; Thomson 2019). A recent study of GB moth biomass concluded that short durations of data generate unreliable estimates of longer-term trends (Macgregor 2019a).

Given that Lepidoptera typically have high population variability (Williams 1961; Taylor & Taylor 1977), I hypothesised that 10-year population trends of butterflies and moths, and resultant IUCN classifications, would be sensitive to start year. I explore this using UKBMS and RIS citizen-science data to derive a series of 10-year trends with different start years for 54 butterfly and 431 macromoth species. Each trend was then compared to IUCN Criterion A thresholds to produce Red List classifications for each date period. Large discrepancies were revealed between classifications that differed by just a single start year. For example, 15 butterfly species met the Red List threshold using trends for 2002-2011, but 29 did so for 2003-2012. In the most extreme example, the difference of a single year reduced the number of qualifying moth species from 62 to 20.

Current IUCN guidelines acknowledge that using data from a longer time period may be advantageous for species that have high population variability (IUCN 2017). However, 10-year trends remain the basis of Criterion A and can be applied without utilising longer-term data. Previous authors have noted this potential problem (de longh & Bal 2007; van Swaay *et al.* 2011), but this is the first time that such impacts have been quantified for insect taxa. My results suggest that it is inappropriate to use 10-year trends in extinction risk assessment of UK Lepidoptera and that this is likely to be the case for many other insect taxa globally. I call for further guidance on Red List assessments of taxa with high levels of population variability.

Chapter 6 Opinions of citizen scientists on open access to UK butterfly and moth occurrence data

Recent studies have examined the motivations of citizen scientists (Hobbs & White 2012; West & Pateman 2016; Richter *et al.* 2018), the benefits that they gain from participation (Merenlender *et al.* 2016; Coventry *et al.* 2019) and impacts on their engagement with conservation (Lewandowski & Oberhauser

2017). However, little work has been undertaken on the views of citizen scientists regarding the onward use of the data they contribute, beyond the project in which they participated (Ganzevoort *et al.* 2017). This is topical due to scientific and ethical pressure for data sharing (Hampton *et al.* 2013), and requirements imposed by public funding bodies and scientific journals for open access to datasets (Reichman *et al.* 2011; Pearce-Higgins *et al.* 2018). It is often suggested, without supporting evidence, that citizen scientists favour open access, but at present many citizen science biodiversity datasets are not fully open (Groom *et al.* 2017).

Through questionnaire surveys of two groups of citizen scientists involved in the BNM and NMRS projects, namely recorders (510 survey respondents) and regional co-ordinators (County Recorders) (104 survey respondents), I characterise views relating to open access. Overall, I found high levels of support for the principle of open access to UK butterfly and moth records; e.g. more than twice as many regional co-ordinators (39.8%) were classified as promoters of open access compared with detractors (16.5%). Despite this, there was much more caution when it came to the practicalities. Only 6.7% of regional co-ordinators and 32.7% of recorders thought that all records should be open at full spatial resolution, and 79.6% of regional co-ordinators felt that data reuse should be limited to non-commercial purposes. There were significant regional differences, however, with co-ordinators in Scotland being more supportive of open access than their counterparts in England.

Knowledge of these opinions, including details about which data should be accessible, when and for what purposes, contributes to the current debate on open access taking place within organisations collecting, curating and utilising species records provided by citizen scientists. Open access to such data would maximise their use in biodiversity conservation (Chandler *et al.* 2017; Sullivan *et al.* 2017; Soroye *et al.* 2018), contribute to ecological research (Farley *et al.* 2018) and increase public trust in science (Soranno *et al.* 2015). Unlike in conventional science though, where researchers are also data gatherers and are able to decide on issues of data access, in citizen science, researchers should also be mindful of the views of the participants. There can be negative consequences of open access to biological records, e.g. harm to threatened

species and habitats (Tulloch *et al.* 2018), and citizen scientists might take the view that the risks outweigh the benefits and cease participation, undermining project viability. My results, and those from the Netherlands (Ganzevoort *et al.* 2017), suggest that participants expect some limitation on data availability. Organisers of citizen science should consider open access issues in the project planning phase and present would-be participants with clear information about onward data availability from the outset.

Future directions

Although much has been achieved using citizen science data to assess the magnitude and causes of biodiversity change in the case study of GB butterflies and moths, there remains huge potential for further improvement in generating reliable trends and, particularly, in extending geographical and taxonomic scope. Citizen science provides cost-effective biodiversity surveillance (Gardiner et al. 2012) but necessitates careful consideration of data quality and specialised analysis to adjust for bias. Data are currently inadequate to assess the vast majority of species in most countries. GB Lepidoptera are intensively recorded by citizen scientists and yet major gaps in our knowledge remain. Long-term population trends are restricted to c.400 of the c.2,500 GB moth species, and no distribution trends exist for the c.1,600 micro-moths. Increased recording and novel statistical methods will both contribute to the production of robust trends for more GB moths in the future. The extensive datasets on GB Lepidoptera provide a model system for the development of new statistical approaches (e.g. Dennis 2017a) that can be applied to other taxa, and for comparing different methods (Norberg et al. 2019). Further research is needed to generate meaningful short-term trends for taxa with highly variable population growth rates. We also need to explore the extent to which mass-participation citizen science can inform species trends and, indeed, whether it can provide additional information about biodiversity change in poorly-monitored habitats such as gardens.

Extending citizen science approaches to other taxa and wider geographical scales is an important next step towards more informative and dependable assessments of global insect biodiversity change (Montgomery *et al.* 2020; Harvey *et al.* 2020). In Europe, there are currently several significant

developments, including the ABLE project (https://butterfly-monitoring.net/able) to extend standardised butterfly transect monitoring to new countries and to rollout a mass-participation butterfly recording scheme, collating data into a pan-European database (https://butterfly-monitoring.net/), and the European Ladybird Survey (https://european-ladybirds.brc.ac.uk/home) with a new smartphone app to facilitate citizen science recording. However, the tropics represent the key information gap and areas such as southern Asia and tropical Africa have been identified as regions where increased citizen science could provide the greatest benefits for global biodiversity assessment (Pocock *et al.* 2018). Scaling-up citizen science to address this gap is a crucial challenge over the next decade (Chandler *et al.* 2017).

New technologies such as eDNA (Ruppert *et al.* 2019) and image recognition cameras (Hogeweg *et al.* 2019) may revolutionise aspects of biodiversity monitoring, but the direct engagement of citizens in gathering data will remain vital to counteract the "extinction of experience" (Miller 2005; Soga & Gaston 2016) and "shifting baseline syndrome" (Soga & Gaston 2018). Citizen science can engender support for biodiversity conservation and encourage civic participation (Turrini *et al.* 2018), although these outcomes need to be measured more effectively (Bela *et al.* 2016). Co-created projects (Trimble & Berkes 2013; Pocock *et al.* 2018), citizen science within formal education (Wals *et al.* 2014; Saunders *et al.* 2018) and balanced reporting of results (McAfee *et al.* 2019) will all build trust in biodiversity science and help deliver the transformative change required to tackle current environmental crises (Díaz *et al.* 2019).

Finally, more needs to be done to make citizen science biodiversity data available to support wider research, policy development and implementation (Chandler *et al.* 2017; Sullivan *et al.* 2017; Montgomery *et al.* 2020). Research priorities should include identifying the relative contributions of anthropogenic drivers to insect declines (which are incompletely understood even for many GB Lepidoptera; Chapter 2) and the design of evidence-based land management techniques to restore biodiversity, even if drivers are not fully known (Harvey *et al.* 2020). There are barriers to overcome in increasing access to citizen science data and new initiatives need to address these from the outset, while long-

running projects, such as those for GB butterflies and moths, should work with participants to promote the benefits of open data and mitigate any negative impacts (Tulloch *et al.* 2018). Immediate actions could include focus groups with GB Lepidoptera recorders to clarify their views on open data e.g. participants favoured only permitting non-commercial reuse of data, but it is unclear what they regard as commercial use of biodiversity information.

Conclusions

Global biodiversity is in steep decline, although data are currently insufficient to estimate rates of change reliably for insects, leading to some injudicious predictions of imminent 'insect armageddon'. In GB however, butterflies and moths are among the best monitored taxa and show clear overall decreases since the 1970s, albeit with a minority of species faring well. Citizen science already makes an enormous contribution to knowledge of biodiversity change in some countries and has the potential to provide much-needed data from poorlystudied regions in order to give a more representative global perspective.

Building on the strong tradition of citizen science Lepidoptera recording in GB, I show that such data can be used to produce a comprehensive assessment of distribution trends for macro-moths (Chapter 3) and robust measures of population change for widespread butterflies (Chapter 4). The former provides essential information to input into the prioritization of moth species for conservation action, vital given the overall declines of moths in GB, and also sheds light on drivers, such as land-use change, climate change and nutrient enrichment, helping to fill knowledge gaps (Chapter 2). Through these analyses, I show that major increases in citizen science engagement can be achieved, benefitting participants and increasing support for biodiversity conservation, without compromising scientific outputs.

The involvement of citizen scientists enables biodiversity monitoring at large spatial and temporal scales. Long-term monitoring is particularly important in the assessment of abundance trends for species with high levels of population variability (Chapter 5); short-term trends, even those measured over the Red List 10-year standard, are easily skewed by frequent peaks and troughs in abundance. However, the involvement of citizen scientists may also place novel

constraints on researchers, unless these are circumvented by project design. I explore one such issue, showing that citizen scientists expect restrictions on the reuse of their records, limiting the benefits of open data (Chapter 6).

Biodiversity loss is a crisis with drastic implications for human society. Citizen science, by providing scientific data to demonstrate and monitor biodiversity loss and by engaging citizens directly with the issue, can play a significant role in attempts to avoid the worst of the predicted impacts and bring about transformative change for a brighter future.

References

Altermatt F (2010) Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B* **277**, 1281–1287.

Altwegg R & Nichols JD (2019) Occupancy models for citizen-science data. *Methods in Ecology and Evolution* **10**, 8–21.

Asher J, Warren M, Fox R, Harding P, Jeffcoate G & Jeffcoate S (2001) *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford University Press, Oxford, UK.

Baldock KC, Goddard MA, Hicks DM, Kunin WE, Mitschunas N, Osgathorpe LM, Potts SG, Robertson KM, Scott AV, Stone GN & Vaughan IP (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B* **282**, 20142849.

Banza P, Belo AD & Evans DM (2015) The structure and robustness of nocturnal Lepidopteran pollen-transfer networks in a biodiversity hotspot. *Insect Conservation and Diversity* **8**, 538–546.

Barlow J, França F, Gardner TA, Hicks CC, Lennox GD, Berenguer E, Castello L, Economo EP, Ferreira J, Guénard B, Leal CG, Isaac V, Lees AC, Parr CL, Wilson SK, Young PJ & Graham NAJ (2018) The future of hyperdiverse tropical ecosystems. *Nature* **559**, 517–526.

Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, Mersey B & Ferrer EA (2011) Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57. Basley K & Goulson D (2018) Effects of field-relevant concentrations of clothianidin on larval development of the butterfly *Polyommatus icarus* (Lepidoptera, Lycaenidae). *Environmental Science* & *Technology* **52**, 3990–3996.

Bela G, Peltola T, Young JC, Balázs B, Arpin I, Pataki G, Hauck J, Kelemen E, Kopperoinen L, Van Herzele A, Keune H, Hecker S, Suškevičs M, Roy HE, Itkonen P, Külvik M, László M, Basnou C, Pino J & Bonn A (2016) Learning and the transformative potential of citizen science. *Conservation Biology* **30**, 990– 999.

Bell JR, Alderson L, Izera D, Kruger T, Parker S, Pickup J, Shortall CR, Taylor MS, Verrier P & Harrington R (2015) Long-term phenological trends, species accumulation rates and climate: Five decades of change in migrating aphids. *Journal of Animal Ecology* **84**, 21–34.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W & Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters* **15**, 365–377.

Belsky J & Joshi NK (2018) Assessing role of major drivers in recent decline of monarch butterfly population in North America. *Frontiers in Environmental Science* **6**, 86.

Bennie J, Davies TW, Cruse D & Gaston KJ (2016) Ecological effects of artificial light at night on wild plants. *Journal of Ecology* **104**, 611–620.

Bennie J, Davies TW, Cruse D, Inger R & Gaston KJ (2018) Artificial light at night causes top-down and bottom-up trophic effects on invertebrate populations. *Journal of Applied Ecology* **55**, 2698–2706.

Bernstein AS (2014) Biological diversity and public health. *Annual Review of Public Health* **35**, 153–167.

Betzholtz P-E, Pettersson LB, Ryrholm N & Franzén M (2012) With that diet, you will go far: trait-based analysis reveals a link between rapid range expansion and a nitrogen-favoured diet. *Proceedings of the Royal Society B* **280**, 20122305.

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J & Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**, 351–354.

Bird TJ, Bates AE, Lefcheck JS, Hill NA, Thomson RJ, Edgar GJ, Stuart-Smith RD, Wotherspoon S, Krkosek M, Stuart-Smith JF, Pecl GT, Barrett N & Frusher S (2014) Statistical solutions for error and bias in global citizen science datasets. *Biological Conservation* **173**, 144–154.

Boakes EH, McGowan PJK, Fuller RA, Chang-qing D, Clark NE, O'Connor K & Mace GM (2010) Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biology* **8**, e1000385.

Botías C, David A, Hill EM & Goulson D (2016) Contamination of wild plants near neonicotinoid seed-treated crops, and implications for non-target insects. *Science of the Total Environment* **566**, 269–278.

Botías C, David A, Horwood J, Abdul-Sada A, Nicholls E, Hill E & Goulson D (2015) Neonicotinoid residues in wildflowers, a potential route of chronic exposure for bees. *Environmental Science & Technology* **49**,12731–12740.

Boyes DH, Fox R, Shortall CR & Whittaker RJ (2019) Bucking the trend: the diversity of Anthropocene 'winners' among British moths. *Frontiers of Biogeography* **11**, e43862.

Braak N, Neve R, Jones AK, Gibbs M & Breuker CJ (2018) The effects of insecticides on butterflies – a review. *Environmental Pollution* **242**, 507–518.

Bradshaw CJA, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Barbet-Massin M, Salles J-M, Simard F & Courchamp F (2016) Massive yet grossly underestimated global costs of invasive insects. *Nature Communications* **7**, 12986.

Breed GA, Stichter S & Crone EE (2013) Climate-driven changes in northeastern US butterfly communities. *Nature Climate Change* **3**, 142–145.

Brereton TM, Botham MS, Middlebrook I, Randle Z, Noble D, Harris S, Dennis EB, Robinson AE, Peck K & Roy DB (2019) *United Kingdom Butterfly Monitoring Scheme report for 2018*. Centre for Ecology & Hydrology, Butterfly

Conservation, British Trust for Ornithology and Joint Nature Conservation Committee.

Brereton TM, Cruickshanks KL, Risely K, Noble DG & Roy DB (2011a) Developing and launching a wider countryside butterfly survey across the United Kingdom. *Journal of Insect Conservation* **15**, 279–290.

Brereton T, Roy DB, Middlebrook I, Botham M & Warren M (2011b) The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation* **15**, 139–151.

Brereton TM, Warren MS, Roy DB & Stewart K (2008) The changing status of the Chalkhill Blue butterfly *Polyommatus coridon* in the UK: the impacts of conservation policies and environmental factors. *Journal of Insect Conservation* **12**, 629–638.

Brook BW, Sodhi NS & Bradshaw CJA (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**, 453–460.

Bubová T, Vrabec V, Kulma M & Nowicki P (2015) Land management impacts on European butterflies of conservation concern: a review. *Journal of Insect Conservation* **19**, 805–821.

Burgess MD, Smith KW, Evans KL, Leech D, Pearce-Higgins JW, Branston CJ, Briggs K, Clark JR, du Feu CR, Lewthwaite K, Nager RG, Sheldon BC, Smith JA, Whytock RC, Willis SG & Phillimore AB (2018) Tritrophic phenological match–mismatch in space and time. *Nature Ecology & Evolution* **2**, 970–975.

Burns F, August T, Eaton M, Noble D, Powney G, Isaac N & Hayhow D (2019). UK Biodiversity Indicators 2019 C4a. Status of UK priority species: relative abundance technical background document.

http://data.jncc.gov.uk/data/1f47d611-dbfc-421a-bc26b019433306d1/UKBI2019-F-C4a.pdf (accessed 22 November 2019).

Burns F, Eaton MA, Barlow KE, Beckmann BC, Brereton T, Brooks DR, Brown PM, Al Fulaij N, Gent T, Henderson I, Noble DG, Parsons M, Powney GD, Roy HE, Stroh P, Walker K, Wilkinson JW, Wotton SR & Gregory RD (2016) Agricultural management and climatic change are the major drivers of biodiversity change in the UK. *PLoS One* **11**, e0151595. Burns F, Eaton MA, Hayhow DB, Outhwaite CL, Al Fulaij N, August TA, Boughey KL, Brereton T, Brown A, Bullock DJ, Gent T, Haysom KA, Isaac N JB, Johns DG, Macadam CR, Mathews F, Noble DG, Powney GD, Sims DW, Smart SM, Stroh P, Walker KJ, Webb JR, Webb TJ & Gregory RD (2018) An assessment of the state of nature in the United Kingdom: A review of findings, methods and impact. *Ecological Indicators* **94**, 226–236.

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque J-F, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Hernández Morcillo M, Oldfield TEE, Pauly D, Quader S Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié J-C & Watson R (2010) Global biodiversity: indicators of recent declines. *Science* **328**. 1164–1168.

Butchart SHM, Stattersfield AJ, Baillie J, Bennun LA, Stuart SN, Akçakaya HR, Hilton-Taylor C & Mace GM (2005) Using Red List indices to measure progress towards the 2010 target and beyond. *Philosophical Transactions of the Royal Society B* **360**, 255–268.

Callaghan CT, Rowley JJL, Cornwell WK, Poore AGB & Major RE (2019) Improving big citizen science data: Moving beyond haphazard sampling. *PLoS Biology* **17**, e3000357.

Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF & Griswold TL (2011) Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the USA* **108**, 662–667.

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS & Naeem S (2012) Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67.

Cardinale BJ, Gonzalez A, Allington GR & Loreau M (2018) Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. *Biological Conservation* **219**,175–183.

Cardoso P, Borges PAV, Triantis KA, Ferrández MA & Martín JL (2011b) Adapting the IUCN Red List criteria for invertebrates. *Biological Conservation* **144**, 2432–2440.

Cardoso P, Erwin TL, Borges PAV & New TR (2011a) The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* **144**, 2647–2655.

Carvalheiro LG, Kunin WE, Keil P, Aguirre-Gutiérrez J, Ellis WN, Fox R, Groom Q, Hennekens S, Van Landuyt W, Maes D, Van de Meutter F, Michez D, Rasmont P, Ode B, Potts SG, Reemer M, Roberts SPM, Schaminée J, WallisDeVries MF & Biesmeijer JC (2013) Species richness declines and biotic homogenization have slowed down for NW-European pollinators and plants. *Ecology Letters* **16**, 870–878.

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM & Palmer TM (2015) Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances* **1**, e1400253.

Ceballos G, Ehrlich PR & Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the USA* **114**, E6089–E6096.

Chagnon M, Kreutzweiser D, Mitchell EAD, Morrissey CA, Noome DA & Van der Sluijs JP (2015) Risks of large-scale use of systemic insecticides to ecosystem functioning and services. *Environmental Science and Pollution Research* **22**, 119–134.

Chandler M, See L, Copas K, Bonde AMZ, Claramunt López B, Danielsen F, Kristoffer Legind J, Masinde S, Miller-Rushing AJ, Newman G, Rosemartin A & Turak E (2017) Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation* **213**, 280–294.

Chapin III FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC & Díaz S (2000) Consequences of changing biodiversity. *Nature* **405**, 234–242. Chase SK & Levine A (2016) A framework for evaluating and designing citizen science programs for natural resources monitoring. *Conservation Biology* **30**, 456–466.

Chen I-C, Hill JK, Shiu H-J, Holloway JD, Benedick S, Chey VK, Barlow HS & Thomas CD (2011) Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Global Ecology and Biogeography* **20**, 34–45.

Clark JA & May RM (2002) Taxonomic bias in conservation research. *Science* **297**, 191–192.

Clausnitzer V, Kalkman VJ, Ram M, Collen B, Baillie JEM, Bedjanič M, Darwall WRT, Dijkstra K-DB, Dow R, Hawking J, Karube H, Malikova E, Paulson D, Schütte K, Suhling F, Villanueva RJ, von Ellenrieder N & Wilson K (2009) Odonata enter the biodiversity crisis debate: The first global assessment of an insect group. *Biological Conservation* **142**, 1864–1869.

Clavel J, Julliard R & Devictor V (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* **9**, 222–228.

Cohen JM, Lajeunesse MJ & Rohr JR (2018) A global synthesis of animal phenological responses to climate change. *Nature Climate Change* **8**, 224–228.

Collen B, Böhm M, Kemp R & Baillie JEM (2012) *Spineless: status and trends of the world's invertebrates*. Zoological Society of London, London, UK.

Collen B, Dulvy NK, Gaston KJ, Gärdenfors U, Keith DA, Punt AE, Regan HM, Böhm M, Hedges S, Seddon M, Butchart SHM, Hilton-Taylor C, Hoffmann M, Bachman SP & Akçakaya HR (2016) Clarifying misconceptions of extinction risk assessment with the IUCN Red List. *Biology Letters* **12**, 20150843.

Collen B, Ram M, Zamin T & McRae L (2008) The tropical biodiversity data gap: addressing disparity in global monitoring. *Tropical Conservation Science* **1**, 75–88.

Connors BM, Cooper AB, Peterman RM & Dulvy NK (2014) The false classification of extinction risk in noisy environments. *Proceedings of the Royal Society B* **281**, 20132935.

Conrad KF, Fox R & Woiwod IP (2007) Monitoring biodiversity: measuring longterm changes in insect abundance. *Insect Conservation Biology*, (ed. AJA Stewart, TR New & OT Lewis), pp. 203–225. CABI publishing, Wallingford, UK.

Conrad KF, Warren M, Fox R, Parsons M & Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation* **132**, 279–291.

Conrad KF, Woiwod IP, Parsons M, Fox R & Warren M (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation* **8**, 119–136.

Conrad KF, Woiwod IP & Perry JN (2002) Long-term decline in abundance and distribution of the garden tiger moth (*Arctia caja*) in Great Britain. *Biological Conservation* **106**, 329–337.

Coventry PA, Neale C, Dyke A, Pateman R & Cinderby S (2019) The mental health benefits of purposeful activities in public green spaces in urban and semi-urban neighbourhoods: a mixed-methods pilot and proof of concept study. *International Journal of Environmental Research and Public Health* **16**, 2712.

Danielsen F, Pirhofer-Walzl K, Adrian TP, Kapijimpanga DR, Burgess ND, Jensen PM, Bonney R, Funder M, Landa A, Levermann N & Madsen J (2014) Linking public participation in scientific research to the indicators and needs of international environmental agreements. *Conservation Letters* **7**, 12–24.

Defra (2019) *UK Biodiversity Indicators 2019*. Department for Environment, Food and Rural Affairs, London, UK.

Deguines N, Julliard R, De Flores M & Fontaine C (2016) Functional homogenization of flower visitor communities with urbanization. *Ecology and Evolution* **6**, 1967–1976.

Deikumah J, McAlpine CA & Maron M (2014) Biogeographical and taxonomic biases in tropical forest fragmentation research. *Conservation Biology* **28**, 1522–1531.

de longh HH & Bal D (2007) Harmonization of Red Lists in Europe: some lessons learned in the Netherlands when applying the new IUCN Red List Categories and Criteria version 3.1. *Endangered Species Research* **3**, 53–60.

Denerley C, Redpath SM, Wal R, Newson SE, Chapman JW & Wilson JD (2019) Breeding ground correlates of the distribution and decline of the Common Cuckoo *Cuculus canorus* at two spatial scales. *Ibis* **161**, 346–358.

Dennis EB, Brereton TM, Morgan BJT, Fox R, Shortall CR, Prescott T & Foster S (2019) Trends and indicators for quantifying moth abundance and occupancy in Scotland. *Journal of Insect Conservation* **23**, 369–380.

Dennis EB, Freeman SN, Brereton T & Roy DB (2013) Indexing butterfly abundance whilst accounting for missing counts and variability in seasonal pattern. *Methods in Ecology and Evolution* **4**, 637–645.

Dennis EB, Morgan BJT, Brereton TM, Roy DB & Fox R (2017b) Using citizen science butterfly counts to predict species population trends. *Conservation Biology* **31**, 1350–1361.

Dennis EB, Morgan BJ, Freeman SN, Brereton TM & Roy DB (2016) A generalized abundance index for seasonal invertebrates. *Biometrics* **72**, 1305–1314.

Dennis EB, Morgan BJT, Freeman SN, Ridout MS, Brereton TM, Fox R, Powney GD & Roy DB (2017a) Efficient occupancy model-fitting for extensive citizen-science data. *PLoS One* **12**, e0174433.

Dennis EB, Morgan BJT, Roy DB & Brereton TM (2017c) Urban indicators for UK butterflies. *Ecological Indicators* **76**, 184–193.

d'Eon-Eggertson F, Dulvy NK & Peterman RM (2015) Reliable identification of declining populations in an uncertain world. *Conservation Letters* **8**, 86–96.

de Sassi C, Lewis OT & Tylianakis JM (2012) Plant-mediated and nonadditive effects of two global change drivers on an insect herbivore community. *Ecology* **93**, 1892–1901.

Devictor V, Van Swaay C, Brereton T, Brotons L, Chamberlain D, Heliölä J, Herrando S, Julliard R, Kuussaari M, Lindström Å, Reif J, Roy DB, Schweiger O, Settele J, Stefanescu C, Van Strien A, Van Turnhout C, Vermouzek Z, WallisDeVries M, Wynhoff I & Jiguet F (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change* **2**, 121– 124. De Vos JM, Joppa LN, Gittleman JL, Stephens PR & Pimm SL (2015) Estimating the normal background rate of species extinction. *Conservation Biology* **29**, 452–462.

Díaz S, Settele J, Brondízio ES, Ngo HT, Agard J, Arneth A, Balvanera P, Brauman KA, Butchart SHM, Chan KMA, Garibaldi LA, Ichii K, Liu J, Subramanian SM, Midgley GF, Miloslavich P, Molnár Z, Obura D, Pfaff A, Polasky S, Purvis A, Razzaque J, Reyers B, Roy Chowdhury R, Shin Y-J, Visseren-Hamakers I, Willis KJ & Zayas CN (2019) Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* **366**, eaax3100.

Dickinson JL, Shirk J, Bonter D, Bonney R, Crain RL, Martin J, Phillips T & Purcell K (2012) The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment* **10**, 291–297.

Di Marco M, Chapman S, Althor G, Kearney S, Besancon C, Butt N, Maina JM, Possingham HP, Rogalla von Bieberstein K, Venter O & Watson JEM (2017) Changing trends and persisting biases in three decades of conservation science. *Global Ecology and Conservation* **10**, 32–42.

Diniz-Filho JA, De Marco PJr & Hawkins BA (2010) Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity* **3**, 172–179.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB & Collen B (2014) Defaunation in the Anthropocene. *Science* **345**, 401–406.

Domroese MC & Johnson EA (2017) Why watch bees? Motivations of citizen science volunteers in the Great Pollinator Project. *Biological Conservation* **208**, 40–47.

Dornelas M, Gotelli NJ, Shimadzu H, Moyes F, Magurran AE & McGill BJ (2019) A balance of winners and losers in the Anthropocene. *Ecology Letters* **22**, 847–854.

Dunn RR (2005) Modern insect extinctions, the neglected majority. *Conservation Biology* **19**, 1030–1036.

Eaton MA, Burns F, Isaac NJB, Gregory RD, August TA, Barlow KE, Brereton T, Brooks DR, Al Fulaij N, Haysom KA, Noble DG, Outhwaite C, Powney GD, Procter D & Williams J (2015) The priority species indicator: measuring the trends in threatened species in the UK. *Biodiversity* **16**, 108–119.

Eisenhauer N, Bonn A & Guerra CA (2019) Recognizing the quiet extinction of invertebrates. *Nature Communications* **10**, 50.

Ellis S, Wainwright D, Dennis EB, Bourn NA, Bulman CR, Hobson R, Jones R, Middlebrook I, Plackett J, Smith RG & Wain M (2019) Are habitat changes driving the decline of the UK's most threatened butterfly: the High Brown Fritillary *Argynnis adippe* (Lepidoptera: Nymphalidae)? *Journal of Insect Conservation* **23**, 351–367.

Eskildsen A, Carvalheiro LG, Kissling WD, Biesmeijer JC, Schweiger O & Høye TT (2015) Ecological specialization matters: long-term trends in butterfly species richness and assemblage composition depend on multiple functional traits. *Diversity and Distributions* **21**, 792–802.

Farley SS, Dawson A, Goring SJ & Williams JW (2018) Situating ecology as a big-data science: current advances, challenges, and solutions. *BioScience* **68**, 563–576.

Fartmann T, Müller C & Poniatowski D (2013) Effects of coppicing on butterfly communities of woodlands. *Biological Conservation* **159**, 396–404.

ffrench-Constant RH, Somers-Yeates R, Bennie J, Economou T, Hodgson D, Spalding A & McGregor PK (2016) Light pollution is associated with earlier tree budburst across the United Kingdom. *Proceedings of the Royal Society B* **283**, 20160813.

Follett R & Strezov V (2015) An analysis of citizen science based research: usage and publication patterns. *PLoS One* **10**, e0143687.

Fonseca CR (2009) The silent mass extinction of insect herbivores in biodiversity hotspots. *Conservation Biology* **23**, 1507–1515.

Forister ML, Cousens B, Harrison JG, Anderson K, Thorne JH, Waetjen D, Nice CC, De Parsia M, Hladik ML, Meese R & van Vliet H (2016) Increasing

neonicotinoid use and the declining butterfly fauna of lowland California. *Biology Letters* **12**, 20160475.

Forister ML, Pelton EM & Black SH (2019) Declines in insect abundance and diversity: We know enough to act now. *Conservation Science and Practice* **1**, e80.

Fox R, Brereton TM, Asher J, August TA, Botham MS, Bourn NAD, Cruickshanks KL, Bulman CR, Ellis S, Harrower CA, Middlebrook I, Noble DG, Powney GD, Randle Z, Warren MS & Roy DB (2015) *The State of the UK's Butterflies 2015*. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, UK.

Fox R, Oliver TH, Harrower C, Parsons MS, Thomas CD & Roy DB (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land use changes. *Journal of Applied Ecology* **51**, 949–957.

Fox R, Parsons MS, Chapman JW, Woiwod IP, Warren MS & Brooks DR (2013) *The State of Britain's Larger Moths 2013*. Butterfly Conservation and Rothamsted Research, Wareham, UK.

Fox R, Randle Z, Hill L, Anders S, Wiffen L & Parsons MS (2011a) Moths Count: recording moths for conservation in the UK. *Journal of Insect Conservation* **15**, 55–68.

Fox R, Warren MS, Brereton TM, Roy DB & Robinson A (2011b) A new red list of British butterflies. *Insect Conservation and Diversity* **4**, 159–172.

Franco AMA, Hill JK, Kitschke C, Collingham YC, Roy DB, Fox R, Huntley B & Thomas CD (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* **12**, 1545–1553.

Freeman SN, Noble DG, Newson SE & Baillie SR (2007) Modelling population changes using data from different surveys: the Common Birds Census and the Breeding Bird Survey. *Bird Study* **54**, 61–72.

Froidevaux JSP, Broyles M & Jones G (2019) Moth responses to sympathetic hedgerow management in temperate farmland. *Agriculture, Ecosystems & Environment* **270–271**, 55–64.

Fuentes-Montemayor E, Goulson D & Park K (2011) The effectiveness of agrienvironment schemes for the conservation of farmland moths: assessing the importance of a landscape-scale management approach. *Journal of Applied Ecology* **48**, 532–542.

Gallai N, Salles JM, Settele J & Vaissiere BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics* **68**, 810–821.

Ganzevoort W, van den Born RJG, Halffman W & Turnhout S (2017) Sharing biodiversity data: citizen scientists' concerns and motivations. *Biodiversity and Conservation* **26**, 2821–2837.

Garbuzov M, Fensome KA & Ratnieks FL (2015) Public approval plus more wildlife: twin benefits of reduced mowing of amenity grass in a suburban public park in Saltdean, UK. *Insect Conservation and Diversity* **8**, 107–119.

Gardiner MM, Allee LL, Brown PM, Losey JE, Roy HE & Smyth RR (2012) Lessons from lady beetles: accuracy of monitoring data from US and UK citizen-science programs. *Frontiers in Ecology and the Environment* 10, 471– 476.

Gaston KJ (2018) Lighting up the nighttime. Science 362, 744-746.

Gaston KJ & Fuller RA (2008) Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution* **23**, 14–19.

Gibbons DW, Donald PF, Bauer H-G, Fornasari L & Dawson IK (2007) Mapping avian distributions: the evolution of bird atlases. *Bird Study* **54**, 324–334.

Gilburn AS, Bunnefeld N, Wilson J, Botham MS, Brereton T, Fox R & Goulson D (2015) Are neonicotinoid insecticides driving declines of widespread butterflies? *PeerJ* **3**, e1402.

Gillingham PK, Alison J, Roy DB, Fox R & Thomas CD (2015) High abundances of species in protected areas in parts of their geographic distributions colonised during a recent period of climatic change. *Conservation Letters* **8**, 97–106.

Gossner MM, Lewinsohn TM, Kahl T, Grassein F, Boch S, Prati D, Birkhofer K, Renner SC, Sikorski J, Wubet T, Arndt H, Baumgartner V, Blaser S, Blüthgen N, Börschig C, Buscot F, Diekötter T, Ré Jorge L, Jung K, Keyel AC, Klein A-M, Klemmer S, Krauss J, Lange M, Müller J, Overmann J, Pašalić E, Penone C, Perović DJ, Purschke O, Schall P, Socher SA, Sonnemann I, Tschapka M, Tscharntke T, Türke M, Venter PC, Weiner CN, Werner M, Wolters V, Wurst S, Westphal C, Fischer M, Weisser WW & Allan E (2016) Land-use intensification causes multitrophic homogenization of grassland communities. *Nature* **540**, 266–269.

Grenis K & Murphy SM (2019) Direct and indirect effects of light pollution on the performance of an herbivorous insect. *Insect Science* **26**, 770–776.

Gripenberg S, Hamer N, Brereton T, Roy DB & Lewis OT (2011) A novel parasitoid and a declining butterfly: cause or coincidence? *Ecological Entomology* **36**, 271–281.

Groenendijk D & Ellis WN (2011) The state of the Dutch larger moth fauna. *Journal of Insect Conservation* **15**, 95–101.

Groom Q, Weatherdon L & Geijzendorffer IR (2017) Is citizen science an open science in the case of biodiversity observations? *Journal of Applied Ecology* 54, 612–617.

Gunnarsson B, Knez I, Hedblom M & Sang ÅO (2017) Effects of biodiversity and environment-related attitude on perception of urban green space. *Urban Ecosystems* **20**, 37–49.

Guo F, Lenoir J & Bonebrake TC (2018) Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications* **9**, 1315.

Habel JC, Samways MJ & Schmitt T (2019a) Mitigating the precipitous decline of terrestrial European insects: Requirements for a new strategy. *Biodiversity and Conservation* **28**, 1343–1360.

Habel JC, Trusch R, Schmitt T, Ochse M & Ulrich W (2019b) Long-term largescale decline in relative abundances of butterfly and burnet moth species across south-western Germany. *Scientific Reports* **9**, 14921.

Habel JC, Ulrich W, Biburger N, Seibold S & Schmitt T (2019c) Agricultural intensification drives butterfly decline. *Insect Conservation and Diversity* **12**, 289–295.

Hahn, M, Schotthöfer, A, Schmitz, J, Franke, LA & Brühl, CA (2015) The effects of agrochemicals on Lepidoptera, with a focus on moths, and their pollination service in field margin habitats. *Agriculture, Ecosystems & Environment* **207**, 153–162.

Hall DM, Camilo GR, Tonietto RK, Ollerton J, Ahrné K, Arduser M, Ascher JS, Baldock KC, Fowler R, Frankie G & Goulson D (2017) The city as a refuge for insect pollinators. *Conservation Biology* **31**, 24–29.

Halley JM, Monokrousos N, Mazaris AD, Newmark WD & Vokou D (2016) Dynamics of extinction debt across five taxonomic groups. *Nature Comm*unications **7**, 12283.

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D & de Kroon H (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* **12**, e0185809.

Hampton SE, Strasser CA, Tewksbury JJ, Gram WK, Budden AE, Batcheller AL, Duke CS & Porter JH (2013) Big data and the future of ecology. *Frontiers in Ecology and the Environment* **11**, 156–162.

Harmon J, Stephens E & Losey J (2007) The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. *Journal of Insect Conservation* **11**, 85–94.

Harvey JA, Heinen R, Armbrecht I, Basset Y, Baxter-Gilbert JH, Bezemer TM, Böhm M, Bommarco R, Borges PAV, Cardoso P, Clausnitzer V, Cornelisse T, Crone EE, Dicke M, Dijkstra K-DB, Dyer L, Ellers J, Fartmann T, Forister ML, Furlong MJ, Garcia-Aguayo A, Gerlach J, Gols R, Goulson D, Habel J-C, Haddad NM, Hallmann CA, Henriques S, Herberstein ME, Hochkirch A, Hughes AC, Jepsen S, Jones TH, Kaydan BM, Kleijn D, Klein A-M, Latty T, Leather SR, Lewis SM, Lister BC, Losey JE, Lowe EC, Macadam CR, Montoya-Lerma J, Nagano CD, Ogan S, Orr MC, Painting CJ, Pham T-H, Potts SG, Rauf A, Roslin TL, Samways MJ, Sanchez-Bayo F, Sar SA, Schultz CB, Soares AO, Thancharoen A, Tscharntke T, Tylianakis JM, Umbers KDL, Vet LEM, Visser ME, Vujic A, Wagner DL, WallisDeVries MF, Westphal C, White TE, Wilkins VL, Williams PH, Wyckhuys KAG, Zhu Z-R & de Kroon H (2020) International scientists formulate a roadmap for insect conservation and recovery. *Nature Ecology & Evolution* **4**, 174–176.

Hayhow DB, Eaton MA, Stanbury AJ, Burns F, Kirby WB, Bailey N, Beckmann B, Bedford J, Boersch-Supan PH, Coomber F, Dennis EB, Dolman SJ, Dunn E, Hall J, Harrower C, Hatfield JH, Hawley J, Haysom K, Hughes J, Johns DG, Mathews F, McQuatters-Gollop A, Noble DG, Outhwaite CL, Pearce-Higgins JW, Pescott OL, Powney GD & Symes N (2019) *The State of Nature 2019*. The State of Nature partnership, UK.

Haywood BK, Parrish JK & Dolliver J (2016) Place-based and data-rich citizen science as a precursor for conservation action. *Conservation Biology* **30**, 476–486.

Heath J, Pollard E & Thomas JA (1984) *Atlas of Butterflies in Britain and Ireland*. Viking, Harmondsworth, UK.

Herrando S, Brotons L, Anton M, Paramo F, Villero D, Titeux N, Quesada J & Stefanescu C (2016) Assessing impacts of land abandonment on Mediterranean biodiversity using indicators based on bird and butterfly monitoring data. *Environmental Conservation* **43**, 69–78.

Herrera CM (2019) Complex long-term dynamics of pollinator abundance in undisturbed Mediterranean montane habitats over two decades. *Ecological Monographs* **89**, e01338.

Hickling R, Roy DB, Hill JK, Fox R & Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**, 450–455.

Hill JK, Collingham YC, Thomas CD, Blakeley DS, Fox R, Moss D & Huntley B (2001) Impacts of landscape structure on butterfly range expansion. *Ecology Letters* **4**, 313–321.

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J & Huntley B (2002) Responses of butterflies to 20th century climate warming: implications for future ranges. *Proceedings of the Royal Society B* **269**, 2163–2171. Hill MO (2012) Local frequency as a key to interpreting species occurrence data when recording effort is not known. *Methods in Ecology and Evolution* **3**, 195–205.

Hillebrand H, Blasius B, Borer ET, Chase JM, Downing JA, Eriksson BK, Filstrup CT, Harpole WS, Hodapp D, Larsen S, Lewandowska AM, Seabloom EW, Van de Waal DB & Ryabov AB (2018) Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. *Journal of Applied Ecology* **55**, 169–184.

Hobbs SJ & White PCL (2012) Motivations and barriers in relation to community participation in biodiversity recording. *Journal for Nature Conservation* **20**, 364–373.

Hogeweg L, Zeegers T, Katramados I & Jongejans E (2019) Smart Insect Cameras. *Biodiversity Information Science and Standards* **3**, e39241.

IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES secretariat, Bonn, Germany.

Isaac NJB & Pocock MJO (2015) Bias and information in biological records. *Biological Journal of the Linnean Society* **115**, 522–531.

Isaac NJB, van Strien AJ, August TA, de Zeeuw MP & Roy DB (2014) Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution* **5**, 1052–1060.

Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES & Loreau M (2011) High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199–202.

IUCN (2012) *IUCN Red List Categories and Criteria. Version 3.1. 2nd Edition.* IUCN Species Survival Commission, Gland, Switzerland.

IUCN (2017) *Guidelines for Using the IUCN Red List Categories and Criteria. Version 13.* IUCN, Gland, Switzerland and Cambridge, UK. IUCN (2018) The IUCN Red List of Threatened Species. Version 2018-2. IUCN, Gland, Switzerland.

Jordan RC, Gray SA, Howe DV, Brooks WR & Ehrenfeld JG (2011) Knowledge gain and behavioral change in citizen-science programs. *Conservation Biology* **25**, 1148–1154.

Kalkman VJ, Boudot J-P, Bernard R, Conze KJ, De Knijf G, Dyatlova E, Ferreira S, Jović M, Ott J, Riservato E & Sahlén G (2010) *European Red List of dragonflies*. Publications Office of the European Union, Luxembourg.

Kearney MR, Briscoe NJ, Karoly DJ, Porter WP, Norgate M & Sunnucks P (2010) Early emergence in a butterfly causally linked to anthropogenic warming. *Biology Letters* **6**, 674–677.

Kelling S, Johnston A, Bonn A, Fink D, Ruiz-Gutierrez V, Bonney R, Fernandez M, Hochachka WM, Julliard R, Kraemer R & Guralnick R (2019) Using semistructured surveys to improve citizen science data for monitoring biodiversity. *BioScience* **69**, 170–179.

Kerr JT, Pindar A, Galpern P, Packer L, Potts SG, Roberts SM, Rasmont P, Schweiger O, Colla SR, Richardson LL, Wagner DL, Gall LF, Sikes DS & Pantoja A (2015) Climate change impacts on bumblebees converge across continents. *Science* **349**, 177–180.

Kleijn D, Winfree R, Bartomeus I, Carvalheiro LG, Henry M, Isaacs R, Klein A-M, Kremen C, M'Gonigle LK, Rader R, Ricketts TH, Williams NM, Lee Adamson N, Ascher JS, Báldi A, Batáry P, Benjamin F, Biesmeijer JC, Blitzer EJ, Bommarco R, Brand MR, Bretagnolle V, Button L, Cariveau DP, Chifflet R, Colville JF, Danforth BD, Elle E, Garratt MPD, Herzog F, Holzschuh A, Howlett BG, Jauker F, Jha S, Knop E, Krewenka KM, Le Féon V, Mandelik Y, May EA, Park MG, Pisanty G, Reemer M, Riedinger V, Rollin O, Rundlöf M, Sardiñas HS, Scheper J, Sciligo AR, Smith HG, Steffan-Dewenter I, Thorp R, Tscharntke T, Verhulst J, Viana BF, Vaissière BE, Veldtman R, Westphal C & Potts SG (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, **6**. 7414. Klop E, Omon B & WallisDeVries MF (2015) Impact of nitrogen deposition on larval habitats: the case of the Wall Brown butterfly *Lasiommata megera*. *Journal of Insect Conservation* **19**, 393–402.

Knop E, Zoller L, Ryser R, Gerpe C, Hörler M & Fontaine C (2017) Artificial light at night as a new threat to pollination. *Nature* **548**, 206–209.

Kobori H, Dickinson JL, Washitani I, Sakurai R, Amano T, Komatsu N, Kitamura W, Takagawa S, Koyama K, Ogawara T & Miller-Rushing AJ (2016) Citizen science: a new approach to advance ecology, education, and conservation. *Ecological Research* **31**, 1–19.

Koh LP, Dunn RR, Sodhi NS, Colwell RK, Proctor HC & Smith VS (2004) Species coextinctions and the biodiversity crisis. *Science* **305**, 1632–1634.

Kosmala M, Wiggins A, Swanson A & Simmons B (2016) Assessing data quality in citizen science. *Frontiers in Ecology and the Environment* **14**, 551–560.

Kurze S, Heinken T & Fartmann T (2017) Nitrogen enrichment of host plants has mostly beneficial effects on the life-history traits of nettle-feeding butterflies. *Acta Oecologica* **85**, 157–164.

Kurze S, Heinken T & Fartmann T (2018) Nitrogen enrichment in host plants increases the mortality of common Lepidoptera species. *Oecologia* **188**, 1227–1237.

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Rodà F, Stefanescu C, Teder T, Zobel M & Steffan-Dewenter I (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution* **24**, 564–571.

Lakeman-Fraser P, Gosling L, Moffat AJ, West SE, Fradera R, Davies L, Ayamba MA & van der Wal R (2016) To have your citizen science cake and eat it? Delivering research and outreach through Open Air Laboratories (OPAL). *BMC Ecology* **16**(Suppl 1), 57–70.

Lang BJ, Dixon PM, Klaver RW, Thompson JR & Widrlechner MP (2019) Characterizing urban butterfly populations: the case for purposive point-count surveys. *Urban Ecosystems* **22**, 1083–1096. Lawson CR, Bennie JJ, Thomas CD, Hodgson JA & Wilson RJ (2014) Active management of protected areas enhances metapopulation expansion under climate change. *Conservation Letters* **7**, 111–118.

Leather SR (2018) "Ecological Armageddon" – more evidence for the drastic decline in insect numbers. *Annals of Applied Biology* **172**, 1–3.

Lehikoinen A, Brotons L, Calladine J, Campedelli T, Escandell V, Flousek J, Grueneberg C, Haas F, Harris S, Herrando S, Husby M, Jiguet F, Kålås JA, Lindström Å, Lorrillière R, Molina B, Pladevall C, Calvi G, Sattler T, Schmid H, Sirkiä PM, Teufelbauer N & Trautmann S (2019) Declining population trends of European mountain birds. *Global Change Biology* **25**, 577–588.

Le Viol I, Jiguet F, Brotons L, Herrando S, Lindström Å, Pearce-Higgins JW, Reif J, Van Turnhout C & Devictor V (2012) More and more generalists: two decades of changes in the European avifauna. *Biology Letters* **8**, 780–782.

Lewandowski EJ & Oberhauser KS (2017) Butterfly citizen scientists in the United States increase their engagement in conservation. *Biological Conservation* **208**, 106–112.

Lewandowski E & Specht H (2015) Influence of volunteer and project characteristics on data quality of biological surveys. *Conservation Biology* **29**, 713–723.

Lewis OT & Senior MJM (2011) Assessing conservation status and trends for the world's butterflies: the Sampled Red List Index approach. *Journal of Insect Conservation* **15**, 121–128.

Lister BC & Garcia A (2018) Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences of the USA* **115**, E10397–E10406.

Losey JE & Vaughan M (2006) The economic value of ecological services provided by insects. *BioScience* **56**, 311–323.

Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Milner-Gulland EJ & Stuart SN (2008) Quantification of extinction risk: International Union for the Conservation of Nature's (IUCN) system for classifying threatened species. *Conservation Biology* **22**, 1424–1442. Macgregor CJ, Pocock MJO, Fox R & Evans DM (2015) Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review. *Ecological Entomology* **40**, 187–198.

Macgregor CJ, Pocock MJO, Fox R & Evans DM (2019b) Effects of street lighting technologies on the success and quality of pollination in a nocturnally pollinated plant. *Ecosphere* **10**, e02550.

Macgregor CJ, Thomas CD, Roy DB, Beaumont MA, Bell JR, Brereton T, Bridle JR, Dytham C, Fox R, Gotthard K, Hoffmann AA, Martin G, Middlebrook I, Nylin S, Platts PJ, Rasteiro R, Saccheri IJ, Villoutreix R, Wheat CW & Hill JK (2019c) Climate-induced phenology shifts linked to range expansions in species with multiple reproductive cycles per year. *Nature Communications* **10**, 1–10.

Macgregor CJ, Williams JH, Bell JR & Thomas CD (2019a) Moth biomass increases and decreases over 50 years in Britain. *Nature Ecology and Evolution* **3**, 1645–1649.

Maclean IMD & Wilson RJ (2011) Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences of the USA* **108**, 12337–12342.

MacLean SA & Beissinger SR (2017) Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. *Global Change Biology* **23**, 4094–4105.

Maes D, Verovnik R, Wiemers M, Brosens D, Beshkov S, Bonelli S, Buszko J, Cantú-Salazar L, Cassar L-F, Collins S, Dincă V, Djuric M, Dušej G, Elven H, Franeta F, Garcia-Pereira P, Geryak Y, Goffart P, Gór A, Hiermann U, Höttinger H, Huemer P, Jakšić P, John E, Kalivoda H, Kati V, Kirkland P, Komac B, Kőrösi A, Kulak A, Kuussaari M, L'Hoste L, Lelo S, Mestdagh X, Micevski N, Mihoci I, Mihut S, Monasterio-León Y, Morgun DV, Munguira ML, Murray T, Stadel Nielsen P, Ólafsson E, Õunap E, Pamperis LN, Pavlíčko A, Pettersson LB, Popov S, Popović M, Pöyry J, Prentice M, Reyserhove L, Ryrholm N, Šašić M, Savenkov N, Settele J, Sielezniew M, Sinev S, Stefanescu C, Švitra G, Tammaru T, Tiitsaar A, Tzirkalli E, Tzortzakaki O, van Swaay CAM, Lykke Viborg A, Wynhoff I, Zografou K & Warren MS (2019) Integrating national Red Lists for prioritising conservation actions for European butterflies. *Journal of Insect Conservation* **23**, 301–330.

Mair L, Hill JK, Fox R, Botham M, Brereton T & Thomas CD (2014) Abundance changes and habitat availability drive species' responses to climate change. *Nature Climate Change* **4**, 127–131.

Majerus MEN (2002) Moths. HarperCollins Publishers, London, UK.

Manfrin A, Singer G, Larsen S, Weiß N, van Grunsven RHA, Weiß N-S, Wohlfahrt S, Monaghan MT & Hölker F (2017) Artificial light at night affects organism flux across ecosystem boundaries and drives community structure in the recipient ecosystem. *Frontiers in Environmental Science* **5**, 61.

Mangels J, Fiedler K, Schneider FD & Blüthgen N (2017) Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists. *Biodiversity and Conservation* **26**, 3385–3405.

Mantyka-pringle CS, Martin TG & Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and metaanalysis. *Global Change Biology* **18**, 1239–1252.

Martay B, Brewer MJ, Elston DA, Bell JR, Harrington R, Brereton TM, Barlow KE, Botham MS & Pearce-Higgins JW (2017) Impacts of climate change on national biodiversity population trends. *Ecography* **40**, 1139–1151.

Mason SC, Palmer G, Fox R, Gillings S, Hill JK, Thomas CD & Oliver TH (2015) Geographical range margins of a wide range of taxonomic groups continue to shift polewards. *Biological Journal of the Linnean Society* **115**, 586–597.

Mattila N, Kaitala V, Komonen A, Kotiaho JS & Päivinen J (2006) Ecological determinants of distribution decline and risk of extinction in moths. *Conservation Biology* **20**,1161–1168.

McAfee D, Doubleday ZA, Geiger N & Connell SD (2019) Everyone loves a success story: optimism inspires conservation engagement. *BioScience* **69**, 274–281.

McCain C, Szewczyk T & Bracy Knight K (2016) Population variability complicates the accurate detection of climate change responses. *Global Change Biology* **22**, 2081–2093.

McDermott Long O, Warren R, Price J, Brereton TM, Botham MS & Franco AM (2017) Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? *Journal of Animal Ecology* **86**, 108–116.

McGill BJ, Dornelas M, Gotelli NJ & Magurran AE (2015) Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Evolution* **30**, 104–113.

McKinley DC, Miller-Rushing AJ, Ballard HL, Bonney R, Brown H, Cook-Patton SC, Evans DM, French RA, Parrish JK, Phillips TB, Ryan SF, Shanley LA, Shirk JL, Stepenuck KF, Weltzin JF, Wiggins A, Boyle OD, Briggs RD, Chapin III SF, Hewitt DA, Preuss PW & Soukup MA (2017) Citizen science can improve conservation science, natural resource management, and environmental protection. *Biological Conservation* **208**, 15–28.

McKinney ML (1999) High rates of extinction and threat in poorly studied taxa. *Conservation Biology* **13**, 1273–1281.

McKinney ML & Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* **14**, 450–453.

Merckx T (2015) Rewilding: pitfalls and opportunities for moths and butterflies. *Rewilding European Landscapes*, (ed. HM Pereira & LM Navarro), pp. 107–125. Springer, Cham, Switzerland.

Merckx T, Souffreau C, Kaiser A, Baardsen LF, Backeljau T, Bonte D, Brans KI, Cours M, Dahirel M, Debortoli N, de Wolf K, Engelen JMT, Fontaneto D, Gianuca AT, Govaert L, Hendrickx F, Higuti J, Lens L, Martens K, Matheve H, Matthysen E, Piano E, Sablon R, Schön I, van Doninck K, de Meester L & van Dyck H (2018) Body-size shifts in aquatic and terrestrial urban communities. *Nature* **558**, 113–116.

Merckx T & Van Dyck H (2019) Urbanization-driven homogenization is more pronounced and happens at wider spatial scales in nocturnal and mobile flying insects. *Global Ecology and Biogeography* **28**, 1440–1455.

Merenlender AM, Crall AW, Drill S, Prysby M & Ballard H (2016) Evaluating environmental education, citizen science, and stewardship through naturalist programs. *Conservation Biology* **30**, 1255–1265. Miller JR (2005) Biodiversity conservation and the extinction of experience. *Trends in Ecology & Evolution* **20**, 430–434.

Miller-Rushing A, Primack R & Bonney R (2012) The history of public participation in ecological research. *Frontiers in Ecology and the Environment* **10**, 285–290.

Molina-Martínez A, León-Cortés JL, Regan HM, Lewis OT, Navarrete D, Caballero U & Luis-Martínez A (2016) Changes in butterfly distributions and species assemblages on a Neotropical mountain range in response to global warming and anthropogenic land use. *Diversity and Distributions* **22**, 1085– 1098.

Montgomery GA, Dunn RR, Fox R, Jongejans E, Leather SR, Saunders ME, Shortall CR, Tingley MW & Wagner DL (2020) Is the insect apocalypse upon us? How to find out. *Biological Conservation* **241**, 108327.

Mora C, Tittensor DP, Adl S, Simpson AGB & Worm B (2011) How many species are there on Earth and in the ocean? *PLoS Biology* **9**, e1001127.

Muratet A & Fontaine B (2015) Contrasting impacts of pesticides on butterflies and bumblebees in private gardens in France. *Biological Conservation* **182**, 148–154.

Newbold T, Adams GL, Albaladejo Robles G, Boakes EH, Braga Ferreira G, Chapman AS, Etard A, Gibb R, Millard J, Outhwaite CL & Williams JJ (2019) Climate and land-use change homogenise terrestrial biodiversity, with consequences for ecosystem functioning and human well-being. *Emerging Topics in Life Sciences* **3**, 207–219.

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Borger L, Bennett DJ, Choimes A, Collen B, Day J, De Palma A, Diaz S, Echeverria-Londono S, Edgar MJ, Feldman A, Garon M, Harrison MLK, Alhusseini T, Ingram DJ, Itescu Y, Kattge J, Kemp V, Kirkpatrick L, Kleyer M, Correia DLP, Martin CD, Meiri S, Novosolov M, Pan Y, Phillips HRP, Purves DW, Robinson A, Simpson J, Tuck SL, Weiher E, White HJ, Ewers RM, Mace GM, Scharlemann JPW & Purvis A (2015) Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50.

Nieto A, Roberts SPM, Kemp J, Rasmont P, Kuhlmann M, García Criado M, Biesmeijer JC, Bogusch P, Dathe HH, De la Rúa P, De Meulemeester T, Dehon M, Dewulf A, Ortiz-Sánchez FJ, Lhomme P, Pauly A, Potts SG, Praz C, Quaranta M, Radchenko VG, Scheuchl E, Smit J, Straka J, Terzo M, Tomozii B, Window J & Michez D (2014) *European Red List of bees*. Publications Office of the European Union, Luxembourg.

Nijssen ME, WallisDeVries MF & Siepel H (2017) Pathways for the effects of increased nitrogen deposition on fauna. *Biological Conservation* **212**, 423–431.

Nilsson SG, Franzén M & Pettersson L (2013) Land-use changes, farm management and the decline of butterflies associated with semi-natural grasslands in southern Sweden. *Nature Conservation* **6**, 31–48.

Norberg A, Abrego N, Blanchet FG, Adler FR, Anderson BJ, Anttila J, Araújo MB, Dallas T, Dunson D, Elith J, Foster SD, Fox R, Franklin J, Godsoe W, Guisan A, O'Hara B, Hill NA, Holt RD, Hui FKC, Husby M, Kålås JA, Lehikoinen A, Luoto M, Mod HK, Newell G, Renner I, Roslin T, Soininen J, Thuiller W, Vanhatalo J, Warton D, White M, Zimmermann NE, Gravel D & Ovaskainen O (2019) A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels. *Ecological Monographs* **89**, e01370.

Northrup JM, Rivers JW, Yang Z & Betts MG (2019) Synergistic effects of climate and land-use change influence broad-scale avian population declines. *Global Change Biology* **25**, 1561–1575.

Öckinger E, Hammarstedt O, Nilsson SG & Smith HG (2006) The relationship between local extinctions of grassland butterflies and increased soil nitrogen levels. *Biological Conservation* **128**, 564–573.

Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, Petersen JD, Pöyry J, Settele J, Summerville KS & Bommarco R (2010) Lifehistory traits predict species responses to habitat area and isolation: a crosscontinental synthesis. *Ecology Letters* 13, 969–979.

Oliver TH, Isaac NJB, August TA, Woodcock BA, Roy DB & Bullock JM (2015a) Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications* **6**, 10122. Oliver TH, Marshall HH, Morecroft MD, Brereton T, Prudhomme C & Huntingford C (2015b) Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change* **5**, 941– 945.

Outhwaite CL, Powney GD, August TA, Chandler RE, Rorke S, Pescott OL, Harvey M, Roy HE, Fox R, Roy DB, Alexander K, Ball S, Bantock T, Barber T, Beckmann BC, Cook T, Flanagan J, Fowles A, Hammond P, Harvey P, Hepper D, Hubble D, Kramer J, Lee P, MacAdam C, Morris R, Norris A, Palmer S, Plant CW, Simkin J, Stubbs A, Sutton P, Telfer M, Wallace I & Isaac NJB (2019) Annual estimates of occupancy of bryophytes, lichens and invertebrates in the UK, 1970–2015. *Scientific Data* **6**, 259.

Owens ACS & Lewis SM (2018) The impact of artificial light at night on nocturnal insects: A review and synthesis. *Ecology and Evolution* **8**, 11337–11358.

Pagel J, Anderson BJ, O'Hara RB, Cramer W, Fox R, Jeltsch F, Roy DB, Thomas CD & Schurr FM (2014) Quantifying range-wide variation in population trends from local abundance surveys and widespread opportunistic occurrence records. *Methods in Ecology and Evolution* **5**, 751–760.

Palmer G, Platts PJ, Brereton T, Chapman JW, Dytham C, Fox R, Pearce-Higgins JW, Roy DB, Hill JK & Thomas CD (2017) Climate change, climatic variation and extreme biological responses. *Philosophical Transactions of the Royal Society B* **372**, 20160144.

Pardo I, Pata MP, Gómez D & García MB (2013) A novel method to handle the effect of uneven sampling effort in biodiversity databases. *PLoS One* **8**, e52786.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**, 637–369.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Laila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA & Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579–583. Parsons M (2010) The changing moth and butterfly fauna of Britain – the first decade of the twenty-first century (2000–2009). *Entomologist's Record and Journal of Variation* **122**, 13–22.

Pearce-Higgins JW, Baillie SR, Boughey K, Bourn NAD, Foppen RPB, Gillings S, Gregory RD, Hunt T, Jiguet F, Lehikoinen A, Musgrove AJ, Robinson RA, Roy DB, Siriwardena GM, Walker KJ & Wilson JD (2018) Overcoming the challenges of public data archiving for citizen science biodiversity recording and monitoring schemes. *Journal of Applied Ecology* **55**, 2544–2551.

Pearce-Higgins JW, Beale CM, Oliver TH, August TA, Carroll M, Massimino D, Ockendon N, Savage J, Wheatley CJ, Ausden MA, Bradbury RB, Duffield SJ, Macgregor NA, McClean CJ, Morecroft MD, Thomas CD, Watts O, Beckmann BC, Fox R, Roy HE, Sutton PG, Walker KJ & Crick HQP (2017) A national-scale assessment of climate change impacts on species: assessing the balance of risks and opportunities for multiple taxa. *Biological Conservation* **213**, 124–134.

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Rashid Sumaila U & Walpole M (2010) Scenarios for global biodiversity in the 21st century. *Science* **330**, 1496–1501.

Pescott OL, Simkin JM, August TA, Randle Z, Dore AJ & Botham MS (2015) Air pollution and its effects on lichens, bryophytes, and lichen-feeding Lepidoptera: review and evidence from biological records. *Biological Journal of the Linnean Society* **115**, 611–635.

Pfeifer M, Lefebvre V, Peres CA, Banks-Leite C, Wearn OR, Marsh CJ, Butchart SHM, Arroyo-Rodríguez V, Barlow J, Cerezo A, Cisneros L, D'Cruze N, Faria D, Hadley A, Harris SM, Klingbeil BT, Kormann U, Lens L, Medina-Rangel GF, Morante-Filho JC, Olivier P, Peters SL, Pidgeon A, Ribeiro DB, Scherber C, Schneider-Maunoury L, Struebig M, Urbina-Cardona N, Watling JI, Willig MR, Wood EM & Ewers RM (2017) Creation of forest edges has a global impact on forest vertebrates. *Nature* **551**, 187–191.

Pillai P & Gouhier TC (2019) Not even wrong: The spurious measurement of biodiversity's effects on ecosystem functioning. *Ecology* **100**, e02645.

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM & Sexton JO (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246752.

Pimm SL, Russell GJ, Gittleman JL & Brooks TM (1995) The future of biodiversity. *Science* **269**, 347–350.

Pisa LW, Amaral-Rogers V, Belzunces LP, Bonmatin JM, Downs CA, Goulson D, Kreutzweiser DP, Krupke C, Liess M, McField M, Morrissey CA, Noome DA, Settele J, Simon-Delso N, Stark JD, Van der Sluijs JP, Van Dyck H & Wiemers M (2015) Effects of neonicotinoids and fipronil on non-target invertebrates. *Environmental Science and Pollution Research* **22**, 68–102.

Platts PJ, Mason SC, Palmer G, Hill JK, Oliver TH, Powney GD, Fox R & Thomas CD (2019) Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. *Scientific Reports* **9**, 15039.

Pocock MJO, Chandler M, Bonney R, Thornhill I, Albin A, August T, Bachman S, Brown PMJ, Gasparini Fernandes Cunha D, Grez A, Jackson C, Peters M, Romer Rabarijaon N, Roy HE, Zaviezo T & Danielsen F (2018) A vision for global biodiversity monitoring with citizen science. *Advances in Ecological Research* **59**, 169–223.

Pocock MJO, Roy HE, Preston CD & Roy DB (2015) The Biological Records Centre: a pioneer of citizen science. *Biological Journal of the Linnean Society* **115**, 475–493.

Pocock MJO, Tweddle JC, Savage J, Robinson LD & Roy HE (2017) The diversity and evolution of ecological and environmental citizen science. *PLoS One* **12**, e0172579.

Pollard E (1977) A method for assessing changes in the abundance of butterflies. *Biological Conservation* **12**, 115–134.

Pollard E & Yates TJ (1993) *Monitoring Butterflies for Ecology and Conservation*. Chapman & Hall, London, UK.

Powney GD, Carvell C, Edwards M, Morris RKA, Roy HE, Woodcock BA & Isaac NJB (2019) Widespread losses of pollinating insects in Britain. *Nature Communications* **10**, 1018.

Powney GD & Isaac NJB (2015) Beyond maps: a review of the applications of biological records. *Biological Journal of the Linnean Society* **115**, 532–542.

Pöyry J, Carvalheiro LG, Heikkinen RK, Kühn I, Kuussaari M, Schweiger O, Valtonen A, van Bodegom PM & Franzén M. (2017) The effects of soil eutrophication propagate to higher trophic levels. *Global Ecology and Biogeography* 26, 18–30.

Pöyry J, Leinonen R, Söderman G, Nieminen M, Heikkinen RK & Carter TR (2011) Climate-induced increase of moth multivoltinism in boreal regions. *Global Ecology and Biogeography* **20**, 289–298.

Prosser RS, Anderson JC, Hanson ML, Solomon KR & Sibley PK (2016) Indirect effects of herbicides on biota in terrestrial edge-of-field habitats: A critical review of the literature. *Agriculture, Ecosystems & Environment* **232**, 59– 72.

Rada S, Schweiger O, Harpke A, Kühn E, Kuras T, Settele J & Musche M (2019) Protected areas do not mitigate biodiversity declines: A case study on butterflies. *Diversity and Distributions* **25**, 217–224.

Ramírez-Restrepo L & MacGregor-Fors I (2017) Butterflies in the city: a review of urban diurnal Lepidoptera. *Urban Ecosystems* **20**, 171–182.

Randle Z, Evans-Hill LJ, Parsons MS, Tyner A, Bourn NAD, Davis AM, Dennis EB, O'Donnell M, Prescott T, Tordoff GM & Fox R (2019) *Atlas of Britain & Ireland's Larger Moths*. Pisces Publications, Newbury, UK.

Régnier C, Achaz G, Lambert A, Cowie RH, Bouchet P & Fontaine B (2015) Mass extinction in poorly known taxa. *Proceedings of the National Academy of Sciences of the USA* **112**, 7761–7766.

Reichman OJ, Jones MB & Schildhauer MP (2011) Challenges and opportunities of open data in ecology. *Science* **331**, 703–705.

Riesch H & Potter C (2014) Citizen science as seen by scientists: Methodological, epistemological and ethical dimensions. *Public Understanding of Science* **23**, 107–120.

Richter A, Hauck J, Feldmann R, Kühn E, Harpke A, Hirneisen N, Mahla A, Settele J & Bonn A (2018) The social fabric of citizen science - drivers for longterm engagement in the German butterfly monitoring scheme. *Journal of Insect Conservation* **22**, 731–743.

Rodrigues ASL, Pilgrim JD, Lamoreux JF, Hoffmann M & Brooks TM (2006) The value of the IUCN Red List for conservation. *Trends in Ecology & Evolution* **21**, 71–76.

Roy DB, Rothery P & Brereton T (2007) Reduced-effort schemes for monitoring butterfly populations. *Journal of Applied Ecology* **44**, 993–1000.

Roy DB & Sparks TH (2000) Phenology of British butterflies and climate change. *Global Change Biology* **6**, 407–416.

Roy HE, Adriaens T, Isaac NJ, Kenis M, Onkelinx T, Martin GS, Brown PM, Hautier L, Poland R, Roy DB, Comont R, Eschen R, Frost R, Zindel R, Van Vlaenderen J, Nedvěd O, Ravn HP, Grégoire J, de Biseau J & Maes D (2012) Invasive alien predator causes rapid declines of native European ladybirds. *Diversity and Distributions* **18**, 717–725.

Roy HE, Baxter E, Saunders A & Pocock MJO (2016) Focal plant observations as a standardised method for pollinator monitoring: opportunities and limitations for mass participation citizen science. *PLoS One* **11**, e0150794.

Ruppert KM, Kline RJ & Rahman MS (2019) Past, present, and future perspectives of environmental DNA (eDNA) metabarcoding: A systematic review in methods, monitoring, and applications of global eDNA. *Global Ecology and Conservation* **10**, e00547.

Russell C & Schultz CB (2010) Effects of grass-specific herbicides on butterflies: an experimental investigation to advance conservation efforts. *Journal of Insect Conservation* **14**, 53–63.

Rytkönen S, Vesterinen EJ, Westerduin C, Leviäkangas T, Vatka E, Mutanen M, Välimäki P, Hukkanen M, Suokas M & Orell M (2019) From feces to data: A metabarcoding method for analyzing consumed and available prey in a bird-insect food web. *Ecology and Evolution* **9**, 631–639.

Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M & Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774.

Sánchez-Bayo F & Wyckhuys KAG (2019) Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation* **232**, 8–27.

Saunders ME (2019) No simple answers for insect conservation: media hype has missed the biggest concern that ecologists and entomologists have about six-legged life: how little we know about it. *American Scientist* **107**, 148–151.

Saunders ME, Janes JK, O'Hanlon JC (2020) Moving On from the insect apocalypse narrative: engaging with evidence-based insect conservation. *BioScience* **70**, 80–89.

Saunders ME, Roger E, Geary WL, Meredith F, Welbourne DJ, Bako A, Canavan E, Herro F, Herron C, Hung O & Kunstler M (2018) Citizen science in schools: Engaging students in research on urban habitat for pollinators. *Austral Ecology* **43**, 635–642.

Sax DF & Gaines SD (2003) Species diversity: From global decreases to local increases. *Trends in Ecology & Evolution* **18**, 561–566.

Schmucki R, Pe'Er G, Roy DB, Stefanescu C, Van Swaay CA, Oliver TH, Kuussaari M, Van Strien AJ, Ries L, Settele J & Musche M (2016) A regionally informed abundance index for supporting integrative analyses across butterfly monitoring schemes. *Journal of Applied Ecology* **53**, 501–510.

Seibold S, Gossner MM, Simons NK, Blüthgen N, Müller J, Ambarlı D, Ammer C, Bauhus J, Fischer M, Habel JC, Linsenmair KE, Nauss T, Penone C, Prati D, Schall P, Schulze E-D, Vogt J, Wöllauer S & Weisser WW (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* **574**, 671–674.

Shortall CR, Moore A, Smith E, Hall MJ, Woiwod IP & Harrington R (2009) Long-term changes in the abundance of flying insects. *Insect Conservation and Diversity* **2**, 251–260.

Silvertown J (2009) A new dawn for citizen science. *Trends in Ecology* & *Evol*ution **24**, 467–471.

Simmons BI, Balmford A, Bladon AJ, Christie AP, De Palma A, Dicks LV, Gallego-Zamorano J, Johnston A, Martin PA, Purvis A, Rocha R, Wauchope HS, Wordley CFR, Worthington TA & Finch T (2019) Worldwide insect declines: An important message, but interpret with caution. *Ecology and Evolution* **9**, 3678–3680.

Smart SM, Thompson K, Marrs RH, Le Duc MG, Maskell LC & Firbank LG (2006) Biotic homogenization and changes in species diversity across humanmodified ecosystems. *Proceedings of the Royal Society B* **273**, 2659–2665.

Soga M & Gaston KJ (2016) Extinction of experience: evidence, consequences and challenges of loss of human-nature interactions. *Frontiers in Ecology and the Environment* **14**, 94–101.

Soga M & Gaston KJ (2018) Shifting baseline syndrome: causes, consequences, and implications. *Frontiers in Ecology and the Environment* **16**, 222–230.

Somers-Yeates R, Hodgson D, McGregor PK, Spalding A & Ffrench-Constant RH (2013) Shedding light on moths: shorter wavelengths attract noctuids more than geometrids. *Biology Letters* **9**, 20130376.

Soranno PA, Cheruvelil KS, Elliott KC & Montgomery GM (2015) It's good to share: why environmental scientists' ethics are out of date. *BioScience* **65**, 69–73.

Soroye P, Ahmed N & Kerr JT (2018) Opportunistic citizen science data transform understanding of species distributions, phenology, and diversity gradients for global change research. *Global Change Biology* **24**, 5281–5291.

Staley JT, Botham MS, Amy SR, Hulmes S & Pywell RF (2018) Experimental evidence for optimal hedgerow cutting regimes for Brown hairstreak butterflies. *Insect Conservation and Diversity* **11**, 213–218.

Staley JT, Botham MS, Chapman RE, Amy SR, Heard MS, Hulmes L, Savage J & Pywell RF (2016) Little and late: How reduced hedgerow cutting can benefit Lepidoptera. *Agriculture, Ecosystems & Environment* **224**, 22–28.

Stark JD, Chen XD & Johnson CS (2012) Effects of herbicides on Behr's metalmark butterfly, a surrogate species for the endangered butterfly, Lange's metalmark. *Environmental Pollution 164*, 24–27.

Stefanescu C, Peñuelas J & Filella I (2003) Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology* **9**, 1494–1506.

Stephenson PJ, Bowles-Newark N, Regan E, Stanwell-Smith D, Diagana M,
Höft R, Abarchi H, Abrahamse T, Akello C, Allison H, Banki O, Batieno B,
Dieme S, Domingos A, Galt R, Githaiga CW, Guindo AB, Hafashimana DLN,
Hirsch T, Hobern D, Kaaya J, Kaggwa R, Kalemba MM, Linjouom I, Manaka B,
Mbwambo Z, Musasa M, Okoree E, Rwetsiba A, Siam AB & Thiombiano A
(2016) Unblocking the flow of biodiversity data for decision-making in Africa. *Biological Conservation* 213, 335–340.

Stevens CJ, David TI & Storkey J (2018) Atmospheric nitrogen deposition in terrestrial ecosystems: Its impact on plant communities and consequences across trophic levels. *Functional Ecology* **32**, 1757–1769.

Storkey J, Macdonald AJ, Bell JR, Clark IM, Gregory AS, Hawkins NJ, Hirsch PR, Todman LC & Whitmore AP (2016) The unique contribution of Rothamsted to ecological research at large temporal scales. *Advances in Ecological Research* **55**, 3–42.

Strasser BJ, Baudry J, Mahr D, Sanchez G, Tancoigne E (2019) "Citizen Science"? Rethinking science and public participation. *Science and Technology Studies* **32**, 52–76.

Stuart SN, Wilson EO, McNeely JA, Mittermeier RA & Rodríguez JP (2010) The barometer of life. *Science* **328**, 177.

Suggitt AJ, Wilson RJ, Isaac NJB, Beale CM, Auffret AG, August T, Bennie JJ, Crick HQP, Duffield S, Fox R, Hopkins JJ, Macgregor NA, Morecroft MD, Walker KJ & Maclean IMD (2018) Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change* **8**, 713–717.

Sullivan BL, Phillips T, Dayer AA, Wood CL, Farnsworth A, Iliff MJ, Davies IJ, Wiggins A, Fink D, Hochachka WM, Rodewald AD, Rosenberg KV, Bonney R &

Kelling S (2017) Using open access observational data for conservation action: A case study for birds. *Biological Conservation* **208**, 5–14.

Sumner S, Bevan P, Hart AG & Isaac NJ (2019) Mapping species distributions in 2 weeks using citizen science. *Insect Conservation and Diversity* **12**, 382–388.

Sumner S, Law G & Cini A (2018) Why we love bees and hate wasps. *Ecological Entomology* **43**, 836–845.

Sutherland WJ, Armstrong-Brown S, Armsworth PR, Brereton T, Brickland J, Campbell CD, Chamberlain DE, Cooke AI, Dulvy NK, Dusic NR, Fitton MG, Freckleton RP, Godfray HCJ, Grout N, Harvey HJ, Hedley C, Hopkins JJ, Kift NB, Kirby J, Kunin WE, Macdonald DW, Marker B, Naura M, Neale AR, Oliver T, Osborn D, Pullin AS, Shardlow MEA, Showler DA, Smith PL, Smithers RJ, Solandt J-L, Spencer J, Spray CJ, Thomas CD, Thompson J, Webb SE, Yalden DW & Watkinson AR (2006) The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology* **43**, 617–627.

Taylor LR & Taylor RA (1977) Aggregation, migration and population mechanics. *Nature* **265**, 415–421.

Termaat T, van Strien AJ, van Grunsven RH, De Knijf G, Bjelke U, Burbach K, Conze KJ, Goffart P, Hepper D, Kalkman VJ & Motte G (2019) Distribution trends of European dragonflies under climate change. *Diversity and Distributions* **25**, 936–950.

Thackeray SJ, Helaouet P, Johns DG, Jones ID, Bacon PJ, Brereton TM, Carvalho L, Clutton-Brock TH, Duck C, Edwards M, Elliott JM, Hall SJG, Harrington R, Pearce-Higgins JW, Pemberton JM, Sparks TH, Thompson PM, White I, Winfield IJ, Henrys PA, Hemming D, Leech DI, Bell JR, Botham MS, Burthe S, Mackay EB, Massimino D, Høye TT, Kruuk LEB, Wanless S & Atkinson S (2016) Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535**, 241–245.

Theobald EJ, Ettinger AK, Burgess HK, DeBey LB, Schmidt NR, Froehlich HE, Wagner C, HilleRisLambers J, Tewksbury J, Harsch MA & Parrish JK (2015) Global change and local solutions: Tapping the unrealized potential of citizen science for biodiversity research. *Biological Conservation* **181**, 236–244.

Thomas CD (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society B* **267**, 139–145.

Thomas CD, Franco AM & Hill JK (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution* **21**, 415–416.

Thomas CD, Hill JK, Anderson BJ, Bailey S, Beale CM, Bradbury RB, Bulman CR, Crick HQ, Eigenbrod F, Griffiths HM & Kunin WE (2011) A framework for assessing threats and benefits to species responding to climate change. *Methods in Ecology and Evolution* **2**, 125–142.

Thomas CD, Jones TH & Hartley SE (2019) "Insectageddon": A call for more robust data and rigorous analyses. *Global Change Biology* **25**, 1891–1892.

Thomas J (1980) Why did the large blue become extinct in Britain? *Oryx* **15**, 243–247.

Thomas JA (1995) The conservation of declining butterfly populations in Britain and Europe: priorities, problems and successes. *Biological Journal of the Linnean Society* **56**, 55–72.

Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B* **360**, 339–357.

Thomas JA (2016) Butterfly communities under threat. Science 353, 216-218.

Thomas JA, Edwards M, Simcox DJ, Powney GD, August TA & Isaac NJ (2015) Recent trends in UK insects that inhabit early successional stages of ecosystems. *Biological Journal of the Linnean Society* **115**, 636–646.

Thomas JA, Simcox DJ & Clarke RT (2009) Successful conservation of a threatened *Maculinea* butterfly. *Science* **325**, 80–83.

Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT & Lawton JH (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**, 1879–1881.

Thomson JD (2019) Progressive deterioration of pollination service detected in a 17-year study vanishes in a 26-year study. *New Phytologist* **224**, 1151–1159.

Tilman D, Isbell F & Cowles JM (2014) Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* **45**, 471–493.

Tittensor DP, Walpole M, Hill SLL, Boyce DG, Britten GL, Burgess ND, Butchart SHM, Leadley PW, Regan EC, Alkemade R, Baumung R, Bellard C, Bouwman L, Bowles-Newark NJ, Chenery AM, Cheung WWL, Christensen V, Cooper HD, Crowther AR, Dixon MJR, Galli A, Gaveau V, Gregory RD, Gutierrez NL, Hirsch TL, Höft R, Januchowski-Hartley SR, Karmann M, Krug CB, Leverington FJ, Loh J, Kutsch Lojenga R, Malsch K, Marques A, Morgan DHW, Mumby PJ, Newbold T, Noonan-Mooney K, Pagad SN, Parks BC, Pereira HM, Robertson T, Rondinini C, Santini L, Scharlemann JPW & Schindler S (2014) A mid-term analysis of progress toward international biodiversity targets. *Science* **346**, 241–244.

Trimble M & Berkes F (2013) Participatory research towards co-management: lessons from artisanal fisheries in coastal Uruguay. *Journal of Environmental Management* **128**, 768–778.

Troudet J, Grandcolas P, Blin A, Vignes-Lebbe R & Legendre F (2017) Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports* **7**, 9132.

Tulloch AIT, Auerbach N, Avery-Gomm S, Bayraktarov E, Butt N, Dickman CR, Ehmke G, Fisher DO, Grantham H, Holden MH, Lavery TH, Leseberg, NP, Nicholls M, O'Connor J, Roberson L, Smyth AK, Stone Z, Tulloch V, Turak E, Wardle GM & Watson JEM (2018) A decision tree for assessing the risks and benefits of publishing biodiversity data. *Nature Ecology and Evolution* **2**, 1209– 1217.

Turrini T, Dörler D, Richter A, Heigl F & Bonn A (2018) The threefold potential of environmental citizen science - Generating knowledge, creating learning opportunities and enabling civic participation. *Biological Conservation* **225**, 176–186.

Ubach A, Páramo F, Gutiérrez C & Stefanescu C (2019) Vegetation encroachment drives changes in the composition of butterfly assemblages and species loss in Mediterranean ecosystems. *Insect Conservation and Diversity* DOI: 10.1111/icad.12397 Valtonen A, Hirka A, Szőcs L, Ayres MP, Roininen H & Csóka G (2017) Longterm species loss and homogenization of moth communities in Central Europe. *Journal of Animal Ecology* **86**, 730–738.

VanDerWal J, Murphy HT, Kutt AS, Perkins GC, Bateman BL, Perry JJ & Reside AE (2013) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change* **3**, 239–243.

Van Dyck H, Bonte D, Puls R, Gotthard K & Maes D (2015) The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? *Oikos* **124**, 54–61.

Van Dyck H, van Strien AJ, Maes D & van Swaay CAM (2009) Declines in common, widespread butterflies in a landscape under intense human use. *Conservation Biology* **23**, 957–965.

Van Geffen KG, Groot AT, Van Grunsven RHA, Donners M, Berendse F & Veenendaal EM (2015a) Artificial night lighting disrupts sex pheromone production in a Noctuid moth. *Ecological Entomology* **40**, 401–408.

Van Geffen KG, Van Eck E, De Boer RA, Van Grunsven RHA, Salis L, Berendse F & Veenendaal EM (2015b) Artificial light at night inhibits mating in a Geometrid moth. *Insect Conservation and Diversity* **8**, 282–287.

Van Langevelde F, Braamburg-Annegarn M, Huigens ME, Groendijk R, Poitevin O, van Deijk JR, Ellis WN, van Grunsven RHA, de Vos R, Vos RA, Franzén M & WallisDeVries MF (2018) Declines in moth populations stress the need for conserving dark nights. *Global Change Biology* **24**, 925–932.

Van Langevelde F, Van Grunsven RHA, Veenendaal EM & Fijen TPM (2017) Artificial night lighting inhibits feeding in moths. *Biology Letters* **13**, 20160874.

van Strien AJ, van Swaay CAM, van Strien-van Liempt WTFH, Poot MJM & WallisDeVries MF (2019) Over a century of data reveal more than 80% decline in butterflies in the Netherlands. *Biological Conservation* **234**, 116–122.

van Swaay C, Maes D, Collins S, Munguira ML, Šašić M, Settele J, Verovnik R, Warren M, Wiemers M, Wynhoff I & Cuttelod A (2011) Applying IUCN criteria to

invertebrates: How red is the Red List of European butterflies? *Biological Conservation* **144**, 470–478.

van Swaay CAM, Nowicki P, Settele J & van Strien AJ (2008) Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation* **17**, 3455–3469.

Vaughan N (1997) The diets of British bats (Chiroptera). *Mammal Review* **27**, 77–94.

Vellend M, Baeten L, Myers-Smith IH, Elmendorf SC, Beauséjour R, Brown CD, De Frenne P, Verheyen K & Wipf S (2013) Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proceedings of the National Academy of Sciences of the USA **110**, 19456–19459.

Visconti P, Bakkenes M, Baisero D, Brooks T, Butchart SH, Joppa L, Alkemade R, Di Marco M, Santini L, Hoffmann M, Maiorano L, Pressey RL, Arponen A, Boitani L, Reside AE, Vuuren DP & Rondinini C (2016) Projecting global biodiversity indicators under future development scenarios. *Conservation Letters* **9**, 5–13.

Wagner DL (2020) Insect declines in the Anthropocene. *Annual Review of Entomology* **65**, 457–480.

WallisDeVries MF & van Swaay CAM (2006) Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biology* **12**, 1620–1626.

WallisDeVries MF & van Swaay CA (2017) A nitrogen index to track changes in butterfly species assemblages under nitrogen deposition. *Biological Conservation* **212**, 448–453.

Wals AE, Brody M, Dillon J & Stevenson RB (2014) Convergence between science and environmental education. *Science* **344**, 583–584.

Wang Wei J, Lee BPY-H & Bing Wen L (2016) Citizen science and the urban ecology of birds and butterflies - a systematic review. *PLoS One* **11**, e0156425.

Warren MS (1994) The UK status and suspected metapopulation structure of a threatened European butterfly, the marsh fritillary *Eurodryas aurinia*. *Biological Conservation* **67**, 239–249.

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D & Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69.

Warren MS & Key RS (1991) Woodlands: past, present and potential for insects. *The Conservation of Insects and their Habitats*, (ed. NM Collins & JA Thomas), pp. 155–211. Academic Press, London, UK.

Warren MS, Thomas CD & Thomas JA (1984) The status of the health fritillary butterfly *Mellicta athalia* Rott. in Britain. *Biological Conservation* **29**, 287–305.

Warren R, Price J, Graham E, Forstenhaeusler N & VanDerWal J (2018) The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C. *Science* **360**, 791–795.

Wepprich T, Adrion JR, Ries L, Wiedmann J & Haddad NM (2019) Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLoS One* **14**, e0216270.

West S & Pateman R (2016) Recruiting and retaining participants in citizen science: what can be learned from the volunteering literature? *Citizen Science: Theory and Practice* **1**, 15.

White ER (2019) Minimum time required to detect population trends: the need for long-term monitoring programs. *BioScience* **69**, 40–46.

Williams CB (1948) The Rothamsted light trap. *Proceedings of the Royal Entomological Society of London Series A* **23**, 80–85.

Williams CB (1961) Studies in the effect of weather conditions on the activity and abundance of insect populations. *Philosophical Transactions of the Royal Society B* **244**, 331–378.

Wilson EO (1987) The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* **1**, 344–346.

Wilson JF, Baker D, Cook M, Davis G, Freestone R, Gardner D, Grundy D, Lowe N, Orridge S & Young H (2015) Climate association with fluctuation in annual abundance of fifty widely distributed moths in England and Wales: a citizen-science study. *Journal of Insect Conservation* **19**, 935–946. Woiwod IP, Gould P & Conrad KF (2005) The Rothamsted light-trap network - shedding light on a common moth problem. *Atropos* **26**, 5–18.

Worm B, Hilborn R, Baum JK, Branch TA, Collie JS, Costello C, Fogarty MJ, Fulton EA, Hutchings JA, Jennings S, Jensen OP, Lotze HK, Mace PM, McClanahan TR, Minto C, Palumbi SR, Parma AM, Ricard D, Rosenberg AA, Watson R & Zeller D (2009) Rebuilding global fisheries. *Science* **325**, 578–585.

WWF (2018) *Living Planet Report - 2018: Aiming Higher*. WWF, Gland, Switzerland.

Yang LH & Gratton C (2014) Insects as drivers of ecosystem processes. *Current Opinion in Insect Science* **2**, 26–32.

Young M (1997) The Natural History of Moths. T & AD Poyser, London, UK.

Young MR & Barbour DA (2004) Conserving the New Forest burnet moth in Scotland, responses to grazing reduction and consequent vegetation changes. *Journal of Insect Conservation* **8**, 137–148.

Zingg S, Ritschard E, Arlettaz R & Humbert JY (2019) Increasing the proportion and quality of land under agri-environment schemes promotes birds and butterflies at the landscape scale. *Biological Conservation* **231**, 39–48.

Chapter 2: The decline of moths in Great Britain: a review of possible causes

Slightly modified from:

Fox R (2013) The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity* **6**, 5–19.

Abstract

Population declines among insects are inadequately quantified, yet of vital importance to national and global biodiversity assessments and have significant implications for ecosystem services. Substantial declines in abundance and distribution have been reported recently within a species-rich insect taxon, macro-moths, in Great Britain and other European countries. These declines are of concern because moths are important primary consumers and prey items for a wide range of other taxa, as well as contributing to ecosystem services such as pollination.

I summarise these declines and review potential drivers of change. Direct evidence for causes of moth declines is extremely limited, but correlative studies and extrapolation from closely related taxa suggest that habitat degradation (particularly because of agricultural intensification and changing silviculture) and climate change are likely to be major drivers. There is currently little evidence of negative population-level effects on moths caused by chemical or light pollution, non-native species or direct exploitation.

I make suggestions for future research with a focus on quantifying impacts of land management practices, light pollution and climate change on moth population dynamics and developing evidence-based measures that can be incorporated into agri-environment schemes and other policy initiatives to help reverse the widespread decline of moths in Great Britain and beyond.

Introduction

The Earth is undergoing a period of substantial decreases in biodiversity and mass extinction of species (Pimm *et al.* 1995; Dirzo & Raven 2003; Butchart *et al.* 2010; May 2010; Mooney 2010), which threaten ecosystem services and the

welfare of the human race (Balmford & Bond 2005; Millennium Ecosystem Assessment 2005; Schröter *et al.* 2005; Biesmeijer *et al.* 2006; Rockström *et al.* 2009; UK National Ecosystem Assessment 2011). However, the decline and extinction rates of insects, which comprise the majority of terrestrial biodiversity, are inadequately quantified and poorly understood (McKinney 1999; Dunn 2005; Thomas 2005). A contributory factor to this knowledge gap is the highly variable population dynamics of many insect species (Wilson & Roy 2009). Long time series of data are required to identify significant directional trends amid the statistical 'noise' of population cycles and short-term responses to stochastic environmental events (Conrad *et al.* 2004).

Until recently, large spatial-scale assessments of long-term insect trends were restricted to a few charismatic, well-studied, but species-poor, taxa such as butterflies and bumblebees, in some developed nations, particularly in western Europe (Maes & Van Dyck 2001; Warren *et al.* 2001; Fox *et al.* 2006a; Fitzpatrick *et al.* 2007; Kosior *et al.* 2007; Goulson *et al.* 2008; van Swaay *et al.* 2008; Van Dyck *et al.* 2009; Cameron *et al.* 2011). Thomas *et al.* (2004b) showed that butterfly declines exceeded comparable changes among birds and vascular plants in Great Britain (GB). These examples provide insight into insect diversity trends, but concerns remain over how representative they are across insect taxa (e.g. Hambler & Speight 2004; but see Thomas & Clarke 2004).

Recently, studies of moths have generated the first evidence of national-scale declines in a species-rich insect taxon (Conrad *et al.* 2006; Mattila *et al.* 2006, 2008; Groenendijk & Ellis 2011). Such studies are important as they corroborate the use of taxa such as butterflies as indicators of wider insect biodiversity trends, but also because the greater diversity of moths may facilitate an improved understanding of the drivers of change and the impacts that insect declines will have on other organisms, communities and ecosystem functioning.

This article reviews current knowledge about moth declines and the potential drivers of change in GB (and elsewhere in western Europe). The five main causes of biodiversity loss and changes in ecosystem services in the UK (UK National Ecosystem Assessment 2011) are examined in relation to moths, as well as an additional potential driver, light pollution. This review is topical at a

time of resurgent interest in ecological research on moths, stimulated, in part, by the discovery of the widespread and substantial declines in this taxon (Sutherland *et al.* 2006).

Moth declines in GB and beyond

Although national-level extinctions (Parsons 2003) and decreased distribution and abundance of selected diurnal macro-moths had already been documented (Groenendijk & van der Meulen 2004), the analyses of the Rothamsted Insect Survey (RIS) monitoring data yielded the first quantitative understanding of the severity of population decline among moths.

The RIS, a nationwide network monitoring UK moth populations, has been operated by Rothamsted Research since 1968 and provides one of the longestrunning and most spatially extensive datasets of a species-rich insect taxon anywhere in the world (Conrad et al. 2007; Woiwod & Gould 2008). Monitoring at one RIS site (Rothamsted, UK) commenced in 1933 and has demonstrated a substantial decrease in abundance and diversity of moths during the 1950s (Woiwod & Gould 2008). Furthermore, detailed national studies of an individual species, Garden Tiger Arctia caja, also demonstrated severe population and site occupancy declines for this once-common species and paved the way for a more comprehensive assessment (Conrad et al. 2002). Analysis of a 35-year dataset (1968-2002) for 337 macro-moth species (those for which adequate data were available) revealed significant decreases (Conrad et al. 2004). The total abundance of individual macro-moths caught by the RIS network decreased in the whole of GB (31% decrease over 35 years) and in southern GB (44% decrease) (Conrad et al. 2006). The total abundance of moths did not decrease in northern GB, a finding corroborated by a smaller study of RIS data from a single site by Salama et al. (2007) and also by butterfly trends (Brereton et al. 2011).

Conrad *et al.* (2006) also found that 66% of the 337 species studied had negative population trends and that 21% of the species had decline rates >30% 10 year⁻¹ (equivalent to the IUCN threshold levels for Red List threat categories). That these 337 species are considered widespread and generally common in GB (Skinner 2009; Waring *et al.* 2009) underscored the significance

of Conrad *et al.*'s findings for biodiversity conservation (Fox *et al.* 2006b). A similar proportion of species had undergone substantial population decreases in northern GB and southern GB, but many more species had increased in the north and this appears to account for the lack of a significant trend in overall moth abundance there compared to the south (Fox *et al.* 2006b).

Parallel decreases in the abundance or distribution of macro-moths have now been reported from other European countries. Groenendijk and Ellis (2011) found a pattern of change among 733 macro-moth species in the Netherlands, which was strikingly similar to the British findings: 71% of Dutch species decreased in abundance and the total abundance of moths decreased by onethird (1980-2009). Both studies also highlighted a minority of species that had markedly increased in abundance.

Utilising long-term distribution records, Mattila *et al.* (2006, 2008) showed significant overall decreases in the distribution of macro-moths in the families Geometridae and Noctuidae (590 species in total) in Finland and a study of Lepidoptera at a nature reserve in southern Sweden revealed high rates of local extinction over a 50-year period (27% of 597 study species were deemed to have become extinct versus 4% that had colonised the area) (Franzén & Johannesson 2007). Preliminary analysis of the new National Moth Recording Scheme dataset in the UK also indicated severe distribution declines among some macro-moth species (Fox *et al.* 2011b).

Several of these studies examined ecological traits and life history attributes in relation to rates of distribution or population change, but the results varied considerably. For example, in GB and the Netherlands, species overwintering in the adult life-cycle stage had positive population trends over time (Conrad *et al.* 2004; Groenendijk & Ellis 2011), whereas Mattila *et al.* (2006) found adult overwintering to be a significant predictor of increased extinction risk and Franzén and Johannesson (2007) found no effects of overwintering strategy on species persistence. However, range size and larval specificity correlated consistently with rates of decline or extinction risk, mirroring studies on butterflies (Warren *et al.* 2001; Koh *et al.* 2004; Nilsson *et al.* 2008). Rarer species were associated with greater losses or increased likelihood of extinction

(Franzén & Johannesson 2007; Groenendijk & Ellis 2011) and monophagous species were more likely to have declined or become extinct than less-specialised species (Franzén & Johannesson 2007; Mattila *et al.* 2008).

Taken together, these studies provide overwhelming evidence of moth declines on a large geographical scale and mirror previous studies of less species-rich taxonomic groups such as butterflies. Such losses are likely to have substantial impacts at higher and lower trophic levels, because of the importance of moths as herbivores, pollinators and prey items (e.g. Proctor *et al.* 1996; Vaughan 1997; Wilson *et al.* 1999; Wickramasinghe *et al.* 2004; Devoto *et al.* 2011) and may affect the delivery of some ecosystem services. Yet, the causes of pervasive moth declines are poorly understood.

Drivers of change in moth populations

Habitat loss, degradation and fragmentation

The destruction and modification of habitats by human activity is regarded as the foremost cause of global biodiversity loss (Diamond *et al.* 1989; Brooks *et al.* 2002; Dirzo & Raven 2003; Fahrig 2003). Habitat loss (including deterioration in quality and the isolation effects of fragmentation) has also been identified as the principle driver of butterfly declines in Europe (e.g. Asher *et al.* 2001; Maes & Van Dyck 2001; Warren *et al.* 2001; Wenzel *et al.* 2006; Bulman *et al.* 2007; Hanski & Pöyry 2007; Van Dyck *et al.* 2009; Öckinger *et al.* 2010). Consequently, it seems probable that habitat loss will have influenced moth abundance and distributions in GB (Fox *et al.* 2006b), although habitat degradation patterns vary geographically and, therefore, impacts on species are expected to differ between areas. It is possible that the better performance, on average, of moth populations in northern GB stems from lower levels of habitat degradation relative to the southern half of GB, although a climatic explanation, or a combination of both, is also plausible (see section Climate change and Chapter 3).

There is little direct evidence for habitat loss, degradation or fragmentation effects on moth populations in GB (or elsewhere). However, as for butterflies, there is considerable circumstantial evidence that the widespread destruction of semi-natural habitats has had a severe impact on specialist moths, and it has been implicated in the extinction of species, including Reed Tussock *Laelia coenosa* and Gypsy Moth *Lymantria dispar* because of wetland drainage, and Spotted Sulphur *Acontia trabealis* as a result of afforestation and agricultural intensification (Majerus 2002). Habitat changes may also have played a role in the declines of species such as *Pyrausta sanguinalis* in sand dunes, Straw Belle *Aspitates gilvaria* and Black-veined Moth *Siona lineata* on unimproved grassland, Shoulder-striped Clover *Heliothis maritima* and Speckled Footman *Coscinia cribraria* on lowland heath and Barberry Carpet *Pareulype berberata* in hedgerows (Fox *et al.* 2010).

Fragmentation effects have been detected in few empirical studies of moths (Öckinger *et al.* 2010), but generally biodiversity impacts from fragmentation *per* se tend to be relatively small compared to the effects of habitat loss and habitat quality (Thomas *et al.* 2001; Fahrig 2003; Hodgson *et al.* 2009). In addition, theory predicts that mobile species are less likely to experience negative effects of isolation. Mobility is poorly understood in most moth species (apart from long-distance migrants, e.g. Chapman *et al.* 2011), but recent evidence suggests that many species are relatively mobile (Franzén & Nilsson 2007; Merckx *et al.* 2009a, 2010a,b; Betzholtz & Franzén 2011; Slade *et al.* 2013; but see Nieminen 1996; Nieminen *et al.* 1999). Thus, while fragmentation might be expected to be important for some specialised species with low to intermediate mobility (Thomas 2000), it is unlikely to be a principle driver of the declines of many widespread moths in GB and elsewhere.

In contrast, it seems highly plausible that the widespread destruction of seminatural habitats that took place across GB during the 20th century had substantial impacts on moths. These were rarely documented through sitebased population monitoring at the time (although see Woiwod & Gould 2008), and land-use change effects cannot easily be assessed retrospectively. However, recent research has started to shed light on the impacts of land use on moth populations, by contrasting different levels of management intensity.

Agricultural management. Agriculture is a dominant and socioeconomically important land use in GB and much of Europe and is also of great importance for biodiversity (Bignal & McCracken 1996; Halada *et al.* 2011). However,

agricultural intensification generally reduces habitat area, quality and heterogeneity through the interlinked impacts of increased agrochemical use, changes in tillage/grazing practices and larger cropped areas and is widely recognised as a major driver of biodiversity decline (Donald *et al.* 2001; Benton *et al.* 2002, 2003; Robinson & Sutherland 2002; Kleijn *et al.* 2009). The substantial drop in moth abundance and diversity recorded on farmland at Rothamsted between the 1940s and 1960s was concomitant with agricultural intensification of the surrounding land (Woiwod & Gould 2008). Specific changes included a move from grassland to arable cultivation, removal of hedgerows and uncultivated areas to increase field size and built development. A number of other recent studies have also implicated aspects of intensification with reduced moth populations (see below).

Taylor and Morecroft (2009) reported significant increases in moth abundance and species richness on a farm in southern England, following organic conversion and simultaneous entry into an agri-environment scheme (AES) and the adoption of less-intensive farming techniques. Wickramasinghe et al. (2004) found significantly higher species richness and diversity of moths on organic farms than on conventional ones in a study of 24 pairs of (livestock and mixed) farms in GB. The authors ascribed this difference to the reduced use of agrochemicals, but many other factors could also be responsible. Pocock and Jennings (2008) conducted a similar study, but were able to separate out several different elements of intensification. They found the greatest effects on moth abundance related to the presence or absence of field boundaries (moths benefited from boundaries), both in arable and in pasture fields, with relatively little impact from either agrochemical inputs or the switch from hay to silage cropping regimes. This corroborates findings that the area of hedges and bushes in the local environment around RIS traps on the Rothamsted Estate was an important predictor of moth abundance and diversity (Woiwod & Gould 2008).

Work by Merckx *et al.* (2009a,b, 2010a,b) also highlighted the importance of field boundaries for moths in agricultural settings. The presence of hedgerow trees and 6m-wide grassy field margins were both significantly correlated with increased moth abundance and diversity (Merckx *et al.* 2009b). Such field

margins, but not hedgerow trees, were management options for which 'entry level' AES payments were available at the time of the studies. Hedgerow trees had the greater effect, but only when targeted management advice resulted in elevated levels of AES uptake in the surrounding landscape (Merckx *et al.* 2009b). Hedgerow trees had a positive impact on a wide range of moths, not just those species that utilise them as larval hostplants, possibly because they provide sheltered micro-climates in relatively exposed landscapes (Merckx *et al.* 2010a).

Another study (Fuentes-Montemayor *et al.* 2011) found benefits for moths from AES management at farms in Scotland. Conversion of conventional arable or improved pasture fields to more species-rich grassland under AES resulted in increased abundance and species richness of moths. Other AES options, including the creation of extensively managed margins, also led to increased moth numbers and abundance, but no effects were found for AES hedgerow management.

Agricultural use of chemicals, both fertilizers and pesticides, increased enormously as an integral part of agricultural intensification during the latter half of the 20th century. With direct and indirect (e.g. via impacts on larval hostplants, nectar sources, vegetation structure and composition) effects on many taxa both within cropped areas and on field margins (Freemark & Boutin 1995; McLaughlin & Mineau 1995; Longley & Sotherton 1997), these agrochemicals may have played a prominent role in the decline of moths in GB. However, disentangling the relative contributions of fertilizers or pesticides from other elements of agricultural intensification at a landscape or national scale is problematic (Benton *et al.* 2003; although see Gibbs *et al.* 2009).

Ongoing agricultural development will alter patterns of agrochemical use and the nature of the substances deployed. Such changes may increase or decrease potential impacts on biodiversity and should be evaluated prior to introduction. For example, genetically modified herbicide-tolerant crops alter pesticide regimes and aim to improve the efficacy of weed control, with potential impacts on plants and associated invertebrates both within the crop and on field margins (Roy *et al.* 2003). Novel crops (e.g. biofuel and biomass), increasing resistance to pesticides and changing food security conditions may drive increased intensification and additional exposure to existing and future agrochemicals (Sutherland *et al.* 2008).

Often, subtle aspects of habitat quality are vital for population persistence. Change in the grazing intensity of agricultural land is known to alter habitat quality critically for many taxa, including butterflies, vascular plants and some specialist moth species. For example, increased intensity of livestock grazing almost led to the extinction of New Forest Burnet *Zygaena viciae* from GB (Young & Barbour 2004). Experimental reduction of the high intensity of livestock grazing typical of commercial upland agriculture led to significant increases in moth abundance and species richness (Littlewood 2008). While less-intensive grazing may benefit grassland insects, the permanent abandonment of traditional pastoral agriculture, leading to rapid ecological succession, can be detrimental (Balmer & Erhardt 2000; Bourn & Thomas 2002; Öckinger *et al.* 2006; van Swaay *et al.* 2006; Settele *et al.* 2009; Stefanescu *et al.* 2009). Such abandonment is thought to have contributed to declines of moth species in GB such as Forester *Adscita statices* and Narrow-bordered Bee Hawk-moth *Hemaris tityus* (M. Parsons pers. comm.).

Woodland management. Native broad-leaved and coniferous woodlands are important habitats for a wide range of taxa in GB, including a high proportion of the macro-moth species. Although woodlands of high biodiversity value have been destroyed, the net amount of broad-leaved woodland has increased in GB over recent decades, in stark contrast to the amount of other semi-natural habitats. And yet, the changing status of key monitored taxa, such as birds, butterflies and plants, clearly indicates a decrease in woodland biodiversity (Fuller *et al.* 2005; van Swaay *et al.* 2006; Carey *et al.* 2008; Fox *et al.* 2011a). A range of factors are responsible for these declines but, for butterflies, the main causes appear to be altered structural diversity, botanical communities and micro-climatic conditions associated with a shift towards high-forest management (including the cessation of traditional practices such as coppicing), leading to increasing shade and fewer open, early-successional habitats (Warren & Key 1991; Sparks *et al.* 1996; Asher *et al.* 2001; van Swaay *et al.* 2006; Clarke *et al.* 2011). Conrad *et al.* (2004) found that moth species utilising

deciduous trees as larval hostplants tended to have negative population trends in GB, while the few species (such as Spruce Carpet *Thera britannica* and Pine Beauty *Panolis flammea*) that exploit coniferous trees generally increased. The latter is hardly surprising, given the massive expansion of conifer plantations (a 20-fold increase, 1800-1980) in GB.

Moth species assemblages vary between woodland types and along geographical gradients, but also within woods (e.g. species associated with mature trees, others with edge habitats or open, grassland conditions in rides and glades) and even between age-classes of managed areas such as coppice coupes (Broome *et al.* 2011).

Merckx et al. (2012) assessed the macro-moth response to standard woodland conservation management practises in a landscape-scale study in southern England. They found that moth abundance increased with the amount of shelter: open, recently coppiced areas had the lowest abundance and standard (narrow) forest rides and blocks of mature woodland had the highest. However, common management techniques to open up woodland for the benefit of taxa such as butterflies, including coppicing and ride widening, did benefit the overall species richness of moths in the woodland landscape. Wide rides, although containing relatively low abundance levels of moths, were as rich in species as the standard rides and mature woodland. Moreover, the introduction of increased structural and micro-climatic heterogeneity increased overall species richness by providing niches for moths that were not found elsewhere in the woods. The authors caution, however, against opening up the sheltered latesuccessional cores of woodlands as these support high abundance and species richness of many specialist and conservation priority moths that are not found in more open habitats.

Most woodland specialist moths may have benefited from the switch to highforest management in broad-leaved woodland habitats over recent decades, although they will have been impacted detrimentally by conversion to coniferous forestry. However, it is equally clear that many moths, mostly generalist species of more open habitats (but also some specialists such as *Anania funebris* and

Drab Looper *Minoa murinata*) will have undergone substantial decreases in abundance and distribution as a result of changing woodland management.

Urbanisation. The impacts of urbanisation on biodiversity are complex. Increasing urban land cover typically replaces and fragments semi-natural habitat, leading to decreases in biodiversity, particularly among specialist species (Bergerot *et al.* 2010; Gaston & Evans 2010; UK National Ecosystem Assessment 2011). However, urbanisation can also cause increases in biodiversity among particular taxa (McKinney 2008). In addition to habitat loss, urbanisation also generates other environmental changes that might alter biodiversity including local climatic effects, chemical, light and sound pollution and the introduction of non-native species. Thus, urbanisation impacts on moths need also to be considered in the context of the effects of climate, pollution and non-native species (see below).

Although reduced levels of moth abundance and diversity have long been associated with urbanisation (Taylor *et al.* 1978), there do not appear to have been any published studies of the specific impacts of urbanisation on the moth fauna of GB, nor of the relative value for moths of habitat fragments in urban surroundings compared with other degraded land-uses such as intensive agriculture. In California, Rickman & Connor (2003) found no consistent differences between leaf-mining moth communities of remnant habitats in urban versus agricultural settings.

Urban greenspace, including private gardens, supports diverse moth communities. As with agriculture, intensive management of gardens and parks (including pesticide use) is expected to reduce moth numbers, although quantitative studies are lacking. Recent trends for reduction in garden size, both in new-build developments and through in-fill (building new housing in existing gardens), and loss of vegetated area to hard surfaces (e.g. driveways, parking, patios, decking) and garden buildings (e.g. sheds, greenhouses) (Loram *et al.* 2008; Smith 2010; UK National Ecosystem Assessment 2011) will have reduced resources available to moths, but no population-level studies have been conducted.

In contrast, increased public awareness of biodiversity and interest in 'wildlife gardening' may have improved habitat quality in some gardens and parks, and the cultivation of non-native plants has provided opportunities for a few native and newly-colonising moth species (see section Non-native species).

Habitat loss summary. Direct evidence of the impact of historical habitat loss, decreasing quality or fragmentation on moth abundance or diversity is largely lacking. However, the weight of contemporary evidence suggests that reducing the intensity of agricultural management (including at field boundaries) and reinstating traditional management to recently neglected broadleaved woodlands increase moth abundance and diversity at the landscape scale. The implication is that the predominant trends in land-use management in 20th-century GB and concomitant loss of breeding habitat must have resulted in considerable declines for many moth species.

Chemical pollution

Eutrophication (increased soil and water fertility caused by unintended nutrient inputs from fossil fuel combustion and agriculture) is altering the plant composition and vegetation structure of many habitats, often in conjunction with other drivers such as management intensity and climate change (Bobbink *et al.* 1998; Van der Wal *et al.* 2003; Hartley & Mitchell 2005). Biodiversity of plant and insect populations (e.g. butterflies) correlates negatively with nitrogen input (Pollard *et al.* 1998; Stevens *et al.* 2004; Öckinger *et al.* 2006; WallisDeVries & van Swaay 2006), so there may be substantial, unquantified impacts on moth populations resulting from such chemical pollution.

Links between other forms of chemical pollution and moth populations appear completely unstudied in GB. It has been suggested that the population increases seen amongst moths that utilise lichens and algae as larval hostplants (e.g. the footman moths in sub-family Lithosiinae) might be linked to the recovery of some of these organisms following amelioration of sulphur dioxide pollution (Fox *et al.* 2006b). However, there is no direct evidence for such causality. Similarly, while there has been much research into the impacts of pollution by heavy metals and other chemicals on humans, other vertebrates and plants (e.g. Sharma & Agrawal 2005), there have been few studies involving moths. Negative fitness impacts of chemical pollution on moth larvae have been shown in Europe (Mitterböck & Fuhrer 1988; van Ooik *et al.* 2007; van Ooik & Rantala 2010), but population effects have not been established.

In summary, there is no evidence currently available to suggest that chemical pollution in its many, complex and interacting forms is a driver of change in moth populations in GB. However, as a key constituent of agricultural intensification and through negative effects on the insects themselves, larval hostplants and other essential resources, it is probable that chemical inputs in the form of herbicides, insecticides and fertilizers have contributed to the decline of GB moth populations.

Light pollution

Many moth species are attracted to artificial light, although the mechanistic basis for this behaviour is not entirely clear (Young 1997). Artificial light elicits a wide range of responses in many animal and plant species, but there is insufficient knowledge about impacts in the wild, especially among invertebrates (Longcore & Rich 2004; Rich & Longcore 2006; Sutherland *et al.* 2006; Poot *et al.* 2008; Royal Commission on Environmental Pollution 2009; Stone *et al.* 2009; Bruce-White & Shardlow 2011).

Outdoor lighting can cause direct mortality, increase exposure to predators and have disruptive effects on various elements of moth behaviour and life cycles (Frank 2006; Bruce-White & Shardlow 2011). However, such effects vary between species, populations and even individuals, as well as with the spectral composition of the light sources. Furthermore, direct impacts of light pollution must be quantified separately from the other effects of urbanisation and habitat loss that usually accompany an increase in lighting levels.

Unfortunately, despite a massive increase in background light levels in GB and many other parts of the globe, there have been few studies on the impact of outdoor lighting on moths (e.g. Eisenbeis 2006; van Langevelde *et al.* 2011) and none that have assessed population-level or community-level effects.

Conrad *et al.* (2006) undertook a comparison of moth population trends from the RIS network using satellite data on the change in background illumination levels in GB. There was no significant difference between total moth abundance in areas exposed to increased background light levels and those unaffected. However, illumination data were available for only a short period (1992-2000), and therefore this finding does not preclude light pollution as a driver of long-term moth declines in GB.

In summary, although the attraction of moths to artificial light has been known for centuries and disruptive and fitness-reducing impacts of such attraction have been demonstrated, light pollution remains uninvestigated as a possible cause of population-level changes in moths.

Climate change

Climate change has already caused considerable modification of geographical range, abundance and phenology for many species globally (Parmesan & Yohe 2003; Gregory *et al.* 2009; Thackeray *et al.* 2010; Chen *et al.* 2011) and is perceived to be a major threat to biodiversity (Thomas *et al.* 2004a; Pounds *et al.* 2006; Thomas *et al.* 2006; Ohlemüller *et al.* 2008; Bálint *et al.* 2011; Maclean & Wilson 2011).

In GB (and elsewhere in north-west Europe), moderate levels of climate warming may bring opportunities for thermally-constrained species such as insects and there is strong evidence, for example, that some butterflies have already expanded their ranges and flight periods in response to climate change (Roy & Sparks 2000; Warren *et al.* 2001; Hill *et al.* 2002; Davies *et al.* 2006; Menéndez *et al.* 2007). At the same time, climate change may threaten other species through the loss of thermally suitable habitat space (Franco *et al.* 2006; Wilson *et al.* 2007; Maes *et al.* 2010), altered phenological synchrony with hostplants (Singer & Parmesan 2010) and even hybridization (Mallet *et al.* 2011).

Established links between climate change and the decline of moths in GB are limited at present. Population trends of a small group of northerly distributed species (i.e. those with a southern range margin within GB) decreased compared with southerly distributed moths (Conrad *et al.* 2004), and Morecroft *et al.* (2009) found significant decreasing population trends for moth species with more northerly European distributions at northern, upland sites in the UK Environmental Change Network.

In addition, several studies have found links between winter conditions and moth declines, indicative of climatic influence. Population levels of Garden Tiger correlate closely, and negatively, with winter precipitation and mean spring temperature, suggesting a link between climate change and the severe decline (89% decrease in population index,1968-2002) of this moth (Conrad *et al.* 2002). Furthermore, studies of moth declines in both GB and the Netherlands found significant relationships between overwintering life-cycle stage and species trend; moths that overwinter in the egg stage had declined (on average) more than others (Conrad *et al.* 2004; Groenendijk & Ellis 2011; and a similar result for butterflies in WallisDeVries & van Swaay 2006). Species overwintering as larvae or pupae had also decreased, while species that are adults during the winter had, on average, increased in both countries.

Another effect of winter and early spring climate has been observed on Winter Moth *Operophtera brumata* populations in the Netherlands. The synchrony of larval hatching date with the availability of its larval food resource (bud burst of *Quercus robur*) decreased over time, because of larvae hatching in advance of bud burst (Visser & Holleman 2001). The degree of synchrony was reduced by warmer spring temperatures combined with no change in the incidence of days with frost during the winter. Such asynchrony is predicted to cause a large increase in larval mortality, which is a major driver of population dynamics in this species. Thus, prolonged or high levels of asynchrony might cause population decreases in this moth species, although intense selection pressure to restore synchrony (or adaptive asynchrony) may rapidly redress this problem (van Asch *et al.* 2007; Both *et al.* 2009; Singer & Parmesan 2010).

In contrast, climate change is also expected to benefit elements of GB's moth fauna. There is already some evidence for range expansion and increased abundance among southerly distributed moth species (i.e. those with a northern range margin in GB). Morecroft *et al.* (2009) found that species with the most

southerly distributions at the European scale showed significant increases in population levels at 10 sites in the UK. The moth species with the greatest population increases in GB according to Conrad *et al.* (2006) also had increased distribution size, and the northern range margins of a sample of eight macro-moth species had shifted northwards considerably (mean 79.5km 10 year⁻¹ northward shift, 1982-2009), rivalling the largest equivalent results for butterflies and Odonata (Hill *et al.* 2002; Hickling *et al.* 2005; Fox *et al.* 2011b). This intimates that southern moths may conform to the general pattern of poleward range expansions recorded among other taxa in GB and globally (Hickling *et al.* 2006; Chen *et al.* 2011). The study by Salama *et al.* (2007) in central Scotland found that increasing moth diversity was positively correlated with mean annual temperature.

The absence of moth abundance decline in northern GB compared with significant decreases in southern GB appears to relate to a greater proportion of species with increasing population trends in the north (Conrad *et al.* 2006; Fox *et al.* 2006b; Scottish Government 2007). This pattern is consistent with poleward range expansion and increasing abundance of some moth species through northern GB in response to climate change. However, other factors, such as different patterns of land use and land-use change in northern GB, could equally be responsible.

Other generally positive climate change impacts on moths in GB include increased immigration (Sparks *et al.* 2005; Morecroft *et al.* 2009), colonisation (Parsons 2003, 2010) and phenological change. The latter includes many examples of advancement and increased duration of flight period and additional generations in apparent response to climate warming, both in GB and elsewhere in Europe (e.g. Fletcher 2006, 2009; Salama *et al.* 2007; Altermatt 2010; Pöyry *et al.* 2011).

In summary, although the evidence is limited at present, GB moths appear to be responding to climate change in qualitatively similar ways to butterflies. There are suggestions of climatic effects leading to the decline of some species, but also clear evidence of apparently positive impacts on species populations and distributions. Future climate change may, of course, alter this balance if new conditions are unsuitable for moth species in GB, plus the interaction between climate change and habitat loss, for example through sea-level rises, may damage specialist moth communities of coastal wetland habitats (e.g. Fisher's Estuarine Moth *Gortyna borelii*; Ringwood *et al.* 2004).

Non-native species

Globally, non-native species are regarded as a principle driver of biodiversity decline and an ongoing threat to species and habitats (Mack *et al.* 2000; Manchester & Bullock 2000; Gurevitch & Padilla 2004; McGeoch *et al.* 2010). Many species of non-native plants, vertebrates and invertebrates are established in GB, and there are numerous negative impacts on native biodiversity (Brown *et al.* 2008; Lack 2010; Lever 2010; Holt *et al.* 2011).

There have been no quantitative assessments of the impact of non-native species on moth populations in GB. Nonetheless, negative effects might be expected via the influence of invasive plant species and introduced animals (e.g. deer) on habitat quality and larval hostplant resources. Examples of specific impacts include the invasion of semi-natural habitats of Slender Scotch Burnet *Zygaena loti*, Transparent Burnet *Z. purpuralis* and *Eudarcia richardsoni* by *Cotoneaster* spp. shrubs (M. Parsons & T. Prescott, pers. comm.). Experiments in the United States found that non-native woody plants supported significantly lower abundance and species richness of moth and butterfly larvae than native trees and shrubs, even if the alien plants were in the same genus as the native hostplants (Burghardt *et al.* 2010). The impact of new predators is even more poorly understood, with species such as Harlequin Ladybird *Harmonia axyridis* and the parasitic fly *Sturmia bella* spreading rapidly and having the potential to impact on moth populations as well as other insects (Brown *et al.* 2011; Gripenberg *et al.* 2011).

Set against these examples is the success of some colonising and rapidly increasing moths that utilise non-native plants as larval hosts (Parsons 2003, 2010; Conrad *et al.* 2006; Fox *et al.* 2011b). Blair's Shoulder-knot *Lithophane leautieri*, for example, utilises Cupressaceae trees and shrubs and, having become established on the south coast of GB in the mid-20th century, spread rapidly northwards (146km 10 year⁻¹, 1982-2009) and increased substantially in

abundance (16.5% year⁻¹, 1968-2002). Other Cupressaceae-feeding moths show similar patterns, including recent colonists (e.g. Cypress Carpet *Thera cupressata* and Cypress Pug *Eupithecia phoeniceata*) and native species (e.g. Juniper Carpet *T. juniperata* and Juniper Pug *E. pusillata*). The latter moths were formerly restricted to semi-natural habitats where their only native larval hostplant Juniper *Juniperus communis* occurs but, in recent decades, both moths have colonised many gardens in which ornamental Cupressaceae species have been planted (Waring *et al.* 2009).

Non-native species have not been directly linked with moth declines or extinctions in GB as yet, though there is clear potential for negative impacts. On the contrary, non-native plants have enabled new moths to colonise GB and a few native species to extend their distributions.

Exploitation of populations

Collecting of wild specimens of macro-moths was once an integral part of the natural history study of this taxon in GB. In modern times, despite an increase in popular interest in macro-moths, collecting of specimens is less commonplace. Although over-collecting has often been postulated as a cause of decline or extinction for rare moths and butterflies in GB, there is little evidence to support the assertion (Young 1997; Asher *et al.* 2001), contrary to other taxa (Diamond *et al.* 1989; Roberts & Hawkins 1999; Jackson *et al.* 2001; Rosser & Mainka 2002; Dirzo & Raven 2003). Indeed, the large population sizes, phased emergence and short lifespan of many moth species also make it theoretically unlikely that anything but highly organised, exhaustive collecting could impact on any but the rarest localised species. Nevertheless, responsible collecting is strongly urged by relevant UK organisations, and there is a widely accepted code of conduct (Invertebrate Link 2002).

Young (1997) considered New Forest Burnet to be the only moth species for which there was credible evidence of extinction caused by collecting in GB. After discovery in 1869, nine sites were found in the New Forest in southern England, attracting large numbers of collectors, and the moth became extinct in 1927. The extinction proved short-lived, however, as another, isolated colony of the moth was later discovered in Scotland. The precise location of this remaining colony has not been publicised to reduce potential damage from collecting.

Synthesis: why have GB moths declined?

Substantial decreases have occurred in overall abundance of macro-moths and the populations of many widespread species in GB and north-western Europe. In some cases, parallel reductions in distribution have been recorded (Conrad *et al.* 2002; Fox *et al.* 2011b). However, direct evidence to explain the trends is very limited. Correlative results and extrapolation from better-studied insect taxa (e.g. butterflies) provide the basis for our current understanding of the probable causes of moth declines and can be summarised as follows:

Multiple drivers of change

This review indicates the influence of multiple drivers in the decline of GB moths. This is expected as it is improbable that each species in a diverse taxon would be affected by the same environmental and ecological factors. Various elements of habitat degradation, including habitat destruction, reduction in quality, loss of heterogeneity, and increased isolation, resulting from major land-use changes of the 20th century (agricultural intensification, changing woodland management, urbanisation) are very likely to have had an adverse impact on moths. For habitat specialist moths, this is a simple truth – the total area of semi-natural habitats such as unimproved calcareous grassland, heathland, fens and lowland raised bogs has decreased substantially. Generalist moths may also have been affected detrimentally by such losses but are, in addition, likely to have declined as changing land management (increased intensity in agricultural landscapes and a switch to high-forest silviculture) reduced available niches.

Research in agricultural and woodland settings show that moth abundance and species richness increase in response to techniques that reverse recent changes in management intensity. There is also correlative evidence that habitats subject to lower levels of management intensity change (e.g. organic farms) have higher abundance and species richness of moths.

Other drivers appear to be important too. There is strong evidence of both positive and negative climate change impacts. Currently, the impacts of chemical and light pollution and non-native species are insufficiently studied and understood to assess accurately. Thus far, most of the recognised impacts of non-native plants are positive, providing novel niches. Of the potential drivers of change considered in this paper, only direct exploitation of moth populations, in the form of collecting, is considered to be negligible in impact across the taxon.

Interactions and synergies

Evidence from other taxa suggests that multiple drivers of population change are likely to interact, often in complex ways, and may produce synergies (Travis 2003; Brook *et al.* 2008). Thus, one driver, such as habitat loss, may act to reduce populations to levels where synergistic processes, both intrinsic (e.g. population dynamics, inbreeding depression) and external (e.g. other drivers such as climate change), and stochastic effects form amplifying feedback loops and drive species towards extinction. Such synergies have yet to be identified for moths in GB, but some have been elucidated for butterflies (e.g. interactions between habitat loss and the negative implications of isolation for populations, and between climate change and nitrogen pollution (WallisDeVries & van Swaay 2006; Bulman *et al.* 2007; Hanski & Pöyry 2007)).

The human activities that shape the environment tend to generate complex mixtures of change. For example, agricultural intensification causes habitat loss, but also changes spatiotemporal structure and heterogeneity, and chemical inputs alter botanical communities. Urbanisation also causes habitat loss, along with changes to the climatic environment, background lighting levels and chemical pollution. Isolating the relative contributions of these drivers to moth declines within the real world of human land use is an enormous challenge that has, as yet, received little attention.

Future perspectives

Much moth research to date has focused on species that are economic pests on agricultural or forestry crops. The conservation biology of moths has been neglected as a research topic, particularly in comparison with butterflies and, as

a result, although widespread declines of moth faunas have been identified recently from GB and other countries, knowledge of the underlying causes is scant. Fortunately, this has started to change. Ecologists are taking a greater interest in moths, spurred on by the pressing need to understand the causes and implications of biodiversity decline and the opportunities afforded by an ecologically-diverse and species-rich taxon supported by large surveillance and monitoring datasets. Sutherland et al. (2006) highlighted the need to understand the causes of moth declines as one of 100 ecological questions of high policy relevance, Butterfly Conservation continues to raise awareness of the declines among the public and policy makers alike (e.g. Fox *et al.* 2006b) and the UK Government added 71 species of widespread but rapidly-declining macro-moths to the UK Biodiversity Action Plan as Priority Species with the intention of stimulating research into causal factors and amelioration measures. The maintenance of recording and monitoring schemes gathering spatially extensive, long-term, time-series data on moths is vital to underpin future research and conservation.

It is hoped, therefore, that the next decade will see a continued surge in research interest leading to better comprehension of the changes taking place in GB's moth fauna. The following issues and questions are proposed to help understand and reverse the decline.

1. What is the complete picture of change for GB moths? Overall abundance has decreased, but the differing trends between northern and southern halves of GB provide a natural contrast that might shed light on the causes of change. Are the differences due to less-intensive land use and more extensive semi-natural habitats in northern GB or do they arise from climate change driving increases in range and abundance for southerly distributed moth species? Furthermore, population and/or distribution trends have been calculated for fewer than half of the c.900 macro-moth species and only a tiny proportion of the c.1600 micro-moths. Long-term distribution data have now been gathered by the National Moth Recording Scheme for all macro-moths in the UK (Fox *et al.* 2011b), and could be used to generate distribution trends and estimates of range margin shift. Revised national population trends from the ongoing RIS would also yield more up-to-date

information, and critical statistical analysis might yield further insight into the underlying causes. Trend analyses are currently impossible for all but a small minority of micro-moths (e.g. the Pyralidae), but greater co-ordination of micro-moth recording at the national level could generate suitable data in the medium term.

- 2. As agricultural intensification is considered to be a major driver of moth declines in GB, improved understanding of the impacts of different elements of agricultural management is required. Identification of the key factors that depress moth abundance and diversity would facilitate efforts to reverse the trends (e.g. through AES). For example, 'What are the relative impacts of initial loss of habitat to cropped land versus the subsequent agricultural management?', 'How important is local habitat heterogeneity?' and 'What role do pesticides play in relation to other aspects of crop cultivation?'
- 3. More research is needed into land-management techniques that attempt to mitigate against biodiversity loss (Warren & Bourn 2011). If moth declines are to be reversed and wider biodiversity policy targets met, evidence-based AES prescriptions, woodland management practices and urban landscape designs are needed. Currently, there is little evidence that AES have benefited biodiversity, despite huge budget expenditure, at the national and European scale (Kleijn et al. 2011; but see Brereton et al. 2008). Crucially, the impact of such management techniques on populations is a vital but seldom addressed issue. Most studies, including those on moths, focus on recording changes in the abundance and species richness of adult animals in relation to management treatments and make no assessment of reproduction, immature stages or population dynamics (e.g. Feber et al. 1996; Pywell et al. 2004; Merckx et al. 2009b; Haaland et al. 2011). Management techniques may simply concentrate mobile adults within the landscape (e.g. at nectar resources) without contributing substantially to improved fitness or increased population levels. Worse still, interventions aimed at improving biodiversity might have a negative impact via sourcesink effects (Severns 2011).

- 4. An equally critical question concerns the optimal targeting of AES for maximum benefit and cost-effectiveness. Theoretical and (limited) empirical evidence suggests benefits from clustering AES participation in the landscape (Merckx *et al.* 2009b; Gabriel *et al.* 2010), targeting extensively farmed land that retains relatively high levels of biodiversity (Kleijn *et al.* 2009) and, conversely, focusing on 'simple' landscapes where agriculture already dominates and semi-natural habitats are isolated (Tscharntke *et al.* 2005). An associated debate concerns the relative merits of setting land aside (or taking land out of cultivation) for biodiversity conservation (land sparing) versus reducing the intensity of agricultural management on farmland to benefit wildlife at the expense of production (land sharing) (Green *et al.* 2005; Hodgson *et al.* 2010). Apart from the recent work of Merckx *et al.* (2009b), there is no information on these contrasting strategies that relates directly to moths in GB.
- 5. The impact of outdoor, artificial lighting and background light pollution on moths and other nocturnal biodiversity is a topic requiring urgent ecological research (Sutherland *et al.* 2006). It is imperative that such studies aim to elucidate and quantify population-level effects and that research focuses on artificial lighting of types and intensities commonly experienced by wild moth populations. Does artificial light cause negative population-level effects in moth populations through increased mortality and disruption of life-cycles and behaviour? If so, what measures can be taken to reduce these impacts (e.g. through choice of lighting type, power, quantity and orientation, placement of lights and the periods that they are operated)?
- 6. Finally, although many impacts of climate change have been recorded for butterflies and other taxa in GB, little is known about the responses of moths to weather and climate (with the exception of Garden Tiger, Conrad *et al.* 2002). It would be insightful to assess the range margin shifts of all macromoth species in GB, utilising the National Moth Recording Scheme database, and to attempt to relate shifts to climate change, habitat and larval hostplant distribution. In addition, the species richness of the macro-moth fauna in GB provides a good opportunity to detect poleward or uphill retreats

of high-altitude or northerly distributed species, which have proved rather elusive thus far.

The requirement for a research and conservation response elicited by the recently discovered widespread declines of moths in GB and beyond is substantial and challenging. These declines are one of the clearest signals yet of catastrophic biodiversity loss caused by anthropogenic environmental and land-use changes, which is of great conservation concern and threatens ecosystem services upon which the human race depends. Understanding and taking measures to reverse the declines of diverse insect faunas, such as GB macro-moths, are vital steps back from the brink.

Acknowledgments

I thank John Hopkins for the original suggestion of this paper, Thomas Merckx for sharing unpublished results, and Aldina Franco, Thomas Merckx, Mark Parsons, Martin Warren, Ian Woiwod and Mark Young for constructive comments that greatly improved earlier drafts.

References

Altermatt F (2010) Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B* **277**, 1281–1287.

Asher J, Warren M, Fox R, Harding P, Jeffcoate G & Jeffcoate S (2001) *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford University Press, Oxford, UK.

Bálint M, Domisch S, Engelhardt CHM, Haase P, Lehrian S, Sauer J, Theissinger K, Pauls SU & Nowak C (2011) Cryptic biodiversity loss linked to global climate change. *Nature Climate Change* **1**, 313–318.

Balmer O & Erhardt A (2000) Consequences of succession on extensively grazed grasslands for central European butterfly communities: rethinking conservation practices. *Conservation Biology* **14**, 746–757.

Balmford A & Bond W (2005) Trends in the state of nature and their implications for human well-being. *Ecology Letters* **8**, 1218–1234.

Benton TG, Bryant DM, Cole L & Crick HQP (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology* **39**, 673–687.

Benton TG, Vickery JA & Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution* **18**, 182–188.

Bergerot B, Julliard R & Baguette M (2010) Metacommunity dynamics: decline of functional relationship along a habitat fragmentation gradient. *PLoS One* **5**, e11294.

Betzholtz P-E & Franzén M (2011) Mobility is related to species traits in noctuid moths. *Ecological Entomology* **36**, 369–376.

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J & Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**, 351–354.

Bignal EM & McCracken DI (1996) Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology* **33**, 413–424.

Bobbink R, Hornung M & Roelofs JGM (1998) The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* **86**, 717–738.

Both C, van Asch M, Bijlsma R, van den Berg AB & Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* **78**, 73–83.

Bourn NAD & Thomas JA (2002) The challenge of conserving grassland insects at the margins of their range in Europe. *Biological Conservation* **104**, 285–292.

Brereton T, Roy DB, Middlebrook I, Botham M & Warren M (2011) The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation* **15**, 139–151.

Brereton TM, Warren MS, Roy DB & Stewart K (2008) The changing status of the Chalkhill Blue butterfly *Polyommatus coridon* in the UK: the impacts of conservation policies and environmental factors. *Journal of Insect Conservation* **12**, 629–638. Brook BW, Sodhi NS & Bradshaw CJA (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**, 453–460.

Brooks TM, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G & Hilton-Taylor C (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* **16**, 909–923.

Broome A, Clarke S, Peace A & Parsons M (2011) The effect of coppice management on moth assemblages in an English woodland. *Biodiversity and Conservation* **20**, 729–749.

Brown PMJ, Frost R, Doberski J, Sparks T, Harrington R & Roy HE (2011) Decline in native ladybirds in response to the arrival of *Harmonia axyridis*: early evidence from England. *Ecological Entomology* **36**, 231–240.

Brown PMJ, Roy, HE, Rothery P, Roy DB, Ware RL & Majerus MEN (2008) *Harmonia axyridis* in Great Britain: analysis of the spread and distribution of a non-native coccinellid. *BioControl* **53**, 55–68.

Bruce-White C & Shardlow M (2011) A Review of the Impact of Artificial Light on Invertebrates. Buglife, Peterborough, UK.

Bulman CR, Wilson RJ, Holt AR, Gálvez Bravo L, Early RI, Warren MS & Thomas CD (2007) Minimum viable metapopulation size, extinction debt, and the conservation of a declining species. *Ecological Applications* **17**, 1460–1473.

Burghardt KT, Tallamy DW, Philips C & Shropshire KJ (2010) Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere* **1**, article 11.

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque J-F, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Hernández Morcillo M, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié J-C & Watson R (2010) Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168.

Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF & Griswold TL (2011) Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the USA* **108**, 662–667.

Carey PD, Wallis SM, Emmett BE, Maskell LC, Murphy J, Norton LR, Simpson IC & Smart SS (2008) *Countryside Survey: UK Headline Messages from 2007*. Centre for Ecology & Hydrology, Lancaster, UK.

Chapman JW, Drake VA & Reynolds DR (2011) Recent insights from radar studies of insect flight. *Annual Review of Entomology* **56**, 337–356.

Chen I-C, Hill JK, Ohlemüller R, Roy DB & Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026.

Clarke SA, Green DG, Bourn NA & Hoare DJ (2011) *Woodland management for butterflies and moths: a best practice guide*. Butterfly Conservation, Wareham, UK.

Conrad KF, Fox R & Woiwod IP (2007) Monitoring biodiversity: measuring longterm changes in insect abundance. *Insect Conservation Biology*, (ed. AJA Stewart, TR New & OT Lewis), pp. 203–225. CABI publishing, Wallingford, UK.

Conrad KF, Warren M, Fox R, Parsons M & Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation* **132**, 279–291.

Conrad KF, Woiwod IP, Parsons M, Fox R & Warren M (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation* **8**, 119–136.

Conrad KF, Woiwod IP & Perry JN (2002) Long-term decline in abundance and distribution of the garden tiger moth (*Arctia caja*) in Great Britain. *Biological Conservation* **106**, 329–337.

Davies ZG, Wilson RJ, Coles S & Thomas CD (2006) Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology* **75**, 247–256.

Devoto M, Bailey S & Memmott J (2011) The 'night-shift': nocturnal pollentransport networks in a boreal pine forest. *Ecological Entomology* **36**, 25–35.

Diamond JM, Ashmole NP & Purves PE (1989) The present, past and future of human-caused extinctions. *Philosophical Transactions of the Royal Society B* **325**, 469–477.

Dirzo R & Raven PH (2003) Global state of biodiversity and loss. *Annual Review of Environmental Resources* **28**, 137–167.

Donald PF, Green RE & Heath MF (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society B* **268**, 25–29.

Dunn RR (2005) Modern insect extinctions, the neglected majority. *Conservation Biology* **19**, 1030–1036.

Eisenbeis G (2006) Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. *Ecological Consequences of Artificial Night Lighting*, (ed. C Rich & T Longcore), pp. 281–304. Island Press, Washington DC, USA.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review* of Ecology, Evolution, and Systematics **34**, 487–515.

Feber RE, Smith H & Macdonald DW (1996) The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology* **33**, 1191–1205.

Fletcher CH (2006) Changes in the behaviour of double-brooded macro moths in Yorkshire. *Entomologist's Record and Journal of Variation* **118**, 105–113.

Fletcher CH (2009) The effects of climatic warming on flight time of moths in Yorkshire. *Entomologist's Record and Journal of Variation* **121**, 109–118.

Fitzpatrick U, Murray TE, Paxton RJ & Brown MJF (2007) Building on IUCN regional Red Lists to produce lists of species of conservation priority: a model with Irish bees. *Conservation Biology* **21**, 1324–1332.

Fox R, Asher J, Brereton T, Roy D & Warren M (2006a) *The State of Butterflies in Britain and Ireland*. Pisces Publications, Newbury, UK.

Fox R, Conrad KF, Parsons MS, Warren MS & Woiwod IP (2006b) *The State of Britain's Larger Moths*. Butterfly Conservation and Rothamsted Research, Wareham, UK.

Fox R, Conrad KF, Parsons MS, Warren MS & Woiwod IP (2010). Moths. *Silent Summer: the State of the Wildlife in Britain and Ireland*, (ed. N Maclean), pp. 448–470. Cambridge University Press, Cambridge, UK.

Fox R, Brereton TM, Roy DB, Asher J & Warren MS (2011a) *The State of the UK's Butterflies 2011*. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, Dorset, UK.

Fox R, Randle Z, Hill L, Anders S, Wiffen L & Parsons MS (2011b) Moths Count: recording moths for conservation in the UK. *Journal of Insect Conservation* **15**, 55–68.

Franco AMA, Hill JK, Kitschke C, Collingham YC, Roy DB, Fox R, Huntley B & Thomas CD (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* **12**, 1545–1553.

Frank KD (2006) Effects of artificial night lighting on moths. *Ecological Consequences of Artificial Night Lighting*, (ed. C Rich & T Longcore), pp. 305– 344. Island Press, Washington DC, USA.

Franzén M & Johannesson M (2007) Predicting extinction risk of butterflies and moths (Macrolepidoptera) from distribution patterns and species characteristics. *Journal of Insect Conservation* **11**, 367–390.

Franzén M & Nilsson SG (2007) What is the minimum landscape size for dispersal studies? *Journal of Animal Ecology* **76**, 1224–1230.

Freemark KE & Boutin C (1995) Impacts of agricultural herbicide use on terrestrial wildlife in temperate landscapes: a review with special reference to North America. *Agriculture, Ecosystems and Environment* **52**, 67–91.

Fuentes-Montemayor E, Goulson D & Park K (2011) The effectiveness of agrienvironment schemes for the conservation of farmland moths: assessing the importance of a landscape-scale management approach. *Journal of Applied Ecology* **48**, 532–542. Fuller RJ, Noble DG, Smith KW & Vanhinsbergh D (2005) Recent declines in populations of woodland birds in Britain: a review of possible causes. *British Birds* **98**, 116–143.

Gabriel D, Sait SM, Hodgson JA, Schmutz U, Kunin WE & Benton TG (2010) Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters* **13**, 858–869.

Gaston KJ & Evans KL (2010) Urbanisation and development. *Silent summer: the State of the Wildlife in Britain and Ireland*, (ed. N Maclean), pp. 72–83. Cambridge University Press, Cambridge, UK.

Gibbs KE, Mackey RL & Currie DJ (2009) Human land use, agriculture, pesticides and losses of imperiled species. *Diversity and Distributions* **15**, 242–253.

Goulson D, Lye GC & Darvill B (2008) Decline and conservation of bumble bees. *Annual Review of Entomology* **53**, 191–208.

Green RE, Cornell SJ, Scharlemann JPW & Balmford A (2005) Farming and the fate of wild nature. *Science* **307**, 550–555.

Gregory RD, Willis SG, Jiguet F, Voříšek P, Klvaňová A, van Strien A, Huntley B, Collingham YC, Couvet D & Green RE (2009) An indicator of the impact of climatic change on European bird populations. *PLoS One* **4**, e4678.

Gripenberg S, Hamer N, Brereton T, Roy DB & Lewis OT (2011) A novel parasitoid and a declining butterfly: cause or coincidence? *Ecological Entomology* **36**, 271–281.

Groenendijk D & Ellis WN (2011) The state of the Dutch larger moth fauna. *Journal of Insect Conservation* **15**, 95–101.

Groenendijk D & van der Meulen J (2004) Conservation of moths in the Netherlands: population trends, distribution patterns and monitoring techniques of day-flying moths. *Journal of Insect Conservation* **8**,109–118.

Gurevitch J & Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* **19**, 470–474.

Haaland C, Naisbit RE & Bersier L-F (2011) Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity* **4**, 60–80.

Halada L, Evans D, Romão C & Petersen J-E (2011) Which habitats of European importance depend on agricultural practices? *Biodiversity and Conservation* **20**, 2365–2378.

Hambler C & Speight MR (2004) Extinction rates and butterflies. *Science* **305**, 1563.

Hanski I & Pöyry J (2007) Insect populations in fragmented habitats. *Insect Conservation Biology*, (ed. AJA Stewart, TR New & OT Lewis), pp. 175–202. CABI, Wallingford, UK.

Hartley SE & Mitchell RJ (2005) Manipulation of nutrients and grazing levels on heather moorland: changes in *Calluna* dominance and consequences for community composition. *Journal of Ecology* **93**, 990–1004.

Hickling R, Roy DB, Hill JK & Thomas CD (2005) A northward shift of range margins in British Odonata. *Global Change Biology* **11**, 502–506.

Hickling R, Roy DB, Hill JK, Fox R & Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**, 450–455.

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J & Huntley B (2002) Responses of butterflies to 20th century climate warming: implications for future ranges. *Proceedings of the Royal Society B* **269**, 2163–2171.

Hodgson JA, Kunin WE, Thomas CD, Benton TG & Gabriel D (2010) Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale. *Ecology Letters* **13**, 1358–1367.

Hodgson JA, Thomas CD, Wintle BA & Moilanen A (2009) Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology* **46**, 964–969.

Holt CA, Fuller RJ & Dolman PM (2011) Breeding and post-breeding responses of woodland birds to modification of habitat structure by deer. *Biological Conservation* **144**, 2151–2162.

Invertebrate Link (JCCBI) (2002) A code of conduct for collecting insects and other invertebrates. *British Journal of Entomology and Natural History* **15**, 1–6.

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ & Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–637.

Kleijn D, Kohler F, Báldi A, Batáry P, Concepción ED, Clough Y, Díaz M, Gabriel D, Holzschuh A, Knop E, Kovács A, Marshall EJP, Tscharntke T & Verhulst J (2009) On the relationship between farmland biodiversity and landuse intensity in Europe. *Proceedings of the Royal Society B* **276**, 903–909.

Kleijn D, Rundlöf M, Scheper J, Smith HG & Tscharntke T (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution* **26**, 474–481.

Koh LP, Sodhi NS & Brook BW (2004) Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology* **18**, 1571–1578.

Kosior A, Celary W, Olejnikzak P, Fijal J, Krol W, Solarz W & Plonka P (2007) The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. *Oryx* **41**, 79–88.

Lack A (2010) Plant introductions. *Silent Summer: the State of the Wildlife in Britain and Ireland*, (ed. N Maclean), pp. 53–71. Cambridge University Press, Cambridge, UK.

Lever C (2010) Vertebrate animal introductions. *Silent Summer: the State of the Wildlife in Britain and Ireland*, (ed. N Maclean), pp. 36–52. Cambridge University Press, Cambridge, UK.

Littlewood NA (2008) Grazing impacts on moth diversity and abundance on a Scottish upland estate. *Insect Conservation and Diversity* **1**, 151–160.

Longcore T & Rich C (2004) Ecological light pollution. *Frontiers in Ecology and the Environment* **2**, 191–198.

Longley M & Sotherton NW (1997) Factors determining the effects of pesticides upon butterflies inhabiting arable farmland. *Agriculture, Ecosystems & Environment* **61**, 1–12.

Loram A, Warren PH & Gaston KJ (2008) Urban domestic gardens (XIV): the characteristics of gardens in five cities. *Environmental Management* **42**, 361–376.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M & Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**, 689–710.

Maclean IMD & Wilson RJ (2011) Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences of the USA* **108**, 12337–12342.

Maes D, Titeux N, Hortal J, Anselin A, Decleer K, De Knijf G, Fichefet V & Luoto M (2010) Predicted insect diversity declines under climate change in an already impoverished region. *Journal of Insect Conservation* **14**, 95–101.

Maes D & Van Dyck H (2001) Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biological Conservation* **99**, 485–498.

Majerus MEN (2002) Moths. HarperCollins, London, UK.

Mallet J, Wynne IR & Thomas CD (2011) Hybridisation and climate change: brown argus butterflies in Britain (*Polyommatus* subgenus *Aricia*). *Insect Conservation and Diversity* **4**, 192–199.

Manchester SJ & Bullock JM (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. *Journal of Applied Ecology* **37**, 845–864.

Mattila N, Kaitala V, Komonen A, Kotiaho JS & Päivinen J (2006) Ecological determinants of distribution decline and risk of extinction in moths. *Conservation Biology* **20**,1161–1168.

Mattila N, Kotiaho JS, Kaitala V & Komonen A (2008) The use of ecological traits in extinction risk assessments: a case study on geometrid moths. *Biological Conservation* **141**, 2322–2328.

May RM (2010) Ecological science and tomorrow's world. *Philosophical Transactions of the Royal Society B* **365**, 41–47.

McGeoch MA, Butchart SHM, Spear D, Marais E, Kleynhans EJ, Symes A, Chanson J & Hoffmann M (2010) Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. *Diversity and Distributions* **16**, 95–108.

McKinney ML (1999) High rates of extinction and threat in poorly studied taxa. *Conservation Biology* **13**, 1273–1281.

McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems* **11**, 161–176.

McLaughlin A & Mineau P (1995) The impact of agricultural practices on biodiversity. *Agriculture Ecosystems and Environment* **55**, 201–212.

Menéndez R, González-Megías A, Collingham Y, Fox R, Roy DB, Ohlemüller R & Thomas CD (2007) Direct and indirect effects of climate and habitat factors on specialist and generalist butterfly diversity. *Ecology* **88**, 605–611.

Merckx T, Feber RE, Dulieu RL, Townsend MC, Parsons MS, Bourn NAD, Riordan P & Macdonald DW (2009a) Effect of field margins on moths depends on species mobility: field-based evidence for landscape-scale conservation. *Agriculture, Ecosystems and Environment* **129**, 302–309.

Merckx T, Feber RE, Hoare DJ, Parsons MS, Kelly CJ, Bourn NAD & Macdonald DW (2012) Conserving threatened Lepidoptera: towards an effective woodland management policy in landscapes under intense human land-use. *Biological Conservation* **149**, 32–39.

Merckx T, Feber RE, Mclaughlan C, Bourn NAD, Parsons MS, Townsend MC, Riordan P & Macdonald DW (2010a) Shelter benefits less mobile moth species: The field-scale effect of hedgerow trees. *Agriculture, Ecosystems and Environment* **138**, 147–151.

Merckx T, Feber RE, Parsons MS, Bourn NAD, Townsend MC, Riordan P & Macdonald DW (2010b) Habitat preference and mobility of *Polia bombycina*: are non-tailored agri-environment schemes any good for a rare and localised species? *Journal of Insect Conservation* **14**, 499–510.

Merckx T, Feber RE, Riordan P, Townsend MC, Bourn NAD, Parsons MS & Macdonald DW (2009b) Optimizing the biodiversity gain from agri-environment schemes. *Agriculture, Ecosystems and Environment* **130**, 177–182.

Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: synthesis*. Island Press, Washington DC, USA.

Mitterböck F & Fuhrer E (1988) Effects of fluoride-polluted spruce leaves on nun moth caterpillars (*Lymantria monacha*). *Journal of Applied Entomology* **105**, 19–27.

Mooney HA (2010) The ecosystem-service chain and the biological diversity crisis. *Philosophical Transactions of the Royal Society B* **365**, 31–39.

Morecroft MD, Bealey CE, Beaumont DA, Benham S, Brooks DR, Burt TP, Critchley CNR, Dick J, Littlewood NA, Monteith DT, Scott WA, Smith RI, Walmsley C & Watson H (2009) The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation* **142**, 2814–2832.

Nieminen M (1996) Migration of moth species in a network of small islands. *Oecologia* **108**, 643–651.

Nieminen M, Rita H & Uuvana P (1999) Body size and migration rate in moths. *Ecography* **22**, 697–707.

Nilsson SG, Franzén M & Jönsson E (2008) Long-term land-use changes and extinction of specialised butterflies. *Insect Conservation and Diversity* **1**, 197–207.

Ohlemüller R, Anderson BJ, Araújo MB, Butchart SHM, Kudrna O, Ridgely RS & Thomas CD (2008) The coincidence of climatic and species rarity: high risk to small-range species from climate change. *Biology Letters* **4**, 568–572.

Öckinger E, Hammarstedt O, Nilsson SG & Smith HG (2006) The relationship between local extinctions of grassland butterflies and increased soil nitrogen levels. *Biological Conservation* **128**, 564–573.

Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, Petersen JD, Pöyry J, Settele J, Summerville KS & Bommarco R (2010) Lifehistory traits predict species responses to habitat area and isolation: a crosscontinental synthesis. *Ecology Letters* **13**, 969–979.

Parmesan C & Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.

Parsons MS (2003) The changing moth fauna of Britain during the twentieth century. *Entomologist's Record and Journal of Variation* **115**, 49–66.

Parsons M (2010) The changing moth and butterfly fauna of Britain – the first decade of the twenty-first century (2000–2009). *Entomologist's Record and Journal of Variation* **122**, 13–22.

Pimm SL, Russell GJ, Gittleman JL & Brooks TM (1995) The future of biodiversity. *Science* **269**, 347–350.

Pocock MJO & Jennings N (2008) Testing biotic indicator taxa: the sensitivity of insectivorous mammals and their prey to the intensification of lowland agriculture. *Journal of Applied Ecology* **45**, 151–160.

Pollard E, Woiwod IP, Greatorex-Davies JN, Yates TJ & Welch RC (1998) The spread of coarse grasses and changes in numbers of Lepidoptera in a woodland nature reserve. *Biological Conservation* **84**, 17–24.

Poot H, Ens BJ, Vries HD, Donners MAH, Wernand MR & Marquenie JM (2008) Green light for nocturnally migrating birds. *Ecology and Society* **13**, 47.

Pounds JA, Bustamante MR, Coloma LA, Consuegra JA, Fogden MP, Foster PN, La Marca E, Masters KL, Merino-Viteri A, Puschendorf R, Ron SR, Sánchez-Azofeifa GA, Still CJ & Young BE (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167.

Pöyry J, Leinonen R, Söderman G, Nieminen M, Heikkinen RK & Carter TR (2011) Climate-induced increase of moth multivoltinism in boreal regions. *Global Ecology and Biogeography* **20**, 289–298.

Proctor M, Yeo P & Lack A (1996) *The Natural History of Pollination*. Harper Collins, London, UK.

Pywell RF, Warman EA, Sparks TH, Greatorex-Davies JN, Walker KJ, Meek WR, Carvell C, Petit S & Firbank LG (2004) Assessing habitat quality for butterflies on intensively managed arable farmland. *Biological Conservation* 118, 313–325.

Rich C & Longcore T (Eds.) (2006) *Ecological Consequences of Artificial Night Lighting*. Island Press, Washington DC, USA.

Rickman JK & Connor EF (2003) The effect of urbanization on the quality of remnant habitats for leaf-mining Lepidoptera on *Quercus agrifolia*. *Ecography* **26**, 777–787.

Ringwood Z, Hill J & Gibson C (2004) Conservation management of *Gortyna borelii lunata* (Lepidoptera: Noctuidae) in the United Kingdom. *Journal of Insect Conservation* **8**, 173–183.

Roberts CM & Hawkins JP (1999) Extinction risk in the sea. *Trends in Ecology* & *Evolution* **14**, 241–246.

Robinson RA & Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* **39**, 157–176.

Rockström J, Steffen W, Noone K, Persson Å, Chapin III FS, Lambin EF, Lenton TM, Scheffer M, Folke C, Schellnhuber HJ, Nykvist B, de Wit CA, Hughes T, van der Leeuw S, Rodhe H, Sörlin S, Snyder PK, Costanza R, Svedin U, Falkenmark M, Karlberg L, Corell RW, Fabry VJ, Hansen J, Walker B, Liverman D, Richardson K, Crutzen P & Foley JA (2009) A safe operating space for humanity. *Nature* **461**, 472–475.

Rosser AM & Mainka SA (2002) Overexploitation and species extinctions. *Conservation Biology* **16**, 584–586.

Roy DB, Bohan DA, Haughton AJ, Hill MO, Osborne JL, Clark SJ, Perry JN, Rothery P, Scott RJ, Brooks DR, Champion GT, Hawes C, Heard MS & Firbank LG (2003) Invertebrates and vegetation of field margins adjacent to crops subject to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society B* **358**, 1879–1898.

Roy DB & Sparks TH (2000) Phenology of British butterflies and climate change. *Global Change Biology* **6**, 407–416.

Royal Commission on Environmental Pollution (2009) *Artificial light in the environment*. The Stationery Office, Norwich, UK.

Salama NKG, Knowler JT & Adams CE (2007) Increasing abundance and diversity in the moth assemblage of east Loch Lomondside, Scotland over a 35 year period. *Journal of Insect Conservation* **11**, 151–156.

Schröter D, Cramer W, Leemans R, Prentice IC, Araújo MB, Arnell NW, Bondeau A, Bugmann H, Carter TR, Gracia CA, de la Vega-Leinert AC, Erhard M, Ewert F, Glendining M, House JI, Kankaanpää S, Klein RJT, Lavorel S, Lindner M, Metzger MJ, Meyer J, Mitchell TD, Reginster I, Rounsevell M, Sabaté S, Sitch S, Smith B, Smith J, Smith P, Sykes MT, Thonicke K, Thuiller W, Tuck G, Zaehle S & Zierl B (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science* **310**, 1333–1337.

Scottish Government (2007) *Scotland's Biodiversity Indicators*. The Scottish Government, Edinburgh, UK.

http://www.scotland.gov.uk/Resource/Doc/202855/0054080.pdf (accessed 12th September 2011).

Settele J, Dover J, Dolek M & Konvička M (2009) Butterflies of European ecosystems: impact of land use and options for conservation management. *Ecology of Butterflies in Europe* (ed. J Settele, T Shreeve, M Konvička & H Van Dyck), pp. 353–370. Cambridge University Press, Cambridge, UK.

Severns PM (2011) Habitat restoration facilitates an ecological trap for a locally rare, wetland-restricted butterfly. *Insect Conservation and Diversity* **4**, 184–191.

Sharma RK & Agrawal M (2005) Biological effects of heavy metals: an overview. *Journal of Environmental Biology* **26**, 301–313.

Singer MC & Parmesan C (2010) Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B* **365**, 3161–3176.

Skinner B (2009) Colour Identification Guide to Moths of the British Isles. Apollo Books, Stenstrup, Denmark.

Slade EM, Merckx T, Riutta T, Bebber DP, Redhead D, Riordan P & Macdonald DW (2013) Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. *Ecology* **94**, 1519–1530.

Smith C (2010) *London: garden city*? London Wildlife Trust, Greenspace Information for Greater London and the Greater London Authority, London, UK. Sparks TH, Greatorex-Davies JN, Mountford JO, Hall ML & Marrs RH (1996) The effects of shade on the plant communities of rides in plantation woodland and implications for butterfly conservation. *Forest Ecology and Management* **80**,197–207.

Sparks TH, Roy DB & Dennis RLH (2005) The influence of temperature on migration of Lepidoptera into Britain. *Global Change Biology* **11**, 507–514.

Stefanescu C, Peñuela J & Filella I (2009) Rapid changes in butterfly communities following the abandonment of grasslands: a case study. *Insect Conservation and Diversity* **2**, 261–269.

Stevens CJ, Dise NB, Mountford JO & Gowing DJ (2004) Impact of nitrogen deposition on the species richness of grasslands. *Science* **303**, 1876–1879.

Stone EL, Jones G & Harris S (2009) Street lighting disturbs commuting bats. *Current Biology* **19**, 1123–1127.

Sutherland WJ, Armstrong-Brown S, Armsworth PR, Brereton T, Brickland J, Campbell CD, Chamberlain DE, Cooke AI, Dulvy NK, Dusic NR, Fitton MG, Freckleton RP, Godfray HCJ, Grout N, Harvey HJ, Hedley C, Hopkins JJ, Kift NB, Kirby J, Kunin WE, Macdonald DW, Marker B, Naura M, Neale AR, Oliver T, Osborn D, Pullin AS, Shardlow MEA, Showler DA, Smith PL, Smithers RJ, Solandt J-L, Spencer J, Spray CJ, Thomas CD, Thompson J, Webb SE, Yalden DW & Watkinson AR (2006) The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology* **43**, 617–627.

Sutherland WJ, Bailey MJ, Bainbridge IP, Brereton T, Dick JTA, Drewitt J, Dulvy NK, Dusic NR, Freckleton RP, Gaston KJ, Gilder PM, Green RE, Heathwaite L, Johnson SM, Macdonald DW, Mitchell R, Osborn D, Owen RP, Pretty J, Prior SV, Prosser H, Pullin AS, Rose P, Stott A, Tew T, Thomas CD, Thompson DBA, Vickery JA, Walker M, Walmsley C, Warrington S, Watkinson AR, Williams RJ, Woodroffe R & Woodroof HJ (2008) Future novel threats and opportunities facing UK biodiversity identified by horizon scanning. *Journal of Applied Ecology* **45**, 821–833.

Taylor LR, French RA & Woiwod IP (1978) The Rothamsted Insect Survey and the urbanization of land in Great Britain. *Perspectives in Urban Entomology* (ed. GW Frankie & CS Koehler), pp. 31–65. Academic Press, New York, USA.

Taylor ME & Morecroft MD (2009) Effects of agri-environment schemes in a long-term ecological time series. *Agriculture, Ecosystems and Environment* **130**, 9–15.

Thackeray SJ, Sparks TH, Frederiksenz M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliott JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ & Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* **16**, 3304–3313.

Thomas CD (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society B* **267**, 139–145.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beamont LJ, Collingham YC, Erasmus BFN, Ferreira de Siqueira M, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL & Williams SE (2004a) Extinction risk from climate change. *Nature* **427**,145–148.

Thomas CD, Franco AMA & Hill JK (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution* **21**, 415–416.

Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B* **360**, 339–357.

Thomas JA, Bourn NAD, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, Curtis R & Goodger B (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society B* **268**, 1791–1796.

Thomas JA & Clarke RT (2004) Extinction rates and butterflies. *Science* **305**, 1563–1565.

Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT & Lawton JH (2004b) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**, 1879–1881.

Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society B* **270**, 467–473.

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I & Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* **8**, 857–874.

UK National Ecosystem Assessment (2011) *The UK National Ecosystem* Assessment: Synthesis of the Key Findings. UNEP-WCMC, Cambridge, UK.

van Asch M, van Tienderen PH, Holleman LJ & Visser ME (2007) Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Global Change Biology* **13**, 1596–1604.

Van der Wal R, Pearce I, Brooker R, Scott D, Welch D & Woodin S (2003) Interplay between nitrogen deposition and grazing causes habitat degradation. *Ecology Letters* **6**, 141–146.

Van Dyck H, van Strien AJ, Maes D & van Swaay CAM (2009) Declines in common, widespread butterflies in a landscape under intense human use. *Conservation Biology* **23**, 957–965.

van Langevelde F, Ettema JA, Donners M, WallisDeVries MF & Groenendijk D (2011) Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation* **144**, 2274–2281.

van Ooik T & Rantala MJ (2010) Local adaptation of an insect herbivore to a heavy metal contaminated environment. *Annales Zoologici Fennici* **47**, 215–222.

van Ooik T, Rantala MJ & Saloniemi I (2007) Diet-mediated effects of heavy metal pollution on growth and immune response in the geometrid moth *Epirrita autumnata*. *Environmental Pollution* **145**, 348–354.

van Swaay CAM, Nowicki P, Settele J & van Strien AJ (2008) Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation* **17**, 3455–3469.

van Swaay C, Warren MS & Lois G (2006) Biotope use and trends of European butterflies. *Journal of Insect Conservation* **10**, 189–209.

Vaughan N (1997) The diets of British bats (Chiroptera). *Mammal Review* **27**, 77–94.

Visser ME & Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society B* **268**, 289–294.

WallisDeVries MF & van Swaay CAM (2006) Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biology* **12**, 1620–1626.

Waring P, Townsend M & Lewington R (2009) *Field Guide to the Moths of Great Britain and Ireland*. British Wildlife Publishing, Gillingham, UK.

Warren MS & Bourn NAD (2011) Ten challenges for 2010 and beyond to conserve Lepidoptera in Europe. *Journal of Insect Conservation* **15**, 321–326.

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D & Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69.

Warren MS & Key RS (1991) Woodlands: past, present and potential for insects. *The Conservation of Insects and their Habitats*, (ed. NM Collins & JA Thomas), pp. 155–211. Academic Press, London, UK.

Wenzel M, Schmitt T, Weitzel M & Seitz A (2006) The severe decline of butterflies on western German calcareous grasslands during the last 30 years: a conservation problem. *Biological Conservation* **128**, 542–552.

Wickramasinghe LP, Harris S, Jones G & Jennings N (2004) Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. *Conservation Biology* **18**, 1283–1292.

Wilson JD, Morris AJ, Arroyo BE, Clark SC & Bradbury RB (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems and Environment* **75**, 13–30.

Wilson RJ, Gutiérrez D, Gutiérrez J & Monserrat VJ (2007) An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology* **13**, 1873–1887.

Wilson RJ & Roy DB (2009) Butterfly population structure and dynamics. *Ecology of butterflies in Europe* (ed. J Settele, T Shreeve, M Konvička & H Van Dyck), pp. 81–96. Cambridge University Press, Cambridge, UK.

Woiwod IP & Gould PJL (2008) Long-term moth studies at Rothamsted. *The Moths of Hertfordshire* (ed. CW Plant), pp. 31–44. Hertfordshire Natural History Society, Welwyn Garden City, UK.

Young M (1997) The Natural History of Moths. T. & A.D. Poyser, London, UK.

Young MR & Barbour DA (2004) Conserving the New Forest burnet moth in Scotland, responses to grazing reduction and consequent vegetation changes. *Journal of Insect Conservation* **8**, 137–148.

Chapter 3: Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes

Slightly modified from:

Fox R, Oliver TH, Harrower C, Parsons MS, Thomas CD & Roy DB (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology* **51**, 949–957.

Abstract

Species' distributions are likely to be affected by a combination of environmental drivers. We used a dataset of 11 million species occurrence records over the period 1970-2010 to assess changes in the frequency of occurrence of 673 macro-moth species in Great Britain. Groups of species with different predicted sensitivities showed divergent trends, which we interpret in the context of land-use and climatic changes.

A diversity of responses was revealed: 260 moth species declined significantly whereas 160 increased significantly. Overall, frequencies of occurrence declined, mirroring trends in less species-rich, yet more intensively studied taxa. Geographically widespread species, which were predicted to be more sensitive to land-use than to climate change, declined significantly in southern Britain, where the cover of urban and arable land has increased. Moths associated with low nitrogen and open environments (based on their larval hostplant characteristics) declined most strongly, which is also consistent with a land-use change explanation. Some moths that reach their northern (leading edge) range limit in southern Britain increased, whereas species restricted to northern Britain (trailing edge) declined significantly, consistent with a climate change explanation. Not all species of a given type behaved similarly, suggesting that complex interactions between species' attributes and different combinations of environmental drivers determine frequency of occurrence changes.

Our findings are consistent with large-scale responses to climatic and land-use changes, with some species increasing and others decreasing. We suggest that

land-use change (e.g. habitat loss, nitrogen deposition) and climate change are both major drivers of moth biodiversity change, acting independently and in combination. Importantly, the diverse responses revealed in this species-rich taxon show that multifaceted conservation strategies are needed to minimise negative biodiversity impacts of multiple environmental changes. We suggest that habitat protection, management and ecological restoration can mitigate combined impacts of land-use change and climate change by providing environments that are suitable for existing populations and also enable species to shift their ranges.

Introduction

The main drivers of global biodiversity change have been identified (Millennium Ecosystem Assessment 2005), but their impacts vary spatially, temporally and taxonomically. Drivers may also interact to produce synergistic or opposing effects (Travis 2003; Brook *et al.* 2008; Schweiger *et al.* 2010), but there are few empirical examples, particularly for insects, which comprise the majority of terrestrial biodiversity (Collen *et al.* 2012). Unquantified change and a resultant lack of evidence-based conservation, present pressing biological and strategic management challenges.

Here, we utilise a substantial dataset of species occurrence records to examine long-term changes of a species-rich insect taxon (Lepidoptera: macro-moths) in Great Britain (GB). Large-scale, comprehensive assessments of biodiversity changes in speciose insect taxa are rare (Thomas 2005; Mattila *et al.* 2008, 2009; Jeppsson *et al.* 2010). Moths constitute one of the largest groups of herbivorous insects, forming key links in food webs, inflicting damage (as well as pollination) on their plant hosts, and providing a major food source for insectivorous animals in many ecosystems (Strong *et al.* 1984).

We calculate long-term changes in frequency of occurrence of 673 lepidopteran species in GB and evaluate the trends in relation to species' predicted sensitivities to recent climatic and habitat changes. Habitat modification, particularly agricultural intensification, is considered the pre-eminent cause of recent species declines in GB and other western European countries (Warren & Key 1991; Robinson & Sutherland 2002; Kleijn *et al.* 2009). In parallel, climate

change is eliciting changes in the geographical range, abundance, phenology and biotic interactions of Lepidoptera species (Parmesan 2006). Climate change provides a shifting context for the impacts of habitat modification, either amplifying or ameliorating species' responses depending upon ecological traits and biogeographical situation.

Gradients of land use, climate and species' distributions combine conveniently to provide distinct (often opposite) predictions of changes to species' occurrence in GB. Northern GB retains a higher proportion of semi-natural habitats than southern GB, where levels of land conversion to intensive agriculture and urbanisation have been greater (Morton et al. 2011). Therefore, moth species that are not strongly constrained by climate and occur widely in GB, might be expected to decline in the south while remaining relatively stable in the north, in response to land-use changes. On the other hand, many insect species (including many macro-moths) reach the north-western climatic limit of their European range within southern GB. These species should benefit from climate change, leading to the opposite prediction – they should potentially increase as the climate has warmed (Hickling et al. 2006). In contrast, arcticalpine species that are restricted to northern and montane areas in GB might be expected to decline in response to regional warming. By considering warmadapted, cold-adapted and relatively climate-insensitive (within GB) species across a broad gradient of land-use intensity, we attempt to tease apart the effects of change in land use and climate on GB moths.

Land-use changes involve altered management (e.g. increased fertilizer input) as well as conversion from one land-use type to another. We considered these effects by analysing the occurrence changes of moths that are monophagous on larval hostplants that possess different environmental requirements. Trait-based analyses of plant trends have been linked to drivers of change (Carey *et al.* 2008), utilising Ellenberg indicator values to characterise the realized niches of plants along environmental gradients, such as those relating to soil chemistry and light availability (Ellenberg 1979). Thus, by considering the Ellenberg indicator values of moth larval hosts, we can examine links between drivers of botanical change and changes to the frequency of occurrence of moths.

Here, we test three hypotheses: (i) macro-moth species will show a wide diversity of changes as they respond to diverse drivers, but will have declined overall, mirroring wider biodiversity trends. (ii) The responses of species with different geographic distributions (southern, northern, widespread) are expected to differ because the effects of climate and land use may differ between these species categories. (iii) Moth occurrence trends will be associated with hostplant attributes (Ellenberg indicator values); specifically, moths that use types of plant that are in decline, such as those associated with low nitrogen soil conditions, will also be in decline.

We found support for each hypothesis, enabling us to assess long-term moth biodiversity change. These results will guide future research into drivers of biodiversity change and inform ecological management to buffer species from negative impacts.

Materials and Methods

Data sources

GB species occurrence records for macro-moths (here defined as Lepidoptera families: Hepialidae, Cossidae, Zygaenidae, Limacodidae, Sesiidae, Lasiocampidae, Saturniidae, Endromidae, Drepanidae, Geometridae, Sphingidae, Notodontidae, Erebidae, Nolidae and Noctuidae) for the period 1970-2010 were obtained from the National Moth Recording Scheme database: 11,074,870 records were extracted. These were collated from volunteer observers during recording for distribution atlases organised by the Biological Records Centre and Butterfly Conservation (Heath & Emmet 1983; Hill *et al.* 2010) (accessible via the National Biodiversity Network http://data.nbn.org.uk).

Interspecies detectability differences can be an issue with analysis of occurrence data (MacKenzie *et al.* 2006; Kéry, Gardner & Monnerat 2010), so we only considered within-species changes over time. New knowledge of species' biology or novel collection methods may also alter detectability (Jeppsson *et al.* 2010). Thus, non-resident species and those subject to taxonomic revision since 1970 were excluded from the analysis. We also excluded species for which recording methodologies changed (e.g. most Sesiidae were excluded because the recent introduction of pheromone lures

has greatly improved detection rates) and species that occurred in <10 grid squares in the 1970-1999 period, as no range margin could be determined for these species (see next section). This left 673 species (10,462,519 records in total) for our analysis.

Each species occurrence was attributed to a 10km x 10km grid square of the GB Ordnance Survey (OS) National Grid (hereafter 'grid squares') for analysis. The records cover 93% of GB grid squares.

Classification of southern, northern and widespread species

Range margins were determined as the mean latitude of the 10 most northerly or southerly occupied grid squares in 1970-1999 (Hickling *et al.* 2006), the baseline period for our analysis. Species were then classified into three groups, based on the 488km North gridline (OS National Grid). 'Southern species' had a northern (cold) range margin that occurred in the southern half of GB (i.e. south of 488km North OS). 'Northern species' had a southern (warm) range margin north of 488km North. 'Widespread species' did not meet either criteria, occurring in both northern and southern GB (Fig. 1). There was little evidence of taxonomic bias between these groups (Fig. A3.1).

Analysis of changes in frequency of occurrence

Temporal and spatial variation in recording intensity (Boakes *et al.* 2010) must be accounted for in analyses of species occurrence data (Ponder *et al.* 2001; Hedenäs *et al.* 2002; Telfer *et al.* 2002; Hassall & Thompson 2010; Pardo *et al.* 2013). We interpreted moth occurrence data using the program Frescalo to determine temporal trends for each species (Hill 2012). This method utilises the presence or absence of 'benchmark' species to assess recording intensity at a given location. A local set of benchmark species was defined for each (focal) grid square, based on species occurrence data in surrounding 'neighbourhoods'. The fraction of benchmark species observed in a focal square enables recording effort to be estimated, which can then be used to adjust the observed frequencies of species occurrence. The adjusted frequencies are then used to assess trends over time (see Hill 2012 and Appendix 3 for detailed explanation). Frescalo was applied to the total moth dataset (673 species), split into two time periods of roughly equal numbers of records, 1970-1999 versus 2000-2010. For each time period, a grid square was categorised as having species detected (1) or not-detected (0) (giving a sample of 720,969 data points). Neighbourhoods were defined based on spatial proximity and floristic similarity using 1970 onwards vascular plant data from Preston *et al.* (2002). For each location in our analysis, the corresponding neighbourhood was defined as the 50 most floristically similar (using a spatial smoothing kernel) grid squares selected from the 100 geographically closest squares to each location (Appendix 3).

Change in moth species' frequency of occurrence was estimated by considering the relative reporting rate (RRR; Appendix 3) of each species in each time period (1970-1999 and 2000-2010) (Hill 2012). Temporal trends for each species were expressed as the yearly change in RRR, calculated as the overall change between the mid-points of the two time periods (i.e. 1984 and 2005 respectively) divided by the number of intervening years. The significance of these trends was determined using a z-test by:

$$z = \frac{t_2 - t_1}{\sqrt{{\sigma_1}^2 + {\sigma_2}^2}}$$

where t_1 and t_2 are the relative reporting rates of a given species from the first and second time periods and σ_1^2 and σ_2^2 are the variances associated with the RRR for periods t_1 and t_2 respectively. Trends in RRR were determined to be significant (at the 95% confidence level) if |z| > 1.96. The analyses of Frescalo trends were carried out in R v2.9.2 (R Development Core Team 2009).

Finally, for widespread species, RRR trends were recalculated separately for the northern and southern halves of GB, dividing the data along the 488km North gridline.

Correlation with host plant and environmental variables

We tested host plant effects for the subset of 56 GB macro-moths that are monophagous (Skinner 2009; Waring *et al.* 2009) on vascular plant species for which distribution and trait (Ellenberg indicator values) data were available.

Long-term GB distribution changes of the plants (1930-1960 versus 1987-1999) and Ellenberg values were derived from PLANTATT (Hill *et al.* 2004). We used all Ellenberg values in PLANTATT (soil nitrogen, soil pH, soil moisture and shade tolerance) excluding salt tolerance, for which there was insufficient variation for the plants in our analysis.

We tested whether changes in frequency of occurrence (Δ RRR year⁻¹) of the 56 moth species were correlated with distribution change of their hostplants. We fitted a multiple regression of moth changes against their host's Ellenberg values for light, moisture, reaction (pH) and nitrogen. In all these statistical models, we included species distribution grouping ('southern' or 'widespread' species; no northern species were part of the monophagous group) as a control variable. Regressions were fitted in R with moth Δ RRR year⁻¹ as a response variable and either plant distribution change or Ellenberg traits as explanatory variables. Initially, model residuals did not conform to normality, so three outlying data points were removed to rectify this (Shapiro test for normality of residuals: W = 0.9776, p = 0.42, n = 53), although results were qualitatively similar when including these data. We considered the phylogenetic nonindependence of species by fitting a mixed effects model with genus and family as random effects. Higher-level phylogenetic relationships are not well resolved in Lepidoptera so a full comparative analysis using a phylogeny was not possible (Mutanen et al. 2010). We used the Ime4 and ImerTest packages (Bates et al. 2008; with significance of variables assessed using Satterthwaite's approximation for degrees of freedom, Kuznetsova et al. 2013).

Results

British macro-moth species decreased significantly in frequency of occurrence between the periods 1970-1999 and 2000-2010 (Wilcoxon signed-rank test on Δ RRR year⁻¹ using all species: V = 87558, n = 673, *p* < 0.001): 260 of the 673 species exhibited significant declines (*p* < 0.05), with a further 157 species showing a tendency to decline. In contrast, 160 species increased significantly (*p* < 0.05) in frequency of occurrence, with 96 others showing a tendency to increase. Thus, 420 (62%) of the species have undertaken significant changes in frequency, with 1.6 times as many decreasing as increasing (Table A3.1). The magnitude of these changes was relatively similar between groups (median

138

 Δ RRR year¹ for significantly increasing species = 0.006 [range 0.002-0.033]; significantly declining species: median = -0.006 [range = -0.024 - -0.002]; Table A3.1). The results reveal a wide diversity of occurrence changes among moths.

Geographically limited species showed contrasting trends (Fig. 1). Species restricted to northern GB (trailing edges of distributions) declined significantly in frequency of occurrence (with 94% of species declining; V = 10, n = 17, p = 0.002). In contrast, species confined to southern GB did not show a significant change overall (V = 8575, n = 186, p = 0.87): 24% of species declined significantly while 27% increased significantly.

On average, geographically widespread species decreased in frequency of occurrence (V= 39066, n = 470, p < 0.001; Fig. 3.1): 45% of individual species in this group declined significantly. When trends for widespread species were recalculated separately for southern and northern GB, we found disproportionately larger declines in the south (Fig. 3.2). There was no significant change in frequency of occurrence of widespread species in northern GB (V = 53569, n = 470, p = 0.55), but a significant decline in the south (V = 37017, n = 470, p = < 0.001).

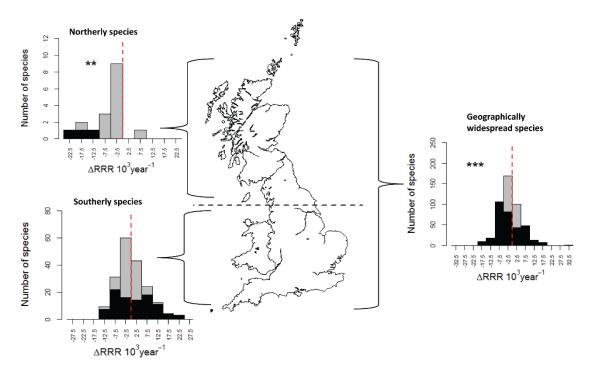
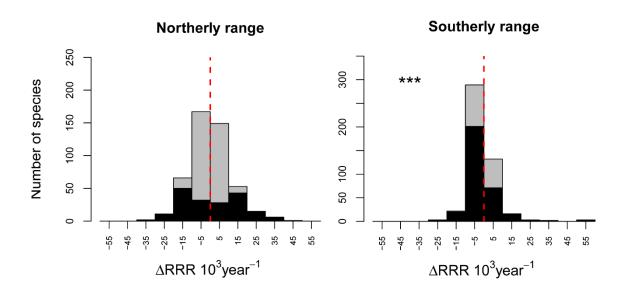
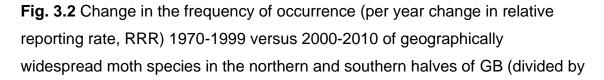


Fig. 3.1 Change in frequency of occurrence (per year change in relative reporting rate, RRR) 1970-1999 versus 2000-2010 for southerly distributed, northerly distributed and geographically widespread moths. Significant results shown as ** p < 0.01 and *** p < 0.001. Species with individually significant changes (p < 0.05) are shown in black. Change values are multiplied by 10³ to improve axis legibility.





488km North OS gridline, see Fig. 3.1). Species with individually significant changes (p < 0.05) are shown in black. Change values are multiplied by 10^3 to improve axis legibility.

Changes in frequency of occurrence of monophagous macro-moths and distribution changes of their larval hostplants were not significantly linked (linear regression: slope = 0.002, t = 1.33, p = 0.19, R² = 0.03; mixed model: slope = 0.002, t = 1.99, p = 0.057; n = 53 species for both; Fig. A3.2). However, there was a negative relationship between moth species' trends and their hostplant Ellenberg light values and a positive correlation between moth trends and host Ellenberg nitrogen values (Table 3.1; Fig. 3.3). Moths utilising larval hostplants growing in open, low-fertility conditions declined over time compared to species using plants in more shaded, nitrogen-rich environments. There were no relationships between moth trends and Ellenberg values for moisture or reaction.

Table 3.1 Relationships from a multiple regression and linear mixed model of host plant Ellenberg indicator values on change in frequency of occurrence of monophagous moth species (n = 53 for both). Significant results (p < 0.05) shown in bold text. Species distribution grouping (Distribution) ('southern' or 'ubiquitous' species; no northern species were part of the 53 species) was included as a covariate, with the intercept representing southern species.

	Model 1 multiple regression				Model 2 mixed effects			
					(phylogenetic control)			
Coefficient	Coefficent	SE	t	р	Coefficent	SE	t	р
Intercept	0.0057	0.0050	1.14	0.261	0.0042	0.0049	0.849	0.401
Light	-0.0014	0.0005	-2.64	0.011	-0.0011	0.0005	-2.179	0.035
Moisture	-0.0007	0.0006	-1.20	0.236	-0.0006	0.0005	-1.139	0.261
Reaction	-0.0004	0.0005	-0.89	0.378	-0.0007	0.0005	-1.432	0.160
Nitrogen	0.0013	0.0006	2.32	0.025	0.0015	0.0005	2.772	0.008
Distribution	0.0006	0.0012	0.52	0.607	0.0006	0.0012	0.477	0.636

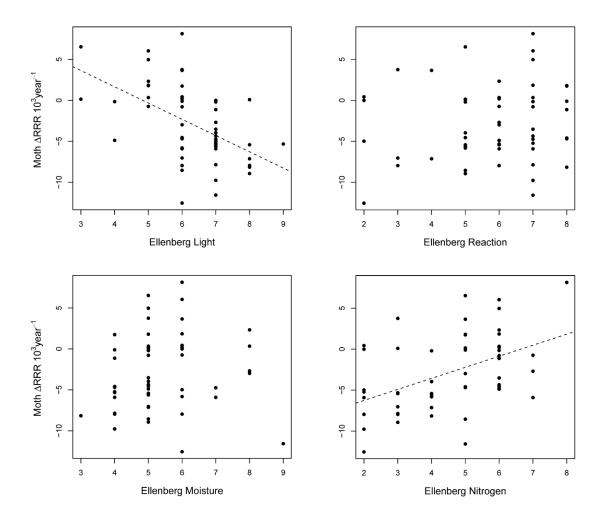


Fig. 3.3 Change in the frequency of occurrence (per year change in relative reporting rate, RRR) 1970-1999 versus 2000-2010 of monophagous moth species in relation to host plant Ellenberg indicator values. Change values are multiplied by 10³ to improve axis legibility. Dashed lines are from univariate regressions.

Discussion

Macro-moth species in GB decreased overall in frequency of occurrence between 1970-1999 and 2000-2010, in keeping with a significant decrease in GB macro-moth abundance over a similar period (Conrad *et al.* 2006), moth distribution trends in other countries (Mattila *et al.* 2008; Groenendijk & Ellis 2011) and declines in other insect taxa (Warren *et al.* 2001; Cameron *et al.* 2011). It provides further evidence that invertebrates are as negatively impacted by environmental change as vertebrates (Thomas *et al.* 2004; Collen *et al.* 2012). The diversity of trends suggests that combinations of different drivers are resulting in a mixture of responses. The occurrence trends were calculated using the Frescalo method to control for spatiotemporal variation in recorder effort (Hill 2012). Without controlling for this bias, variation in the intensity of recording can confound assessments of species occurrence over time. The method estimated frequency of occurrence, which is a function of both local abundance and distribution extent (Appendix 3, Fig. A3.3, A3.4).

The Frescalo method makes a number of assumptions. One is that the probability of finding a species in a locality can be estimated by its frequency in the neighbourhood (floristically similar grid squares in close spatial proximity). We believe this is reasonable because moth species tend to be associated with specific ecotypes and plant communities and because plant communities are generally good indicators of a range of local environmental conditions (e.g. soil structure, pH, moisture levels and microclimate; Ellenberg 1979). A second potential consideration of the Frescalo method is that poorly recorded neighbourhoods cannot provide information about local species frequency. This was not an issue in the current analysis of moth data at 10km resolution with neighbourhoods of 50 grid squares, but it could be if analyses were conducted at finer spatiotemporal scales. Finally, the Frescalo method may have limited applicability for less speciose taxonomic groups that have few potential benchmark species.

Our results demonstrate different patterns of change in the frequency of occurrence among macro-moths with different geographical distributions and hostplant traits, providing full or partial support for each of our hypotheses. Moths as a whole decreased in frequency of occurrence, as did northern and geographically widespread species, while southerly distributed species showed no overall trend. Additional analyses showed that geographically widespread species only decreased in the southern half of GB and showed no overall trend in the north. Correlations between trends of monophagous moths and Ellenberg indicator values of their hostplants revealed mixed findings.

The development of an understanding of the drivers of moth biodiversity change in GB is a vital step for conservation biologists and practitioners. We propose an interpretation of our findings based on two major drivers of change for GB biodiversity: habitat modification and climate change. There is growing indirect evidence of the impacts of these drivers on GB moths (Merckx *et al.* 2012; Fox 2013), but we acknowledge that other factors may be involved and drive changes in the occurrence of individual species.

The overall decrease in moth frequencies, and that of the subset of geographically widespread species, is consistent with a response to high levels of habitat modification, as for butterflies (Warren *et al.* 2001), although it does not exclude other explanations.

Our second set of hypotheses related to the performances of three geographically defined groups of moths. Southerly distributed (warmth associated) species were predicted to increase in response to regional climate warming (Fig. A3.5), but they also inhabit the parts of GB with the highest levels of land-use change. Some of these species increased and others decreased (resulting in no overall significant trend in this group, Fig. 3.1). This might reflect a diversity of habitat and climatic sensitivities, although such results could also be due to the species being insensitive to recent changes in climate and land-use.

In northern GB, cold-adapted species have declined; a response consistent with synergistic negative effects of climate change and habitat modification (as found for four northern GB butterfly species, Franco *et al.* 2006). This is in keeping with other studies implicating climate change in the retraction of warm range margins of cold-adapted Lepidoptera (Thomas *et al.* 2006; Chen *et al.* 2011; Dieker *et al.* 2011). Specific conservation measures may be required for these trailing edge populations (Hampe & Petit 2005), including steps to minimise negative land-use impacts and the protection of climatic refugia.

Geographically widespread species only decreased, on average, in southern GB; population monitoring has yielded similar findings (Conrad *et al.* 2006; Fox *et al.* 2011). Almost all of the widespread species also occur in warmer parts of Europe, and are unlikely, therefore, to have experienced a climatic deterioration of conditions in southern GB, although there may be exceptions (e.g. Garden Tiger *Arctia caja* Conrad, Woiwod & Perry 2002) due, for example, to local

climatic adaptation. A greater proportion of widespread species is increasing in northern GB (Fig. 3.2) perhaps reflecting the positive impacts of climate change for some species.

Southern GB has undergone greater loss of semi-natural habitats since the early 20th century than the north. Comparison of 10km grid square resolution land cover data for 1931-1941 with 2000 data suggests an increase in arable and urban land of 20% and 6%, respectively, in southern GB, and a 4% decrease of arable and 1% increase in urban land in the north (T. Jucker pers. comm.; Jucker 2010). Although these habitat conversion trends have slowed recently, the overall pattern of greater habitat modification in the south has been retained and ongoing degradation in habitat quality (e.g. loss of botanical species richness in linear features) has been recorded (Haines-Young *et al.* 2003; Carey *et al.* 2008). We suggest that the decline of widespread moth species in southern GB is predominantly linked to habitat modification. Further research is needed to assess whether these rates of decline will cause regional extinctions, and to identify effective conservation strategies in the wider countryside (Kleijn *et al.* 2011).

The variation among species is as revealing as the overall trends (Table A3.1). Sixteen of the 17 northern species showed a declining trend, suggesting relatively consistent responses to drivers of change. In contrast, many southern species increased significantly while others decreased significantly; a pattern also seen among widespread species. Given that species vary in their habitat associations and likely responsiveness to different elements of climate, it is not surprising that simultaneous habitat and climatic changes generate increases in frequency in some species and declines in others (Menéndez *et al.* 2007).

Much recent research has focussed on species' traits as predictors of biodiversity decline (Mattila *et al.* 2008; Öckinger *et al.* 2010), but success in explaining climate change responses has been limited (Angert *et al.* 2011). We examined traits of the plant hosts of moths, which are expected to reflect sensitivity to land-use changes more than the climate (Firbank *et al.* 2008; Kleijn *et al.* 2009).

Surprisingly, we found no significant relationship between changes in hostplant distributions and frequency of occurrence of dependent moths (Fig. A3.2). However, specialist moths rarely occupy the entire range of their larval hosts (Quinn *et al.* 1997), and change in hostplant distribution might occur in parts of the range unoccupied by the associated moth. In addition, thresholds of hostplant abundance, quality and local distribution may determine moth persistence (Menéndez & Thomas 2000), but these are not accounted for in assessments of distribution change. Finally, the lack of association may stem from the inherent differences in the measures being compared (frequency of occurrence change for moths versus distribution change for plants).

We did find significant correlations between changes in the frequency of occurrence of moth species and Ellenberg values of hostplants for two predictors, showing that monophagous moths that utilise plant species associated with high light intensity and low-fertility soils tended to decrease most strongly (as have plants with these traits, Carey *et al.* 2008). Decreases among plants and their specialist herbivores associated with open, nutrient-poor conditions can be attributed to habitat modification directly, through changing agricultural and woodland management, and also indirectly, for example due to eutrophication of the environment (Warren & Key 1991; Firbank *et al.* 2008; Kleijn *et al.* 2009; Payne *et al.* 2013). Such impacts, mediated through botanical communities (Payne *et al.* 2013), have rarely been recorded among herbivores (Hendriks *et al.* 2013). Although enrichment may be reversible on individual sites, new approaches to the management of nutrients in the wider countryside will be required to address declines of species restricted to low nutrient environments (Robertson & Vitousek 2009).

Synergistic climate change interactions, both negative and positive, may also occur. Warmer conditions extend the growing season (Menzel & Fabrian 1999) leading to increased plant growth, particularly if coupled with rising soil fertility. Thus, climate change could favour shade-tolerant species and could, perversely, reduce warm microclimatic niches required by invertebrates (WallisDeVries & van Swaay 2006; Oliver *et al.* 2012). On the other hand, for moth species that utilise plants favoured in high-nitrogen environments,

146

eutrophication may facilitate climate-driven range expansion (Betzholtz *et al.* 2012).

Understanding species' responses to the drivers of biodiversity change is vital to develop adaptive conservation strategies (Mawdsley et al. 2009). The diverse patterns of change revealed by our study suggest that drivers of trends are likely to differ between species, necessitating multifaceted approaches to conservation. Nevertheless, a generic solution is to maintain existing highquality habitats and create new areas (Lawton et al. 2010). This will minimise declines (e.g. of widespread species in the south) and maximise increases (e.g. of southern species), regardless of whether species are responding most strongly, or in combination, to land-use or climatic changes. Hence, conservation strategies should aim to retain sufficient quantity and quality of habitat to minimise negative synergistic effects (Oliver et al. 2010; Araújo et al. 2011), while facilitating the exploitation of opportunities created by climate warming (Hodgson et al. 2011; Thomas et al. 2012). This requires the protection of remaining habitats from deleterious impacts, but also sufficient knowledge of land management techniques to maximise habitat quality. Such knowledge is limited for moths but can start by identifying landscape elements and management practices associated with enhanced species richness and abundance (Fuentes-Montemayor et al. 2011; Merckx et al. 2012).

Acknowledgements

We are indebted to the volunteers who contributed moth records and to the County Recorders, Zoë Randle and Les Evans-Hill who collated them. NMRS funders included the Heritage Lottery Fund, Environment Agency, Redwing Trust, Natural England, Countryside Council for Wales, Northern Ireland Environment Agency, Royal Entomological Society and Scottish Natural Heritage. DR, CH and TO were part-funded by the Natural Environment Research Council and Joint Nature Conservation Committee partnership supporting the Biological Records Centre. We thank Les Evans-Hill for data extraction, Mark Hill for analysis advice and T. Jucker and G. Powney for historic land cover data. We also thank Tomas Pärt, Tobias Jeppsson, Michael Pocock and an anonymous reviewer for improvements to the manuscript.

References

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ & Chunco AJ (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters* **14**, 677–689.

Araújo MB, Alagador D, Cabeza M, Nogues-Bravo D & Thuiller W (2011) Climate change threatens European conservation areas. *Ecology Letters* **14**, 484–492.

Bates D, Maechler M & Dai B (2008) *Ime4: Linear mixed-effects models using S4 classes.* R package version 0.999375-20. Available from http://lme4.r-forge.r-project.org/.

Betzholtz P-E, Pettersson LB, Ryrholm N & Franzén M (2012) With that diet, you will go far: trait-based analysis reveals a link between rapid range expansion and a nitrogen-favoured diet. *Proceedings of the Royal Society B* **280**, 20122305.

Boakes EH, McGowan PJK, Fuller RA, Chang-qing D, Clark NE, O'Connor K & Mace GM (2010) Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biology* **8**, e1000385.

Brook BW, Sodhi NS & Bradshaw CJA (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**, 453–460.

Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF & Griswold TL (2011) Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the USA* **108**, 662–667.

Carey PD, Wallis S, Chamberlain PM, Cooper A, Emmett BA, Maskell LC, McCann T, Murphy J, Norton LR, Reynolds B, Scott WA, Simpson IC, Smart SM & Ullyett JM (2008) *Countryside Survey: UK results from 2007*. NERC Centre for Ecology & Hydrology, Lancaster, UK.

Chen I-C, Hill JK, Shiu H-J, Holloway JD, Benedick S, Chey VK, Barlow HS & Thomas CD (2011) Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Global Ecology and Biogeography* **20**, 34–45.

Collen B, Böhm M, Kemp R & Baillie JEM (2012) *Spineless: status and trends of the world's invertebrates*. Zoological Society of London, London, UK.

Conrad KF, Warren M, Fox R, Parsons M & Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation* **132**, 279–291.

Conrad KF, Woiwod IP & Perry JN (2002) Long-term decline in abundance and distribution of the garden tiger moth (*Arctia caja*) in Great Britain. *Biological Conservation* **106**, 329–337.

Dieker P, Drees C & Assmann T (2011) Two high-mountain burnet moth species (Lepidoptera, Zygaenidae) react differently to the global change drivers climate and land-use. *Biological Conservation* **144**, 2810–2818.

Ellenberg H (1979) Zeigerwerte von Gefässpflanzen Mitteleuropas. *Scripta Geobotanica* **9**, 1–122.

Firbank LG, Petit S, Smart S, Blain A & Fuller RJ (2008) Assessing the impacts of agricultural intensification on biodiversity: a British perspective. *Philosophical Transactions of the Royal Society B* **363**, 777–787.

Fox R (2013) The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity* **6**, 5–19.

Fox R, Brereton TM, Asher J, Botham MS, Middlebrook I, Roy DB & Warren MS (2011) *The State of the UK's Butterflies 2011*. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, UK.

Franco AMA, Hill JK, Kitschke C, Collingham YC, Roy DB, Fox R, Huntley B & Thomas CD (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* **12**, 1545–1553.

Fuentes-Montemayor E, Goulson D & Park K (2011) The effectiveness of agrienvironment schemes for the conservation of farmland moths: assessing the importance of a landscape-scale management approach. *Journal of Applied Ecology* **48**, 532–542.

Groenendijk D & Ellis WN (2011) The state of the Dutch larger moth fauna. *Journal of Insect Conservation* **15**, 95–101. Haines-Young R, Barr CJ, Firbank LG, Furse M, Howard DC, McGowan G, Petit S, Smart SM & Watkins JW (2003) Changing landscapes, habitats and vegetation diversity across Great Britain. *Journal of Environmental Management* **67**, 267–281.

Hampe A & Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* **8**, 461–467.

Hassall C & Thompson DJ (2010) Accounting for recorder effort in the detection of range shifts from historical data. *Methods in Ecology and Evolution* **1**, 343–350.

Heath J & Emmet AM (1983) *The Moths and Butterflies of Great Britain and Ireland*. Harley Books, Colchester, UK.

Hedenäs L, Bisang I, Tehler A, Hamnede M, Jaederfelt K & Odelvik G (2002) A herbarium-based method for estimates of temporal frequency changes: mosses in Sweden. *Biological Conservation* **105**, 321–331.

Hendriks RJJ, Carvalheiro LG, Kleukers RMJC & Biesmeijer JC (2013) Temporal-spatial dynamics in Orthoptera in relation to nutrient availability and plant species richness. *PLoS One* **8**, e71736.

Hickling R, Roy DB, Hill JK, Fox R & Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**, 450–455.

Hill L, Randle Z, Fox R & Parsons M (2010) *Provisional Atlas of the UK's Larger Moths*. Butterfly Conservation, Wareham, UK.

Hill MO (2012) Local frequency as a key to interpreting species occurrence data when recording effort is not known. *Methods in Ecology and Evolution* **3**, 195–205.

Hill MO, Preston CD & Roy DB (2004) *PLANTATT. Attributes of British and Irish plants: status, size, life history, geography and habitats.* Centre for Ecology and Hydrology, Wallingford, UK.

Hodgson JA, Moilanen A, Wintle BA & Thomas CD (2011) Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology* **48**, 148–152.

Jeppsson T, Lindhe A, Gärdenfors U & Forslund P (2010) The use of historical collections to estimate population trends: A case study using Swedish longhorn beetles (Coleoptera: Cerambycidae). *Biological Conservation* **143**, 1940–1950.

Jucker T (2010) Climate and land use drive compositional changes in the flora of Scotland at distinct spatial scales. MSc thesis, Imperial College London, UK.

Kéry M, Gardner B & Monnerat C (2010) Predicting species distributions from checklist data using site-occupancy models. *Journal of Biogeography* **37**, 1851–1862.

Kleijn D, Kohler F, Báldi A, Batáry P, Concepción ED, Clough Y, Díaz M, Gabriel D, Holzschuh A, Knop E, Kovács A, Marshall EJP, Tscharntke T & Verhulst J (2009) On the relationship between farmland biodiversity and landuse intensity in Europe. *Proceedings of the Royal Society B* **276**, 903–909.

Kleijn D, Rundlöf M, Scheper J, Smith HG & Tscharntke T (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution* **26**, 474–481.

Kuznetsova A, Brockhoff PB & Christensen R (2013) *ImerTest: tests for random and fixed effects for linear mixed effect models* (Imer objects of Ime4 package).

Lawton JH, Brotherton PNM, Brown VK, Elphick C, Fitter AH, Forshaw J, Haddow RW, Hilborne S, Leafe RN, Mace GM, Southgate MP, Sutherland WJ, Tew TE, Varley J & Wynne GR (2010) *Making Space for Nature: a review of England's wildlife sites and ecological network*. Report to Defra.

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL & Hines JE (2006) Occupancy estimation and modelling: inferring patterns and dynamics of species. Elsevier, Burlington, USA.

Mattila N, Kotiaho JS, Kaitala V & Komonen A (2008) The use of ecological traits in extinction risk assessments: a case study on geometrid moths. *Biological Conservation* **141**, 2322–2328.

Mattila N, Kotiaho JS, Kaitala V, Komonen A & Pälvinen J (2009) Interactions between ecological traits and host plant type explain distribution change in Noctuid moths. *Conservation Biology* **23**, 703–709.

Mawdsley JR, O'Malley R & Ojima DS (2009) A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conservation Biology* **23**, 1080–1089.

Menéndez R & Thomas CD (2000) Metapopulation structure depends on spatial scale in the host-specific moth, *Wheeleria spilodactylus* (Lepidoptera: Pterophoridae). *Journal of Animal Ecology* **69**, 935–951.

Menéndez R, González-Megías A, Collingham Y, Fox R, Roy DB, Ohlemüller R & Thomas CD (2007) Direct and indirect effects of climate and habitat factors on specialist and generalist butterfly diversity. *Ecology* **88**, 605–611.

Menzel A & Fabrian P (1999) Growing season extended in Europe. *Nature* **397**, 659.

Merckx T, Marini L, Feber RE & Macdonald DW (2012) Hedgerow trees and extended-width field margins enhance macro-moth diversity: implications for management. *Journal of Applied Ecology* **49**, 1396–1404.

Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: synthesis*. Island Press, Washington DC, USA.

Morton D, Rowland C, Wood C, Meek L, Marston C, Smith G, Wadsworth R & Simpson IC (2011) *Countryside Survey: final report for LCM2007 - the new UK land cover map.* NERC Centre for Ecology & Hydrology, Lancaster, UK.

Mutanen M, Wahlberg N & Kaila L (2010) Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings of the Royal Society B* **277**, 2839–2848.

Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, Petersen JD, Pöyry J, Settele J, Summerville KS & Bommarco R (2010) Lifehistory traits predict species responses to habitat area and isolation: a crosscontinental synthesis. *Ecology Letters* **13**, 969–979.

Oliver TH, Roy DB, Hill JK, Brereton T & Thomas CD (2010) Heterogeneous landscapes promote population stability. *Ecology Letters* **13**, 473–484.

Oliver TH, Thomas CD, Hill JK, Brereton T & Roy DB (2012) Habitat associations of thermophilous butterflies are reduced despite climatic warming. *Global Change Biology* **18**, 2720–2729. Pardo I, Pata MP, Gómez D & García MB (2013) A novel method to handle the effect of uneven sampling effort in biodiversity databases. *PLoS One* **8**, e52786.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**, 637–369.

Payne RJ, Dise NB, Stevens CJ, Gowing DJ & BEGIN Partners (2013) Impact of nitrogen deposition at the species level. *Proceedings of the National Academy of Sciences of the USA* **110**, 984–987.

Ponder WF, Carter GA, Flemons P & Chapman RR (2001) Evaluation of museum collection data for use in biodiversity assessment. *Conservation Biology* **15**, 648–657.

Preston CD, Pearman DA & Dines TD (2002) New Atlas of the British and Irish Flora. Oxford University Press, Oxford, UK.

Quinn RM, Gaston KJ & Roy DB (1997) Coincidence between consumer and host occurrence: macrolepidoptera in Britain. *Ecological Entomology* **22**, 197–208.

R Development Core Team (2009) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Robertson GP & Vitousek PM (2009) Nitrogen in agriculture: Balancing the cost of an essential resource. *Annual Review of Environment and Resources* **34**, 97–125.

Robinson RA & Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* **39**, 157–176.

Schweiger O, Biesmeijer JC, Bommarco R, Hickler T, Hulme PE, Klotz S, Kühn I, Moora M, Nielsen A, Ohlemüller R, Petanidou T, Potts SG, Pyšek P, Stout JC, Sykes MT, Tscheulin T, Vilà M, Walther G-R, Westphal C, Winter M, Zobel M & Settele J (2010) Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biological Reviews* **85**, 777–795.

Skinner B (2009) Colour Identification Guide to Moths of the British Isles. Apollo Books, Stenstrup, Denmark.

Strong DR, Lawton JH & Southwood TRE (1984) *Insects on plants: Community patterns and mechanisms.* Blackwell, Oxford, UK.

Telfer MG, Preston CD & Rothery P (2002) A general method for measuring relative change in range size from biological atlas data. *Biological Conservation* **107**, 99–109.

Thomas CD, Franco AMA & Hill JK (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution* **21**, 415–416.

Thomas CD, Gillingham PK, Bradbury RB, Roy DB, Anderson BJ, Baxter JM, Bourn NAD, Crick HQP, Findon RA, Fox R, Hodgson JA, Holt AR, Morecroft MD, O'Hanlon NJ, Oliver TH, Pearce-Higgins JW, Procter DA, Thomas JA, Walker KJ, Walmsley, CA, Wilson RJ & Hill JK (2012) Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences of the USA* **109**, 14063–14068.

Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B* **360**, 339–357.

Thomas JA, Telfer MG, Roy DB, Preston C, Greenwood JJD, Asher J, Fox R, Clarke RT & Lawton JH (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**, 1879–1881.

Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society B* **270**, 467–473.

WallisDeVries MF & van Swaay CAM (2006) Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biology* **12**, 1620–1626.

Waring P, Townsend M & Lewington R (2009) *Field guide to the Moths of Great Britain and Ireland*. British Wildlife Publishing, Gillingham, UK.

Warren MS & Key RS (1991) Woodlands: past, present and potential for insects. *The Conservation of Insects and their Habitats* (ed. NM Collins & JA Thomas), pp. 155–211. Academic Press, London, UK.

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D & Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69.

Chapter 4: Using citizen science butterfly counts to predict species population trends

Slightly modified from:

Dennis EB, Morgan BJT, Brereton TM, Roy DB & Fox R (2017) Using citizen science butterfly counts to predict species population trends. *Conservation Biology* **31**, 1350–1361.

Abstract

Citizen scientists are increasingly engaged in gathering biodiversity information, but trade-offs are often required between public engagement goals and reliable data collection. We compared population estimates for 18 widespread butterfly species derived from the first four years (2011-2014) of a short-duration citizen science project (Big Butterfly Count, BBC) with those from long-running, standardized monitoring data collected by experienced observers (UK Butterfly Monitoring Scheme, UKBMS). BBC data are gathered during an annual threeweek period, whereas UKBMS sampling takes place over six months each year.

An initial comparison with UKBMS data restricted to the three-week BBC period revealed that species population changes were significantly correlated between the two sources. The short-duration sampling season rendered BBC counts susceptible to bias caused by inter-annual phenological variation in the timing of species' flight periods. The BBC counts were positively related to butterfly phenology and sampling effort. Annual estimates of species abundance and population trends predicted from models including BBC data and weather covariates as a proxy for phenology correlated significantly with those derived from UKBMS data.

Overall, citizen science data obtained using a simple sampling protocol produced comparable estimates of butterfly species abundance to data collected through standardized monitoring methods. Although caution is urged in extrapolating from this UK study of a small number of common, conspicuous insects, we found that mass-participation citizen science can simultaneously contribute to public engagement and biodiversity monitoring. Mass-participation citizen science is not an adequate replacement for standardized biodiversity monitoring but may extend and complement it (e.g., through sampling different land-use types), as well as serving to reconnect an increasingly urban human population with nature.

Introduction

Citizen science, the participation of members of the public in gathering research and monitoring data, is increasing rapidly across many scientific disciplines, including biodiversity conservation (Dickinson et al. 2012; Follett & Strezov 2015). Public involvement in biodiversity recording and monitoring has a long history in some countries (Miller-Rushing et al. 2012; Pocock et al. 2015). Distinction can be made, however, between citizen science projects in which standardized protocols are used to conduct systematic, repeatable sampling in long-term studies (e.g. the Breeding Bird Survey; Gregory & Baillie 1998) or for hypothesis-driven enquiry (e.g. Conker Tree Science; Pocock & Evans 2014) and schemes reliant on opportunistic sampling undertaken with relatively unstructured protocols (e.g. eBird; Sullivan et al. 2009). Opportunistic schemes with simple sampling protocols reduce barriers to participation (e.g. time commitment, prior knowledge) and may thus engage large numbers of new, inexperienced citizen scientists. Although these increase sample size and public outreach, the data gathered may lack credibility (Riesch & Potter 2014; Lewandowski & Specht 2015). Standardized schemes may have much greater barriers to participation and therefore rely on fewer dedicated, skilled volunteers. However, the abilities of these participants to undertake biodiversity monitoring may be comparable with those of professional scientists (Chase & Levine 2016). Biodiversity citizen science projects often involve trade-offs between the goals of public engagement and education (counteracting the extinction of experience; Soga & Gaston 2016) and the collection of reliable data for research (Chase & Levine 2016; Lakeman-Fraser et al. 2016).

Many aspects of citizen science biodiversity research have been examined, including the quality of observations (Lewandowski & Specht 2015), participants' motivations (Hobbs & White 2012), and the development of new data-analysis techniques (Bird *et al.* 2014). However, few studies have compared population trends based on relatively unstructured sampling undertaken by mass-participation citizen science with those derived from long-

term systematic monitoring and none, to our knowledge, involving terrestrial invertebrates. We derived and compared species population trends from two contrasting citizen science projects in the United Kingdom (UK) - the Big Butterfly Count (BBC) and UK Butterfly Monitoring Scheme (UKBMS).

The BBC is an annual survey of widespread butterfly species launched in 2010 that encourages participation by members of the general public (www.bigbutterflycount.org). It seeks to engage people with little or no experience with biodiversity monitoring and aims to enhance public awareness and interaction with nature and to gather species-abundance data. To minimize barriers to participation, the sampling protocol is simple: 15-minute counts of 18 butterfly species and two diurnal moths over three weeks in the summer. Consequently, and thanks to a high media profile, BBC has met its aims of mass-participation (mean = 47,636 people involved per year 2013-2015) and raising awareness but, given the target audience, likelihood of identification mistakes, and simple method, counts may not provide a meaningful indication of butterfly population change.

The UKBMS, initiated in 1976, has a robust, standardized recording protocol in which weekly fixed-route counts are conducted over six months each year at >1,000 sites. High levels of commitment and identification skills are required so participants tend to be experienced amateur butterfly observers or professional conservationists, and the high-quality data generated are used to produce population trend estimates for 56 of 59 regularly breeding UK butterfly species, as biodiversity indicators by government (Brereton *et al.* 2011a; Eaton *et al.* 2015), and in scientific research (e.g. Dennis *et al.* 2013; Oliver *et al.* 2015b; Thackeray *et al.* 2016). We tested the validity of BBC data for estimating species trends by determining whether population changes derived from BBC data were comparable with those from UKBMS.

Butterfly abundance differs throughout the year as one or more broods emerge. These phenological patterns vary year to year in response to the weather (Sparks & Yates 1997) and show long-term trends due to climate change (Roy & Sparks 2000). Because the BBC runs for just three weeks each summer, inter-annual variation in counts for each species may result from differing

157

phenology rather than real population changes. We assessed temporal variation in phenology with respect to the BBC survey period to determine its influence on estimates of annual change. Furthermore, we investigated whether population-change estimates from the BBC, in conjunction with weather covariates, can provide an accurate indicator of how populations are faring. In the rapidly expanding field of citizen science, we sought to provide a rare test of the validity of a mass-participation approach to biodiversity monitoring.

Methods

Big Butterfly Count

The BBC runs annually in late July and early August during the peak in overall abundance of butterflies. In 2010, the scheme ran for nine days. Since 2011, the BBC occurs over a period of up to 24 days each year (Table A4.1), although participants can additionally submit counts taken throughout July and August. Due to this difference, we excluded 2010 data from analyses and used BBC data from 2011 to 2014. Participants count 18 widespread butterflies (Table A4.2) and two day-flying moths for 15 minutes during bright weather. No training is provided, sightings are submitted online, and minimal verification of sightings is undertaken. Counts can be undertaken anywhere in the UK. If counting from a fixed position, the maximum number of each species seen at any time is recorded rather than an additive total so as to reduce double counting. BBC data are summarized in Table A4.3 and show the scheme's rapid growth. Sightings are spatially referenced and land-use type is recorded by the participant. The majority of counts are taken in gardens (65% on average, Table A4.4). An average of 12%, 11%, and 4% are taken in fields, other rural, and woodland sites, respectively, and a small number are taken in other land-use types.

UK Butterfly Monitoring Scheme

The UKBMS counts are undertaken along line transects, typically 2-4km, with systematic, standardized methods (Pollard & Yates 1993). In 2014, 1,223 UKBMS transects were monitored (Brereton *et al.* 2015). Counts can be made throughout the main season for UK butterfly activity; the core period is April-September. A 5m wide fixed transect route is walked weekly at specified times of the day and weather conditions, and all butterflies seen are identified and

counted. In practice approximately 30% of core-season weekly counts are missed (Dennis *et al.* 2013). Transect counts are used to generate annual indices of relative abundance from which population trends can be calculated.

Comparisons of BBC and UKBMS data

We compared species abundance estimates from the two schemes in three ways. First, we examined agreement through direct comparison of annual growth rates. Second, we investigated the effects of sampling effort and phenology. Finally, we tested whether UKBMS trends may be predicted over 36 years (1980-2015) and 10 years (2006-2015) based on BBC data and an appropriate weather variable acting as a proxy for butterfly phenology.

The BBC and UKBMS are inherently different, independent datasets, and although sample locations are self-selected by participants in both schemes, the representation of habitats may differ. Overall UK coverage of each scheme is shown in Fig. A4.1. Most BBC counts are undertaken in gardens, whereas UKBMS locations are biased toward semi-natural habitats that are often managed to benefit biodiversity (Brereton *et al.* 2011b). We compared the habitats covered by the schemes by summarizing land-cover data from 2007 (Morton *et al.* 2014) in the 1km squares sampled in each scheme. For each UKBMS transect, the central 1km x 1km grid square was used to characterize the habitat.

Comparison of annual growth rates

To make an initial direct comparison between the two schemes, we limited the UKBMS data to counts made within the BBC survey period each year and restricted the analysis to the 18 butterfly species counted by the BBC (Table A4.2). Because BBC data are available for only a three-week period, by initially restricting the UKBMS data to the same period we could directly compare the two schemes in the absence of seasonal differences, for example due to multiple broods (which are sampled by the UKBMS).

Following Roy *et al.* (2015), we determined annual population growth rates for each species from the two datasets. In brief, we defined $\mu_{i,t}$ as the expected total count of a species at site *i* in year *t* across *vi*,*t* visits, and regarded this as

the realisation of a Poisson random variable. Annual proportional changes in abundance were assumed to be the same across sites, such that we estimated annual growth rate (*Rt*) as

$$R_{t} = \log\left(\frac{\mu_{i,t+1}/\nu_{i,t+1}}{\mu_{i,t}/\nu_{i,t}}\right)$$
(1)

which leads to

$$\log(\mu_{i,t}) = \sum_{j=1}^{t-1} R_j + \log(\mu'_{i,1}) + \log(v_{i,t})$$
(2)

where $\mu'_{i,t} = \mu_{i,t}/v_{i,t}$. Standard generalized linear model (GLM) software, for example in R (R Core Team 2016), may be used to fit this model. However, the many sites represented in the BBC data each require the estimation of a site parameter each year; hence, the model described is computationally challenging to fit to BBC data with standard GLM software because of the amount of computer memory required. Therefore, we adopted a concentrated (or profile) likelihood approach (Morgan 2008; Pawitan 2013) that reduces the number of parameters to estimate and results in efficient model fitting (Dennis *et al.* 2016).

With the notation $S_i = \log(\mu'_{i,1})$, apart from an additive constant, the loglikelihood may be written as

$$l = \text{Log}(L) = \sum_{i=1}^{S} \sum_{t=1}^{T} \left[-\exp\{\sum_{j=1}^{t-1} R_j + S_i + \log(v_{i,t})\} + y_{i,t}\{\sum_{j=1}^{t-1} R_j + S_i + \log(v_{i,t})\} \right].$$
(3)

Then for site *i* we obtain

$$\frac{\partial l}{\partial S_i} = \sum_{t=1}^{T} \left[-\exp\{\sum_{j=1}^{t-1} R_j + S_i + \log(v_{i,t})\} + y_{i,t} \right],$$
(4)

and equating to zero gives

$$S_i = \log\left\{\frac{\sum_{t=1}^T y_{i,t}}{\sum_{t=1}^T v_{i,t} \exp\left(\sum_{j=1}^{t-1} R_j\right)}\right\}.$$
(5)

Substituting Eq. (5) into Eq. (3) results in a concentrated likelihood that can be maximized simply with respect to $\{R \ j\}$. We maximized the likelihood with the *optim* function in R and the BFGS algorithm (Nocedal & Wright 1999).

We estimated the net change, *N*, over *T* years for each survey with

$$\widehat{N} = \sum_{t=1}^{T} \widehat{R}_t, \tag{6}$$

where the variance of \hat{N} is the sum of all the entries of the covariance matrix for the growth rates. We adjusted for overdispersion by scaling standard errors with the square root of the ratio of the Pearson chi-square statistic to its degrees of freedom.

Effects of phenology and effort

Seasonality of life-cycle phenology results in differences in counts of adult butterflies throughout the year and complicates the analysis of population data (Rothery & Roy 2001; Dennis *et al.* 2013, 2016). We used UKBMS data to establish how the BBC data were influenced by changes in flight-period phenology. Seasonal abundance patterns for each species in each year were estimated by fitting an appropriate generalized abundance index model (GAI) (Dennis *et al.* 2016) to the UKBMS data (without date restriction, in contrast to the comparison of annual population growth rates). For univoltine and bivoltine species, a phenomenological GAI is based on the assumption that the flight period of each brood follows a normal distribution (μ , mean flight date; σ , standard deviation). For species with complex seasonal flight patterns, which are difficult to model parametrically, a GAI was fitted using a spline to describe the seasonal variation. The approach used for each species is in Table A4.2.

For each univoltine and bivoltine species, we plotted the total BBC count per day and the estimated annual seasonal pattern from the UKBMS GAI. The BBC counts from all dates were used, rather than only the official three-week sampling period. We explored the relationship between BBC data and sampling effort and phenology. For each species, a negative-binomial model with log link was fitted using the glm.nb function from the MASS package (Venables & Ripley 2002) in R. The response was the total BBC count per day, and

161

measures of effort (log counts per day) and phenology based on the estimated seasonal pattern from the UKBMS were covariates. We also modelled the number of counts per day (rather than the total BBC count); however, this measure was right skewed and therefore less satisfactory. The estimated seasonal pattern from the GAI (which sums to unity across the season) formed the measure of phenology for a given day and year. This is in anticipation of positive associations between BBC count and both sampling effort and the timing of sampling coinciding with the peak in species' seasonal patterns.

Predicting UKBMS species trends from BBC data

We assessed whether UKBMS species' population trends were described by the BBC data with weather covariates as a proxy for phenology. We used a simple linear model to regress UKBMS abundance indices for 2011-2014 on BBC data and weather covariates and the index for the previous year (autoregression) to account for potential density dependence.

We used a GAI to estimate UKBMS indices. In a given year, the GAI produces a relative abundance, *Ni*, for each site *i* (Dennis *et al.* 2016). Given the variation in UKBMS sites between years, we fitted a Poisson GLM with year and site factors and used scaled predicted year effects as indices of abundance (Dennis *et al.* 2013).

We used BBC data from the official three weeks of sampling as a covariate in the linear model; the sum of the total counts per day was scaled by daily effort (defined as the log of the number of counts for all species for that day). However, scaling by the numbers of counts produced similar results.

Average monthly mean temperatures (Parker *et al.* 1992) and total rainfall (Alexander & Jones 2000) for central England for spring (March-May) and summer (June-August) were used as weather covariates. All weather covariates were standardized to have zero mean and unit variance. The maximum correlation between weather covariates was 0.67.

Potential longer-term (rather than for 2011-2014 only) effects of weather and density dependence were accounted for by fitting a linear model to the GAI

index values for 1980-2014; the index values in the previous year and the four weather covariates were explanatory variables. The products of the slope coefficients and covariates from each model were included as optional offsets in the linear models to allow for potential longer-term effects than those for 2011-2014 only.

We used the dredge function in the MuMIn package (Barton 2016) in R to select models based on the Akaike information criterion (AIC). Given the few years for which BBC data were available, we allowed up to two variables only and only one weather covariate (either as a covariate for 2011-2014 or as an offset for weather from 1980 to 2014). The relative importance of the BBC and weather covariates was assessed using the relaimpo package (Grömping 2006) in R.

Each year UKBMS data are collated (from online and hard copy sources) and verified. Unverified UKBMS data were available for 2015 online; hence, a GAI was fitted to incorporate these data and estimate an index of abundance for 2015. We compared this 2015 index, estimated from observed UKBMS data, with the abundance index predicted from the BBC linear model with the lowest AIC. An abundance index for 2015 was also predicted for each of the candidate models, and we assessed the model with the prediction closest to the index from the observed UKBMS data.

Population trends were compared by fitting linear models to the index of abundance, where the index for 2015 had either been estimated from UKBMS data or predicted from the best linear model. We estimated percent change over two periods (long-term for 1980-2015 and short term for 2006-2015) and calculated percent change with respect to the previous year. In doing so we assessed whether predicting the 2015 index from the BBC affected the overall UKBMS trend estimates.

Results

Comparison of BBC and UKBMS data

A greater proportion of 1km squares sampled in the BBC were classified as urban than were transects in the UKBMS (Table A4.5). This was expected given that most BBC counts were undertaken in gardens. The UKBMS squares contained a greater proportion of broadleaf woodland than the BBC, but the two schemes showed similar coverage of arable farmland and improved grassland.

Comparison of annual growth rates

There was a significant correlation between net species population changes from the two schemes for 2011-2014 ($\rho = 0.84$, $\rho < 0.001$) (Fig. 4.1). There was also a significant correlation (p < 0.01) between each of the year-to-year changes (Fig. A4.2). From 2011 to 2014, 11 of the 18 species had significantly positive and three had significantly negative change in abundance in the BBC, whereas 11 species had significantly positive and six had significantly negative change in the UKBMS. The remainder showed nonsignificant trends (Table A4.6). Population changes estimated from the two schemes were similar. although the BBC growth rates were less precise and tended to underestimate UKBMS growth rates. Changes were generally of a similar magnitude and were always of the same sign, with the exception of Comma Polygonia c-album and Small White *Pieris rapae*, and in no cases were the changes significantly different from zero and in opposite directions (Table A4.6). Nevertheless, there were significant differences in net change 2011-2014 between the two schemes for 11 species, and confidence intervals for BBC results were on average twice the width of the UKBMS results (0.38 and 0.19 respectively). Estimates of overdispersion were greater than unity for both schemes (Table A4.7). The BBC confidence intervals narrowed in 2013-2014 (average width 0.18) relative to 2012-2013 (0.38) because of the increasing number of counts (Table A4.3).

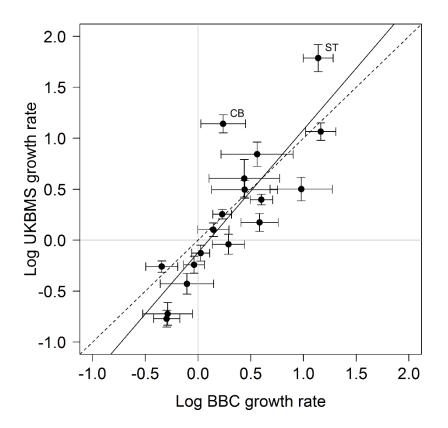
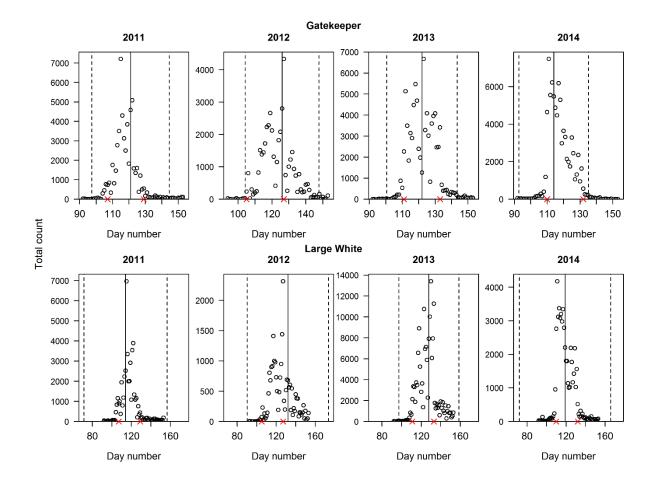
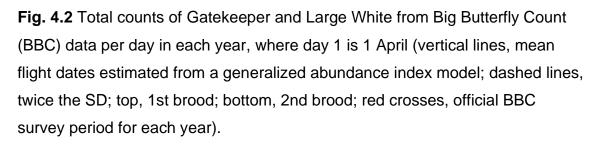


Fig. 4.1 Comparison of estimated log growth rates of populations of 18 butterfly species from Big Butterfly Count (BBC) and UK Butterfly Monitoring Scheme (UKBMS) counts for 2011-2014 (error bars, 95% confidence intervals; solid grey lines, zero growth; dashed line, equal growth rates between the datasets; solid black line, fitted linear regression between the growth rates based on BBC and UKBMS data). The Small Tortoiseshell *Aglais urticae* (ST) and Common Blue *Polyommatus icarus* (CB) have the greatest differences.

Effects of phenology and effort

Overlaying total daily abundance of each species from BBC counts with phenology information from the UKBMS, revealed how BBC population estimates may be influenced by inter-annual variation in the timing of species' flight periods (examples in Fig. 4.2 & Fig. A4.3). For Gatekeeper *Pyronia tithonus* the peak flight period was fairly central in the BBC recording period in 2011 and 2013 but fell at the end of period in 2012 and near the beginning in 2014. For Large White *Pieris brassicae* timing of the second brood varied; in 2012 in particular, the peak fell outside the BBC period.





Regressing the BBC counts on measures for effort and phenology showed good agreement between the counts and expected values, given the simplicity of the model used (Fig. 4.3 & Fig. A4.4). Residual deviance values suggested a good fit for the negative binomial model compared with the Poisson model (Table A4.8).

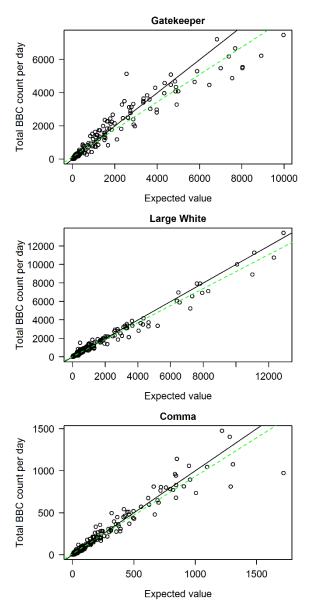


Fig. 4.3 Total counts of three butterfly species (Gatekeeper, univoltine; Large White, bivoltine; Comma, multivoltine) from Big Butterfly Count (BBC) data per day versus the expected value from a negative-binomial model with log-link in which the response variable is the total count per day and measures of effort (log number of counts made) and phenology (from the corresponding generalized abundance index model curve) are covariates (black line, equal expected values and total counts; green dashed line, fitted linear regression through the points).

Predicting UKBMS species trends from BBC data

The BBC was a covariate in the best model (in terms of AIC) for 13 of 18 species (Table 4.1), in conjunction with summer rainfall, spring temperature, and spring rainfall each for three species; summer temperature for two; and

offset long-term spring rainfall and autoregression for one species each. Of the 11 species where BBC and a weather covariate were in the best model, the relative importance of BBC exceeded the weather covariate for eight species (Table A4.9). For five species, BBC was not included in the best model, but autoregression was important. The observed 2015 index of abundance was within the 95% confidence interval of the best model for 10 out of 18 species, and only four species showed major discrepancies (Fig. 4.4).

Table 4.1 Estimated population trends (percent changes) in relative abundance for 18 UK butterfly species for the best models and selected covariates in terms of Akaike information criterion (AIC) or predicted index closest to the observed 2015 UKBMS index, relative to observed UKBMS populations trends estimated from the generalized abundance index model. SPRt = spring temperature, SPRr = spring rainfall, SUMt = summer temperature, SUMr = summer rainfall, auto = auto-regression, of = offset variable. * = significant at p < 0.01.

	Best fit		1980-2015		2006-2015	
Species	AIC	Prediction	Observed	Best AIC	Observed	Best AIC
Brimstone	bbc+SPRt	SUMr+of(auto)	35.9	35.1	-0.5	-2.2
Comma	bbc+SUMr	bbc+SUMr	10.9 *	10.9 *	-5.4	-5.5
Common Blue	bbc+SUMr	bbc+SUMr	-9.0	-8.9	5.2	5.5
Gatekeeper	bbc+SPRt	bbc+SUMr	-12.5 *	-12.4 *	-1.7	-1.3
Green-veined White	auto+SUMr	bbc+SPRt	-4.1	-2.8	6.6	11.2
Holly Blue	bbc+of(auto)	bbc+of(SUMr)	4.1	1.4	-6.1	-14.1
Large Skipper	auto+SPRt	auto+SPRt	-12.9 *	-13.5 *	-13.5	-15.6
Large White	bbc+SPRr	SPRt	-7.5	-7.0	-3.9	-2.3
Marbled White	auto+SUMr	auto+SUMt	-0.7	1.3	10.2	17.3
Meadow Brown	bbc+SPRt	SUMt+of(auto)	-4.7	-4.9 *	2.4	1.7
Painted Lady	bbc+SUMr	bbc+SUMt	-0.3	-4.3	-36.9	-46.0
Peacock	auto+SPRt	auto+of(SPRt)	-1.0	3.0	6.5	20.3
Red Admiral	auto+SPRt	auto+bbc	13.9	14.9 *	-11.9	-9.3
Ringlet	bbc+SUMt	of(SPRr)	12.3 *	11.3 *	7.9	5.2
Small Copper	bbc+of(SPRr)	SUMt+of(auto)	-14.2 *	-12.6 *	-11.8	-6.1
Small Tortoiseshell	bbc+SPRr	of(SPRr)	-27.0 *	-27.4 *	30.2 *	27.7
Small White	bbc+SPRr	bbc+of(auto)	-7.2	-6.2	0.1	3.3
Speckled Wood	bbc+SUMt	bbc+of(SPRr)	8.2 *	8.0 *	0.6	0

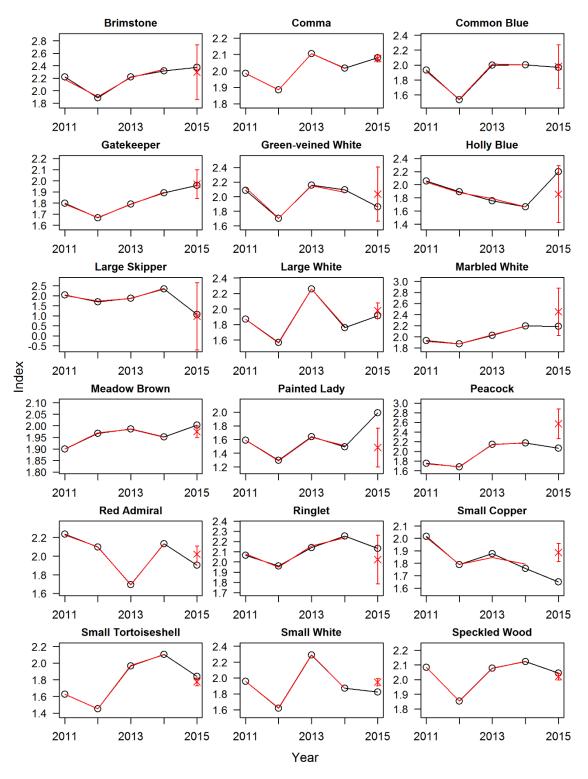


Fig. 4.4 Comparison of the generalized abundance index from UK Butterfly Monitoring Scheme (UKBMS) data (black) and predicted butterfly abundance indices from the best model in terms of Akaike information criterion (red) (vertical line, 95% confidence intervals for the 2015 prediction).

There were significant correlations between estimated population trends (Fig. 4.5), where the values for 2015 were from the observed data or predicted from

the best model: $\rho = 0.99$ for 1980-2015, $\rho = 0.95$ for 2006-2015, $\rho = 0.75$ for 2014-2015, where all $\rho < 0.001$. For 1980-2015, the difference between the two trends was < 5% for all species. For 2006-2015 and 2014-2015, the difference was < 5% for 13 and 10 species, respectively, out of 18. Significant trends were correctly identified for the seven species with significant UKBMS trends for 1980-2015, although two further species were predicted to have significant trends. There was greater correlation between the trends when the model with the best 2015 prediction was used (Fig. A4.5, Fig. A4.6).

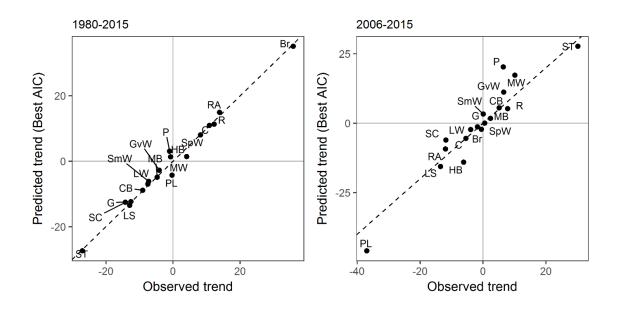


Fig. 4.5 Comparison of linear trends in relative butterfly abundance from the generalized abundance index model. The indices for 2015 are from observed data or predicted from the best model in terms of Akaike information criterion (solid grey lines, 0% change in relative abundance; dashed line, equal population trends). Abbreviations are for species common names (Table A4.2).

Discussion

Citizen science appears to offer opportunities for largescale, cost-effective biodiversity monitoring. However, the reliability of species trends may be compromised in citizen science projects that prioritize public outreach goals because there is often a trade-off between mass participation and scientific rigor. This reliability has rarely been tested empirically by comparing opportunistic citizen science data with standardized sampling data. Munson *et al.* (2010) found that eBird transect checklists predict bird species occurrence almost as accurately as highly standardized North American Breeding Bird Survey data. In contrast, Snäll *et al.* (2011) reported only weak overall correlation between opportunistic bird reports in Sweden and annual count data from a standardized transect-style survey. In the only terrestrial invertebrate examples we are aware of, Warren *et al.* (2001) and Oliver *et al.* (2015a) found correlations between UK butterfly species' occurrence trends assessed with opportunistic recording-scheme data and UKBMS population trends.

Population change estimates from the BBC and UKBMS using only counts from the official three-week BBC period were significantly correlated ($\rho = 0.84$). This compares favourably with the value of 0.75 obtained by Roy *et al.* (2015) when they compared population trends from the UKBMS with the Wider Countryside Butterfly Survey, in which a reduced-effort UKBMS sampling protocol is used in randomly selected locations (Brereton *et al.* 2011b).

The temporal distribution of BBC counts showed a potential mismatch with annual phenological variation, and the BBC data were well described by measures of recording effort and phenology. Simple annual proportional changes in abundance calculated from the BBC could result from varying phenology and effort rather than true population changes and may mask or falsely predict declines and increases. This demonstrates that the results of snap-shot citizen science biodiversity projects, which often take place at fixed points during the year, are vulnerable to bias from temporal factors that are not normally measured in such projects, as well as from variation in participation.

Despite the limited number of years and lack of standardization or verification, linear models based on BBC data and simple weather covariates were surprisingly successful at predicting the UKBMS abundance index for 2015 and consequently correcting for the effects of changing phenology. The BBC was an important variable for 13 out of 18 butterfly species, and the difference between the two trends was < 5% for all species in 1980-2015. Predictions of population trends were good even for species that are not straightforward to identify for inexperienced participants (e.g. three *Pieris* species: Large, Small and Greenveined White). The significant correlation and similar estimates of population trends between the two schemes validates the use of BBC data in assessing abundance change for these UK butterfly species. We used only four years of BBC data; over time one would expect even better predictions from BBC.

Species with the poorest model predictions of the 2015 abundance index, and consequently greatest differences in trend estimates relative to the UKBMS, tended to be those recorded in fewer locations by the BBC. Wider confidence intervals for the prediction of the 2015 index were also associated with species recorded in fewer BBC locations. Species may be less well recorded by the BBC due to reduced population densities in locations such as gardens, where most counts are undertaken. This may be addressed by encouraging BBC observers to sample other land-use types. Population trends for some species may also be better described by alternative climatic covariates. For example, trends for migratory Painted Lady *Vanessa cardui* and Red Admiral *V. atalanta* may be better explained by weather from parts of their ranges outside the UK.

This study concerns only 18 widespread butterfly species in the UK; therefore, caution should be applied in extrapolating our conclusions to other taxa and areas. Relative to many invertebrate taxa, butterflies are conspicuous and popular, and, in the context of butterfly monitoring, the UK benefits from low species richness, high human population density, and a tradition of amateur natural history recording.

From a biodiversity conservation perspective, the limitations of BBC relative to the UKBMS are clear. The UKBMS provides population trends for all but one of the threatened butterfly species on the British Red List (18 of 19 species), whereas BBC primarily counts just 18 common butterfly species (all also monitored by the UKBMS). Even in the UK, mass-participation citizen science is unlikely to provide reliable data on the large number of threatened, habitatspecialist invertebrates.

Nevertheless, the BBC data, as validated by our results, provide the potential for additional or improved assessments of biodiversity change. For example,

there is increasing interest in the biodiversity of urban areas, both as potential refuges for species whose habitats have been degraded in intensively farmed countryside and for the opportunities it affords for human-wildlife interactions and associated human well-being (Goddard *et al.* 2010; Shanahan *et al.* 2015). Sampling protocols developed for use in semi-natural habitat or open countryside may not be easily implemented in built areas and private gardens. The BBC samples more urban habitat than the UKBMS, and the majority of counts are undertaken in private gardens; hence, the BBC could provide a new biodiversity indicator for the performance of butterfly populations in gardens and parks, providing a valuable tool to engage the public and managers of urban greenspace.

The sampling of private gardens and urban areas as part of BBC also provides potentially useful population data for common butterfly species to complement UKBMS sampling of semi-natural habitat and the farmed landscape. While not of highest conservation priority, trends of common species are, nevertheless, of considerable interest due to the significance of such species to ecosystem function (Gaston & Fuller 2008). In the UK, the overall abundance of widespread butterflies decreased by 25% over 40 years (Fox *et al.* 2015), and many widespread species have significant negative population trends in the UK and the Netherlands (Van Dyck *et al.* 2009). Currently, the drivers of these declines are poorly understood. The BBC and UKBMS data could be combined in an integrated analysis (Pagel *et al.* 2014) representative of a wider range of land-use types, although variation in the scale and accuracy of the two surveys would need to be addressed, for example, by weighting different likelihood components (Francis 2011).

In practice, the financial costs of mass-participation citizen science versus standardized monitoring are an important factor, particularly where a new scheme is to be implemented. Both schemes incur considerable annual expenditure due to the essential involvement of professional staff, but the cost of running BBC is about a quarter that of the UKBMS. Aside from minor coordination, the primary cost of BBC arises from the need for media promotion to engage the public. Despite a larger overall cost due to greater coordination needs, it could be argued that the UKBMS is more cost-effective because data

173

are collected for many more species, including those that are the main focus of conservation. Both schemes also require an online data system, however, as the primary monitoring method for UK butterflies, the UKBMS incurs additional costs associated with data validation, which is not undertaken in the BBC.

The UKBMS operating costs are contingent on the assumption that an adequate network of skilled, trained volunteers already exists or can be mobilized quickly. Without this, the start-up costs and lead-in time for a monitoring scheme would be substantially greater than for mass-participation citizen science, for example, if paid professionals were required (Carvell *et al.* 2016). As we have shown with the BBC, mass-participation citizen science may, in some instances and with suitable adjustments (e.g., for effort and phenology), provide meaningful estimates of population trends for common, easily identifiable species. Even if this is not the case (or cannot be tested), by raising awareness and providing informal education, citizen science projects may provide a means to develop the necessary pool of skilled, engaged volunteers to enable the establishment of standardized biodiversity monitoring of additional areas and of taxa that are not currently well-monitored.

Despite relatively simplistic modelling and only a few years of available data, and contrary to the scepticism with which mass-participation citizen science is sometimes viewed, we found that BBC can produce population change estimates for common butterflies comparable to standardized monitoring data collected by skilled recorders. These results establish BBC as an example of a citizen science win win (Chase & Levine 2016; Lakeman-Fraser *et al.* 2016); a project focused on outreach and public engagement that generates meaningful scientific output.

Acknowledgments

We are extremely grateful to all the citizen scientists who gathered data for BBC and UKBMS. The BBC is run by Butterfly Conservation and received funding from Marks & Spencer. The UKBMS is operated by the Centre for Ecology & Hydrology, the Butterfly Conservation and the British Trust for Ornithology and funded by a multi-agency consortium including Defra, Joint Nature Conservation Committee, Forestry Commission, Natural England, Natural Resources Wales, Natural Environment Research Council, and Scottish Natural Heritage. We thank S. Freeman for helpful advice and M. Kéry and an anonymous reviewer for constructive comments.

References

Alexander L & Jones P (2000) Updated precipitation series for the UK and discussion of recent extremes. *Atmospheric Science Letters* **1**,142–150.

Barton K (2016) MuMIn: multi-model inference. R package. Version, 1.15.6. R Foundation, Vienna. Available from https://CRAN.Rproject.org/package=MuMIn (accessed December 2015).

Bird TJ, Bates AE, Lefcheck JS, Hill NA, Thomson RJ, Edgar GJ, Stuart-Smith RD, Wotherspoon S, Krkosek M, Stuart-Smith JF, Pecl GT, Barrett N & Frusher S (2014) Statistical solutions for error and bias in global citizen science datasets. *Biological Conservation* **173**, 144–154.

Brereton TM, Botham MS, Middlebrook I, Randle Z & Roy DB (2015) *United Kingdom Butterfly Monitoring Scheme Report for 2014*. Centre for Ecology & Hydrology and Butterfly Conservation, Wallingford, Oxfordshire, UK.

Brereton TM, Cruickshanks KL, Risely K, Noble DG & Roy DB (2011b) Developing and launching a wider countryside butterfly survey across the United Kingdom. *Journal of Insect Conservation* **15**, 279–290.

Brereton TM, Roy DB, Middlebrook I, Botham MS & Warren MS (2011a) The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation* **15**, 139–151.

Carvell C, Isaac NJB, Jitlal M, Peyton J, Powney GD, Roy DB, Vanbergen AJ, O'Connor RS, Jones CM, Kunin WE, Breeze TD, Garratt MPD, Potts SG, Harvey M, Ansine J, Comont RF, Lee P, Edwards M, Roberts SPM, Morris RKA, Musgrove AJ, Brereton T, Hawes C & Roy HE (2016) *Design and testing of a national pollinator and pollination monitoring framework*. Final summary report to the Department for Environment, Food and Rural Affairs, Scottish Government and Welsh Government: project WC1101. Centre for Ecology & Hydrology, Wallingford, Oxfordshire, UK. Chase SK & Levine A (2016) A framework for evaluating and designing citizen science programs for natural resources monitoring. *Conservation Biology* **30**, 456–466.

Dennis EB, Freeman SN, Brereton T & Roy DB (2013) Indexing butterfly abundance whilst accounting for missing counts and variability in seasonal pattern. *Methods in Ecology and Evolution* **4**, 637–645.

Dennis EB, Morgan BJT, Freeman SN, Brereton TM & Roy DB (2016) A generalised abundance index for seasonal invertebrates. *Biometrics* **72**, 1305–1314.

Dickinson JL, Shirk J, Bonter D, Bonney R, Crain RL, Martin J, Phillips T & Purcell K (2012) The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment* **10**, 291–297.

Eaton MA, Burns F, Isaac NJB, Gregory RD, August TA, Barlow KE, Brereton T, Brooks DR, Al Fulaij N, Haysom KA, Noble DG, Outhwaite C, Powney GD, Procter D & Williams J (2015) The priority species indicator: measuring the trends in threatened species in the UK. *Biodiversity* **16**, 108–119.

Follett R & Strezov V (2015) An analysis of citizen science based research: usage and publication patterns. *PLoS One* **10**, e0143687.

Fox R, Brereton TM, Asher J, August TA, Botham MS, Bourn NAD, Cruickshanks KL, Bulman CR, Ellis S, Harrower CA, Middlebrook I, Noble DG, Powney GD, Randle Z, Warren MS & Roy DB (2015) *The State of the UK's Butterflies 2015*. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, UK.

Francis RICC (2011) Data weighting in statistical fisheries stock assessment models. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 1124–1138.

Gaston KJ & Fuller RA (2008) Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution* **23**, 14–19.

Goddard MA, Dougill AJ & Benton TG (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology & Evolution* **25**, 90–98.

Gregory RD & Baillie SR (1998) Large-scale habitat use of some declining British birds. *Journal of Applied Ecology* **35**, 785–799.

Grömping U (2006) Relative importance for linear regression in R: The Package relaimpo. *Journal of Statistical Software* **17**, 1–27.

Hobbs SJ & White PCL (2012) Motivations and barriers in relation to community participation in biodiversity recording. *Journal for Nature Conservation* **20**, 364–373.

Lakeman-Fraser P, Gosling L, Moffat AJ, West SE, Fradera R, Davies L, Ayamba MA & van der Wal R (2016) To have your citizen science cake and eat it? Delivering research and outreach through Open Air Laboratories (OPAL). *BMC Ecology* **16**(Suppl 1), 57–70.

Lewandowski E & Specht H (2015) Influence of volunteer and project characteristics on data quality of biological surveys. *Conservation Biology* **29**, 713–723.

Miller-Rushing A, Primack R & Bonney R (2012) The history of public participation in ecological research. *Frontiers in Ecology and the Environment* **10**, 285–290.

Morgan BJT (2008) *Applied Stochastic Modelling*. 2nd edition. CRC, Chapman & Hall, Boca Raton, USA.

Morton RD, Rowland CS, Wood CM, Meek L, Marston CG & Smith GM (2014) Land Cover Map 2007 (1km percentage aggregate class, GB). Version 1.2. NERC-Environmental Information Data Centre.

Munson MA, Caruana R, Fink D, Hochachka WM, Iliff M, Rosenberg KV, Sheldon D, Sullivan BL, Wood C & Kelling S (2010) A method for measuring the relative information content of data from different monitoring protocols. *Methods in Ecology and Evolution* **1**, 263–273.

Nocedal J & Wright SJ (1999) *Numerical Optimization*. Springer, New York, USA.

Oliver TH, Isaac NJB, August TA, Woodcock BA, Roy DB & Bullock JM (2015a) Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications* **6**, 10122. Oliver TH, Marshall HH, Morecroft MD, Brereton T, Prudhomme C & Huntingford C (2015b) Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change* **5**, 941– 945.

Pagel J, Anderson BJ, O'Hara RB, Cramer W, Fox R, Jeltsch F, Roy DB, Thomas CD & Schurr FM (2014) Quantifying range-wide variation in population trends from local abundance surveys and widespread opportunistic occurrence records. *Methods in Ecology and Evolution* **5**, 751–760.

Parker DE, Legg TP & Folland CK (1992) A new daily central England temperature series, 1772-1991. *International Journal of Climatology* **12**, 317–342.

Pawitan Y (2013) *In all likelihood: statistical modelling and inference using likelihood.* Oxford University Press, Oxford, UK.

Pocock MJO & Evans DM (2014) The success of the Horse-Chestnut Leafminer, *Cameraria ohridella*, in the UK revealed with hypothesis-led citizen science. *PLoS One* **9**, e86226.

Pocock MJO, RoyHE, Preston CD & Roy DB (2015) The Biological Records Centre: a pioneer of citizen science. *Biological Journal of the Linnean Society* **115**, 475–493.

Pollard E & Yates TJ (1993) *Monitoring Butterflies for Ecology and Conservation*. Chapman & Hall, London, UK.

R Core Team (2016) *R: A language and environment for statistical computing*. R Foundation, Vienna, Austria.

Riesch H & Potter C (2014) Citizen science as seen by scientists: Methodological, epistemological and ethical dimensions. *Public Understanding of Science* **23**, 107–120.

Rothery P & Roy DB (2001) Application of generalized additive models to butterfly transect count data. *Journal of Applied Statistics* **28**, 897–909.

Roy DB & Sparks TH (2000) Phenology of British butterflies and climate change. *Global Change Biology* **6**, 407–416.

Roy DB, Ploquin EF, Randle Z, Risely K, Botham MS, Middlebrook I, Noble D, Cruickshanks K, Freeman SN & Brereton TM (2015) Comparison of trends in butterfly populations between monitoring schemes. *Journal of Insect Conservation* **19**, 313–325.

Shanahan DF, Fuller RA, Bush R, Lin BB & Gaston KJ (2015) The health benefits of urban nature: How much do we need? *BioScience* **65**, 476–485.

Snäll T, Kindvall O, Nilsson J & Pärt T (2011) Evaluating citizen-based presence data for bird monitoring. *Biological Conservation* **144**, 804–810.

Soga M & Gaston KJ (2016) Extinction of experience: evidence, consequences and challenges of loss of human-nature interactions. *Frontiers in Ecology and the Environment* **14**, 94–101.

Sparks TH & Yates TJ (1997) The effect of spring temperature on the appearance dates of British butterflies 1883–1993. *Ecography* **20**, 368–374.

Sullivan BL, Wood CL, Iliff MJ, Bonney RE, Fink D, Kelling S (2009) eBird: a citizen-based bird observation network in the biological sciences. *Biological Conservation* **142**, 2282–2292.

Thackeray SJ, Helaouet P, Johns DG, Jones ID, Bacon PJ, Brereton TM, Carvalho L, Clutton-Brock TH, Duck C, Edwards M, Elliott JM, Hall SJG, Harrington R, Pearce-Higgins JW, Pemberton JM, Sparks TH, Thompson PM, White I, Winfield IJ, Henrys PA, Hemming D, Leech DI, Bell JR, Botham MS, Burthe S, Mackay EB, Massimino D, Høye TT, Kruuk LEB, Wanless S & Atkinson S (2016) Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535**, 241–245.

Van Dyck H, van Strien AJ, Maes D & van Swaay CAM (2009) Declines in common, widespread butterflies in a landscape under intense human use. *Conservation Biology* **23**, 957–965.

Venables WN & Ripley BD (2002) *Modern Applied Statistics with* S. 4th edition. Springer, New York, USA.

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D &

Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69.

Chapter 5: Insect population trends and the IUCN Red List process

Published as:

Fox R, Harrower CA, Bell JR, Shortall CR, Middlebrook I & Wilson RJ (2019) Insect population trends and the IUCN Red List process. *Journal of Insect Conservation* **23**, 269–278.

Abstract

Reliable assessment of extinction risk is a key factor in the preparation of Red Lists and in prioritizing biodiversity conservation. Temporal population trends can provide important evidence for such assessments, but imperfect sampling (observation errors) and short-term stochastic variation in population levels caused by environmental variability (process errors) can reduce the reliability of trends and lead to incorrect quantification of extinction risk. The assessment of insect taxa is likely to be particularly prone to these problems, due to the highly dynamic nature of many insect populations, driven by short life-cycles and sensitivity to environmental factors such as the weather. Using long-term United Kingdom monitoring data for 54 butterfly and 431 macro-moth species, we demonstrate the impact of insect population variability on the assessment of extinction risk using the International Union for Conservation of Nature (IUCN) Red List Criterion A (reduction in population size over the last 10 years). For both taxa, varying the start year of the 10-year population trend had a substantial effect on whether particular species met Red List thresholds and on the overall number of species assessed as threatened. We conclude that for these insect taxa strict application of the 10-year rule produces Red List classifications that are unacceptably biased by the start year. Use of long-term trends with adjustment based on species performance over the last decade may offer a pragmatic solution to this problem. We call for further IUCN guidance for practitioners undertaking Red List assessments of taxa with populations that have high temporal variability.

Introduction

Biodiversity conservation practitioners rely on robust assessments of extinction risk (at global, regional, national and even local scales) to prioritise the use of limited resources. The Red List process developed by the International Union

for Conservation of Nature (IUCN) plays an important role both as the global standard for extinction risk assessment (Miller *et al.* 2007; Mace *et al.* 2008) and, indirectly, in catalysing conservation activity. The Red List process itself is solely an objective, quantitative assessment of threat across taxa. Nevertheless, by providing a key input into prioritisation decisions made by practitioners and as a consequence of increased public and political support stemming from the credibility and reputation of the process, Red Lists are frequently a starting point for the development of conservation initiatives (Rodrigues *et al.* 2006; Hoffmann et al. 2008; Azam *et al.* 2016).

The IUCN process utilises criteria with quantitative thresholds based on population and distribution size and rate of decline in order to classify taxa into Red List threat categories (IUCN 2001). The development, application and misuse of these criteria have been documented (Akçakaya et al. 2006; Mace et al. 2008; Collen et al. 2016), as have the wider problems of applying them to insects and other invertebrates due to data constraints (e.g. Cardoso et al. 2011; van Swaay et al. 2011; Azam et al. 2016). Criterion A "Reduction in population size" depends solely on measures of population decline over a (potentially short) time-period of the most recent 10 years or three generations, whichever is longer, hereafter referred to as the "10-year rule" for simplicity. Thus widespread and common species, with large population sizes and ranges, can qualify as being threatened with extinction on Red Lists if they are undergoing rapid decline. Criterion A is justified because even large populations would eventually be driven to extinction by continuing decline (Mace et al. 2008), especially as other negative feedback loops may come into play at low population densities (e.g. Allee effects, genetic inbreeding), but also because the reduction in abundance of common and widespread species may be of particular significance to ecosystem structure and functioning (Gaston & Fuller 2008; Winfree et al. 2015).

However, the reliable measurement of species population trends that indicate extinction risk (and are being driven by anthropogenic processes such as habitat loss or climate change) for use in Red List Criterion A is made difficult by imperfect sampling (observation errors) and short-term stochastic variation in population levels caused by environmental variability (process errors) (Connors

et al. 2014). Inaccurate detection of underlying species population trends can result in incorrect Red List classification (false positives i.e. incorrectly classifying a species as threatened and false negatives i.e. failing to classify a species that should be listed as threatened).

Investigations, using both empirical and simulated data, show that as process errors (and observation errors) increase, the reliable detection of population declines decreases across a range of different statistical techniques (Wilson et al. 2011; McCain et al. 2016). Trends assessed over short time periods, such as those required under the IUCN 10-year rule, are particularly sensitive to process errors, resulting in high levels of false positive and false negative species assessments (Connors et al. 2014; d'Eon-Eggertson et al. 2015). Concern has also been raised over the fundamental assumption that short-term declines are reliable predictors of ongoing decline (and, therefore, extinction risk) and authors have regularly advocated the use of long-term population data, where available, to improve the accuracy of extinction risk assessment (Dunn 2002; Porszt et al. 2012; Keith et al. 2015; White 2019). These findings undermine confidence in the classification of extinction risk using Criterion A in its current form (White 2019). However, these studies are based almost exclusively on vertebrate examples, where biological traits (e.g. generation times, population growth rates) and specific environmental drivers (e.g. human exploitation) may differ markedly from those of insects. Indeed, Connors et al. (2014) predict that the lowest rates of false-positive and false-negative classification errors under IUCN Red List Criterion A will occur for large-bodied, long-lived animal species.

These findings do not bode well for the application of Criterion A to insects. Most insect species have very short generation times (\leq 1 year), meaning that the 10-year rule is applied as a 10-year population trend over the most recent 10 years. By comparison, the same rule applied to long-lived vertebrates would see trends measured over longer time periods equating to three generations of the species concerned. In addition, the poikilothermic and ectothermic physiology of many insects results in climatic sensitivity that can drive large fluctuations in population size from generation to generation, particularly near altitudinal or latitudinal range margins (Oliver *et al.* 2014). Short-term climatic variation is a principal driver of inter-annual population change in UK butterflies and moths (Roy *et al.* 2001; Oliver *et al.* 2015; Palmer *et al.* 2017), alongside density dependence (Mills *et al.* 2017).

Due to anticipated high levels of process error (as well as potential observation error), 10-year population trends of insects may not be sufficiently reliable to enable the accurate classification of extinction risk in the Red List process, but rather reflect spurious responses to short-term environmental stochasticity. Thus, Red List classifications based on such trends are likely to be strongly affected by the start date of the 10-year trend, determined typically by factors such as policy development or funding availability that are unrelated to the population dynamics of the taxa being assessed.

The difficulty of detecting underlying declines from natural population fluctuations in short-term butterfly trends has been recognised previously (e.g. van Strien *et al.* 1997). Furthermore, the impact of temporal scale of trend measurement has been noted in comparisons of Red Lists produced using long-term versus 10-year trends (de longh & Bal 2007; van Swaay *et al.* 2011), and authors have recommended or developed adjustments to assessments under IUCN Criterion A to take long-term trends into consideration (Maes *et al.* 2012). In response, current IUCN guidance acknowledges this issue and sanctions optional use of data over a longer period to model population decline, especially for species with highly variable population levels, while still requiring trends to be measured over the most recent 10 years (IUCN 2017). Nevertheless, the 10-year rule remains fundamental to IUCN Criterion A and practitioners can continue to assess the threat levels of short-lived species based on just a decade of population data.

The purpose of this study is to highlight, from a practitioner's perspective, problems with the application of 10-year population trends in the Red Listing of insects and to seek further advice from IUCN. Specifically, we quantify, for the first time, the direct implications of high levels of inter-annual population variation (process errors) on Red List classification under IUCN Criterion A. Our assessment of two United Kingdom (UK) insect taxa for which standardised population monitoring data are available, butterflies and macro-moths, is then used to consider whether the 10-year rule is appropriate for such taxa.

Methods and results

We consider two case studies using UK insect population data for butterflies and macro-moths derived from long-term (40+ years) monitoring schemes to assess the impact of species' population variability on Red Listing using IUCN Criterion A. Although butterflies and moths are closely related taxa in the Order Lepidoptera, considering them as separate case studies is appropriate and informative as the monitoring schemes and datasets for each are independent and utilise different methodologies (fixed-width line counts for butterflies and point counts using light-traps for macro-moths) to sample diurnal and nocturnal insect communities respectively. In addition, long-running time series of standardised abundance for insect taxa are rare in the UK and globally; the only other insect taxon for which data are available over a comparable duration in the UK are aphids (Order Hemiptera, Superfamily Aphidoidea), although the geographical coverage is much less extensive (Thomas 2005).

We also varied two aspects of the assessment method in each case study: standardisation of time periods across species and the use of population trends with or without statistical significance. First, in the butterfly case study, the 10-year periods being compared were standardised (i.e. they started in the same year for each species), whereas in the macro-moth case study, the 10-year time periods varied between species according to data availability. Second, butterfly population trends were assessed against the IUCN threat category thresholds irrespective of whether the trends were statistically significant, while in the macro-moth study only statistically significant population trends were used in the assessment. These alternatives were used to represent the range of different approaches likely to be employed by practitioners undertaking Red List assessment depending on the form and availability of data.

It should be noted that the case studies do not represent the application of a complete Red List process, but are indicative assessments of the potential impact of one IUCN criterion on the outcome. A full Red List procedure would utilise other criteria based on geographical range and population size (depending on data availability) and also, when carried out at a regional level, an important additional consideration is the potential for the extinction risk of a taxon to be influenced by movement of individuals into or out of the region being

assessed (IUCN 2012). However, our consideration of Criterion A in isolation is relevant because threatened Red List status is conferred under the precautionary principle - as long as a taxon meets the threshold for a single criterion then it can be classified as threatened. Thus, false positive assessments under Criterion A (or any criterion) could exert substantial influence over completed Red Lists.

Case study 1: UK butterflies

We considered the impact of arbitrary start date on the Red List outcomes for UK butterflies based on published 10-year population trends derived by linear regression from the UK Butterfly Monitoring Scheme (UKBMS) over six consecutive years (www.ukbms.org; Pollard & Yates 1993; Roy et al. 2015). The standardised, annual monitoring of butterfly abundance by the UKBMS at over 1,000 sites generates robust population data used by the Government to assess biodiversity trends (Brereton et al. 2011; Eaton et al. 2015). Despite low observation error, 10-year UKBMS population trends for many species fluctuate considerably from year to year, reflecting stochastic environmental variation (process error) (Table A5.1). The 10-year population trends for each species were assessed against the IUCN Criterion A2 thresholds (A2 being for population trends where the reduction or its causes may not have ceased or may not be understood or may not be reversible) and species allocated to threat categories accordingly. Trend values were utilised in the assessment irrespective of their statistical significance (in contrast to the macro-moth case study). Thus, six classifications were produced using population trends for six 10-year periods, each starting one year after the previous one (i.e. 2001-2010, 2002-2011, 2003-2012, 2004-2013, 2005-2014 and 2006-2015). In addition, the median, lower and upper quartile population trends were calculated for each species from the six 10-year trend values and these were also assessed against IUCN Criterion A2.

Fifty-four species (of the 59 resident or common migrant butterfly species present in the UK) had UKBMS 10-year population trends for all six periods considered. There was considerable variation in the total number of species qualifying for Red List categories between classifications and for individual species across classifications. An average of 18.5 species met the IUCN

Criterion A2 thresholds for threatened status (i.e. Critically Endangered \geq 80% population decrease, Endangered \geq 50% decrease or Vulnerable \geq 30% decrease) per period, but the number of species qualifying ranged from 13 (24% of species) to 29 (54% of species) (Table 5.1). Twenty species (37% of the total) were consistently classified across the six different time periods (i.e. they either always (3 species) or never (17 species) qualified as threatened), but 34 species (63%) qualified as threatened in some periods and not others (Table 5.2). Removing the three common migratory species from the sample had no qualitative effect on the overall pattern.

Using the median population change value over the six 10-year periods for the Red List assessment produced 18 threatened species, the lower quartile trend value led to 25 threatened species and the upper quartile trend just 8 species (Table 5.1). The threat category assigned to a particular species frequently differed between the median, lower and upper quartile values (Table 5.2).

Table 5.1 Number of UK butterfly species (of 54 species assessed) meeting Red List threat thresholds under IUCN Criterion A2 (reduction in population size) on basis of 10-year UKBMS population trends over different year ranges and the median, lower and upper quartile trend values across the periods. CR = Critically Endangered (decrease \geq 80%), EN = Endangered (decrease \geq 50%), VU = Vulnerable (decrease \geq 30%). These classifications do not represent the final outcomes of a full Red List process.

	2001-	2002-	2003-	2004-	2005-	2006-	Median	Lower	Upper
	2010	2011	2012	2013	2014	2015		Qrt	Qrt
CR	2	4	5	5	2	2	2	6	1
EN	10	8	14	11	7	4	11	12	4
VU	6	3	10	4	7	7	5	7	3
Total	18	15	29	20	16	13	18	25	8

Table 5.2 Red List threat thresholds met by UK butterflies under IUCN Criterion A2 (reduction in population size) on basis of 10-year UKBMS population trends over different year ranges, and the median (MT), lower (LQ) and upper quartile (UQ) values of these trends. CR = Critically Endangered (decrease \geq 80%), EN = Endangered (decrease \geq 50%), VU = Vulnerable (decrease \geq 30%). Empty cells indicate that the species did not qualify as threatened. Species are ranked by the total number of classifications in which they reach Red List thresholds. These classifications do not represent the final outcomes of a full Red List process. * Common migrant species in the UK.

	2001	2002	2003	2004	2005	2006				
Taxon	- 10	- 11	- 12	- 13	- 14	- 15	Total	мт	LQ	UQ
Colias croceus*	EN	CR	CR	CR	EN	VU	6	EN	CR	EN
Melitaea athalia	EN	EN	EN	CR	EN	CR	6	EN	CR	EN
Vanessa cardui*	VU	CR	CR	CR	CR	CR	6	CR	CR	CR
Pyronia tithonus	VU	VU	EN	EN	VU		5	VU	EN	VU
Thecla betulae	EN	EN	EN	EN	EN		5	EN	EN	EN
Thymelicus lineola	CR	CR	CR	CR	EN		5	CR	CR	EN
Argynnis adippe	EN	EN	CR	EN			4	EN	EN	
Euphydryas aurinia			EN	EN	EN	EN	4	EN	EN	
Lasiommata megera	EN	EN	EN	EN			4	EN	EN	VU
Leptidea sinapis	EN	EN	EN	EN			4	EN	EN	
Limenitis camilla			VU	EN	VU	VU	4	VU	VU	
Satyrium pruni			VU	CR	CR	EN	4	EN	CR	
Satyrium w-album			EN	EN	EN	EN	4	EN	EN	VU
Thymelicus acteon	CR	CR	CR	EN			4	EN	CR	
Thymelicus sylvestris	EN	EN	EN	VU			4	VU	EN	
Aglais urticae	EN	EN	EN				3	EN	EN	
Apatura iris			EN		VU	VU	3		VU	
Celastrina argiolus				EN	EN	VU	3	VU	EN	
Coenonympha tullia				EN	VU	EN	3		EN	
Hamearis lucina	EN	EN	EN				3		EN	
Polyommatus										
bellargus			VU		VU	VU	3	VU	VU	
Aricia agestis			VU	VU			2			
Callophrys rubi				VU	VU		2		VU	
Erebia aethiops	EN	VU					2		VU	
Gonepteryx rhamni			VU	VU			2			

Hesperia comma	VU		EN			2	VU	
Maniola jurtina		VU	VU			2		
Plebejus argus	VU		VU			2		
Vanessa atalanta*				VU	VU	2	VU	
Aglais io			VU			1		
Aricia artaxerxes	VU					1		
Boloria euphrosyne	VU					1		
Lycaena phlaeas					VU	1		
Pieris brassicae			VU			1		
Pieris rapae			EN			1		
Polygonia c-album			VU			1		
Polyommatus icarus			EN			1		
Anthocharis								
cardamines						0		
Aphantopus								
hyperantus						0		
Argynnis aglaja						0		
Argynnis paphia						0		
Boloria selene						0		
Coenonympha								
pamphilus						0		
Cupido minimus						0		
Erynnis tages						0		
Favonius quercus						0		
Hipparchia semele						0		
Maculinea arion						0		
Melanargia galathea						0		
Ochlodes sylvanus						0		
Pararge aegeria						0		
Pieris napi						0		
Polyommatus coridon						0		
Pyrgus malvae						0		

Case study 2: UK macro-moths

A second case study, using population data for 431 UK macro-moths (hereafter "moths"), was undertaken to assess the wider applicability of the results for butterflies.

Monitoring of adult moth numbers has been carried out across the UK since 1968, as part of the Rothamsted Insect Survey (RIS) run by Rothamsted Research (www.rothamsted.ac.uk/insect-survey). Standardised light-traps operate at approximately 80-100 sites annually, on every night of the year and all moths attracted into the traps are retained for identification by professional staff or expert volunteers (Conrad *et al.* 2004). The data have been used to assess long-term change in moth biodiversity, including as part of official Government indicators (Conrad *et al.* 2006; Eaton *et al.* 2015; Burns *et al.* 2018).

For this case study, we present a preliminary analysis of RIS abundance data using the Generalized Abundance Index (GAI) approach (Dennis et al. 2016). RIS count data were extracted for UK resident moth species in the families Hepialidae, Cossidae, Sesiidae, Limacodidae, Zygaenidae, Drepanidae, Lasiocampidae, Endromidae, Saturniidae, Sphingidae, Geometridae, Notodontidae, Erebidae, Noctuidae and Nolidae (Agassiz, Beavan & Heckford 2013). Species that occur in the UK only as immigrants were excluded. Daily species count data for the full RIS time series (1960-2015) were analysed using the GAI method and trends assessed using linear regression. The data were not filtered prior to analysis, but *post hoc* tests on the GAI for the entire time series of data for each species were used to identify statistically unreliable models. Species were excluded from the case study where the results contained indices for less than 10 years and/or where the number of years with missing indices was greater than 30% of the total series. In addition, the annual index values and their standard errors were assessed and species exhibiting extreme indices (indices <zero or >4) or exceptionally large standard errors (standard error >1) were also excluded from the case study.

Having excluded species that did not meet the minimum statistical requirements, a series of five, overlapping 10-year population trends were calculated for the remaining species. First, in keeping with the IUCN 10-year rule, GAI values for the most recent 10 years available for each moth species were used to derive a population trend by fitting linear regressions. The key parameters (e.g. slope, intercept, statistical significance) of each of these linear models were stored, and measures of annual growth rate and proportional

change over the 10-year time period were calculated from these parameters. For the majority of species the most recent 10-year period was 2006-2015. However, as data availability varied from species to species, e.g. because rapidly declining species become so scarce that they are no longer caught at all in the RIS monitoring network, the start/end year of this most recent 10-year period was not the same for all species.

Next, this process was repeated four times for every moth species, on each occasion starting the 10-year period one year earlier. Only the GAI values for each 10-year period were used to calculate the population trend in each instance. This resulted in five 10-year population trends per species, each trend lagged by one year: t (the most recent 10 years), t-1, t-2, t-3 and t-4. For the majority of species, the five trends covered the periods 2006-2015, 2005-2014, 2004-2013, 2003-2012 and 2002-2011, but some extended back into the 1990s and, in one case, the 1980s. For each time period, 10-year species population trends that were statistically significant at p < 0.05 were then assessed against IUCN Criterion A2 thresholds to provide a threat (extinction risk) classification.

Population trends for a total of 431 moth species, which had statistically reliable long-term GAI models, were assessed across five overlapping 10-year time periods (Table A5.2). 109 species (25% of the total) had statistically significant 10-year population trends that met IUCN Criterion A2 thresholds for Red List threat categories (i.e. Critically Endangered ≥80% population decrease, Endangered ≥50% decrease or Vulnerable ≥30% decrease) in at least one of the five time periods. The remaining 322 species (75% of the total) did not meet these conditions in any of the five 10-year periods. However, of the 109 species that qualified as threatened, only five (4.6%) did so in all five of the time periods; the remaining 104 moth species were variable, qualifying for the Red List in some time periods but not in others, despite the fact that the five time periods were offset by only one year in each case.

The number of moths qualifying under Criterion A2 varied considerably between the time periods (Table 5.3). Most dramatically, the difference of a single year between period t-3 and t-4 reduced the number of qualifying species from 62 (14% of the total number of species assessed) to just 20 (5%). While appropriate for use in this case study and for demonstrating the variation in trend magnitude from year to year, it should be noted that this is a preliminary analysis of RIS data and the proportional change values over time for individual species may differ when a more detailed analysis is carried out.

Table 5.3 Number of UK macro-moth species (of 431 species assessed) meeting Red List threat thresholds under IUCN Criterion A2 (reduction in population size) on the basis of preliminary 10-year RIS population trends representing the most recent 10-year period (t) and preceding 10-year periods each starting one year earlier than the previous (t-1, t-2, t-3, t-4). These classifications do not represent the final outcomes of a full Red List process.

	t	t-1	t-2	t-3	t-4
Critically Endangered	14	17	13	13	4
Endangered	27	24	35	37	11
Vulnerable	5	5	9	12	5
Total	46	46	57	62	20

Discussion

The case studies using UK butterfly and macro-moth population time series revealed large discrepancies between Criterion A Red List classifications produced using trends that differed by just a single year. For individual species, the temporal patterns of Red List qualification might reflect genuinely improving or deteriorating levels of extinction risk. On the other hand, and as indicated by the dynamic nature of many species population trends between years (Table A5.1, Table A5.2), patterns may be artefacts of process errors driven by environmental (particularly climatic) variability. Whatever the specific cause of the intra-species variation, the application of the 10-year rule, and specifically the requirement for the population trend to be measured over the most recent 10 years, leads, in our opinion, to a scientifically unacceptable dependency of the Red List classification outcome on the year in which the process is undertaken.

The use and misuse of IUCN Red List criteria has been considered frequently in the literature (Eaton *et al.* 2005; Akçakaya *et al.* 2006; Collen *et al.* 2016), but

the specific issue concerning the use of short-term (the most recent 10 years or three generations) population trends to classify insect taxa under Criterion A has not been addressed. Many insect species naturally undergo highly variable and erratic population dynamics, due to environmental variation (Williams 1961) or density-dependence effects (Hanski 1990), and, as illustrated in the case studies using UK butterflies and moths, this may impact significantly on the Red List classifications.

Studies using vertebrate population data have concluded that longer time series can improve the assessment of extinction risk under Criterion A, and practitioners undertaking Red Listing of butterflies have highlighted the same issue (van Swaay et al. 2011; Maes et al. 2012). Indeed the current IUCN guidelines reflect this, suggesting that using data from a longer time period to fit a statistical model of population decline may be preferable for species that have widely fluctuating or oscillating population dynamics (in Section 4.5.1, IUCN 2017). Nevertheless, the IUCN guidelines go on to stress that having fitted the model, the proportional decline should still be calculated over the most recent 10 years or three generations, as per the 10-year rule. In light of our results, we do not consider this guidance to be sufficient. It is optional, dependent on the availability of long-term data and relies on practitioners being familiar with the detailed IUCN guidance. Even if applied, the requirement to calculate change over the most recent 10 years is unlikely to ameliorate the problem illustrated by our case studies, as high levels of inter-annual population variability within the 10-year period are still likely to strongly skew trends and therefore Red List assessments. More fundamentally, the 10-year rule remains the basis of IUCN Criterion A and can be used to determine the extinction risk of species without use of longer-term data. Our results, quantifying the impacts of 10-year trend start year on the number and identity of species meeting Red List thresholds, suggest that this is inappropriate for UK butterflies and macro-moths and potentially for many other insect and invertebrate taxa around the world.

An obvious solution to the problem is to measure population trends over a longer period of time rather than the last 10 years. Linear trends over the 40+ year time series available for both UK butterflies and moths dampen the effects of annual variation, providing a more robust assessment of population change.

From such long-term population trends, annual rates of change can be used to calculate a 10-year trend for each species that can be assessed against the IUCN Criterion A thresholds. The important distinction is that this is a population change measured over an average 10-year period of a longer time interval, rather than being measured over the most recent 10 years.

This approach brings other benefits too. IUCN guidance explicitly warns against interpreting the downward phase of population cycles as a reduction under Criterion A (Section 4.5, IUCN 2017). While there are well-established cases of population periodicity in moths (e.g. Berryman 1996; Johnson *et al.* 2006; Bell *et al.* 2012), for most species it is unclear whether populations are truly cyclical or simply erratic, making it difficult to apply the IUCN guidance. Trends derived from a long-term time series will be less prone to misinterpretation and misclassification caused by unrecognised population cyclicity. In addition, if practitioners determine that only statistically significant population trends should be used to assign species to Red List threat categories, trends calculated over just the most recent 10 years are unlikely to attain significance, when populations are naturally variable, even if reductions (or increases) are very large, as a result of the small number of data points.

Despite all of these benefits, the key problem with adopting such an approach for Red Listing is that the IUCN guidelines are clear that Criterion A should represent the recent population trend of a taxon and not take account of historical declines. Indeed the 10-year rule is specifically there to ensure that species that have undergone major declines in the past, but are currently stable or recovering, are not classified as threatened under the IUCN Red List process (unless there is sufficient evidence of future threats to support a projected decline that meets threshold levels) (Section 5.4 and 5.5, IUCN 2017).

As a compromise, which avoids the spurious variability of the 10-year rule yet embraces the spirit of reflecting recent population decline, we propose a twostep process to the implementation of IUCN Criterion A with insect population trends. First, long-term data are used to derive an average 10-year trend over the full time series, which is then assessed against the IUCN quantitative thresholds to produce a provisional threat classification for each species. Second, a population trend derived just from the last 10 years of data is calculated for each species and used to adjust the provisional threat classification using expert judgement. Thus, the threat status of species with a long-term population decline but recent stability or recovery would be downgraded, while that of species with both long-term and recent declines would be maintained, or even be increased if the recent trend shows an increasing rate of population reduction. As with all elements of the Red Listing process, it would be essential to document the basis for upgrading or downgrading the threat category of each species to ensure transparency.

An alternative approach to adjusting the classification produced by Criterion A was implemented by Maes *et al.* (2012) when applying the IUCN criteria to butterflies in Flanders (Belgium). They calculated 10-year rates of change (from occurrence rather than abundance data) and applied the IUCN Criterion A thresholds to produce an initial classification for each species. They then upgraded species by one Red List category if they had shown >50% historical distribution decline over a longer time period (c.30 years).

The IUCN Red List process is an important force in biodiversity conservation and has been successfully applied at global, regional and national levels to a wide range of taxa, including insects and other invertebrates (Collen *et al.* 2012). This has been aided in recent years by the development of new statistical techniques to extract reliable trends from species occurrence data (Isaac *et al.* 2014; Maes *et al.* 2015; Dennis *et al.* 2017). Long- and short-term temporal trends can now be derived from annual indices generated by occupancy modelling (Burns *et al.* 2018) and could be used with Criterion A to facilitate Red List assessment of many more invertebrate taxa in many more countries and regions. To our knowledge, the sensitivity of occupancy trends to inter-annual variability has not been examined and this should be a focus of further research prior to the use of such trends under the 10-year rule in Red List assessment for insects.

Robust population monitoring remains the gold standard, however, for measuring biodiversity change (Roy *et al.* 2007; Morecroft *et al.* 2009) and the geographical and taxonomic extent of such schemes for insects continues to

expand (van Swaay *et al.* 2008; Carvell *et al.* 2018; Matechou *et al.* 2018). Where available, population monitoring data should be utilised in Red List assessments, yet the natural variability of insect populations presents a dilemma for conservation practitioners in applying the Red List '10-year rule'. Given the variability illustrated here with case studies on UK butterfly and macro-moth populations, practitioners should be extremely wary of assigning extinction risk to insects based on only the last 10 years of population data as per IUCN Criterion A. Our examples suggest that longer time series of data are required to produce a robust assessment, but trends measured over a long time period are likely to be less indicative of the current extinction risk of a species. While we have proposed one possible compromise solution to ameliorate this issue, and other practitioners may adopt other approaches, further consideration and advice from IUCN on the application of Criterion A for species with high process errors would be very welcome.

Acknowledgements

We would like to thank all of the volunteers involved in gathering the UK butterfly and moth population data. We are grateful to Dr Nick Isaac and two anonymous reviewers for helpful comments on earlier drafts of this paper. The Rothamsted Insect Survey, a National Capability, is funded by the Biotechnology and Biological Sciences Research Council under the Core Capability Grant BBS/E/C/000J0200. We are grateful to collaborators and staff who have contributed to the Rothamsted Insect Survey light-trap network since the 1960s. The UK Butterfly Monitoring Scheme is operated by the Centre for Ecology & Hydrology, Butterfly Conservation and the British Trust for Ornithology, and funded by a multi-agency consortium including the Joint Nature Conservation Committee, Forestry Commission, Natural England, the Natural Environment Research Council, Natural Resources Wales and Scottish Natural Heritage.

References

Agassiz DJL, Beavan SD & Heckford RJ (2013) A checklist of the Lepidoptera of the British Isles. Royal Entomological Society, St Albans, UK.

Akçakaya HR, Butchart SHM, Mace GM, Stuart SN & Hilton-Taylor C (2006) Use and misuse of the IUCN Red List Criteria in projecting climate change impacts on biodiversity. *Global Change Biology* **12**, 2037–2043.

Azam CS, Gigot G, Witte I & Schatz B (2016) National and subnational Red Lists in European and Mediterranean countries: current state and use for conservation. *Endangered Species Research* **30**, 255–266.

Bell JR, Burkness EC, Milne AE, Onstad DW, Abrahamson M, Hamilton KL & Hutchison WD (2012) Putting the brakes on a cycle: bottom-up effects damp cycle amplitude. *Ecology Letters* **15**, 310–318.

Berryman AA (1996) What causes population cycles of forest Lepidoptera? *Trends in Ecology & Evolution* **11**, 28–32.

Brereton T, Roy DB, Middlebrook I, Botham M & Warren M (2011) The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation* **15**, 139–151.

Burns F, Eaton MA, Hayhow DB, Outhwaite CL, Al Fulaij N, August TA, Boughey KL, Brereton T, Brown A, Bullock DJ, Gent T, Haysom KA, Isaac NJB, Johns DG, Macadam CR, Mathews F, Noble DG, Powney GD, Sims DW, Smart SM, Stroh P, Walker KJ, Webb JR, Webb TJ & Gregory RD (2018) An assessment of the state of nature in the United Kingdom: A review of findings, methods and impact. *Ecological Indicators* **94**, 226–236.

Cardoso P, Borges PAV, Triantis KA, Ferrández MA & Martín JL (2011) Adapting the IUCN Red List criteria for invertebrates. *Biological Conservation* **144**, 2432–2440.

Carvell C & Pollinator Monitoring and Research Partnership (2018) *Establishing a UK Pollinator Monitoring and Research Partnership progress report January 2018.* Centre for Ecology & Hydrology and PMRP. Available from https://www.ceh.ac.uk/sites/default/files/Pollinator Monitoring and Research Partnership_Progress report_January 2018.pdf (accessed 22 September 2018).

Collen B, Böhm M, Kemp R & Baillie JEM (2012) *Spineless: status and trends of the world's invertebrates*. Zoological Society of London, London, UK.

Collen B, Dulvy NK, Gaston KJ, Gärdenfors U, Keith DA, Punt AE, Regan HM, Böhm M, Hedges S, Seddon M, Butchart SHM, Hilton-Taylor C, Hoffmann M, Bachman SP & Akçakaya HR (2016) Clarifying misconceptions of extinction risk assessment with the IUCN Red List. *Biology Letters* **12**, 20150843.

Connors BM, Cooper AB, Peterman RM & Dulvy NK (2014) The false classification of extinction risk in noisy environments. *Proceedings of the Royal Society B* **281**, 20132935.

Conrad KF, Warren M, Fox R, Parsons M & Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation* **132**, 279–291.

Conrad KF, Woiwod IP, Parsons M, Fox R & Warren M (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation* **8**, 119–136.

d'Eon-Eggertson F, Dulvy NK & Peterman RM (2015) Reliable identification of declining populations in an uncertain world. *Conservation Letters* **8**, 86–96.

de longh HH & Bal D (2007) Harmonization of Red Lists in Europe: some lessons learned in the Netherlands when applying the new IUCN Red List Categories and Criteria version 3.1. *Endangered Species Research* **3**, 53–60.

Dennis EB, Morgan BJT, Freeman SN, Brereton TM & Roy DB (2016) A generalised abundance index for seasonal invertebrates. *Biometrics* **72**, 1305–1314.

Dennis EB, Morgan BJT, Freeman SN, Ridout MS, Brereton TM, Fox R, Powney GD & Roy DB (2017) Efficient occupancy model-fitting for extensive citizen-science data. *PLoS One* **12**, e0174433.

Dunn EH (2002) Using decline in bird populations to identify needs for conservation action. *Conservation Biology* **16**, 1632–1637.

Eaton MA, Burns F, Isaac NJB, Gregory RD, August TA, Barlow KE, Brereton T, Brooks DR, Al Fulaij N, Haysom KA, Noble DG, Outhwaite C, Powney GD, Procter D & Williams J (2015) The priority species indicator: measuring the trends in threatened species in the UK. *Biodiversity* **16**, 108–119.

Eaton MA, Gregory RD, Noble DG, Robinson JA, Hughes J, Procter D, Brown AF & Gibbons DW (2005) Regional IUCN Red Listing: the process as applied to birds in the United Kingdom. *Conservation Biology* **19**, 1557–1570.

Gaston KJ & Fuller RA (2008) Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution* **23**, 14–19.

Hanski I (1990) Density dependence, regulation and variability in animal populations. *Philosophical Transactions of the Royal Society B* **330**, 141–150.

Hoffmann M, Brooks TM, Fonseca GAB, Gascon C, Hawkins AFA, James RE, Langhammer P, Mittermeier RA, Pilgrim JD, Rodrigues ASL & Silva JMC (2008)
Conservation planning and the IUCN Red List. *Endangered Species Research* 6, 113–125.

Isaac NJB, van Strien AJ, August TA, de Zeeuw MP & Roy DB (2014) Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution* **5**, 1052–1060.

IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1*. IUCN Species Survival Commission, Gland, Switzerland and Cambridge, UK.

IUCN (2012) Guidelines for Application of IUCN Red List Criteria at Regional and National Levels: Version 4.0. IUCN, Gland, Switzerland and Cambridge, UK.

IUCN Standards and Petitions Subcommittee (2017) *Guidelines for Using the IUCN Red List Categories and Criteria. Version 13.* IUCN, Gland, Switzerland and Cambridge, UK.

Johnson DM, Liebhold AM & Bjørnstad ON (2006) Geographical variation in the periodicity of gypsy moth outbreaks. *Ecography* **29**, 367–374.

Keith D, Akcakaya HR, Butchart SHM, Collen B, Dulvy NK, Holmes EE & Hutchings JA (2015) Temporal correlations in population trends: Conservation implications from time-series analysis of diverse animal taxa. *Biological Conservation* **192**, 247–257.

Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Milner-Gulland EJ & Stuart SN (2008) Quantification of extinction risk: International Union for the Conservation of Nature's (IUCN) system for classifying threatened species. *Conservation Biology* **22**, 1424–1442.

Maes D, Isaac NJB, Harrower CA, Collen B, van Strien AJ & Roy DB (2015) The use of opportunistic data for IUCN Red List assessments. *Biological Journal of the Linnean Society* **115**, 690–706.

Maes D, Vanreusel W, Jacobs I, Berwaerts K & Van Dyck H (2012) Applying IUCN Red List criteria at a small regional level: A test case with butterflies in Flanders (north Belgium). *Biological Conservation* **145**, 258–266.

Matechou E, Freeman SN & Comont R (2018) Caste-specific demography and phenology in bumblebees: modelling *BeeWalk* data. *Journal of Agricultural, Biological and Environmental Statistics* **23**, 427–445.

McCain C, Szewczyk T & Bracy Knight K (2016) Population variability complicates the accurate detection of climate change responses. *Global Change Biology* **22**, 2081–2093.

Miller RM, Rodríguez JP, Aniskowicz-Fowler T, Bambaradeniya C, Boles R, Eaton MA, Gärdenfors U, Keller V, Molur S, Walker S & Pollock C (2007) National threatened species listing based on IUCN criteria and regional guidelines: Current status and future perspectives. *Conservation Biology* **21**, 684–696.

Mills SC, Oliver TH, Bradbury RB, Gregory RD, Brereton T, Kühn E, Kuussaari M, Musche M, Roy DB, Schmucki R, Stefanescu C, van Swaay C & Evans KL (2017) European butterfly populations vary in sensitivity to weather across their geographical ranges. *Global Ecology and Biogeography* **26**, 1374–1385.

Morecroft MD, Bealey CE, Beaumont DA, Benham S, Brooks DR, Burt TP, Critchley CNR, Dick J, Littlewood NA, Monteith DT, Scott WA, Smith RI, Walmsley C & Watson H (2009) The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation* **142**, 2814–2832.

Oliver TH, Marshall HH, Morecroft MD, Brereton T, Prudhomme C & Huntingford C (2015) Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change* **5**, 941– 945. Oliver TH, Stefanescu C, Páramo F, Brereton T & Roy DB (2014) Latitudinal gradients in butterfly population variability are influenced by landscape heterogeneity. *Ecography* **37**, 863–871.

Palmer G, Platts PJ, Brereton T, Chapman JW, Dytham C, Fox R, Pearce-Higgins JW, Roy DB, Hill JK & Thomas CD (2017) Climate change, climatic variation and extreme biological responses. *Philosophical Transactions of the Royal Society B* **372**, 20160144.

Pollard E & Yates TJ (1993) *Monitoring Butterflies for Ecology and Conservation*. Chapman & Hall, London, UK.

Porszt EJ, Peterman RM, Dulvy NK, Cooper AB & Irvine JR (2012) Reliability of indicators of decline in abundance. *Conservation Biology* **26**, 894–904.

Rodrigues ASL, Pilgrim JD, Lamoreux JF, Hoffmann M & Brooks TM (2006) The value of the IUCN Red List for conservation. *Trends in Ecology & Evolution* **21**, 71–76.

Roy DB, Ploquin EF, Randle Z, Risely K, Botham MS, Middlebrook I, Noble D, Cruickshanks K, Freeman SN & Brereton TM (2015) Comparison of trends in butterfly populations between monitoring schemes. *Journal of Insect Conservation* **19**, 313–324.

Roy DB, Rothery P & Brereton T (2007) Reduced-effort schemes for monitoring butterfly populations. *Journal of Applied Ecology* **44**, 993–1000.

Roy DB, Rothery P, Moss D, Pollard E & Thomas JA (2001) Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology* **70**, 201–217.

Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B* **360**, 339–357.

van Strien AJ, van de Pavert R, Moss D, Yates TJ, van Swaay CAM & Vos P (1997) The statistical power for two butterfly monitoring schemes to detect trends. *Journal of Applied Ecology* **34**, 817–828.

van Swaay C, Maes D, Collins S, Munguira ML, Šašić M, Settele J, Verovnik R, Warren M, Wiemers M, Wynhoff I & Cuttelod A (2011) Applying IUCN criteria to

invertebrates: How red is the Red List of European butterflies? *Biological Conservation* **144**, 470–478.

van Swaay CAM, Nowicki P, Settele J & van Strien AJ (2008) Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation* **17**, 3455–3469.

White ER (2019) Minimum time required to detect population trends: the need for long-term monitoring programs. *BioScience* **69**, 40–46.

Williams CB (1961) Studies in the effect of weather conditions on the activity and abundance of insect populations. *Philosophical Transactions of the Royal Society B* **244**, 331–378.

Wilson HB, Kendall BE & Possingham HP (2011) Variability in population abundance and the classification of extinction risk. *Conservation Biology* **25**, 747–757.

Winfree R, Fox JW, Williams NM, Reilly JR & Cariveau DP (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters* **18**, 626–635.

Chapter 6: Opinions of citizen scientists on open access to UK butterfly and moth occurrence data

Published as:

Fox R, Bourn NAD, Dennis EB, Heafield RT, Maclean IMD & Wilson RJ (2019) Opinions of citizen scientists on open access to UK butterfly and moth occurrence data. *Biodiversity and Conservation* **28**, 3321–3341.

Abstract

Citizen science plays an increasingly important role in biodiversity research and conservation, enabling large volumes of data to be gathered across extensive spatial scales in a cost-effective manner. Open access increases the utility of such data, informing land-use decisions that may affect species persistence, enhancing transparency and encouraging proliferation of research applications. However, open access provision of recent, fine-scale spatial information on the locations of species may also prompt legitimate concerns among contributors regarding possible unintended negative conservation impacts, violations of privacy and commercial exploitation of volunteer-gathered data. Here we canvas the attitudes towards open access of contributors (104 regional coordinators and 510 recorders) of species occurrence records to two of the largest citizen science biodiversity recording schemes, the UK's Butterflies for the New Millennium project and National Moth Recording Scheme. We find that while the majority of participants expressed support for open access in principle, most were more cautious in practice, preferring to limit the spatial resolution of records, particularly of threatened species, and restrict commercial reuse of data. In addition, citizen scientists' opinions differed between UK countries, taxonomic groups and the level of involvement volunteers had in the schemes. In order to maintain successful and democratic citizen science schemes. organisers, funders and data users must understand and respect participants' expectations and aspirations regarding open data while seeking to optimise data use for scientific and societal benefits.

Introduction

There is growing expectation and demand for open access to data in many areas of public life including science. In addition to the accepted scientific

requirements of transparency and reproducibility, and the responsibility of public funding, this demand has been driven by the development of "big data" technologies enabling the storage and analysis of huge quantities of information (Arzberger *et al.* 2004; Farley *et al.* 2018). Scientists are increasingly willing to share data publicly (Tenopir *et al.* 2015), enabling other researchers to utilise and build upon freely-available archived data, resulting in benefits for society. An open access culture has developed in some scientific fields, notably genetics and genomics (Noor *et al.* 2006), although even here ethical concerns remain (McGuire *et al.* 2011; McEwen *et al.* 2013; Choudhury *et al.* 2014).

Ecologists, however, have been relatively slow to embrace open data, despite its potential to address many urgent, global, environmental pressures (Hampton *et al.* 2013; Poisot *et al.* 2013; Kenall *et al.* 2014; Soranno *et al.* 2015). Progress towards a more open approach in ecology is hindered by technological and cultural barriers, but solutions and incentives have emerged, alongside new obligations for public data archiving from funding organisations and scientific journals (Reichman *et al.* 2011; Michener 2015; Nosek *et al.* 2015; Culina *et al.* 2018a). Nevertheless, concerns remain about open access to ecological data, and while the views of scientists and organisations have been reported (Moles *et al.* 2013; Mills *et al.* 2015; Pearce-Higgins *et al.* 2018; Tulloch *et al.* 2018), the opinions of citizen scientists themselves have been overlooked.

Ecological data gathered through citizen science projects are increasingly useful, particularly for biodiversity monitoring and conservation (Chandler *et al.* 2017; Sullivan *et al.* 2017; Soroye *et al.* 2018). Unrestricted access to and reuse of citizen science ecological data maximises the societal and scientific returns on the efforts of volunteers; for example disclosure of locations of threatened species can encourage informed decision making about land-use changes that might impact biodiversity, improve species' trend assessments, facilitate applied scientific research and help engage landowners, funders, politicians and the public in conservation (Tulloch *et al.* 2018). However, in the context of open access, citizen science data differ fundamentally from those collected in professional scientific research because the data are contributed by volunteers, who have their own views on data accessibility. It is widely expected that citizen science ecological data will be open access (Groom *et al.* 2017; Robinson *et al.*

2018), perhaps because it is supposed that people who contribute willingly and without material reward to citizen science projects would assume, or even insist, that their data are freely shared and publicly accessible. This assumption may not be justified, in part because the large number of citizen scientists are bound to encompass a diversity of views but also, specifically, because some participants have been engaged in gathering ecological data under different data exchange principles long before the advent of the "big data" era and the contemporary pressure for open access. Indeed, while the term citizen science was coined in the mid-1990s and the field has burgeoned since then (Silvertown 2009; Pocock et al. 2017), there is a long tradition of amateur naturalists gathering ecological, and particularly biogeographical, information (Miller-Rushing et al. 2012; Pocock et al. 2015; Strasser et al. 2019). In this tradition, the individual's motivation to observe and study nature may have little to do with science or biodiversity conservation, leading to mismatches and tensions between the expectations of the scientific establishment and these participants in projects that are nowadays labelled as 'citizen science' (Ellis & Waterton 2004).

Thus, while some citizen science projects have an explicitly open data ethos (e.g. eBird, Sullivan et al. 2014), others do not (Groom et al. 2017). This may simply be because projects and their participants are continuing the historical legacy of mindsets, relationships and practices formed long before the advent of modern citizen science (Strasser et al. 2019) and do not conform to its expectations around open access. Alternatively, access to data may be restricted deliberately due to legitimate concerns from project organisers (Pearce-Higgins et al. 2018; Tulloch et al. 2018). One such concern is that unintended negative consequences of open access, for example harm to threatened species, could lead citizen scientists to cease participation, undermining project viability. It is important, therefore, that organisers, funders and users of citizen science are mindful of the views of participants regarding open access. While the motivations of citizen scientists taking part in biodiversity projects have been surveyed (Evans et al. 2005; Hobbs & White 2012; Wright et al. 2015; Domroese & Johnson 2017), their attitudes towards the onward use of the data that they contribute, and on the specific issue of open access to data, have rarely been considered (Ganzevoort et al. 2017).

These issues are of interest and importance to governmental and nongovernmental organisations involved in conservation and research. For example, the charity Butterfly Conservation runs long-term citizen science schemes focussed on butterflies and moths (Lepidoptera) in the United Kingdom (UK). The schemes rely upon collaboration between paid staff (organising and promoting the schemes, managing databases, undertaking research and providing feedback to participants) and unpaid volunteers (undertaking species recording, computerisation and verification of records). Tens of thousands of volunteers are involved annually and the schemes have generated datasets that underpin assessments of UK Lepidoptera biodiversity change (e.g. Fox et al. 2014; Fox et al. 2015) and the delivery of species conservation (Ellis et al. 2012), as well as research e.g. into the impacts of environmental drivers such as climate change (e.g. Mason et al. 2015; Martay et al. 2017; Pearce-Higgins et al. 2017). In most cases, the data assembled through these schemes are not currently open access. Yet, given the considerable potential benefits for both biodiversity protection and scientific research of increasing access to these data, as well as the ethical impetus towards greater inclusivity (Soranno et al. 2015), the availability of these datasets should be reviewed and weighed against possible negative repercussions (e.g. impacts on threatened species or habitats, intrusion on participants' privacy or damage to partnerships with private landowners who have allowed access to otherwise closed land).

Therefore, to inform such a review and to provide practical recommendations to designers, organisers and funders of similar citizen science projects, we conducted surveys of volunteer participants in Butterfly Conservation recording schemes to seek a nuanced understanding of their views on open access to butterfly and moth occurrence data. Our study extends the approach of Ganzevoort *et al.* (2017), the only similar survey that we are aware of, by exploring the influence of spatial resolution, deferred data release and species threat on the attitudes of two different groups of volunteers with differing roles and levels of involvement in citizen science schemes, as well as contrasting the opinions of recorders of different taxa and in different UK countries. Our principal aim was to document the attitudes of these different groups of participants and understand how these may influence transition towards more

open models of data accessibility. We did not seek to explore the motivations or values underlying participants' attitudes to open access and acknowledge that, as a result, the findings in this respect are limited. However, in addition to quantifying opinions, we sought to test the following hypotheses: 1) if the main concerns of citizen scientists related to potential damage to butterflies, moths or their habitats, rather than about privacy, confidentiality or intellectual property rights, then they would be more reluctant to allow open access to records of threatened species compared to widespread ones and 2) that unwillingness to make threatened species records open access would be ameliorated by limiting (blurring) spatial location information and postponing the release of records for long periods (five or more years).

Methods

Focal citizen science projects

The opinions towards open access of contributors to two UK-wide citizen science projects organised by Butterfly Conservation, Butterflies for the New Millennium (BNM; Asher *et al.* 2001) and the National Moth Recording Scheme (NMRS; Fox *et al.* 2011), were ascertained by questionnaires. The BNM was launched in 1995 and has, to date, collated 12.7 million butterfly species occurrence records covering the period 1690-2017. The NMRS commenced in 2006, initially focusing on macro-moth occurrence records (although it has now been extended to include all moth species), and has compiled 25 million macro-moth records for the period 1746-2016. These projects are among the largest citizen science biodiversity monitoring schemes globally, but the majority of BNM and NMRS records are not currently open access.

The flow of species occurrence records through the BNM and NMRS projects is organised in the same way. Observations made by citizen scientist recorders are sent to regional co-ordinators (also known as County Recorders), who are expert volunteers with the responsibility to collate and verify sightings for their area and maintain a local dataset of records. Copies of these local datasets are then pooled annually and, following further checks, added to the BNM or NMRS databases. At the time of this study, the BNM project included 65 regional coordinators and the NMRS 94. A few individuals fulfilled both roles for their area. The total numbers of citizen scientist recorders participating in the BNM and NMRS annually is unknown, because of inconsistencies in the way that individual recorder identities are logged across the schemes. However, given that each scheme currently collates c.1 million new records per annum, it is likely that there are tens of thousands of contributors at present. Some recorders take part in one but not the other scheme, whereas others contribute sightings to both.

The BNM and NMRS schemes collate opportunistic sightings of species from any location in the UK and on any date. Although there are minimum information standards for valid sightings, there are no sampling protocols – participants can record where, when and for as long as they wish. This traditional model of natural history recording (Pocock *et al.* 2015), separates the schemes on the one hand from systematic monitoring programmes with rigorous sampling protocols undertaken by experienced amateur or professional naturalists (e.g. the UK Butterfly Monitoring Scheme, Brereton *et al.* 2011; North American Breeding Bird Survey, Sauer *et al.* 2013) and, on the other, from modern citizen science projects that often aim to engage people with no previous involvement (e.g. Big Butterfly Count, Dennis *et al.* 2017; Great Pollinator Project, Domroese & Johnson 2017). Thus, while all BNM and NMRS participants are volunteers, their natural history expertise and recording behaviour vary greatly, as has been found in other biodiversity surveillance projects (Boakes *et al.* 2016; Everett & Geoghegan 2016).

Although it is difficult to categorize BNM and NMRS recorders on the basis of levels of engagement or expertise, different volunteer roles within the schemes provide a clear dichotomy; individual regional co-ordinators are essential to the functioning of the schemes in a way that individual recorders are not, as without a regional co-ordinator in place no new records for that area will be provided to the scheme. While the opinions of both groups are important, the integral role of regional co-ordinators in the operation of the schemes necessitates an understanding of their attitudes to data sharing of the records in their custodianship as part of any prospective shift toward open access to the BNM and NMRS data. In addition, as curators of local datasets of species occurrence records, regional co-ordinators are likely to be familiar with the pros and cons of open access and, as expert naturalists, their views will be shaped by the

traditions of data exchange within amateur natural history (Ellis & Waterton 2005; Ellis *et al.* 2005).

Questionnaires

Separate questionnaires were designed to elucidate the views of regional coordinators and recorders and surveys were undertaken in May and June 2017. A longer questionnaire was used for regional co-ordinators so that we could gain a detailed understanding of the views of this key group of volunteers, while a much shorter, 'light touch' and entirely anonymous questionnaire was developed for recorders to maximise participation in the study.

Regional co-ordinator questionnaire

The guestionnaire for regional co-ordinators (Appendix 6) aimed to ascertain the current level of support for and against open access and to gauge how such attitudes vary between volunteers in schemes for different taxa, in different countries and in response to perceived risk of negative impacts. Even when data are made publicly accessible, potential risks to species, habitats, sites or citizens can be moderated by restricting the information that is made available, by delaying the release of data and by legally restricting the uses to which data can be put. Thus, general support for open access was assessed by responses on a 10-point numerical scale (from 1 = serious reservations to 10 = strongly in favour), but subsequent questions asked participants to consider the appropriate spatial resolution of open records (i.e. how much records are blurred to conceal the precise location of species occurrence, with options of full capture resolution or blurring to 1km x 1km square, 2km x 2km square or 10km x 10km square), whether there should be a time lag before records are made public (with options of no lag, 5 year, 10 year or 20 year lags) and on the type of Creative Commons license that should be applied to open access UK butterfly and moth data. Developed as an alternative to traditional 'all rights reserved' copyright, Creative Commons licenses enable the copyright holder to choose which rights to reserve and which to waive, and have been widely adopted in many fields of human endeavour, including biodiversity monitoring (Hagedorn et al. 2011; Groom et al. 2017). Regional co-ordinators were asked for their opinion on the most appropriate of three Creative Commons licenses for UK butterfly and moth occurrence data; Zero (CC0), which has no restrictions on

reuse, Attribution (CC-BY), which requires users to acknowledge the author/source, and Attribution-NonCommercial (CC-BY-NC), which requires acknowledgement and restricts reuse to non-commercial applications.

In addition to controlling data availability and use, the rarity or threat levels of taxa are likely to influence the perception of risk stemming from open access. The questionnaire sought to quantify this by asking respondents to consider the appropriate spatial resolution for open access records separately for widespread and threatened species. 'Widespread' and 'threatened' were not defined, so respondents used their own interpretation. In addition, regional co-ordinators were asked whether there were taxa or specific populations of taxa in their area that would require a more restrictive approach than the various open access options already discussed.

In total, the regional co-ordinator questionnaire included six questions with multiple-choice or scaled answers. Respondents were asked to provide their name and the geographical area for which they fulfil the role of regional co-ordinator. Questions were not obligatory and not all respondents completed all questions.

The questionnaire was sent by email attachment as a Microsoft Word document with a covering letter (Appendix 6) to all UK regional co-ordinators in the BNM and NMRS networks on 10 May 2017. Regional co-ordinators were given until the end of May 2017 to respond, although responses received by 7 June 2017 were included in the analysis.

Recorder questionnaire

A simpler questionnaire (Appendix 6) was designed to canvas recorders' views on open access and how recording behaviour might change in response to it. Just four multiple-choice questions were asked; two to segment respondents by UK country and taxonomic interest (recording butterflies, moths or both) and two relating to open access. Recorders were asked for their preferred open access spatial resolution for their own records via the BNM and NMRS schemes. Three options were provided: all records open at full capture resolution (i.e. the same level of spatial resolution as submitted by the recorder), widespread species at full resolution but scarce/threatened species at a summary (i.e. blurred) resolution, and all records at summary resolution. Secondly, to quantify the impacts (positive or negative) of moving to open access, recorders were asked about their likely behaviour towards the schemes if all records were made fully accessible. Four options were available; withhold future records from the schemes, blur the resolution of future contributed records, continue to participate as before, and increase support for the schemes by submitting more records.

All four questions were obligatory and the survey was anonymous. The questionnaire was an online survey designed using DotMailer (www.dotmailer.com). In late May 2017, the online questionnaire was promoted to recorders by the UK regional co-ordinators. It remained live for just over two weeks with data being extracted on 13 June 2017.

Analysis

For each questionnaire, analysis was carried out on the aggregated responses but also separately after categorizing respondents by geographic or taxonomic interest, to test for differences between citizen scientists in different constituent countries of the UK (England, Scotland, Wales; Northern Ireland could not be tested separately due to a low sample size of responses to both questionnaires) and between recorders of butterflies, moths and both taxa. In addition, for the regional co-ordinator questionnaire data, we divided respondents into promoters, neutrals (passives) and detractors on the basis of their general support (on a 10-point scale) for open access to butterfly and moth records, using a slightly modified Net Promoter Score (NPS) methodology (Reichheld 2003; Keiningham et al. 2007). We classified those who scored 9 or 10 as promoters of open access, those who scored 5-8 as neutral and those scoring 1-4 as open access detractors. In standard NPS classification, scores as high as 6 are designated as detractors, but we increased the neutral segment to reflect better the range of views of our respondents. Categorising in this way enabled us to compare the opinions of regional co-ordinators with different levels of overall support for the principle of open access to the questions about specific details of record resolution, temporal delays in data release and species threat status.

Each comparison was analysed initially using Pearson Chi-squared and linearby-linear association tests (Agresti 2002), accounting for the presence of ordinal variables. Where significant associations were found, cumulative link models with logit link were fitted, then Tukey-adjusted pairwise differences were investigated via least-squares means (LSM). All analyses were undertaken in R version 3.5.1 (R Core Team 2018) using the packages ordinal (Christensen 2018), coin (Hothorn *et al.* 2008) and emmeans (Lenth 2018). Goodness of fit for the cumulative link models was checked using likelihood ratio tests (nominal_test and scale_test in the ordinal package), in particular to assess whether the proportional odds assumption was satisfied. In some cases this assumption was not met, suggesting that the cumulative link model may not be appropriate, and in these instances pairwise differences among the explanatory variables were either assessed using the Cochran-Armitage test (with *p* values adjusted to account for false discovery rate) or only considered on the basis of summary statistics and figures.

Ethics statement

Butterfly Conservation conforms strictly to appropriate legislation and codes of conduct relating to personal data and both questionnaires were designed and implemented in this context. For the regional co-ordinator questionnaire, full informed consent was obtained from all participants for the use of anonymised, aggregated responses in this research paper. Participants consented to the secure storage of data and access to the data by Butterfly Conservation employees involved in its analysis, and to publication of the arising results, for a period of five years, after which the data will be destroyed. Regional co-ordinator responses were anonymized prior to analysis. The online recorder questionnaire was completely anonymous and no personal data were collected. Participation in the questionnaires was voluntary and respondents were informed that the purpose was to gather views relating to open access to UK butterfly and moth occurrence data to aid the ongoing management and development of recording scheme data by Butterfly Conservation and other citizen science organisers.

Results

Regional co-ordinators

Survey coverage

Completed questionnaires were received from 104 regional co-ordinators representing response rates of 69% for the BNM and 68% for the NMRS networks. Responses were received from all four UK countries: 60 England, 2 Northern Ireland, 28 Scotland, 14 Wales.

Support for open access

Using our modified NPS scale, 39.8% of 103 regional co-ordinators who responded to this question were classified as open access promoters, 43.7% as neutrals and 16.5% as detractors. There was no difference in NPS value between respondents responsible for butterfly records, moth records and those who cover both taxa ($\chi^2 = 3.257$, df = 2, *p* = 0.196), although regional co-ordinators for butterflies generally appeared to have more moderate NPS values than other co-ordinators, with smaller proportions in both the promoter and detractor classes (Fig. A6.1).

Levels of general support for open access (measured with NPS) varied significantly between countries (Fig. 6.1, $\chi^2 = 9.766$, df = 2, p = 0.008); regional co-ordinators in Scotland were more in favour of open access than their counterparts in England (England – Scotland contrast: LSM estimate = -0.485, z ratio = -3.252, p = 0.003). Respondents from Wales had similar NPS scores to those from Scotland, but the difference with England was not statistically significant (England – Wales contrast: LSM estimate = -0.364, z ratio = -1.852, p = 0.153).

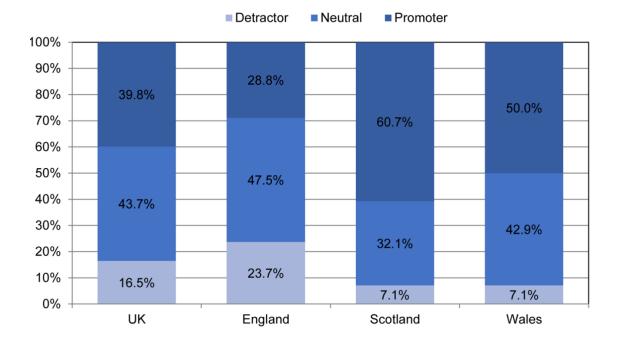
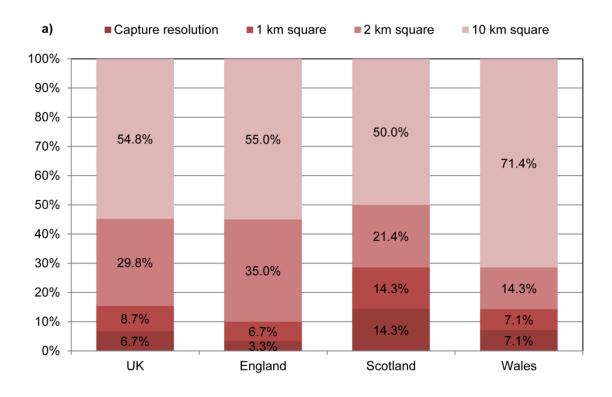


Fig. 6.1 Levels of general support for open access, assessed by modified NPS categories, among regional co-ordinators from UK, England, Scotland and Wales (Northern Ireland not shown separately due to low sample size).

Spatial resolution of records

For records of threatened species, only 6.7% of the 104 regional co-ordinators were in favour of open access at full capture resolution (Fig. 6.2a). The majority (54.8%) preferred records of such species to be accessible only at 10km x 10km square (hereafter '10km square') scale, the coarsest resolution offered in the questionnaire, with a further 29.8% in favour of 2km x 2km square (hereafter '2km square') scale. Attitudes were very different for records of widespread species. For these, 37.5% of regional co-ordinators were in favour of open access at full capture resolution, while a further 40.4% supported open access at 1km x 1km square (hereafter '1km square') resolution and 17.3% chose the 2km square scale (Fig. 6.2b). Only 4.8% (5 of 104 respondents) preferred the coarsest resolution option (10km square) for records of widespread species. These results provide support for our hypotheses, suggesting that fear of ecological damage underlies regional co-ordinators' concerns about open access (as they were much more restrictive about records of threatened species than widespread ones) and also that these concerns can be ameliorated by blurring the spatial resolution of accessible records.



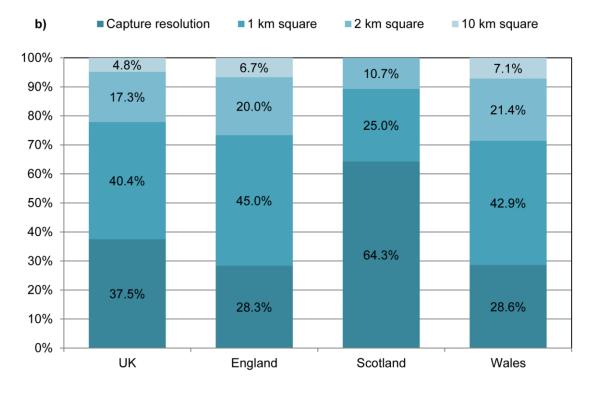


Fig. 6.2 Preferred resolution of open access records of a) threatened species and b) widespread species among regional co-ordinators from UK, England, Scotland and Wales (Northern Ireland not shown separately due to low sample size).

For threatened species records there was no apparent difference between the responses from regional co-ordinators in different countries ($\chi^2 = 3.364$, df = 2, p = 0.186), but there was a significant difference for widespread species ($\chi^2 = 9.513$, df = 2, p = 0.009); regional co-ordinators in Scotland favoured finer resolution of open access records of widespread species than those in England (Scotland – England contrast: LSM estimate = -0.585, z ratio = -3.493, p = 0.001) (Fig. 2b). There was also a tendency for regional co-ordinators in Scotland to favour finer resolution access than those in Wales (Scotland – Wales contrast: LSM estimate = -0.604, z ratio = -2.298, p = 0.056). For example, in Scotland, 64.3% supported capture resolution access for widespread species compared to 28.3% in England and 28.6% in Wales.

There was a significant negative relationship between NPS category and preferred spatial resolution for both threatened (linear-by-linear association test Z = -3.794, p = 0.0001) and widespread species (Z = -5.197, p = <0.0001), with detractors favouring the coarsest resolutions. For records of widespread species, detractors favoured a coarser resolution than both neutrals (detractors – neutrals contrast: LSM estimate = 0.995, z ratio = 4.358, p = <0.0001) and promoters (detractors – promoters contrast: LSM estimate = 1.396, z ratio = 6.207, p = <0.0001), and neutrals favoured a coarser resolution than promoters (neutrals – promoters contrast: LSM estimate = 0.401, z ratio = 2.690, p = 0.020).

Based on the goodness-of-fit tests, the cumulative link model was not reliable for pairwise contrasts between NPS categories and preferred spatial resolution for records of threatened species, but the responses suggest that detractors favoured coarser resolutions than neutrals who, in turn, favoured coarser resolutions than promoters (Fig. A6.2). None of the regional co-ordinators who classified as detractors or neutrals and only 17.1% of promoters were in favour of capture resolution open access for threatened species records. Even at the 2km square scale, only 17.6% detractors and 44.4% of neutrals were supportive, compared to the majority (58.5%) of promoters who were in favour of open access to records of threatened species at this resolution or even finer. In contrast, all of the regional co-ordinators classified as promoters or neutrals were in favour of open access to widespread species records at 2km square

resolution, along with 70.6% of detractors. However, even for records of widespread species there was only limited support for full resolution open access, with 61.0% promoters, 28.9% neutrals and just 5.9% detractors (corresponding to one respondent) in favour.

The preferred spatial resolution of open access records of threatened species differed between regional co-ordinators covering butterflies, moths or both taxa ($\chi^2 = 9.376$, df = 2, p = 0.009) but there was no apparent difference for widespread species ($\chi^2 = 0.852$, df = 2, p = 0.653). Regional co-ordinators for butterflies preferred finer resolution open access for threatened species records than their moth counterparts (butterfly co-ordinators – moth co-ordinators contrast: LSM estimate = -0.627, z ratio = -3.441, p = 0.002) or for those covering both taxa (butterfly co-ordinators – co-ordinators of both taxa contrast: LSM estimate = -0.676, z ratio = -3.101, p = 0.006). Only 28.9% of regional co-ordinators for butterflies considered that the coarsest resolution (10km square) was required for open access records of threatened species, while 68.1% of regional co-ordinators for moths felt this was the appropriate resolution, as did 73.7% of co-ordinators responsible for both taxa.

Time lags

Of the 100 regional co-ordinators that responded to the question about time lags, 74 favoured no delay to records being made open access, 21 supported a 5-year lag, 1 a 10-year lag and 4 a 20-year lag. NPS was significantly related to time lag (linear-by-linear association test Z = -5.351, p = <0.0001), with higher NPS correlated with shorter time lags. We were unable to undertake pairwise comparisons between NPS categories and time lags as the models did not satisfy goodness-of-fit tests. However, the significant relationship supports our hypothesis that concerns about open access can be lessened by deferring the release of records, at least among those regional co-ordinators who are generally more concerned about open access.

There was no apparent difference in the responses on time lags between regional co-ordinators covering different taxa ($\chi^2 = 2.371$, df = 2, p = 0.306), but there was between countries ($\chi^2 = 8.495$, df = 2, p = 0.014); only 11% (3 of 28 respondents) of regional co-ordinators in Scotland and 8% (1 of 13

respondents) in Wales advocated any time lag at all, and all of these were at the 5-year level, while 39% of 57 respondents in England were in favour of a delay in the release of records, including 9% who supported at least a 10-year delay. The difference in opinion on time lags was statistically significant (at the 5% level) between regional co-ordinators in England and Scotland (Cochran–Armitage test Z = 2.403, p = 0.049), but not between England and Wales (Cochran–Armitage test Z = 1.780, p = 0.113).

Additional restrictions for species or colonies

70.1% of 97 regional co-ordinators who answered this question stated that no additional restrictions on open access were required for species and/or sites in their area beyond those provided by constraints on spatial resolution and time lags.

Creative Commons licences

Of the 103 regional co-ordinators who answered this question, 79.6% favoured the Attribution-NonCommercial licence (CC-BY-NC), the most restrictive of the three Creative Commons licence options offered on the questionnaire. Only 3.9% of respondents selected the most open licence option (CC0).

Opinions about Creative Commons licences differed between countries (χ^2 = 8.105, df = 2, *p* = 0.017). 46.2% of regional co-ordinators in Wales favoured the more open licences (CC0 and CC-BY), compared to 21.4% in Scotland and just 15.0% in England, but none of the pairwise comparisons were statistically significant (at the 5% level) using cumulative link models. There was no difference in views on Creative Commons licences between regional co-ordinators responsible for different taxa (χ^2 = 0.659, df = 2, *p* = 0.719).

Recorders

Survey coverage

A total of 510 people completed the online questionnaire aimed at contributors of occurrence records to the BNM and NMRS. 25.3% identified as butterfly recorders, 25.5% as moth recorders and 49.2% stated that they recorded both groups. 367 (72.0%) respondents record mainly in England, 80 (15.7%) in Scotland, 58 (11.4%) in Wales and 5 (1.0%) in Northern Ireland.

Spatial resolution of open access to own records

32.7% of respondents preferred full open access, opting for public access to all their records at capture resolution. A further 50.8% indicated that they were happy for their records of widespread species (but not those of scarce/ threatened species) to be available at full capture resolution. Thus, for widespread species, 83.5% of respondents supported open access at capture resolution. In contrast, 16.5% of citizen scientists opposed capture resolution open access to any of their records (i.e. the spatial resolution of all records should be blurred to obscure precise locations), along with the 50.8% of respondents who thought that their records of scarce/threatened species should be blurred. Thus, 67.3% of respondents were against open access at capture resolution for some of their records. There were no significant differences between the views of recorders of different taxa ($\chi^2 = 2.022$, df = 2, p = 0.364) or in the different countries ($\chi^2 = 2.324$, df = 2, p = 0.313). The overall pattern, with a majority of recorders preferring to have their records of scarce/threatened species blurred but those of widespread species available at capture resolution provides further support for our two hypotheses; concern about ecological harm resulting from open access appears to be widespread among recorders and can be reduced by blurring the spatial resolution of records that are made publicly accessible.

Future support for open access recording schemes

The majority of respondents (76.7%) indicated that their participation in the projects would be affected positively (4.5% would provide more records) or unaffected (72.2%) if all records were made open access in full detail. In contrast, the results suggest that the participation in the recording schemes of 23.3% of respondents would be detrimentally impacted, either due to them reducing the precision of the records they submit (21.2%) or withholding records entirely (2.2%). There were no significant differences in responses between countries ($\chi^2 = 1.267$, df = 2, *p* = 0.531) or between recorders of different taxa ($\chi^2 = 2.393$, df = 2, *p* = 0.302).

Discussion

We have shown that while there are high levels of support in principle for open access among UK citizen scientists that contribute, collate and verify

Lepidoptera occurrence data, they do not endorse full capture resolution open access nor unrestricted use of such data. Among the two groups of citizen scientists surveyed, only 6.7% of regional co-ordinators and 32.7% of recorders stated that records of all butterfly and moth species (widespread and threatened) should be open access at capture resolution, and 79.6% of regional co-ordinators felt that data reuse should be limited to non-commercial purposes. These findings are broadly similar to those in the only other study of citizen scientists' opinions that we are aware of; Ganzevoort *et al.* (2017) surveyed the demographics, motivations and views on data ownership and sharing of nearly 2,200 volunteer biodiversity recorders in the Netherlands. They found that only 12.3% of biodiversity recorders in the Netherlands supported unconditional reuse of their data, while 36.7% were opposed to commercial use of their data.

Current limitations to access and reuse of citizen science data are often attributed to the scientists or organisations running citizen science projects, who may face a range of technological, economic and cultural barriers and disincentives to data sharing (Reichman *et al.* 2011; Schmidt *et al.* 2016; Groom *et al.* 2017; Pearce-Higgins *et al.* 2018). However, our UK results and those from the Netherlands suggest that some limitation is in accordance with the wishes and expectations of citizen science participants.

Citizen scientist support for open access

Despite data quality concerns (Kosmala *et al.* 2016; Aceves-Bueno *et al.* 2017; Specht & Lewandowski 2018), citizen science has great potential to address pressing matters in biodiversity monitoring, conservation and research (Theobald *et al.* 2015; Chandler *et al.* 2017; Pocock *et al.* 2018). Open access to citizen science data would maximise this potential through increased reuse and the application of new 'big data' techniques and cross-disciplinary studies (Culina *et al.* 2018b; Farley *et al.* 2018; Ma *et al.* 2018; Tulloch *et al.* 2018), as well as yielding benefits of increased transparency and public trust in science (Soranno *et al.* 2015).

Surveys of citizen scientists' motivations suggest support for these goals, with factors such as contributing to biodiversity conservation and science ranking highly (Hobbs & White 2012; Wright *et al.* 2015; West & Pateman 2016;

Ganzevoort et al. 2017; Lewandowski & Oberhauser 2017). In keeping with this, our surveys of attitudes among UK citizen scientists suggest general support for open access, albeit with some concern about threatened species. 39.8% of UK regional co-ordinators were classified as promoters of open access on the basis of NPS, with a further 43.7% as neutrals, and support was stronger in some UK countries (60.7% promoters in Scotland and 50.0% promoters in Wales). Among the much larger group of recorders, 32.7% felt that all their records should be open access at capture resolution and 76.7% indicated that they would maintain or enhance their participation if the data were to be made completely open. Considering just records of widespread species, 37.5% of regional co-ordinators and 83.5% of recorders were in favour of open access at capture resolution, with the proportion of regional co-ordinators in favour rising to 77.9% if records were restricted to 1km square resolution. In their survey of Dutch biodiversity recorders, Ganzevoort et al. (2017) also found evidence of general support for open access; 76.1% of citizen scientists regarded the data they contributed as a public good or as belonging to the organisation running the recording scheme i.e. they did not consider the data to be their personal property.

Concerns and alleviating factors

Set against this general desire for data to be available and utilised are clear signals from our results and from other studies of concern regarding inappropriate use (Pearce-Higgins *et al.* 2018). As we did not ask participants about the motivations underlying their opinions on open access, discussion of their concerns must be speculative. It is well established that many citizen scientists want their records to contribute towards biodiversity conservation (e.g. Hobbs & White 2012; Lewandowski & Oberhauser 2017) but may be concerned that open access to data will undermine this goal. Threats to species (e.g. collectors targeting rare species, deliberate habitat destruction by landowners to avoid conservation responsibility/land-use restrictions, accidental damage to sites by naturalists wanting to see scarce species) are real (Tulloch *et al.* 2018), but the levels of perceived risk are subjective and individualistic. Such concerns may also engender support for licences that prohibit commercial reuse; citizen scientists appear to support uses of their data that are likely to benefit biodiversity conservation, but not those that are thought to cause harm (Ellis &

Waterton 2005; Ganzevoort *et al.* 2017). The perceived commodification of volunteer-gathered records, which runs counter to the traditional culture of data exchange within natural history, and a lack of transparency and feedback about the onward uses of the data may also contribute to restrictive attitudes towards licensing (Ellis & Waterton 2005). Other concerns may exist around privacy and the potential malicious use of personal information (e.g. names and locations of recorders) derived from species occurrence data (Bowser *et al.* 2014).

We extended the previous study by Ganzevoort *et al.* (2017) to gain a more nuanced understanding of these concerns and explored how citizen scientists' attitudes to open access were moderated by variation in spatial and temporal factors. We hypothesised that if concerns about open access related to potential damage to individual organisms, populations and habitats, then citizen scientists would be more restrictive with records of threatened species than widespread ones. Additionally, we posited that restricting the spatial resolution of publicly accessible data or delaying the release of data may both be expected to reduce the perceived risk. Other commonly raised fears around the personal privacy of the recorders themselves and of private land where charismatic species are present (which may be subject to trespass if the precise locations are made public) might also be ameliorated by such restrictions.

We found strong evidence to support both our hypotheses. There was a clear effect of spatial scale on attitudes to open access for UK Lepidoptera records (but not for the use of deferred release of data i.e. time lags). 37.5% of regional co-ordinators were in favour of capture resolution open access for records of widespread species and this rose cumulatively as the spatial scale was coarsened, such that 77.9% were in favour at 1km square resolution and 95.2% in favour at 2km square resolution. The impact of spatial resolution on open access opinions was even more pronounced when considering records of threatened species; regional co-ordinators were more cautious, with only 6.7% in favour at capture resolution, rising cumulatively to 15.4% at 1km square and 45.2% at 2km square resolution. Similar patterns were found when regional co-ordinators were grouped by general levels of support for open access (NPS categories) and each analysed separately.

The survey of recorders also suggested that spatial scale was an important factor in citizen scientists' attitudes towards open data. Generally, recorders were more supportive than regional co-ordinators of open access at capture resolution. Nevertheless, two-thirds (67.3%) of recorders felt that some (i.e. threatened species) or all of their records should be blurred to a coarser resolution than capture level for open access.

Therefore, although we did not attempt to determine the rationale underlying the opinions of citizen scientists, these results support both our hypotheses. The greater unwillingness to release records of threatened species at full capture resolution compared to records of widespread species suggests that the main concerns of citizen scientists relate to potential negative ecological impacts, rather than unease about privacy, confidentiality or intellectual property rights. Second, for the majority of contributors these concerns can be alleviated by blurring spatial location information. Interestingly, most respondents did not support deferral of the open release of records in addition to spatial restrictions, although 26.0% were in favour of a delay of at least five years.

Differences between roles, countries and taxa

The differing nature of the roles of regional co-ordinators and recorders and the fact that they were asked different questions makes it inappropriate to undertake a direct statistical comparison of their views. In addition, it is probable that some regional co-ordinators also completed the recorder questionnaire and so the two samples may not be independent. The findings on spatial resolution suggest, however, that the regional co-ordinators were more restrictive, on average, than recorders in their attitudes to open access. Further work is required to elucidate the causes of the seemingly greater risk aversion among regional co-ordinators, as our questionnaires did not examine the reasons underlying stated opinions. They may stem from complex combinations of ecological (e.g. increased awareness of possible threats to species), legal (e.g. concerns about acts of trespass and personal data under the General Data Protection Regulation), personal (e.g. greater time investment in the data), ethical (e.g. a sense of responsibility as custodians of records contributed by other citizen scientists) and cultural (e.g. traditional principles of data exchange in natural history) considerations. The latter may be particularly important given

that regional co-ordinators are amateur expert naturalists, whereas recorders are a much more diverse group ranging from committed amateur naturalists to complete beginners (e.g. see Everett & Geoghegan 2016). Irrespective of the causes, however, if restrictions on open access to recording scheme data, informed by the views of regional co-ordinators, are contrary to the wishes of most citizen scientist participants, this may risk demotivation, loss of support and, ultimately, reduced levels of species recording.

Significant differences were found between the opinions of regional coordinators in England and Scotland. Regional co-ordinators in Scotland had higher NPS values than their counterparts in England, indicating greater support in general for the principles of open access to Lepidoptera occurrence records. This predisposition was reflected in attitudes to more specific options, whereby regional co-ordinators in Scotland favoured finer spatial scale resolution of open access records for widespread species and shorter time lags before records are released than their colleagues in England.

The causes of these differences are not known and require further research. However, we speculate that two factors may contribute to these contrasting attitudes. First, long-term abundance trends of butterflies and moths differ geographically within the UK. The abundance of 337 species of widespread moths has decreased significantly in southern Britain (most of England and all of Wales) but not in northern Britain (Scotland plus part of northern England) (Conrad *et al.* 2006). Similarly, the abundance of wider countryside butterflies has decreased significantly in England but not in Scotland (Fox *et al.* 2015). Thus, regional co-ordinators in England, where greater declines have occurred, might be more sensitive to potential adverse effects on butterflies and moths arising from open access to data and this results in more restrictive attitudes than regional co-ordinators in Scotland.

Second, there are substantial differences between Scotland and the rest of the UK in the legal framework relating to public access to land. The Land Reform (Scotland) Act 2003 confers a public 'right to roam' over almost all land in Scotland, while similar rights (under the Countryside and Rights of Way Act 2000) cover only c.8% - 12% of the total land area of England and Wales

(Lovett 2012). The situation is even more restrictive in Northern Ireland. Regional co-ordinators in Scotland may have reduced concerns, therefore, compared to their counterparts in other UK countries, about either exposing acts of trespass by recorders or inadvertently encouraging others to trespass on private land (thereby undermining relationships between recorders and landowners) as a result of records being made open access.

Interestingly, the online survey of recorders found no significant differences between UK countries. This suggests that the differing attitudes of regional coordinators in England and Scotland relates to their roles as custodians of local datasets.

In contrast to the clear country-level differences, attitudes of regional coordinators varied very little depending on the taxon (butterflies, moths or both) for which they have responsibility. The only significant result in our analysis was that regional co-ordinators for butterflies favoured finer spatial resolution open access for records of threatened species than regional co-ordinators who cover moths or both taxa. Possible reasons for this might include that there are more UK populations of the most threatened butterflies than the most threatened moths, that sites for threatened butterflies are often well known already or that extra visitors to sites of threatened butterflies are likely to be less intrusive for landowners than those wanting to see threatened moths if the latter are nocturnal. There were no significant differences between the opinions of recorders based on taxon of interest.

Wider applicability

The wider applicability of our findings depends on the representativeness of our sampling. With 69% and 68% response rates among regional co-ordinators, we can have high confidence that our results are representative of this key group of UK Lepidoptera-recording volunteers. However, we do not know how many people participate annually in the BNM and NMRS recording schemes, so we cannot measure the response rate for our online questionnaire aimed at recorders. While 510 responses is reasonable for statistical analysis, it likely represents only a small proportion of the total number of citizen science contributors to these projects. In addition, the sample is likely to be biased, as

the online survey was not distributed randomly or systematically but promoted to recorders by the regional co-ordinators. This clearly limits our ability to generalise from the findings.

Another limitation stems from variation between participants. Analyses of this variation have classified citizen scientists by expertise in species identification and by temporal and spatial patterns of participation in particular projects (Ponciano & Brasileiro 2014; Boakes et al. 2016; Everett & Geoghegan 2016; Johnston et al. 2018). Boakes et al. (2016), for example, categorised citizen scientists undertaking biodiversity recording as 'dabbler', 'steady' or 'enthusiast' depending on their temporal participation, while Everett & Geoghegan (2016) utilised a continuum of engagement, on the basis of past involvement in natural history. While all citizen scientists can contribute useful data, their motivations and strength of commitment to particular projects vary considerably between individuals and also over time for individuals. It is likely that attitudes towards open access to citizen science data would also vary between individuals and over time, and might covary with other metrics describing the engagement behaviour of citizen scientists. By definition, given their role and responsibilities to the BNM and NMRS projects, the regional co-ordinators that took part in our study are highly motivated, committed and knowledgeable volunteers, many of whom have a passion for biodiversity conservation. Their views on open access are of fundamental importance for the ongoing development of the BNM and NMRS projects, but cannot reasonably be generalised to the thousands of citizens who participate to a greater or lesser extent in the schemes. Similarly, as the recorders who responded to our online questionnaire were not selected at random, it is likely that these may also be a biased sample, with views on open access that might differ from less active or more recent participants.

Even within our sampled audience of citizen scientists, we found evidence of differences in attitude towards open access between countries. Whatever the causes, this variation within the UK suggests that there will also be differences between the UK and other countries. This limits the applicability of our results but stresses the importance of seeking the opinions of and establishing dialogue with citizen scientists on this issue, rather than making assumptions.

Practical recommendations for citizen science

A key factor in the creation of a citizen science project is the development of a comprehensive yet clear data policy (James 2011). This needs to take into account not only the requirements of the project itself, and its aspirations for future data sharing and scientific publication, but also any legal requirements for open access imposed by funding organisations. For example, in the UK Butterfly Monitoring Scheme, a systematic monitoring programme run by Butterfly Conservation and partner organisations, it is a condition of longstanding financial support from government departments and agencies that data are made freely available under an Open Government Licence. Schemes such as those addressed in this study, which are not bound by funder requirements regarding open data, provide an opportunity to plan data access in the light of contributors' attitudes. A data policy must, of course, also comply with relevant legislation relating to the protection of personal data, such as the European Union's General Data Protection Regulation. The use of widely recognised licences, such as Creative Commons licences, is recommended to ensure clarity for both participants and prospective data users, as well as compatibility with other projects and data repositories (e.g. the Atlas of Living Australia, www.ala.org.au) locally and globally. Most importantly, we recommend that any data policy developed for a citizen science project should be actively disseminated to potential contributors to ensure that they are aware of the uses to which their data will be put and are therefore able to make an informed choice prior to participation.

Despite its limitations, our study provides useful information on the development of open access data policies that is of wider relevance to biodiversity citizen science projects. In particular, the heterogeneity of views present in these relatively small samples shows that organisers would be well-advised to consult with potential participants on matters of data access in advance as part of project development. Similarly, funding organisations, statutory agencies and policy makers may wish to reflect on the diversity of views revealed by our questionnaires, and previous studies (e.g. Ellis *et al.* 2005), in their drive for open citizen science data. Our results suggest that the cultural context is likely to be extremely important in influencing attitudes to open access among citizen scientists; not only are these likely to differ substantially between nationalities, but also between participants with different roles in projects and levels of past engagement with natural history and citizen science.

Conclusions

In order to maximise the scientific and societal benefits of citizen science, the views and motivations of participants must be considered. Our study shows that, contrary to common assumptions, UK citizen scientists taking part in butterfly and moth recording have diverse, in some cases polarised, views on open access and there was substantial variation between different countries and between volunteers with different roles. Overall, many participants are supportive, in principle, of open access to the data they gather, but are mindful of possible negative ecological impacts that may result. Our results suggest that the majority of participants favour increasing access to these data, and that the concerns of many could be ameliorated by limiting the spatial resolution of open records, particularly of threatened species, and licencing reuse for non-commercial purposes. Globally, citizen science schemes have great potential to help address the enormous challenges facing biodiversity, but to do so effectively, must be responsive to the changing attitudes and new opportunities afforded by open data.

Acknowledgements

We are grateful to all of the volunteer regional co-ordinators and recorders who contribute to the BNM and NMRS projects and, in particular, to those who participated in the surveys of opinion reported here. We would like to thank Dr Katie Cruickshanks and two anonymous reviewers for helpful comments on previous drafts of this paper. The BNM and NMRS are run by Butterfly Conservation and receive financial support from Natural England.

References

Aceves-Bueno E, Adeleye AS, Feraud M, Huang Y, Tao M, Yang Y & Anderson SE (2017) The accuracy of citizen science data: a quantitative review. *Bulletin of the Ecological Society of America* **98**, 278–290.

Agresti A (2002) *Categorical Data Analysis*. 2nd edition. John Wiley & Sons, Hoboken, USA.

Arzberger P, Schroeder P, Beaulieu A, Bowker G, Casey K, Laaksonen L, Moorman D, Uhlir P & Wouters P (2004) An international framework to promote access to data. *Science* **303**, 1777–1778.

Asher J, Warren M, Fox R, Harding P, Jeffcoate G & Jeffcoate S (2001) *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford University Press, Oxford, UK.

Boakes EH, Gliozzo G, Seymour V, Harvey M, Smith C, Roy DB & Haklay M (2016) Patterns of contribution to citizen science biodiversity projects increase understanding of volunteers' recording behaviour. *Scientific Reports* **6**, 33051.

Bowser A, Wiggins A, Shanley L, Preece J & Henderson S (2014) Sharing data while protecting privacy in citizen science. *Interactions* **21**, 70–73.

Brereton TM, Roy DB, Middlebrook I, Botham MS & Warren MS (2011) The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation* **15**, 139–151.

Chandler M, See L, Copas K, Bonde AMZ, Claramunt López B, Danielsen F, Kristoffer Legind J, Masinde S, Miller-Rushing AJ, Newman G, Rosemartin A & Turak E (2017) Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation* **213**, 280–294.

Choudhury S, Fishman JR, McGowan ML & Juengst ET (2014) Big data, open science and the brain: lessons learned from genomics. *Frontiers in Human Neuroscience* **8**, 239.

Christensen, RHB (2018) Ordinal – regression models for ordinal data. R package version 2018.8-25. Available from http://www.cran.r-project.org/ package=ordinal/ (accessed 19 October 2018).

Conrad KF, Warren M, Fox R, Parsons M & Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation* **132**, 279–291.

Culina A, Baglioni M, Crowther TW, Visser ME, Woutersen-Windhouwer S & Manghi P (2018a) Navigating the unfolding open data landscape in ecology and evolution. *Nature Ecology and Evolution* **2**, 420–426.

Culina A, Crowther TW, Ramakers JJC, Gienapp P & Visser ME (2018b) How to do meta-analysis of open datasets. *Nature Ecology and Evolution* **2**,1053–1056.

Dennis EB, Morgan BJT, Brereton TM, Roy DB & Fox R (2017) Using citizen science butterfly counts to predict species population trends. *Conservation Biology* **31**, 1350–1361.

Domroese MC & Johnson EA (2017) Why watch bees? Motivations of citizen science volunteers in the Great Pollinator Project. *Biological Conservation* **208**, 40–47.

Ellis R, Grove-White R, Vogel J & Waterton C (2005) *Nature: who knows?* English Nature, the Natural History Museum and Lancaster University, Lancaster, UK.

Ellis R & Waterton C (2004) Environmental citizenship in the making: the participation of volunteer naturalists in UK biological recording and biodiversity policy. *Science and Public Policy* **31**, 95–105.

Ellis R & Waterton C (2005) Caught between the cartographic and the ethnographic imagination: the whereabouts of amateurs, professionals, and nature in knowing biodiversity. *Environment and Planning D Society and Space* **23**, 673–693.

Ellis S, Bourn NAD & Bulman CR (2012) *Landscape-scale Conservation for Butterflies and Moths: Lessons from the UK*. Butterfly Conservation, Wareham, UK.

Evans C, Abrams E, Reitsma R, Roux K, Salmonsen L & Marra PP (2005) The Neighborhood Nestwatch Program: Participant outcomes of a citizen-science ecological research project. *Conservation Biology* **19**, 589–594.

Everett G & Geoghegan H (2016) Initiating and continuing participation in citizen science for natural history. *BMC Ecology* **16**, 15–22.

Farley SS, Dawson A, Goring SJ & Williams JW (2018) Situating ecology as a big-data science: current advances, challenges, and solutions. *BioScience* **68**, 563–576.

Fox R, Brereton TM, Asher J, August TA, Botham MS, Bourn NAD, Cruickshanks KL, Bulman CR, Ellis S, Harrower CA, Middlebrook I, Noble DG, Powney GD, Randle Z, Warren MS & Roy DB (2015) *The State of the UK's Butterflies 2015*. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, UK.

Fox R, Oliver TH, Harrower C, Parsons MS, Thomas CD & Roy DB (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land use changes. *Journal of Applied Ecology* **51**, 949–957.

Fox R, Randle Z, Hill L, Anders S, Wiffen L & Parsons MS (2011) Moths Count: recording moths for conservation in the UK. *Journal of Insect Conservation* **15**, 55–68.

Ganzevoort W, van den Born RJG, Halffman W & Turnhout S (2017) Sharing biodiversity data: citizen scientists' concerns and motivations. *Biodiversity and Conservation* **26**, 2821–2837.

Groom Q, Weatherdon L & Geijzendorffer IR (2017) Is citizen science an open science in the case of biodiversity observations? *Journal of Applied Ecology* **54**, 612–617.

Hagedorn G, Mietchen D, Morris RA, Agosti D, Penev L, Berendsohn WG & Hobern D (2011) Creative Commons licenses and the non-commercial condition: Implications for the re-use of biodiversity information. *ZooKeys* **150**, 127–149.

Hampton SE, Strasser CA, Tewksbury JJ, Gram WK, Budden AE, Batcheller AL, Duke CS & Porter JH (2013) Big data and the future of ecology. *Frontiers in Ecology and the Environment* **11**, 156–162.

Hobbs SJ & White PCL (2012) Motivations and barriers in relation to community participation in biodiversity recording. *Journal of Nature Conservation* **20**, 364–373.

Hothorn T, Hornik K, van de Wiel MA & Zeileis A (2008) Implementing a class of permutation tests: the coin package. *Journal of Statistical Software* **60**, 257–263.

James T (2011) *Running a biological recording scheme or survey*. National Biodiversity Network, Nottingham, UK.

Johnston A, Fink D, Hochachka WM & Kelling S (2018) Estimates of observer expertise improve species distributions from citizen science data. *Methods in Ecology and Evolution* **9**, 88–97.

Keiningham TL, Cooil B, Andreassen TW & Aksoy L (2007) A longitudinal examination of net promoter and firm revenue growth. *Journal of Marketing* **71**, 39–51.

Kenall A, Harold S & Foote C (2014) An open future for ecological and evolutionary data? *BMC Evolutionary Biology* **14**, 66.

Kosmala M, Wiggins A, Swanson A & Simmons B (2016) Assessing data quality in citizen science. *Frontiers in Ecology and the Environment* **14**, 551–560.

Lenth R (2018) emmeans: estimated marginal means, aka least-squares means. R package version 1.2.4. Available from https://CRAN.R-project.org/ package=emmeans (accessed 19 October 2018).

Lewandowski EJ & Oberhauser KS (2017) Butterfly citizen scientists in the United States increase their engagement in conservation. *Biological Conservation* **208**, 106–112.

Lovett JA (2012) The right to exclude meets the right of responsible access: Scotland's bold experiment in public access legislation. *Probate & Property* **26**, 52–59.

Ma A, Bohan DA, Canard E, Derocles SAP, Gray C, Lu X, Macfadyen S, Romero GQ & Kratina P (2018) A Replicated Network Approach to 'Big Data' in Ecology. *Advances in Ecological Research* **59**, 225–264.

Martay B, Brewer MJ, Elston DA, Bell JR, Harrington R, Brereton TM, Barlow KE, Botham MS & Pearce-Higgins JW (2017) Impacts of climate change on national biodiversity population trends. *Ecography* **40**, 1139–1151.

Mason SC, Palmer G, Fox R, Gillings S, Hill JK, Thomas CD & Oliver TH (2015) Geographical range margins of a wide range of taxonomic groups continue to shift polewards. *Biological Journal of the Linnean Society* **115**, 586–597. McEwen JE, Boyer JT & Sun KY (2013) Evolving approaches to the ethical management of genomic data. *Trends in Genetics* **29**, 375–382.

McGuire AL, Basford M, Dressler LG, Fullerton SM, Koenig BA, Li R, McCarty CA, Ramos E, Smith ME, Somkin CP, Waudby C, Wolf WA & Clayton EW (2011) Ethical and practical challenges of sharing data from genome-wide association studies: The eMERGE Consortium experience. *Genome Research* **21**, 1001–1007.

Michener WK (2015) Ecological data sharing. Ecological Informatics 29, 33-44.

Miller-Rushing A, Primack R & Bonney R (2012) The history of public participation in ecological research. *Frontiers in Ecology and the Environment* **10**, 285–290.

Mills JA, Teplitsky C, Arroyo B, Charmantier A, Becker PH, Birkhead TR, Bize P, Blumstein DT, Bonenfant C, Boutin S, Bushuev A, Cam E, Cockburn A, Côté SD, Coulson JC, Daunt F, Dingemanse NJ, Doligez B, Drummond H, Espie RHM, Festa-Bianchet M, Frentiu F, Fitzpatrick JW, Furness RW, Garant D, Gauthier G, Grant PR, Griesser M, Gustafsson L, Hansson B, Harris MP, Jiguet F, Kjellander P, Korpimäki E, Krebs CJ, Lens L, Linnell JDC, Low M, McAdam A, Margalida A, Merilä J, Møller AP, Nakagawa S, Nilsson J-A, Nisbet ICT, van Noordwijk AJ, Oro D, Pärt T, Pelletier F, Potti J, Pujol B, Réale D, Rockwell RF, Ropert-Coudert Y, Roulin A, Sedinger JS, Swenson JE, Thébaud C, Visser ME, Wanless S, Westneat DF, Wilson AJ & Zedrosser A (2015) Archiving primary data: solutions for long-term studies. *Trends in Ecology & Evolution* **30**, 581–589.

Moles AT, Dickie JB & Flores-Moreno H (2013) A response to Poisot *et al.*: Publishing your dataset is not always virtuous. *Ideas in Ecology and Evolution* **6**, 20–22.

Noor MA, Zimmerman KJ & Teeter KC (2006) Data sharing: how much doesn't get submitted to GenBank? *PLoS Biology* **4**, e228.

Nosek BA, Alter G, Banks GC, Borsboom D, Bowman SD, Breckler SJ, Buck S, Chambers CD, Chin G, Christensen G, Contestabile M, Dafoe A, Eich E, Freese J, Glennerster R, Goroff D, Green DP, Hesse B, Humphreys M, Ishiyama J, Karlan D, Kraut A, Lupia A, Mabry P, Madon T, Malhotra N, MayoWilson E, McNutt M, Miguel E, Levy Paluck E, Simonsohn U, Soderberg C, Spellman BA, Turitto J, VandenBos G, Vazire S, Wagenmakers EJ, Wilson R & Yarkoni T (2015) Promoting an open research culture. *Science* **348**, 1422– 1425.

Pearce-Higgins JW, Baillie SR, Boughey K, Bourn NAD, Foppen RPB, Gillings S, Gregory RD, Hunt T, Jiguet F, Lehikoinen A, Musgrove AJ, Robinson RA, Roy DB, Siriwardena GM, Walker KJ, Wilson JD (2018) Overcoming the challenges of public data archiving for citizen science biodiversity recording and monitoring schemes. *Journal of Applied Ecology* **55**, 2544–2551.

Pearce-Higgins JW, Beale CM, Oliver TH, August TA, Carroll M, Massimino D, Ockendon N, Savage J, Wheatley CJ, Ausden MA, Bradbury RB, Duffield SJ, Macgregor NA, McClean CJ, Morecroft MD, Thomas CD, Watts O, Beckmann BC, Fox R, Roy HE, Sutton PG, Walker KJ & Crick HQP (2017) A national-scale assessment of climate change impacts on species: assessing the balance of risks and opportunities for multiple taxa. *Biological Conservation* **213**, 124–134.

Pocock MJO, Chandler M, Bonney R, Thornhill I, Albin A, August T, Bachman S, Brown PMJ, Gasparini Fernandes Cunha D, Grez A, Jackson C, Peters M, Romer Rabarijaon N, Roy HE, Zaviezo T & Danielsen F (2018) A vision for global biodiversity monitoring with citizen science. *Advances in Ecological Research* **59**, 169–223.

Pocock MJO, Roy HE, Preston CD & Roy DB (2015) The Biological Records Centre: a pioneer of citizen science. *Biological Journal of the Linnean Society* **115**, 475–493.

Pocock MJO, Tweddle JC, Savage J, Robinson LD & Roy HE (2017) The diversity and evolution of ecological and environmental citizen science. *PLoS One* **12**, e0172579.

Poisot T, Mounce R & Gravel D (2013) Moving toward a sustainable ecological science: Don't let data go to waste! *Ideas in Ecology and Evolution* **6**, 11–19.

Ponciano L & Brasileiro F (2014) Finding volunteers' engagement profiles in human computation for citizen science projects. *Human Computation* **1**, 247–266.

R Core Team (2018) *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Reichheld FF (2003) The one number you need to grow. *Harvard Business Review* **81**, 46–54.

Reichman OJ, Jones MB & Schildhauer MP (2011) Challenges and opportunities of open data in ecology. *Science* **331**, 703–705.

Robinson LD, Cawthray JL, West SE, Bonn A & Ansine J (2018) Ten principles of citizen science. *Citizen Science: innovation in open science, society and policy*, (ed. S Hecker, M Haklay, A Bowser, Z Makuch, J Vogel & A Bonn), pp. 27–40. UCL Press, London, UK.

Sauer JR, Link WA, Fallone JE, Pardieck KL & Ziolkoqski DJ (2013) The North American Breeding Bird Survey 1966–2011: summary analysis and species accounts. *North American Fauna* **97**, 1–32.

Schmidt B, Gemeinholzer B & Treloar A (2016) Open data in global environmental research: the Belmont Forum's open data survey. *PLoS One* **11**, e0146695.

Silvertown J (2009) A new dawn for citizen science. *Trends in Ecology* & *Evolution* **24**, 467–471.

Soranno PA, Cheruvelil KS, Elliott KC & Montgomery GM (2015) It's good to share: why environmental scientists' ethics are out of date. *BioScience* **65**, 69–73.

Soroye P, Ahmed N & Kerr JT (2018) Opportunistic citizen science data transform understanding of species distributions, phenology, and diversity gradients for global change research. *Global Change Biology* **24**, 5281–5291.

Specht H & Lewandowski E (2018) Biased assumptions and oversimplifications in evaluations of citizen science data quality. *Bulletin of the Ecological Society of America* **99**, 251–256.

Strasser BJ, Baudry J, Mahr D, Sanchez G, Tancoigne E (2019) "Citizen Science"? Rethinking science and public participation. *Science and Technology Studies* **32**, 52–76.

Sullivan BL, Aycrigg JL, Barry JH, Bonney RE, Bruns N, Cooper CB, Damoulas T, Dhondt AA, Dietterich T, Farnsworth A, Fink D, Fitzpatrick JW, Fredericks T, Gerbracht J, Gomes C, Hochachka WM, Iliff MJ, Lagoze C, La Sorte FA, Merrifield M, Morris W, Phillips TB, Reynolds M, Rodewald AD, Rosenberg KV, Trautmann NM, Wiggins A, Winkler DW, Wong W-K, Wood CL, Yu J & Kelling S (2014) The eBird enterprise: an integrated approach to development and application of citizen science. *Biological Conservation* **169**, 31–40.

Sullivan BL, Phillips T, Dayer AA, Wood CL, Farnsworth A, Iliff MJ, Davies IJ, Wiggins A, Fink D, Hochachka WM, Rodewald AD, Rosenberg KV, Bonney R & Kelling S (2017) Using open access observational data for conservation action: A case study for birds. *Biological Conservation* **208**, 5–14.

Tenopir C, Dalton ED, Allard S, Frame M, Pjesivac I, Birch B, Pollock D & Dorsett K (2015) Changes in data sharing and data reuse practices and perceptions among scientists worldwide. *PLoS One* **10**, e0134826.

Theobald EJ, Ettinger AK, Burgess HK, DeBey LB, Schmidt NR, Froehlich HE, Wagner C, HilleRisLambers J, Tewksbury J, Harsch MA & Parrish JK (2015) Global change and local solutions: Tapping the unrealized potential of citizen science for biodiversity research. *Biological Conservation* **181**, 236–244.

Tulloch AIT, Auerbach N, Avery-Gomm S, Bayraktarov E, Butt N, Dickman CR, Ehmke G, Fisher DO, Grantham H, Holden MH, Lavery TH, Leseberg, NP, Nicholls M, O'Connor J, Roberson L, Smyth AK, Stone Z, Tulloch V, Turak E, Wardle GM & Watson JEM (2018) A decision tree for assessing the risks and benefits of publishing biodiversity data. *Nature Ecology and Evolution* **2**, 1209– 1217.

West S & Pateman R (2016) Recruiting and retaining participants in citizen science: what can be learned from the volunteering literature? *Citizen Science: Theory and Practice* **1**, 15.

Wright DR, Underhill LG, Keene M & Knight AT (2015) Understanding the motivations and satisfactions of volunteers to improve the effectiveness of citizen science programs. *Society & Natural Resources* **28**, 1013–1029.

Appendix 1: Richard Fox Peer-reviewed publications

Asher J, Fox R & Warren MS (2011) British butterfly distributions and the 2010 target. *Journal of Insect Conservation* **15**, 291–299.

Banza P, Macgregor CJ, Belo ADF, Fox R, Pocock MJO & Evans DM (2019) Wildfire alters the structure and seasonal dynamics of Mediterranean nocturnal pollen transport networks. *Functional Ecology* **33**, 1882–1892.

Bishop TR, Botham MS, Fox R, Leather SR, Chapman DS & Oliver TH (2013) The utility of distribution data in predicting phenology. *Methods in Ecology and Evolution* **4**, 1024–1032.

Boyes DH, Fox R, Shortall CR & Whittaker RJ (2019) Bucking the trend: the diversity of Anthropocene 'winners' among British moths. *Frontiers of Biogeography* **11**, e43862.

Buckley LB, Waaser S, MacLean HJ & Fox R (2011) Does including physiology improve species distribution model predictions of responses to recent climate change? *Ecology* **92**, 2214–2221.

Carvalheiro LG, Kunin WE, Keil P, Aguirre-Gutiérrez J, Ellis WN, Fox R, Groom Q, Hennekens S, Van Landuyt W, Maes D, Van de Meutter F, Michez D, Rasmont P, Ode B, Potts SG, Reemer M, Roberts SPM, Schaminée J, WallisDeVries MF & Biesmeijer JC (2013) Species richness declines and biotic homogenization have slowed down for NW-European pollinators and plants. *Ecology Letters* **16**, 870–878.

Conrad KF, Warren M, Fox R, Parsons M & Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation* **132**, 279–291.

Conrad KF, Woiwod IP, Parsons M, Fox R & Warren M (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation* **8**, 119–136.

Dapporto L, Ciolli G, Dennis RLH, Fox R & Shreeve T (2015) A new procedure for extrapolating turnover regionalization at mid-small spatial scales, tested on British butterflies. *Methods in Ecology and Evolution* **6**, 1287–1297.

Davies H, Brereton TM, Roy DB & Fox R (2007) Government targets for protected area management: will threatened butterflies benefit? *Biodiversity and Conservation* **16**, 3719–3736.

Dennis EB, Brereton TM, Morgan BJT, Fox R, Shortall CR, Prescott T & Foster S (2019) Trends and indicators for quantifying moth abundance and occupancy in Scotland. *Journal of Insect Conservation* **23**, 369–380.

Dennis EB, Morgan BJT, Brereton TM, Roy DB & Fox R (2017) Using citizen science butterfly counts to predict species population trends. *Conservation Biology* **31**, 1350–1361.

Dennis EB, Morgan BJT, Fox R, Roy DB & Brereton TM (2019) Functional data analysis of multi-species abundance and occupancy data sets. *Ecological Indicators* **104**, 156–165.

Dennis EB, Morgan BJT, Freeman SN, Ridout MS, Brereton TM, Fox R, Powney GD & Roy DB (2017) Efficient occupancy model-fitting for extensive citizen-science data. *PLoS One* **12**, e0174433.

Dennis RLH, Shreeve TG, Isaac NJB, Roy DB, Hardy PB, Fox R & Asher J (2006) The effects of visual apparency on bias in butterfly recording and monitoring. *Biological Conservation* **128**, 486–492.

Dyer RJ, Gillings S, Pywell RF, Fox R, Roy DB & Oliver TH (2017) Developing a biodiversity-based indicator for large-scale environmental assessment: a case study of proposed shale gas extraction sites in Britain. *Journal of Applied Ecology* **54**, 872–882.

Fox R (2013) The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity* **6**, 5–19.

Fox R, Bourn NAD, Dennis EB, Heafield RT, Maclean IMD & Wilson RJ (2019) Opinions of citizen scientists on open access to UK butterfly and moth occurrence data. *Biodiversity and Conservation* **28**, 3321–3341.

Fox R, Harrower CA, Bell JR, Shortall CR, Middlebrook I & Wilson RJ (2018) Insect population trends and the IUCN Red List process. *Journal of Insect Conservation* **23**, 269–278. Fox R, Oliver TH, Harrower C, Parsons MS, Thomas CD & Roy DB (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology* **51**, 949–957.

Fox R, Randle Z, Hill L, Anders S, Wiffen L & Parsons MS (2011) Moths Count: recording moths for conservation in the UK. *Journal of Insect Conservation* **15**, 55–68.

Fox R, Warren MS, Brereton TM, Roy DB & Robinson A (2011) A new red list of British butterflies. *Insect Conservation and Diversity* **4**, 159–172.

Franco AMA, Anderson BJ, Roy DB, Gillings S, Fox R, Moilanen A & Thomas CD (2009) Surrogacy and persistence in reserve selection: landscape prioritisation for multiple taxa in Britain. *Journal of Applied Ecology* **46**, 82–91.

Franco AMA, Hill JK, Kitschke C, Collingham YC, Roy DB, Fox R, Huntley B & Thomas CD (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* **12**, 1545–1553.

Gilburn AS, Bunnefeld N, Wilson J, Botham MS, Brereton T, Fox R & Goulson D (2015) Are neonicotinoid insecticides driving declines of widespread butterflies? *PeerJ* **3**, e1402.

Gillingham PK, Alison J, Roy DB, Fox R & Thomas CD (2015) High abundances of species in protected areas in parts of their geographic distributions colonised during a recent period of climatic change. *Conservation Letters* **8**, 97–106.

Gillingham PK, Bradbury RB, Roy DB, Anderson BJ, Baxter JM, Bourn NAD, Crick HQP, Findon RA, Fox R, Franco A, Hill JK, Hodgson JA, Holt AR, Morecroft MD, O'Hanlon NJ, Oliver TH, Pearce-Higgins JW, Procter DA, Thomas JA, Walker KJ, Walmsley CA, Wilson RJ & Thomas CD (2015) The effectiveness of protected areas in the conservation of species with changing geographical ranges. *Biological Journal of the Linnean Society* **115**, 707–717.

Hickling R, Roy DB, Hill JK, Fox R & Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**, 450–455.

Hill JK, Collingham YC, Thomas CD, Blakeley DS, Fox R, Moss D & Huntley B (2001) Impacts of landscape structure on butterfly range expansion. *Ecology Letters* **4**, 313–321.

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J & Huntley B (2002) Responses of butterflies to 20th century climate warming: implications for future ranges. *Proceedings of the Royal Society B* **269**, 2163–2171.

Macgregor CJ, Evans DM, Fox R & Pocock MJO (2017) The dark side of street lighting: impacts on moths and evidence for the disruption of nocturnal pollen transport. *Global Change Biology* **23**, 697–707.

Macgregor CJ, Kitson JJN, Fox R, Hahn C, Lunt DH, Pocock MJO & Evans DM (2019) Construction, validation, and application of nocturnal pollen transport networks in an agro-ecosystem: a comparison using light microscopy and DNA metabarcoding. *Ecological Entomology* **44**, 17–29.

Macgregor CJ, Pocock MJO, Fox R & Evans DM (2015) Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review. *Ecological Entomology* **40**, 187–198.

Macgregor CJ, Pocock MJO, Fox R & Evans DM (2019) Effects of street lighting technologies on the success and quality of pollination in a nocturnally pollinated plant. *Ecosphere* **10**, e02550.

Macgregor CJ, Thomas CD, Roy DB, Beaumont MA, Bell JR, Brereton T, Bridle JR, Dytham C, Fox R, Gotthard K, Hoffmann AA, Martin G, Middlebrook I, Nylin S, Platts PJ, Rasteiro R, Saccheri IJ, Villoutreix R, Wheat CW & Hill JK (2019) Climate-induced phenology shifts linked to range expansions in species with multiple reproductive cycles per year. *Nature Communications* **10**, 4455.

Mair L, Hill JK, Fox R, Botham M, Brereton T & Thomas CD (2014) Abundance changes and habitat availability drive species' responses to climate change. *Nature Climate Change* **4**, 127–131.

Mair L, Thomas CD, Anderson BJ, Fox R, Botham M & Hill JK (2012) Temporal variation in responses of species to four decades of climate warming. *Global Change Biology* **18**, 2439–2447.

Mason SC, Hill JK, Thomas CD, Powney GD, Fox R, Brereton T & Oliver TH (2018) Population variability in species can be deduced from opportunistic citizen science records: a case study using British butterflies. *Insect Conservation and Diversity* **11**, 131–142.

Mason SC, Palmer G, Fox R, Gillings S, Hill JK, Thomas CD & Oliver TH (2015) Geographical range margins of a wide range of taxonomic groups continue to shift polewards. *Biological Journal of the Linnean Society* **115**, 586–597.

Menéndez R, González-Megías A, Collingham Y, Fox R, Roy DB, Ohlemüller R & Thomas CD (2007) Direct and indirect effects of climate and habitat factors on specialist and generalist butterfly diversity. *Ecology* **88**, 605–611.

Menéndez R, González-Megías A, Hill JK, Braschler B, Willis SG, Collingham Y, Fox R, Roy DB & Thomas CD (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society B* **273**, 1465–1470.

Moilanen A, Franco AMA, Early RI, Fox R, Wintle B & Thomas CD (2005) Prioritizing multiple-use landscapes for conservation: methods for large multispecies planning problems. *Proceedings of the Royal Society B* **272**, 1885– 1891.

Montgomery GA, Dunn RR, Fox R, Jongejans E, Leather SR, Saunders ME, Shortall CR, Tingley MW & Wagner DL (2020) Is the insect apocalypse upon us? How to find out. *Biological Conservation* **241**, 108327.

Norberg A, Abrego N, Blanchet FG, Adler FR, Anderson BJ, Anttila J, Araújo MB, Dallas T, Dunson D, Elith J, Foster SD, Fox R, Franklin J, Godsoe W, Guisan A, O'Hara B, Hill NA, Holt RD, Hui FKC, Husby M, Kålås JA, Lehikoinen A, Luoto M, Mod HK, Newell G, Renner I, Roslin T, Soininen J, Thuiller W, Vanhatalo J, Warton D, White M, Zimmermann NE, Gravel D & Ovaskainen O (2019) A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels. *Ecological Monographs* **89**, e01370.

Outhwaite CL, Powney GD, August TA, Chandler RE, Rorke S, Pescott OL, Harvey M, Roy HE, Fox R, Roy DB, Alexander K, Ball S, Bantock T, Barber T, Beckmann BC, Cook T, Flanagan J, Fowles A, Hammond P, Harvey P, Hepper D, Hubble D, Kramer J, Lee P, MacAdam C, Morris R, Norris A, Palmer S, Plant CW, Simkin J, Stubbs A, Sutton P, Telfer M, Wallace I & Isaac NJB (2019) Annual estimates of occupancy of bryophytes, lichens and invertebrates in the UK, 1970–2015. *Scientific Data* **6**, 259.

Ovaskainen O, Roy DB, Fox R & Anderson BJ (2016) Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. *Methods in Ecology and Evolution* **7**, 428–436.

Pagel J, Anderson BJ, O'Hara RB, Cramer W, Fox R, Jeltsch F, Roy DB, Thomas CD & Schurr FM (2014) Quantifying range-wide variation in population trends from local abundance surveys and widespread opportunistic occurrence records. *Methods in Ecology and Evolution* **5**, 751–760.

Palmer G, Platts PJ, Brereton T, Chapman JW, Dytham C, Fox R, Pearce-Higgins JW, Roy DB, Hill JK & Thomas CD (2017) Climate change, climatic variation and extreme biological responses. *Philosophical Transactions of the Royal Society B* **372**, 20160144.

Pateman RM, Hill JK, Roy DB, Fox R & Thomas CD (2012) Temperaturedependent alterations in host use drive rapid range expansion in a butterfly. *Science* **336**, 1028–1030.

Pearce-Higgins JW, Beale CM, Oliver TH, August TA, Carroll M, Massimino D, Ockendon N, Savage J, Wheatley CJ, Ausden MA, Bradbury RB, Duffield SJ, Macgregor NA, McClean CJ, Morecroft MD, Thomas CD, Watts O, Beckmann BC, Fox R, Roy HE, Sutton PG, Walker KJ & Crick HQP (2017) A national-scale assessment of climate change impacts on species: assessing the balance of risks and opportunities for multiple taxa. *Biological Conservation* **213**, 124–134.

Platts PJ, Mason SC, Palmer G, Hill JK, Oliver TH, Powney GD, Fox R & Thomas CD (2019) Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. *Scientific Reports* **9**, 15039.

Pocock MJO, Roy HE, Fox R, Ellis WN & Botham M (2017) Citizen science and invasive alien species: predicting the detection of the oak processionary moth *Thaumetopoea processionea* by moth recorders. *Biological Conservation* **208**, 146–154.

Rapacciuolo G, Roy DB, Gillings S, Fox R, Walker K & Purvis A (2012) Climatic associations of British species distributions show good transferability in time but low predictive accuracy for range change. *PLoS One* **7**, e40212.

Redhead JW, Fox R, Brereton T & Oliver TH (2016) Assessing species' habitat associations from occurrence records, standardised monitoring data and expert opinion: A test with British butterflies. *Ecological Indicators* **62**, 271–278.

Stefanescu C, Páramo F, Åkesson S, Alarcón M, Ávila A, Brereton T, Carnicer J, Cassar LF, Fox R, Heliölä J, Hill JK, Hirneisen N, Kjellén N, Kühn E, Kuussaari M, Leskinen M, Liechti F, Musche M, Regan EC, Reynolds DR, Roy DB, Ryrholm N, Schmaljohann H, Settele J, Thomas CD, van Swaay C & Chapman JW (2013) Multi-generational long-distance migration of insects: studying the painted lady butterfly in the Western Palaearctic. *Ecography* **36**, 474–486.

Suggitt AJ, Wilson RJ, August TA, Fox R, Isaac NJB, Macgregor NA, Morecroft MD & Maclean IMD (2015) Microclimate affects landscape level persistence in the British Lepidoptera. *Journal of Insect Conservation* **19**, 237–253.

Suggitt AJ, Wilson RJ, Isaac NJB, Beale CM, Auffret AG, August T, Bennie JJ, Crick HQP, Duffield S, Fox R, Hopkins JJ, Macgregor NA, Morecroft MD, Walker KJ & Maclean IMD (2018) Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change* **8**, 713–717.

Thomas CD, Gillingham PK, Bradbury RB, Roy DB, Anderson BJ, Baxter JM, Bourn NAD, Crick HQP, Findon RA, Fox R, Hodgson JA, Holt AR, Morecroft MD, O'Hanlon NJ, Oliver TH, Pearce-Higgins JW, Procter DA, Thomas JA, Walker KJ, Walmsley CA, Wilson RJ & Hill JK (2012) Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences of the USA* **109**, 14063–14068.

Thomas JA, Telfer MG, Roy DB, Preston C, Greenwood JJD, Asher J, Fox R, Clarke RT & Lawton JH (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**, 1879–1881.

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D &

Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69.

Willis SG, Hill JK, Thomas CD, Roy DB, Fox R, Blakeley DS & Huntley B (2009) Assisted colonization in a changing climate: a test-study using two U.K. butterflies. *Conservation Letters* **2**, 45–51.

Willis SG, Thomas CD, Hill JK, Collingham YC, Telfer MG, Fox R & Huntley B (2009) Dynamic distribution modelling: predicting the present from the past. *Ecography* **32**, 5–12.

Wilson RJ, Thomas CD, Fox R, Roy DB & Kunin WE (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature* **432**, 393–396.

Appendix 2: Affiliations of co-authors

James R. Bell Rothamsted Insect Survey, Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK

Nigel A.D. Bourn Butterfly Conservation, Manor Yard, Wareham, Dorset, BH20 5QP, UK

Tom M. Brereton Butterfly Conservation, Manor Yard, Wareham, Dorset, BH20 5QP, UK

Emily B. Dennis Butterfly Conservation, Manor Yard, Wareham, Dorset, BH20 5QP, UK School of Mathematics, Statistics and Actuarial Science, University of Kent, Canterbury, Kent, CT2 7FS, UK

Colin A. Harrower NERC Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK

Richard T. Heafield Butterfly Conservation, Manor Yard, Wareham, Dorset, BH20 5QP, UK

Ilya M. D. Maclean Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall, TR10 9FE, UK

Ian Middlebrook Butterfly Conservation, Manor Yard, Wareham, Dorset, BH20 5QP, UK

Byron J.T. Morgan School of Mathematics, Statistics and Actuarial Science, University of Kent, Canterbury, Kent, CT2 7FS, UK Tom H. Oliver

NERC Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK

Mark S. Parsons Butterfly Conservation, Manor Yard, Wareham, Dorset, BH20 5QP, UK

David B. Roy NERC Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK

Chris R. Shortall Rothamsted Insect Survey, Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK

Chris D. Thomas Department of Biology, University of York, York, Yorkshire, YO10 5DD, UK

Robert J. Wilson

Biosciences, College of Life and Environmental Sciences, University of Exeter, Prince of Wales Road, Exeter, Devon, EX4 4PS, UK National Museum of Natural Sciences (MNCN-CSIC), 28006 Madrid, Spain Appendix 3: Supporting Information for Chapter 3: Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes

Frescalo analysis of distribution change

Frescalo is a method that can be applied to species occurrence data to assess variation in recorder effort and produce trends in species frequency over time (Hill 2012). The method requires two parameters to be identified by users, although sensitivity analyses suggest that precise values are not critical (see supporting Information in Hill 2012). The first parameter is the standard neighbourhood frequency Φ , which generally reflects how well the species group is recorded. The default value of Φ is 0.74, but the Frescalo program provides an output value of phi using a convergence algorithm which scales local neighbourhood frequencies by sampling effort multipliers. For groups that are not completely recorded, Hill (2012) suggests setting Φ greater than the 98th percentile of observed values of local neighbourhood frequency. Therefore, for the analysis of the entire Great Britain (GB) macro-moth dataset we increased the value of Φ to 0.89, to remain above this 98th percentile. For the analysis where northern and southern halves of geographically widespread species distributions were assessed separately we used a Φ value of 0.94 for southern hectads (10km x 10km grid squares), which were relatively better recorded than northern hectads, where we set the value of Φ to 0.74.

The second input parameter required by Frescalo is the R*, the proportion of species treated as benchmark species. The most common species in a local neighbourhood are used as 'benchmarks' to give an indication of how well recorded a given hectad is, and this is then used to modify the reporting frequency of the focal species in order to inform on the probability of occurrence. Ideally, the benchmark species should be relatively stable in frequency over time, but sensitivity analyses have shown that the method is robust to dynamic benchmark species (see Supporting Information in Hill 2012). We retained the default value of 0.27 for this parameter.

Following the methods in Hill (2012), the probability of reporting species in a given hectad in a given time period depends on 1) recorder effort, which is

measured as the proportion of benchmark species reported from the hectad in that time period, 2) the time-independent probability of the species occurring in that hectad and 3) the Relative Reporting Rate (RRR) for the time period. The RRR is the ratio of the rate at which the focal species is reported to the rate at which the benchmark species are reported within the range of occupancy of the focal species in a given time period. In order that values of RRR for rare species are of comparable magnitude to those for commoner species, this is relativized by dividing by the time-independent probability of finding the focal species, also within its range of occupancy. Relative Reporting Rate is obtained iteratively through the formula given in Hill (2012). Hence, although it is a measure without units, the change in Relative Reporting Rate (Δ RRR) between time periods describes temporal changes in the estimated species frequency across all hectads, i.e. a negative Δ RRR indicates a decline in species frequency.

As described in Chapter 3, the significance of these trends can be determined by:

$$z = \frac{t_2 - t_1}{\sqrt{\sigma_2^2 + \sigma_1^2}}$$

where t_1 and t_2 are the Relative Reporting Rates of a given species from the first and second time periods and σ_1^2 and σ_2^2 are the variances associated with the RRR for periods t_1 and t_2 respectively.

The Frescalo method estimates species' frequency of occurrence, which is a function of both local abundance and distribution extent. In practice, these two variables are inextricably linked because the probability of a species being recorded in a grid square depends both on local abundance and on recording effort. In theory, changes in frequency of occurrence could relate solely to variation in local abundance with no distribution change. However, because we aggregated data over broad time periods in our study (thereby increasing recording effort), and the fact that changes in frequency of occurrence calculated for macro-moths correlated significantly with the raw number of occupied grid squares (Figs A3.3 & A3.4), it is likely that changes in frequency described here also reflect changes in moth distribution extents in GB.

References

Hill MO (2012) Local frequency as a key to interpreting species occurrence data when recording effort is not known. *Methods in Ecology and Evolution* **3**, 195–205.

Table A3.1 Change in frequency of occurrence (measured as annual change in relative reporting rate; Δ RRR year⁻¹) 1970-99 versus 2000-10 for 673 resident GB macro-moths.

Taxon	Δ RRR year ⁻¹	z	Signif
Abraxas			
grossulariata	-0.0085	-5.40	p<0.05
A. sylvata	-0.0040	-3.98	p<0.05
Abrostola	0.0120	6.91	n <0.05
tripartita	0.0139	6.81	p<0.05
A. triplasia	-0.0002	-0.22	NS
Acasis viretata	0.0083	7.66	p<0.05
Achlya flavicornis	0.0007	0.82	NS
Acronicta aceris	0.0078	4.94	p<0.05
A. alni	-0.0015	-1.62	NS
A. euphorbiae	-0.0013	-0.54	NS
A. leporina	0.0022	2.19	p<0.05
A. megacephala	0.0036	2.82	p<0.05
A. menyanthidis	-0.0055	-4.52	p<0.05
A. psi	-0.0071	-6.58	p<0.05
A. rumicis	0.0016	1.16	NS
A. tridens	-0.0051	-5.25	p<0.05
Actebia praecox	-0.0076	-4.78	p<0.05
Adscita geryon	-0.0052	-2.24	p<0.05
A. statices	-0.0041	-3.60	p<0.05
Aethalura punctulata	-0.0044	-4.74	p<0.05
Agriopis aurantiaria	-0.0054	-6.77	p<0.05
A. leucophaearia	-0.0034	-1.30	NS
A. marginaria	-0.0038	-3.78	p<0.05
A. marginana Agrochola	-0.0030	-5.70	μς0.05
circellaris	-0.0010	-1.05	NS
A. helvola	-0.0064	-7.87	p<0.05
A. litura	-0.0061	-5.67	p<0.05
A. lota	0.0024	2.39	p<0.05
A. lychnidis	-0.0038	-3.01	p<0.05
A. macilenta	0.0033	3.43	p<0.05
Agrotis cinerea	-0.0082	-5.50	p<0.05
A. clavis	0.0016	1.46	NS

		-	
A. exclamationis	-0.0109	-3.73	p<0.05
A. puta	0.0100	5.05	p<0.05
A. ripae	-0.0017	-0.72	NS
A. segetum	-0.0029	-2.38	p<0.05
A. trux	-0.0045	-1.72	NS
A. vestigialis	-0.0103	-6.37	p<0.05
Alcis jubata	-0.0016	-1.14	NS
A. repandata	-0.0018	-0.66	NS
Aleucis distinctata	-0.0116	-2.59	p<0.05
Allophyes oxyacanthae	-0.0020	-1.81	NS
Alsophila aescularia	-0.0014	-1.20	NS
Amphipoea crinanensis	-0.0036	-2.36	p<0.05
A. fucosa	-0.0019	-1.28	NS
A.lucens	0.0003	0.25	NS
A. oculea	-0.0028	-3.41	p<0.05
Amphipyra tragopoginis	-0.0160	- 11.14	p<0.05
Anaplectoides prasina	0.0017	1.77	NS
Anarta cordigera	-0.0249	-3.33	p<0.05
A. melanopa	-0.0003	-0.09	NS
A. myrtilli	-0.0052	-5.30	p<0.05
Angerona prunaria	-0.0042	-2.87	p<0.05
Anticlea badiata	-0.0020	-1.98	p<0.05
A. derivata	0.0029	2.88	p<0.05
Anticollix sparsata	-0.0116	-3.18	p<0.05
Antitype chi	-0.0080	-7.53	p<0.05
Apamea anceps	-0.0020	-1.57	NS
A. crenata	0.0000	-0.03	NS
A. epomidion	-0.0008	-0.84	NS
A. furva	-0.0074	-6.37	p<0.05
A. lithoxylaea	-0.0042	-2.88	p<0.05

A. monoglypha	-0.0105	-1.63	NS
A. oblonga	-0.0111	-5.85	p<0.05
A. ophiogramma	-0.0003	-0.37	NS
A. remissa	-0.0032	-2.51	p<0.05
A. scolopacina	0.0031	2.96	p<0.05
A. sordens	-0.0064	-5.59	p<0.05
A. sublustris	-0.0008	-0.56	NS
A. unanimis	0.0009	1.03	NS
A. zeta	-0.0013	-0.54	NS
Apeira syringaria	-0.0022	-2.27	p<0.05
Aplocera			P
efformata	-0.0025	-2.04	p<0.05
A. plagiata	-0.0060	-6.67	p<0.05
Apocheima	0.0004	4.00	NO
hispidaria	-0.0021	-1.69	NS
Apoda limacodes Aporophyla	0.0098	4.19	p<0.05
australis	-0.0014	-0.39	NS
A. nigra	0.0080	7.34	p<0.05
Archanara algae	-0.0034	-0.75	NS
A. dissoluta	-0.0004	-0.28	NS
A. geminipuncta	0.0031	2.15	p<0.05
A. sparganii	0.0110	5.40	p<0.05
Archiearis notha	-0.0045	-2.37	p<0.05
A. parthenias	-0.0006	-0.57	NS
		-	
Arctia caja	-0.0161	10.23	p<0.05
A. villica	-0.0041	-2.68	p<0.05
Arenostola phragmitidis	-0.0003	-0.17	NS
Aspitates gilvaria	-0.0039	-0.88	NS
Asteroscopus	0.0000	0.00	
sphinx	-0.0020	-1.98	p<0.05
Asthena albulata	-0.0009	-0.88	NS
Atethmia	0.0000		
centrago Atolmis	0.0060	5.44	p<0.05
rubricollis	0.0134	12.30	p<0.05
Autographa			
bractea	-0.0063	-4.92	p<0.05
A. jota	-0.0087	-6.54	p<0.05
A. pulchrina	-0.0090	-5.17	p<0.05
Axylia putris	0.0060	2.69	p<0.05
		3.39	p<0.05
Bena bicolorana	0.0035	0.00	
	0.0035 0.0028	1.22	NS
Bena bicolorana			NS NS
Bena bicolorana Biston betularia B. strataria Blepharita	0.0028 0.0018	1.22 1.69	NS
Bena bicolorana Biston betularia B. strataria Blepharita adusta	0.0028	1.22	
Bena bicolorana Biston betularia B. strataria Blepharita adusta Brachionycha	0.0028 0.0018 -0.0068	1.22 1.69 -7.77	NS p<0.05
Bena bicolorana Biston betularia B. strataria Blepharita adusta	0.0028 0.0018	1.22 1.69	NS

		1	
Bupalus piniaria	-0.0057	-5.42	p<0.05
Cabera exanthemata	0.0028	1.68	NS
Cabera pusaria	-0.0042	-1.89	NS
Callimorpha	0.0042	1.00	
dominula	0.0033	1.82	NS
Callistege mi	-0.0024	-2.66	p<0.05
Calliteara			
pudibunda	0.0142	6.92	p<0.05
Calophasia Iunula	0.0165	3.86	p<0.05
Campaea	0.0105	5.00	μ<0.05
margaritata	0.0076	2.81	p<0.05
Camptogramma			
bilineata	-0.0193	-7.86	p<0.05
Caradrina morpheus	-0.0046	-3.15	p<0.05
Carsia sororiata			
Carsia soronata Catarhoe	-0.0035	-2.21	p<0.05
cuculata	-0.0049	-3.08	p<0.05
C. rubidata	-0.0029	-2.18	p<0.05
Catocala fraxini	-0.0005	-0.27	NS
C. nupta	0.0001	0.12	NS
C. promissa	-0.0028	-0.71	NS
Celaena	0.0020	0.71	110
haworthii	-0.0046	-3.76	p<0.05
C. leucostigma	-0.0018	-1.95	NS
Cepphis			
advenaria	-0.0037	-1.41	NS
Cerapteryx graminis	-0.0157	- 10.23	p<0.05
Cerastis			P Noree
leucographa	-0.0026	-1.59	NS
C. rubricosa	-0.0015	-1.46	NS
Cerura vinula	-0.0073	-8.32	p<0.05
Charanyca	0.0000	5.00	
trigrammica	0.0068	5.30	p<0.05
Charissa obscurata	-0.0088	-7.08	p<0.05
Chesias legatella	-0.0048	-5.15	p<0.05
C. rufata	-0.0071	-5.32	p<0.05
Chiasmia	0.0071	5.02	P 10.00
clathrata	-0.0093	-7.53	p<0.05
Chilodes	0.0000	0.00	
maritimus	0.0009	0.62	NS
Chlorissa viridata	-0.0075	-3.19	p<0.05
Chloroclysta citrata	-0.0095	-8.43	p<0.05
C. concinnata	-0.0156	-2.64	p<0.05
C. miata	-0.0044	-4.89	p<0.05
C. siterata	0.0189	16.94	
_			p<0.05
C. truncata Chloroclystis v-	0.0108	3.60	p<0.05
•			
ata	0.0033	2.53	p<0.05
ata Chortodes brevilinea	0.0033	2.53 -1.12	p<0.05 NS

	1		
C. elymi	-0.0100	-2.37	p<0.05
C. extrema	0.0027	0.49	NS
C. fluxa	-0.0047	-1.84	NS
C. pygmina	0.0016	1.56	NS
Cidaria fulvata	-0.0044	-3.47	p<0.05
Cilix glaucata	-0.0020	-1.21	NS
Cleora cinctaria	-0.0039	-1.10	NS
Cleorodes			
lichenaria	0.0033	2.60	p<0.05
Clostera curtula	0.0058	4.40	p<0.05
C. pigra	-0.0075	-6.11	p<0.05
Coenobia rufa	0.0068	6.10	p<0.05
Coenocalpe			
lapidata	-0.0014	-0.40	NS
Colocasia coryli	0.0068	5.43	p<0.05
Colostygia multistrigaria	-0.0013	-1.47	NS
C. olivata	-0.0069	-5.59	p<0.05
C. pectinataria Colotois	0.0130	4.04	p<0.05
pennaria	0.0000	-0.05	NS
Comibaena			
bajularia	-0.0032	-2.48	p<0.05
Conistra ligula	0.0026	2.77	p<0.05
C. rubiginea	0.0109	5.91	p<0.05
C. vaccinii	0.0064	5.15	p<0.05
Coscinia			
cribraria	-0.0100	-2.16	p<0.05
Cosmia affinis	-0.0043	-4.01	p<0.05
C. diffinis	-0.0083	-7.08	p<0.05
C. pyralina	-0.0051	-3.94	p<0.05
C. trapezina	-0.0002	-0.14	NS
Cosmorhoe	0.0000	0.04	- 0.05
ocellata	-0.0060	-3.91	p<0.05
Cossus cossus	-0.0026	-2.81	p<0.05
Craniophora ligustri	0.0112	9.60	p<0.05
Crocallis	0.0112	0.00	P \$0.00
elinguaria	-0.0042	-2.02	p<0.05
Cryphia	0.000.	0.00	
domestica	0.0004	0.30	NS
C. muralis	0.0037	1.96	p<0.05
Cucullia absinthii	-0.0065	-4.06	p<0.05
C. asteris	-0.0087	-3.91	p<0.05
C. chamomillae	-0.0056	-5.87	p<0.05
C. umbratica	-0.0054	-5.97	p<0.05
Cybosia			
mesomella	-0.0014	-1.16	NS
Cyclophora albipunctata	-0.0014	-1.13	NS
C. annularia	0.0050	3.05	p<0.05
C. linearia	0.0065	5.88	p<0.05

C. pendularia	-0.0002	-0.10	NS
C. porata	-0.0076	-6.34	p<0.05
C. punctaria	0.0081	6.84	p<0.05
Cymatophorima			
diluta	-0.0038	-3.14	p<0.05
Dasypolia templi	-0.0043	-3.44	p<0.05
Deilephila	0.0114	E 40	n -0.05
elpenor	0.0114	5.42	p<0.05
D. porcellus Deileptenia	0.0056	5.58	p<0.05
ribeata	0.0039	3.76	p<0.05
Deltote bankiana	0.0054	0.98	NS
D. uncula	-0.0063	-4.33	p<0.05
Diachrysia			
chrysitis	-0.0043	-1.68	NS
D. chryson	-0.0027	-0.87	NS
D. sannio	-0.0018	-1.41	NS
Diaphora mendica	0.0006	0.50	NS
Diarsia brunnea	-0.0043	-4.04	p<0.05
Diarsia brunnea D. dahlii	-0.0059	-5.81	p<0.05 p<0.05
D. mendica	-0.0089	-3.78	p<0.05
D. rubi	0.0074	3.39	p<0.05
Dicallomera	0.0074	5.59	μ<0.05
fascelina	-0.0013	-0.85	NS
Dichonia aprilina	0.0035	4.01	p<0.05
Dicycla oo	-0.0040	-1.49	NS
Diloba		-	
caeruleocephala	-0.0137	13.37	p<0.05
Discestra trifolii Discoloxia	-0.0057	-5.13	p<0.05
blomeri	-0.0001	-0.09	NS
Drepana		0.00	
falcataria	0.0029	2.35	p<0.05
Drymonia dodonaea			
	_0 0004	_0.20	NC
	-0.0004	-0.39	NS
D. ruficornis	-0.0004 0.0041	-0.39 4.00	NS p<0.05
D. ruficornis Dryobotodes eremita Dypterygia	0.0041	4.00 1.41	p<0.05 NS
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula	0.0041 0.0013 -0.0012	4.00 1.41 -0.83	p<0.05 NS NS
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria	0.0041 0.0013 -0.0012 -0.0062	4.00 1.41 -0.83 -5.37	p<0.05 NS NS p<0.05
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria Earias clorana	0.0041 0.0013 -0.0012	4.00 1.41 -0.83	p<0.05 NS NS
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria Earias clorana Ecliptopera	0.0041 0.0013 -0.0012 -0.0062 0.0080	4.00 1.41 -0.83 -5.37 4.85	p<0.05 NS NS p<0.05 p<0.05
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria Earias clorana Ecliptopera silaceata	0.0041 0.0013 -0.0012 -0.0062	4.00 1.41 -0.83 -5.37	p<0.05 NS NS p<0.05
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria Earias clorana Ecliptopera	0.0041 0.0013 -0.0012 -0.0062 0.0080	4.00 1.41 -0.83 -5.37 4.85	p<0.05 NS NS p<0.05 p<0.05
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria Earias clorana Ecliptopera silaceata Ectropis bistortata	0.0041 0.0013 -0.0012 -0.0062 0.0080 0.0074 0.0049	4.00 1.41 -0.83 -5.37 4.85 4.11 3.62 -	p<0.05 NS p<0.05 p<0.05 p<0.05 p<0.05
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria Earias clorana Ecliptopera silaceata Ectropis bistortata E. crepuscularia	0.0041 0.0013 -0.0012 -0.0062 0.0080 0.0074	4.00 1.41 -0.83 -5.37 4.85 4.11	p<0.05 NS NS p<0.05 p<0.05 p<0.05
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria Earias clorana Ecliptopera silaceata Ectropis bistortata E. crepuscularia Egira	0.0041 0.0013 -0.0012 -0.0062 0.0080 0.0074 0.0049 -0.0102	4.00 1.41 -0.83 -5.37 4.85 4.11 3.62 - 11.74	p<0.05 NS p<0.05 p<0.05 p<0.05 p<0.05
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria Earias clorana Ecliptopera silaceata Ectropis bistortata E. crepuscularia	0.0041 0.0013 -0.0012 -0.0062 0.0080 0.0074 0.0074 -0.0022	4.00 1.41 -0.83 -5.37 4.85 4.11 3.62 -	p<0.05 NS p<0.05 p<0.05 p<0.05 p<0.05 p<0.05 NS
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria Earias clorana Ecliptopera silaceata Ectropis bistortata E. crepuscularia Egira conspicillaris Eilema caniola	0.0041 0.0013 -0.0012 -0.0062 0.0080 0.0074 0.0074 -0.0049 -0.0102 -0.0022 0.0095	4.00 1.41 -0.83 -5.37 4.85 4.11 3.62 - 11.74 -0.58 3.57	p<0.05 NS p<0.05 p<0.05 p<0.05 p<0.05 p<0.05 p<0.05 NS p<0.05
D. ruficornis Dryobotodes eremita Dypterygia scabriuscula Dyscia fagaria Earias clorana Ecliptopera silaceata Ectropis bistortata E. crepuscularia Egira conspicillaris	0.0041 0.0013 -0.0012 -0.0062 0.0080 0.0074 0.0074 -0.0022	4.00 1.41 -0.83 -5.37 4.85 4.11 3.62 - 11.74 -0.58	p<0.05 NS p<0.05 p<0.05 p<0.05 p<0.05 p<0.05 NS

E griscolo	0.0235	13.11	n <0.05
E. griseola			p<0.05
E. lurideola	0.0171	6.34	p<0.05
E. pygmaeola	0.0061	0.94	NS
E. sororcula	0.0209	16.11	p<0.05
Elaphria venustula	0.0024	0.92	NS
Electrophaes	0.0024	0.92	110
corylata	-0.0034	-3.18	p<0.05
Ematurga			
atomaria	-0.0070	-6.44	p<0.05
Enargia	0.0040	0.00	NO
paleacea Endromis	-0.0010	-0.63	NS
versicolora	-0.0065	-1.63	NS
Ennomos	0.0000		
alniaria	0.0014	0.94	NS
E. autumnaria	-0.0016	-0.76	NS
E. erosaria	-0.0093	-9.68	p<0.05
E. fuscantaria	0.0035	2.78	p<0.05
E. quercinaria	-0.0033	-3.54	p<0.05
Entephria	0.0000	-	p <0.00
caesiata	-0.0167	10.62	p<0.05
E. flavicinctata	-0.0011	-0.33	NS
Epione			
repandaria	-0.0008	-0.84	NS
Epirrhoe	0.0010	0.22	NO
alternata	0.0012	0.23	NS
E. galiata	-0.0046	-4.23	p<0.05
E. rivata	-0.0048	-4.71	p<0.05
E. tristata	-0.0080	-6.25	p<0.05
Epirrita autumnata	-0.0037	-3.90	p<0.05
E. christyi	-0.0043	-4.32	p<0.05
E. dilutata	-0.0055	-6.29	p<0.05
E. filigrammaria	-0.0078	-6.44	p<0.05
Erannis defoliaria	-0.0061	-6.25	p<0.05
Eremobia	0.0001	0.20	μ<0.05
ochroleuca	-0.0010	-0.52	NS
Eriogaster			
lanestris	-0.0015	-1.32	NS
Euchoeca	0 0022	2.51	D-0 05
nebulata	0.0023		p<0.05
Euclidia glyphica Eugnorisma	-0.0014	-1.24	NS
depuncta	-0.0042	-2.62	p<0.05
E. glareosa	-0.0006	-0.53	NS
	0.0000	-	
Eulithis mellinata	-0.0094	10.23	p<0.05
E. populata	-0.0125	-8.05	p<0.05
E. prunata	0.0014	1.36	NS
E. pyraliata	-0.0052	-2.70	p<0.05
E. testata		-6.92	
E. testata Euphyia	-0.0070	-0.92	p<0.05
biangulata	0.0001	0.06	NS
			25

	1	r	1
E. unangulata	-0.0040	-3.20	p<0.05
Eupithecia abbreviata	0.0070	7.05	n -0.0E
	0.0079	7.25	p<0.05 NS
E. abietaria			
E. absinthiata	0.0027	2.68	p<0.05
E. assimilata	0.0039	4.70	p<0.05
E. centaureata	0.0008	0.57	NS
E. distinctaria	-0.0080	-4.28	p<0.05
E. dodoneata	0.0060	5.92	p<0.05
E. egenaria	0.0060	1.35	NS
E. exiguata	0.0069	6.40	p<0.05
E.expallidata	-0.0064	-4.14	p<0.05
E. haworthiata	-0.0001	-0.07	NS
E. icterata	-0.0101	-9.26	p<0.05
E. indigata	0.0016	1.61	NS
E. innotata	-0.0064	-5.23	p<0.05
E. insigniata	-0.0080	-3.63	p<0.05
E. inturbata	0.0003	0.29	NS
E. irriguata	-0.0071	-3.23	p<0.05
E. lariciata	-0.0033	-3.63	p<0.05
E. linariata	-0.0032	-3.15	p<0.05
E. millefoliata	0.0058	2.18	p<0.05
E. nanata	-0.0050	-4.95	p<0.05
E. phoeniceata	0.0081	3.78	p<0.05
E. pimpinellata	-0.0079	-4.72	p<0.05
E. plumbeolata	-0.0037	-2.53	p<0.05
E. pulchellata	0.0037	3.21	p<0.05
E. pusillata	-0.0040	-3.98	p<0.05
			p<0.05
E. pygmaeata	-0.0027	-1.99	
E.satyrata	-0.0063	-5.81	p<0.05
E. simpliciata	-0.0022	-1.85	NS
E.subfuscata	-0.0009	-0.82	NS
E.subumbrata	-0.0037	-2.58	p<0.05
E. succenturiata	-0.0077	-6.47	p<0.05
E. tantillaria	-0.0006	-0.63	NS
E. tenuiata	0.0007	0.82	NS
E. tripunctaria	0.0030	2.97	p<0.05
E. trisignaria	0.0006	0.54	NS
E. valerianata	-0.0030	-2.10	p<0.05
E. venosata	-0.0062	-6.54	p<0.05
E. virgaureata	0.0051	4.72	p<0.05
E. vulgata	0.0028	1.95	NS
E.	0.0405	4.40	- 0.05
quadripunctaria	0.0135	4.46	p<0.05
Euplexia lucipara	0.0003	0.18	NS
Euproctis chrysorrhoea	0.0048	3.32	p<0.05
E. similis	-0.0040	-1.87	NS
	0.0040	1.07	

Eupsilia				H.s
transversa	0.0034	3.41	p<0.05	Heri
Eurois occulta	0.0029	2.88	p<0.05	grise
Euthrix potatoria	0.0019	0.85	NS	H. ta
Euxoa cursoria	-0.0066	-3.02	p<0.05	Hete
		-	1	ase
E. nigricans	-0.0124	14.20	p<0.05	Hop
E. obelisca	-0.0062	-2.88	p<0.05	alsir
E. tritici	-0.0092	-8.91	p<0.05	Н. а
Falcaria				H. b
lacertinaria	-0.0014	-1.36	NS	Hori
Furcula bicuspis	0.0015	1.10	NS	H. v
F. bifida	0.0000	-0.05	NS	Hyd
F. furcula	0.0024	2.44	p<0.05	mica
Gastropacha		-		Н. р
quercifolia	-0.0144	13.33	p<0.05	Hyd
Geometra	0.0044	0.70	- 0.05	flam
papilionaria Gnophos	-0.0044	-3.72	p<0.05	H. s Hyd
obfuscata	-0.0140	-5.03	p<0.05	furca
Gortyna flavago	0.0040	3.90	p<0.05	H. ir
Graphiphora	0.0040	-	μ<0.05	
augur	-0.0184	18.62	p<0.05	<u>H.</u> r
Gymnoscelis				Hyla
rufifasciata	0.0159	10.83	p<0.05	Hyle
Habrosyne	0.0000	4.40	NO	Hylo
pyritoides	0.0030	1.18	NS	Нур
Hada plebeja	-0.0011	-1.12	NS	Н. р
Hadena albimacula	-0.0081	-1.83	NS	Нур
H. bicruris	-0.0008	-0.69	NS	hum
				Нур
H. compta	0.0004	0.29	NS	pune Hyp
H. confusa	-0.0055	-5.65	p<0.05	robo
H. luteago	-0.0001	-0.03	NS	Нур
H. perplexa	-0.0050	-5.15	p<0.05	Idae
H. rivularis	-0.0020	-2.17	p<0.05	I. bis
Hecatera				
bicolorata	-0.0064	-6.34	p<0.05	<i>I. co</i>
Heliophobus reticulata	-0.0070	-6.99	p<0.05	I. dil
Heliothis	0.0070	0.00	p<0.00	I. dii
maritima	-0.0125	-1.84	NS	I. en
H. viriplaca	-0.0032	-1.63	NS	I. fu
Hemaris				I. m
fuciformis	-0.0025	-1.88	NS	I. ru
H. tityus	0.0015	1.25	NS	I. se
Hemistola				I. sti
chrysoprasaria	0.0032	2.45	p<0.05	1. su
Hemithea	0.0031	1 71	NS	
aestivaria Hepialus	0.0031	1.71	СИ	I. sy
fusconebulosa	-0.0008	-0.58	NS	I. tri
H. hecta	-0.0070	-8.37	p<0.05	Ipim
H. humuli	-0.0058	-3.99	p<0.05	I. su
				Itam
H. lupulinus	0.0020	1.21	NS	52
			<u> </u>	. •)

	0.0040	0.00	NO
H. sylvina Herminia	0.0010	0.82	NS
grisealis	0.0035	2.64	p<0.05
H. tarsicrinalis	0.0107	1.39	NS
Heterogenea	0.0107	1.00	110
asella	0.0037	0.82	NS
Hoplodrina		a - 4	
alsines	0.0050	2.71	p<0.05
H. ambigua	0.0118	7.43	p<0.05
H. blanda	0.0037	2.58	p<0.05
Horisme tersata	-0.0047	-3.14	p<0.05
H. vitalbata	0.0018	1.13	NS
Hydraecia	0 0020	1 77	NC
micacea	0.0029	1.77	NS
H. petasitis	-0.0059	-4.64	p<0.05
Hydrelia flammeolaria	0.0040	3.86	p<0.05
H. sylvata	0.0007	0.49	NS
Hydriomena	0.0007	0.10	
furcata	-0.0148	-5.35	p<0.05
H. impluviata	0.0003	0.38	NS
H. ruberata	-0.0059	-5.55	p<0.05
Hylaea fasciaria	-0.0026	-2.54	p<0.05
Hyles gallii	-0.0027	-2.10	p<0.05
Hyloicus pinastri	0.0138	8.91	p<0.05
Hypena crassalis	0.0011	0.68	NS
H. proboscidalis	0.0081	2.45	p<0.05
Hypenodes	0.0001	2.45	ρ<0.05
humidalis	0.0005	0.32	NS
Hypomecis			
punctinalis	-0.0005	-0.33	NS
Hypomecis roboraria	-0.0002	-0.10	NS
Hyppa rectilinea	-0.0002	-0.28	NS
Idaea aversata	0.0093	2.75	p<0.05
I. biselata	0.0089	4.33	p<0.05
I. contiguaria	-0.0049	-1.23	NS
I. dilutaria	-0.0098	-2.08	p<0.05
I. dimidiata	0.0065	3.41	p<0.05
I. emarginata	-0.0052	-3.63	p<0.05
I. fuscovenosa	0.0015	1.09	NS
I. muricata	-0.0051	-1.89	NS
I. rusticata	0.0159	7.36	p<0.05
I. seriata	0.0047	4.36	p<0.05
I. straminata	-0.0023	-2.37	p<0.05
I. subsericeata	-0.0038	-3.10	p<0.05
I. sylvestraria	-0.0054	-2.08	p<0.05
I. trigeminata	0.0070	4.39	p<0.05
Ipimorpha retusa	-0.0009	-0.64	NS
I. subtusa	0.0011	1.11	NS
ltame brunneata	0.0052	2.19	p<0.05

[
Jodia croceago	-0.0061	-3.71	p<0.05
Jodis lactearia	-0.0053	-5.40	p<0.05
Jordanita			
globulariae	-0.0078	-1.88	NS
Lacanobia	-0.0025	_2 02	D-0.05
contigua	-0.0035	-2.93	p<0.05
L. oleracea	0.0025	1.02	NS
L. suasa	-0.0010	-0.83	NS
L. thalassina	-0.0043	-3.80	p<0.05
L. w-latinum	-0.0002	-0.16	NS
Lampropteryx		o (-	
otregiata	0.0063	3.45	p<0.05
L. suffumata	0.0020	1.82	NS
Laothoe populi	0.0087	3.18	p<0.05
Larentia clavaria	-0.0034	-3.35	p<0.05
Lasiocampa	0.0005	4	- 0.05
quercus	-0.0065	-5.54	p<0.05
L. trifolii	0.0007	0.23	NS
Laspeyria flexula	0.0030	2.30	p<0.05
Leucochlaena	0.0100	-1.36	NS
oditis	-0.0108		
Leucoma salicis	-0.0051	-4.34	p<0.05
Ligdia adustata	0.0018	1.31	NS
Lithomoia solidaginis	-0.0080	-6.21	p<0.05
Lithophane	-0.0000	-0.21	μ<0.05
hepatica	0.0126	13.13	p<0.05
L. leautieri	0.0108	8.76	p<0.05
L. ornitopus	0.0082	7.61	p<0.05
L. semibrunnea	0.0019	1.85	NS
Lithosia quadra	0.00102	7.52	p<0.05
Lithostege	0.0102	1.52	μ<0.05
griseata	0.0080	1.84	NS
Lobophora			
halterata	-0.0008	-0.78	NS
Lomaspilis	0.0040	0.54	
marginata Lomographa	0.0013	0.51	NS
bimaculata	0.0039	3.48	p<0.05
L. temerata	0.0085	4.78	p<0.05
Luperina nickerlii	0.0020	0.37	NS
•			
L. testacea	-0.0030	-1.76	NS
Lycia hirtaria	-0.0031	-2.69	p<0.05
L. lapponaria	-0.0044	-1.24	NS
Lycia zonaria	-0.0056	-0.95	NS
Lycophotia	0.0070	4.0.4	n -0.05
porphyrea	-0.0076	-4.84	p<0.05
Lygephila pastinum	-0.0005	-0.49	NS
Lymantria dispar	-0.0014	-0.35	NS
	0.0129	8.44	
L. monacha Macaria	0.0129	0.44	p<0.05
alternata	0.0081	3.98	p<0.05
	0.0001	0.00	P 10100

-0.0040	-0.66	NS
	-3,10	p<0.05
0.0006	0.46	NS
	-	
-0.0136	17.65	p<0.05
0 0005	0.20	NS
0.0000	0.20	
0.0183	14.01	p<0.05
0 0004	- 10	0.05
-0.0061	-5.16	p<0.05
-0.0089	-1.48	NS
	-	
-0.0187	10.84	p<0.05
-0.0096	-7.77	p<0.05
0.0076	3.10	p<0.05
		•
-0.0056	-1.83	NS
-0 0048	-2.84	p<0.05
-0.0040	-2.04	μ<0.00
-0.0142	11.61	p<0.05
0.00.10	0.00	- 0.05
-0.0046	-3.38	p<0.05
0.0045	3.36	p<0.05
		1 2.00
-0.0050	-5.99	p<0.05
0.0009	0.75	NS
		p<0.05
0.0074	4.41	p<0.05
0.0071	4.96	p<0.05
-0.0049	-1.72	NS
0.0050	1.41	NS
0.0018	1.96	NS
0.0100	40.00	- 0.05
		p<0.05
		p<0.05
		p<0.05
		NS
-0.0044	-2.38	p<0.05
-0.0074	-2.22	p<0.05
-0.0021	-0.61	NS
0.0117	4.42	p<0.05
-0.0053	-2.22	p<0.05
-0.0043	-2.60	p<0.05
-0.0002	-0.10	NS
-0.0008	-0.63	NS
-0.0037	-0.89	NS
0.0008	0.67	NS
	-0.0031 0.0006 0.0136 0.0183 0.0183 -0.0061 -0.0089 -0.0187 -0.0096 0.0076 -0.0050 -0.0045 -0.0045 0.0045 0.0045 0.0045 0.0074 0.0050 0.0074 0.0074 0.0071 0.0050 0.0073 0.0074 0.00074 0.00074 0.0004 0.00	-0.0031-3.100.00060.46-0.013617.650.00050.200.018314.01-0.0061-5.16-0.0089-1.48-0.018710.84-0.0096-7.770.00763.10-0.0056-1.83-0.0048-2.84-0.0048-2.84-0.0048-2.84-0.00453.36-0.0046-3.380.00453.36-0.0046-3.380.0045-5.990.00090.75-0.0045-4.180.00744.410.00744.410.00741.96-0.0049-1.720.00501.410.00744.96-0.0049-1.720.00501.410.00744.96-0.0045-0.334-0.0045-0.3140.0074-2.220.0054-2.38-0.0044-2.38-0.0045-0.41-0.0045-0.42-0.0045-0.42-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22-0.0045-2.22

M. turca	0.0013	0.66	NS
M. unipuncta	0.0073	5.00	p<0.05
Naenia typica	-0.0034	-3.74	p<0.05
Nebula salicata	-0.0093	-7.06	p<0.05
	0.0035	1.14	NS
Noctua comes			
N. fimbriata	0.0074	5.43	p<0.05
N. interjecta	0.0030	2.05	p<0.05
N. janthe	0.0053	1.92	NS
N. orbona	-0.0058	-4.78	p<0.05
N. pronuba	0.0198	2.20	p<0.05
Nola confusalis	0.0063	6.31	p<0.05
N. cucullatella	-0.0060	-4.34	p<0.05
Nonagria typhae	0.0007	0.71	NS
Notodonta	0.000.0	4.00	
dromedarius	0.0064	4.23	p<0.05
N. ziczac	0.0060	3.77	p<0.05
Nudaria mundana	-0.0041	-3.47	p<0.05
Nycteola	0.0041	5.47	P \$0.00
revayana	0.0068	7.00	p<0.05
Ochropacha			
duplaris	0.0000	0.00	NS
Ochropleura plecta	0.0161	3.94	p<0.05
Odezia atrata	-0.0085	-6.43	p<0.05
Odezla allata	-0.0005	-0.45	p<0.00
bidentata	-0.0010	-0.69	NS
Odontosia			
carmelita	-0.0019	-1.34	NS
Oligia fasciuncula	-0.0007	-0.39	NS
O. latruncula	-0.0043	-4.16	p<0.05
O. strigilis	-0.0067	-6.22	p<0.05
O. versicolor	0.0000	-0.05	NS
Omphaloscelis	0.0000	0.00	
lunosa	0.0044	3.47	p<0.05
Operophtera			
brumata	-0.0071	-6.14	p<0.05
O. fagata	-0.0066	-7.00	p<0.05
Opisthograptis luteolata	0.0095	1 76	NS
	0.0085	1.76	
Orgyia antiqua	0.0002	0.23	NS
O. recens	-0.0054	-1.67	NS
Oria musculosa	-0.0143	-5.48	p<0.05
Orthonama vittata	-0.0027	-2.92	p<0.05
Orthosia cerasi	0.0100	5.48	
			p<0.05
O. cruda	0.0049	3.92	p<0.05
O. gothica	0.0103	4.55	p<0.05
O. gracilis	-0.0013	-1.31	NS
O. incerta	0.0069	4.35	p<0.05
O. miniosa	-0.0040	-3.55	p<0.05

O. munda	0.0063	5.66	p<0.05
O. opima	-0.0047	-4.37	p<0.05
O. populeti	-0.0021	-2.01	p<0.05
Ourapteryx sambucaria	-0.0019	-0.96	NS
Pachycnemia	-0.0013	-0.30	110
hippocastanaria	-0.0010	-0.38	NS
Panemeria			
tenebrata	-0.0048	-5.27	p<0.05
Panolis flammea	0.0055	6.29	p<0.05
Papestra biren	-0.0031	-3.06	p<0.05
, Paracolax			
tristalis	-0.0098	-2.58	p<0.05
Paradarisa			
consonaria	0.0021	1.64	NS
Paradrina	0.0022	-2.91	n <0.05
clavipalpis Parascotia	-0.0032	-2.91	p<0.05
fuliginaria	0.0047	2.35	p<0.05
Parasemia			
plantaginis	-0.0070	-7.06	p<0.05
Parastichtis			
suspecta	-0.0032	-3.27	p<0.05
P. ypsillon	-0.0011	-1.16	NS
Parectropis	0.0040	4.00	NO
similaria Daginhila	0.0019	1.28	NS
Pasiphila chloerata	-0.0008	-0.53	NS
P. debiliata	0.0004	0.19	NS
		4.16	
P. rectangulata Pechipogo	0.0056	4.10	p<0.05
strigilata	-0.0081	-6.66	p<0.05
Pelosia			
muscerda	0.0074	1.81	NS
Pelurga comitata	-0.0077	-7.75	p<0.05
Perconia			
strigillaria	-0.0034	-2.06	p<0.05
Peribatodes	0.0047	0.70	NO
rhomboidaria	0.0017	0.79	NS
Peridea anceps	-0.0001	-0.08	NS
Perizoma affinitata	-0.0007	-0.73	NS
P. albulata	-0.0054	-6.45	p<0.05
			•
P. alchemillata	-0.0027	-1.93	NS
P. bifaciata	-0.0030	-2.92	p<0.05
P. blandiata	-0.0054	-3.23	p<0.05
P. didymata	-0.0147	- 11.78	p<0.05
			•
P. flavofasciata	-0.0010	-0.96	NS
P. minorata	-0.0089	-4.30	p<0.05
P. sagittata	-0.0124	-2.78	p<0.05
P. taeniata	0.0000	0.00	NS
Petrophora	0.0000		
chlorosata	0.0038	2.31	p<0.05
Phalera bucephala	0.0006	0.35	NS
Sucepitala	0.0000	0.55	110

Pheosia gnoma	0.0028	1.82	NS	Pyrrhia um
P. tremula	0.0055	4.18	p<0.05	Rheumapte
Phibalapteryx				cervinalis
virgata	-0.0059	-2.81	p<0.05	R. hastata
Phigalia pilosaria	-0.0005	-0.52	NS	R. undulata
Philereme	0.0000	0.00	NO	Rhizedra lu
transversata	0.0000	0.03	NS	Rhyacia
P. vetulata	-0.0035	-2.41	p<0.05	simulans
Phlogophora meticulosa	0.0111	4.30	p<0.05	Rivula seri
Photedes	0.0111	4.30	p<0.05	Rusina
captiuncula	-0.0079	-2.57	p<0.05	ferruginea
P. minima	-0.0058	-5.22	p<0.05	Saturnia pa Schrankia
Phragmatobia			1	costaestrig
fuliginosa	0.0061	3.67	p<0.05	S. taenialis
Phytometra				Scolioptery
viridaria	-0.0049	-5.00	p<0.05	libatrix
Plagodis	0.0060	E 26	n 10.0E	Scopula
dolabraria	0.0069	5.26	p<0.05	emutaria
P. pulveraria	-0.0036	-3.70	p<0.05	S. floslacta
Plemyria rubiginata	-0.0006	-0.68	NS	S. imitaria
Plusia festucae	0.0060	5.59	p<0.05	S. immutat
P. putnami	0.0061	4.12	p<0.05	S.
Poecilocampa	0.0001	4.12	p<0.05	marginepu
populi	-0.0022	-2.49	p<0.05	S. ornata
<u></u>		-	P	S. rubigina
Polia bombycina	-0.0120	11.35	p<0.05	S. ternata
P. nebulosa	-0.0037	-3.69	p<0.05	Scotoptery
P. trimaculosa	-0.0088	-6.32	p<0.05	bipunctaria
Polychrysia		-		S. chenope
moneta	-0.0094	10.51	p<0.05	S. luridata
Polymixis flavicincta	0.0022	1 77	NS	S. mucrona
	0.0022	1.77		Selenia de
P. lichenea	-0.0017	-1.00	NS	S. lunularia
P. xanthomista	-0.0054	-1.23	NS	
Polyploca ridens	0.0020	1.80	NS	S. tetraluna Selidosem
Protodeltote	0.0120	0.00	n 40.05	brunnearia
pygarga Protolampra	0.0130	9.88	p<0.05	Semiaspila
sobrina	-0.0069	-1.59	NS	ochrearia
Pseudoips				Sesia
prasinana	0.0048	4.45	p<0.05	bembecifo
Pseudopanthera	0.0050	4 50	0.05	Setina irro
macularia	-0.0053	-4.58	p<0.05	Shargacuc lychnitis
Pseudoterpna pruinata	-0.0094	-9.10	p<0.05	-
Pterapherapteryx	0.0004	5.10	p<0.00	S. verbasc Sideridis
sexalata	-0.0004	-0.36	NS	albicolon
Pterostoma				Simyra
palpina	0.0044	2.95	p<0.05	albovenos
Ptilodon	0.004.4	0 70		Smerinthu
capucina	-0.0014	-0.72	NS	ocellata
P. cucullina Ptilophora	0.0069	2.87	p<0.05	Charlette
PTIIODDOra				Spaelotis r
plumigera	-0.0045	-1.27	NS	Spargania

Pyrrhia umbra-0.0032-2.95p<0.05				
cervinalis -0.0037 -2.84 p<0.05 R. hastata -0.0040 -3.55 p<0.05		-0.0032	-2.95	p<0.05
R. hastata -0.0040 -3.55 $p<0.05$ R. undulata -0.0001 -0.15 NS Rhizedra lutosa 0.0012 1.31 NS Rhyacia - - - simulans -0.0163 13.56 $p<0.05$ Rivula sericealis 0.0333 16.09 $p<0.05$ Rusina - - $p<0.05$ Rusina -0.0056 -4.01 $p<0.05$ Saturnia pavonia -0.0079 -7.04 $p<0.05$ Schrankia - - $p<0.05$ Schrankia - 0.0023 -1.19 NS Scoliopteryx - - NS S Ibbarix -0.0020 -0.65 NS S. S. floslactata -0.0010 -1.10 NS S. S. imitaria 0.0032 2.09 $p<0.05$ S. immutata -0.0022 -0.88 NS S. ornata -0.0025 -1.84 NS		0.0007		0.05
R. undulata -0.0001 -0.15 NS Rhizedra lutosa 0.0012 1.31 NS Rhyacia - - simulans -0.0163 13.56 p<0.05				
Rhizedra lutosa 0.0012 1.31 NS Rhyacia - - - simulans -0.0163 13.56 p<0.05				
Rhyacia - - simulans -0.0163 13.56 $p<0.05$ Rivula sericealis 0.0333 16.09 $p<0.05$ Rusina - $p<0.05$ $question a pavonia$ -0.0079 -7.04 $p<0.05$ Saturnia pavonia -0.0079 -7.04 $p<0.05$ $p<0.05$ Schrankia $o.00023$ -1.19 NS costaestrigalis 0.0023 -1.19 NS Scoliopteryx 1.38 NS libatrix -0.0020 -0.655 NS S. floslactata -0.0010 -1.10 NS S. floslactata -0.0003 -0.78 NS S. imitaria 0.0032 2.09 $p<0.05$ S. immutata -0.0002 -0.88 NS S. ornata -0.0025 -1.84 NS S. ornata -0.0025 -1.84 NS S. ornata -0.0025 -1.84 NS S. ornata -0.0076 <	R. undulata			
simulans -0.0163 13.56 p<0.05 Rivula sericealis 0.0333 16.09 p<0.05		0.0012	1.31	NS
Rivula sericealis 0.0333 16.09 $p<0.05$ Rusina -0.0056 -4.01 $p<0.05$ Saturnia pavonia -0.0079 -7.04 $p<0.05$ Schrankia -0.0023 -1.19 NS costaestrigalis 0.0023 -1.19 NS Scoliopteryx -0.0018 -1.38 NS libatrix -0.0010 -1.10 NS Scopula -0.0020 -0.65 NS emutaria -0.0020 -0.65 NS S. floslactata -0.0008 -0.78 NS S. imitaria 0.0022 -0.88 NS S. immutata -0.0025 -1.84 NS S. ornata -0.0025 -1.84 NS S. ternata -0.0057 -3.45 $p<0.05$ S. huridata -0.0020 -0.09 NS S. ternata -0.0050 -4.36 $p<0.05$ S. nucronata -0.0076 -8.65 $p<0.05$ S. lunidata		0.0400	-	
Rusina ferruginea-0.0056-4.01 $p<0.05$ Saturnia pavonia-0.0079-7.04 $p<0.05$ Schrankia costaestrigalis0.0085 8.96 $p<0.05$ S. taenialis-0.0023-1.19NSScoliopteryx libatrix-0.0018-1.38NSScopula emutaria-0.0020-0.65NSS. floslactata-0.0010-1.10NSS. imitaria0.00322.09 $p<0.05$ S. imitaria0.00322.09 $p<0.05$ S. imitaria0.0003-0.19NSS. ornata-0.0003-0.19NSS. ornata-0.0022-0.88NSS. rubiginata0.00340.93NSS. ternata-0.0057-3.45 $p<0.05$ S. huridata-0.0050-4.36 $p<0.05$ S. luridata-0.0050-4.36 $p<0.05$ S. luridata-0.0022-0.09NSS. lunularia-0.0023-0.09NSS. lunularia-0.0050-4.36 $p<0.05$ S. lunularia-0.0076-8.65 $p<0.05$ S. tetralunaria0.00281.41NSSesia bembeciformis-0.0031-2.11 $p<0.05$ Shargacucullia lychnitis-0.0077-3.55 $p<0.05$ Sideridis albicolon-0.0031-2.09 $p<0.05$ Simerinthus ocellata-0.0077-0.18NSS. verbasci-0.0031-2.11 $p<0.05$ Simerinthus 				
ferruginea -0.0056 -4.01 p<0.05 Saturnia pavonia -0.0079 -7.04 p<0.05		0.0333	16.09	p<0.05
Saturnia pavonia -0.0079 -7.04 $p<0.05$ Schrankia 0.0085 8.96 $p<0.05$ S. taenialis -0.0023 -1.19 NS Scoliopteryx -0.0018 -1.38 NS libatrix -0.0020 -0.65 NS S. floslactata -0.0020 -0.65 NS S. floslactata -0.0020 -0.65 NS S. imitaria 0.0032 2.09 $p<0.05$ S. imitaria 0.0032 2.09 $p<0.05$ S. imitaria 0.0032 2.09 $p<0.05$ S. immutata -0.0022 -0.88 NS S. ornata -0.0025 -1.84 NS S. ornata -0.0057 -3.45 $p<0.05$ S. turbiginata -0.0057 -3.45 $p<0.05$ S. turbiginata -0.0057 -3.45 $p<0.05$ S. turbiginata -0.0076 -8.65 $p<0.05$ S. nucronata -0.0076		-0.0056	-4 01	n<0.05
Schrankia costaestrigalis 0.0085 8.96 $p<0.05$ S. taenialis -0.0023 -1.19 NS Scoliopteryx -0.0018 -1.38 NS libatrix -0.0020 -0.65 NS Scopula -0.0010 -1.10 NS scopula -0.0003 2.09 $p<0.05$ S. floslactata -0.0003 -0.19 NS S. imitaria 0.0032 2.09 $p<0.05$ S. imitaria -0.0003 -0.19 NS S. ornata -0.0022 -0.88 NS S. ornata -0.0025 -1.84 NS S. ternata -0.0057 -3.45 $p<0.05$ S. ternata -0.0050 -4.36 $p<0.05$ S. lunidata -0.0076 -8.65 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$				
costaestrigalis 0.0085 8.96 $p<0.05$ S. taenialis -0.0023 -1.19 NS Scoliopteryx -0.0018 -1.38 NS Scopula -0.0020 -0.65 NS S. filoslactata -0.0010 -1.10 NS S. filoslactata -0.0003 2.09 $p<0.05$ S. imitaria 0.0032 2.09 $p<0.05$ S. imitaria -0.0003 -0.19 NS S. imitaria -0.0022 -0.88 NS S. ornata -0.0022 -0.88 NS S. rubiginata 0.0034 0.93 NS S. ternata -0.0025 -1.84 NS Scotopteryx p<0.05		-0.0073	-7.04	p<0.00
S. taenialis -0.0023 -1.19 NS Scoliopteryx -0.0018 -1.38 NS Scopula -0.0020 -0.65 NS S. floslactata -0.0010 -1.10 NS S. floslactata -0.0003 2.09 $p<0.05$ S. imitaria 0.0032 2.09 $p<0.05$ S. imitaria -0.0003 -0.19 NS S. immutata -0.0022 -0.88 NS S. ornata -0.0022 -0.88 NS S. rubiginata 0.0034 0.93 NS S. ternata -0.0025 -1.84 NS Scotopteryx bipunctaria -0.0057 -3.45 $p<0.05$ S. huridata -0.0019 -6.49 $p<0.05$ S. luridata -0.0022 -0.09 NS S. lunularia -0.0019 -6.49 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.0028 1.41 NS Seesia - - - bembeciformis		0.0085	8.96	p<0.05
Scoliopteryx libatrix -0.0018 -1.38 NS Scopula -0.0020 -0.65 NS S. floslactata -0.0010 -1.10 NS S. floslactata -0.0008 -0.78 NS S. imitaria 0.0032 2.09 $p<0.05$ S. immutata -0.0008 -0.78 NS S. -0.0003 -0.19 NS S. ornata -0.0022 -0.88 NS S. ornata -0.0025 -1.84 NS S. ternata -0.0057 -3.45 $p<0.05$ S. ternata -0.0057 -3.45 $p<0.05$ S. luridata -0.0050 -4.36 $p<0.05$ S. luridata -0.0050 -4.36 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ Selidosema - - - brunnearia -0.0078 1.41 NS Sesia -<	S. taenialis	-0.0023	-1.19	
libatrix -0.0018 -1.38 NS Scopula -0.0020 -0.65 NS S. floslactata -0.0010 -1.10 NS S. imitaria 0.0032 2.09 $p<0.05$ S. imitaria -0.0008 -0.78 NS S. imitaria -0.0003 -0.19 NS S. imitaria -0.0022 -0.88 NS S. ornata -0.0022 -0.88 NS S. ornata -0.0025 -1.84 NS S. ternata -0.0057 -3.45 $p<0.05$ S. ternata -0.0057 -3.45 $p<0.05$ S. luridata -0.0050 -4.36 $p<0.05$ S. nucronata -0.0050 -4.36 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ Selidosema - - - ochrearia 0.0028 1.41 NS Sesia -		-	-	
emutaria -0.0020 -0.65 NS S. floslactata -0.0010 -1.10 NS S. imitaria 0.0032 2.09 $p<0.05$ S. immutata -0.0008 -0.78 NS S. -0.0003 -0.19 NS S. ornata -0.0022 -0.88 NS S. ornata -0.0025 -1.84 NS S. ternata -0.0057 -3.45 $p<0.05$ S. ternata -0.0057 -3.45 $p<0.05$ S. chenopodiata -0.0022 -0.88 NS S. luridata -0.0057 -3.45 $p<0.05$ S. huridata -0.0050 -4.36 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.0028 1.41 NS Selidosema - - - brunnearia -0.0037 -3.55 $p<0.05$ Setina irrorella	libatrix	-0.0018	-1.38	NS
S. floslactata -0.0010 -1.10 NS S. imitaria 0.0032 2.09 $p<0.05$ S. immutata -0.0008 -0.78 NS S. -0.0003 -0.19 NS S. ornata -0.0022 -0.88 NS S. ornata -0.0025 -1.84 NS S. rubiginata 0.0034 0.93 NS S. ternata -0.0025 -1.84 NS Scotopteryx -0.0057 -3.45 $p<0.05$ S. huridata -0.0050 -4.36 $p<0.05$ S. luridata -0.0022 -0.09 NS S. luridata -0.0050 -4.36 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.0028 1.41 NS Seeia - - - brunnearia -0.0037 -3.55 $p<0.05$ Setina irrorella -0.0031 -2.11 $p<0.05$ Shargacucullia - <		0.0000	0.05	
S. imitaria 0.0032 2.09 $p<0.05$ S. immutata -0.0008 -0.78 NS S. -0.0003 -0.19 NS S. ornata -0.0022 -0.88 NS S. ornata -0.0022 -0.88 NS S. ornata -0.0025 -1.84 NS S. ternata -0.0057 -3.45 $p<0.05$ S. chenopodiata -0.0057 -3.45 $p<0.05$ S. luridata -0.0082 -8.30 $p<0.05$ S. luridata -0.0022 -0.09 NS S. lunularia -0.0076 -8.65 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.00028 1.41 NS Selidosema -0.0037 -3.55 $p<0.05$ Setina irrorella -0.0037 -3.55 $p<0.05$ Setina irrorella -0.0031 -2.11 $p<0.05$ Shargacucullia -0.0031 -2.86 $p<0.05$ Sideridis -0.00031				
S. immutata -0.0008 -0.78 NS S. -0.0003 -0.19 NS S. ornata -0.0022 -0.88 NS S. ornata -0.0025 -1.84 NS S. ternata -0.0057 -3.45 $p<0.05$ S. chenopodiata -0.00119 -6.49 $p<0.05$ S. luridata -0.0022 -0.09 NS S. nucronata -0.0082 -8.30 $p<0.05$ S. luridata -0.0020 -0.09 NS S. nucronata -0.0007 -4.36 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.0028 1.41 NS Selidosema - - - brunnearia -0.0077 -3.55 $p<0.05$ Setina irrorella -0.0037 -3.55 $p<0.05$ Setina irrorella -0.0031 -2.11 $p<0.05$ Shargacucullia - - - lychnitis -0.00				
marginepunctata -0.0003 -0.19 NS S. ornata -0.0022 -0.88 NS S. rubiginata 0.0034 0.93 NS S. ternata -0.0025 -1.84 NS Scotopteryx - - - bipunctaria -0.0057 -3.45 p<0.05				•
marginepunctata -0.0003 -0.19 NS S. ornata -0.0022 -0.88 NS S. rubiginata 0.0034 0.93 NS S. ternata -0.0025 -1.84 NS Scotopteryx - - - bipunctaria -0.0057 -3.45 p<0.05	S. immutata	-0.0008	-0.78	NS
S. ornata -0.0022 -0.88 NS S. rubiginata 0.0034 0.93 NS S. ternata -0.0025 -1.84 NS Scotopteryx -0.0057 -3.45 p<0.05	-	0.0000	0.40	NO
S. rubiginata 0.0034 0.93 NS S. ternata -0.0025 -1.84 NS Scotopteryx -0.0057 -3.45 p<0.05				
S. ternata -0.0025 -1.84 NS Scotopteryx -0.0057 -3.45 $p<0.05$ S. chenopodiata -0.0119 -6.49 $p<0.05$ S. luridata -0.0082 -8.30 $p<0.05$ S. luridata -0.0082 -8.30 $p<0.05$ S. nucronata -0.0002 -0.09 NS Selenia dentaria -0.0076 -8.65 $p<0.05$ S. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.0033 2.67 $p<0.05$ Selidosema - - $p<0.05$ brunnearia -0.0098 -3.07 $p<0.05$ Semiaspilates - - $p<0.05$ ochrearia 0.0028 1.41 NS Sesia - - $p<0.05$ Shargacucullia -0.0037 -3.55 $p<0.05$ Shargacucullia - - $p<0.05$ Sideridis - - $p<0.05$ Sideridis - - $p<0.05$ Simyra - <				
Scotopteryx bipunctaria -0.0057 -3.45 $p<0.05$ S. chenopodiata -0.0119 -6.49 $p<0.05$ S. luridata -0.0082 -8.30 $p<0.05$ S. mucronata -0.0050 -4.36 $p<0.05$ Selenia dentaria -0.0002 -0.09 NS S. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.0033 2.67 $p<0.05$ S. tetralunaria -0.0098 -3.07 $p<0.05$ Selidosema - - - brunnearia -0.0028 1.41 NS Sesia - - - ochrearia 0.0028 1.41 NS Sesia - - - - bembeciformis -0.0037 -3.55 $p<0.05$ Shargacucullia lychnitis -0.0007 -0.18 NS S S. verbasci -0.0031 -2.86 $p<0.05$ Sideridis albicolon -0.0042 <td></td> <td></td> <td></td> <td></td>				
bipunctaria -0.0057 -3.45 $p<0.05$ S. chenopodiata -0.0119 -6.49 $p<0.05$ S. luridata -0.0082 -8.30 $p<0.05$ S. mucronata -0.0050 -4.36 $p<0.05$ Selenia dentaria -0.0002 -0.09 NSS. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.0033 2.67 $p<0.05$ Selidosema -0.0098 -3.07 $p<0.05$ Semiaspilates -0.0098 -3.07 $p<0.05$ Sesia -0.0037 -3.55 $p<0.05$ Setina irrorella -0.0037 -3.55 $p<0.05$ Shargacucullia -0.0037 -3.55 $p<0.05$ Shargacucullia -0.0031 -2.86 $p<0.05$ Sideridis -0.0031 -2.86 $p<0.05$ Sideridis -0.0042 -2.09 $p<0.05$ Simyra -0.0057 2.11 $p<0.05$ Smerinthus 0.0057 2.11 $p<0.05$ Spaelotis ravida 0.0011 0.12 NSSpargania -0.0175 13.65 $p<0.05$		-0.0025	-1.84	NS
S. chenopodiata -0.0119 -6.49 $p<0.05$ S. luridata -0.0082 -8.30 $p<0.05$ S. mucronata -0.0050 -4.36 $p<0.05$ Selenia dentaria -0.0002 -0.09 NS S. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.0033 2.67 $p<0.05$ Selidosema - - $p<0.05$ brunnearia -0.0098 -3.07 $p<0.05$ Semiaspilates - - $p<0.05$ semiaspilates - - $p<0.05$ Setina irrorella -0.0037 -3.55 $p<0.05$ Shargacucullia - - $p<0.05$ lychnitis -0.0037 -3.55 $p<0.05$ Shargacucullia - - $p<0.05$ Sideridis - - $p<0.05$ Sideridis - - $p<0.05$ Simyra - - $p<0.05$ albovenosa 0.0057 2.11 $p<0.05$ Smerinthus -	Scotopteryx	-0.0057	-3 15	n-0.05
S. luridata -0.0082 -8.30 $p<0.05$ S. mucronata -0.0050 -4.36 $p<0.05$ Selenia dentaria -0.0002 -0.09 NS S. lunularia -0.0076 -8.65 $p<0.05$ S. lunularia 0.0033 2.67 $p<0.05$ S. tetralunaria 0.0033 2.67 $p<0.05$ Selidosema - - $p<0.05$ Selidosema - - $p<0.05$ Seniaspilates - $p<0.05$ $p<0.05$ Sesia - - $p<0.05$ Sesia - - $p<0.05$ Setina irrorella -0.0037 -3.55 $p<0.05$ Shargacucullia - - $p<0.05$ Iychnitis -0.0031 -2.11 $p<0.05$ Sideridis - - $p<0.05$ Sideridis - - $p<0.05$ Simyra - - $p<0.05$ Simyra - - $p<0.05$ Smerinthus - - $p<0.05$				
S. mucronata -0.0050 -4.36 $p<0.05$ Selenia dentaria -0.0002 -0.09 NS S. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.0033 2.67 $p<0.05$ Selidosema -0.0098 -3.07 $p<0.05$ Selidosema -0.0098 -3.07 $p<0.05$ Semiaspilates -0.0028 1.41 NS ochrearia 0.0028 1.41 NS Sesia - - - bembeciformis -0.0037 -3.55 $p<0.05$ Setina irrorella -0.0031 -2.11 $p<0.05$ Shargacucullia - - - lychnitis -0.0007 -0.18 NS S. verbasci -0.0031 -2.86 $p<0.05$ Sideridis - - - albicolon -0.0042 -2.09 $p<0.05$ Simyra - - - albovenosa 0.0057 2.11 $p<0.05$ Smerinthus - -				
Selenia dentaria -0.0002 -0.09 NS S. lunularia -0.0076 -8.65 p<0.05				
S. lunularia -0.0076 -8.65 $p<0.05$ S. tetralunaria 0.0033 2.67 $p<0.05$ Selidosema -0.0098 -3.07 $p<0.05$ Semiaspilates 0.0028 1.41 NS Sesia -0.0037 -3.55 $p<0.05$ Setina irrorella -0.0037 -3.55 $p<0.05$ Setina irrorella -0.0037 -3.55 $p<0.05$ Shargacucullia -0.0031 -2.11 $p<0.05$ Shargacucullia -0.0007 -0.18 NS S. verbasci -0.0031 -2.86 $p<0.05$ Sideridis -0.0042 -2.09 $p<0.05$ Simyra -0.0057 2.11 $p<0.05$ Simyra -0.0057 2.11 $p<0.05$ Smerinthus -0.0007 0.12 NS $ocellata$ 0.0001 0.12 NS Spaelotis ravida -0.0175 13.65 $p<0.05$				
S. tetralunaria 0.0033 2.67 $p<0.05$ Selidosema -0.0098 -3.07 $p<0.05$ Semiaspilates 0.0028 1.41 NS Sesia -0.0037 -3.55 $p<0.05$ Sesia -0.0037 -3.55 $p<0.05$ Sesia -0.0037 -3.55 $p<0.05$ Setina irrorella -0.0081 -2.11 $p<0.05$ Shargacucullia -0.0007 -0.18 NS S. verbasci -0.0031 -2.86 $p<0.05$ Sideridis $albicolon$ -0.0042 -2.09 $p<0.05$ Simyra $albovenosa$ 0.0057 2.11 $p<0.05$ Smerinthus -0.0042 -2.09 $p<0.05$ Smerinthus -0.0057 2.11 $p<0.05$ Spaelotis ravida -0.00175 13.65 $p<0.05$				
Selidosema brunnearia-0.0098-3.07 $p<0.05$ Semiaspilates ochrearia0.00281.41NSSesia bembeciformis-0.0037-3.55 $p<0.05$ Setina irrorella-0.0081-2.11 $p<0.05$ Shargacucullia lychnitis-0.0007-0.18NSS. verbasci-0.0031-2.86 $p<0.05$ Sideridis albicolon-0.0042-2.09 $p<0.05$ Simyra albovenosa0.00572.11 $p<0.05$ Smerinthus ocellata0.00010.12NSSpaelotis ravida-0.017513.65 $p<0.05$	S. lunularia	-0.0076	-8.65	p<0.05
brunnearia -0.0098 -3.07 p<0.05 Semiaspilates ochrearia 0.0028 1.41 NS Sesia -0.0037 -3.55 p<0.05		0.0033	2.67	p<0.05
Semiaspilates ochrearia 0.0028 1.41 NSSesia bembeciformis -0.0037 -3.55 $p<0.05$ Setina irrorella -0.0081 -2.11 $p<0.05$ Shargacucullia lychnitis -0.0007 -0.18 NSS. verbasci -0.0031 -2.86 $p<0.05$ Sideridis albicolon -0.0042 -2.09 $p<0.05$ Simyra albovenosa 0.0057 2.11 $p<0.05$ Smerinthus ocellata 0.0001 0.12 NSSpaelotis ravida -0.0175 13.65 $p<0.05$		0.0000	o c=	
ochrearia 0.0028 1.41 NS Sesia -0.0037 -3.55 $p<0.05$ bembeciformis -0.0081 -2.11 $p<0.05$ Setina irrorella -0.0081 -2.11 $p<0.05$ Shargacucullia -0.0007 -0.18 NS S. verbasci -0.0031 -2.86 $p<0.05$ Sideridis -0.0042 -2.09 $p<0.05$ Simyra - - - albovenosa 0.0057 2.11 $p<0.05$ Smerinthus - - - ocellata 0.0001 0.12 NS Spaelotis ravida -0.0175 13.65 $p<0.05$		-0.0098	-3.07	p<0.05
Sesia -0.0037 -3.55 $p<0.05$ bembeciformis -0.0081 -2.11 $p<0.05$ Setina irrorella -0.0081 -2.11 $p<0.05$ Shargacucullia -0.0007 -0.18 NS lychnitis -0.0031 -2.86 $p<0.05$ Sideridis -0.0042 -2.09 $p<0.05$ Sideridis -0.0057 2.11 $p<0.05$ Simyra - - - albovenosa 0.0057 2.11 $p<0.05$ Smerinthus - - - ocellata 0.0001 0.12 NS Spaelotis ravida -0.0175 13.65 $p<0.05$		0.0028	1 4 1	NS
bembeciformis-0.0037-3.55 $p<0.05$ Setina irrorella-0.0081-2.11 $p<0.05$ Shargacucullia lychnitis-0.0007-0.18NSS. verbasci-0.0031-2.86 $p<0.05$ Sideridis albicolon-0.0042-2.09 $p<0.05$ Simyra albovenosa0.00572.11 $p<0.05$ Smerinthus ocellata0.00010.12NSSpaelotis ravida-0.017513.65 $p<0.05$		0.0020		
Setina irrorella -0.0081 -2.11 $p<0.05$ Shargacucullia lychnitis -0.0007 -0.18 NS S. verbasci -0.0031 -2.86 $p<0.05$ Sideridis albicolon -0.0042 -2.09 $p<0.05$ Simyra albovenosa 0.0057 2.11 $p<0.05$ Smerinthus ocellata 0.0001 0.12 NS Spaelotis ravida -0.0175 13.65 $p<0.05$		-0.0037	-3.55	p<0.05
Shargacucullia lychnitis -0.0007 -0.18 NS S. verbasci -0.0031 -2.86 $p<0.05$ Sideridis -0.0042 -2.09 $p<0.05$ Simyra -0.0057 2.11 $p<0.05$ Smerinthus 0.0057 2.11 $p<0.05$ Spaelotis ravida -0.0175 13.65 $p<0.05$	Setina irrorella	-0.0081	-2.11	
S. verbasci -0.0031 -2.86 $p<0.05$ Sideridis -0.0042 -2.09 $p<0.05$ Simyra -0.0042 -2.09 $p<0.05$ Simyra -0.0057 2.11 $p<0.05$ Smerinthus 0.0057 2.11 $p<0.05$ Spaelotis ravida 0.0001 0.12 NS Spaelotis ravida -0.0175 13.65 $p<0.05$	Shargacucullia			
Sideridis albicolon-0.0042-2.09 $p<0.05$ Simyra albovenosa0.00572.11 $p<0.05$ Smerinthus ocellata0.00010.12NSSpaelotis ravida-0.017513.65 $p<0.05$ Spargania	lychnitis		-0.18	NS
albicolon -0.0042 -2.09 $p<0.05$ Simyra 2.11 $p<0.05$ albovenosa 0.0057 2.11 $p<0.05$ Smerinthus 0.0001 0.12 NS ocellata -0.0175 13.65 $p<0.05$ Spaelotis ravida -0.0175 13.65 $p<0.05$		-0.0031	-2.86	p<0.05
Simyra albovenosa0.00572.11p<0.05Smerinthus ocellata0.00010.12NSSpaelotis ravida-0.017513.65p<0.05		0.0010	0.00	
albovenosa 0.0057 2.11 p<0.05 Smerinthus 0.0001 0.12 NS ocellata 0.0001 0.12 NS Spaelotis ravida -0.0175 13.65 p<0.05		-0.0042	-2.09	p<0.05
Smerinthus ocellata0.00010.12NSSpaelotis ravida-0.017513.65p<0.05	-	0.0057	2 1 1	D<0.05
ocellata 0.0001 0.12 NS Spaelotis ravida -0.0175 13.65 p<0.05		0.0007	<u> </u>	μ το.00
Spargania		0.0001	0.12	NS
Spargania			-	
		-0.0175	13.65	p<0.05
iuciuala -0.0037 -0.94 NS		0.0027	0.04	NC
	เนติเนลเล	-0.0037	-0.94	112

Sphinx ligustri	0.0011	0.81	NS	Watsonalla binaria	0.
Spilosoma Iubricipeda	0.0010	0.38	NS	W. cultraria	0.
S. luteum	0.0059	2.40	p<0.05	Xanthia aurago	0.
S. urticae	-0.0021	-1.05	NS	X. citrago	0
Standfussiana	0.0021			X. gilvago	-0
lucernea	-0.0056	-3.63	p<0.05	X. icteritia	-0
Stauropus fagi	0.0045	3.16	p<0.05	X. ocellaris	-0
Stilbia anomala	-0.0091	-7.37	p<0.05	X. togata	0.
Syngrapha interrogationis	-0.0016	-1.29	NS	Xanthorhoe	0.
Tethea ocularis	0.0040	3.05	p<0.05	X. decoloraria	
T. or	-0.0019	-1.57	NS		-0
Tetheella				X. designata	0
fluctuosa	0.0015	0.73	NS	X. ferrugata	-0
Thalpophila matura	-0.0077	-6.12	p<0.05	X. fluctuata	-0
Thera britannica	0.0152	13.16	p<0.05	X. montanata	-0
T. cognata	-0.0034	-1.92	NS	X. quadrifasiata	0
T. cupressata	0.0248	8.24	p<0.05	X. spadicearia	-0
T. firmata	0.0033	3.43	p<0.05	Xestia agathina	0.
T. juniperata	0.0001	0.08	NS	X. alpicola	-0
T. obeliscata	-0.0014	-1.07	NS	X. ashworthii	-0
T. primaria	-0.0074	-8.38	p<0.05	X. baja	-0
Tholera cespitis	-0.0070	-8.37	p<0.05	X. castanea	-0
T. decimalis	-0.0081	-8.20	p<0.05	X. c-nigrum	0
Thumatha senex	-0.0013	-1.09	NS	X. ditrapezium	-0
	0.0002	0.14	NS	X. rhomboidea	0
Thyatira batis				X. sexstrigata	-0
Timandra comae Trichiura	0.0063	3.26	p<0.05	X. triangulum	0
crataegi	-0.0087	-8.84	p<0.05	X. xanthographa	0
Trichopteryx				Xylena exsoleta	-0
carpinata	0.0032	3.27	p<0.05	X. vetusta	0
T. polycommata	-0.0043	-1.96	NS	Xylocampa	
Triphosa dubitata	-0.0049	-6.07	p<0.05	areola Zanclognatha	0
Trisateles	-0.0049	-0.07	μ<0.05	tarsipennalis	0
emortualis	0.0115	2.27	p<0.05	Zeuzera pyrina	0
Tyria jacobaeae	0.0044	2.14	p<0.05	Zygaena	
Tyta luctuosa	-0.0011	-0.85	NS	filipendulae	-0
Venusia				Z. lonicerae	-0
cambrica	-0.0020	-1.56	NS	Z.purpuralis	-0
				Zygaena trifolii	-0

Watsonalla binaria	0.0033	2.40	p<0.05
W. cultraria	0.0000	0.12	NS
	0.0069	5.64	p<0.05
Xanthia aurago			
X. citrago	0.0022	2.41	p<0.05
X. gilvago	-0.0051	-5.90	p<0.05
X. icteritia	-0.0034	-2.94	p<0.05
X. ocellaris	-0.0068	-2.49	p<0.05
X. togata	0.0005	0.54	NS
Xanthorhoe biriviata	0.0029	1.03	NS
X. decoloraria	-0.0100	-6.06	p<0.05
X. designata	0.0123	7.97	p<0.05
X. ferrugata	-0.0108	-8.47	p<0.05
X. fluctuata	-0.0060	-2.41	p<0.05
X. montanata	-0.0134	-2.48	p<0.05
X. quadrifasiata	0.0046	3.01	p<0.05
X. spadicearia	-0.0001	-0.08	NS
Xestia agathina	0.0000	0.00	NS
X. alpicola	-0.0021	-0.75	NS
X. ashworthii	-0.0096	-1.89	NS
X. baja	-0.0085	-7.17	p<0.05
X. castanea	-0.0032	-3.15	p<0.05
X. c-nigrum	0.0062	3.28	p<0.05
X. ditrapezium	-0.0024	-2.22	p<0.05
X. rhomboidea	0.0011	0.89	NS
X. sexstrigata	-0.0023	-1.88	NS
X. triangulum	0.0041	2.14	p<0.05
X. xanthographa	0.0040	1.56	NS
Xylena exsoleta	-0.0045	-5.59	p<0.05
X. vetusta	0.0050	5.53	p<0.05
Xylocampa		4 70	0.05
areola Zapalagnatha	0.0062	4.70	p<0.05
Zanclognatha tarsipennalis	0.0104	7.05	p<0.05
Zeuzera pyrina	0.0020	1.53	NS
Zygaena			
filipendulae	-0.0018	-1.45	NS
Z. lonicerae	-0.0035	-2.86	p<0.05
Z.purpuralis	-0.0164	-1.43	NS
Zygaena trifolii	-0.0097	-8.67	p<0.05

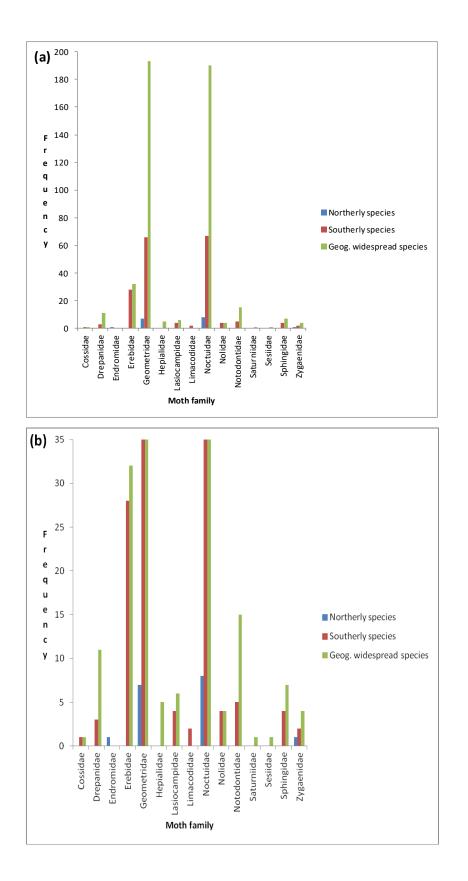


Fig. A3.1 The frequency (a), and proportion (b), of moths in different distribution groupings (northerly, southerly, geographically widespread) by taxonomic family.

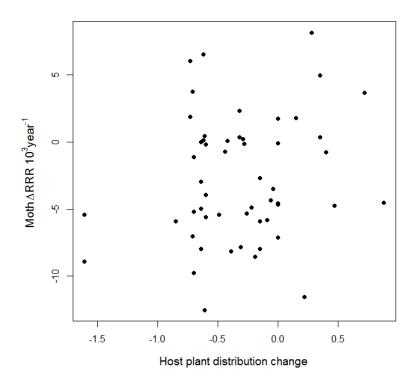
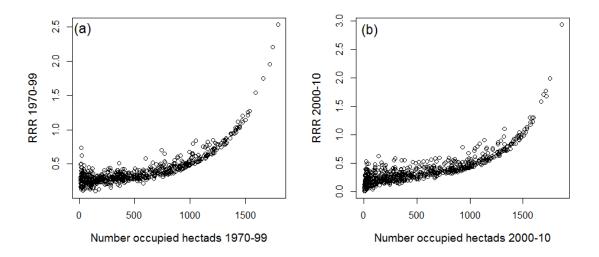
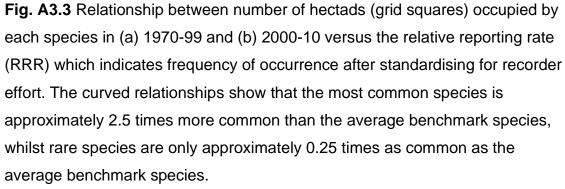


Fig. A3.2 Change in the frequency of occurrence of monophagous moth species 1970-99 versus 2000-10 in relation to change in host plant distribution between 1970 and 1987 (with outliers removed as per main text).





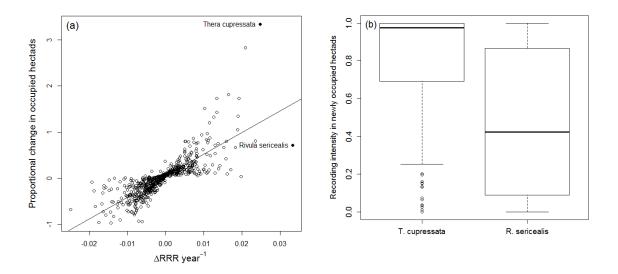


Fig. A3.4 Change in moth frequency of occurrence versus proportional change in hectads. Panel (a) shows the relationship between change in moth frequency of occurrence (Δ RRR) using the Frescalo method which controls for spatiotemporal variation in recorder effort versus proportional change in hectads (grid squares) listed as occupied. The time periods under consideration are 1970-99 versus 2000-10. The correlation is significant ($F_{1,161} = 1301$, p < 0.001). We select two outliers from this relationship, both with large positive RRR trends, to demonstrate how the Frescalo method accounts for variation in recorder effort (shown in panel (b)). Panel (a) suggests that the species T. cupressata has a greater increase in records than expected from changes in frequency relative to benchmark species (which inform on recorder effort). Hence, the large increase in number of records is partly due to increased recording effort in these locations in the latter period. In contrast, R. sericealis has fewer records than expected which indicates relatively less recording effort focussed in areas where this species occurs. Panel (b) shows the recording intensity in hectads newly occupied by the two moths in the latter period. Recording intensity is calculated as the proportion of benchmarks species recorded in a hectad. Hence, this confirms that T. cupressata has expanded into well recorded areas, whilst R. sericealis has expanded into poorly recorded areas.

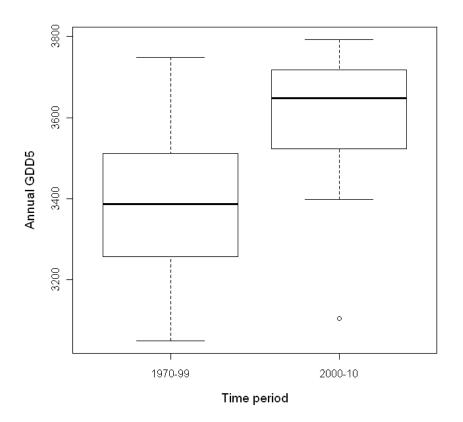


Fig. A3.5 Annual accumulated temperatures (growing degree days > 5°C; GDD5; calculated from daily mean temperature data from the UK Met Office Central England Temperature dataset; http://www.metoffice.gov.uk/hadobs/ hadcet/) during the two recording periods. The box and whisker plots show median annual GDD5, upper and lower quartiles and 95th percentiles. Annual GDD5 values were significantly higher in the latter period (t-test: t = 2.84, df = 17.71, p = 0.01).

Appendix 4: Supporting Information for Chapter 4: Using citizen science butterfly counts to predict species population trends

Year	Period
2010	24 th July – 1 st August
2011	16 th July – 7 th August
2012	14 th July – 5 th August
2013	20 th July – 11 th August
2014	19 th July – 10 th August
2015	17 th July – 9 th August

Table A4.1 Official Big Butterfly Count period for each year. The period

 changes each year to include weekends in order to maximise participation.

Table A4.2 Common UK butterflies counted by the Big Butterfly Count (BBC) and considered in Chapter 4. Voltinism refers to the assumed species' seasonal pattern, where U and B represent univoltine and bivoltine species, respectively, and S represents species with more than two broods or a complicated seasonal pattern (where a spline rather than phenomenological generalised abundance index (GAI) was fitted to the UKBMS data). nSq is the number of 1km squares in which the species was recorded by the BBC in the period 2010-2015.

Common name	Species	Species	Voltinism	nSq
Marbled White	Melanargia galathea	MW	U	7818
Large Skipper	Ochlodes sylvanus	LS	U	12226
Ringlet	Aphantopus	R	U	25351
Meadow Brown	Maniola jurtina	MB	U	49277
Gatekeeper	Pyronia tithonus	G	U	65175
Brimstone	Gonepteryx rhamni	В	В	13673
Holly Blue	Celastrina argiolus	HB	В	15120
Common Blue	Polyommatus icarus	СВ	В	24033
Green-veined White	Pieris napi	GvW	В	28187
Large White	Pieris brassicae	LW	В	75801
Small White	Pieris rapae	SmW	В	81553
Small Copper	Lycaena phlaeas	SC	S	11584
Painted Lady	Vanessa cardui	PL	S	13867
Speckled Wood	Pararge aegeria	SpW	S	28010
Comma	Polygonia c-album	С	S	34952
Red Admiral	Vanessa atalanta	RA	S	45018
Small Tortoiseshell	Aglais urticae	ST	S	47904
Peacock	Aglais io	Ρ	S	56907

 Table A4.3 Summary of Big Butterfly Count data 2011-2015.

Year	2011	2012	2013	2014	2015
Number of 15 minute counts	28715	24074	44108	42768	49090
Mean number of counts per location	1.31	1.35	1.48	1.50	1.23
Mean number of species seen per count	4.00	3.24	4.52	4.12	4.01

Table A4.4 Percentage of Big Butterfly Count counts recorded in differenthabitat categories each year.

Location	2011	2012	2013	2014	2015
Field	13.2	18.1	10.2	9.1	11.7
Garden	65.1	54.7	67.3	70.1	65.8
Other rural	10.5	14.6	11.0	10.1	11.1
Other urban	2.4	3.5	4.5	3.5	3.5
Park	3.3	3.9	3.4	3.6	3.6
School	0.8	0.2	0.4	0.3	0.3
Wood	4.6	5.0	3.3	3.3	4.0

Table A4.5 Mean and standard error (SE) of the percentage habitat types(LCM2007) for 1km squares sampled by the UK Butterfly Monitoring Scheme(UKBMS) and Big Butterfly Count (BBC) 2010-2014.

Habitat type	UKBM	1S	BBC		
	Mean	SE	Mean	SE	
Broadleaf woodland	13.77	0.34	7.76	0.04	
Coniferous woodland	4.39	0.25	1.53	0.02	
Arable and Horticulture	27.55	0.54	23.19	0.08	
Improved Grassland	26.38	0.42	24.37	0.06	
Semi-natural grassland	7.90	0.23	4.85	0.03	
Mountain, heath & bog	3.92	0.25	1.20	0.02	
Saltwater	0.36	0.06	0.37	0.01	
Freshwater	1.05	0.09	0.86	0.01	
Coastal	1.62	0.17	1.09	0.02	
Urban & Suburban	9.80	0.38	33.36	0.11	

Table A4.6 Estimated net population change 2011-2014 (log growth rate) from Big Butterfly Count (BBC) and the UK Butterfly Monitoring Scheme (UKBMS), with 95% confidence intervals. Asterisks indicate significant change (p < 0.05).

Common name	BBC		UKBMS		Difference	
Brimstone	0.44 (0.13, 0.76)	*	0.50 (0.41, 0.58)	*	-0.05 (-0.38, 0.27)	
Comma	0.29 (0.14, 0.44)	*	-0.04 (-0.14, 0.06)		0.33 (0.15, 0.51)	*
Common Blue	0.24 (0.03, 0.45)	*	1.14 (1.05, 1.23)	*	-0.90 (-1.13, -0.67)	*
Gatekeeper	0.23 (0.14, 0.32)	*	0.25 (0.21, 0.30)	*	-0.02 (-0.12, 0.08)	
Green-veined White	0.15 (0, 0.29)		0.10 (0.04, 0.17)	*	0.04 (-0.12, 0.2)	
Holly Blue	-0.29 (-0.52, -0.05)	*	-0.72 (-0.83, -0.61)	*	0.44 (0.18, 0.70)	*
Large Skipper	0.98 (0.68, 1.27)	*	0.50 (0.39, 0.62)	*	0.48 (0.16, 0.80)	*
Large White	-0.04 (-0.14, 0.06)		-0.24 (-0.32, -0.16)	*	0.20 (0.07, 0.33)	*
Marbled White	0.56 (0.22, 0.90)	*	0.84 (0.72, 0.96)	*	-0.28 (-0.65, 0.08)	
Meadow Brown	0.60 (0.50, 0.71)	*	0.40 (0.35, 0.45)	*	0.20 (0.09, 0.32)	*
Painted Lady	0.44 (0.11, 0.77)	*	0.61 (0.42, 0.79)	*	-0.17 (-0.55, 0.22)	
Peacock	1.16 (1.02, 1.31)	*	1.06 (0.98, 1.15)	*	0.10 (-0.07, 0.27)	
Red Admiral	-0.30 (-0.42, -0.17)	*	-0.77 (-0.85, -0.69)	*	0.47 (0.32, 0.62)	*
Ringlet	0.58 (0.41, 0.76)	*	0.17 (0.09, 0.26)	*	0.41 (0.21, 0.61)	*
Small Copper	-0.10 (-0.36, 0.15)		-0.43 (-0.53, -0.33)	*	0.32 (0.05, 0.60)	*
Small Tortoiseshell	1.14 (1, 1.28)	*	1.79 (1.65, 1.92)	*	-0.65 (-0.84, -0.45)	*
Small White	0.03 (-0.06, 0.11)		-0.13 (-0.21, -0.05)	*	0.15 (0.04, 0.27)	*
Speckled Wood	-0.34 (-0.49, -0.19)	*	-0.26 (-0.31, -0.20)	*	-0.08 (-0.25, 0.08)	

Table A4.7 Overdispersion estimated by the ratio of the Pearson Chi-squaredstatistic to its degrees of freedom. UKBMS = UK Butterfly Monitoring Scheme,BBC = Big Butterfly Count.

Species	UKBMS	BBC
Brimstone	2.48	1.40
Comma	1.55	1.35
Common Blue	10.14	2.26
Gatekeeper	14.01	3.23
Green-veined White	7.27	2.38
Holly Blue	0.89	1.41
Large Skipper	3.27	2.65
Large White	6.18	2.95
Marbled White	8.36	3.63
Meadow Brown	27.33	4.06
Painted Lady	0.74	1.81
Peacock	6.80	4.06
Red Admiral	2.00	1.65
Ringlet	11.87	3.07
Small Copper	2.30	1.78
Small Tortoiseshell	3.18	2.79
Small White	7.99	2.68
Speckled Wood	3.59	1.64

Table A4.8 Residual deviance, degrees of freedom (df) and associated ratios from fitting a Poisson and negative-binomial GLM where the response is the total Big Butterfly Count count per day and measures of effort (log number of counts made) and phenology (from the corresponding GAI curve) as covariates.

		Residual de	eviance	Rati	io
Species	df	Poisson	NegBin	Poisson	NegBin
Brimstone	216	2362.6	253.5	10.9	1.2
Comma	230	1602.4	282.7	7.0	1.2
Common Blue	230	7362	261.3	32.0	1.1
Gatekeeper	230	11380	283.7	49.5	1.2
Green-veined White	222	4452.6	285	20.1	1.3
Holly Blue	215	1559.3	274.3	7.3	1.3
Large Skipper	207	3019.7	240.6	14.6	1.2
Large White	232	9695.7	263.9	41.8	1.1
Marbled White	203	5598.1	230.9	27.6	1.1
Meadow Brown	234	31229.3	266	133.5	1.1
Painted Lady	223	2306.8	256.3	10.3	1.1
Peacock	229	35926.9	258	156.9	1.1
Red Admiral	233	5711	270.7	24.5	1.2
Ringlet	229	9034.6	264.1	39.5	1.2
Small Copper	220	2103.3	264.6	9.6	1.2
Small Tortoiseshell	234	13983.2	255.5	59.8	1.1
Small White	235	5484.7	327.5	23.3	1.4
Speckled Wood	233	2782.7	279	11.9	1.2

Table A4.9 Relative importance (Grömping 2006) of Big Butterfly Count (BBC) and weather for each species. The same conclusions were obtained by considering all possible regressions based on AIC.

Species	BBC	Weather
Small Tortoiseshell	0.99	0.01
Large White	0.88	0.12
Gatekeeper	0.84	0.16
Speckled Wood	0.84	0.16
Small White	0.83	0.17
Brimstone	0.71	0.29
Meadow Brown	0.66	0.34
Comma	0.52	0.48
Ringlet	0.42	0.58
Common Blue	0.41	0.59
Painted Lady	0.24	0.76

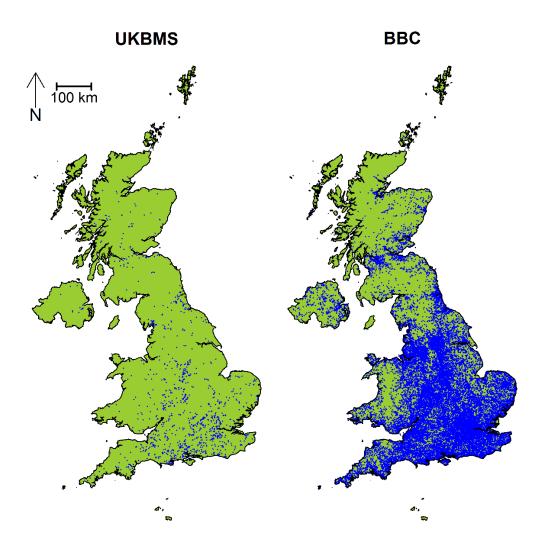


Fig. A4.1 Locations of UK Butterfly Monitoring Scheme (UKBMS= 1,462 transects) and Big Butterfly Count (BBC= 65,197 1km squares surveyed) counts from 2011-2014 (shown in blue).

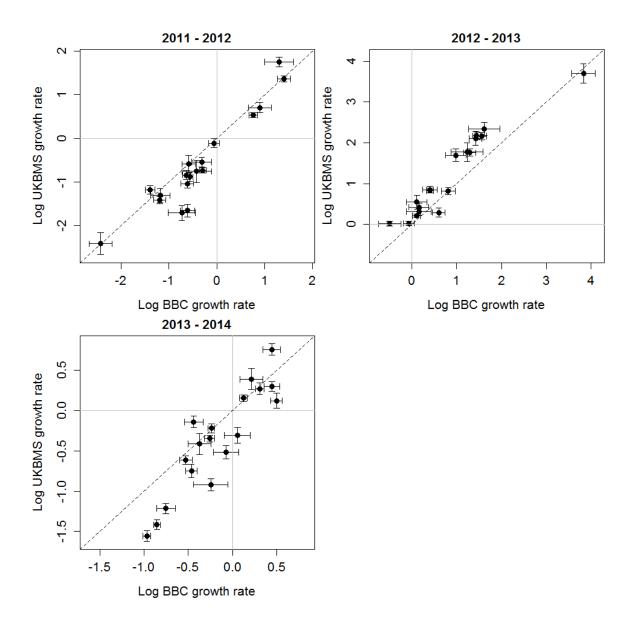
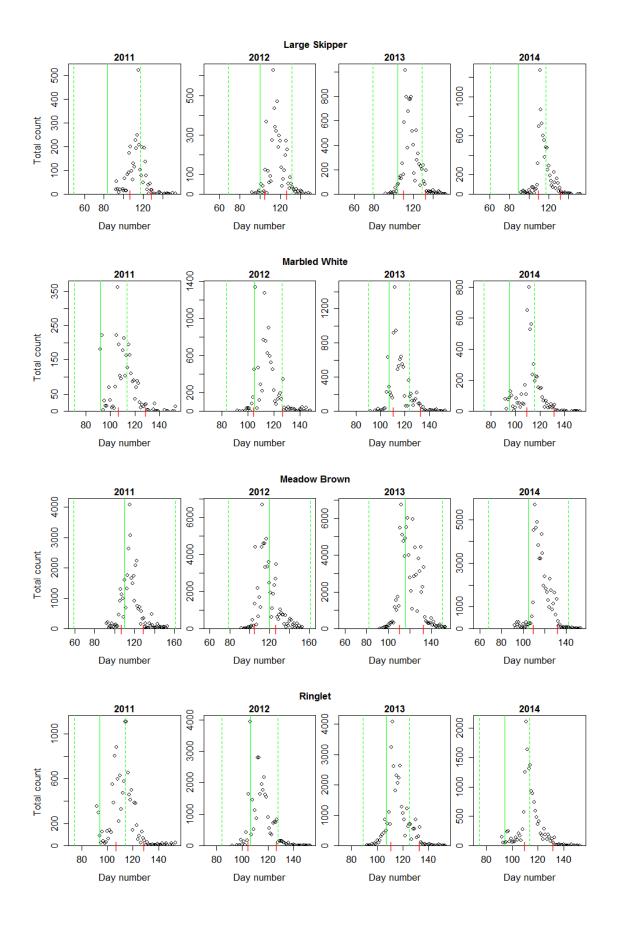
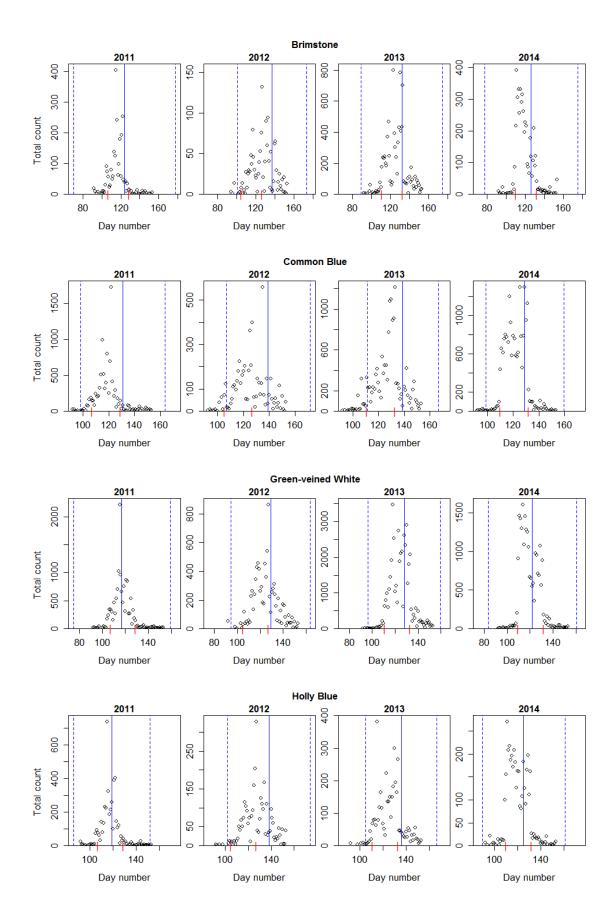


Fig. A4.2 Comparison of estimated year-to-year log growth rates from the Big Butterfly Count (BBC) and UK Butterfly Monitoring Scheme (UKBMS) for 2011 to 2014. Error bars represent 95% confidence intervals. Solid grey lines represent zero growth and dashed lines represents equal growth rates from the BBC and UKBMS.





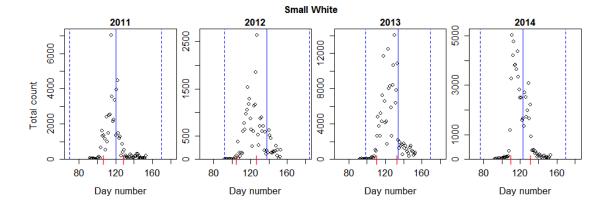


Fig. A4.3 Total counts of nine species from Big Butterfly Count data per day in each year, where day 1 is 1st April (vertical lines, mean flight dates estimated from a GAI; dashed lines, twice SD; green = 1st brood ; blue = 2nd brood; red lines on x-axis show the official BBC survey period for each year).

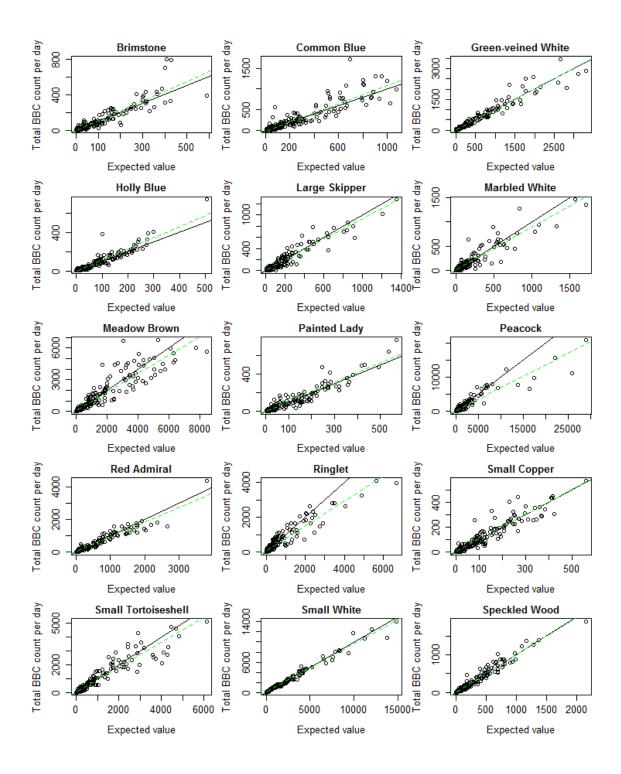


Fig. A4.4 Total counts for each butterfly species from Big Butterfly Count (BBC) data per day versus the expected value from a negative-binomial GLM in which the response variable is the total count per day and measures of effort (log number of counts made) and phenology (from the corresponding GAI curve) are covariates (black line, equal expected values and total counts; green dashed line, fitted linear regression through the points).

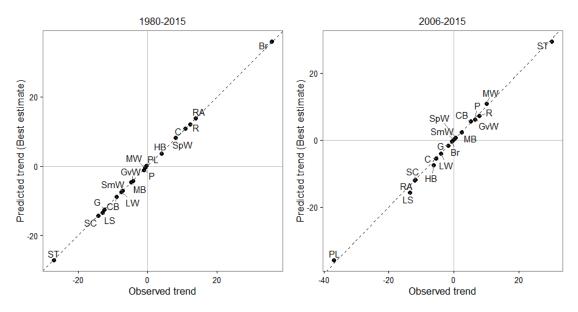


Fig. A4.5 Comparison of linear trends in relative abundance from the GAI index, where 2015 is from observed data or predicted from the model with the best estimate of the index in 2015 (solid grey lines, 0% change in relative abundance; dashed line, equal population trends). Abbreviations are for species common names (Table A4.2).

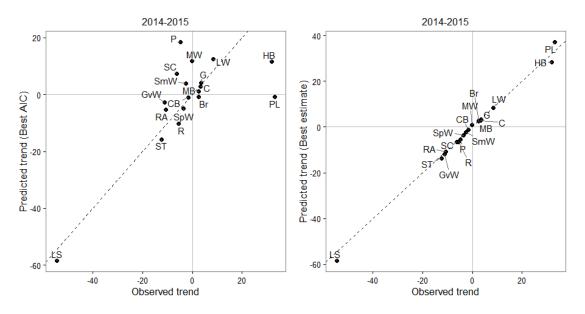


Fig. A4.6 Comparison of percentage changes in relative abundance 2014-2015, where 2015 is from observed data or predicted from the model with the best estimate of the index in 2015 (solid grey lines, 0% change in relative abundance; dashed line, equal population trends). Abbreviations are for species common names (Table A4.2).

Appendix 5: Supporting Information for Chapter 5: Insect population trends and the IUCN Red List process

Table A5.1 UK butterfly species' 10-year population trends over six overlapping date periods, and the median (MT), lower (LQ) and upper quartile (UQ) values of these trends. Shading indicates Red List classification against IUCN Criterion A2 (reduction in population size) thresholds: dark shading = Critically Endangered (population decrease \geq 80%), intermediate shading = Endangered (population decrease \geq 80%), is shading = Vulnerable (population decrease \geq 30%). * common migrants in the UK.

Taxon name	2001- 2010	2002- 2011	2003- 2012	2004- 2013	2005- 2014	2006- 2015	LQ	МТ	UQ
Aglais io	-9	-17	-30	-6	21	33	-15	-7.5	14.25
Aglais urticae	-72	-75	-77	-28	146	216	-74.25	-50	102.5
Anthocharis cardamines	19	36	59	32	59	66	33	47.5	59
Apatura iris	-15	-24	-55	-19	-35	-32	-34.25	-28	-20.25
Aphantopus hyperantus	51	38	14	38	72	64	38	44.5	60.75
Argynnis adippe	-69	-64	-81	-74	0	46	-72.75	-66.5	-16
Argynnis aglaja	99	88	12	30	18	6	13.5	24	73.5
Argynnis paphia	137	80	-2	-3	6	8	0	7	62
Aricia agestis	53	44	-35	-34	-11	8	-28.25	-1.5	35
Aricia artaxerxes	-44	-20	-27	-9	6	19	-25.25	-14.5	2.25
Boloria euphrosyne	-41	-11	10	23	45	87	-5.75	16.5	39.5
Boloria selene	16	40	17	6	3	5	5.25	11	16.75
Callophrys rubi	-12	-15	-26	-40	-34	-2	-32	-20.5	-12.75
Celastrina argiolus	-29	-28	-23	-60	-61	-31	-52.75	-30	-28.25
Coenonympha pamphilus	5	7	-22	0	18	27	1.25	6	15.25
Coenonympha tullia	171	130	-6	-60	-49	-56	-54.25	-27.5	96
Colias croceus*	-59	-97	-98	-88	-57	-32	-94.75	-73.5	-57.5
Cupido minimus	37	83	0	-25	-27	-19	-23.5	-9.5	27.75
Erebia aethiops	-50	-44	-5	40	24	23	-34.25	9	23.75
Erynnis tages	3	31	49	57	69	90	35.5	53	66
Euphydryas aurinia	4	42	-52	-66	-64	-62	-63.5	-57	-10
Favonius quercus	-9	-15	-8	-25	-10	-17	-16.5	-12.5	-9.25
Gonepteryx rhamni	3	-5	-30	-30	-1	37	-23.75	-3	2
Hamearis lucina	-71	-51	-58	24	67	80	-56.25	-13.5	56.25
Hesperia comma	-33	-19	-55	-23	12	53	-30.5	-21	4.25
Hipparchia semele	26	43	18	25	10	-7	12	21.5	25.75
Lasiommata megera	-57	-62	-67	-56	-25	-17	-60.75	-56.5	-32.75
Leptidea sinapis	-61	-55	-59	-56	-18	41	-58.25	-55.5	-27.25
Limenitis camilla	80	21	-44	-50	-45	-43	-44.75	-43.5	5
Lycaena phlaeas	42	30	-16	-19	-19	-46	-19	-17.5	18.5

Maniola jurtina	-23	-30	-31	-25	-15	13	-28.75	-24	-17
Melanargia galathea	-17	-16	-28	-16	25	62	-16.75	-16	14.75
Melitaea athalia	-72	-72	-76	-82	-79	-84	-81.25	-77.5	-73
Ochlodes sylvanus	-14	3	-18	-16	23	41	-15.5	-5.5	18
Pararge aegeria	33	12	-20	-9	4	-5	-8	-0.5	10
Phengaris arion	23	-7	4	-11	-20	25	-10	-1.5	18.25
Pieris brassicae	54	8	-40	-1	-28	-20	-26	-10.5	5.75
Pieris napi	21	20	-16	26	72	38	20.25	23.5	35
Pieris rapae	-5	-14	-55	10	9	-1	-11.75	-3	6.5
Plebejus argus	-30	-15	-40	2	-9	-6	-26.25	-12	-6.75
Polygonia c-album	11	-6	-39	-25	-28	-26	-27.5	-25.5	-10.75
Polyommatus bellargus	99	-1	-46	-23	-43	-46	-45.25	-33	-6.5
Polyommatus coridon	21	15	13	77	55	66	16.5	38	63.25
Polyommatus icarus	16	-11	-52	-27	1	30	-23	-5	12.25
Pyrgus malvae	-11	23	63	12	0	-5	-3.75	6	20.25
Pyronia tithonus	-37	-46	-62	-67	-44	-6	-58	-45	-38.75
Satyrium pruni	334	319	-40	-89	-87	-78	-84.75	-59	229.2 5
Satyrium w-album	-26	-22	-69	-74	-77	-74	-74	-71.5	-36.75
Thecla betulae	-53	-50	-75	-75	-58	-5	-70.75	-55.5	-50.75
Thymelicus acteon	-93	-92	-88	-53	39	200	-91	-70.5	16
Thymelicus lineola	-90	-92	-91	-81	-66	16	-90.75	-85.5	-69.75
Thymelicus sylvestris	-71	-66	-66	-31	27	121	-66	-48.5	12.5
Vanessa atalanta*	-27	-13	-25	-14	-40	-45	-36.75	-26	-16.75
Vanessa cardui*	-40	-84	-94	-89	-84	-88	-88.75	-86	-84

Table A5.2 UK macro-moth 10-year population trends for the most recent 10year period (t) for each of 431 species, and preceding 10-year periods each starting one year earlier than the previous (t-1, t-2, t-3, t-4) and the Red List categories appropriate to each trend according to IUCN Criterion A2 (reduction in population size). Trend values given in bold indicate statistically significant trends at p < 0.05. These classifications do not represent the final outcomes of a full Red List process.

Taxon	Period	t	Period	t-1	Period	t-2	Period	t-3	Period t	-4
Abraxas grossulariata	-47.8		-75.0	EN	-79.0	EN	-63.8		-20.6	
Abraxas sylvata	23.2		50.8		116.0		41.2		2.8	
Abrostola tripartita	-8.4		0.3		-21.3		-35.9		0.4	
Abrostola triplasia	39.9		7.0		-21.2		-58.4		-61.5	
Acasis viretata	-28.0		6.4		22.2		15.7		-16.6	
Achlya flavicornis	-40.8		10.6		57.6		30.1		13.0	
Acronicta alni	-51.3		-75.5	EN	-78.4		-19.6		34.1	
Acronicta psi	-39.5		-35.6		-55.9		-68.6	EN	-66.9	EN
Acronicta rumicis	-69.9	EN	-58.3	EN	-57.9	EN	-54.7		-11.3	
Aethalura punctulata	-42.8		-25.9		-21.8		23.9		118.9	
Agriopis leucophaearia	-45.8		-4.9		100.8		301.0		337.4	
Agrochola circellaris	23.8		67.0		76.9		6.4		109.4	
Agrochola helvola	-18.0		-5.6		35.5		-23.2		-0.6	
Agrochola litura	31.9		25.8		30.6		-26.5		-3.5	
Agrochola lota	7.0		14.1		-3.4		-0.4		15.6	
Agrochola lychnidis	181.6		70.3		-10.3		-38.3		-21.1	
Agrochola macilenta	4.3		-10.6		12.5		6.5		59.9	
Agrotis clavis	15.4		10.0		1.2		33.6		35.7	
Agrotis exclamationis	-15.8		-39.8		-52.7		-21.5		10.9	
Agrotis puta	-55.9		-48.2		-51.5		-51.0		1.5	
Agrotis segetum	-40.2		-62.1		-72.4		-52.0		105.3	
Agrotis vestigialis	11.3		73.2		-20.5		81.0		43.5	
Alcis jubata	-52.0		5.1		31.3		38.5		15.6	
Alcis repandata	-1.5		3.1		10.7		11.4		27.8	
Allophyes oxyacanthae	8.8		45.0		49.4		91.4		92.6	
Alsophila aescularia	1.3		10.7		0.1		11.8		12.3	
Amphipoea crinanensis	14.3		-37.3		-49.7		-1.4		91.6	
Amphipoea oculea	-25.1		-9.3		-22.9		-13.1		36.2	
Amphipyra berbera	-26.5		138.4		327.4		460.1		605.4	
Amphipyra pyramidea	-63.7		-75.0	EN	-74.1	EN	-56.3		-24.7	
Amphipyra tragopoginis	-27.4		-52.6		-60.2	EN	-61.9	EN	-46.5	VU
Anaplectoides prasina	-3.7		-31.0		-21.3		-36.7		-4.7	
Anarta trifolii	-46.8		-82.4		-86.8		-27.0		-43.2	
Anorthoa munda	5.5		46.7		57.4		110.0		45.0	
Anticlea derivata	-18.2		-13.8		-33.7		1.7		38.7	
Antitype chi	209.6		65.1		56.9		11.5		-29.9	
Apamea anceps	-67.2		-54.0		-53.2		-35.1		55.6	
Apamea crenata	-26.6		6.0		-24.4		-17.3		25.0	
Apamea lithoxylaea	20.4		50.1		3.8		10.5		57.1	

Apamea monoglypha	15.7		2.1		-40.8		-26.0		-0.9	
Apamea remissa	2.4		28.8		-14.8		-27.9		29.4	
Apamea scolopacina	155.0		112.1		61.6		35.1		15.5	
Apamea sordens	-70.6	EN	-38.8		-22.0		11.1		123.9	
Apeira syringaria	-49.4		-58.0		-59.6		-65.5	EN	-29.9	
Aplocera efformata	-36.4		-37.3		-44.0		-22.0		38.7	
Aplocera plagiata	-69.9		-51.7		-20.2		-31.8		-37.7	
Apocheima hispidaria	-1.7		181.8		414.3		198.9		52.9	
Aporophyla	160.8		125.7		23.4		-73.8	EN	-62.1	
lueneburgensis									/	
Aporophyla lutulenta	-6.4		-18.7		-38.3		-25.9		58.4	
Aporophyla nigra	-40.3		-43.7		-47.1	VU	-47.8	VU	-12.6	
Apterogenum ypsillon	-85.3		-59.4		52.2		92.6		560.0	
Arctia caja	60.8	~ ~	44.6	~ ~	-7.2	~ ~	-19.9		-42.0	
Aspitates ochrearia	-90.9	CR	-96.7	CR	-87.1	CR	-83.0	CR	-67.0	EN
Asteroscopus sphinx	-3.0		10.9		87.2		113.7		126.2	
Asthena albulata	-40.8		-57.7		-70.2	EN	-56.0		-5.3	
Atethmia centrago	-25.3		-18.1		33.5		5.3		54.5	
Autographa bractea	-8.9		33.4		30.0		-15.6		-45.9	
Autographa jota	155.8		245.1		175.7		49.7		5.6	
Autographa pulchrina	84.3		121.4		121.3		26.0		-14.0	
Axylia putris	10.4		-19.1	00	-40.2		-40.1		-24.9	
Bena bicolorana	-73.6		-88.1	CR	-1.6		85.3		28.6	
Biston betularia	-78.2	EN	-58.6	EN	-56.6	EN	-55.4	EN	-45.4	VU
Biston strataria	19.9		58.1		46.2		53.0		69.5	
Brachylomia viminalis	59.4		17.6		13.6		28.8		29.0	
Bryophila domestica	-4.4		-24.0		-43.0		-58.4	EN	-64.2	EN
Bupalus piniaria	166.1		-4.6		-42.7		-31.0		-24.1	
Cabera exanthemata	3.5		33.9		39.0		5.5	141	48.2	
Cabera pusaria	20.8		16.4		-19.4		-39.4	VU	-30.4	
Calliteara pudibunda	-14.4		-23.9		-43.5		-24.9		31.0	
Campaea margaritata	27.0	1/11	57.8		43.7		21.9		33.4	
Camptogramma bilineata	-37.8	VU	-37.4		-32.9		-26.8		6.4	
Caradrina clavipalpis	-85.5	CR	-92.7	CR	-93.3	CR	-84.5	CR	-75.8	EN
Caradrina morpheus	70.7		36.9		0.6		-6.1		-7.0	
Catarhoe rubidata	-91.9	CR	-85.8	CR	-60.9	EN	-36.6		118.9	
Catocala nupta	41.7		60.1		122.2		54.6		146.3	
Celaena haworthii	198.2		224.7		275.7		27.9		21.7	
Ceramica pisi	-49.4		-58.0		-70.4	EN	-57.2		-41.6	
Cerapteryx graminis	-41.0		28.5		83.8		31.5		75.6	
Cerastis leucographa	69.5		256.4		357.0		118.7		-0.5	
Cerastis rubricosa	-17.5		-12.0		-42.7		4.1		9.2	
Charanyca trigrammica	4.0		4.4		2.6		116.6		96.1	
Chesias legatella	-40.9		-51.6		-34.7		-59.8		-17.1	
Chesias rufata	58.7		15.9		69.2		-6.5		-73.1	
Chiasmia clathrata	-40.9		-43.0		-64.8	EN	-68.0	EN	-51.4	
Chloroclysta miata	-2.1		52.5		70.8		21.9		40.1	
Chloroclysta siterata	-6.3		29.6		54.1		37.8		63.2	
Chloroclystis v-ata	4.0		37.1		1.5		18.1		104.3	
Cidaria fulvata	-11.6		-6.7		-18.4		-51.3		-30.1	
Cilix glaucata	-21.8		-21.0		-44.1	VU	-52.1	EN	-32.1	
Cirrhia icteritia	-27.2		-2.7		24.2		27.2		63.1	

Cleorodes lichenaria	6.7		0.3		-26.8		-28.4		-11.9
Clostera curtula	-32.2		6.7		22.6		79.3		73.5
Coenobia rufa	-21.1		-35.5		-73.5	EN	-84.4	CR	-68.0
Coenotephria salicata	-19.9		24.2		9.0		-31.3		14.8
Colocasia coryli	-21.5		5.3		-30.1		-20.3		6.1
Colostygia pectinataria	-7.2		4.2		40.9		48.2		41.5
Colotois pennaria	-1.3		23.3		11.7		28.6		23.7
Comibaena bajularia	-82.1	CR	-74.2		-71.6		-43.2		214.3
Conistra ligula	36.8	-	44.9		27.3		78.6		124.3
Conistra rubiginea	-43.7		73.6		17.1		-3.6		37.3
Conistra vaccinii	56.2		46.9		44.7		60.0		61.4
Cosmia affinis	14.4		76.1		58.1		51.1		97.9
Cosmia pyralina	-40.5		-11.6		-14.5		7.0		154.3
Cosmia trapezina	-40.4		-2.0		50.8		22.2		77.1
Cosmorhoe ocellata	6.8		-6.4		-35.9		-51.0	EN	-29.1
Craniophora ligustri	26.7		11.8		-19.6		-46.9		-30.5
Crocallis elinguaria	-21.4		-6.3		-7.9		2.8		19.7
Cybosia mesomella	45.6		24.1		-3.0		2.4		-0.7
Cyclophora albipunctata	-34.7		-45.5		-70.0	EN	-39.6		-22.4
Cyclophora linearia	-74.2		-27.0		-53.1	213	-58.9		-20.5
Cyclophora punctaria	-60.2	EN	-44.0		-62.8	EN	-66.8	EN	-40.1
Cymatophorina diluta	-98.5	CR	-96.9	CR	-91.5	CR	-47.7		-10.0
Dasypolia templi	178.5	ÖN	413.0	ÖN	476.6	ÖN	82.5		-28.8
Deilephila elpenor	3.6		-37.5		-70.7	EN	-48.5	VU	-39.8
Deileptenia ribeata	-24.9		-12.9		-29.0	213	-54.6	EN	-23.4
Deltote pygarga	680.5		255.0		78.8		32.2	<u> </u>	79.5
Deltote uncula	9.7		1.5		25.8		-21.8		23.4
Denticucullus pygmina	16.0		66.0		93.7		44.9		66.8
Diachrysia chrysitis	10.5		20.3		40.3		13.5		6.1
Diacrisia sannio	26.4		5.4		-39.3		-35.0		-49.9
Diaphora mendica	-37.2		-32.1		-13.1		89.9		126.8
Diarsia brunnea	32.5		20.6		5.5		11.4		28.2
Diarsia dahlii	68.8		42.8		38.0		-0.9		23.9
Diarsia mendica	61.3		18.4		-6.8		-10.4		-14.7
Diarsia rubi	13.1		-4.6		-28.0		-21.5		12.2
Diloba caeruleocephala	-72.0		-26.8		-31.7		13.6		-21.5
Drepana falcataria	-20.0		-24.8		-48.9	VU	-49.0	VU	-13.0
Drymonia dodonaea	5.9		-2.9		-20.8		-18.0		-3.4
Drymonia ruficornis	-74.7		-76.1		-78.5		-23.3		24.2
Dryobotodes eremita	-37.4		-24.4		-22.1		-30.6		-5.1
Dypterygia scabriuscula	-13.2		1.3		-74.6	EN	-85.6	CR	-64.3
Dyscia fagaria	13.4		-41.6		20.4		-17.9		-35.6
Dysstroma citrata	4.0		34.1		37.0		-14.5		-14.1
Dysstroma truncata	39.4		73.7		84.6		19.2		27.8
Earophila badiata	2.7		8.4		8.3		63.7		51.4
Ecliptopera silaceata	15.5		85.6		60.6		9.6		28.7
Ectropis sp.	6.8		8.3		5.8		17.8		38.4
Eilema complana	-6.5		-42.7		-43.9		-47.0		-25.4
Eilema depressa	96.9		73.1		29.4		5.4		37.4
Eilema griseola	61.2		80.6		33.3		12.6		19.8
Eilema lurideola	-3.2		-4.2		-19.4		2.6		12.7
Electrophaes corylata	32.2		49.5		11.0		4.5		24.5
			.0.0						20

Ennomos alniaria	-50.9	EN	-49.4	VU	-35.6		-43.0		-22.0	Ĩ
Ennomos erosaria	111.9		40.4		-30.1		-45.7		-22.4	
Ennomos fuscantaria	2.0		-22.9		-43.9		-72.2	EN	-59.2	EN
Ennomos quercinaria	36.4		81.9		77.5		-3.1		-28.0	
Entephria caesiata	333.0		534.4		351.8		141.1		-39.9	
Epione repandaria	13.1		32.5		25.0		23.8		44.7	
Epirrhoe alternata	17.3		5.7		-22.6		-50.7	EN	-39.4	
Epirrhoe galiata	-50.4		-31.5		-61.3		-84.8	CR	-76.3	EN
Epirrhoe rivata	-47.5	VU	-30.8		3.4		-7.1		31.0	
Epirrita autumnata	1.8		7.5		-19.8		-13.4		-23.4	
Epirrita christyi	9.2		33.6		54.4		31.7		30.4	
Epirrita dilutata	-16.5		-7.5		12.7		16.8		23.8	
Epirrita filigrammaria	-42.2		-54.1		-54.6		-78.5	EN	-57.1	
Eremobia ochroleuca	175.5		101.8		33.5		-4.2		-12.2	
Euchoeca nebulata	-68.6		-75.1	EN	-72.9	EN	-83.3	CR	-33.3	
Eugnorisma depuncta	-78.0	EN	-77.1	EN	-55.5		-65.2		-39.1	
Eugnorisma glareosa	-13.6		-54.8		-50.4		-27.9		-12.9	
Eulithis populata	100.9		97.0		46.8		-9.9		-3.5	
Eulithis prunata	-15.9		40.7		40.1		-31.8		-45.1	
Eulithis testata	8.0		-11.4		-30.2		-55.2	EN	-36.4	
Euphyia biangulata	-63.2	EN	-55.7	EN	-53.1		-30.3		21.2	
Euphyia unangulata	-59.7	EN	-61.4	EN	-57.2		-51.7		-35.9	
Eupithecia abbreviata	-42.2		3.0		28.7		69.1		90.3	
Eupithecia absinthiata	35.2		13.4		-23.6		-48.6		29.3	
Eupithecia assimilata	-52.2		-25.5		-25.8		-26.9		38.5	
Eupithecia centaureata	-50.7		-36.2		-34.1		-58.5	EN	-37.1	
Eupithecia distinctaria	-78.9	EN	-70.5		-78.5	EN	-64.9		-82.3	CR
Eupithecia exiguata	-53.5	EN	-45.2		-40.4		-25.1		50.2	
Eupithecia haworthiata	-3.3		-20.0		-51.5		-59.9		4.7	
Eupithecia icterata	24.4		12.5		-4.1		-33.6		-31.4	
Eupithecia innotata	-81.3	CR	-84.7	CR	-68.3		-25.3		57.1	
Eupithecia intricata	-4.1		-32.1		-22.2		-29.0		-26.4	
Eupithecia inturbata	30.0		-32.8		-30.0		-26.1		-6.5	
Eupithecia lariciata	-71.2	EN	-42.1		43.4		309.7		504.5	
Eupithecia linariata	-88.2	CR	-89.7	CR	-88.7	CR	-88.7	CR	-75.4	
Eupithecia nanata	-43.1		-24.3		-32.6		-43.4		-45.7	
Eupithecia plumbeolata	319.9		336.1		75.5		35.3		131.5	
Eupithecia pulchellata	1.6		37.8		-5.5		-11.8		51.7	
Eupithecia pusillata	-36.0		-24.3		2.5		-16.7		56.0	
Eupithecia simpliciata	65.5		-57.1		-82.4	CR	-75.5		-55.6	
Eupithecia subfuscata	-46.0		-39.1		-47.7		-21.0		157.8	
Eupithecia subumbrata	20.1		80.5		49.8		1.4		25.1	
Eupithecia succenturiata	-6.4		-4.8		-22.2		-62.2	EN	-58.0	
Eupithecia tantillaria	-40.5		-1.0		-1.0		71.4		10.2	
Eupithecia tenuiata	-26.7		-13.4		6.0		20.8		202.6	
Eupithecia tripunctaria	-38.7		-6.5		-12.7		-15.6		119.6	
Eupithecia trisignaria	334.9		463.8		373.6		-23.7		-28.1	
Eupithecia valerianata	-50.1		-80.3	CR	-83.3	CR	-65.8		-3.5	
Eupithecia venosata	-86.0	CR	-88.1	CR	-76.2		-78.6		-68.9	
Eupithecia virgaureata	-59.3		-64.5		-62.6		-58.5		157.6	
Eupithecia vulgata	-22.5		0.5		-11.0		21.9		72.7	
Euplexia lucipara	-0.4		4.1		-17.3		-38.5		-22.6	

Euproctis chrysorrhoea	11.2		-18.5		-30.5		-32.9		55.8	
Euproctis similis	-30.7		-32.2		-45.6		-49.0	VU	-25.9	
, Eupsilia transversa	-10.6		-3.4		13.2		73.3		140.9	
Euthrix potatoria	15.5		-1.4		-32.5		-40.5	VU	-29.7	
Furcula furcula	-64.2		-79.6	EN	-65.4		-78.1		-49.0	
Gandaritis pyraliata	35.1		32.8		27.6		-7.0		-4.7	
Geometra papilionaria	-7.5		-6.3		-19.0		-25.6		-10.3	
Gnophos obfuscata	-92.4		-92.9		-87.0		-72.5		-63.5	
Gortyna flavago	-20.4		11.5		42.9		7.8		49.6	
Graphiphora augur	182.3		92.3		87.7		3.8		19.9	
Griposia aprilina	-6.6		-6.1		13.9		-15.0		6.4	
Gymnoscelis rufifasciata	-68.4	EN	-67.6	EN	-74.3	EN	-67.4	EN	-3.9	
Habrosyne pyritoides	50.0		71.4		96.9		1.4		19.1	
Hada plebeja	-52.4		-27.2		-38.6		-18.6		-25.9	
Hadena confusa	-46.4		-91.9	CR	-97.3	CR	-94.8	CR	-95.5	CR
Hadena perplexa	-4.0		56.7		-42.4		-31.6		-62.0	
Hecatera bicolorata	-39.3		2.5		-26.2		-41.6		1.3	
Helotropha leucostigma	5.6		-20.6		-21.2		-45.5		10.2	
Hemistola chrysoprasaria	-62.4	EN	-49.4	VU	-47.8	VU	-13.0		8.8	
Hemithea aestivaria	2.1		-12.1		-0.7		-9.3		44.3	
Hepialus humuli	-6.6		-31.5		-21.6		-23.5		3.1	
Herminia grisealis	-3.9		-8.3		-16.2		-24.9		2.2	
Herminia tarsipennalis	34.3		50.7		88.8		53.4		69.6	
Hoplodrina alsines	29.0		24.6		15.0		45.0		71.4	
Hoplodrina ambigua	-29.8		-39.9		-57.2		-47.4		42.1	
Hoplodrina blanda	81.8		40.9		0.2		2.6		-14.2	
Horisme tersata	-29.0		-33.4		-23.8		-29.3		1.3	
Horisme vitalbata	-49.7		-57.4		-62.9	EN	-63.5	EN	-13.6	
Hydraecia micacea	34.8		41.1		27.2		-2.5		46.6	
Hydrelia flammeolaria	81.2		-56.0		-78.4	EN	-80.9	CR	-67.6	
Hydrelia sylvata	24.8		-3.1		66.2		28.0		202.0	
Hydria undulata	18.9		-15.4		-30.4		-38.2		17.9	
Hydriomena furcata	134.2		153.9		87.9		14.6		7.8	
Hydriomena impluviata	-23.5		-34.4		-59.4		-56.7		-1.5	
Hydriomena ruberata	204.4		189.9		70.8		-52.1		-52.0	
Hylaea fasciaria	21.9		44.3		25.3		31.4		19.4	
Hypena crassalis	-68.7		-69.1		-29.1		27.0		111.5	
Hypena proboscidalis	-4.7		15.6		26.0		-15.6		6.9	
Hypomecis punctinalis	-49.4	VU	-47.7	VU	-63.4	EN	-61.1	EN	-42.7	
Hypomecis roboraria	-12.4		-5.1		-10.2		18.0		9.9	
Hyppa rectilinea	54.4		60.2		28.1		31.5		0.5	
ldaea aversata	-12.2		-3.5		-19.4		0.8		17.0	
ldaea biselata	7.1		21.4		2.0		-6.5		2.0	
Idaea dimidiata	-30.1		-19.4		-24.4		-21.4		-5.9	
Idaea emarginata	1.4		27.3		-5.4		14.8		34.4	
ldaea fuscovenosa	-37.0		-39.4		-33.0		-1.1		43.5	
Idaea rusticata	88.1		126.8		137.7		164.8		193.4	
Idaea seriata	-36.3		-18.5		-30.5		-38.3		-6.4	
ldaea subsericeata	-57.4		-72.3	EN	-70.9		-77.5	EN	-42.5	
Idaea trigeminata	-32.2		-27.8		-39.6		-8.8		71.3	
Jodis lactearia	57.4		72.1		42.4		13.8		41.5	

Korscheltellus	19.8		-6.6		71.9		60.6		90.9	Í
fusconebulosa Korscheltellus lupulina	-29.0		-31.4		-34.1		-10.9		-17.7	
Lacanobia contigua	-71.7	EN	-57.9		-27.3		48.1		146.4	
Lacanobia oleracea	-48.0		-66.6	EN	-77.0	EN	-77.1	EN	-50.3	
Lacanobia suasa	-14.9		-29.8		-2.7		-25.2		110.5	
Lacanobia thalassina	-1.2		-1.7		-27.5		-24.2		15.9	
Lampropteryx otregiata	19.4		57.9		59.9		23.5		45.8	
Lampropteryx suffumata	76.7		126.7		68.6		70.8		82.4	
Laothoe populi	-11.5		-24.8		-25.0		-14.4		-8.3	
Larentia clavaria	-46.8	VU	-49.2	VU	-30.7		-30.3		-19.5	
Lasiocampa quercus	13.5		-60.2		-66.9		-81.2		-69.2	
Laspeyria flexula	44.9		97.4		109.5		161.1		540.4	
Lateroligia ophiogramma	-50.4		-67.6		-75.0		-74.0		-41.0	
Leucania comma	-69.7	EN	-72.3	EN	-59.2	EN	-49.2		-18.7	
Ligdia adustata	55.6		43.7		-9.5		-29.6		49.0	
Lithophane leautieri	17.5		18.3		51.8		-4.0		-22.4	
Lithophane ornitopus	-29.6		-30.5		-17.1		21.2		205.0	
Lithophane socia	-76.6		-80.5		-62.2		-64.9		-31.9	
Litoligia literosa	-5.8		-8.0		-14.5		-13.2		-63.1	EN
Lobophora halterata	-19.4		-26.8		-42.1		-29.9		-20.3	
Lomaspilis marginata	3.0		-5.2		-14.1		-8.7		22.8	
Lomographa bimaculata	-55.2		-36.9		-47.3		-42.2		24.4	
Lomographa temerata	58.8		42.2		14.7		-4.6		47.5	
Luperina testacea	-0.6		-2.8		-7.3		0.1		19.9	
Lycia hirtaria	102.9		95.4		67.4		138.6		141.8	
Lycophotia porphyrea	-3.2		-20.1		-39.3		-32.8		-34.7	
Lygephila pastinum	9.7		16.7		17.4		79.0		232.3	
Lymantria monacha	60.9		74.2		41.7		15.9		27.3	
Macaria alternata	-46.8		-51.4		-62.0	EN	-52.7		27.7	
Macaria liturata	-73.4	EN	-77.1	EN	-77.3	EN	-72.5	EN	-56.6	
Macaria notata	52.7		-0.7		-49.0		-65.6		-41.8	
Macrothylacia rubi	-15.1		-2.5		-22.8		-10.5		59.2	
Malacosoma neustria	-66.0		-46.9		-41.1		-16.9		44.9	
Mamestra brassicae	-44.1		-49.4		-54.1		-74.1	EN	-60.0	
Melanchra persicariae	31.0		-0.8		-45.4		-76.7	EN	-68.9	
Melanthia procellata	41.3		99.2		133.8		54.2		35.6	
Menophra abruptaria	-40.8		8.2		5.4		27.7		85.8	
Mesapamea	-1.7		-30.9		-42.6		-48.2		-18.9	
secalis/didyma Mesoleuca albicillata	-37.3		-47.4		-46.9		-65.7	EN	-52.9	
Mesoligia furuncula	-51.0		-19.3		2.7		-7.0		21.0	
Mesotyp didymata	133.7		49.0		10.1		-67.2	EN	-74.5	EN
Miltochrista miniata	27.3		-1.6		-3.3		-27.1		1.4	
Mimas tiliae	-77.3		-86.0	CR	-90.2	CR	-82.6		-70.2	
Mniotype adusta	17.4		52.8		34.2		72.9		127.6	
Mythimna albipuncta	215.6		198.9		76.3		78.7		191.5	
Mythimna conigera	12.8		30.0		33.5		75.7		103.7	
Mythimna ferrago	133.2		140.5		93.4		52.8		34.5	
Mythimna impura	-4.8		-20.6		-35.8	VU	-32.9	VU	-19.3	
Mythimna pallens	-76.4	EN	-83.8	CR	-86.2	CR	-92.0	CR	-75.2	EN
Naenia typica	113.9	-	345.8		212.8		109.2		40.4	
Noctua comes	-10.8		-29.7		-24.6		-14.7		29.5	
]	I		I							I

Noctua fimbriata	-12.1		-15.8		-19.5		-4.2		40.3	
Noctua interjecta	-80.0		-69.5		-82.2	CR	-91.8	CR	-82.5	CR
Noctua pronuba	-33.9		-44.8	VU	-47.0	VU	-49.5	VU	-34.1	VU
Nola confusalis	-35.0		-31.1	-	-40.4		-11.9		74.6	
Nola cucullatella	-61.7	EN	-31.4		-9.3		-26.2		7.7	
Notodonta dromedarius	-61.3	EN	-50.7	EN	-50.0	EN	-56.4	EN	-35.5	
Notodonta ziczac	-4.6		0.7		-23.1		-45.1	VU	-29.0	
Nudaria mundana	55.3		144.1		155.4		80.7		67.3	
Nycteola revayana	-65.7	EN	-65.4	EN	-67.6	EN	-64.9	EN	5.9	
Nyctobrya muralis	-26.7		-50.0		-15.5		-67.5		-76.7	
Ochropacha duplaris	-48.2		-28.8		-36.8		-43.5		-7.6	
Ochropleura plecta	-25.3		-15.9		-21.4		-32.3		-2.1	
Odezia atrata	87.9		63.3		57.4		-46.0		-63.3	
Odontopera bidentata	-35.8		13.8		16.1		49.5		32.0	
Odontosia carmelita	28.6		23.5		23.8		5.2		12.1	
Oligia fasciuncula	-20.1		-14.2		14.9		12.4		85.8	
Oligia latruncula	11.3		34.0		7.6		2.0		18.4	
Oligia strigilis	143.0		85.5		49.3		25.7		37.5	
Oligia versicolor	58.1		34.4		-3.5		-14.0		8.8	
Omphaloscelis lunosa	-2.6		-46.3		-71.7	EN	-76.2	EN	-55.6	
Opisthograptis luteolata	9.9		22.2		15.5		4.7		22.4	
Orthonama vittata	31.0		-38.6		-48.7		-53.6		-10.6	
Orthosia cerasi	44.8		62.5		16.3		44.0		5.5	
Orthosia cruda	-4.1		61.0		132.7		235.1		93.8	
Orthosia gothica	34.5		64.9		25.0		42.0		9.3	
Orthosia gracilis	75.5		78.6		73.2		101.1		52.2	
Orthosia incerta	-19.9		14.2		-7.6		27.2		24.8	
Orthosia populeti	-10.8		52.3		274.2		305.7		252.5	
Ourapteryx sambucaria	24.6		22.2		33.9		-17.4		22.3	
Pachycnemia	103.1		248.1		201.1		138.3		520.0	
hippocastanaria Panolis flammea	-65.5		-69.2		-85.9	CR	-50.9		-47.0	
Papestra biren	14.9		97.3		46.4	OIX	-23.6		-51.3	
Paradarisa consonaria	-35.5		-36.9		-9.5		214.9		154.8	
Parascotia fuliginaria	-32.6		-27.3		-47.4	VU	-46.1	VU	-37.2	
Parectropis similaria	1.0		-40.7		-75.4	EN	-69.2	EN	-63.3	EN
Pasiphila debiliata	236.9		194.7		36.1		-9.1		134.9	
Pasiphila rectangulata	-54.9		-57.5		-50.0		-50.5		-16.5	
Pennithera firmata	-31.4		-19.0		28.4		57.2		134.5	
Peribatodes	-44.5	VU	-27.2		-11.0		5.2		27.9	
rhomboidaria										
Peridea anceps	-2.6		-12.2		-53.0	EN	-53.7	EN	-47.8	VU
Perizoma affinitata	33.3		59.1		23.7		-14.5		6.0	
Perizoma albulata	-35.1		-1.5		-27.6		-54.6		-19.4	
Perizoma alchemillata	55.5	~ ~	71.4	~ ~	70.7		60.2		49.6	
Perizoma bifaciata	-92.5	CR	-88.4	CR	-75.9	EN	-12.9	05	36.3	
Perizoma blandiata	-76.5	EN	-73.4	EN	-82.3	CR	-85.1	CR	-55.4	
Perizoma flavofasciata	12.4		18.8		-9.1		-30.1		-5.7	
Petrophora chlorosata	-19.1		-17.7		-22.5		-10.1		42.4	
Phalera bucephala	21.5		-8.8		-31.5		-37.4		-32.0	
Pheosia gnoma	-8.9		-12.3		-13.9		34.4		69.8 7.5	
Pheosia tremula	-43.5 85.9		10.3 70.5		14.7 86.2		50.0 42.5		7.5 186.6	
Philereme transversata	00.9		70.5		00.2		42.0		0.001	

Philereme vetulata	34.0		33.3		-31.4		-33.7	ĺ	-47.9	I
Phlogophora meticulosa	-45.3		-46.8		-46.5		-48.4		-54.8	EN
Photedes fluxa	8.1		12.1		-21.6		71.0		79.6	
Photedes minima	-4.8		-15.7		-25.0		-18.9		-20.4	
Phragmatobia fuliginosa	-40.6		-17.3		-19.2		-18.4		65.1	
Phymatopus hecta	228.1		122.8		42.2		29.0		-6.1	
Phytometra viridaria	165.6		50.9		-50.6		-73.1	EN	-69.7	
Plagodis dolabraria	-7.6		30.0		-25.8		-27.8		13.0	
Plagodis pulveraria	36.4		95.7		70.5		52.3		89.1	
Plemyria rubiginata	-34.6		-27.3		-25.2		-56.1		-54.5	
Plusia festucae	-15.2		20.7		-0.5		-40.6		-36.8	
Plusia putnami	-90.8	CR	-80.2	CR	-69.1	EN	-43.2		0.1	
Poecilocampa populi	18.8	••••	22.7	••••	17.2		35.0		34.4	
Polia nebulosa	169.9		106.2		46.8		18.3		-20.5	
Polymixis flavicincta	-86.9	CR	-91.1	CR	-90.8	CR	-90.1	CR	-86.8	CR
Polymixis lichenea	-93.8	CR	-89.0	CR	-49.0	VU	-15.5	U.V.	12.9	0
Polyploca ridens	-53.6	ÖN	18.4	ÖN	78.4		155.3		177.7	
Pseudoips prasinana	-33.3		-9.7		-4.1		-9.7		-21.9	
Pseudoterpna pruinata	0.8		-2.7		-47.8		-55.2		-23.9	
Pterapherapteryx	-49.2		-47.5		-62.7		-57.5		7.8	
sexalata	10.2		17.0		02.7		07.0		7.0	
Pterostoma palpina	-37.1		-24.2		-29.0		-31.9		9.1	
Ptilodon capucina	23.9		12.8		14.0		-18.3		2.7	
Ptilodon cucullina	-40.5		-18.6		12.9		22.8		34.5	
Rivula sericealis	-57.4		-50.0		-46.3		-47.9		8.4	
Rusina ferruginea	-20.4		-19.5		-19.6		-5.8		8.8	
Saturnia pavonia	-84.2	CR	-83.3	CR	-30.9		11.0		284.3	
Schrankia taenialis	-53.8		51.7		-13.9		-56.2		-14.3	
Scopula floslactata	-58.4	EN	-35.9		-46.4	VU	-41.4	VU	-3.6	
Scopula imitaria	-59.9	EN	-60.5	EN	-62.9	EN	-63.8	EN	-36.1	
Scopula immutata	-17.7		6.9		3.1		-3.6		-9.5	
Scopula marginepunctata	-70.3	EN	-64.6	EN	-50.6		-65.0		-58.5	
Scopula ternata	-80.5	CR	-72.5	EN	-71.2	EN	-23.8		11.7	
Scotopteryx	47.5		66.2		42.6		-0.5		-8.3	
chenopodiata	70.0		70.0		50.0		50.0		C 4	
Scotopteryx luridata	-76.3		-79.3	EN	-56.0		-58.3		6.1	
Scotopteryx mucronata	274.0		752.1		342.1		148.8		-33.5	
Selenia dentaria	13.3		66.0		42.9		16.7		19.5	
Selenia lunularia Selenia tetralunaria	49.1		71.7		-16.1 89.1		-33.7		-14.8	
	50.5		102.7				66.1		83.2	
Sideridis rivularis	1.3		-12.5		-37.0		-64.3	EN	-52.7	
Sideridis turbida	92.9		-0.3		6.2		20.9		45.7	
Spilosoma lubricipeda	6.7		-8.0		-32.0		-23.5		-15.6	
Spilosoma lutea	1.7		-13.6		-29.6		-28.8		-9.0	
Stauropus fagi	-66.8	EN	-69.7	EN	-65.5	EN	-53.1	EN	-36.9	
Stilbia anomala	-19.3		-52.7	EN	-60.4	EN	-38.5		-46.1	
Subacronicta megacephala Syngrapha	-82.5 -66.9		-14.3 -59.0		-45.1 -65.6		-20.6 15.0		36.5 -36.5	
interrogationis Tethea ocularis	-38.3		-43.4		-54.2		-32.0		28.2	
Tethea or	-72.0		-50.3		-32.4		-27.1		-18.9	
Tetheella fluctuosa	64.0		7.4		-46.2		-39.9		-40.8	
Thalpophila matura	3.2		23.1		34.0		24.2		99.8	
I · ·	l		28	36	I		I		I	I

Thera britannica	-56.1		-25.1	17.8	9.8		173.0	
Thera juniperata	-53.0		38.7	98.7	153.7		103.5	
Thera obeliscata	-55.4	EN	-51.4	-45.8	-45.1		-10.3	
Theria primaria	-31.4		6.3	9.8	27.2		19.6	
Tholera cespitis	-18.2		-26.2	8.6	-7.6		35.1	
Tholera decimalis	20.1		96.4	207.7	100.6		209.0	
Thumatha senex	110.8		37.3	25.0	1.5		-27.3	
Thyatira batis	3.0		15.4	11.4	-24.0		7.2	
Tiliacea aurago	-0.1		20.6	-2.1	28.9		141.8	
Timandra comae	3.5		-2.4	-29.9	-53.4		-5.9	
Trichiura crataegi	-50.8		-43.5	-29.3	-16.0		22.5	
Trichopteryx carpinata	-27.2		-14.2	-2.7	30.5		105.9	
Triodia sylvina	23.6		0.7	-29.1	-40.4		-37.2	
Tyria jacobaeae	9.4		3.9	-31.9	72.2		259.5	
Watsonalla binaria	-56.4		-35.3	-56.2	-54.4		39.1	
Xanthia togata	7.7		1.8	31.2	66.8		86.1	
Xanthorhoe decoloraria	140.8		165.1	45.9	-38.2		-67.0	
Xanthorhoe designata	-10.5		29.2	8.8	-28.0		-0.3	
Xanthorhoe ferrugata	-26.4		-5.7	-4.7	-13.4		-10.5	
Xanthorhoe fluctuata	-29.0		-16.3	-26.9	-46.9	VU	-38.6	VU
Xanthorhoe montanata	40.4		63.8	54.5	13.9		17.5	
Xanthorhoe quadrifasciata	140.5		143.3	179.7	92.5		67.4	
Xanthorhoe spadicearia	25.0		81.0	80.1	60.9		101.0	
Xestia agathina	-77.6	EN	-65.5	-51.9	-47.1		0.0	
Xestia baja	16.5		12.5	28.4	16.3		30.3	
Xestia castanea	42.9		50.7	20.2	21.7		3.1	
Xestia c-nigrum	-12.1		-17.9	-15.9	-38.9		0.5	
Xestia ditrapezium	29.7		126.9	80.3	3.6		-6.9	
Xestia sexstrigata	75.5		-20.4	-49.2	-63.1	EN	-37.7	
Xestia triangulum	48.7		57.1	45.6	31.5		66.4	
Xestia xanthographa	-11.2		-26.4	-20.2	-29.2		17.8	
Xylena solidaginis	128.6		539.2	319.1	112.2		193.7	
Xylena vetusta	26.7		54.1	12.8	50.3		58.3	
Xylocampa areola	-34.6		-21.0	-24.2	35.1		38.7	

Appendix 6: Supporting Information for Chapter 6: Opinions of citizen scientists on open access to UK butterfly and moth occurrence data

Questionnaire to BNM and NMRS regional co-ordinators (referred to as County Recorders)

Open Access and butterfly and moth recording scheme data

Please complete this short questionnaire as fully as possible and return it by 31st May 2017. Your specific responses will be anonymous in any results that we share publicly or with partner organisations.

1. Do your responses on this questionnaire relate to (put X in one box)

Butterfly records only	Moth records only	Both	
(BNM scheme)	(NMRS)		

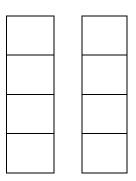
2. Given that there is always some access to records (e.g. via published distribution maps), on a scale from 1 (serious reservations) to 10 (strongly in favour), how much are you in favour of open access to butterfly/moth records? (put X in box below one number)

1	2	3	4	5	6	7	8	9	10

3. Given the balance between maximising use and minimising risk, what spatial resolution would be best for open access butterfly/moth records? (put X in one box in each column)

Common/widespread species Threatened species

Full capture resolution (the resolution of the raw record) 1km square / monad (1km x 1km OS map square) 2km square / tetrad (2km x 2km OS map square) 10km square / hectad (10km x 10km OS map square)



4. Should there be a time lag between records reaching the database and becoming open access? If so, how long should it be? (put X in one box)

20 years	10 years	5 years	No time lag	

5. Are there specific species or colonies of species in your area that would require a different, more restrictive approach to that detailed in Q3 and Q4? (put X in one box)



If yes, please indicate which/how many species:

6. Should BNM and NMRS open access data be provided publicly under a: (put X in one box)

Creative Commons Zero licence	
(no acknowledgment and no limit on use)	
Creative Commons with Attribution licence	
(recording scheme must be acknowledged but no limit on data use	e)
Creative Commons, with Attribution, Non-commercial licence	
(recording scheme must be acknowledged and data cannot be us	ed
for commercial purposes)	

7. Comments (please add anything else you want to tell us re open access and butterfly/moth recording scheme data)

Continue overleaf if necessary

290

Covering letter sent with questionnaire to BNM and NMRS regional coordinators (referred to as County Recorders)

Dear County Recorder,

Open Access and butterfly and moth recording scheme data This letter is being sent to all County Moth Recorders, County Butterfly Recorders, Butterfly Conservation Branch Chairs and other organisations (e.g. certain Local Environmental Records Centres) directly involved in supplying verified county datasets to the Butterflies for the New Millennium (BNM) recording scheme and the National Moth Recording Scheme (NMRS). The aim is to consult you and gather your views, aspirations and concerns about "open access".

In the last decade, there have been increasing calls amongst the scientific and conservation community for data, including biological records, to be made freely and openly accessible to all. This is part of a much wider shift towards open access of data amongst Government and Society, both in the UK and globally. Many arguments are put forward to support open access, ranging from ethical to economic, and government departments, the statutory conservation agencies and some major wildlife charities such as the British Trust for Ornithology have made their biological records open access (although others have not). Conservation decisions, policy, research and public education are increasingly dependent on open access to biological records. It is likely that many of the recorders who provide the raw records expect and assume that their sightings are widely available and being used to the fullest extent to support conservation. In parallel with this consultation, we will also be seeking general opinions from "grass roots" recorders about open access.

Open access means that records are freely available to all i.e. there is no need to seek permission or to pay for access to the data. However, it does not mean that records have to be available at 'full capture resolution' (i.e. the spatial resolution of the original, raw record) or that users can do anything they like with the data.

291

To date, Butterfly Conservation has responded very cautiously to the increasing calls for open access to butterfly and moth records. Currently, only historical (pre-2000) NMRS macro-moth records for the UK and all BNM butterfly records for Scotland are open access under non-commercial use licenses (e.g. via the NBN) and neither are available at full capture resolution.

However, as time passes, it is appropriate to review this position and take stock of the current views of key volunteers, partner organisations and recorders, upon whom our butterfly and moth recording schemes depend. The desire to maximise the use of records for conservation and other public benefits (through being more open with access) must be balanced against the desire to protect sites and species from harm and data from commercial exploitation (through being more restrictive with access). In addition, such considerations will vary from species to species and at different spatial resolutions. For example, some rare and threatened species may be at a greater risk of harm than common and widespread species, and records at summary spatial resolution (e.g. 2km x 2km squares) are of far less use to the commercial sector than fine-scale (full capture resolution) records. As compilers of records, we would ask you to be mindful of the expectations of the recorders who submit their sightings to you, but as the organiser of the UK schemes, Butterfly Conservation will take specific note of your opinion.

The aim of this consultation is to help plan the future for access to Butterfly Conservation's recording scheme datasets (BNM and NMRS) to which you contribute so we need to know your views. I can assure you that Butterfly Conservation's principal concern is to maintain the fantastic and vital recording schemes in which you play an essential part.

I would be extremely grateful if you could take a few minutes to complete the enclosed questionnaire please (either electronically or on paper) and return it by 31st May. Only those people named as County Recorders on the BNM and NMRS lists and BC Branch Chairs will receive this letter, so if you work as part of a team with other key individuals, please feel free to consult with them and submit responses that reflect the group's views.

Many thanks and best wishes

Richard Fox Head of Recording

Questionnaire to UK butterfly and moth recorders contributing to the BNM and NMRS projects

Open public access to butterfly and moth records

You've been asked to complete this brief survey (which should take less than 5 minutes) because you regularly contribute butterfly and/or moth records via your County Recorder to Butterfly Conservation's UK recording schemes (Butterflies for the New Millennium and the National Moth Recording Scheme).

Your answers are anonymous and will help Butterfly Conservation to plan future access to the recording scheme datasets. County Recorders have already been consulted, but as a provider of the sightings on which the schemes rely, your opinions are also very important to us.

The records you provide are already used in many ways by Butterfly Conservation and partner organisations (e.g. statutory conservation agencies, local environmental record centres) including assessing species trends, targeting habitat management, informing planning decisions and in collaborative scientific research. However, the records are not currently openly available to the public, policy makers or scientists to view and use without restriction.

We would be very grateful if you would complete the following short survey by 9th June 2017.

 Do you contribute butterfly records, moth records or both to your County Recorders? *

- ^C Butterfly records
- O Moth records
- ^C Both butterfly and moth records

2) Where is most of your UK butterfly/moth recording done? *

- ^C England ^C Scotland
- ^C Northern Ireland ^C Wales

3) What is your preference for the public accessibility of your butterfly and/or moth records via the national schemes? *

^C All my records should be publicly accessible in full detail (i.e. the grid reference at which you originally submitted the record) to maximise their use

^C My records of widespread species should be publicly accessible in full detail, but my records of scarce/threatened species to be publicly accessible only at a summary level (i.e. my original detailed grid reference is blurred to a coarser resolution such as tetrad 2km x 2km level) so that precise locations cannot be easily identified

^C All my records should be publicly accessible at summary level (i.e. with the grid reference blurred) so that precise locations cannot be easily identified

4) If the UK datasets of butterfly/moth records were openly accessible in full detail to the public, would you be likely to: *

^C Withhold your records from County Recorders and the UK recording schemes?

^C Reduce the precision of the records that you currently provide (e.g. by blurring the grid references of your records before you submit them)?

^C Continue to provide records in exactly the same way?

^C Provide more records to County Recorders and the UK recording schemes?

If you have any other comments that you would like to make on this subject,

please use the box below:

Many thanks for your help!

Richard Fox, Head of Recording, Butterfly Conservation

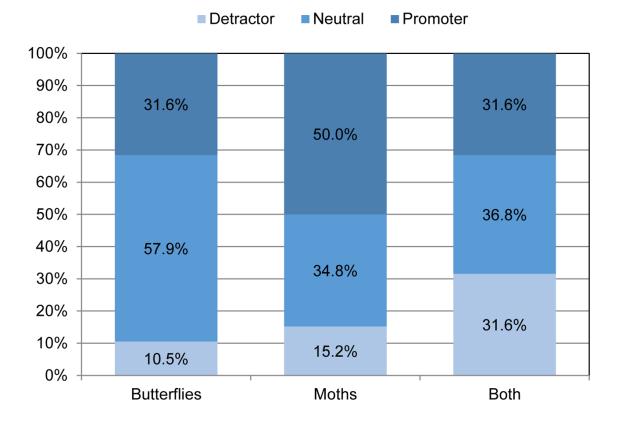
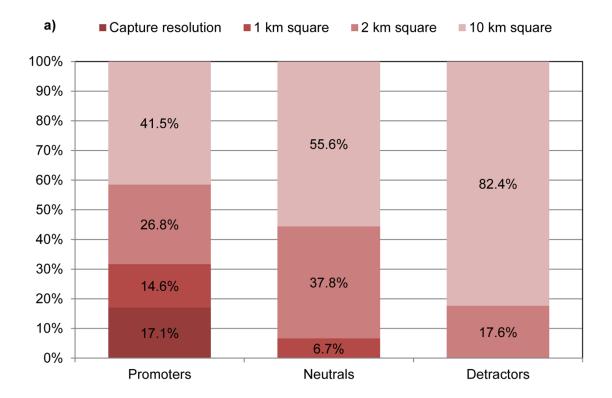


Fig. A6.1 Levels of general support for open access, assessed by modified NPS categories, among regional co-ordinators for butterflies, moths or both taxa.



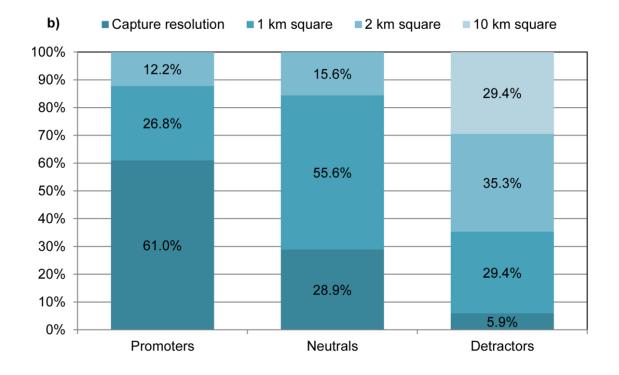


Fig. A6.2 Preferred resolution of open access records of a) threatened species and b) widespread species among regional co-ordinators in different modified NPS categories.