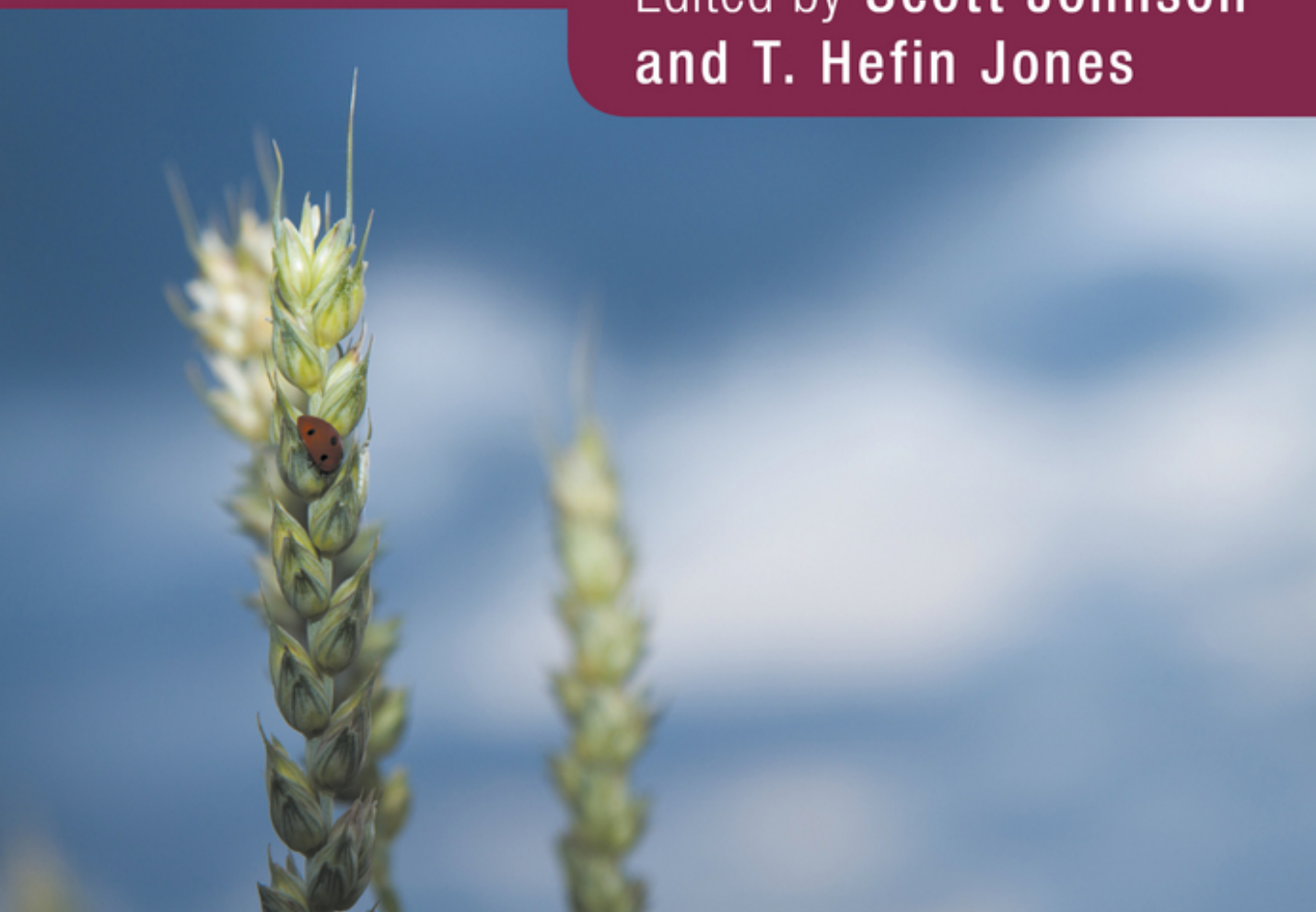


# Global Climate Change and Terrestrial Invertebrates

Edited by **Scott Johnson**  
and **T. Hefin Jones**



**WILEY** Blackwell



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*Edited by*  
*Scott N. Johnson*  
*T. Hefin Jones*

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## Preface

The title of this book should more accurately be 'Global Climate and Atmospheric Change and Terrestrial Invertebrates' because many of the contributors consider the effects of changes in greenhouse gases, especially carbon dioxide, on invertebrates. Our students, past and present, will be bemused because for many years we've laboured the point that carbon dioxide is an atmospheric chemical and not a climatic variable. We decided to use the term climate change as a 'catch all' to include atmospheric change, not just because the title is snappier, but in most peoples' minds, climate change includes components such as greenhouse gases. Public engagement with global climate change research has increased dramatically in the last few decades, helped in part by using accessible language without getting stuck on strict definitions, so we think this is a small compromise to make.

Invertebrates account for over 95% of multicellular life on our planet and represent an unrivalled level of diversity from nematodes which are a few microns in size to the colossal squid (*Mesonychoteuthis hamiltoni*) which can reach 14 metres. While we focus on terrestrial invertebrates in this book, this still represents a massively diverse group which occupy disparate habitats, aboveground and belowground. It would be impossible to provide comprehensive coverage of all groups in a single volume. Our second *mea culpa* is therefore that we have not been able to consider some groups of invertebrates of interest to readers of this book. Our selection of topics reflected those that we considered were ripe for synthesis and could be related to one another in a single volume.

Given the importance of invertebrates to our planet we felt consideration of this group in the context of global climate change was much needed. There are many books on global climate change, some which blend diverse disciplines such as the humanities, economics and science (e.g., Bloom, 2010)<sup>1</sup> and others that cover broad disciplines, such as biology (e.g., Newman et al., 2011).<sup>2</sup> This book aims to fill a gap by taking a more in-depth examination of a crucial group of organisms that shape the world we live in. The book would have not been possible without the work of the 44 contributors throughout the globe and we are indebted to them for their efforts. We sincerely hope that this book will provide a good survey introduction to the issue of global climate change and terrestrial invertebrates.

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- 1 Bloom, A.J. (2010) *Global Climate Change, Convergence of Disciplines*, Sinauer Associates, MA, USA.
- 2 Newman, J.A., Abnand, M., Henry, H.A.L., Hunt, S. & Gedalof, Z. (2011) *Climate Change Biology*, CABI, Wallingford, Oxfordshire, UK.

## 1

# Introduction to Global Climate Change and Terrestrial Invertebrates

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*"If all mankind were to disappear, the world would regenerate back to the rich state of equilibrium that existed ten thousand years ago. If insects were to vanish, the environment would collapse into chaos."*

E. O. Wilson

*"The great ecosystems are like complex tapestries – a million complicated threads, interwoven, make up the whole picture. Nature can cope with small rents in the fabric; it can even, after a time, cope with major disasters like floods, fires, and earthquakes. What nature cannot cope with is the steady undermining of its fabric by the activities of man."*

Gerald Durrell

## 1.1 Background

'Little things that run the world' is how the biologist E.O. Wilson described invertebrates (Wilson, 1987). There is a great deal of truth in this, with invertebrates playing major roles in the functioning and processes of most terrestrial and aquatic ecosystems. In terms of human wellbeing, their influence ranges from the beneficial ecosystem services of pollinators to lethal vectors of human diseases. Invertebrate pests, for example, destroy enough food to feed 1 billion people (Birch et al., 2011) at a time when global populations are expected to exceed 9.7 billion by 2050 and 11.2 billion by 2100 (UN, 2015) and therefore represent a significant challenge to secure global food security (Gregory et al., 2009). Conversely, invertebrates provide an unrivalled array of ecosystem services; globally €153 billion per year via pollination (Gallai et al., 2009), US\$417 billion annually in terms of pest control (Costanza et al., 1997). This latter figure is somewhat dated, but if it increased in line with the general trend for ecosystem services calculated by Costanza et al. (2014) for 2011 this would be closer to US\$1.14 trillion per year.

Besides humankind, invertebrates shape the world around us perhaps more than any other group and their response to climate change is pivotal in future global challenges, including food security, conservation, biodiversity and human health. In this book, we synthesise the current state of knowledge about how terrestrial invertebrates will respond and adapt to predicted changes in our climate and atmosphere, and, in some cases even moderate the impacts of such changes.

## 1.2 Predictions for Climate and Atmospheric Change

Between September 2013 and April 2014 the Fifth Assessment Report of the Intergovernmental Panel for Climate Change (IPCC) was published (IPCC, 2014). Divided into three Working Groups (WGs) and the culmination of the work of over 800 authors, the report not only focusses on the physical science basis of current climate change (WG I), but also assesses the impacts, adaptation strategies and vulnerability related to climate change (WG II) while also covering mitigation response strategies in an integrated risk and uncertainty framework and its assessments (WG III).

The report finds that the warming of the atmosphere and ocean system is *unequivocal*. Many of the associated impacts such as sea level change (among other metrics) have occurred since 1950 at rates unprecedented in the historical record. It states that there is a clear human influence on the climate and declares that it is *extremely likely* that human influence has been the dominant cause of observed warming since 1950, with the level of confidence having increased since the Fourth IPCC Report in 2007 (IPCC, 2007). In noting the current situation the 2014 Report states that (i) it is *likely* (with medium confidence) that 1983–2013 was the warmest 30-year period for 1,400 years; (ii) it is *virtually certain* the upper ocean warmed from 1971 to 2010. This ocean warming accounts, with *high confidence*, for 90% of the energy accumulation between 1971 and 2010; (iii) it can be said with *high confidence* that the Greenland and Antarctic ice sheets have been losing mass in the last two decades and that Arctic sea ice and Northern Hemisphere spring snow cover have continued to decrease in extent; (iv) there is *high confidence* that the sea level rise since the middle of the nineteenth century has been larger than the mean sea level rise of the prior two millennia; (v) concentration of greenhouse gases in the atmosphere has increased to levels unprecedented on Earth in 800,000 years; and (vi) total radiative forcing of the Earth system, relative to 1750, is positive and the most significant driver is the increase in atmospheric concentrations of carbon dioxide (CO<sub>2</sub>).

Relying on the Coupled Model Intercomparison Project Phase 5 (CMIP5), which is an international climate modelling community effort to coordinate climate change experiments, for much of its analysis, the Fifth Report based its predictions on CO<sub>2</sub> concentrations reaching 421 parts per million (ppm), 538 ppm, 670 ppm and 936 ppm by the year 2100. General conclusions drawn from this analysis were that (i) further warming will continue if emissions of greenhouse gases continue; (ii) the global surface temperature increase by the end of the twenty-first century is *likely* to exceed 1.5°C relative to the 1850 to 1900 period for most scenarios, and is *likely* to exceed 2.0°C for many scenarios; (iii) the global water cycle will change, with increases in the disparity between wet and dry regions, as well as wet and dry seasons, with some regional exceptions; (iv) the oceans will continue to warm, with heat extending to the deep ocean, affecting circulation patterns; (v) decreases are *very likely* in Arctic sea ice cover, Northern Hemisphere spring snow cover, and global glacier volume; (vi) global mean sea level will continue to rise at a rate *very likely* to exceed the rate of the past four decades; (vii) changes in climate will cause an increase in the rate of CO<sub>2</sub> production. Increased uptake of CO<sub>2</sub> by the oceans will increase the acidification of the oceans; and (viii) future surface temperatures will be largely determined by cumulative CO<sub>2</sub>, which means climate change will continue even if CO<sub>2</sub> emissions are stopped. This may be a moot point, however, since 2015 saw the largest ever annual increase in atmospheric CO<sub>2</sub> (Le Page, 2016).

## 1.3 General Mechanisms for Climate Change Impacts on Invertebrates

Generally speaking, predicted changes to our climate might affect invertebrates in two ways: (i) by directly affecting invertebrate physiology, performance or behaviour, and (ii) by indirectly affecting

invertebrates via changes to the habitats, resources or organisms they interact with. This is a very simplified way of categorising the impacts of global climate change on invertebrates, but it provides a convenient framework for understanding more complex processes. In this introduction, we do not comprehensively review examples of these mechanisms since they are developed in more detail in subsequent chapters but simply outline the general principles of each. Invertebrates are not just affected by climate change, but they can also moderate its effects on the ecosystem. This seems especially true for soil-dwelling ecosystem engineers (see Chapters 6 and 11) which have the capacity to mitigate the negative effects of drought on plants by changing the hydrological properties of their soil environment.

### 1.3.1 Direct Impacts on Physiology, Performance and Behaviour

As ectotherms, invertebrates are directly and significantly affected by temperature. Increasing temperature generally increases the rate of physiological and developmental processes to a point, whereupon further increases become detrimental. Providing other resources are not limiting, increased rates of development are likely to lead to larger populations of invertebrates and possibly an increased number of generations per year (Bale et al., 2002). This is most tangibly seen in the case of invasive invertebrates that move into warmer regions; the clover root weevil (*Sitona obsoletus*), for example, which is univoltine in the UK undergoes two generations per year since its accidental introduction to New Zealand in the mid-1990s (Goldson & Gerard, 2008). Precipitation changes also have direct impacts on invertebrates. Intense precipitation events can cause physical damage to invertebrates by disrupting flight, reducing foraging efficiency and increasing migration times (Barnett & Facey, 2016), though some invertebrates such as mosquitoes are dependent on heavy rainfall events. Conversely, drought can lead to desiccation, particularly in soft-bodied invertebrates though many have physiological and behavioural adaptations to reduced moisture (Barnett & Facey, 2016). Precipitation events will clearly have greater impacts on terrestrial invertebrates than those in aquatic habitats. Atmospheric changes are generally thought to have negligible direct impacts on invertebrates.

### 1.3.2 Indirect Impacts on Habitats, Resources and Interacting Organisms

Climate change can affect invertebrates indirectly via its impacts on the habitat they occupy, the resources they use or the organisms they interact with. These are enormously varied for different taxa, and can be both positive and negative. Changes in habitat complexity, for instance, could affect foraging behaviour of predatory invertebrates affecting populations of both prey and predator (Facey et al., 2014). Elevated CO<sub>2</sub> concentrations often increase structural complexity of habitats via changes in plant architecture (Pritchard et al., 1999), which potentially explains why web-building predatory spiders can become more abundant under elevated atmospheric CO<sub>2</sub> concentrations (e.g., Hamilton et al., 2012).

Every invertebrate exploits specific resources and, if the supply or nature of these resources is modified by climate change, it seems likely that the invertebrate will also be affected. When climate change affects host plant quantity or quality (e.g., nutritional value or defensive status), for example, many herbivorous insects are affected by this change in their resource (Robinson et al., 2012). Moreover, alterations in herbivore performance will change their quality as a resource for natural enemies that predate or parasitise them (Facey et al., 2014).

Where invertebrate populations are influenced by interactions with other organisms (e.g., mutualism, competition or predation), climate change has the capacity to affect indirectly invertebrates if it has direct impacts on that interacting organism. Changes in temperature and precipitation, for example, often seem to introduce asynchrony between predator and prey life-cycles, which frequently

results in reductions in top-down control of the prey species (Preisser & Strong, 2004; Stireman et al., 2005). Changes in the emissions of volatile organic compounds from plants grown under elevated CO<sub>2</sub> concentrations can alter the foraging efficiency of parasitoids (Vuorinen et al., 2004). Changes in the phenology and range expansions of invertebrates in relation to resources they exploit or organisms they interact with (e.g., natural enemies) is another indirect means that global climate change might affect invertebrates, especially in terms of temporal mismatches (Facey et al., 2014).

## 1.4 Themes of the Book

The following 17 chapters can be divided into four themes; (i) methods for studying invertebrates and climate change, (ii) friends and foes: ecosystem service providers and vectors of disease, (iii) multi-trophic interactions and invertebrate communities and finally (iv) evolution, intervention and emerging perspectives. Some of these chapters use the same case studies and examples but from different perspectives.

### 1.4.1 Methods for Studying Invertebrates and Global Climate Change

This theme describes three mainstream approaches for understanding how invertebrates will respond to global climate change. The first of these, by Palmer and Hill (Chapter 2) considers how historical data, particularly those collected by citizen science projects, can be used to predict changes in geographical distributions of invertebrates. This includes measuring changes in distribution, abundance and changes in the location of species ranges. While these datasets often have taxonomic and spatio-temporal biases, Palmer and Hill present approaches for accounting for such biases, such as fixed effort transects. New ways for analysing existing and future datasets include combining datasets with remotely sensed satellite land cover dataset, meta-genomic DNA barcoding and new dynamic models that incorporate dispersal and evolutionary processes.

Experimental approaches for investigating the impacts of global environmental change on invertebrates are discussed by Lindroth and Raffa (Chapter 3). Such controlled experiments are important for elucidating mechanisms and disentangling interactive relationships quantitatively. These range from reductionist experiments to larger scale approaches, each with inherent strengths and weaknesses. In particular, the authors set out approaches for devising experiments that maximise statistical power and avoid pseudo-replication. In closing, they consider the importance of the often overlooked human dimension of such experiments, emphasising the need for effective team assembly, leadership, project management and communication.

In Chapter 4, Nooten and Andrew describe transplant experimental approaches. This approach involves moving species or entire communities into a new location with a novel climate, usually one that is predicted to occur for the current location. Such experiments have revealed how invertebrates may adapt to warmer climates, potential range shifts of invertebrates, changes in phenology, shifts in species interactions, genotypic and phenotypic responses and community shifts. The authors use network analysis to identify gaps in our knowledge from transplant experiments and stress the importance of understanding whether transplanted species occupy the same niche as they do in their current location.

### 1.4.2 Friends and Foes: Ecosystem Service Providers and Vectors of Disease

In this theme, consideration is given to how global climate change will affect key groups of invertebrates that are of economic and social importance to mankind. In the first of these, Forrest



(Chapter 5) considers how global warming will affect invertebrate pollinators. She considers how warming can cause large-bodied pollinators to overheat, deplete energy reserves, reduce adult body size and increase mortality. These can be considered direct impacts of warming. Indirect impacts include altered plant phenology and changes in floral resource production. Forrest concludes that observed pollinator declines may be partly due to global warming working in concert with habitat loss, pesticide poisoning and pathogen infection.

Chapter 6 by Gerard and Popay considers the impact of global climate change on invertebrates with biological control roles in grasslands. Grassland ecosystems are prone to invasions by exotic pests, but endemic and introduced predators and parasitoids, as well as plant defences and symbionts, play a crucial role in managing weed and pest abundance. Disruption of predator–prey interactions, particularly in terms of asynchrony between life-cycles, could lead to pest outbreaks. Nonetheless, they suggest that the manipulability of grasslands will allow climate change adaptation strategies to be implemented.

Turning to invertebrates with economic pest status, Rose Vineer, Ellse and Wall describe the likely impacts of global climate change on ectoparasites and vectors of veterinary disease in Chapter 7. They note that changes in the phenology and distribution of tick species have already changed in recent years and predicted changes in climate are likely to affect seasonal patterns of blowfly strike. While they suggest climate change may result in increased abundances of ectoparasites, and possibly disease incidence, strategic changes in animal husbandry may help mitigate these impacts.

Invertebrate vectors transmit pathogens that account for almost fifth of the burden of human infectious diseases, and these are the subject of Chapter 8 by Chaves. The chapter focuses on whether global warming could exacerbate vector-borne disease transmission and whether warming will interfere with current programmes to eliminate such diseases. The chapter presents a case study using two mosquito vectors along an altitudinal gradient in Japan to illustrate useful concepts for studying changes in vectors arising through global climate change. The chapter ends with some ideas on the evolutionary implications of climate change for invertebrate vectors and the diseases they transmit.

In the final chapter of this theme, Ryalls and Harrington look at invertebrate vectors of plant diseases focussing on one of the most important groups, aphids, which are responsible for transmitting around 40% of plant viruses. They adopt a ‘disease pyramid’ approach for considering how interactions between aphids, their host plants and viruses determine the overall effect of global climate change on aphids and plant disease incidence. The individual responses of aphids, plants and viruses to global climate change are likely to exacerbate each other, particularly in terms of warming and drought drivers. Ryalls and Harrington conclude that relatively few studies incorporate all these factors interactively, however, so more holistic research is needed to make accurate predictions.

### 1.4.3 Multi-Trophic Interactions and Invertebrate Communities

Related to Chapter 6, Hentley and Wade (Chapter 10) take an in-depth look to how climate change will affect herbivore interactions with their natural enemies. In particular, they produce a comprehensive assessment of 45 studies in this area, pointing to neutral, positive and negative outcomes for insect herbivores. Positive outcomes for herbivores occurred through various mechanisms including reduced rates of parasitism by parasitoids, longer development times for natural enemies, reduced foraging efficiency and phenological mismatches between herbivore and antagonist life cycles. Negative impacts, mostly reported for increased air temperature, arose because of increased rates of parasitism and reduced resistance to such parasites by herbivores. This chapter also discusses the possible mechanisms driving the impact of climate change on herbivore–natural enemy interactions such as altered plant-derived cues which are used by natural enemies to locate their prey.

Moving belowground, Hiltbold and colleagues look at how climate change might affect soil communities of invertebrates in Chapter 11. The authors briefly consider the few studies that have examined overall changes in soil communities, before considering responses of three key groups (nematodes, insect herbivores and earthworms) in more detail in an attempt to understand these community level outcomes. The chapter considers impacts of elevated CO<sub>2</sub> concentrations, elevated air temperatures and altered precipitation patterns. Unlike other chapters, increased warming is likely to have fewer direct impacts on soil-dwelling invertebrates because soils will buffer temperature variation to some extent. Likewise, soil-dwelling invertebrates are already adapted to high concentrations of CO<sub>2</sub>, so impacts are anticipated to be entirely indirect. The authors emphasise the need for longer term studies since soil communities are likely to respond to climate change over longer periods of time than aboveground communities.

Studying linkages between above- and belowground invertebrate communities is a relatively recent development in community ecology, and is the subject of Chapter 12 by Johnson, Ryalls and Staley. In particular, they consider how changes in elevated atmospheric CO<sub>2</sub> and precipitation changes might affect interactions between above- and belowground invertebrates. Studies in this area are scarce, so the chapter puts forward a conceptual framework for these interactions which may be mediated by changes in plant traits, shifts in plant communities and those mediated by plant-derived organic inputs (e.g., frass and litter deposition) entering the soil. Several hypotheses for how climate change may affect these interactions are made.

In terms of broad community responses to atmospheric change, forests are amongst our best studied ecosystems thanks to manipulations in Free Air Carbon dioxide Enrichment (FACE) experiments. These studies are the subject of Chapter 13 by Facey and Gherlenda which focuses on the effects of predicted concentrations of atmospheric CO<sub>2</sub> and ozone on forest invertebrate communities. In general, they conclude that the former tends to increase herbivore susceptibility to attack by natural enemies, whereas the latter generally speeds up herbivore development and causes reductions in natural enemy performance. However, it is suggested that these may be short term responses and that communities may show resilience in the longer term.

While the focus of this book are terrestrial invertebrates, in Chapter 14, Jonsson and Canhoto consider the impacts of global climate change on freshwater invertebrate communities via changes in terrestrial ecosystems. They argue that the effects of climate change mediated via terrestrial ecosystems is at least as important as the direct impacts of climate change, and that these impacts likely will feedback to influence invertebrates and other consumers in terrestrial systems.

Invertebrates are a crucial source of food for vertebrates and Chapter 15 considers this with particular reference to a range of vertebrate taxa. Thomas, Vafidis and Medeiros highlight three climatic drivers for invertebrate–vertebrate interactions. The first arises because global climate change affects invertebrate abundance and therefore, food supply, driving vertebrate population change and potentially causing local extinctions. Secondly, changes in invertebrate communities are likely to induce range shifts in vertebrate populations. Thirdly, invertebrate responses to global climate change are often more rapid than vertebrate responses, potentially introducing temporal mismatches between invertebrate abundance and vertebrate phenology. Invertebrate scarcity, for example, at a time when vertebrates need to provision for their young is particularly problematic.

#### 1.4.4 Evolution, Intervention and Emerging Perspectives

The fourth, and final, theme of the book identifies evolutionary responses to global climate change, intervention and emerging perspectives in our understanding of how invertebrates will evolve to global climate change, potential adaptation strategies and the risk of future biosecurity breaches.

Chapter 16 by Carnicer and colleagues, looks at evolutionary responses of invertebrates to global climate change from the perspective of life-history trade-offs. They consider that such trade-offs will constrain the simultaneous optimisation of correlated suites of traits to environmental change and focus on five particular trade-offs. The chapter also considers the roles of multidecadal climate dynamics and drought regime shifts in long term population responses and evolutionary responses.

Chapter 17 by Arribas and colleagues takes a forward-looking perspective and asks how understanding insect species vulnerability to global climate change might inform conservation strategies. They examine the accumulated background knowledge on vulnerability of insect species to global climate change, recent developments and methods of its assessment and the links with the management options for insect conservation including: (i) monitoring, (ii) reduction of additional threats, (iii) habitat restoration, (iv) increasing habitat connectivity, (v) expansion of reserve networks and (vi) performing assisted dispersal.

Conclusions and Future Perspectives are presented in Chapter 18. We discuss common themes and issues that have arisen in the proceeding chapters, including the need to build on single species study systems and single environmental factor experiments, while observing rigour in experimental design and analysis (see Chapter 3). We also identify the need to investigate how extreme climate change events will affect invertebrates. In closing, we argue that global climate change may severely undermine biosecurity against terrestrial invertebrates since it has the capacity to make previously unsuitable habitats or regions more suitable. Using several examples, we show how movement of exotic invertebrate species into novel environments has the capacity to cause significant harm, especially in terms of food security.

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## **Part I**

### **Methods for Studying Invertebrates and Climate Change**



## 2

## Using Historical Data for Studying Range Changes

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### Summary

Global climates are warming and much of our understanding about the ecological responses of species to climate comes from the analysis of historical data sets. Invertebrates are sensitive to climate changes and so historical distribution data sets from citizen science projects collected over the past few decades provide excellent opportunities to research climate change impacts. In this chapter we review the range of data sets that are available for analysis, the amount of information that is held for different taxa, as well as the types of analyses that such data have been used for. We review the different analytical methods that have been employed to quantify range changes, focussing specifically on analyses of distribution extent and change in location of species' ranges (particularly range boundary shifts). We highlight some of the problems that arise in using these data sets as a consequence of temporal and spatial biases in recorder effort, and we discuss the ways in which researchers have tried to account for these biases. We conclude by highlighting new ways in which the historical data sets might be used in future to address novel research questions, for example, in relation to identifying different components of climate to which species are responding, and the ways in which by combining distribution data with other information we might gain a better understanding of the ecological impacts of climate change.

### 2.1 Introduction

Global climates are changing (IPCC, 2014) and species are responding to these changes (Parmesan & Yohe, 2003), with consequences for communities and ecosystems (Chapin III et al., 2000; Walther et al., 2002; Walther, 2010). Species could potentially respond to climate changes in several ways; species may shift their distributions to track changes, they may respond and adapt to changes in situ without any range shifts, or go extinct. The evidence from analyses of historical records, and from new empirical studies, reveal that the response that is observed is likely to depend on: the taxon and type of species being studied; the location of the study within the species' geographic range; and the extent to which the climate is changing. Thus at leading-edge (cool) range margins of species' distributions, historical data sets have revealed latitudinal range expansions polewards and/or upslope expansions where the climate is improving for the species (e.g., Warren et al., 2001). In contrast, at trailing-edge (warm/dry) range margins, range retractions polewards or uphill have been observed where climatic

conditions have become unfavourable for species (e.g., by becoming too warm and/or too dry for the species; e.g., Wilson et al., 2005; Franco et al., 2006), leading to local extinction of low-latitude and low-elevation populations. Taken together, these responses to climate have resulted in many species shifting their geographical ranges, with greater rates of change being observed in locations that have warmed the most (Chen et al., 2011). These responses, evident in analyses of historical data sets, mirror those seen in the geological record, revealing range shifts by species under past climate changes (e.g. for beetles: Coope, 1978; and chironomids: Brooks & Birks, 2001). Thus, some of the first evidence for human-induced climate change impacts on species and ecosystem came through the analysis of historical data sets, and re-surveys of previous studies (Parmesan et al., 1999). Assuming that the past helps to inform the future, these data sets and analyses have also been used to make projections of the likely responses of species to future climate warming (e.g., Hill et al., 2002; Oliver et al., 2015).

Some of the first studies of climate change impacts on species' distributions were on butterflies in Europe, capitalising in particular on the availability of high resolution data for Britain (Parmesan et al., 1999). Given the extensive data sets that are available for butterflies, which have been analysed to examine climate change impacts, we cite many butterfly examples in this chapter. We have also made considerable use of these UK butterfly data sets in our own research (e.g., Mair et al., 2012; Mason et al., 2015), where we are focussing on gaining a better understanding of the ecological impacts of recent climate change, and we review some of our findings in this chapter. Butterflies have been a very popular taxonomic group for study by the general public in Britain for centuries. The relatively low diversity of butterflies in Britain, but high density of recorders, has resulted in very high temporal and spatial resolution distribution data for ~60 species. There are particularly good records since the 1970s, providing a long-term record of range changes (Heath et al., 1984; Asher et al., 2001; Fox et al., 2006). These distribution data are in addition to transect data (from e.g., the UK Butterfly Monitoring Scheme, UKBMS) documenting population trends in butterflies (Pollard & Yates, 1993; Roy et al., 2001). Other countries also have good records and recording schemes for butterflies, particularly in Europe (Settele et al., 2008; Pöyry et al., 2009; Kudrna et al., 2011; Devictor et al., 2012). Throughout this chapter we use the term 'historical datasets' to refer to datasets spanning the past four to five decades, when many of the current recording schemes were initiated (e.g., 1976 for UKBMS). The number of distribution and abundance records has increased dramatically in more recent decades, as a result of increased interest in citizen science schemes.

Many butterfly species reach either a trailing-edge or leading-edge range margin to their geographical ranges in Britain providing additional potential for analysis of species' range boundary responses from these British data sets (e.g., Hickling et al., 2006; Mason et al., 2015). As with other invertebrates, butterflies are ectothermic (although some are regional heterotherms, e.g., Kingsolver & Moffat, 1982) and activities such as flight, oviposition, and larval development rates are dependent on temperature. Thus, their population dynamics are sensitive to variation in climate. Their short generation times and high mobility also make them sensitive indicators of climate change impacts, and good knowledge of their taxonomy, natural history and ecology (e.g., habitat preferences, dispersal ability, larval host plants) helps to interpret observed responses to climate change and to explore potential mechanisms driving these responses.

The ecological impacts of recent environmental changes are well documented in temperate regions, and invertebrates are often used as indicators of climate change. There are several reasons why invertebrates are studied: these taxa are often well-recorded; their taxonomy is well-resolved (particularly for butterflies) and they can often be identified easily in the field; many species are undergoing rapid declines making them important to study to understand factors responsible for the declines; population dynamics respond quickly and species are sensitive to changing climates; and species occupy



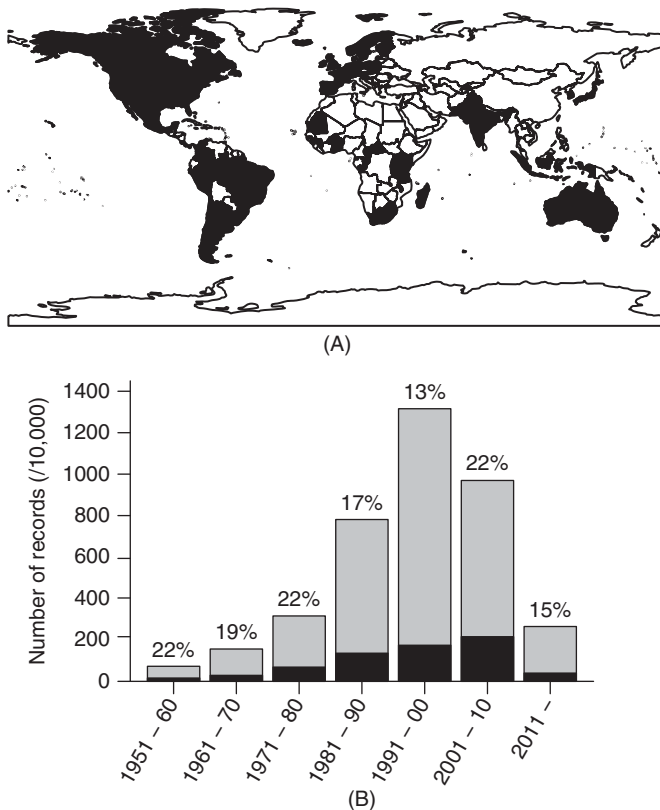
a variety of habitats and have different ecologies (e.g., dispersal abilities, habitat specificities, trophic interactions) making it possible to explore the role of biotic and abiotic factors in the responses of species to environmental changes. Invertebrates span a wide range of life-history traits (e.g., body mass varies by  $\sim 1.5$  orders of magnitude) providing opportunities for comparative analyses of climate change impacts among different species types. In addition, many invertebrates provide vital ecosystem services (e.g., by being pollinators, prey, predators and parasitoids, decomposers) allowing the impacts of climate change to be assessed not only in relation to species but also the ecosystem functions they support (e.g., Biesmeijer et al., 2006; Kerr et al., 2015). Thus the large historical data sets that are available for invertebrates provide an opportunity to quantify and better understand the ecological impacts of climate change on a key group of species.

Some of the first analyses of historical data sets that were carried out highlighted that species' responses to recent environmental changes have been highly heterogeneous, for example in relation to abundance trends (positive or negative), amount of change in geographic range sizes, and direction of range shifts (Warren et al., 2001; Hickling et al., 2006). More recent studies have explored reasons for such variation (e.g., Angert et al., 2011) – such studies are required so that ecologists and conservationists can understand, identify and protect species that are most vulnerable to changes in climate (Pacifi et al., 2015). Thus, the availability of historical data sets that are being regularly updated with new contemporary data provide novel research opportunities to develop new fundamental ecological understanding of the limiting factors to species' ranges, as well as helping in the development of conservation management policies to aid the protection and conservation of species under threat from climate changes. In this chapter we focus particularly on distribution data sets. We review the historical datasets available for studying range changes (section 2.2), describe methods to quantify range changes (section 2.3), and then discuss the challenges and biases of using such data (section 2.4). We conclude by outlining current knowledge gaps and new opportunities for research using these historical data sets (section 2.5).

## 2.2 Review of Historical Data Sets on Species' Distributions

There is a strong causal link between the amount of climate change at study sites and the responses of species' at those locations (Chen et al., 2011; IPCC, 2014). However, to understand the mechanisms driving these changes and the causes of variation among species and taxa (Chen et al., 2011; Mason et al., 2015), scientists and other stakeholders have taken advantage of the large amounts of species' data collected worldwide. For example, information on the extent of occurrence are available for some species (e.g., [www.iucnredlist.org](http://www.iucnredlist.org)), and occurrence data are also available for many species in publically-accessible repositories such as the Global Biodiversity Information Facility (GBIF: [www.gbif.org](http://www.gbif.org)) (Boakes et al., 2010). The GBIF is a repository of  $\sim 570$  million freely accessible occurrence records covering vast geographic areas and many taxonomic groups. The repository includes data from 54 participant countries and 41 international organisations (Fig. 2.1A; [www.gbif.org/participation/participant-list](http://www.gbif.org/participation/participant-list), accessed 15/07/2015). To date, approximately 1.6 million species – including invertebrate and vertebrate animals, fungi, bacteria and plants – are included in the database, and the numbers of records are continually increasing.

We are now in the era of citizen science, which has stemmed from “easier, faster and more accessible” data capture (August et al., 2015). The advent of new technology such as cheap tracking sensors, as well as initiatives such as the data-collection apps for British butterflies (iRecord Butterflies), grasshoppers (iRecord grasshoppers), and ladybirds (iRecord Ladybirds) (August et al., 2015; [www.ceh.ac.uk/citizen-science-apps](http://www.ceh.ac.uk/citizen-science-apps), accessed 06/08/15) have all led to a dramatic increase in the amount



**Figure 2.1** (A) Map of participant countries (black polygons) of the GBIF facility\*, and (B) geo-referenced occurrence records for species in the UK, since 1950 (all 37,673,744 records = grey and black bars; Class: *Insecta* records = black bars, with the percentage of *Insecta* records displayed at the top of each bar). Bars illustrate the increase in records over time. We highlight insect data which comprise ~18% of the c.38 million geo-referenced records held in GBIF for the UK. Summary data were obtained from GBIF.org (accessed 07/08/15). \*note that there are data held in the GBIF database for species that occur outside of these countries.

of data on species' distributions that are available for analysis (Pocock et al., 2015; Sutherland et al., 2015) (Fig. 2.1B; [www.gbif.org/occurrence](http://www.gbif.org/occurrence)). Such data have been used in a wide variety of ways, including identifying species that are likely to invade new areas (Faulkner et al., 2014); exploring the role of species' interactions in determining large-scale distributions of species (Giannini et al., 2013); describing the relationship between beta-diversity and productivity (Andrew et al., 2012); and to predict future distributions of species under potential future climate change (Jones et al., 2013).

The three countries with the most data held in GBIF are the United States which holds ~212 million records ([www.usgs.gov](http://www.usgs.gov)), Sweden which holds ~51 million records ([www.gbif.se](http://www.gbif.se)), and the UK which holds ~50 million records ([www.nbn.org.uk](http://www.nbn.org.uk); although ~10 million of those records are for species occurring outside of the UK). National initiatives such as the UK National Biodiversity Network (NBN) collate data from national, regional and site-based surveys, as well as from incidental sightings and old records from literature and museum/private collections. The data sets that are amassed in such databases have considerable potential to inform, particularly about large-scale patterns occurring as a result of climate change. These patterns and responses of species would otherwise

be impossible to address from short-term surveys involving just a relatively small group of scientists working at small spatial scales. Examples of such uses of GBIF data include Fuller et al. (2012), who modelled the potential future distribution of the malarial vector *Anopheles albimanus* in the Caribbean and northern South America, in order to inform management efforts to limit this species' spread to those upland areas that the authors predicted would become suitable under potential future climate change. To date, over 200 hundred published studies have used data held by the UK Biological Records Centre (BRC) in the last ten years (Powney & Isaac, 2015), including many focussing on climate change topics, for example, studies describing advancement in phenology (Roy & Sparks, 2000) and polewards range shifts of species in response to climate change (e.g. Hickling et al., 2006; Chen et al., 2011; Mason et al., 2015).

Many of these data on species' distributions have come from volunteers, for example an estimated 70,000 people annually in the UK have contributed to national recording schemes (Pocock et al., 2015). In the UK, there are numerous schemes which collect data on a wide range of botanical, vertebrate, and invertebrate species groups, of which invertebrates are by far the most-studied group. For example, 75 of the 88 animal and plant recording schemes listed by the BRC are for invertebrates, ranging from well-studied butterflies and moths that we have already mentioned above, to much-understudied earthworms (Sutherland et al., 2015) ([www.brc.ac.uk/recording-schemes](http://www.brc.ac.uk/recording-schemes), accessed 15/07/2015). Although there are many incidental records from previous centuries, the vast majority of dedicated recording schemes have been set up since the 1960s, but a few have been established as recently as 2006 (Barkfly Recording Scheme: <http://www.brc.ac.uk/schemes/barkfly/homepage.htm>) and 2007 (National Moth Recording Scheme: [www.mothscount.org](http://www.mothscount.org)).

### 2.3 Methods for Using Historical Data to Estimate Species' Range Changes

Global meta-analyses of historical data sets have described the average range shifts of species in both terrestrial and marine ecosystems (Parmesan & Yohe, 2003; Sorte et al., 2010; Chen et al., 2011; Poloczanska et al., 2014), with average shifts in marine ecosystems being reported to be an order of magnitude higher than those in terrestrial systems. Range shifts by species may also vary between temperate and tropical ecosystems (Freeman & Freeman, 2014), although tropical data are lacking. Nonetheless, common to all of these meta-analyses is a consensus that species are shifting on average towards the poles and/or higher elevation, consistent with range shifts being driven by climate (Chen et al., 2011). In support of a causal link with climate, Sorte et al. (2010) found that 70% of the 129 studies of marine range shifts they analysed could be attributed to climate change. The fact that species vary in their rate of range shifting over time (Mair et al., 2012; Mason et al., 2015) provides further support for the important role of climate, and may explain why many studies to date generally provide little support for species' traits being important (Angert et al., 2011, but see e.g., Auer & King, 2014; Sunday et al., 2015). For example, differences in the rates of range shifts among British butterfly species have been shown to be inconsistent over time (Mair et al., 2012); in general, rates of range change were significantly greater in more recent decades (between 1995–1999 and 2005–2009) than in earlier ones (between 1970–1982 and 1995–1999). Such differences in rates of change imply that factors in addition to intrinsic species-specific sensitivities to climate are important in driving species' responses.

The majority of terrestrial data used to estimate range shifts come from the temperate zone, where species are generally considered to be temperature-limited rather than moisture-limited (Chen et al., 2011). A recent meta-analysis found that median latitudinal shifts of species were approximately

17 km per decade (Chen et al., 2011), during a period when the temperature warmed in those study sites by an average of  $\sim 0.6^{\circ}\text{C}$ . This rate of latitudinal shift by species was much faster than previously estimated (Parmesan & Yohe, 2003), even though many species are lagging behind climate changes (Menéndez et al., 2006; Devictor et al., 2012). Studies included in the meta-analysis by Chen et al. (2011) were primarily from data-rich countries, and included data for range shifts of invertebrates from the UK (Franco et al., 2006; Hickling et al., 2006); butterflies in Finland (Pöyry et al., 2009); and intertidal invertebrates along the Chilean coast (Rivadeneira & Fernandez, 2005). Rates of range shifting have also recently been described by Mason et al. (2015), who found that the mean range shifts of nearly 1600 southerly distributed species from 21 taxonomic groups in Britain (19 invertebrate groups, plus birds and herptiles), was  $\sim 20$  km per decade over the past 50 years. However, these are estimates of average range shifts for taxa; the responses of species to climate change vary greatly from species to species within taxonomic groups, with the greatest variation in range changes being observed within, rather than between, taxonomic groups (Chen et al., 2011). For example, Chen et al. (2011) found that the median range shifts of groups of British spiders, ground beetles, butterflies, and grasshoppers and allies were all in the region of 25–70 km over a 25-year period. However, within the group of spiders, for example, range shifts among species varied from an expansion of  $\sim 350$  km in one species to a retraction of  $\sim 100$  km in another species, over the same time period and in the same general GB study area.

### **2.3.1 Measuring Changes in Distribution Size**

In general, two metrics of range change have been used by authors wishing to study responses of species to climate: change in the overall size of species' ranges, and change in the location of species' ranges. Many authors have defined distribution size as the number of occupied squares on gridded maps (i.e., area of occupancy), such as the British Ordnance Survey grid map (e.g., Mair et al., 2012), where the spatial resolution of the estimate of areal extent is dependent on the resolution of the underlying data. Others have quantified distribution size slightly differently, as the extent of occurrence of a species, and have measured this by calculating the area within a polygon encompassing the extremities of a species' distribution (e.g., Lyons et al., 2010). However, this assumes that all areas within a polygon are occupied by the species, which may not necessarily be the case, because species will have much more patchy distributions when defined at finer spatial scales (Jetz et al., 2008). Indeed, microhabitat heterogeneity has been shown to be important in determining the fine-scale spatial distribution of many species including plants (Maclean et al. 2015), small mammals (McCain & King, 2014), frogs (Heard et al., 2015), butterflies, ants, grasshoppers and lizards (Thomas et al., 1999).

### **2.3.2 Measuring Change in the Location of Species Ranges**

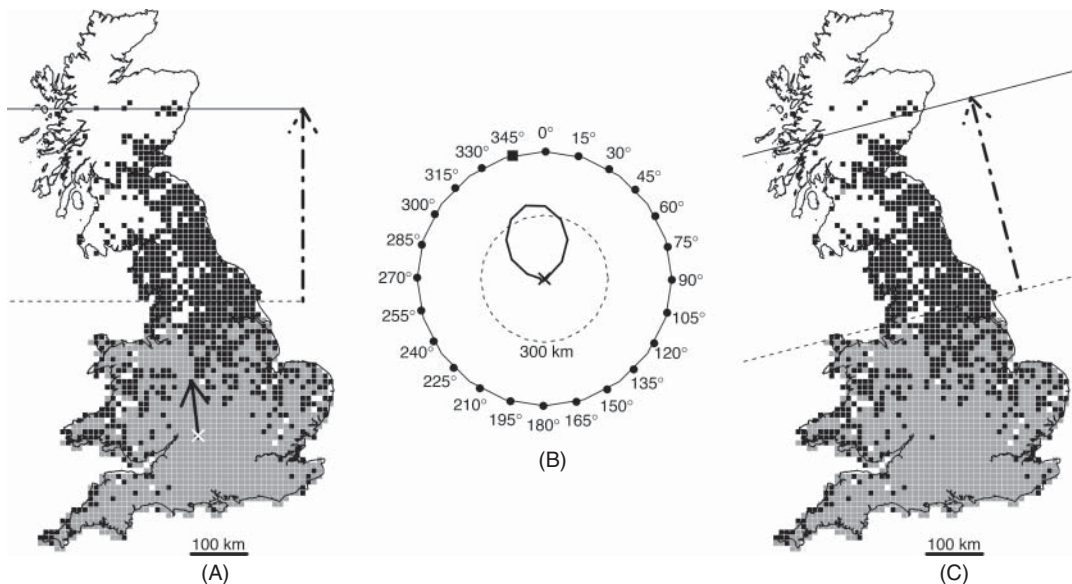
Changes in the locations of species' ranges can be defined by calculating changes in the location of the species' range boundary, or the range core. The vector of change in the location of the centre of a species' range over time has been used to quantify changes in range core locations (e.g., Zuckerberg et al., 2009; Lyons et al., 2010; Mattila et al., 2011; Gillings et al., 2015). Using this approach, Mattila et al. (2011) found that non-threatened butterflies in Finland had shifted their ranges further north than threatened species (30.3 km versus 7.9 km, respectively), and that non-threatened species had shifted in an east-north-east direction ( $73.7^{\circ}$  deg. N) while threatened species showed no consistent angle (i.e., no consistent direction) of change. However, information regarding shifts in the core of the range may not reflect what is happening at the range boundary. For this reason, many studies calculate the change in the location of species' range boundaries, which is expected to be highly sensitive to

climate changes (i.e., to deteriorating climate at species' trailing-edge boundaries, and to improving climate at leading edges).

Arguably the simplest and the most widely used method to measure boundary changes has been to calculate the north/south shift of a species' range boundary between two time periods. This has most often been done by measuring the change in mean latitude of a few (e.g., 10) most northerly or southerly occupied grid squares (e.g., Thomas & Lennon, 1999; Parmesan & Yohe, 2003; Hickling et al., 2005; Franco et al., 2006; Hickling et al., 2006; Mair et al., 2012; Mason et al., 2015). These types of analyses assume that latitudinal shifts are a good approximation of climate changes. However, while latitudinal shifts may be good correlates of temperature change in many regions, species do not necessarily shift their distributions along a north–south axis, because the interaction between changes in temperature and precipitation may result in multidirectional shifts by species (VanDerWal et al., 2013). For example, while species in montane regions have on average shifted upslope to track suitable climates, there is also evidence for down-slope shifts of some species (e.g., Konvicka et al., 2003; Hickling et al., 2006; Chen et al., 2009), possibly to take advantage of local thermal refuges (Dobrowski, 2011). Moreover, invasive species may expand in directions that primarily reflect range infilling patterns rather than climatic limitations (Simmons & Thomas, 2004). In addition, tropical species are expected to have difficulty in reaching suitable climates by latitudinal shifts given the long distances required, and so elevational shifts are expected to dominate (Colwell et al., 2008). Furthermore, focussing on data for a small subset of occupied locations at the range periphery may make estimates of range boundary locations vulnerable to issues of detectability if species distributions are patchy and abundances are low at those range margins. The availability of empty habitats for species to colonise during range shifts, and the shape of the study area may also constrain range boundary shifts and so bias estimates from these relatively simple metrics. For this reason, Gillings et al. (2015) described a new method which allows for estimation of the direction and magnitude of changes in species range boundaries which does not assume north–south shifts, by examining shifts in all directions. Using birds in Britain as exemplar species, these authors calculated changes in the locations of the range margins of species in relation to the full 360° direction over which species could potentially move (Fig. 2.2B), rather than restricting movements to either north or south. Gillings et al. (2015) calculated the mean location of the 20 occupied grid squares furthest along (i.e., closest to the range margin and furthest from the core) each of 24 axes (15° intervals; Fig. 2.2B) running along compass directions centred on the location of the species' range core. In this way, the authors were able to describe the magnitude and direction of range margin shift in multiple directions. Such information allows historical data to be used to examine if species are shifting in different directions, and thus if species may be responding to different aspect of climate and shifting along different environmental gradients. For example in Britain, species responding primarily to temperature might be expected to shift predominantly north–south, depending on which aspect of temperature they were sensitive to, whereas species sensitive to precipitation might be expected to shift along rainfall gradients that run approximately west–east in Britain. The approximately northern shifts of the range margins of British birds were driven by a combination of winter, spring and summer warming, but shifts in the location of the core range of species were not correlated with single climate variables, indicating the individualistic nature of species responses to changes in climate (Gillings et al., 2015).

### **2.3.3 An Invertebrate Example: Quantifying Range Shift by the Comma Butterfly *Polygonia c-album* in Britain**

The choice of method to quantify changes in range boundaries can affect estimates of the direction and magnitude of range shift (Fig. 2.2). We present outputs from the same data analysed in three



**Figure 2.2** Range expansion by the comma butterfly, *Polygonia c-album*, in mainland Britain. Change in distribution is mapped between two time periods: 1970–1985 (grey squares) and 1995–2010 (grey and black squares). To take account of changes in recorder effort over time, in (A) and (C) we only plot well-recorded hectads ( $10 \times 10$  km grid squares; see Section 2.4 for definition of ‘well-recorded’ squares). In (A), the dot-and-dashed arrow denotes a northwards range margin shift of 345 km between the northern range margin in the first (dashed horizontal line) and second (solid horizontal line) time periods. The length and location of the solid arrow in the middle of (A) denotes the location of the range core in 1970–1985 (white cross) and the bearing and magnitude of shift of the range core over the two time periods (98 km at  $353^\circ\text{N}$ ). In (B) the solid line denotes observed range margin change between the two time periods, along each of 24 compass directions ( $0$  to  $345^\circ$ ). These data demonstrate a general shift northwards, with the maximum shift of 356 km occurring along the  $345^\circ$  axis (black square in B). The dotted line in (B) represents a shift of 300 km between the range margins in the earlier and later time periods, along all axes, and is plotted to aid interpretation. In (C), the dot-and-dashed arrow denotes range margin shift of 356 km along the  $345^\circ$  axis, between the range margins in the first (dashed line) and second (solid line) time period. Distribution records were extracted on 16/04/14 from the Butterflies for the New Millennium database.

ways to illustrate this; we calculate: (i) the change in the location of the range core and (ii) changes in range margin locations using the simple north/south method and (iii) using the Gillings et al. (2015) multi-directional method, described above. By presenting these analyses, we illustrate novel ways of analysing historical data that will allow us to gain a much better understanding of species’ responses. We focus on an exemplar invertebrate species, the comma butterfly *Polygonia c-album*, in Britain. This butterfly species is highly dispersive and occurs in a variety of natural and semi-natural habitats in Britain where larvae feed on *Humulus lupulus*, *Urtica dioica* and *Ulmus glabra*. The species reaches a northern range limit in Scotland, and a southern range limit in North Africa. This species has undergone rapid range expansion northwards in the UK over the past few decades (Asher et al., 2001; Braschler & Hill, 2007; Mair et al., 2012) in association with climate warming.

Our analyses of historical data for *P. c-album* revealed that the core of *P. c-album*’s range shifted 98 km over an approximately 25-year period, along a  $353^\circ$  bearing (i.e., approximately north; Fig. 2.2A). However, this shift in the location of the range core of *P. c-album* was much less than the shift at the range periphery. Using the simple north/south method, we estimated that the northern (i.e., leading edge) range margin of *P. c-album* shifted 345 km in Britain between the same time periods (Fig. 2.2A),

consistent with this mobile species responding rapidly to a warming climate (Warren et al., 2001; Braschler & Hill, 2007). Using the multi-directional method of Gillings et al. (2015), the range margin shift was estimated to be marginally greater at 356 km along the 345° axis, in a North-North-West direction (Fig. 2.2B and C). Thus for this species, both methods to calculate changes in the range margin produced broadly similar estimates of range shift, but the simple north–south method was slightly more conservative – a similar conclusion to that reported by Gillings et al. (2015) for birds. However, the multi-directional shift method highlights that *P. c-album* has shifted north-westerly, rather than due north, and this skew is likely to be driven, in part, by the shape of the British coast line. Indeed, the directions in which the greatest proportion of British bird species extended their ranges were also in a similar direction (towards the North-East and West-North-West; Gillings et al., 2015). It would be interesting to carry out these analyses on a broader range of species with different range sizes and in different countries for which range shifts might be less constrained by the location of empty habitats and by coastlines.

Depending on the goal of the study, it may be important that different metrics of range change are calculated, describing different aspects of species' range shifts at the core and the range boundary, as evident for *P. c-album*. In addition, the multi-directional approach we describe in Fig. 2.2 (B and C) could be further developed to take account of species' habitat availability and thus examine direction and magnitude of range shifting that accounts for availability of breeding habitats. Rates of range expansion have been shown to be affected by habitat availability. For example, Hill et al. (2001) found that rates of range expansion by the speckled wood butterfly *Pararge aegeria* in two areas of Britain were up to 45% slower in locations with 24% less breeding habitat (woodland) for this butterfly species. Furthermore, a recent study by Oliver et al. (2015) found that drought-sensitive British butterflies are threatened with extinction due to climate change, but that landscape management – particularly reducing habitat fragmentation – can ameliorate negative climate impacts to improve the probability of species' persistence. Therefore, by taking account of habitat availability it may be possible to gain a better understanding of the role of climate in affecting species' observed and potential future range shifts.

## 2.4 Challenges and Biases in Historical Data

Our ability to detect and describe range shifts is limited by data quality and availability (Fortin et al., 2005). In particular, there are a number of issues that arise due to biases in the taxonomic, spatial and temporal coverage of historical data. In this section, we discuss each of these issues, and their implications for describing and understanding range changes.

### 2.4.1 Taxonomic Bias

As outlined above, there are millions of historical records available for analyses of species' distributions, but data gaps have arisen due to bias in taxonomic coverage (Parmesan, 2006). This is demonstrated by the fact that the majority of studies describing range changes of invertebrates are biased towards a small number of taxonomic groups – usually terrestrial species, and Lepidoptera, in particular. For example, a global meta-analysis of range shifts carried out by Parmesan & Yohe (2003) presented data showing that ~80% of the studies of invertebrate range shifts were of terrestrial rather than marine species. A more recent analysis of range shifts of 1573 species in Britain was biased – due to data availability – towards invertebrates (19 of 21 taxonomic groups studied), and to Lepidoptera in particular (between 40% and 60% of invertebrate species studied, depending on the time period

analysed) (Mason et al., 2015). Marine invertebrates, especially open-ocean species, are often overlooked in studies of range changes (but see e.g., Rivadeneira & Fernandez, 2005; Sorte et al., 2010), despite their important roles as primary producers in those habitats. Thus more studies of a wider range of taxonomic groups are required.

Studies investigating range changes of species often exclude certain groups of species, including ubiquitous species (because there are limited opportunities for range shifting and colonising empty locations); rare species (because of data quality and methodological issues with calculating shifts); migrants (for which it is often difficult to determine breeding range); upland species (for which range shifts uphill are more likely than latitudinal shifts); species that cannot be recorded from ground-based surveys (e.g., canopy species); and species with insufficient data (e.g., Mair et al., 2014; Mason et al., 2015). Many species with insufficient data are often invertebrate species that are ecologically interesting and play important roles in ecosystem functioning, such as processing of organic material, pollination, and as prey items. Sutherland et al. (2015) have recently highlighted the need to identify and carry out surveys for understudied taxonomic groups.

However, along with recognition of the need to collect distribution data for these groups, we also require species-specific information on the taxonomy and ecology of these species (such as life history traits and behaviour; Sutherland et al., 2015), in order to interpret range shifts and to gain a better understanding of mechanisms and environmental drivers of species' responses to climate change, and the consequences for ecosystem functions. Indeed, an additional data-quality issue is the potential for misidentification of species, and therefore potentially incorrect information on the distribution of species (e.g., Johnson, 1993; Meier & Dikow, 2004). As such, many of the current recording schemes have incorporated data validation steps into their data-processing software, and there are an increasing number of online forums, apps and websites (e.g., [www.ispotnature.org](http://www.ispotnature.org)) which allow communities of recorders to help identify species (Sutherland et al., 2015), and reduce misidentification.

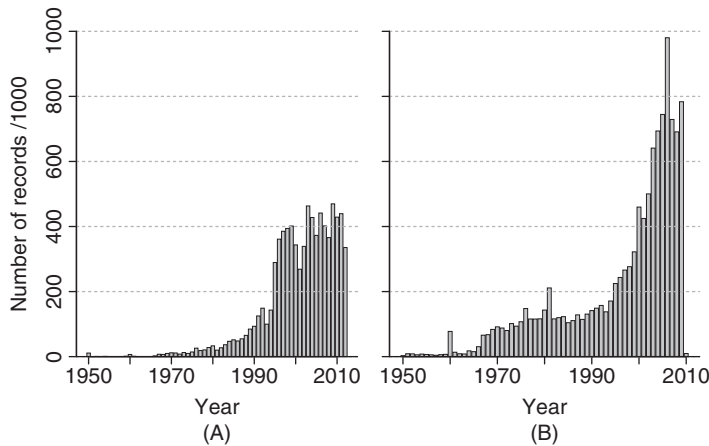
#### **2.4.2 Spatial and Temporal Biases**

In addition to taxonomic biases, there are also biases in the spatial location of records. As we previously mentioned, there is a bias towards terrestrial studies of range shifts (Parmesan, 2006), which stems from, and results in, a relative lack of information of the range shifts of marine invertebrates. However, there are also large discrepancies in the distribution of terrestrial studies and data availability worldwide (Sutherland et al., 2015); the majority of data – and therefore published studies – are from English-speaking locations, and where the gross domestic product (GDP) and security levels are high (Amano & Sutherland, 2013).

Range changes of species in tropical areas are relatively understudied (Colwell et al., 2008; Freeman & Freeman, 2014). Species in these areas are expected to exhibit different rates of change resulting from moisture- rather than temperature limitation (Chen et al., 2011), and so generalisations made from studies outside the tropics may not apply to these species – more data are required to study this. The rise of citizen science projects and new ways to record and identify species (e.g., using DNA barcoding methods) may help amass data for currently poorly studied taxa (e.g., Ji et al., 2013; Tang et al., 2015), recognising that recording species in hyper-diverse tropical regions is challenging because of problems with identification and taxonomy of many invertebrate taxa in these regions.

Historically, naturalists often focussed their data collection in easily-accessible and relatively bio-diverse areas, but more recent surveys are often randomised, increasing the representation of species in different locations and across environmental gradients (Rocchini et al., 2011). However, often there are still geographical biases in data collection for many species groups (e.g., Hill et al., 2010), arising from biases in the spatial location and activity of recorders. Such spatial biases need





**Figure 2.3** Number of (A) butterfly and (B) moth records per year since 1950 (records prior to 1950 are not shown) in the UK. Butterfly records were extracted on 16/04/14 from the Butterflies for the New Millennium database, and moth records were extracted on 08/10/13 from the National Moth Recording Scheme database.

to be taken into account when estimating range shifts, because the (historical) absence of a species in a given location may be due to under-recording, rather than its true absence in that location.

There have been huge increases in the number of records of species collected over time (e.g., Hill et al., 2010), primarily driven by the development of new technologies allowing for faster, easier and cheaper data collection (August et al., 2015). For example, the number of records of butterflies and macro-moths held by Butterfly Conservation in the UK has increased dramatically since the 1970s (Fig. 2.3), and new initiatives to engage amateur observers in data collection will further contribute to these increases in data records (e.g., [www.bigbutterflycount.org](http://www.bigbutterflycount.org), [newforestcicada.info](http://newforestcicada.info) and [www.harlequin-survey.org](http://www.harlequin-survey.org)).

### 2.4.3 Accounting for Temporal and Spatial Biases

For reliable estimates of range changes, ideally there would be complete spatial and temporal coverage at the relevant spatial and temporal scale for the organism of interest, with no spatial or temporal biases. However, this is rarely the case, and temporal and spatial biases must therefore be taken into account (or caveats accepted) when analysing and interpreting historical data on species' ranges. In a few well-studied systems (e.g., birds in the UK), researchers can analyse data obtained through fixed-effort sampling over space and time (Gillings et al., 2015). However, in most other systems, data are collected in a sporadic way, with considerable variation in effort over both space and time.

Earlier on in this chapter we defined historical datasets as those with records spanning the past four to five decades, and as such, many of the examples of distribution changes we have discussed have been calculated over this period. However, as Hickling et al. (2006) state, there needs to be a compromise between leaving a sufficiently large gap between time periods so that range changes can take place, but not so large that substantial amounts of data are excluded. For example, in a recent meta-analysis by Poloczanska et al. (2014), the authors used only the observations from datasets which comprised at least 19 years of data to ensure sufficient time for range changes to be manifest. In general, studies using a longer span of data will be more informative than those using a shorter span of data, and so continued data collection and reporting is essential to increase the robustness of our conclusions about range changes.

Another challenge in analysing range changes using distribution data stems from the fact that recorder effort has increased dramatically in recent decades (e.g., Fig. 2.3). To account for this variation in effort, some studies group data and analyse range changes that occur between time periods rather than analysing annual data (e.g., Mason et al., 2015). Choice of time periods for grouping data may coincide with drives to collect data for taxon-specific Atlases (Isaac et al., 2014; Gillings et al., 2015), because large drops in effort often occur after these Atlas periods. By grouping data in these ways, biases associated with inter-annual variability in both recording effort and species' occurrence can be reduced. While grouping data into discrete time periods is a fairly simple way of dealing with inter-annual variation, more complex methods have been developed to account for temporal changes in recording effort. For example, increases in recording effort over time can be accounted for by sub-sampling locations from the latter time period to match the areal extent and recorder effort of the earlier time period (e.g., Warren et al., 2001); analysing data from only those locations that were visited in all time periods being studied prevents the incorrect assumption that a new sighting of a species is a colonisation when in fact no earlier record exists because the site was not visited (i.e., removing false 'absence' records). However, a single visit may not provide sufficient information to capture a true reflection of a species' presence or absence in a location, especially if the species has low detectability. As such, one can set further limits on how often each location needs to be surveyed before it is included in an analysis. Hickling et al. (2006) set several different thresholds for inclusion/exclusion of locations into analyses, to investigate the consequences of being more or less strict in data selection. Being too strict might be expected to reduce statistical power if too many data are excluded, whereas not being sufficiently strict might introduce too many biases and 'noise' into analyses. Hickling et al. (2006) defined locations as either 'recorded', 'well-recorded' or 'heavily-recorded', depending on whether one species, 10% of species, or 25% of species in the taxonomic group of study were recorded at locations. This approach has since been refined (Mason et al., 2015) to take into account regional variation in species richness, by defining 'well-recorded' locations as having records of 10% of the local species pool, rather than 10% of total UK species richness (Fig. 2.2 uses these 'well-recorded' squares). We demonstrate the consequences of these different thresholds for data on UK butterflies; Fig. 2.4 shows how recorder effort declines from south to north (e.g., comparing A and C; which primarily reflects the density of recorders and centres of human populations in Britain). Fig. 2.4 also shows how refining the method to account for regional species richness rather than total species richness increases the number of locations included in analyses, particularly in northern Britain (black circles in Figs 2.4B & C; reflecting the low diversity of butterflies in these cool and wet northern and upland regions; Fig. 2.4).

Other statistical methods to measure and account for spatial and temporal biases have also been developed (see the review by Isaac et al., 2014). For example, Hill (2012) developed the '*Frescalo*' method to assess and account for bias in recording effort (available from: [www.brc.ac.uk/biblio/frescalo-computer-program-analyse-your-biological-records](http://www.brc.ac.uk/biblio/frescalo-computer-program-analyse-your-biological-records)). Using this approach, a list of 'benchmark' species around each location are defined as those expected to also be present in the focal square, given similarities in environmental attributes, elevation, etc. (Hill, 2012; Balmer et al., 2013). Recording effort can then be estimated as the proportion of benchmark species found at a given location, and the observed frequencies of occurrence adjusted in order to obtain corrected occurrence trends over time (Fox et al., 2014). If all benchmark species were recorded in the focal square in one time period, but only a fraction of them were recorded in another, this indicates a reduction in recording effort in that focal square over time (Balmer et al., 2013). As such, this method can be used to determine spatial patterns in recording effort, as well as changes in recording effort over time, allowing for the production of corrected occurrence trends. This method has been implemented to determine the