

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 (CO₂).

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 CO₂ 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 CO₂ production. Increased uptake of CO₂ by the oceans will increase the acidification of the oceans; and (viii) future surface temperatures will be largely determined by cumulative CO₂, which means climate change will continue even if CO₂ emissions are stopped. This may be a moot point, however, since 2015 saw the largest ever annual increase in atmospheric CO₂ (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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂, 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 CO₂ 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 CO₂ 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 preceding 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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