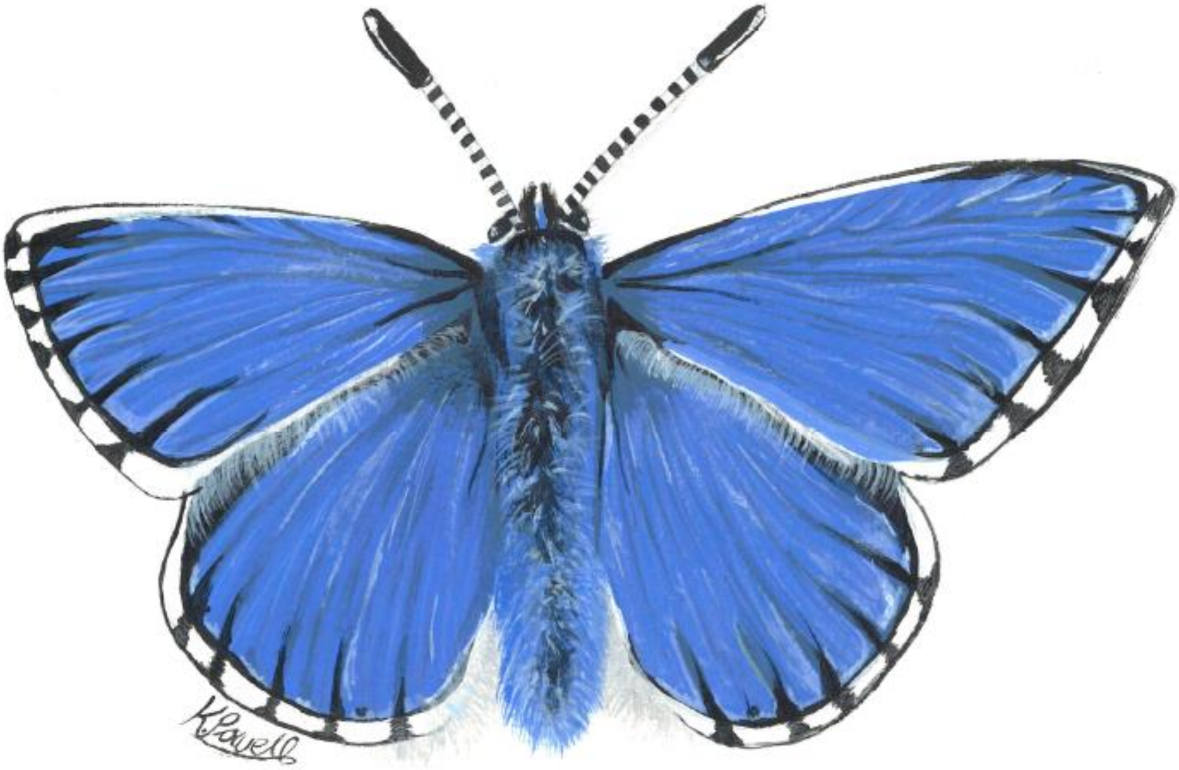
UNIVERSITY OF READING

Insect declines: an exploration of diversity in trends and traits through time

Kathryn Elizabeth Powell



A thesis submitted for the degree of

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Primary supervisor: Dr David Roy

Additional supervisors: Prof Tom Oliver,
Dr Manuela González Suárez, Mr Tim Johns

Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

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Kathryn Elizabeth Powell

Acknowledgements

Over the last few years, I’ve been supervised and supported by the most amazing group of people, without whom I wouldn’t have been able to get to this point at all. I want to thank you all from the bottom of my heart.

To all my supervisors who have been there for me every step of the way. Firstly, David. I honestly couldn’t have wished for a better supervisor than you. You somehow managed to create a perfect hands-off supervisory technique where you let me grow and develop as an independent researcher, whilst never letting me feel alone. You have always, *always* been there when I needed you. You trusted my judgement on chapters, encouraged me to come up with new ideas, and you listened quietly and offered nothing but kind words of encouragement when I came to you with problems, sometimes in tears. You even supported me fully through the tragic death of a friend and fellow student at UKCEH. Thank you for always believing in me and, most of all, for making me finally believe in myself! I can only hope that if I’m ever lucky enough to manage or supervise people in the future I can do even half as good a job as you.

Tom, you’ve always stunned me with your ability to concoct creative ideas, helping to improve the scope of the thesis a million times. Never once have you doubted me and my ability to do this thing, your ambition and unwavering confidence helping me to stick it out through the tough times and take advantage of the good times to succeed. I admire you for all the many different things you do, from science to policy work and even writing books, and want to thank you wholeheartedly for giving me the opportunity to learn from you.

Manuela, thank you for agreeing to come onto the supervisory team when I started the PhD. I am so, so glad that you did. Your impeccable eye for detail and the time and care you dedicated to helping me with my work has improved every single piece of writing I’ve done for the PhD ten-fold. You were always sure to return a piece of work at the start with a kind disclaimer that you tend to ‘over-edit’, trying to ease me into your style. But you never once over-edited; you were just always putting in everything you had to help me improve, and I’ll always be grateful for that. Your obvious commitment to your work and your students inspires me to one day be as dedicated as you. Thank you for everything you’ve done for me.

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As my supervisors, I hope you are all proud of me, and of this thesis, which is a huge collective effort from us all.

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I have many co-authors of either published or potential papers in this thesis to thank, who are outside of my supervisory team. Marc in Canada, a very special thanks for everything you’ve contributed – not only to the two chapters with your name on them, but to my personal and professional development. I’ve enjoyed working with you so much this past year, and I’ll forever be grateful that you agreed to take me into your fold for 3 months in Sherbrooke, despite coming back with a piece of my finger missing! You taught me a lot in such a short space of time, and you always make me strive to be better. Maxim, I’ll never forget the time I spent at the Insectarium; thank you for showing me something different from my day-to-day and opening my eyes to the potential of research and communication to benefit the wider community. Some of the happiest days of my PhD have been spent surrounded by the fluttering of thousands of butterfly wings in the vivarium, and I have you to thank for this. Dom and Nick – somehow, you both managed to reignite in me a love for maths and algebra that I was *so* sure was dead and buried under the weight of my A-levels. Thank you both for working with me on what might be my favourite chapter of the thesis in the end, and for teaching me so much. Judy, Marc B, Colin, Richard, Dan, Yueming and Andrew - thank you for all the time and effort you’ve given; I’ve loved collaborating with you all on the work that we’ve done together. You’ve all contributed something unique and amazing to the manuscripts and I am so thankful for the opportunity to work with you.

Doing a PhD can be tough at times, especially during a global pandemic, but is made so much lighter by having supportive colleagues. The student community at UKCEH has something special that I hope it never loses. There are too many people in this group to individually acknowledge, but I want you to know that you’ve all played such a special role in my life the last few years. I’ve made some life-long friends in this community, and our mutual love and support for each other is one of the greatest gifts I will have received from my time spent here. We’ve stuck together through the highs and the lows, providing each other with comfort and support, even through the very darkest of times. Doug, I wish you could know the imprint you left on our lives. I wish you could understand what you meant to us and see your legacy at UKCEH, including a meadow full of ragwort and cinnabar moths. Your weird cactus is still thriving in the office, though it sits on my desk now. An inspiration always, and my reason for now loving moths.

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Impact statement

Academic Publications

Of the five research chapters in this thesis (Chapter 2, Chapter 3, Chapter 4, Chapter 5, and Chapter 6), one is published, and two are currently submitted to journals and under peer review at the time of writing.

The published paper is Chapter 2:

> **Powell, K. E.,** Johns, T., González Suárez, M., Oliver, T. H., & Roy, D. B. (2022). Abundance trends for river macroinvertebrates vary across taxa, trophic group, and river typology. *Global Change Biology*. https://doi.org/10.1111/gcb.16549

The two under review are Chapter 3 (*Journal of Insect Conservation and Diversity*), and Chapter 5 (*Ecology and Evolution*). There is a preprint available for Chapter 3, although the text was altered before resubmission to Journal of Insect Conservation and Diversity and subsequent addition to this thesis, to improve the narrative of the paper. The reference for this preprint can be found below:

> **Powell, K. E.,** Garrett, D., Roy, D. B., Oliver, T., Larrivée, M., & Bélisle, M. (2023). Complex temporal trends in biomass and abundance of Diptera driven by the impact of agricultural intensity on community-level turnover [Preprint]. Preprints. https://doi.org/10.22541/au.168206055.54698060/v1

Other publications

This PhD was crucial in my undertaking of a POST fellowship. From this experience, the following publication was produced:

> **Powell, K.E.,** & Wentworth, J. (2021). Local nature recovery strategies [POST note]. Parliamentary Office for Science and Technology, UK Parliament. https://post.parliament.uk/research-briefings/post-pn-0652/

Grants

I was successful in securing an award to conduct a project in Canada through the Globalink Doctoral exchange scheme in 2022. This was a joint award that contained two parts, granted by UKRI and Mitacs.

Globalink Doctoral Exchange Scheme Grant (1) Awarded August 2022
Total funding: GBP 8,000

Funding agency: UKRI
Grant reference: NE/X007553/1
Research institution: University of Reading
Co-investigators: David Roy, Marc Bélisle, Maxim Larrivée
Secondary institutions: Université de Sherbrooke, Espace pour la vie, UK Centre for Ecology & Hydrology

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Grant reference: FR98096
Research institution: Université de Sherbrooke
Co-investigators: Tom Henry Oliver, Maxim Larrivée, David Roy
Secondary institutions: UK Centre for Ecology & Hydrology, Espace pour la vie, University of Reading

Personal Impact

As well as my belief that this thesis has contributed in some way to our scientific knowledge of insect population changes and functional ecology, I am pleased to say that the process of producing it has impacted my life considerably through improving my knowledge and skills in research. I have learned how to process large datasets of temporal and spatial data in R, honed my coding and statistical skills, found new ways of modelling data, trifled with techniques to understand causal inference like using path analysis and have begun to introduce theoretical approaches to my work to sit alongside empirical examples. I have gained confidence in communicating about the biodiversity crisis and my contribution to the field of insect declines and functional ecology, and now thoroughly enjoy doing so at events like international conferences. I have nurtured my growing enthusiasm for making policy-impact, and have dabbled in several ways of doing so, including producing policy briefings for parliament, and being involved in policy research groups. I’ve had the chance to travel and live in Canada through a small research grant during my PhD, making a network of colleagues there that I hope to continue to work with in the future. I’ll be forever grateful for the immense opportunity to learn and grow over the last few years, and am excited for whatever comes next, regardless of the outcome of the defence of this thesis.

Author Contributions

Chapter 2: Abundance trends for river macroinvertebrates vary across taxa, trophic group, and river typology

This work was conducted in collaboration with Tom Oliver (University of Reading), Tim Johns (Environment Agency), Manuela González Suárez (University of Reading), Judy England (Environment Agency) and David Roy (UK Centre for Ecology and Hydrology). I conducted all data processing, statistical analysis, interpretation and writing of the manuscript; D.R. and T.J. conceived the original ideas behind the paper that became this chapter; T.J. and J.E. helped with the background and the interpretation; T.O. helped with statistical analysis; M.G.S. helped with interpretation of results and all authors contributed to review of the manuscript. The chapter is published as a paper in Global Change Biology (https://doi.org/10.1111/gcb.16549) and is included in this thesis in its final form for publication.

Chapter 3: Complex temporal trends in biomass and abundance of Diptera driven by the impact of agricultural intensity on community-level turnover

This work was conducted in collaboration with Daniel Garrett (University of Saskatchewan), David Roy, Tom Oliver, Maxim Larrivée (Insectarium de Montréal) and Marc Bélisle (Université de Sherbrooke). I contributed to the conceptualisation of the project, and conducted all data analysis, interpretation and writing of the manuscript. D.G. conducted all data processing prior to analysis and helped with interpretation of results. D.R. and T.O. reviewed and edited the work; M.L. gave provisions to the project and M.B. conceptualised the ideas and contributed to the interpretation of the findings. All authors contributed to review of the manuscript prior to submission to a journal (Insect Conservation and Diversity, at the time of writing). Manuela González Suárez also reviewed this manuscript.

Chapter 4: Diptera communities lose larger species and homogenise under agricultural intensification

This work was conducted in collaboration with Dominic Brass (UK Centre for Ecology and Hydrology), Nick Isaac (UK Centre for Ecology and Hydrology) and Marc Bélisle. I conducted the mathematical modelling and the writing of the manuscript. D.B. helped build the theory and the modelling for 'scenario 1' and contributed toward the interpretation of our findings; N.I. conceived the ideas behind the manuscript, and M.B. supervised the work and contributed to editing. All authors, as well as Tom Oliver, Manuela González Suárez, and David Roy all helped review this manuscript.

Chapter 5: Asynchrony in terrestrial insect abundance corresponds with species' traits mediating exposure and sensitivity to environmental perturbations

This work was conducted in collaboration with Tom Oliver, Manuela González Suárez, Richard Comont (Bumblebee Conservation Trust), Colin Harrower (UK Centre for Ecology and Hydrology), Marc Botham (UK Centre for Ecology and Hydrology), and David Roy. I conceptualised the idea behind the manuscript, conducted data processing and all analysis, and wrote the manuscript. R.C., C.H. and M.B. all contributed to raw data processing and interpretation of results, and T.O., M.G.S. and D.R. contributed to reviewing and editing the manuscript before submission to a journal (Ecology and Evolution, at the time of writing).

Chapter 6: Predicting trends in ecosystem function provided by lepidopteran and freshwater insect communities

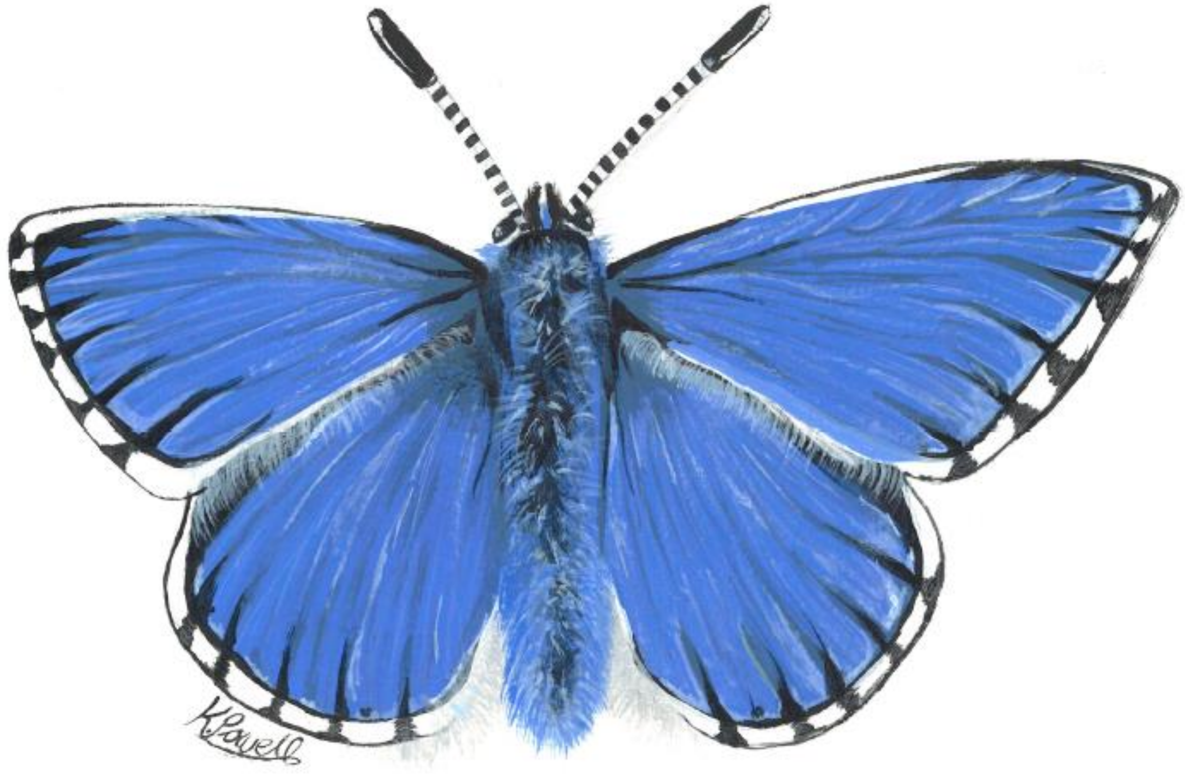
This work was conducted in collaboration with Yueming Qu (UK Centre for Ecology and Hydrology), Arran Greenop (UK Centre for Ecology and Hydrology), Manuela González Suárez, Tom Oliver, and David Roy. I conceptualised the manuscript, conducted all processing of abundance data and terrestrial taxonomic trait data, conducted all processing of code and the statistical analyses, and wrote the manuscript. Y.Q. processed the freshwater taxonomic trait data and the land cover map 2016 data and co-wrote the relevant parts of the methods in the manuscript; A.G. helped conceptualise the hypervolume methods and contributed toward R scripts, M.G.S. helped with interpretation of findings, and M.G.S., T.O. and D.R. all reviewed and edited the manuscript.

Contents

Abstract

Biodiversity is undergoing rapid transformation due to human activities, and yet healthy, biodiverse systems are essential for humankind. Although evidence is lacking for most parts of the world and many species groups, the evidence we do have for biodiversity change shows that not only are vulnerable species disappearing at unprecedented rates, but the abundance of what were once common species is declining. This is potentially disrupting the processes on which the functioning of ecosystems relies. Insects and other arthropods are diverse organisms that are essential for providing ecosystem functions and are under threat from an array of environmental pressures. Yet, the scope of declines and their wider impacts are not fully understood. In this thesis, I aim to address knowledge gaps around the extent of insect declines and the relationship between insect abundance, diversity, and ecosystem functions, by focussing on functional traits. Chapter 1 introduces the current literature around the relationship between biodiversity and ecosystem function and the recent exploding interest in insect declines, pointing out the major sources of controversy in this area. In Chapter 2, I explore how the abundance of freshwater insects and other invertebrates has changed over time in England. I reveal heterogeneity in trends amongst different taxa, trophic groups and across different river systems, warning against sweeping statements of declines. In Chapter 3, I investigate how environmental pressures impact insect communities, quantifying change in abundance and biomass of Diptera under intensive agriculture in Québec, Canada. Chapter 4 expands on this, using theoretical relationships between body size, population size and the number of species to predict declines in the number and population sizes of large species and a positive impact on small species of Diptera. Chapter 5 demonstrates that diversity in functional traits, such as body size, can contribute to resilience in insect communities by being positively associated with population asynchrony. In Chapter 6, I predict how functional diversity described by trait spaces has changed over the past few decades under abundance change for a variety of insect taxa in the UK. The final chapter summarises the key findings and presents thoughts on the direction of future research and conservation actions. Overall, the thesis extends our understanding of the consequences of insect declines, imparting evidence that links environmental drivers of biodiversity change through to the undermining of long-term functional resilience.

Chapter 1



Chapter 1

Introduction

The global biodiversity crisis

Out of an estimated 8 million animal and plant species, 1 million are potentially under threat of extinction (Ferrier et al., 2019). There is emerging consensus that we are currently witnessing the 6th mass extinction on planet earth (Barnosky et al., 2011; Ceballos et al., 2015a; Johnson et al., 2017), and, due to the recognised anthropogenic influence on this global change (Díaz et al., 2019), the dawning of a new geological epoch known as the 'Anthropocene' (Lewis & Maslin, 2015). Moving beyond extinction rates and species loss, abundance of individuals is declining at an equally alarming rate according to the WWF's 'Living Planet Index', suggesting an average 69% decline has taken place since 1970 for 16,000 species (WWF, 2022). This is greatly concerning, as such change not only indicates the increasing potential for future extinctions (Ferrier et al., 2019), but the deterioration of ecological interactions and, consequentially, vital ecosystem functions and services (Valiente-Banuet et al., 2015).

The causes of the ecological crisis are embedded in human activity, and are comprehensively synthesised in the recent Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services Global Assessment (IPBES, 2019). Land-use change, particularly agricultural expansion, is the lead cause of biodiversity loss on land (Foley et al., 2005; IPBES, 2019; Pimm & Raven, 2000), followed by the direct species exploitation and resource extraction through activities such as wild-harvesting, hunting, logging, fishing, and forestry (Bradshaw et al., 2009; WWF, 2022). Industrial fishing is the largest cause of marine biodiversity loss (IPBES, 2019). Climate change is also increasingly recognised as a major driver of biodiversity change around the world, both directly and indirectly through interaction with other causes of biodiversity loss, particularly land / sea use change and habitat removal (Bellard et al., 2012; Newbold et al., 2019; Oliver & Morecroft, 2014). Other drivers such as invasive non-native species and pollution are also important causes of biodiversity change

(Capinha et al., 2015; IPBES, 2019; Simberloff et al., 2013). Although awareness and recognition of these anthropogenic impacts on biodiversity has increased over recent decades, the drive for unbounded economic expansion by governments around the world is continuing to stimulate the unsustainable exploitation and consumption of natural resources that lies at the root of these drivers (Dasgupta, 2021).

Insect Declines – What does the evidence say?

Due to the historical bias in biodiversity research toward vertebrates, most empirical evidence for ongoing biodiversity loss and consequential conservation efforts are directed by population data from this taxonomic group (Leather, 2013; Stefano et al., 2023). Invertebrates, however, make up the majority of animal life on earth; insects alone make up an estimated 75-90% of all animal species, and yet we currently lack a unified consensus over how insects fare in the biodiversity crisis, at both global and regional scales (Stork, 2018; Stork et al., 2015; Wilson, 1987). However, a spate of articles in recent years on this topic have been partly motivated by findings of researchers in Germany, who reported a 76% loss in flying insect biomass in under 3 decades in 2017 (Hallmann et al., 2017). The emergence of papers such as Lister & Garcia (2018) and Sánchez-Bayo & Wyckhuys (2019) led to sensationalist headlines that insect populations were suddenly and inexplicably collapsing on a global scale, and the coining of terms such as ‘Ecological Armageddon’ (Leather, 2018).

In spite of the findings of some of these articles being disputed due to some inadequate methodologies and interpretation (see Mupepele et al., 2019; Simmons et al., 2019; Thomas et al., 2019), the message emerging from this trend is important, and the notion that insects and other arthropods are suffering declines in both diversity and abundance has been recognised among entomologists for nearly two decades (Conrad et al., 2006; Fox, 2013; Kunin, 2019; Potts et al., 2010; Shortall et al., 2009; Wagner, 2020). In line with the findings of the IPBES report, land use change is considered the most significant driver of insect biodiversity loss, with climate change exacerbating its effects on insect populations (Outhwaite et al., 2022; Raven & Wagner, 2021; Wagner, 2020). Particularly, the intensification of agricultural practices, which comes with habitat and resource depletion, monoculturalisation, soil degradation and increased use of chemical fertiliser and pesticides, can be devastating to insect populations (Goulson, 2019; Tscharntke et al., 2005). Such expansion of hostile land use around the world reduces the capacity of insects to escape the encroaching effects of climate change, such as intolerable background temperatures and heightened and more frequent weather extremes (Newbold et al., 2019; Outhwaite et al., 2022; Raven & Wagner, 2021).

Despite the headlines on insect declines, some studies indicate that there may be some variation in the direction of insect trends. For example, increases in the abundance of freshwater insect species have been found using meta-analyses of data from a wide range of surveys (van Klink et al., 2020), with a similar conclusion being made for the occupancy of freshwater insect species in the UK (Outhwaite et al., 2020), and there is some indication that study sites in North America show no net decline in insects (Crossley et al., 2020). What's more, studies claiming substantial declines in insect populations have been disputed by others, who suggest such trends are rendered not significant once certain previously ignored factors are taken into consideration (Daskalova et al., 2021; Seibold et al., 2019). The ways in which trends in insect populations and biodiversity have been measured, the quality of the data and the temporal, spatial and taxonomic scales used in analyses may partly help explain heterogeneity across studies in the conclusions around insects (Didham, Basset, et al., 2020). The question of how wide-ranging these declines are across taxonomic, temporal and spatial scales is difficult to answer without further extensive examination of long-term data where it already exists (mainly in northern and western Europe and North America), and rigorous data collection where it is lacking (for example in tropical and subtropical regions; Didham, Basset, et al., 2020; Wagner, 2020).

Insect-mediated ecosystem functions and services: Why are insect declines so important?

Insect declines, although inherently important from the perspective of conserving the planet's extraordinary diversity, could potentially be disastrous from a wider ecological point of view. Insects and other types of arthropods, through playing key roles in ecosystem functioning, are vital for the provision of essential ecosystem services – i.e., the direct and indirect contributions of natural ecosystems to human well-being (see Table 1). Insects play key roles in plant pollination services, including pollinating a large proportion of commercially viable crops (Fijen et al., 2018); are necessary for nutrient recycling through the turnover of plant and animal material into nutrients for other species (through predation, herbivory and decomposition, e.g. Stadler & Michalzik, 2000); provide pest control services (Ramsden et al., 2017); and are a vital energy source for many keystone predators (Garrett et al., 2022; Jackson & Resh, 1989; Macadam & Stockan, 2015).

The sheer abundance and diversity of insects make them an inherently key component and foundational unit of almost all ecosystems across the planet; it is easy, therefore, to speculate on how the removal or decline of insect species could disrupt entire networks of organisms and potentially lead to the collapse of ecosystem function (Cardoso & Leather, 2019; Goulson, 2019). However, given a lack of lack of long-term data for insect-mediated ecosystem functioning, there are large gaps in our understanding of whether insects are declining at unprecedented rates and how this impacts the provision and resilience of related ecosystem functions.

The biodiversity-ecosystem function relationship: Insects and beyond

Understanding the relationship between biodiversity and ecosystem services generally is important for postulating how vital functions and services provided by insects may be affected by insect biodiversity and population change. Such a relationship is thought to be complex and is often context-dependent, and while they have been well-documented for plant species (Lavorel, 2013), there are fewer empirical examples demonstrating our understanding within the animal world, especially for insects (Brousseau et al., 2018; Noriega et al., 2018a).

Table 1. Summary of a range of ecosystem functions and services provided by insects with some examples from the literature.

Ecosystem service type	Ecosystem Function	Example taxa	Key References
Provisioning	Direct food provision	Blattodea, Hemiptera	(Fombong & Kinyuru, 2018).
	Livestock feed	Diptera (e.g., Stratiomyidae)	(Lalander et al., 2019).
	Medicine	Diptera	(Sun et al., 2014)
Supporting	Seed dispersal	Hymenoptera	(Leal et al., 2014)
	Sediment filtration	Freshwater insects e.g., Trichoptera	(Macadam & Stockan, 2015)
	Soil water infiltration	Blattodea	(Cheik et al., 2018)
	Dung removal	Coleoptera	(Carvalho et al., 2020)
	Nutrient recycling	All	(Dreyer et al., 2015)
	Decomposition	Blattodea, Coleoptera, Collembola, Thysanura	(Ulyshen & Wagner, 2013)
Regulatory	Pollination (e.g., of economically important crops)	Hymenoptera (e.g., Apoidea) Lepidoptera	(Fijen et al., 2018)
	Pest Control (e.g., predation and parasitism)	Hymenoptera Coleoptera	(Ramsden et al., 2017)
	Prey species for apex predators	Ephemeroptera, Diptera, Trichoptera (& General)	(Michel & Overdorff, 1995)
	Herbivory	Hemiptera, Lepidoptera, Coleoptera	(Carson & Root, 1999)
Cultural	Ecotourism	Lepidoptera, Diptera	(Nallakumar, 2003)
	General wellbeing	(General)	(Morley et al., 2013)
	Education	(General)	(Macadam & Stockan, 2015)

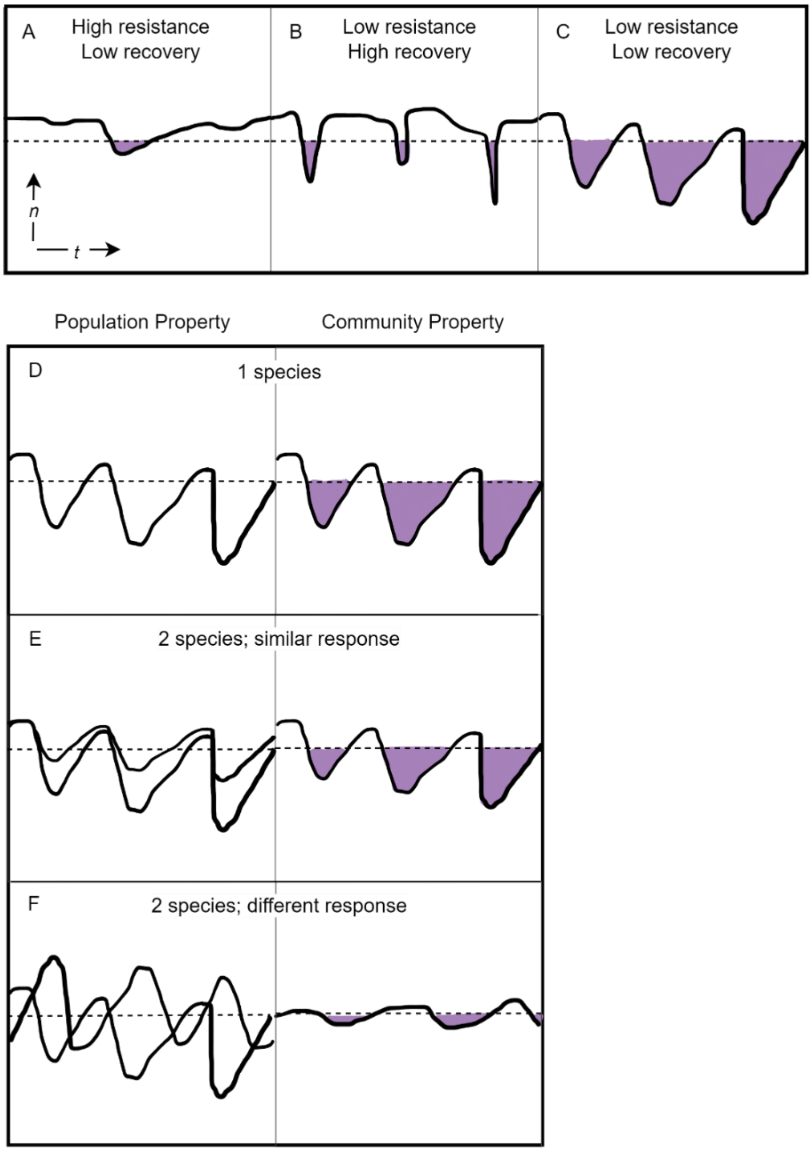


Figure 1. Simplified demonstration of the concept of resilience, and how biodiversity can support it, using abundance of a population or community (*n*) through time (*t*). The resilience of a population, community, or the function it provides, can be described as a combination of resistance (A) and recovery (B). The dotted line represents the hypothetical community abundance level required for the provision of a particular function; the shaded areas are where the abundance is insufficient, and, therefore, represent the level of functional deficiency. With low resistance and recovery in the abundance of species in communities, i.e., low resilience, there is greater functional deficiency over time (C). D-F show how increasing the number of species (left-hand side) can lead to greater resilience (right-hand side) and lower functional deficiency, and this occurs particularly when species are responding differently in time to drivers of abundance change (F). Figure concept adapted and synthesised from Oliver, Heard, et al. (2015) and Hooper et al. (2005).

Richness of taxa, genes, traits

In general, biodiversity change can alter the *level* and the *resilience* of ecological functions (Oliver, Isaac, et al., 2015). ‘Resilience’ of ecosystem functions is broadly defined as the ability of an ecosystem function or service to persist at the same level of production following an environmental perturbation and is comprised of ‘resistance’ (the ability to remain unchanged; Figure 1A) and ‘recovery’ (the ability to ‘bounce back’ to previous levels of function; Figure 1B). Resilience can be created through:

- Functional Redundancy**:** where there is a buffer zone for an ecosystem function to continue after an environmental perturbation, due to an *excess* of present species, genes, or traits providing an equal function in the event of general species loss (Biggs et al., 2020).

- Complementarity: Resulting from spatial or temporal niche partitioning, species can co-exist and ‘complement’ each other to increase the mean community abundance over time, as well as resulting in an ‘insurance’ policy. When the occurrence of a particular environmental perturbation varies in space or time, it may negatively affect one species but not others (or even favour others), and so the unaffected species persist and continue to provide the function. This can also be described as the ‘portfolio effect’ (Figure 1D - F), where a greater number of species results in a more stable community abundance (Thibaut & Connolly, 2013).

A resilient suite of functional traits

Species possess physiological, behavioural, and ecological characteristics which can be described as ‘functional traits’ with respect to an associated function. ‘Response traits’ may affect how an individual’s fitness responds to environmental change, and can therefore influence how a population changes under certain environmental stressors (McGill et al., 2006), whereas ‘effects traits’ determine the impact an organism has on ecosystem processes

(Díaz & Cabido, 2001). The fact that some traits can be both response and effects traits, or indeed that there is high correlation between the possession of certain response and effects traits due to the inheritance of trait combinations under evolutionary processes, is assumed to make ecosystem functions vulnerable to collapse under environmental perturbations (Díaz et al., 2013).

Functional redundancy or complementarity may become inconsequential to ecological resilience in a situation where the set of 'buffer' species possess a limited number of response traits – for example, all species in one community being susceptible to a weather event, such as a drought, due to the effects of environmental filtering on the types of traits present in the community (Hooper et al., 2005). This effect is demonstrated in Figure 1E, where even though an increased number of species are present, the similarity between their abundance dynamics leads to restrictions on the change in resilience (Loreau & De Mazancourt, 2008; Loreau & de Mazancourt, 2013). Logically then, differences in the response of species to environmental perturbations is thought to contribute to the resilience of a community or an ecosystem and its functions (Elmqvist et al., 2003; Walker et al., 1999, Figure 1F). This has been found in soil invertebrate communities, where complementarity of a diverse range of traits in a population can result in higher multi-functionality in an ecosystem (Heemsbergen et al., 2004), and in pollinator communities where response diversity - measured as population asynchrony - results in stabilisation of the pollination process (Winfree & Kremen, 2009), and trait diversity itself corresponds with increased pollination effects (Woodcock et al., 2019).

The constraints placed on the definition of 'functional' traits, and 'response' and 'effects' traits, have been loosened somewhat for some, under the argument that all traits are in some way related to an organism's function, having been accumulated through evolutionary forces, and shaped through abiotic and biotic interactions (Dawson et al., 2021; Violle et al., 2007). The opening up of the use of traits to understand how organisms interact with the environment around them has allowed ecologists to predict, using various methods of calculating trait diversity, how the provision and resilience of ecosystem functions might vary over space and time and under environmental change (e.g., Greenop et al., 2021; Greenwell et al., 2019; Oliver, Isaac, et al., 2015).

Persistence and abundance of functionally dominant species

In some ecosystems, particular functions may be dominated by individual species or a small subset of a community (Senapathi et al., 2021). Functional redundancy and complementarity might be low, but changing species richness may not have a great impact on ecosystem function due to the continued persistence of the ecologically dominant species. Although fewer examples exist, pollination, as well as grazer and scavenger ecosystem services have been shown to operate under this phenomenon; in each case, the continued provision of the ecosystem function correlates most strongly with the abundance of one functionally dominant species or community subset (Duffy et al., 2001; Henderson et al., 2019; Senapathi et al., 2021; Winfree et al., 2015). However, where the provision of function is reliant on dominant species, and that species declines in abundance, it is suggested that changing biotic interactions under abundance loss means that the presence of minor species can then increase and compensate for the loss of dominant species, as has been demonstrated in plant communities (Walker et al., 1999). Hence, both diversity and dominance can be important aspects of maintaining community and functional stability (Senapathi et al., 2021).

Species turnover and colonisations

Rather than the ‘buffering’ effect which occurs because of functional redundancy amongst species in an ecosystem, species turnover has been shown in several instances to provide a ‘compensatory effect’. As a result of local dispersal of individuals, shifting range boundaries or the introduction of non-native species, turnover in a community can result in the recovery of ecosystem processes from perturbations through the replacement or coexistence of species with new-arrivals providing the same function (Little & Altermatt, 2018).

Research gaps, aims and objectives

Although the research area of insect declines is growing by the day, many gaps remain around our understanding of the extent of declines in space and time, across different habitats and continents, and how this translates into functional impacts. With this thesis, I aim to address various aspects of these research gaps, to continue expanding our scientific knowledge of insect declines and ecosystem function. To achieve this, I make use of a range of long-term datasets on insect and other arthropod abundance, biomass, and diversity change over time, and introduce trait-based methods to uncover previously undiscovered spatial and temporal patterns for several insect taxa in empirical data. I amalgamate and make use of new and

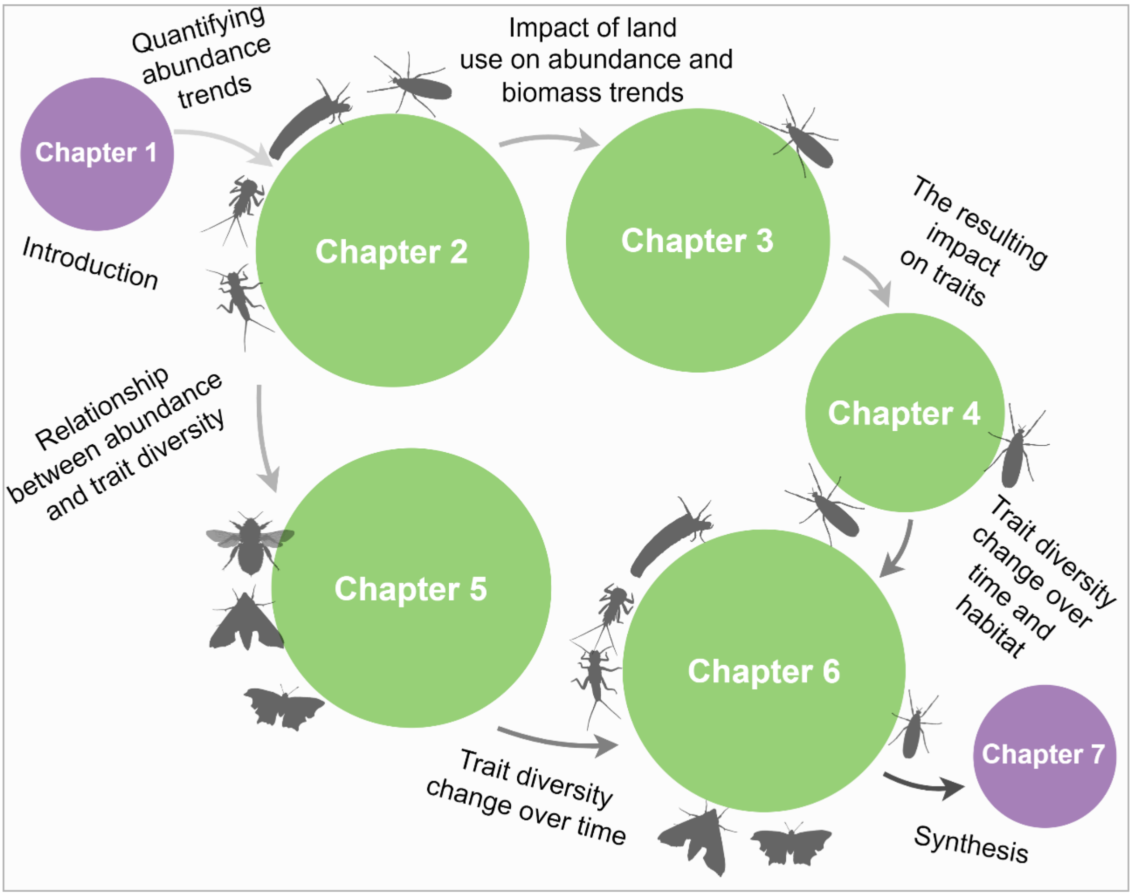


Figure 2. Visual representation of the structure of the thesis. Arrows and text around arrows highlight the relationship between chapters. Icons represent the taxonomic focus of each chapter. Chapters 3 / 4 and 5 represent two alternative flows from understanding the relationship between abundance, trait diversity, the environment and time.

emerging data on species' traits to further our understanding of the mechanisms underlying response diversity, asynchrony and resilience amongst insects and use our knowledge of macroecological relationships to predict how communities of some insects and their functional traits change over time under increasing environmental pressures. The following explains in further detail how I carried this out through addressing specific research aims and objectives in my thesis chapters, the flow and connection between which is highlighted in Figure 2.

- *Chapter 2: "Abundance trends for river macroinvertebrates vary across taxa, trophic group and river typology".* Riverine macroinvertebrates are important components of freshwater and terrestrial ecosystems, through decomposing organic inputs, regulating nutrient flow and providing food for fish, birds, and bats. There is some suggestion that previous devastation of rivers in the UK caused by gross pollution is being reversed by recent water quality improvements, and this is having a positive effect on macroinvertebrate occupancy and diversity. In this chapter, I explore the newly open-access Environment Agency macroinvertebrate data to quantify and compare macroinvertebrate abundance trends across different taxa, functional groups, and river types in England. I find increases in abundance for several sensitive taxa such as Plecoptera, but high heterogeneity across taxa, river types, and functional groups, including significant declines in decomposer organisms.

- *Chapter 3: "Complex temporal trends in biomass and abundance of Diptera driven by the impact of agricultural intensity on community-level turnover".* One of the greatest drivers of insect declines across the world is an increase in the intensification of agriculture to feed a growing human population as efficiently as possible. In this chapter, I use a decades' worth of abundance and biomass data from Diptera traps in Québec (Canada) to model the impact of agricultural intensification on Diptera communities over time. I find a surprising increase in the abundance of Diptera caught in traps over time and with increasing agricultural intensity, but biomass trends move in the opposite direction. Using 'offset' models, I predict that the average size of Diptera is declining in these insect communities, and that this underlies the divergence between total abundance and biomass trends that we have found. My findings imply potentially profound negative consequences for their aerial predators, which rely on these larger-bodied flies for survival.

Chapter 4: “Diptera communities lose larger species and homogenise under agricultural intensification”. Despite my predictions that Diptera are declining in body size on average over time in the Québec study area for Chapter 3, I had little knowledge of what this could mean for different species, due to a lack of data that would help me untangle the relative impacts of agriculture on different types of Diptera. In this Chapter, I work under macroecological assumptions of body size and abundance distributions within ecological communities, to develop theory around how Diptera communities are changing over time and space in our study area given the results of our previous models in Chapter 3. Under this theory, I predict that, with agricultural intensification, small species are selected for, undergoing local colonisations and population booms. Meanwhile, the opposite occurs for large Diptera species, which suffer population collapse. Under my assumptions, I show that Diptera communities become depauperate in species and their traits homogenised.

Chapter 5: “Asynchrony in terrestrial insect abundance corresponds with diversity in exposure and sensitivity to environmental perturbations”. As previously mentioned, the difference between species’ responses to environmental perturbations can contribute to greater resilience in ecosystem functions, and trait diversity can be directly linked to greater multifunctionality (Figure 1). However, the degree to which trait diversity can support functioning through disrupting synchrony between species’ populations is not known, especially in insect communities where trait-based studies are relatively new, and our understanding of the types of traits that could lead to such a phenomenon is poor. In this chapter, I look at our wider understanding of how traits and trait diversity relate to population asynchrony / response diversity, as a means of understanding the mechanisms of resilience in insect-mediated ecosystem functions. Using long term data from monitoring programmes for butterflies, moths and bumblebees in the UK, and newly-published and synthesised trait data, I find a strong and positive association between trait dissimilarity and abundance asynchrony, and find this relationship is strongest for what I refer to as ‘exposure traits’ – those governing the spatial and temporal exposure of individuals to likely abiotic factors.

- *Chapter 6: “Predicting long-term trends in ecosystem function provided by lepidopteran and freshwater insect communities”.* Long-term monitoring datasets for insects in the UK have been extensively studied to understand insect biodiversity and abundance trends, some of them such as the freshwater macroinvertebrate dataset used for this purpose earlier in this thesis, but we are yet to understand how this translates across to trends in ecosystem functioning. In this chapter, I study the temporal change in functional diversity in insect communities, using n-dimensional hypervolumes built from monitoring and trait data to construct functional indices. I revisit taxa previously explored in this thesis, comparing across freshwater and terrestrial taxonomic groups, and explore trends in functional diversity across different habitat types in the UK. I use the understanding of general relationships between traits, asynchrony, and resilience to infer that function provided by freshwater and moth communities are most vulnerable in urban and semi-natural habitats respectively.

- *Chapter 7: Discussion.* In this chapter I summarise the findings of this thesis, the contribution of my work to research on insect declines and ecosystem functioning and the implications of my work for insect conservation in this area. I discuss the caveats of my research, and the remaining knowledge gaps that I hope future research in this area will continue to fill.

Chapter 2

Chapter 2

Abundance trends for river macroinvertebrates vary across taxa, trophic group, and river typology

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Abstract

There is mounting evidence that terrestrial arthropods are declining rapidly in many areas of the world. It is unclear whether freshwater invertebrates, which are key providers of ecosystem services, are also declining. We addressed this question by analysing a long-term dataset of macroinvertebrate abundance collected from 2002 to 2019 across 5009 sampling sites in English rivers. Patterns varied markedly across taxonomic groups. Within trophic groups we detected increases in the abundance of carnivores by 19% and herbivores by 14.8%, whilst we estimated decomposers have declined by 21.7% in abundance since 2002. We also found heterogeneity in trends across rivers belonging to different typologies based on geological dominance and catchment altitude, with organic lowland rivers having generally higher rates of increase in abundance across taxa and trophic groups, with siliceous lowland rivers having the most declines. Our results reveal a complex picture of change in freshwater macroinvertebrate abundance between taxonomic groups, trophic levels and river typologies. Our analysis helps with identifying priority regions for action on potential environmental stressors where we discover macroinvertebrate abundance declines.

Keywords: insect declines, freshwater macroinvertebrates, river macroinvertebrates, river typology, biodiversity change, abundance trends, spatial heterogeneity, ecological status, ecosystem function

Introduction

Biodiversity is rapidly changing across the globe (Díaz et al., 2019). Long-term datasets suggest widespread declines in richness, abundance and biomass of terrestrial insects and other arthropods, including steep declines in biomass of flying insects in areas of Europe (Didham, Barbero, et al., 2020; Hallmann et al., 2017, 2019; Wagner et al., 2021). The spatial and taxonomic extent of these declines are unclear, as well as whether declines are spread across both terrestrial and freshwater systems, and this is further complicated by reported abundance and biomass increases across several taxa at the local scale (Crossley et al., 2020).

Declines in arthropod abundance could have negative consequences on ecosystems, as these taxa underpin vital ecosystem functions and services (Noriega et al., 2018a; Schowalter et al., 2018). Freshwater macroinvertebrates provide a range of key ecological functions and associated ecosystem services in both freshwater and terrestrial systems (Macadam & Stockan, 2015). For example, benthic invertebrates constitute a significant part of the diet of a range of fish, bird and mammal species (Michel & Overdorff, 1995). Burrowing and sedentary macroinvertebrates create structural habitat complexity, benefitting other invertebrate and fish species (Covich et al., 1999). Macroinvertebrate communities are also essential regulators of nutrient cycles in freshwater ecosystems (Cuffney et al., 1990; Hieber & Gessner, 2002), with the activity of detritivorous macroinvertebrates, such as ‘shredders’ and ‘grazers’, being essential for breaking down organic matter such as leaf litter entering streams from riparian habitats (Graça, 2001). This process, along with herbivorous consumption of macrophytes, stimulates the transfer of nutrients to other organisms, thereby regulating the water self-purification of freshwater systems and supporting diverse and complex food webs (Graça, 2001; Wallace & Webster, 1996). The reduction of macroinvertebrate abundance across different taxa and feeding groups will likely have negative consequences for these ecosystem functions and services, in particular given that ecosystem functions are largely driven by the abundance of common species (Winfree et al., 2015).

Biodiversity change in freshwater macroinvertebrate communities has previously been explored in terms of species richness, prevalence, occurrence and distribution changes (Environment Agency, 2021; Fried-Petersen et al., 2020; Jourdan et al., 2018; Outhwaite et al., 2020; Vaughan & Ormerod, 2012b). In contrast to the commentary on terrestrial species, taxonomic richness and prevalence (the number of species within families) as well as occurrence (the presence of species across space) of freshwater macroinvertebrates has been found to have increased over the last two decades in some areas, such as Great Britain (Outhwaite et al., 2020; Vaughan & Ormerod, 2012b). This has been largely attributed to water quality improvements, such as a decrease in phosphate load and catchment acidification from very poor levels before the 1990s, despite other pressures on freshwater ecosystems, such as climate change, intensifying over the same time period (Vaughan & Gotelli, 2019; Vaughan & Ormerod, 2012b, 2012a; Whelan et al., 2022). Other reported trends in freshwater macroinvertebrates, however, are complex, and are thought to be driven by a range of environmental pressures beyond climate change and water quality alone, such as catchment and floodplain land use change and intensification, habitat modification (both the surrounding terrestrial habitats and within the river banks and bed), and flow regulation (Domisch et al., 2011; Feld & Hering, 2007). The fact that freshwater ecosystems are likely highly susceptible to multiple stressors makes untangling trends over space and time, at the hands of a few select environmental drivers, particularly challenging (Leps et al., 2015), with different stressors changing in relative importance depending on the scale of the study (Feld & Hering, 2007; Sundermann et al., 2013).

A meta-analysis of invertebrate trends across continents (van Klink et al., 2020) revealed differences between freshwater and terrestrial abundance, with the former increasing. However, this study did not explore underlying differences among taxa or across space (Desquilbet et al., 2020; Jähnig et al., 2021). Overlooked heterogeneity can mask local patterns that affect the provision of important ecosystem functions and services. Heterogeneity in trend patterns may partly be explained by underlying hydrological, geological and geographical conditions, which constitute ‘river typology’. A ‘typological approach’, as we use in this study, categorises rivers, based on the underlying geology around sites and catchment altitude. Using river typologies allows for a more holistic consideration of the environment and the many interacting drivers of community change, as different river types capture broadly different conditions and pressures in freshwater ecosystems (Lyche Solheim et al., 2019; Schmitt et al., 2011). For example, the geological conditions at sites generally affect the filtration of pollutants into rivers and the way in which rivers are fed, which could influence the severity of the environmental pressures on freshwater ecosystems (Berrie, 1992). Calcareous rivers are usually fed by groundwater sources, the water having filtered through more porous sediment (limestone and chalk), whereas rivers dominated by other geological sediment types (siliceous and organic peat rivers) tend to be surface-water fed (Berrie, 1992). Surface water is more susceptible to flow changes and surface conditions, which can exacerbate the effects of warming water temperatures and nutrient inputs when at low flow, as well as affect colonisation rates of macroinvertebrates when at higher flows (Eveleens et al., 2019; Ledger & Milner, 2015; Mosley, 2015; Piniewski et al., 2017). Other typological features, such as altitude, may influence abundance trends of macroinvertebrates, given that the uplands are generally more vulnerable to climate warming effects than lowland rivers (Orr et al., 2008; Worrall et al., 2004). On the other hand, lowland rivers often flow through urban areas and may be more susceptible to other pressures on freshwater ecosystems such as the disruption of food webs by invasive species (Mathers et al., 2016), which have increased over recent decades, in lowland rivers of England (Johns et al., 2018). Understanding where abundance of important invertebrates has declined, including freshwater macroinvertebrates, has been hampered by a lack of long-term data from standardised monitoring schemes (Isaac & Pocock, 2015; Powney et al., 2015; Thomas et al., 2019). Long-term trends in large systems are also difficult to characterise with statistical confidence as sampling effort is often limited compared to the system scale, causing high fluctuation in interannual variation (Cauvy-Fraunié et al., 2020). An exception is abundance data for riverine freshwater macroinvertebrates collected over multiple decades by the Environment Agency (EA); the government authority responsible for monitoring the health and water quality of freshwaters in England. These data have primarily been used for the qualitative determination of environmental quality across waterbodies and catchments, in alignment with monitoring requirements, such as for the European Union Water Framework Directive (WFD, 2000).

Here, we realise the potential of this dataset to identify long-term abundance changes for freshwater macroinvertebrates across diverse rivers and regions in England. We use the dataset to characterise and compare trends in: 1) the abundance of different taxonomic groups (at family level and above) of riverine macroinvertebrates, 2) the abundance change of different trophic groups, to shed light on the potential functional changes within rivers, and 3) the spatial pattern of long-term trends across different types of river.

Methods

Macroinvertebrate Abundance

Abundance data for riverine macroinvertebrates in England were extracted from the EA's ecological monitoring database (Environment Agency, 2020b). The data were filtered to only include three-minute kick-sample data as the primary method for sampling freshwater invertebrates (approximately 99% of samples). Three-minute kick-samples are a standardised, internationally-recognised, semi-quantitative approach to assessing macroinvertebrate ecology and water quality in rivers using invertebrate diversity indicators (Furse et al., 1981; Murray-Bligh, 1999).

Prior to the implementation of the European Union Water Framework Directive in 2000 (WFD, 2000), abundance estimates were based on categories (0-9, 10-99, 100-999 etc.). In 2002, the EA started recording more exact abundance estimates and enacting improved quality control procedures, whereby one in every ten samples were independently re-analysed. Hence, although the original dataset covered sampling years from 1991, our analysis was restricted to the years 2002-2019.

Data were further filtered to only include sites sampled for a minimum of three years out of a total of eighteen in both spring (March to May) and autumn (September to November) to avoid seasonal bias. In order to test whether this was an appropriate minimum time series length to use in our models, we ran equivalent analyses with sites sampled in both seasons for a minimum of 10 years (see Supporting information, Figure S1-S3). Trends across the two datasets were significantly positively correlated (Pearson's correlation coefficient, r = 0.83), but limiting the dataset to sites sampled across a minimum of 10 years in both seasons greatly reduced the number of sites across river typology categories. This has the potential to introduce spatial bias into our models and, therefore, we report on the more extensive dataset analysis.

After filtering the dataset according to these criteria, our final dataset from 2002-2019 included 67,757 individual macroinvertebrate samples from 5,009 sites (out of 10,136 sites in the original dataset). This equates to an average of 3,764 samples a year, covering 2,774 waterbodies distributed across the 10 river basins defined under the European Union Water Framework Directive in England: Anglian, Humber, North West, Northumbria, Severn, Solway Tweed, South East, South West and Thames (Figure 1). The final dataset provides a wide national distribution of sites representative of the main river conditions, albeit with a bias towards mid to lower perennial reaches (reflective of the purpose of the monitoring programmes instigated for environmental quality monitoring, rather than a river's intrinsic biodiversity).

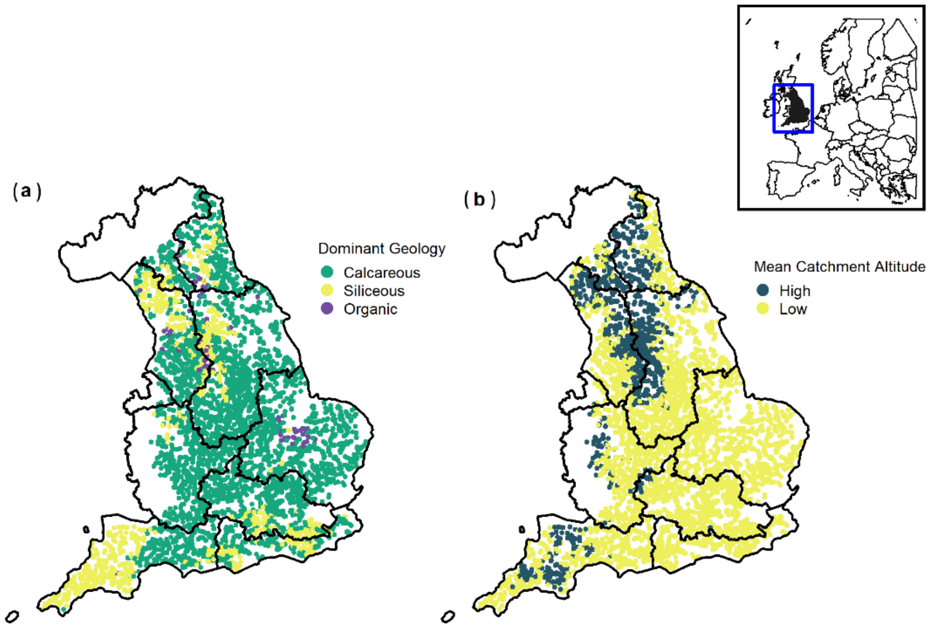

Figure 1. Map of the site locations in England (n = 5009) selected for mixed models, coloured by river typology (n = 6; (a) three dominant geological substrate types – calcareous, organic, and siliceous, and (b) two mean catchment altitude categories – high and low). The number of sites within each typology is as follows; Calcareous High: 525, Calcareous Low: 3289, Organic High: 72, Organic Low: 45, Siliceous High: 525, Siliceous Low: 553. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Taxonomic groups

The identification of macroinvertebrates in the database, including within individual samples, is given at a mixture of taxonomic levels, meaning species-level trends in abundance change could not be calculated due to a lack of consistency between and within samples. Instead, we pooled and analysed the data at two different levels: 1) wider taxonomic groups (non-insect freshwater macroinvertebrates: annelids, molluscs, Turbellaria and crustaceans, and individual insect orders: Ephemeroptera, Trichoptera, Plecoptera, Coleoptera, Diptera, Megaloptera, Hemiptera and Odonata); and 2) taxonomic families, representing observations for which this level of identification was available.

Trophic Groups

We also pooled and analysed data considering main trophic groups (carnivores, herbivores and decomposers). We allocated macroinvertebrate dietary preferences for each genus where this level of identification was given in the dataset, according to the main food source described in the functional and morphological traits database for European freshwater macroinvertebrates (Tachet et al., 2010). Tachet et al. (2010) use a fuzzy-coded system whereby dietary components are given a score between 0 and 5 describing the affinity for the following dietary components: 'microorganisms', 'detritus < 1mm', 'dead plant > = 1mm', 'living microphytes', 'living macrophytes', 'dead animal > = 1mm', 'living microinvertebrates', 'living macroinvertebrates', and 'vertebrates'. In most cases, abundance data were entered at the family or higher taxonomic group level in the EA database; for those cases, diet scores were estimated as weighted means of the diet score data (values between 0-5) for that grouping, weighting based on the relative abundance of taxa identified in our abundance dataset. Hence, taxa included in (Tachet et al., 2010) but not recorded in rivers in England by the EA data were excluded when calculating average family or group dietary scores, and more common and abundant genera had a proportionally greater influence over average dietary scores. This allowed the final diet scores at the group-level to reflect the probability of the individual identified at this higher level possessing a particular dietary trait. Genera, families and higher taxonomic groupings were allocated to trophic groups based on items with highest dietary scores: carnivores had highest scores for ‘vertebrates’, ‘living macroinvertebrates’, ‘living microinvertebrates’; herbivores had highest scores for ‘living macrophytes’ or ‘living microphytes’; and decomposers had highest scores for ‘dead plant ≥1mm’, ‘dead animal ≥1mm’ and ‘detritus’. Freshwater invertebrates could be included in more than one trophic group if distinct diet items had equally high scores (as may occur in omnivores). No genera, family or group in our abundance dataset had highest dietary scores (preference) for microorganisms.

River Typology

To categorise sampling sites by typology, we used criteria from the EU Water Framework Directive’s descriptions of river typologies (Water Framework Directive UKTAG, 2003), including the dominant geology at the site and mean catchment altitude. We used river typology data held by UK Centre for Ecology and Hydrology and used for the River Invertebrate Classification Tool (Scottish Environment Protection Agency, 2023) which modelled the proportion of different sediments (chalk, limestone, clay, hard rock and peat) located along rivers to calculate the dominant geological sediment at sampling sites. Where sites were dominated by chalk or limestone, sites were classified as 'Calcareous'. Where the dominant sediment type was clay or hard rock, sites were classified as 'Siliceous'. We classified sites dominated by peat as 'Organic'. Thirty-eight sites were excluded from the analysis, due to missing or multiple dominant geologies in the RICT typology data. Sites were also grouped by mean catchment altitude: mean altitudes ≥200m were categorised as 'high', and < 200m as 'low'. The combination of these classifications resulted in 6 river typologies for our analyses: ‘Calcareous / High Altitude’, ‘Calcareous / Low Altitude’, ‘Organic / High Altitude’, ‘Organic / Low Altitude’, ‘Siliceous / High Altitude’, and ‘Siliceous / Low Altitude’ (Table 1).

Table 1. Criteria used for categorising sites by river typology.

Type	Dominant Geology	Mean Catchment Altitude (m)	Number of Sites
I	Calcareous	≥ 200 (High)	525
II	Calcareous	< 200 (Low)	3289
III	Organic	≥ 200 (High)	72
IV	Organic	< 200 (Low)	45
V	Siliceous	≥ 200 (High)	525
VI	Siliceous	< 200 (Low)	553

Statistical Analysis

To test whether macroinvertebrate abundance changed over time on a national scale, we fitted hierarchical generalised linear mixed regression models (GLMM; Bates et al., 2015) for various response variables calculated as the sum of counts per sample for the three aggregated groups (wider taxonomic groups, taxonomic families, and trophic groups). Poisson GLMMs were chosen to fit the left-skewed count data, where there were high frequencies of low abundances within groups. For all three aggregated datasets (wider taxonomic groups, taxonomic families, and trophic groups) we fitted a national-level model with year as the sole fixed factor to describe general patterns. For the wider taxonomic group and trophic group datasets we additionally fitted a river-typology model including year, river typology and their interaction as fixed factors to explore trend variation among typologies. In all models, to facilitate interpretation, year was converted to an integer from 0-17, with 0 representing 2002 and 17 corresponding to 2019. In both models the random effects structure included: random intercepts and slopes for each site to account for spatial pseudoreplication and within-site variation in temporal trends; random intercepts for year to account for within-year pseudoreplication (Daskalova et al., 2021); and random intercepts for each observation to account for non-zero-inflated over-dispersion of counts in the data (Harrison et al., 2018). The use of ‘year’ in both the fixed and random effects of the model allowed us to examine the influence of increasing years on abundance of macroinvertebrates, whilst reducing the impact of ‘particularly good’ or ‘particularly bad’ years for macroinvertebrates and decreasing the chance of identifying significant trends driven by outlier effects.

We evaluate models using Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) and tested for differences in abundance trends at the river typology level using analysis of variance tests (ANOVA, Figure S4 and Table S1). AIC was used over AICc due to adequate sample size and a corresponding reduced likelihood of overfitting. Models were fitted with the *lme4* package in R (Bates et al., 2015) and we used the ‘*ggeffects’* R package (Lüdecke, 2018) to get predicted values for each year from which we calculated overall percentage change (Ψ) and annual growth rate (AGR) as:

$$\Psi = ((y_n - y_1) / y_1) * 100 \qquad [2]$$

and

$$AGR = \Psi / (n-1) \qquad [3]$$

Where y_n is the model estimate of the abundance value for the final year of the time series (2019), y_1 is the estimated abundance value for the starting year of the time series (2002), and n is the number of years total in the time series.

In addition to linear models, we explored potential non-linear patterns at the national scale (rather than in different river types) using multi-level hierarchical Generalised Additive Mixed Effect Models (GAMMs) using the ‘mgcv’ package in R (Wood, 2022). For these models we used the same modelling format expressed above for GLMMs, using the function gam() to include year as a smoothed fixed effect, and random smooths at the site and observation level. We focus on the GLMM format to report our results, in order to calculate and compare changes in abundance and annual growth rates in a consistent way across taxon and trophic groups. The results of these additional analyses are included in the Supporting information (Figure S5 and Table S5).

As sampling effort is not typically uniform across years and river typology, we explored temporal patterns of sampling effort within and across sites and rivers of different typologies (see Supporting information, Figure S1, S2). Changes in sampling effort between years did not correspond to changes in macroinvertebrate abundance, which varied between different groups. We found no significant effect of total samples taken across river types on macroinvertebrate abundance trends ($\beta = -0.00495$, s.e. = 0.003, d.f. = 88; $p > 0.05$; Figure S3).

All statistical analyses were completed in R (version 4.0.0) (R Core Team, 2020).

Results

National Trends

Taxonomic group abundance

Across the taxonomic groups we studied, we found large differences in baseline abundance values that reflect the relative proportion of these groups living in freshwater ecosystems. The highly abundant groups include annelids, crustaceans, molluscs, Coleoptera, Ephemeroptera and Trichoptera. Groups with low baseline abundance in samples include Plecoptera, Megaloptera, Odonata, Hemiptera and Turbellaria. The difference between these baseline abundances can be explored through the geometric mean values presented in Figure 2 and 4.

We found major differences in the national-scale abundance trends among the 12 macroinvertebrate taxonomic groups evaluated (Figure 2b-d, Table 2). Among non-insect macroinvertebrates, we found large declines in annelids and Turbellaria, resulting in 46% and 51.8% total abundance loss respectively over the 18-year period (Table 2). In contrast, the abundance of crustaceans and molluscs remained largely stable (Figure 2d). Similarly, abundance trends differed among insect orders. Trichoptera, Plecoptera, and Coleoptera showed estimated increases of 50.8%, 142.1% and 48.6% respectively over the 18-year period (Table 2). Trends for Diptera, Hemiptera, Megaloptera, and Odonata were stable, while Ephemeroptera significantly decreased in abundance, by an estimated 19.5% over the time period we studied (Figure 2b,c, Table 2).

Data aggregated to families also showed variable trends (Figure 3, Table S3). Almost half of all analysed families (82 out of 166) show “no change” with no significant linear abundance trends over time, including families for which significant trends were found at higher taxonomic levels (e.g. Turbellaria and annelids; Table 2). Of the significant family trends, an approximately even number of families were found to increase in abundance (41 families) and decrease in abundance (43 families; Table S3).

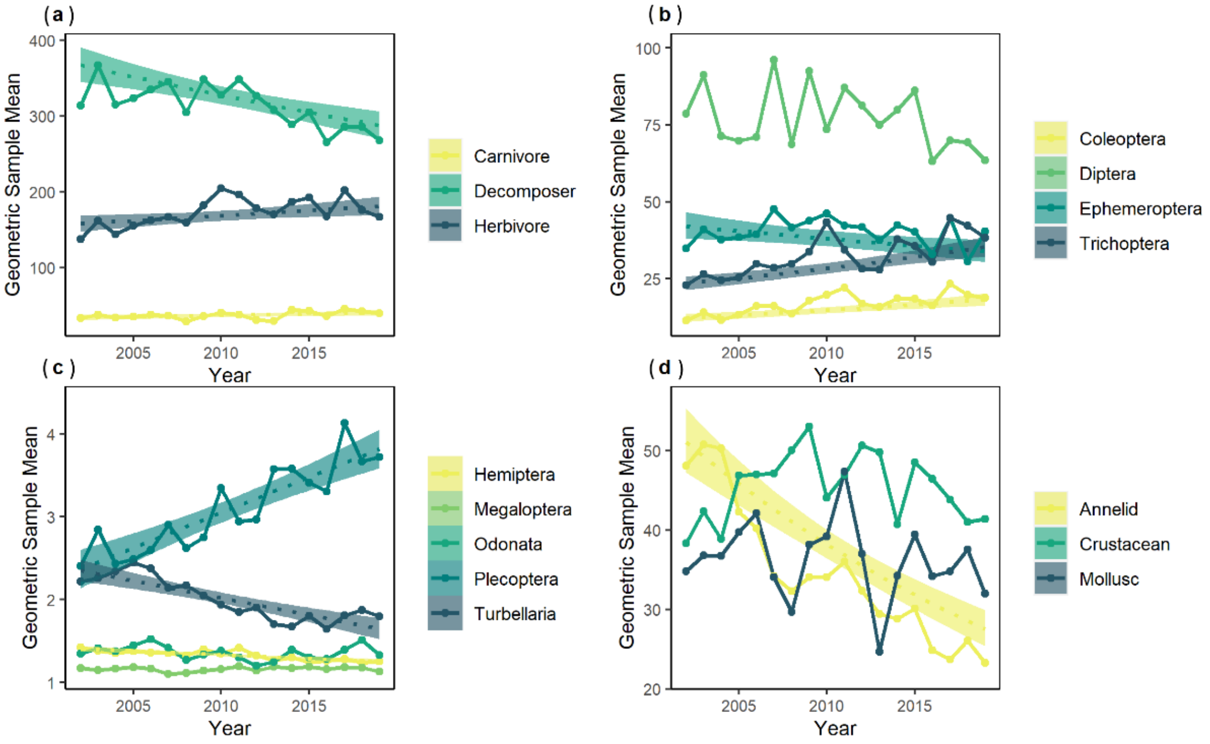

Figure 2. Abundance of river macroinvertebrates from 2002-2019 for groups: (a) trophic groups: Carnivores, Herbivores and Decomposers; (b) insect groups of high mean abundance: Coleoptera (beetles), Diptera (true flies), Ephemeroptera (mayfly), Trichoptera (caddisfly); (c) insect and other invertebrate groups of low mean abundance: Hemiptera (true bugs), Megaloptera (alderfly), Odonata (dragonfly and damselfly), Plecoptera (stonefly) and Turbellaria (flatworms), and (d) other invertebrate groups, of higher mean abundance: Annelids (segmented worms), Crustaceans, and Molluscs. Abundance is presented as the geometric mean, shown with a solid line. Dashed lines show the model predictions based on the raw data for groups where the effect of ‘year’ on abundance was significant ($p \leq 0.05$), with shaded envelopes indicating 95% confidence intervals.

Trophic group abundance

Both herbivore and carnivore abundances increased, by an estimated 14.8% and 19% respectively over 18 years. Over the same time period, decomposers decreased in abundance by approximately 21.7% (Figure 2a, Table 2)

Trends by river typology

Models that allowed for trends to vary across river typologies identified significant typological variation in trends (Table S2).

Wider taxonomic group abundance

Abundance trends for wider taxonomic groups across river typologies in some cases diverged from their national averages (Figure 5). For example, Ephemeroptera decreased in calcareous and siliceous rivers at low altitude (most sites) but were stable across other typologies and increased in calcareous rivers at higher altitudes by 29% (Table S2). At a national level, Odonata showed stable (non- significant) trends, but Odonata trends increased significantly in calcareous rivers at high altitudes, with an estimated abundance increase of 123% (Table S2). In contrast, other groups showed little divergence from the overall national abundance trend when river typology was taken into account; for example, annelids had no positive trends across river typologies, and only organic rivers and low altitudes were found to have stable, non-significant trends for this group. Turbellaria, the invertebrate group with highest overall decline at the national scale, were found to be significantly increasing over time in this same type of river (organic rivers at low altitude; an increase of 550%. Table S2). Estimates for all taxonomic groups and river typologies are shown in Table S2.

Trophic group abundance

Abundance trends in trophic groups also varied amongst river typologies (Figure 4, and Tables S1 and S2). For example, herbivorous macroinvertebrates had no significant trends across half of our river typologies, only increasing in abundance in calcareous rivers and organic rivers at low altitude (Table S2. Figure 4). Although trends for herbivore abundance were significant and positive in calcareous rivers at high altitude over the long-term, the geometric mean

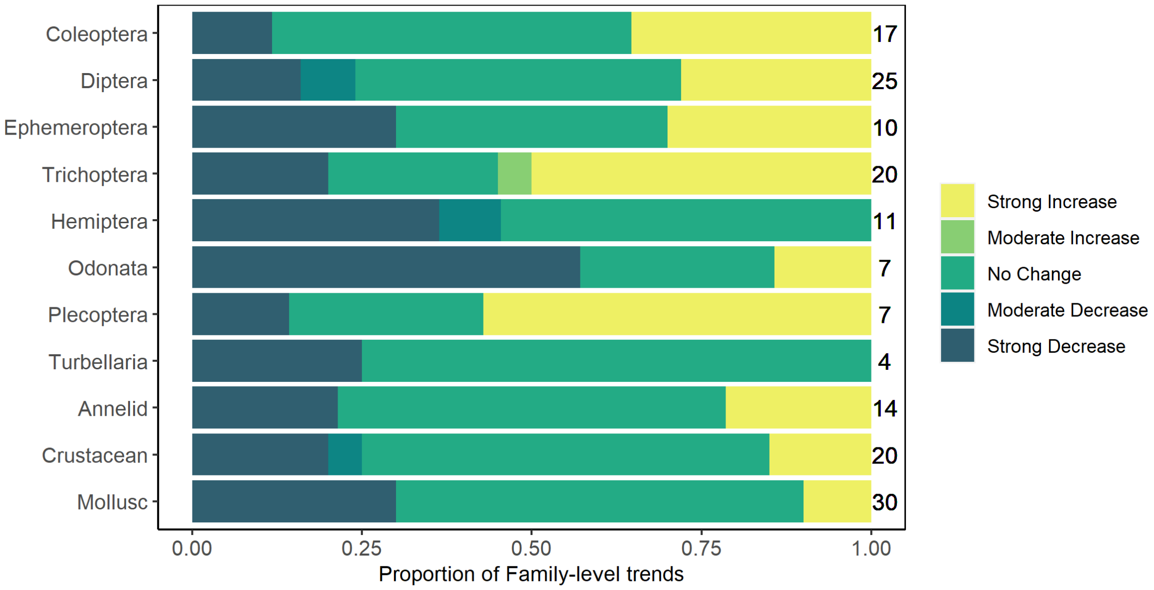

Figure 3. Proportion of family-level trends analysed that show: a) Strong Increases (where the annual growth rate ≥ 2.81%, leading to a doubling of abundance over 25 years); b) Moderate Increases (where the annual growth rate is between 1.16% and 2.81%); c) No Change (where trends were insignificant – all trends with growth rates between -1.14% and 1.16% were insignificant), d) Moderate Decreases (where the annual growth rate is between -2.73% and -1.14%); and e) Strong Decreases (where the annual growth rate ≤ -2.73%, representing at least a halving of abundance over 25 years). N = 67,753 site-sample combinations. Family trends are represented as proportion of families we were able to analyse (given data limitations) within wider taxonomic groups, with the total number of families analysed given on the right of each bar.

abundance progressively decreases over the last 4 years of data collection (years 2015-2019; Figure 4a). This pattern also exists for herbivores in organic and silicious rivers at high altitudes, which had no significant trend over the long-term (Figure 4b,c). Supporting Figure S5 shows the results of GAMMs, including herbivores in the top right panel; these supplementary results show a non-linear trend that captures this short-term decline toward the end of the time series.

Table 2. Summary of coefficients for fixed effects (year), and random effects variance, of generalised linear mixed models of macroinvertebrate abundance including year as a fixed effect. Significant trends ($p < 0.05$) are highlighted in bold text. ‘AGR (%)’ = Annual Growth Rate (%), and ‘Total Change’ = Total percentage change over the 18-year time period

Taxonomic Group	**Intercept**		**Slope**			**Random Effects (θ)**				**AGR (%)**	**Total Change (%)**
	Estimate	**S.E.**	**Estimate**	**S.E.**	**P Value**	**Site (intercept)**	**Site (slope)**	**Year (intercept)**	**OLRE**		
Carnivore	3.513	0.057	0.01	0.005	< 0.05	1.072	0.061	0.111	0.881	1.06	19
Herbivore	5.053	0.037	0.008	0.003	< 0.05	1.059	0.057	0.066	0.867	0.82	14.8
Decomposer	5.921	0.034	-0.014	0.003	< 0.001	0.832	0.052	0.062	0.83	-1.21	-21.7
Annelid	3.97	0.043	-0.036	0.004	< 0.001	1.122	0.07	0.079	1.068	-2.56	-46
Coleoptera	2.477	0.058	0.023	0.005	< 0.001	2.038	0.104	0.099	0.986	2.7	48.6
Crustacean	3.762	0.055	0.005	0.005	0.281	1.937	0.088	0.094	1.118	0.49	8.8
Diptera	4.477	0.06	-0.007	0.005	0.18	0.839	0.049	0.117	1.166	-0.65	-11.7
Ephemeroptera	3.752	0.056	-0.013	0.005	< 0.01	1.691	0.075	0.099	1.279	-1.08	-19.5
Hemiptera	-2.057	0.075	-0.012	0.006	0.056	2.929	0.112	0.108	1.639	-1	-18
Megaloptera	-2.632	0.118	0.001	0.011	0.917	2.636	0.121	0.215	1.548	0.1	1.9
Mollusc	3.536	0.073	0.007	0.007	0.311	1.777	0.086	0.138	1.156	0.66	11.9
Odonata	-2.056	0.18	0.009	0.016	0.574	2.992	0.089	0.351	1.336	0.93	16.8
Plecoptera	-1.218	0.104	0.052	0.008	< 0.001	4.496	0.092	0.157	1.331	7.89	142.1
Trichoptera	3.128	0.052	0.024	0.004	< 0.001	1.934	0.084	0.088	1.016	2.82	50.8
Turbellaria	-0.002	0.082	-0.043	0.007	< 0.001	2.462	0.148	0.143	1.517	-2.88	-51.8

Carnivores increased on a national scale, but again their trends were found to be stable in siliceous rivers and organic rivers at high altitude, with only calcareous rivers and organic rivers at low altitude showing significant trends. Finally, we found decomposers to be declining across all river typologies apart from low altitude calcareous rivers (where there were no significant trends) and organic rivers and low altitude, where decomposer macroinvertebrates were found to be significantly increasing in abundance (Table S2; Figure 4).

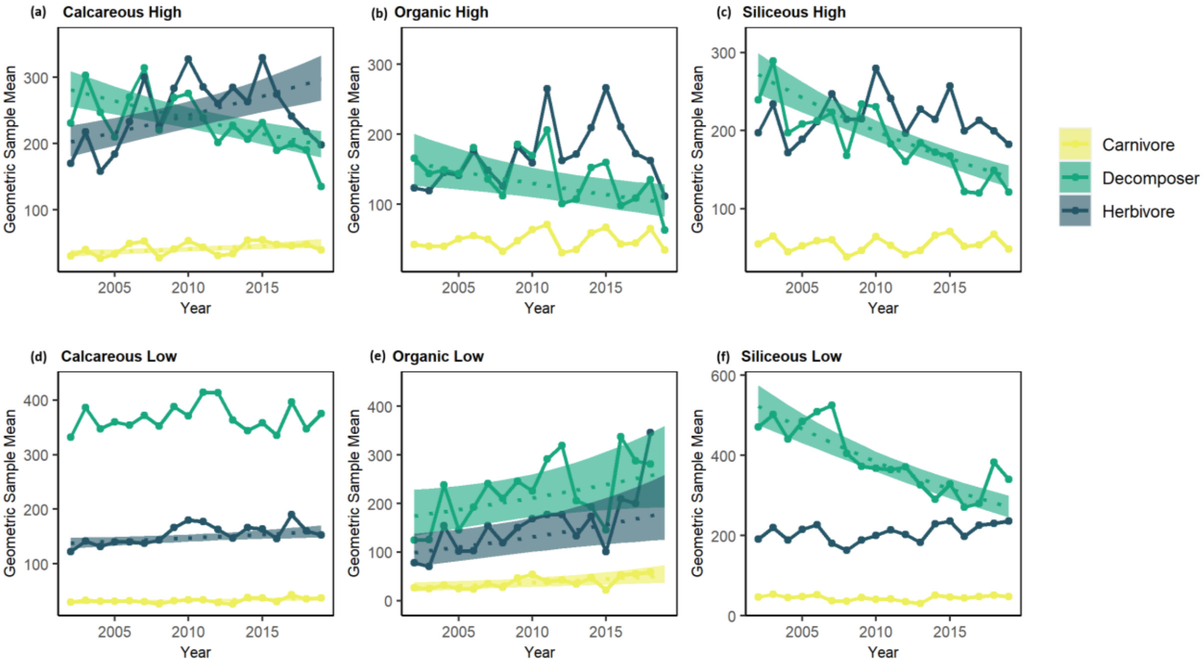

Figure 4. Abundance of river macroinvertebrates from 2002-2019 for Carnivores, Herbivores and Decomposers in samples taken from rivers of different river typology category. Abundance is presented as the geometric mean number of individuals per 3-minute kick sample shown with a solid line. Dashed lines show model predictions based on the raw data for groups where the effect of ‘year’ on abundance was significant ($p \leq 0.05$), with shaded envelopes indicating 95% confidence intervals, for the following typology categories: (a) Calcareous High (n = 7233), (b) Organic High (n = 1099), (c) Siliceous High (n = 8032), (d) Calcareous Low (n = 44566), (e) Organic Low (n = 599), and (f) Siliceous Low (n = 6228), where n = number of site-sample combinations.

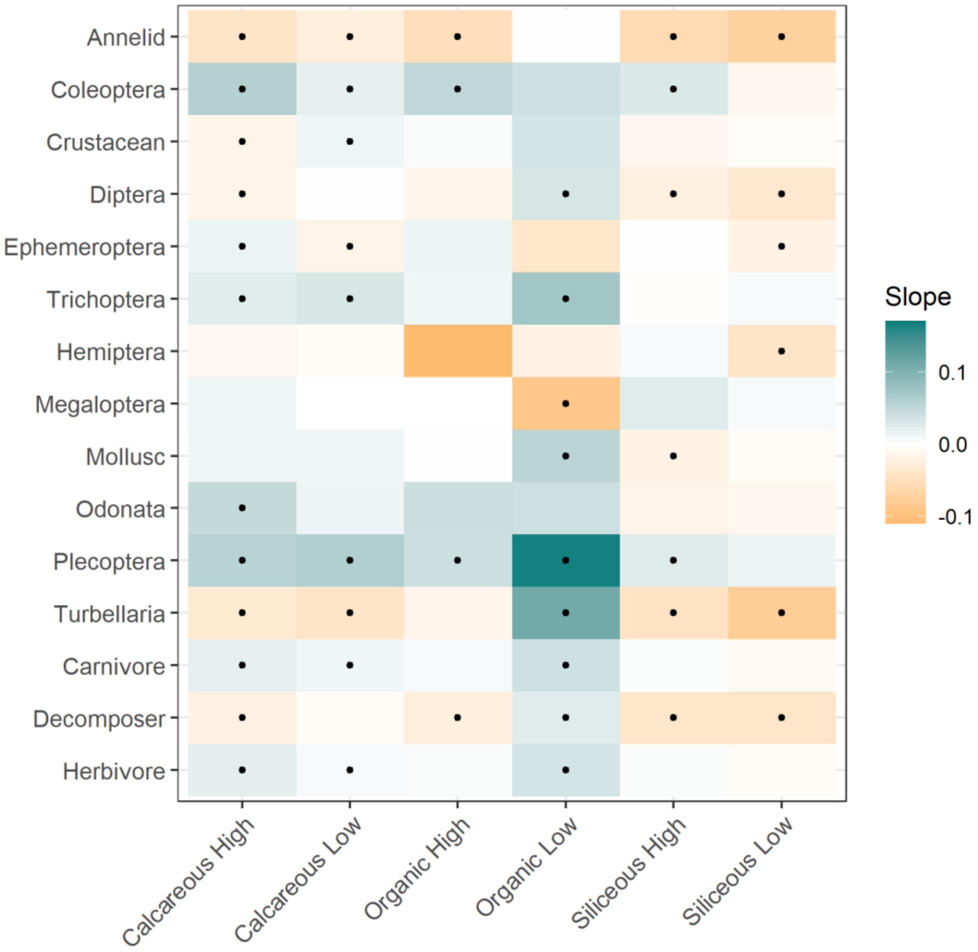

Figure 5. Trend slopes (β values) for the models testing the interaction between year and river typology category (model 2), for each broader taxonomic and trophic group. Significant trends ($p \leq 0.05$) are represented by a black dot. The number of sample-site combinations for each river typology is as follows; Calcareous High: n = 7233, Calcareous Low: n = 44566, Organic High: n = 1099, Organic Low: n = 599, Siliceous High: n = 8032, and Siliceous Low: n = 6228

Discussion

Our study capitalizes on a unique long-term abundance data to describe and compare changes in abundance of freshwater macroinvertebrates at a national scale and across different types of rivers. We report a range of positive, negative, and stable trends in macroinvertebrate abundance over time, with the direction of these trends depending on taxonomic and trophic groupings and varying with river typology. Stable trends have been reported in recent meta-analyses of freshwater invertebrates across continental scales and in the USA (Crossley et al., 2020; van Klink et al., 2020); however, these studies did not quantify spatial and taxonomic heterogeneity in abundance patterns, as we do here. Although our results find that abundance trends are inherently complex within freshwater macroinvertebrate communities, there may be important consequences for changes in ecosystem function provision through a shift in the abundance within different trophic levels. Our results have implications for management of freshwater ecosystems, highlighting particular river types that are most susceptible to invertebrate abundance declines.

Heterogeneity of trends

Although many indicators suggest we are losing biodiversity around the globe (Johnson et al., 2017), caution is required when inferring widespread losses from higher level groupings (e.g. by Order or trophic level) (Leung et al., 2020). While there is evidence of decline in many terrestrial invertebrates (Wagner et al., 2021), here we show stable and increasing trends among several freshwater macroinvertebrate taxa in England. We also show that although freshwater ecosystems in England do not appear to be suffering general macroinvertebrate declines at the national level, the pattern of change across taxonomic groups and across space is more complex and variable than simplistic summary statements allow for. We must consider this spatial and taxonomic variation as an important part of the conversation around the state of invertebrate populations and biodiversity change (Cardinale et al., 2018; Chase et al., 2018, 2019). This complexity is likely to be representative of heterogeneity in multiple environmental stressors, which is at risk of being overlooked if different ecological scales are not considered (Simmons et al., 2021).

Our work highlights the value of long-term abundance data collected through standardised monitoring schemes to reveal complexity, and new patterns of heterogeneity not observed in previous studies of freshwater ecosystems using presence/absence and diversity metrics. Of the family-level trends that we were able to quantify, almost half of all trends are non-significant; coupled with the positive trends, we found no evidence that most families are declining in abundance. In addition, we observed variation in family-level trends within wider taxonomic groups – showing that although total abundance may not be changing significantly in some groups, there could be significant turnover in biodiversity within groups as some families increase and some decrease in abundance over time. One extreme example, Odonata, showed no significant trend in total abundance overall, but most families showed strong declines in abundance. Their declining trends were masked when analysed together because the most abundant odonatan family, Libellulidae, has had largely stable population sizes since 2002, and a few other families showed increases. Conversely, we found families with contrasting trends in groups for which overall estimates showed significant declines or increases including Ephemeroptera, Trichoptera, Plecoptera, annelids, and Turbellaria.

Drivers of freshwater macroinvertebrate abundance change

Most comparable studies have identified water quality improvement in England over the last few decades as an explanatory factor for macroinvertebrate biodiversity trends (Environment Agency, 2021; Outhwaite et al., 2020; Vaughan & Gotelli, 2019; Vaughan & Ormerod, 2012b, 2014). We found annelid worms, which are often associated with poor water quality due to their high tolerance to organic pollution (Armitage et al., 1983), have declined significantly across all-but-one of the river typology categories – organic lowland rivers. By contrast, we found other macroinvertebrate groups generally associated with better water quality due to higher sensitivity, such as some families of Plecoptera and Trichoptera, to have generally increased (Table S2). Within groups and orders of macroinvertebrates, different families can vary in their sensitivity to environmental drivers such as organic and chemical pollution (Hellawell, 1986). For example, for Trichoptera abundance, several more pollution-tolerant families, such as Hydropsychidae and Hydroptilidae have not changed in abundance over time (Table S3), and several more sensitive taxa such as Goeridae and Odontoceridae have increased. However, the state of water quality improvement has halted and even reversed in the last four years in England; this warrants further investigation into how these recent changes in water quality may affect abundance and other indicators for macroinvertebrates going forward (Environment Agency, 2020a).

On the other hand, Ephemeroptera, also generally linked to high water quality, significantly decreased in abundance in our national-scale analysis (Figure 2). Despite this our family-level analysis shows that a number of sensitive families which score higher for water quality indication within Ephemeroptera are increasing, such as Ephemeridae, Siphlonuridae and Heptageniidae, whereas families which are less sensitive to pollution such as Baetidae were either stable or in decline. Beyond water pollution, other drivers of change such as light pollution can disproportionately affect taxa such as Ephemeroptera, and although we do not test for environmental drivers, the presence of a wide range of stressors such as these may contribute to the different patterns seen across broader groups of taxa (Kriska et al., 1998).

Conditions and impacts affecting different types of rivers could also drive variation in trends. Broadly speaking, calcareous rivers tend to have more positive trends across taxonomic and trophic groups than siliceous rivers, which appear to have largely negative trends (with some exceptions in both cases). The calcareous rivers in England, which include limestone rivers and rarer chalk streams and rivers, are typically fed more by groundwater than surface waters in England and, as a result, tend to be subject to different river conditions to siliceous and organic rivers (Berrie, 1992). Calcareous rivers can provide a more stable environment than surface water-fed siliceous rivers for freshwater species. This is because the former are generally less susceptible to fluctuations in flows, flood events and droughts, and the resulting ‘wash out’, high velocity, temperature and dissolved oxygen fluctuations, along with pollutant concentrations, that come with flow changes (Eveleens et al., 2019; Ledger & Milner, 2015; Mosley, 2015; Piniewski et al., 2017). It is possible that rivers with higher base flows are providing a more stable environment to support richer invertebrate communities benefiting from the wide scale water quality improvements documented elsewhere (Vaughan & Ormerod, 2012b). However, Whelan et al. (2022), shows that changes in water quality in the UK are complex; although phosphate loading and acidification appear to have recovered somewhat, catchments with intensive agriculture are likely to be fairing worse than pre-1960 levels of water quality (Whelan et al., 2022).

Organic sites – in areas dominated by peatland – generally have the strongest increases in macroinvertebrates, especially in lowland rivers. There are much fewer organic river sites in England than siliceous and calcareous rivers, and our trends are likely inherently susceptible to spatial autocorrelation due to the aggregation of sites in areas dominated by particular sediment types. For example, there is an aggregation of lowland organic sites in Anglia, which lie in the Fens (Figure 1). We note that Diptera are either significantly decreasing or have no significant trend in other sites; this is likely driven by the families that tend to be found in high abundance but that we found to be strongly declining, such as Chrinomidae and Simuliidae. However, Diptera increase significantly within organic lowland sites; if driven by Chirnomid and Simuliid abundance change this would not support our hypothesis that these particular sites are subject to significant increases in water quality.

Ecosystem functioning

Ecosystem functions and services are often disproportionately driven by the abundance of common species (Larsen et al., 2018; Winfree et al., 2015), and so monitoring population and group-level changes of macroinvertebrate abundance – instead of occurrence, which is more sensitive to rare and vulnerable species – can ultimately contribute to a more detailed understanding of ecosystem function (Greenwell et al., 2019). Freshwater macroinvertebrates support a number of different ecosystem functions and services (Macadam & Stockan, 2015), but namely they constitute the bulk of the diet of many fish, bird and bat species, including some rare and protected species in England such as the Daubenton's bat (*Myotis daubentonii*) and the Eurasian Dipper (*Cinclus cinclus*), whose diet is largely made up of Trichoptera. Identifying long term declines in the abundance of families and wider taxonomic groups of freshwater macroinvertebrates can inform on the availability of food sources for these higher trophic levels.

Trophic level changes such as those we show here may have consequences for regulatory ecosystem services associated with freshwater systems such as water self-purification processes (Ostroumov, 2017). We suggest that an increasing abundance of herbivorous and declining decomposer abundance represents a trophic level shift within macroinvertebrate communities, although they are still largely dominated by decomposers. Herbivorous invertebrate increases are being driven by a number of increasing families within Coleoptera, Trichoptera and Plecoptera, whilst carnivorous abundance increases reflect increases in invertebrate-feeding Coleoptera, crustaceans, Odonata and Megaloptera (in some river typologies). Decomposer abundance decline reflects changes in some abundant dipteran and annelid families. Decomposer declines may be driven by lower abundances in pollution-tolerant groups such as oligochaetes and flow regime change and sediment pollution, but regardless of the drivers these declines could result in stagnation of the self-purification process through leaf-litter breakdown and removal, a vital process in freshwater ecosystem functions (Mustonen et al., 2016). Further analyses would be needed to investigate the potential repercussions of the trophic level changes we highlight in this study.

Limitations and caveats

Although we discuss the potential consequences of our findings for ecosystem functions and services, future studies using biomass and dietary preference data (Lu et al. 2016) could give a more nuanced picture of the functional consequences of temporal invertebrate community change. Using biomass would provide a more accurate picture of the state of food and energy availability for predator species in freshwater ecosystems. Similarly, combining biomass data with other functional traits could reveal more about ecosystem functions such as decomposition, as organisms with larger biomass consume larger amounts of food. If, for example, decomposer declines are driven to a significant degree by Chironomids, which we found to be declining significantly over time, then hypothetically, increases in other decomposers of higher biomass could prevent or mitigate the loss of function. Biomass data and organic matter feeding/decomposition rates are not captured in this monitoring scheme but extending monitoring to consider a functional trait approach holds promise for future research.

Additionally, our method of calculating dietary preferences may have resulted in some taxa having greater influence over results, for example where the fuzzy-coded data in Tachet et al. (2015) sum to greater values across dietary components, meaning we had a potentially reduced capacity to estimate the diet of some individuals which were not identified down to genus level, though we do not think this would have had much of an impact on our results due to our method of weighting by genus presence.

We emphasise the importance of long-term data to evaluate biodiversity changes, but even analyses covering nearly two decades, such as the one analysed here, have limitations. We were not able to resolve species or genus-level trends, which has limited our ability to understand the potential reasons for increases and declines identified in our dataset. Although we discuss family-level trends in the context of water quality changes (due to different families varying in response to water quality improvement and pollution), within families there is also variation amongst species in their sensitivity to water quality metrics, or their ‘saprobic index’, which we were not able to capture in this analysis (Metcalfe, 1989). Nor were we able to calculate absolute abundance change earlier than 2002, due to the limitations of the dataset explained earlier. Although our study presents a range of trends from declines to stable and increasing abundance of freshwater macroinvertebrates since 2002, current population sizes may actually be much lower in English rivers than 50 or 100 years ago.

Finally, the dynamics of invertebrate trends are difficult to capture and model over the long term due to high interannual variation that is inherent across these taxa (Baranov et al., 2020; Cauvy-Fraunié et al., 2020); this appears to also be the case with our data, shown in Figures 2 and 3. We have chosen to model long-term abundance change of macroinvertebrates using hierarchical linear modelling, and whilst this approach allows us to provide our best estimate of how abundance has changed on average since 2002, the models presented do not capture changes from one year to the next, nor explain occasional short-term non-linear patterns in geometric means. For example, some patterns that appear to buck the linear trend - such as herbivore abundance in the latter years of the dataset – may well be better represented by non-linear modelling such as using generalised additive models; for this reason, we provide additional models in the Supporting information that represent these short-term patterns. Other important questions about macroinvertebrate abundance change in the UK and more widely remain, such as the stability and resilience of these communities over time under fluctuating environmental extremes, which are increasing under climate and land use change pressures (Fried-Petersen et al., 2020; Jourdan et al., 2018).

Implications and recommendations

Our work has important implications for policy in the UK and beyond. In the wake of the UK's exit from the European Union, new policies and targets have been created to replace EU biodiversity and environmental policy, for example, the UK Government's 25 Year Environment Plan and the Environment Act (2021). This legislation has triggered new targets in England to halt the decline of species abundance by 2030 and increase abundance by 10% by 2042 (although these are currently subject to change). Although we were unable to identify species-level trends using this dataset, our higher taxonomic level and trophic abundance trends highlight particular groups, such as Ephemeroptera, that have fared worse than other groups of macroinvertebrates, warranting further investigation into invertebrate abundance declines in England. Our analysis also highlights particular river types where macroinvertebrates have declined at higher rates, in particular, siliceous rivers, which are less likely to be resilient to ex situ environmental pressures, such as pollution from agricultural run-off. We suggest this could help direct future management and conservation interventions toward particular river types whose macroinvertebrate communities are more vulnerable.

In view of our use of a Water Framework Directive-based typological approach to river characterisation in this study, we suggest that our results could be used in the future to compare across river systems across Europe, where there are similar macroinvertebrate sampling procedures and typological classifications of rivers. We hope this approach could be used to investigate trends and direct further research and management on a European-wide scale for different types of river typologies based on patterns of abundance change across macroinvertebrate communities. Following the UK's exit from the European Union, regardless of future legislation following the EU Water Framework Directive, we recommend that future monitoring of macroinvertebrate communities in England under the Environment Agency continue to use the same sampling and monitoring protocol to make new data on abundance and biodiversity comparable to past data, as well as to the rest of Europe.

In conclusion, extensive monitoring schemes and detailed analyses that explore taxonomic, functional and spatial nuances are necessary if we are to better understand the extent of biodiversity change around the world. Further studies are needed to predict how the provision and resilience of key ecosystem functions provided by freshwater communities are affected by abundance changes within individual invertebrate taxa and for specific catchments, and to identify key anthropogenic drivers to aid targeted ecosystem management.

Acknowledgements

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Supporting Information

Figures

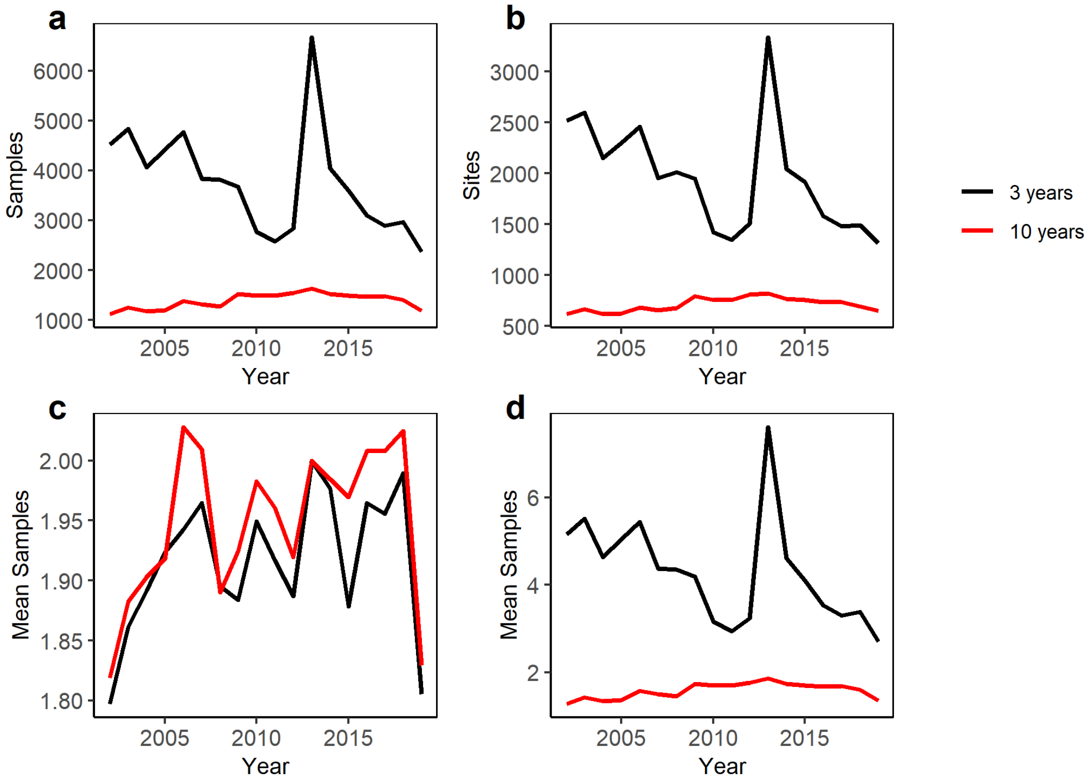


Figure S1. Comparison of sampling effort between two potential datasets to use for mixed effects models – one including only sites sampled in both spring and autumn for at least three years between 2002 and 2019 (black) and the other including only sites sampled in both spring and autumn for at least 10 years between 2002 and 2019 (red). Panel a shows the total number of samples taken each year; panel b shows the total number of sites included in the analysis each year; panel c. shows the mean number of samples taken per site included in the analysis each year, and d. shows the mean number of samples taken per total number of sites in the dataset each year.

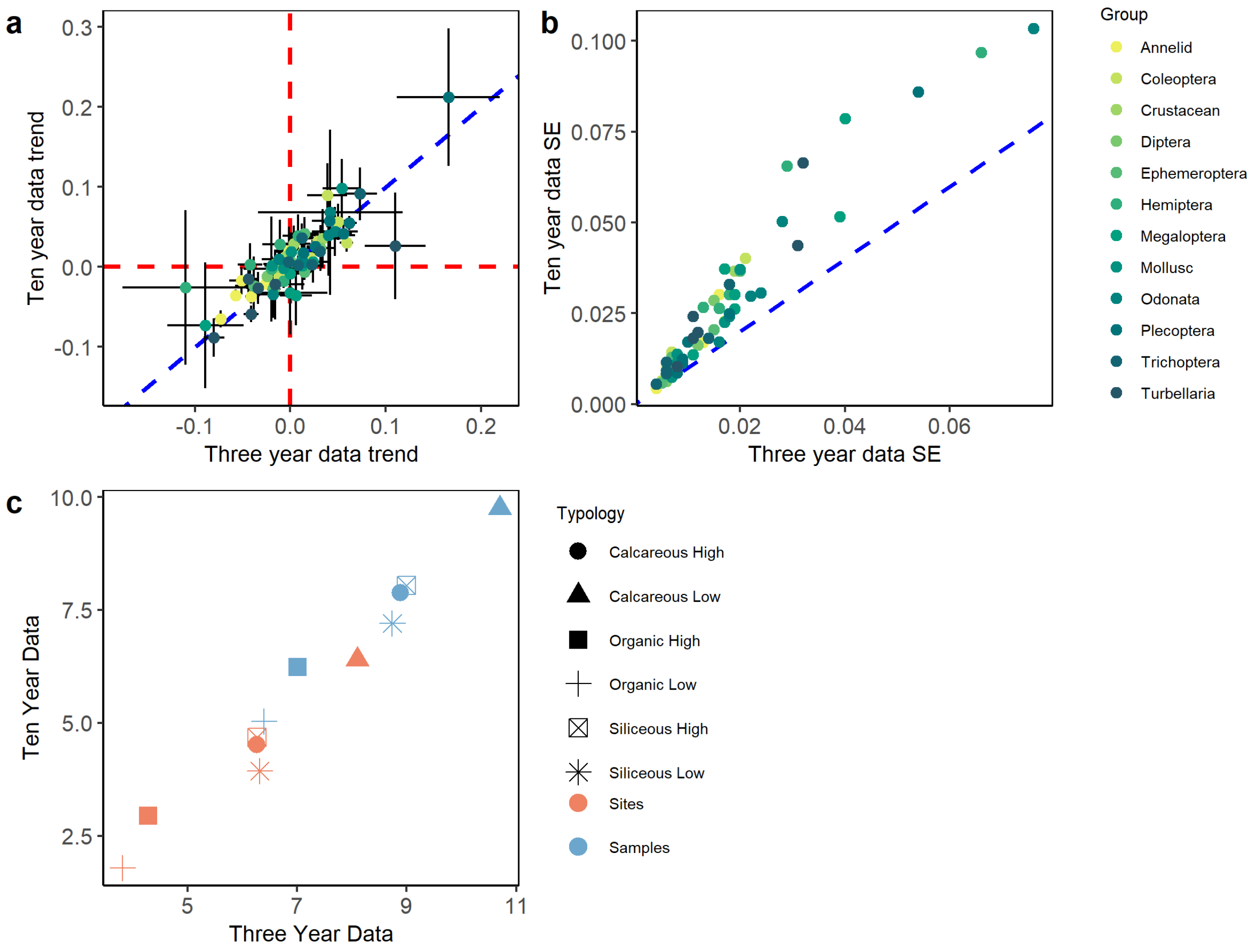


Figure S2. Comparison between two potential datasets to use for mixed effects models – one including only sites sampled in both spring and autumn for at least three years between 2002 and 2019 and the other including only sites sampled in both spring and autumn for at least 10 years between 2002 and 2019. Panel a: comparison of trends extracted from mixed effect model outputs including standard errors (Pearson's correlation coefficient = 0.85); panel b: comparison of the standard error for trends extracted from mixed effect model outputs (Pearson's correlation coefficient = 0.97); panel c. comparison of the number of sites and samples used in analyses (presented as $\log_e$ values due to scale differences).

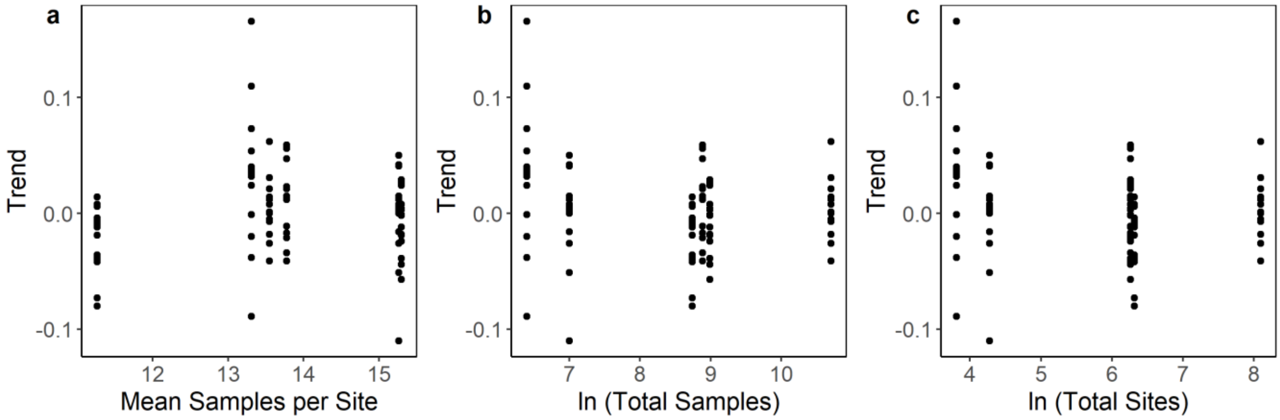


Figure S3. The relationship between a. the mean number of samples taken per site within each river typology; b. the total number of samples taken within river typologies and c. the total number of sites within each river typology; and the group-level trends extracted from final mixed effect model outputs (lm; $\beta = -0.00495$, s.e. = 0.003, d.f. = 88; $p > 0.05$)

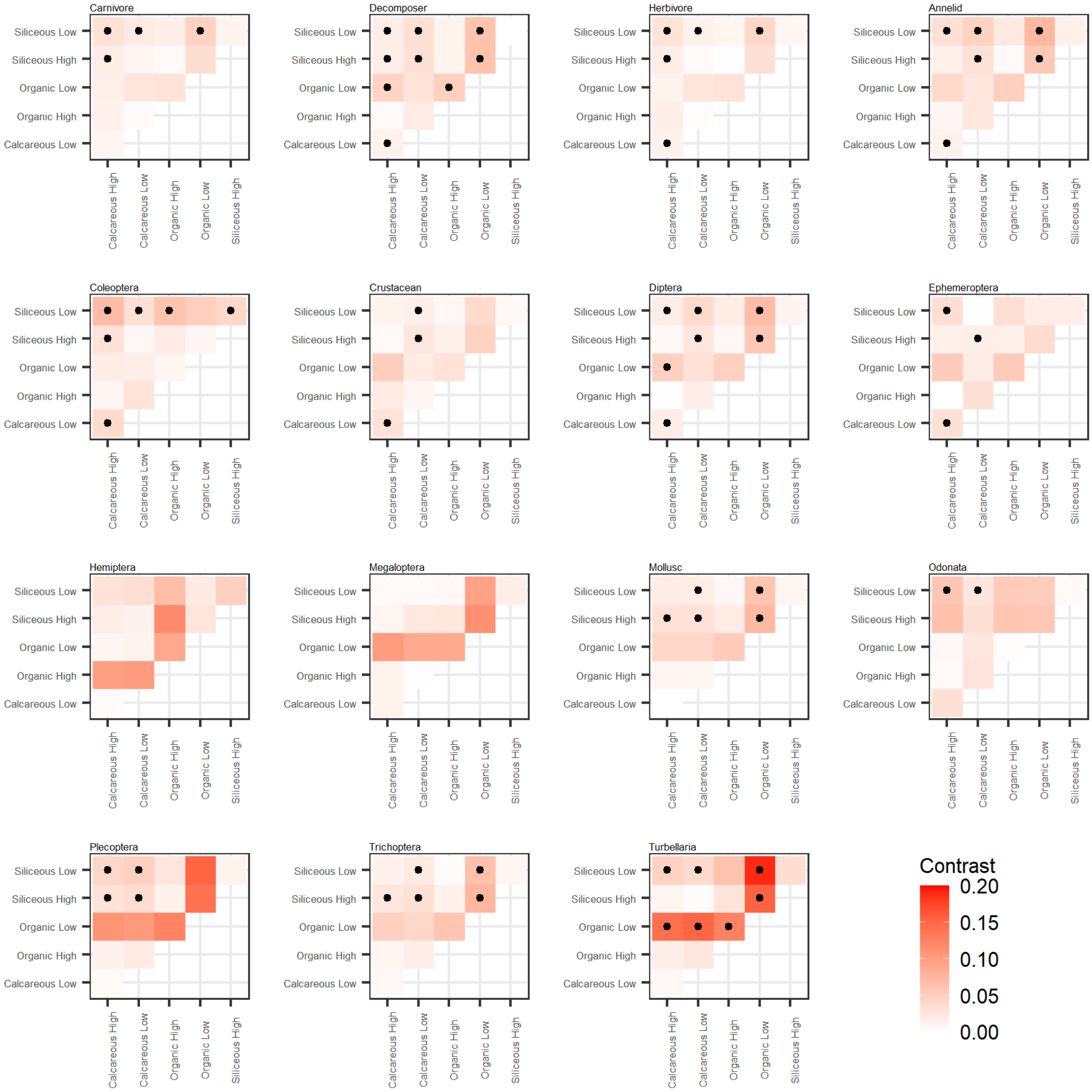


Figure S4. The contrast between different river typology trends in macroinvertebrate abundance change, for each trophic and taxonomic group, according to Tukey pairwise comparison tests. Darker colours show higher contrasts between river typologies, meaning there is a larger difference between their trends. Black dots show where the contrasts between trends are significant at the p ≤ 0.05 level.

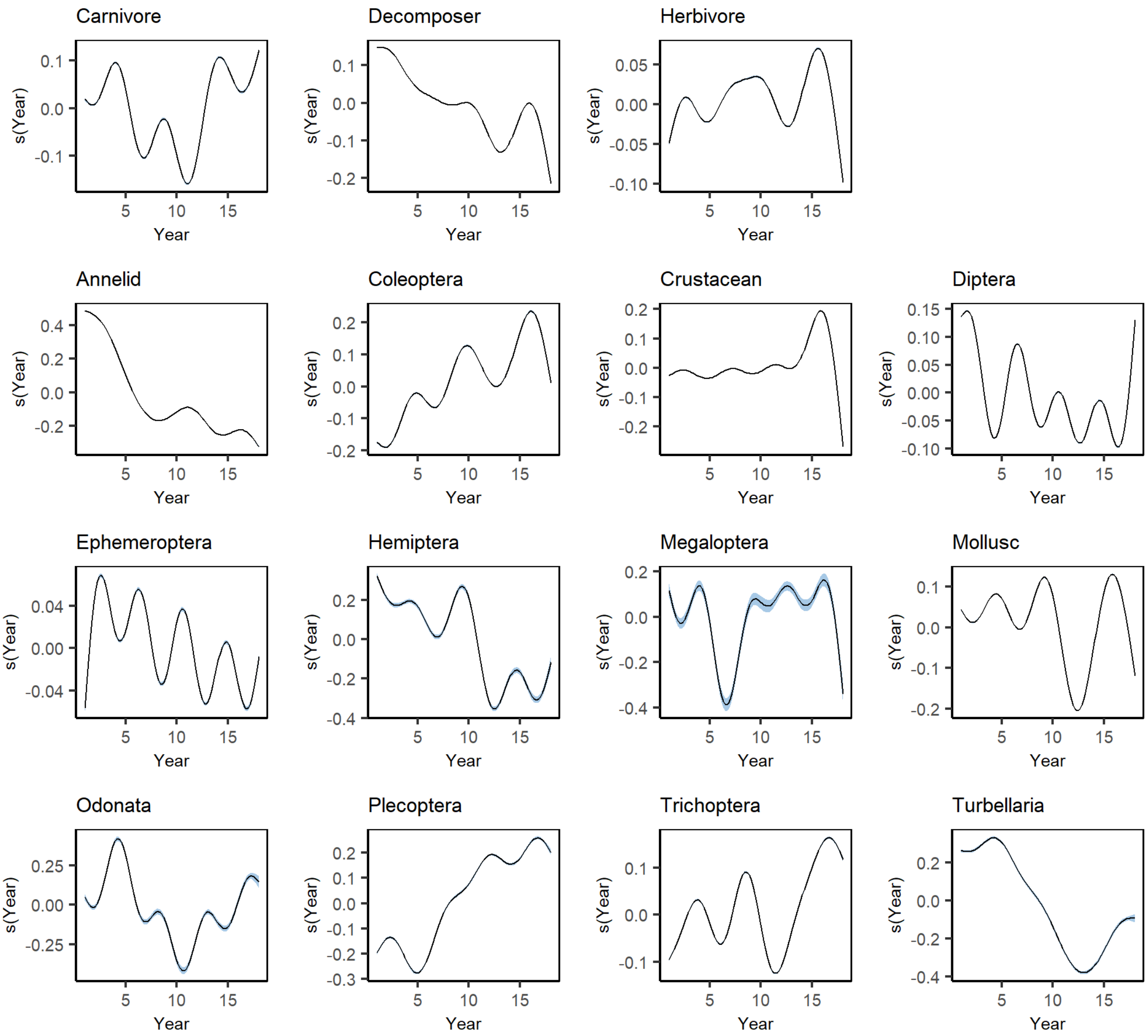


Figure S5. Plotted smooths of 'Year' fixed effects from GAMM trials, fitting site and observations as smoothed random effects in models. 'Year' is presented as integers 1-18 for the years 2002-2019. Approximate significance of smoothed terms can be found in Table S5.

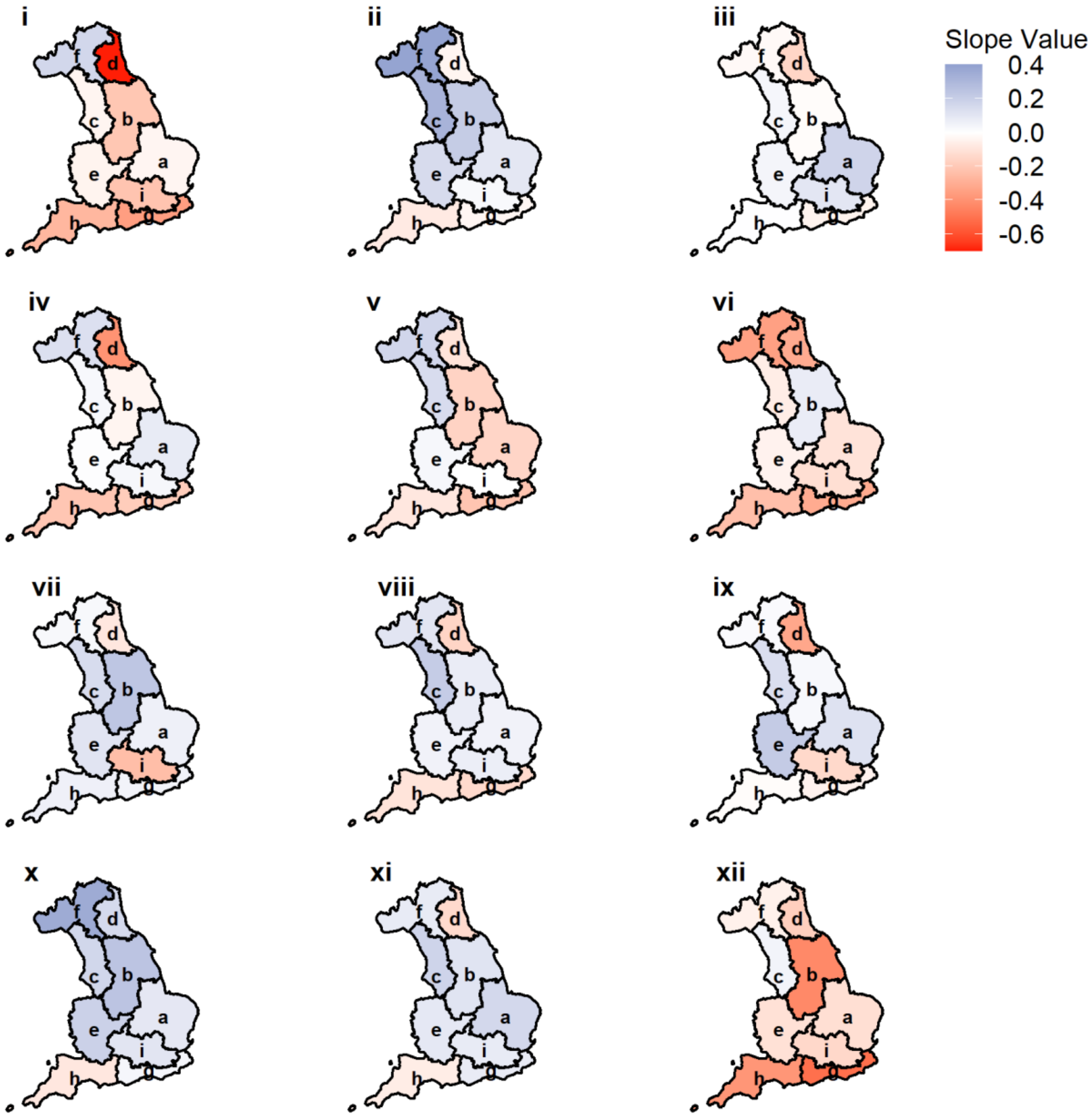


Figure S6. Map of English river basin district boundaries coloured by slope values extracted from models exploring spatial variation in trends, for i) annelids, ii) coleoptera, iii) crustaceans, iv) Diptera, v) Ephemeroptera, vi) Hemiptera, vii) Megaloptera, viii) molluscs, ix) Odonata, x) Plecoptera, xi) Trichoptera and xii) Turbellaria. Labels of river basins and the number of site:sample combinations are as follows; a) Anglian, n = 12071; b) Humber; n = 15396, c) North West, n = 7519; d) Northumbria, n = 3017; e) Severn, n = 6727; f) Solway Tweed, 2101; g) South East, 4103; h) South West, n = 7027, and i) Thames, n = 8808. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Tables

Table S1. Anova outputs for model comparisons across each trophic and taxonomic group to test whether abundance trends varied significantly across river typologies. All model comparison outputs show that including river typology in the model improves the model significantly ($p < 0.05$). Model 1 and Model 2 include a ‘year’ effect only and a ‘year * typology interaction effect respectively.

Taxonomic Group	**AIC**		**BIC**		**X^2**	**d.f.**	**P value**
	Model 1	**Model 2**	**Model 1**	**Model 2**			
Carnivore	685760	685509	685824	685664	271	10	≤ 0.001
Herbivore	888601	888338	888665	888493	283	10	≤ 0.001
Decomposer	962839	962061	962903	962216	799	10	≤ 0.001
Annelid	703202	702302	703266	702457	921	10	≤ 0.001
Coleoptera	592003	591699	592067	591854	324	10	≤ 0.001
Crustacean	743626	741428	743690	741583	2218	10	≤ 0.001
Diptera	816119	815917	816183	816072	222	10	≤ 0.001
Ephemeroptera	743089	742327	743153	742482	782	10	≤ 0.001
Hemiptera	128902	128034	128965	128189	888	10	≤ 0.001
Megaloptera	92840	92370	92904	92525	490	10	≤ 0.001
Mollusc	715103	712865	715167	713021	2257	10	≤ 0.001
Odonata	140179	138864	140243	139019	1335	10	≤ 0.001
Plecoptera	285504	282614	285568	282769	2910	10	≤ 0.001
Trichoptera	683651	683325	683715	683480	346	10	≤ 0.001
Turbellaria	260237	260064	260301	260219	193	10	≤ 0.001

Table S2. Summary of trends across river typologies, for models including a year * typology effect across taxonomic and trophic. 'AGR' = Annual Growth Rate (%), and '% Change' = Total percentage change over the 18 year time period.

Group	River Typology	Intercept		Slope			AGR	% Change
		Estimate	S.E.	Estimate	S.E.	P value		
Annelid	Calcareous High	3.429	0.069	-0.041	0.006	≤ 0.001	-2.78	-50.0
	Calcareous Low	4.101	0.045	-0.026	0.004	≤ 0.001	-1.99	-35.9
	Organic High	2.701	0.167	-0.051	0.013	≤ 0.001	-3.23	-58.1
	Organic Low	3.502	0.193	-0.001	0.016	0.968	-0.06	-1.1
	Siliceous High	3.462	0.069	-0.057	0.006	≤ 0.001	-3.45	-62.0
	Siliceous Low	4.39	0.068	-0.073	0.006	≤ 0.001	-3.96	-71.3
Coleoptera	Calcareous High	2.532	0.106	0.059	0.007	≤ 0.001	9.62	173.1
	Calcareous Low	2.257	0.062	0.021	0.005	≤ 0.001	2.40	43.3
	Organic High	2.136	0.265	0.05	0.017	≤ 0.01	7.47	134.4
	Organic Low	1.584	0.318	0.039	0.021	0.06	5.26	94.6
	Siliceous High	2.824	0.106	0.029	0.007	≤ 0.001	3.56	64.1
	Siliceous Low	3.549	0.103	-0.012	0.007	0.1	-1.03	-18.5
Crustacean	Calcareous High	2.927	0.093	-0.017	0.007	< 0.05	-1.39	-24.9
	Calcareous Low	4.285	0.056	0.013	0.005	≤ 0.01	1.37	24.7
	Organic High	0.597	0.244	0.004	0.017	0.808	0.40	7.3
	Organic Low	4.128	0.269	0.034	0.019	0.075	4.32	77.7
	Siliceous High	1.366	0.096	-0.012	0.007	0.104	-1.00	-18.0
	Siliceous Low	4.045	0.091	-0.004	0.007	0.534	-0.39	-7.0
Diptera	Calcareous High	4.593	0.075	-0.017	0.007	≤ 0.01	-1.43	-25.7
	Calcareous Low	4.417	0.06	0.001	0.006	0.794	0.14	2.5
	Organic High	4.007	0.148	-0.016	0.012	0.17	-1.34	-24.1
	Organic Low	3.348	0.172	0.032	0.015	< 0.05	4.05	72.9
	Siliceous High	4.56	0.075	-0.024	0.006	≤ 0.001	-1.88	-33.9
	Siliceous Low	4.819	0.074	-0.036	0.007	≤ 0.001	-2.57	-46.2
Ephemeroptera	Calcareous High	4.742	0.093	0.015	0.007	< 0.05	1.60	28.8
	Calcareous Low	3.411	0.058	-0.018	0.005	≤ 0.001	-1.50	-26.9
	Organic High	4.117	0.228	0.015	0.015	0.308	1.61	29.0
	Organic Low	2.799	0.274	-0.038	0.02	0.052	-2.65	-47.7
	Siliceous High	4.627	0.093	-0.001	0.007	0.84	-0.13	-2.3
	Siliceous Low	4.062	0.092	-0.019	0.007	≤ 0.01	-1.56	-28.1
Hemiptera	Calcareous High	-3.776	0.216	-0.011	0.018	0.524	-0.96	-17.3
	Calcareous Low	-1.604	0.08	-0.007	0.006	0.256	-0.64	-11.6
	Organic High	-3.883	0.675	-0.11	0.066	0.095	-4.70	-84.6
	Organic Low	0.63	0.454	-0.02	0.029	0.495	-1.59	-28.5
	Siliceous High	-3.855	0.211	0.008	0.016	0.636	0.78	14.0
	Siliceous Low	-1.887	0.163	-0.042	0.013	≤ 0.001	-2.82	-50.7
Megaloptera	Calcareous High	-3.918	0.224	0.013	0.019	0.493	1.37	24.6
	Calcareous Low	-2.189	0.121	0	0.011	0.976	0.03	0.5
	Organic High	-3.304	0.496	0	0.039	0.992	-0.04	-0.7
	Organic Low	-1.566	0.477	-0.089	0.04	< 0.05	-4.33	-78.0
	Siliceous High	-4.161	0.231	0.024	0.019	0.199	2.84	51.2
	Siliceous Low	-3.013	0.197	0.006	0.017	0.701	0.64	11.6
Mollusc	Calcareous High	2.155	0.101	0.012	0.008	0.142	1.28	23.0
	Calcareous Low	4.052	0.074	0.012	0.007	0.074	1.23	22.1
	Organic High	0.612	0.233	0.001	0.017	0.956	0.09	1.6
	Organic Low	3.958	0.257	0.054	0.02	≤ 0.01	8.34	150.1
	Siliceous High	1.702	0.102	-0.019	0.008	< 0.05	-1.52	-27.4
	Siliceous Low	3.868	0.099	-0.007	0.008	0.37	-0.66	-11.8
Odonata	Calcareous High	-4.978	0.295	0.047	0.024	< 0.05	6.81	122.6
	Calcareous Low	-1.578	0.182	0.014	0.016	0.379	1.53	27.6
	Organic High	-6.061	0.991	0.042	0.076	0.576	5.88	105.9
	Organic Low	0.597	0.461	0.04	0.028	0.151	5.36	96.6

	Siliceous High	-3.987	0.265	-0.018	0.022	0.418	-1.44	-25.9
	Siliceous Low	-1.098	0.219	-0.012	0.018	0.505	-1.02	-18.3
Plecoptera	Calcareous High	1.63	0.169	0.056	0.009	≤ 0.001	8.83	159.0
	Calcareous Low	-2.697	0.106	0.062	0.008	≤ 0.001	10.44	187.9
	Organic High	2.954	0.416	0.041	0.018	< 0.05	5.57	100.2
	Organic Low	-5.564	0.854	0.166	0.054	≤ 0.01	88.23	1588.2
	Siliceous High	3.124	0.168	0.026	0.009	≤ 0.01	3.10	55.8
	Siliceous Low	0.879	0.17	0.014	0.01	0.167	1.44	25.9
Trichoptera	Calcareous High	3.571	0.098	0.023	0.006	≤ 0.001	2.69	48.5
	Calcareous Low	2.833	0.056	0.031	0.004	≤ 0.001	3.79	68.1
	Organic High	3.308	0.249	0.012	0.014	0.387	1.29	23.2
	Organic Low	1.421	0.302	0.073	0.018	≤ 0.001	13.63	245.4
	Siliceous High	4.02	0.098	-0.002	0.006	0.708	-0.22	-3.9
	Siliceous Low	3.749	0.096	0.008	0.006	0.204	0.82	14.8
Turbellaria	Calcareous High	-0.695	0.147	-0.034	0.012	≤ 0.01	-2.41	-43.4
	Calcareous Low	0	0.086	-0.041	0.008	≤ 0.001	-2.77	-49.8
	Organic High	-1.532	0.396	-0.016	0.031	0.604	-1.31	-23.6
	Organic Low	-0.631	0.415	0.11	0.032	≤ 0.001	30.53	549.5
	Siliceous High	0.073	0.144	-0.044	0.011	≤ 0.001	-2.93	-52.8
	Siliceous Low	0.816	0.139	-0.08	0.011	≤ 0.001	-4.13	-74.4
Carnivore	Calcareous High	3.504	0.076	0.021	0.006	≤ 0.001	2.44	44.0
	Calcareous Low	3.38	0.058	0.012	0.005	< 0.05	1.27	22.9
	Organic High	3.695	0.16	0.008	0.012	0.507	0.78	14.0
	Organic Low	3.26	0.185	0.038	0.014	≤ 0.01	5.02	90.4
	Siliceous High	3.999	0.076	0.003	0.006	0.668	0.26	4.7
	Siliceous Low	3.87	0.075	-0.009	0.006	0.15	-0.80	-14.4
Herbivore	Calcareous High	5.29	0.062	0.022	0.005	≤ 0.001	2.58	46.5
	Calcareous Low	4.917	0.039	0.008	0.003	< 0.05	0.85	15.3
	Organic High	5.054	0.151	0.005	0.011	0.627	0.50	9.1
	Organic Low	4.558	0.178	0.035	0.013	≤ 0.01	4.60	82.8
	Siliceous High	5.392	0.062	0.004	0.005	0.409	0.38	6.8
	Siliceous Low	5.369	0.061	-0.006	0.005	0.188	-0.57	-10.2
Decomposer	Calcareous High	5.66	0.052	-0.021	0.004	≤ 0.001	-1.64	-29.6
	Calcareous Low	5.97	0.035	-0.005	0.003	0.092	-0.47	-8.5
	Organic High	5.097	0.125	-0.026	0.009	≤ 0.01	-1.97	-35.5
	Organic Low	5.138	0.145	0.024	0.012	< 0.05	2.83	51.0
	Siliceous High	5.644	0.052	-0.039	0.004	≤ 0.001	-2.68	-48.2
	Siliceous Low	6.298	0.052	-0.039	0.004	≤ 0.001	-2.68	-48.2

Table S3. Summary of family-level trend slopes at the national level, basin effect across trophic groups. 'AGR' = Annual Growth Rate (%). We categorised trends as Strong Increases (where the annual growth rate ≥ 2.81%, leading to a doubling of abundance over 25 years); Moderate Increases (where the annual growth rate is between 1.16% and 2.81%); No Change (where trends were insignificant – all trends with growth rates between -1.14% and 1.16% were insignificant); Moderate Decreases (where the annual growth rate is between -2.73% and -1.14%); and Strong Decreases (where the annual growth rate ≤ -2.73%, representing at least a halving of abundance over 25 years).

Group	Family	Slope	SE	P value	AGR (%)	Trend
Annelid	Erpobdellidae	-0.06	0.01	≤ 0.001	-3.42	Strong Decrease
	Glossiphoniidae	0.16	0.02	≤ 0.001	72.98	Strong Increase
	Piscicolidae	-0.07	0.01	≤ 0.001	-3.80	Strong Decrease
	Lumbricidae	0.06	0.02	≤ 0.01	10.00	Strong Increase
	Hirudinidae	-0.14	0.08	0.06	-5.07	No Change
	Haemopidae	0.02	0.05	0.70	2.32	No Change
	Lumbriculidae	-0.09	0.08	0.30	-4.27	No Change
	Glossoscolecidae	-5.69	1.35	≤ 0.001	-5.56	Strong Decrease
	Ampharetidae	0.31	0.13	< 0.05	1080.08	Strong Increase
	Eunicidae	-0.95	1.39	0.49	-5.56	No Change
	Trochochaetidae	-0.92	1.64	0.57	-5.56	No Change
	Cirratulidae	-1.34	2.23	0.55	-5.56	No Change
	Arenicolidae	-1.00	1.84	0.59	-5.56	No Change
Coleoptera	Dytiscidae	-0.02	0.01	0.06	-1.66	No Change
	Elmidae	0.05	0.01	≤ 0.001	7.01	Strong Increase
	Haliplidae	0.15	0.02	≤ 0.001	61.60	Strong Increase
	Gyrinidae	0.03	0.01	< 0.05	3.28	Strong Increase
	Scirtidae	0.04	0.01	≤ 0.01	4.68	Strong Increase
	Hydrophilidae	-0.06	0.01	≤ 0.001	-3.44	Strong Decrease
	Hygrobiidae	-0.08	0.05	0.11	-4.22	No Change
	Hydraenidae	0.02	0.01	< 0.05	2.92	Strong Increase
	Noteridae	-0.37	0.04	≤ 0.001	-5.55	Strong Decrease
	Dryopidae	0.07	0.02	≤ 0.001	13.41	Strong Increase
	Chrysomelidae	-0.02	0.02	0.36	-1.65	No Change
	Curculionidae	-0.01	0.01	0.12	-1.19	No Change
	Erirhinidae	-1.14	0.98	0.25	-5.56	No Change
	Heteroceridae	-0.99	0.73	0.18	-5.56	No Change
	Staphylinidae	0.07	0.06	0.24	11.61	No Change
	Sphaeriusidae	-1.33	2.20	0.55	-5.56	No Change
	Apionidae	-0.60	0.58	0.30	-5.56	No Change
Crustacean	Asellidae	-0.03	0.01	< 0.05	-2.05	Moderate Decrease
	Crangonyctidae	0.07	0.03	≤ 0.01	13.55	Strong Increase
	Astacidae	0.13	0.02	≤ 0.001	41.40	Strong Increase
	Sphaeromatidae	-1.02	0.69	0.14	-5.56	No Change
	Argulidae	-0.46	0.10	≤ 0.001	-5.55	Strong Decrease
	Palaemonidae	-0.78	0.21	≤ 0.001	-5.56	Strong Decrease
	Mysidae	-0.55	0.18	≤ 0.01	-5.56	Strong Decrease

	Corophiidae	-0.61	0.08	≤ 0.001	-5.56	Strong Decrease
	Niphargidae	0.05	0.02	< 0.05	7.75	Strong Increase
	Daphniidae	-0.01	0.04	0.75	-1.05	No Change
	Sididae	-0.66	0.55	0.23	-5.56	No Change
	Notodelphyidae	-3.18	4.23	0.45	-5.56	No Change
	Paguridae	-1.65	3.04	0.59	-5.56	No Change
	Cambaridae	-2.11	3.48	0.54	-5.56	No Change
	Chirocephalidae	-7.42	7.29	0.31	-5.56	No Change
	Cercopagididae	-2.26	2.57	0.38	-5.56	No Change
	Triopsidae	-1.17	1.87	0.53	-5.56	No Change
	Janiridae	-15.68	38.82	0.69	-5.56	No Change
	Bythocytheridae	-4.67	3.36	0.16	-5.56	No Change
	Oplophoridae	-3.86	3.14	0.22	-5.56	No Change
Diptera	Chironomidae	-0.29	0.04	≤ 0.001	-5.51	Strong Decrease
	Simuliidae	-0.02	0.01	< 0.05	-1.92	Moderate Decrease
	Tipulidae	-0.13	0.02	≤ 0.001	-4.93	Strong Decrease
	Ceratopogonidae	-0.02	0.01	≤ 0.01	-1.91	Moderate Decrease
	Tabanidae	-0.02	0.01	0.11	-1.58	No Change
	Pediciidae	0.11	0.03	≤ 0.001	31.40	Strong Increase
	Limoniidae	0.10	0.03	≤ 0.001	23.01	Strong Increase
	Psychodidae	0.01	0.01	0.23	0.76	No Change
	Stratiomyidae	0.01	0.01	0.59	0.53	No Change
	Empididae	0.00	0.01	0.74	-0.21	No Change
	Muscidae	0.00	0.01	0.94	0.07	No Change
	Ptychopteridae	0.08	0.02	≤ 0.001	15.51	Strong Increase
	Culicidae	-0.02	0.02	0.46	-1.44	No Change
	Chaoboridae	-0.01	0.04	0.72	-1.07	No Change
	Dixidae	0.09	0.01	≤ 0.001	19.64	Strong Increase
	Ephydridae	0.04	0.01	≤ 0.001	5.74	Strong Increase
	Syrphidae	0.02	0.02	0.44	1.81	No Change
	Sciomyzidae	0.03	0.02	0.20	3.68	No Change
	Dolichopodidae	0.04	0.02	< 0.05	4.96	Strong Increase
	Rhagionidae	-0.03	0.02	0.10	-2.16	No Change
	Thaumaleidae	-0.51	0.14	≤ 0.001	-5.55	Strong Decrease
	Lonchopteridae	-0.58	0.17	≤ 0.001	-5.56	Strong Decrease
	Bibionidae	0.11	0.07	0.11	31.66	No Change
	Athericidae	0.15	0.02	≤ 0.001	67.29	Strong Increase
	Scatopsidae	0.13	0.07	0.07	42.54	No Change
Ephemeroptera	Caenidae	-0.06	0.03	< 0.05	-3.68	Strong Decrease
	Ephemeridae	0.29	0.02	≤ 0.001	722.26	Strong Increase
	Baetidae	-0.03	0.02	0.06	-2.24	No Change
	Ephemerellidae	0.01	0.02	0.55	1.38	No Change
	Leptophlebiidae	0.01	0.01	0.56	0.63	No Change
	Heptageniidae	0.10	0.01	≤ 0.001	24.75	Strong Increase
	Plagiotropidaceae	0.26	0.04	≤ 0.001	452.77	Strong Increase
	Siphlonuridae	-0.01	0.05	0.79	-1.14	No Change
	Potamanthidae	-0.67	0.16	≤ 0.001	-5.56	Strong Decrease
	Ameletidae	-0.40	0.09	≤ 0.001	-5.55	Strong Decrease
Hemiptera	Corixidae	-0.02	0.01	< 0.05	-1.67	Moderate Decrease
	Notonectidae	-0.01	0.01	0.47	-0.77	No Change
	Aphelocheiridae	-0.38	0.03	≤ 0.001	-5.55	Strong Decrease

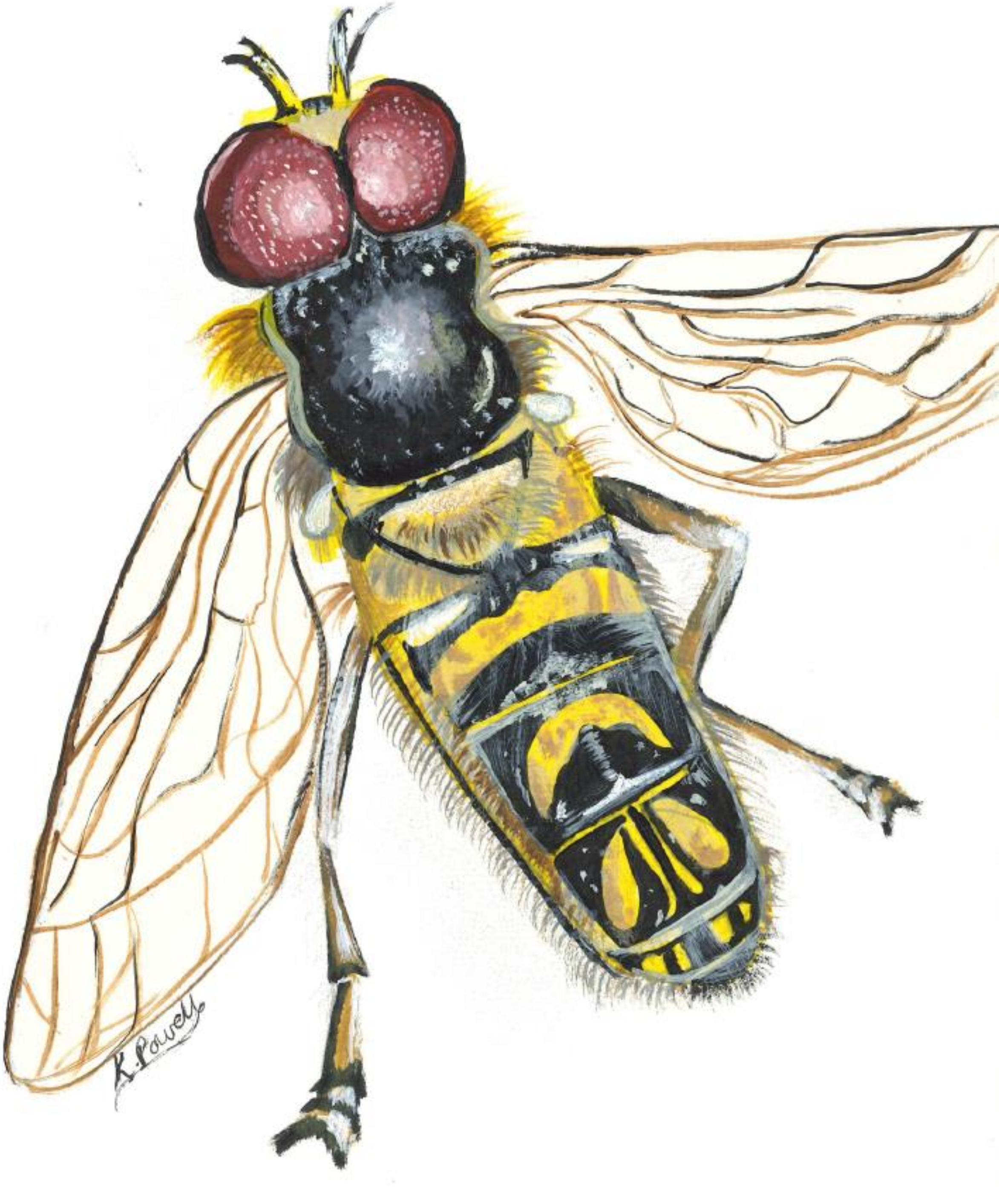
	Naucoridae	-0.33	0.04	≤ 0.001	-5.53	Strong Decrease
	Veliidae	0.01	0.01	0.62	0.50	No Change
	Gerridae	-0.02	0.01	0.13	-1.42	No Change
	Pleidae	0.05	0.03	0.12	6.53	No Change
	Nepidae	0.00	0.01	0.83	-0.30	No Change
	Hydrometridae	-0.10	0.02	≤ 0.001	-4.55	Strong Decrease
	Mesoveliidae	0.03	0.04	0.49	3.09	No Change
	Cicadellidae	-0.58	0.26	< 0.05	-5.56	Strong Decrease
Megaloptera	Sialidae	0.01	0.01	0.51	0.79	No Change
Mollusc	Lymnaeidae	-0.04	0.01	≤ 0.001	-2.81	Strong Decrease
	Sphaeriidae	0.01	0.01	0.34	0.88	No Change
	Bithyniidae	-0.05	0.02	≤ 0.01	-3.37	Strong Decrease
	Valvatidae	-0.07	0.02	≤ 0.001	-3.98	Strong Decrease
	Planorbidae	0.05	0.01	≤ 0.001	7.81	Strong Increase
	Physidae	-0.01	0.01	0.41	-0.73	No Change
	Hydrobiidae	-0.73	0.12	≤ 0.001	-5.56	Strong Decrease
	Tateidae	0.31	0.03	≤ 0.001	1006.03	Strong Increase
	Unionidae	-0.04	0.01	≤ 0.001	-2.87	Strong Decrease
	Neritidae	-0.20	0.02	≤ 0.001	-5.37	Strong Decrease
	Acroloxidae	0.03	0.02	0.08	3.96	No Change
	Viviparidae	-0.37	0.03	≤ 0.001	-5.54	Strong Decrease
	Dreissenidae	-0.47	0.05	≤ 0.001	-5.55	Strong Decrease
	Succineidae	0.06	0.01	≤ 0.001	10.42	Strong Increase
	Gastrodontidae	0.05	0.03	0.08	8.50	No Change
	Cyrenidae	-0.57	0.61	0.34	-5.56	No Change
	Donacidae	-0.69	1.36	0.61	-5.56	No Change
	Carychiidae	-0.07	0.21	0.73	-3.94	No Change
	Hygromiidae	-0.90	0.37	< 0.05	-5.56	Strong Decrease
	Buccinidae	-1.84	2.70	0.50	-5.56	No Change
	Columbellidae	-0.87	0.84	0.30	-5.56	No Change
	Euconulidae	-2.44	1.33	0.07	-5.56	No Change
	Caecidae	-3.98	2.67	0.14	-5.56	No Change
	Lepidomeniidae	-2.39	2.68	0.37	-5.56	No Change
	Tornidae	-0.07	0.21	0.73	-3.94	No Change
	Tellinidae	-1.76	2.23	0.43	-5.56	No Change
	Assimineidae	-0.83	3.87	0.83	-5.56	No Change
	Cocculinidae	-4.01	3.34	0.23	-5.56	No Change
	Ellobiidae	-1.50	3.43	0.66	-5.56	No Change
	Pupillidae	-1.06	5.14	0.84	-5.56	No Change
Odonata	Calopterygidae	0.03	0.02	0.06	3.80	No Change
	Platycnemididae	-0.09	0.02	≤ 0.001	-4.34	Strong Decrease
	Coenagrionidae	-0.07	0.02	≤ 0.001	-3.87	Strong Decrease
	Aeshnidae	-0.12	0.02	≤ 0.001	-4.87	Strong Decrease
	Libellulidae	-0.01	0.03	0.67	-1.20	No Change
	Gomphidae	-0.79	0.28	≤ 0.01	-5.56	Strong Decrease
	Cordulegastridae	0.16	0.01	≤ 0.001	76.35	Strong Increase
Plecoptera	Nemouridae	0.04	0.01	≤ 0.001	4.86	Strong Increase

	Perlodidae	0.05	0.01	≤ 0.001	7.54	Strong Increase
	Leuctridae	0.06	0.01	≤ 0.001	10.27	Strong Increase
	Taeniopterygidae	0.02	0.02	0.25	2.46	No Change
	Chloroperlidae	0.05	0.01	≤ 0.001	7.60	Strong Increase
	Perlidae	-0.25	0.02	≤ 0.001	-5.48	Strong Decrease
	Capniidae	-0.01	0.05	0.77	-1.17	No Change
Trichoptera	Leptoceridae	0.02	0.01	< 0.05	2.80	Moderate Increase
	Goeridae	0.06	0.01	≤ 0.001	10.85	Strong Increase
	Limnephilidae	0.05	0.01	≤ 0.001	6.50	Strong Increase
	Hydropsychidae	0.01	0.01	0.34	0.91	No Change
	Sericostomatidae	0.05	0.01	≤ 0.001	6.84	Strong Increase
	Molannidae	-0.06	0.01	≤ 0.001	-3.39	Strong Decrease
	Polycentropodidae	0.10	0.02	≤ 0.001	23.64	Strong Increase
	Glossosomatidae	0.12	0.02	≤ 0.001	39.78	Strong Increase
	Psychomyiidae	0.00	0.01	0.98	-0.01	No Change
	Rhyacophilidae	0.04	0.01	≤ 0.001	5.05	Strong Increase
	Lepidostomatidae	0.06	0.01	≤ 0.001	11.20	Strong Increase
	Hydroptilidae	-0.01	0.01	0.45	-0.83	No Change
	Phryganeidae	-0.07	0.01	≤ 0.001	-3.79	Strong Decrease
	Beraeidae	0.01	0.07	0.89	1.00	No Change
	Philopotamidae	0.06	0.01	≤ 0.001	10.67	Strong Increase
	Apataniidae	-0.45	0.13	≤ 0.001	-5.55	Strong Decrease
	Brachycentridae	0.09	0.02	≤ 0.001	21.98	Strong Increase
	Ecnomidae	-0.61	0.18	≤ 0.001	-5.56	Strong Decrease
	Odontoceridae	0.04	0.01	≤ 0.001	5.97	Strong Increase
	Ichneumonidae	-1.08	1.14	0.34	-5.56	No Change
Turbellaria	Dugesiidae	0.00	0.02	0.86	-0.38	No Change
	Dendrocoelidae	-0.02	0.01	0.07	-1.62	No Change
	Planariidae	-0.05	0.01	≤ 0.001	-3.36	Strong Decrease
	Dalyelliidae	-8.77	20.97	0.68	-5.56	No Change

Table S5. Summary of final model coefficients (approximate estimates for parametric and smoothed terms, standard error [SE] of parametric terms, approximate significance of smoothed terms, and Un-Biased Risk Estimator [UBRE]) for Generalised Additive Mixed effect Model (GAMM) trials for all taxa and trophic groups.

Group	**Intercept (Parametric term)**	**S.E.**	**S(Year) (Fixed effect)**	**P value**	**S(Site) (Random effect)**	**P value**	**S(OLRE) (Random effect)**	**P value**	**UBRE**
Carnivore	4.44	0.0007	8.89	≤ 0.001	0.99	≤ 0.001	0.99	≤ 0.001	107
Herbivore	5.94	0.0004	8.95	≤ 0.001	1.00	≤ 0.001	0.91	≤ 0.001	352
Decomposer	6.48	0.0003	8.87	≤ 0.001	0.99	≤ 0.001	0.99	≤ 0.001	749
Annelid	4.74	0.0007	8.75	≤ 0.001	0.99	≤ 0.001	1.00	≤ 0.001	211
Coleoptera	4.34	0.0008	8.84	≤ 0.001	1.00	≤ 0.001	1.00	≤ 0.001	122
Crustacean	5.36	0.0004	8.83	≤ 0.001	0.98	≤ 0.001	1.00	≤ 0.001	537
Diptera	5.53	0.0005	8.95	≤ 0.001	1.00	≤ 0.001	0.98	≤ 0.001	377
Ephemeroptera	5.22	0.0005	8.96	≤ 0.001	1.00	≤ 0.001	0.99	≤ 0.001	278
Hemiptera	1.22	0.0038	8.97	≤ 0.001	0.99	≤ 0.001	0.92	≤ 0.001	18
Megaloptera	-0.31	0.0072	8.94	≤ 0.001	0.97	≤ 0.001	0.00	≤ 0.001	3
Mollusc	5.17	0.0005	8.79	≤ 0.001	1.00	≤ 0.001	0.98	≤ 0.001	419
Odonata	0.53	0.0050	8.93	≤ 0.001	0.98	≤ 0.001	0.99	≤ 0.001	7
Plecoptera	3.10	0.0014	8.95	≤ 0.001	0.97	≤ 0.001	0.95	≤ 0.001	74
Trichoptera	4.78	0.0006	8.98	≤ 0.001	0.99	≤ 0.001	0.71	≤ 0.001	179
Turbellaria	1.82	0.0026	8.36	≤ 0.001	0.97	≤ 0.001	1.00	≤ 0.001	31

Chapter 3



Chapter 3

Complex temporal trends in biomass and abundance of Diptera driven by the impact of agricultural intensity on community-level turnover

Abstract

Insect biodiversity and abundance declines have been reported widely and are expected to alter ecosystem functions and processes. Land-use change has been recognised as a major cause of such declines. However, variation in local environmental drivers and the scale of available monitoring data have left large knowledge gaps in which taxa are declining, where declines are the greatest, and how these declines will impact ecosystems. We used 11 years (2006-2016) of monitoring data on 40 farms distributed over ~10,000 km2 in southern Québec, Canada, to quantify the impact of agricultural intensity on temporal trends in abundance and biomass of Diptera (true flies). There was a large difference in temporal trends between farms, which we found to be driven by agricultural landcover. Contrary to expectation, increases in dipteran abundance over time were greater in areas with higher agricultural intensity, especially with an increase in cereal crops. In contrast, declines in biomass were steeper in areas of higher agricultural intensity, although only with greater maize and soy production rather than cereals such as wheat. Variation in forest cover around farms had the least effect on trends. We found steeper declines in biomass per total number of Diptera with increasing agricultural intensive cover, suggesting the presence of community turnover toward smaller-bodied flies with lower individual biomass. Our results imply that land-use may not only alter abundance and species composition of insect species assemblages, but also the distribution of key functional traits such as body size, with potential consequences for ecological processes, and notably, species interactions (e.g., pollinating, or trophic networks).

Keywords: insect declines, biodiversity change, temporal trends, agriculture, intensification, ecological status, ecosystem function, Canada

Introduction

There has been increased awareness of declines in the abundance and diversity of insects and other invertebrates over recent decades (Didham, Barbero, et al., 2020; Goulson, 2019; Hallmann et al., 2017; Montgomery et al., 2019). These declines are typically attributed to two main drivers: changes in land-use and climate (Raven & Wagner, 2021; Wagner et al., 2021). A principal example of land-use change that has impacted insects is the process of agricultural intensification (Leclère et al., 2020; Raven & Wagner, 2021; Sala et al., 2000; Wagner et al., 2021). This process led to the historical shift towards an agricultural production that focuses on increasing the amount of agricultural intervention or input per unit area over increasing the footprint of agricultural lands. Examples of agricultural intensification include the increased removal of marginal and forested habitats, drainage of water bodies, and increasing the amount of area devoted to a small number of crops (Fenoglio et al., 2020; Flick et al., 2012; Habel et al., 2019). Agricultural intensification has resulted in the increased reliance on mechanization and agro-chemical inputs such as fertilizers and pesticides. These practices therefore increase exposure to toxic contaminants and causes the large-scale homogenisation of farmlands and the important resources they provide for insects (Kovács-Hostyánszki et al., 2017; Schreinemachers & Tipraqsa, 2012).

Insects and other invertebrates contribute important ecosystem functions to terrestrial systems, such as being prey for higher trophic levels and supporting abundant predator populations (Schowalter et al., 2018). Diptera (true flies) provide a substantial food source for aerial insectivores – such as birds – in a wide range of ecosystems including agricultural areas (Holland et al., 2006). Long-term declines in dipteran and other insect abundance and biomass due to agricultural intensification are therefore expected to have negative consequences for the long-term abundance and diversity of their predators (Bowler et al., 2019). Indeed, some long-term declines of insectivores coincide with parallel declines in Diptera and other insects (Møller, 2019; Raven & Wagner, 2021; Stanton et al., 2018). Diptera also contribute to crop pollination in agroecosystems, alongside other insects (Rader et al., 2016); the declines in abundance of Diptera could therefore negatively impact on pollination services (Klein et al., 2007; Powney et al., 2019; Rader et al., 2016; Stanley et al., 2015). Diptera also have a larval stage, the larvae occupying different niches to their adult form and carrying out additional ecological functions such as decomposition and nutrient cycling of decaying organic matter in terrestrial and aquatic ecosystems (Graça, 2001). Whilst global syntheses of insect trends increase our understanding of the general state of biodiversity, further work using robust, long-term quantitative monitoring data is vital to understand how the biodiversity and abundance of insects and other invertebrates are changing across space and time, and for understanding the complex array of environmental drivers that affect biodiversity and consequentially ecosystem functioning where such communities provide important ecosystem functions and services (Montgomery et al., 2019; Shortall et al., 2009).

Here, we quantify the impact of agricultural intensification on long-term temporal trends in Diptera abundance and biomass, using a dataset of Diptera samples taken on 40 farms across a gradient of agricultural intensity in Québec, Canada. To understand change in quantity of Diptera, we calculated trends in 1) the total abundance and 2) the total biomass of Diptera over the 11-year time-series, and we asked whether long-term trends in Diptera abundance and biomass are impacted by transition to more intensive agriculture over space and time. As well as quantifying total Diptera, we calculated trends in total Diptera biomass, but ‘offset’ by total abundance caught in samples, as a way of estimating biomass per average number of Diptera and thus the average biomass of the typical individual. This was to understand whether biomass was changing as a function of abundance change alone, or whether other mechanisms of community change may be at play.

Methods

Study area

We monitored Diptera between 2006 and 2016 (11 years) on 40 farms distributed along a ~10,000-km^2 gradient of agricultural intensity in southern Québec, Canada (Figure 1a). Geological differences across the longitudinal gradient of our study area resulted in the eastern section being primarily covered by pasture and forage crops (e.g., hay, alfalfa [*Medicago*

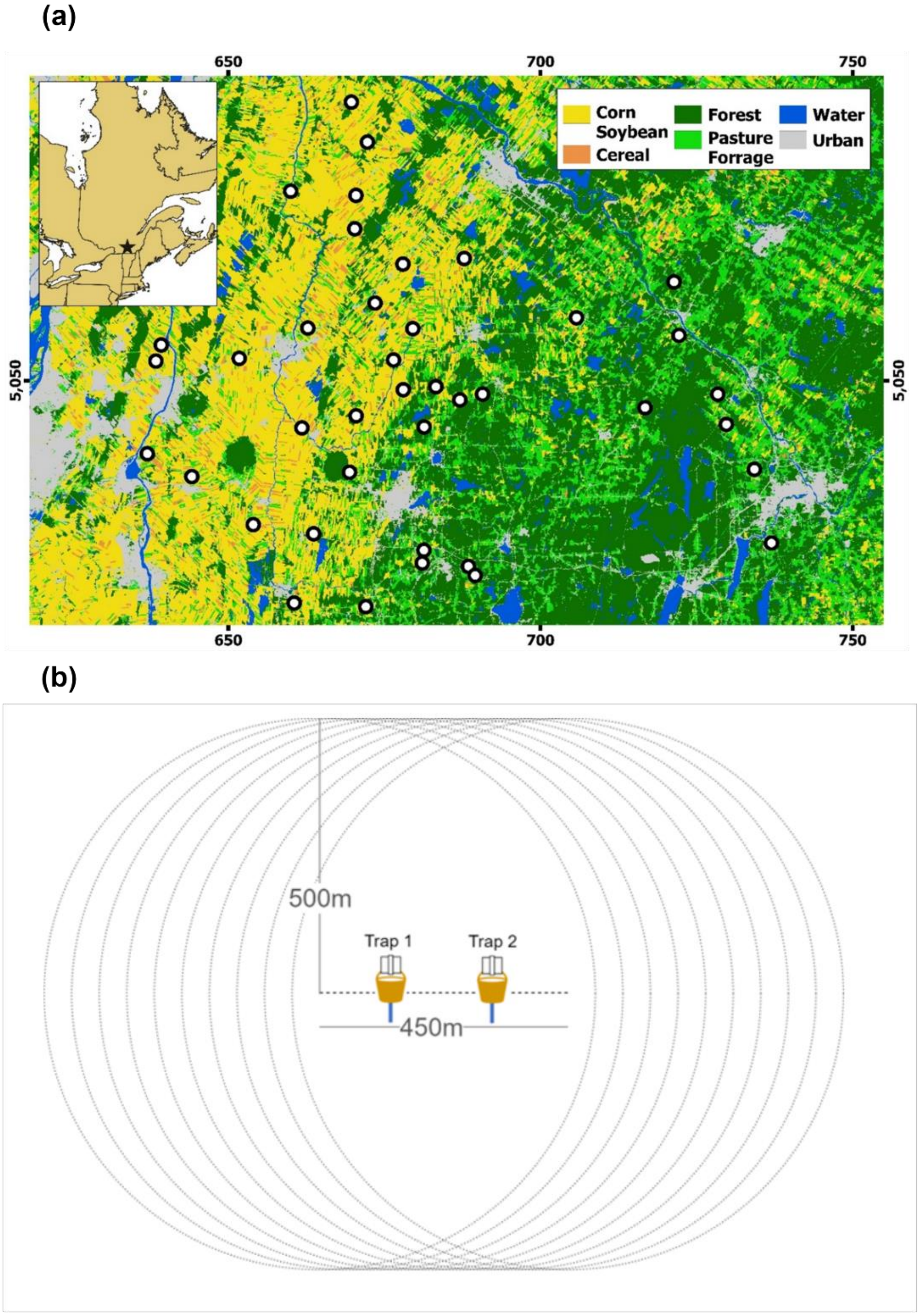


Figure 1. (a) The geographical position of the 40 farms sampled during the study, with the gradient of agricultural intensification and landscape context shown. Inset shows the position of the study site – or farm - in Québec, Canada, indicated by the star symbol. Coordinates are given in metres (‘m’). **(b)** The typical layout of a sampling transect, with the two Diptera traps placed along the transect. Buffers of 500m around 10 centroids placed equidistantly along the transect are shown; these buffers were used to calculate the relative habitat cover surrounding farms.

sativa], and clover [*Trifolium spp.*]) embedded within large expanses of forest. In contrast, the west was primarily composed of large-scale monocultures (principally maize [*Zea mays*], soybean [*Glycine max*], and wheat [*Triticum spp.*]), and small, highly interspersed forest patches (Bélanger & Grenier, 2002; Jobin et al., 2005; Ruiz & Domon, 2009). Between 2011 and 2019, about 100% of the maize and 60% of the soybean were sown as neonicotinoid-coated seeds (MDDELCC, 2015). As a result, neonicotinoids, alongside many other pesticides, were regularly detected in water bodies of the western part of the study area at concentrations threatening to aquatic life – including Diptera species with aquatic larval stages – if chronically exposed (Giroux, 2019; Montiel-León et al., 2019).

Diptera monitoring

Diptera were monitored using two flight-interception traps placed on field margins of each farm (N = 80 per year). Traps were spaced approximately 250 m apart and in a way that avoided blockage from vegetation. Traps consisted of yellow buckets (15 cm deep and 21 cm in diameter) surmounted by two bisecting plexiglass sheets (11.5 cm x 30 cm) and were placed one meter above the ground (Bellavance et al., 2018; Rioux Paquette et al., 2013). Traps were filled with 1 L of saltwater and soap solution. The contents of each trap were collected every two days by straining insects into a tube filled with 70% ethanol. Samples were stored in closed boxes at room temperature until processing. We processed samples collected between 1 June and 15 July. This period was chosen as the sampling protocol was originally created for a project studying the impact of Diptera availability on tree swallow (*Tachycineta bicolor*) fitness (Garrett et al., 2022). Tree swallows are aerial insectivorous birds preying primarily upon Diptera while food provisioning their nestlings during the above 6-week period in our study area. Regardless, the period captured the height of the seasonal abundance of Diptera and was therefore judged to be an appropriate time window for our study (see Figure S3). Diptera were individually counted, then dried in an oven at 60ºC for 24 hours. Once dried, samples were weighed without delay (± 0.0001 g). Due to time constraints and the volume of data, abundance and biomass of insects were recorded at order-level (Diptera).

Landscape context

We defined the landscape context surrounding each farm on a given year based on its habitat composition relative to other farms and years. Every year on each farm, we calculated the relative cover of habitat within 500-m around 10 points, which were positioned 50 m apart from each other along a 450-m transect on which the Diptera traps were positioned (Figure 1b). We then calculated a mean of these habitat values to give the average relative habitat cover around traps, for each farm-year combination. We determined land cover types within each 500-m buffer *in situ* between the middle and the end of July, before crop-harvesting. We delineated the principal land cover types found within each 500-m buffer using orthophotos (scale 1:40 000) in QGIS (QGIS, 2020). Land covers, including crop varieties, were then classified into one of five higher order categories, namely forest, maize and soybean, forage (hay fields, other grasses, alfalfa, clover, pastures, and old fields), and cereals (other than maize and soybean). The relative cover in aquatic habitats in the 500-m buffers was extremely low (0.66% ± 1.07%; mean ± SD) and thus not considered further.

A total of 440 'landscape contexts' (40 farms x 11 years), were determined using the farm scores of a robust principal components analysis (PCA) for compositional data (Filzmoser et al., 2009) fitted on the yearly percent cover of all higher order habitats of each farm by year combination (Figure 2a). The robust PCA was performed using the robCompositions package (Templ et al., 2011) in R v. 3.6.2 (R Core Team, 2020). The first two components explained over 95% of variance in landscape composition; we therefore used the scores for each year-farm combination along these two axes to represent the landscape context of each Diptera sample (see below).

Specifically, the first component (Comp.1) explained 80.34% of the variance in landscape habitat composition and was positively correlated with maize and soybean and negatively with forage and forest cover (Figure 2a). The second component (Comp.2) explained 14.69% of the variance in landscape habitat composition and was negatively correlated with forage and positively with forest cover. Landscape contexts characterized by maximal Comp.1 and minimal Comp.2 values thus comprised a mixture of maize, soybean, and cereals, and were stripped of forest cover. Landscape contexts characterized by minimal Comp.1 and negative Comp.2 values were dominated by forage fields and pastures interspersed by remnant forest cover and are thus referred to as forage landscapes.

Biomass and abundance trends

We took a model comparison approach, using Maximum Likelihood Generalised Linear Mixed Effect Modelling (GLMMs), to estimate temporal trends in Diptera abundance and biomass, and how these trends varied with landscape context. We first started with an identical candidate set of models for each response variable (abundance and biomass). These models focused on interactions between the main covariates of interest (i.e., year and the scores representing landscape context; Figure 2a). We included the ordinal date of sample collection (i.e., 1 May = 150) in each model in the candidate set as a second order polynomial term, due to the quadratic relationship between abundance/biomass and date in seasonally-abundant insects, rising to a peak and then falling again during the sampling season (see Figure S3; (Garrett et al., 2022). We tested two models in which landcover did not influence Diptera values and thus included a model (Base) including only the ordinal date of sample collection (i.e., 1 May = 150), and another with both the date and year of sample collection (‘Temporal’ model). Furthermore, various possible confounding variables, such as climatic and geological factors, may influence local abundance, biomass, and community composition of Diptera, along with the likelihood of trapping individuals independently of their relative abundance or biomass. Many of these factors vary along the longitudinal spatial gradient in this region of Québec, along with the degree of agricultural intensity (Comp.1 values) at farms, potentially confounding the effect of our landscape context values on temporal trends in Diptera. To control for this, we included the longitude of farms as UTM, WGS-84 coordinate reference values in the models that tested the effect of landscape context. Prior to including longitude as a variable, we checked the Variance Inflation Factors using the vif() function in the ‘car’ package in R (J. Fox & Weisberg, 2011), and found no evidence of multi-collinearity between fixed effects that may have distorted the estimation of effect sizes. In order to check whether we should further include the impact of climatic or weather variables in our models, such as temperature and precipitation, due to their potential impacts on the availability of capturable insects, we analysed potential model structures leading to inadequate controls (Cinelli et al., 2020) using Dynamic Acyclic Graphs in DAGgitty software (Textor et al., 2016). Due to the interconnectivity between climatic or weather variables and the variables of interest in our models, DAG analysis showed that controlling directly for climatic or weather variables would bias estimates of the total effect of Year and Comp1 and 2 on our response variables (insect biomass and abundance), and that Longitude alone provides a sufficient adjustment for the models. See Figure S1 for further details.

The main models of interest were those hypothesising landcover acts additively or interactively (on a log scale; see Spake et al., 2023), with the year of sample collection. We therefore included a model with the landscape context terms added interactively with each other and additively with all other covariates (‘Spatio-temporal 1’ model), and then including two-way interaction terms between year and each of the landscape context terms Comp.1 and Comp.2 (‘Spatio-temporal 2’ model). We finally predicted that the year itself would influence the effect of the interaction formed by the two landscape context terms, and therefore included a three-way interaction term between year and the two components (‘Spatio-temporal 3’ model). See Table 1 for a breakdown of terms found within each model.

We then recreated the candidate set of models for biomass (Model Set 1) but included abundance as an ‘offset’ variable in each model, to model the rate of biomass change per number of Diptera across farms (‘Model Set 3’). Each model was subject to the same model comparison approach using AICc values. We used Model Set 3 to test our hypothesis that the average biomass of individual Diptera changed over time yet differentially across the gradient of agricultural intensity. We used abundance as an offset variable as this is a more statistically sound method of modelling rates of change in a response variable than using a ratio (i.e. biomass / abundance) as the response itself, which can lead to spurious correlations between variables (Kronmal, 1993).

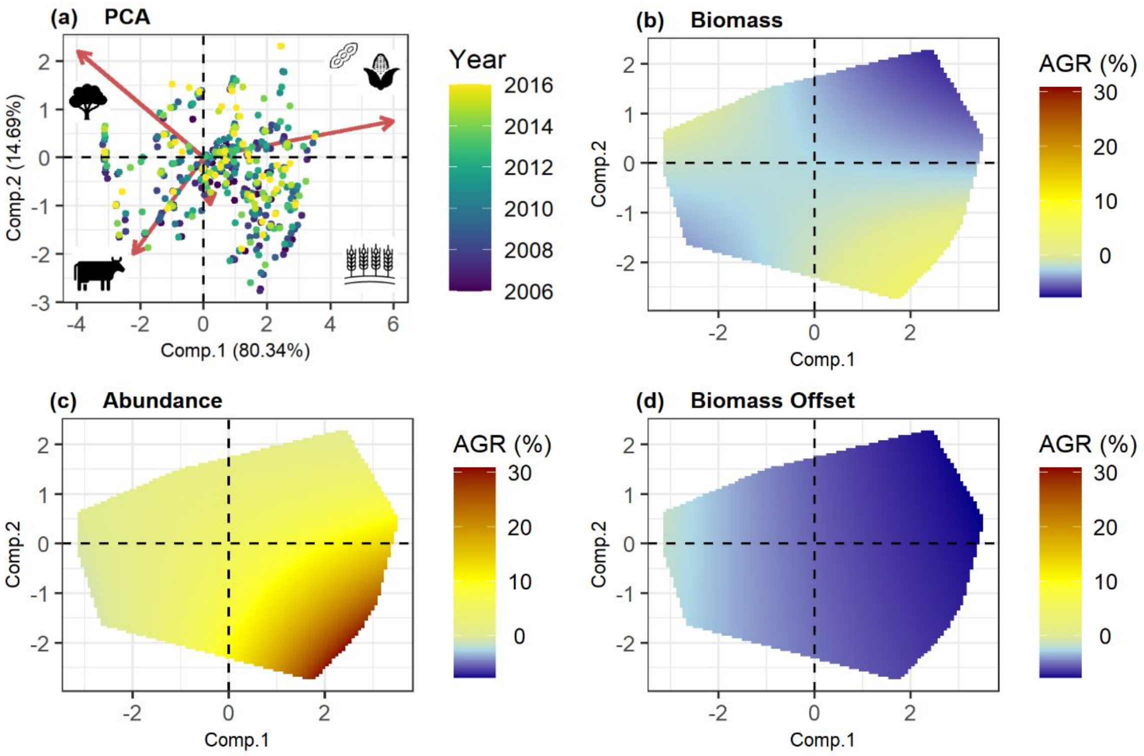


Figure 2. (a) Position of each Farm-Year point (n = 440) along the landscape PCA axes (Comp.1 and Comp.2) used in analyses. Icons represent the dominant landscape features along each axis: forested, maize / soy, other cereals incl. wheat, and pasture. **(b)** Predictions of Annual Growth Rate (AGR), calculated as the average annual percentage change in Diptera biomass from 2006-2016, across the axes Comp.1 and Comp.2. The surface area represents a convex hull of the space within the 2 dimensions of the PCA occupied by our 40 farms, inclusively. Model predictions were produced using the top model from Model Set 1 (Table 2, 'Spatio-Temporal 3'). **(c)** Predictions of Annual Growth Rate (AGR) for Diptera abundance, calculated in the same way as described for biomass, using predictions from Model Set 2 (Table 2, 'Spatio-Temporal 3'); and **(d)** Predictions of Annual Growth Rate (AGR) of Diptera biomass offset by abundance, using predictions from the top model from Model Set 3 (Table 2, 'Spatio-Temporal 2').

Diptera biomass was modelled using a gamma distribution (with a log link function), while Diptera abundance ($\log_e$(abundance+1)) was modelled via a gaussian distribution. Prior to modelling, we rescaled the 'year', 'date' and 'longitude' covariates to give a mean value of 0 and a standard deviation of 1. We compared models using sample corrected Akaike Information Criteria (AICc; Tables 2 and 3). All modelling was conducted using the glmmTMB package in R (Brooks et al., 2017).

Beyond checks of Variance Inflation Factors, other model validation checks included checks on the posterior predictions, residuals versus fitted values, homogeneity of variance, and normality of residuals and random effects. All model checks were completed using the ‘performance’ package in R (Lüdecke, 2021).

Random effect structure

Prior to comparing the fixed effects of different models, we carried out preliminary analyses to establish a random effects structure. The spatial and temporal structure of our sampling regime resulted in the need for both ‘crossed’ and ‘nested’ random effects, such that our final models contained ‘date’ (first and second order polynomials) nested within ‘year’, and ‘farm’ as random intercepts, and ‘date’ nested within ‘year’ as random slopes across farms. We compared this structure with less-complex random effects structures using restricted maximum likelihood and AICc values (Table S2 – supplementary materials). The resulting random effects structure for our models can be written as such using the glmmTMB package:

$$(1 \mid \text{Year} / \text{Date}) + (\text{Year} / \text{Date} \mid \text{Farm})$$

Table 1. Reference table for candidate model set with varying additive and interacting fixed effects structures. The values of landscape PCA axes are represented here as ‘Comp.1’ (farm score on the first axis) and ‘Comp.2’ (farm score on the second axis). See Figure 2 for an understanding of the landscape structure according to Comp.1 and Comp.2. Date is included as a second order polynomial in all models.

Model Name	**Fixed Effects Structure**
Spatio-Temporal3	Date + Longitude + Year * Comp.1 * Comp.2
Spatio-Temporal2	Date + Longitude + Year + Comp.1 + Comp.2 + Year : Comp.1 + Year : Comp.2 + Comp.1 : Comp.2
Spatio-Temporal1	Date + Longitude + Year + Comp.1 * Comp.2
Temp	Date + Year
Base	Date
Null	1 (intercept only, no fixed effects)

Rate of change

For all selected models for biomass, abundance, and biomass offset by abundance ($\log_e$(abundance+1)), we used the 'ggeffects' package in R (Lüdecke, 2018) to predict biomass and abundance for each year of the time series, the values of which were back-transformed from the log-link to the response scale, to calculate marginal and conditional effects of our predictor variables. We then calculated rates of change across the time series for biomass and abundance across the landscape gradients using the following equations for overall percentage change (ψ) and annual growth rate (AGR) as:

$$\psi = 100\frac{(y_n - y_1)}{y_1}$$

and

$$\mathrm{AGR} = \frac{\psi}{n-1}$$

Where y_n is the model estimate of the biomass or abundance value for the final year of the time series (2016), y_1 is the estimated biomass or abundance value for the starting year of the time series (2006), and *n* is the number of years total in the time series.

R version 4.2.2 was used for all data manipulation and analysis outside of QGIS (R Core Team, 2022).

Results

We collected and processed 15,916 insect samples, resulting from 8,614 farm visits over 11 years. Overall mean Diptera biomass (± SD) was 0.030 ± 0.044 g per trap and per farm for each two-day sampling period. While it did not vary greatly between years (range of means: 0.019 g - 0.037 g), the variance within each year was high (range of SD: 0.023 g - 0.059 g. Table S1, Figure S2 and S3). Overall mean Diptera abundance (± SD) was 59.7 ± 79.8 individuals per trap and per farm for each two-day sampling period. The abundance of Diptera was highly variable both between and within years (range of means and SD between years: 24.8 - 98.8 and 27.9 - 126.2 individuals, respectively; range of means and SD within years: 35.2 - 71.9 and 38.1 - 133.1 individuals, respectively; Table S1, Figure S2 and S3).

Biomass trends: Model Set 1

The covariate contributing the most to variation in biomass, from Model Set 1, was ‘Ordinal date’. We found no main effect of ‘Year’ on biomass from our temporal models ($\beta = -0.075 \pm 0.058$, $p = 0.2$; Figure 3a; Table S3: ‘Temporal’ model). However, we found an interaction between Year’, ‘Comp.1’ and ‘Comp.2’, with our model selection process suggesting the fixed effects structure containing a three-way interaction was preferred ($\beta = -0.035 \pm 0.012$, $p \leq 0.01$; Table S3: ‘Spatio-Temporal 3’ model; Table 2, AICc Weight = 0.95). Our model suggested that biomass decreased the most over time in locations that were either a) high in both Comp.1 and Comp.2 scores (e.g., increasing agricultural intensity, dominated by soy and maize

cropping), or b) low in both Comp.1 and 2 scores 1 (e.g., agriculture dominated by pasture and forage landscapes; Figure 2b).

Abundance trends: Model Set 2

Like Model Set 1, ‘Ordinal date’ was found to have the largest effect on abundance from our covariates. However, our predictions for total Diptera abundance over time in samples showed a slight increase, though the estimate of the main effect of ‘Year’ again lacked precision ($\beta = 0.19 \pm 0.118$, $p = 0.12$; Figure 3b; Table S4: ‘Temporal’ model). There were interactions between ‘Year’ and ‘Comp.1’ and ‘Comp.2’, however, with abundance increasing over time at rates that varied with landscape context ($\beta = -0.024 \pm 0.011$, $p < 0.05$; Table S4: ‘Spatio-Temporal 3’ model; Table 2, AICc Weight = 0.78). Our model predicted that abundance increased over time most in locations that were high in Comp.1 scores and low in Comp.2 scores (i.e., in intensively cultivated areas dominated by a diversity of cereal cropping; Figure 2c). We estimated abundance increases in areas of intense cereal cropping of up to 32% per year compared to 2006 levels. In general, abundance increased more slowly over time in locations with lower Comp.1 scores, and, at these low scores of Comp.1, abundance increase over time was similar across locations with varying Comp.2 scores (i.e., was similar across forested and pasture-forage landscapes; Figure 2c).

Biomass offset by abundance: Model Set 3

Including abundance of Diptera within the sample as an offset showed a decline in biomass per individual Diptera over time (β = -0.267 ± 0.079, p ≤ 0.001; Figure 3c, Table S5: 'Temporal' model). We found that the rate of decline in offset biomass varied over 'Comp.1', with Biomass

Table 2. Model Set 1: Comparison between candidate biomass and abundance models, in order from lowest AICc and highest AICcWeight (and therefore the preferred model) first, to highest AICc and lowest AICcWeight last. Log-likelihood values for the top models of Set 1 = 42,594.59; Set 2 = -20,731.31; and Set 3 = 45,495.73. Models were performed on data from 15916 individual insect samples, from 80 traps across 40 farms, on 493 days in total over 11 years. See Table S3-5 for model coefficients.

Model Set	Model	K	Delta_AICc	AICcWt
1	Spatio-Temporal3	24	0.00	0.95
	Spatio-Temporal2	23	6.27	0.04
	Base	16	10.66	0.00
	Temporal	17	11.10	0.00
	Spatio-Temporal1	21	13.63	0.00
	Null	14	52.72	0.00
2	Spatio-Temporal3	24	0.00	0.78
	Spatio-Temporal2	23	2.58	0.22
	Spatio-Temporal1	21	21.74	0.00
	Temporal	17	25.20	0.00
	Base	16	25.55	0.00
	Null	14	33.99	0.00
3	Spatio-Temporal2	23	0.00	0.70
	Spatio-Temporal3	24	1.67	0.30
	Spatio-Temporal1	21	26.40	0.00
	Temporal	17	54.44	0.00
	Base	16	60.54	0.00
	Null	14	92.85	0.00

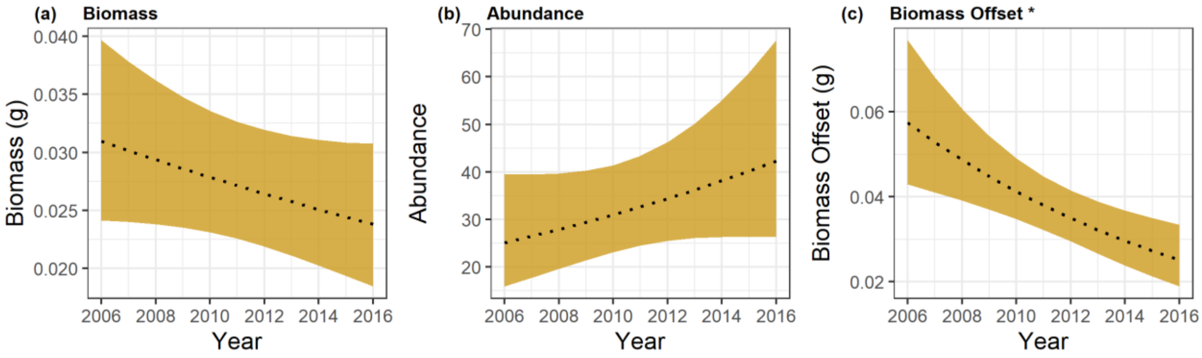


Figure 3. Marginal effect of **(a)** 'Year' on Diptera biomass (predictions from Model Set 1, Table 2 'Spatio-temporal3'), **(b)** abundance (predictions from Model Set 2, Table 2, 'Spatio-temporal3'), and **(c)** biomass offset by abundance (predictions from Model Set 3, Table 2, 'Spatio-temporal2'). The marginal effects on the 'y' axis depict the predictions for the response variables as the level of each predictor is held constant at their mean values. An asterisk (*) indicates a significant effect of 'Year' on the response variable ($p \leq 0.05$). 95% confidence intervals are represented by shaded envelopes.

per number of Diptera declining more over time as agricultural intensity increased toward row-crop production landscapes ($\beta = -0.057 \pm 0.01$, $p \leq 0.001$; Figure 2; Table S5: 'Spatio-Temporal 2' model; Table 2, AICc Weight = 0.7). We found little variation in the rate of decline in the offset biomass over Comp.2 values (Figure 2d).

Discussion

The temporal trends in abundance and biomass of the Diptera community varied with landscape context within the boundaries of our sampling region of Southern Québec. Although our findings are in partial agreement with our hypotheses that intensively cultivated areas focusing on row cropping results in greater biomass declines over time in comparison to less-intensively cultivated areas (dependent on whether there were cereals other than maize and soy growing on farms or not), the abundance trends contradicted our hypotheses, increasing overall and more rapidly so with high-intensity agriculture.

Given that the temporal change in Diptera biomass varied widely from that of abundance, changes in biomass must have been driven by processes other than changes in the number of Diptera, and therefore potentially correspond with community and/or trait turnover. Figure 4 shows the relationship between the temporal trends in dipteran abundance and biomass across the 40 farms in the study; whilst there is a logical general increase in the temporal slope value of biomass as abundance trends increase, more than half of all farms show a rise in abundance but a drop in biomass over time. Almost all other farms still either show biomass to be decreasing faster than abundance or increasing slower than abundance.

We addressed this phenomenon further through offsetting our biomass trends by abundance in additional models (Figure 3c). The decline in biomass per number of Diptera suggests functional and community-level changes are occurring, shifting toward Diptera with lower individual biomass on average over time. Furthermore, an increase in agricultural intensity strengthened the declines of biomass per Diptera, indicating that community turnover is happening more rapidly in areas of more intensive farming practices (Figure 2d). This suggests that species within the community are responding differently to agricultural intensification in space and time, with species with smaller body sizes likely increasing in population size at a greater rate than larger dipteran species. Correlations between traits and population declines of insects in Germany indeed showed that larger insect species, and those that were more abundant and of a higher trophic level, declined the most over time, although this was only tested in forested systems (Staab et al., 2023). In more intensively managed ecosystems, higher disturbance and resource availability can filter life history traits to favour communities with ‘fast’ traits such as faster reproduction, smaller body size and higher relative abundance compared to lower-intensity production systems (Neyret et al., 2023; Hanson et al., 2016). Such traits can enable populations to recover more quickly following ecosystem disturbance, as well as allow competitive exploitation of resources, and are often associated with pest status (Gavina et al., 2018; Kőrösi et al., 2022). The inference from our results, that Diptera communities are moving toward species with lower body mass and higher abundance with intensification of agriculture, aligns with the findings of Neyret et al. (2023).

Alternative or additional mechanisms of change in Dipteran communities that could cause the patterns observed in our results include intraspecific variation in body size and biomass over time and across the landscape gradient. Body size has previously been found to vary amongst individuals of a given species across space in Diptera, according to variables such as local temperature (Atkinson, 1994; Gilbert, 1985). Similar to the way in which environmental variables can 'filter out' species traits, such pressures can also operate within species to filter individuals according to their traits, as well as act on the plasticity of traits like body size to determine the adult phenotype of individuals (Atkinson, 1994). For example, Chironomidae (non-biting midges) are predicted to decrease in size over time with future climate warming (Wonglersak et al., 2021). Further investigation into species-level trends in our study area would help untangle possible interspecific and intraspecific trait mechanisms.

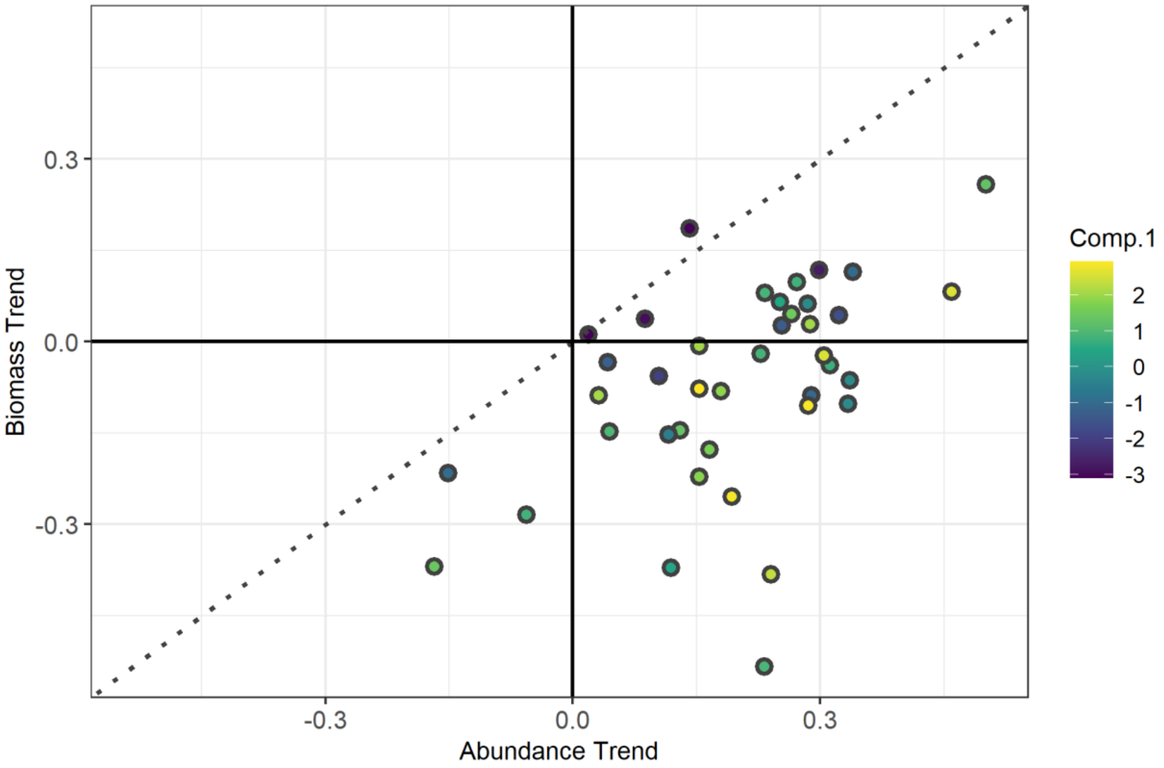


Figure 4. The relationship between the temporal trend in abundance and biomass of Diptera, for each of the 40 farms. The 'trend' values are the slope of 'Year' calculated from adding the random effects of each farm to the main effect of year on abundance and biomass from the 'Temporal' models of model sets 1 and 2 (Tables 2,3; 'Temporal'). The dotted line indicates where the points would be if the relationship between biomass trend and abundance trend on each farm was y = x or 1:1, i.e., abundance and biomass change at the same rate. The 'Comp.1' values indicated in the plot are the mean landscape context values from the first axis of the PCA performed (Figure 2a) for each farm, averaged over 2006-2016.

A complex array of variables determines the characterisation of a landscape and may affect the trends in Diptera abundance and biomass in our study, including the homogenisation of landscapes around farms, and reduction in the abundance and diversity of resources and habitats available to support larger species of Diptera (Forister et al., 2019; Nilsson et al., 2008; Wagner et al., 2021). Agricultural intensification is often accompanied by increased use of pesticides, and artificial and organic fertilisers, which can further compound the exposure of coprophagous Diptera species to pesticides through residue in manure sprayed on fields, or more widely to Diptera species through leaching into waterways (Buijs et al., 2022; Ewald et al., 2015; Schreinemachers & Tipraqsa, 2012; Wagner et al., 2021). Such organic and chemical pollution can alter community structure as some species are considerably more sensitive to these inputs than others (Buendia et al., 2013; Hellawell, 1986; Powell et al., 2022; Timm & Haldna, 2019; Vaughan & Ormerod, 2012b). Typically, species of Diptera with lower biomass, such as chironomids, are more resilient to pollution effects than larger species (De Haas et al., 2005).

Our findings that total abundance and biomass increase at a greater rate in landscapes containing ‘small’ cereals (other than just soy and maize), despite the more rapid decline in biomass per number of individuals on these farms, suggests other cereals support larger populations within Dipteran communities than maize and soy monocultures do. This suggests the increase in Diptera abundance in these more diverse, mixed-crop cereal landscapes results in a compensation of total biomass despite the turnover to lower-biomass individuals, resulting in a greater abundance and biomass of flies even relative to the lower-intensity farms and forested areas (Figure 2).

Change in climatic or weather patterns is yet another possible driver of Diptera biomass (Boggs, 2016). Maximum temperature as well as precipitation levels in the days leading up to Diptera sampling were found by Garrett et al. (2022a) to influence spatial variation in biomass of Diptera in our study area. However, we explored whether there were changes in weather patterns across years that could have explained the temporal trends we found in Diptera communities but found no trend in the maximum or mean temperature nor in precipitation levels over time across our sampling region (Supporting Information, Figure S4a-c). We did, however, find an increase in the proportion of land occupied by intensive agriculture around farms over time, driven by an increase in maize and soy cultivation (Figure S5, S4d-i). If the agricultural shift to converting more forage and pasture toward intensive maize and soy production in our sampling region continues, we may expect further and more significant declines in biomass of Diptera communities in the future.

Our results may be significant in the wider context of biodiversity and ecosystem functioning across our study area. The biomass of Diptera available throughout the summer months in Québec have been found to affect the reproductive success of predators, for example tree swallows, a species in decline in North-Eastern North America (Garrett et al., 2022). Tree swallows have been found to select for larger species of Diptera, such as Calyptratae, over smaller-bodied species in our study area (Bellavance et al., 2018). Our postulation that Diptera communities are shifting toward smaller-bodied individuals over time and with agricultural intensity may therefore have an even stronger impact on tree swallow populations than a reduction in total biomass alone. Furthermore, seeing as birds tend to target different Diptera prey species, we may expect our predictions of community turnover in the region to have a bottom-up effect on predator community composition (Hasegawa, 2023; McCarty & Winkler, 1999; Orłowski & Karg, 2011; Turner, 1982).

Further ecosystem functions may be disrupted by the patterns we find in our study. For example, 70% of commercial crops are reliant on species of Diptera, Hymenoptera and other aerial insects such as Coleoptera for pollination (Klein et al., 2007). Changes to community structure under agricultural intensification could therefore, paradoxically, negatively affect pollination rate and yield, risking future food security (Kovács-Hostyánszki et al., 2017; Ricketts et al., 2008). As well as the sheer number of insects required to pollinate crops and wild plants effectively, functional traits are also found to be important for pollination rates at the individual-level (Woodcock et al., 2019). For example, larger body size of bumblebees increases the amount of pollen they carry on their bodies and their dispersal from plant-to-plant (Greenleaf et al., 2007; Woodcock et al., 2019). Our prediction that Dipteran communities experience temporal species turnover towards lower biomass could thus negatively affect pollination by Dipteran communities if this trait is important for pollination in general.

Although species-level data is more ideal to retain in monitoring programmes, valuable insights can still be gained from using other metrics such as community abundance and biomass in combination. Many monitoring schemes sample with lower intensity, including citizen science schemes, and may not extract biomass information from samples. Using abundance alone in our study would have shown an incomplete picture of biodiversity change in dipteran communities within our sampling area, perhaps leading to the interpretation that agricultural intensification leads to more resilient Diptera communities with increased abundance and diversity. We therefore recommend that, where species information is too time-consuming or not possible to obtain, efforts are made to go beyond abundance metrics, such as using biomass to further understand functional change in insect communities over time.

We also recognise that, although we have obtained very high-resolution temporal data, the length of our time series is relatively short and therefore provides a ‘snapshot’ of trends through time (Didham, Basset, et al., 2020). Whilst we think our analyses deliver valuable insights into changes in dipteran communities under agricultural intensification, the beginning of our sampling period in 2006 is subsequent to much larger agricultural transformations in this region of Québec. Previous land-use change consisted of removal of forest and semi-natural habitat for forage and pasture-dominated agriculture such as dairy farms from the 1950s, and then a transformation of dairy farms to intensive maize and soybean farming in the 1990s (Jobin et al., 2003; Ruiz & Domon, 2009). Therefore, it is probable that the baseline abundance and biomass of Diptera was much higher in the decades prior to our sampling period, and that Diptera biomass and abundance have declined much more rapidly prior to our study, possibly representing a shifting baseline (Didham, Basset, et al., 2020; Soga & Gaston, 2018). The collection of long-term data on insect communities becomes even more important in this light.

Acknowledgements

We are indebted to the farm owners who kindly accepted to partake in our long-term study since 2004. Sincere thanks to the many graduate students, field and lab assistants who helped collect, enter, and proof data throughout the years, notably with respect to insect sample processing. Financial contributions to this work came from multiple sources; KP is grateful to the joint UK Research and Innovation (UKRI) and Mitacs Globalink grant NE/X007553/1 and the Natural Environment Research Council (NERC) SCENARIO Doctoral Training Partnership grant F4114915 for their financial support. Further contributions were made through the Natural Sciences and Engineering Research Council of Canada (NSERC) discovery grants to Fanie Pelletier, Dany Garant and MB and a Steacie fellowship to FP, two team research grants from the Fonds de recherche du Québec—Nature et technologies (FRQNT) to FP, DG and MB, by the Canada Research Chairs program to FP and MB, as well as by New Opportunities Funds of the Canadian Foundation for Innovation (FCI) to FP, DG and MB, the Canadian Wildlife Service of Environment and Climate Change Canada, and the Université de Sherbrooke. T.H.O's contribution was funded by NERC project NE/V006916/1 and D.B.R.'s contribution was supported by the Natural Environment Research Council award number NE/R016429/1 as part of the UK-SCAPE programme delivering National Capability. Finally, we would like to thank the reviewers and editors for greatly improving our manuscript for publication.

Supporting Information

Tables

Table S1. Data summary for abundance and biomass (g) of Diptera caught in traps for each year of time series.

Year	Mean Abund	SD Abund	Min Abund	Max Abund	Sum Abund	Mean Biomass (g)	SD Biomass (g)	Min Biomass (g)	Max Biomass (g)	Sum Biomass (g)
2006	33.828	49.260	1	641	57,981	0.033	0.044	0	0.817	57.278
2007	24.770	27.876	1	450	41,366	0.029	0.054	0	0.988	48.839
2008	42.387	65.043	0	704	46,032	0.030	0.059	0	0.925	40.660
2009	98.768	98.709	0	910	136,892	0.037	0.048	0	0.887	51.275
2010	56.293	65.182	0	821	73,913	0.029	0.033	0	0.303	38.733
2011	59.795	48.325	0	442	80,006	0.033	0.038	0	0.549	44.035
2012	56.993	73.480	0	1,401	67,024	0.031	0.045	0	1.009	36.943
2013	77.374	97.929	0	1,200	116,525	0.026	0.031	0	0.386	39.304
2014	88.771	126.168	0	2,051	127,031	0.028	0.044	0	0.725	40.574
2015	78.641	83.163	0	1,004	122,366	0.034	0.044	0	0.820	52.538
2016	42.968	56.348	0	970	60,370	0.019	0.023	0	0.217	26.939

Tables S2. Comparison of different random effects structures for modelling biomass (a) and abundance (b).

(a)

Modnames	**K**	**AICc**	**Delta_AICc**	**ModelLik**	**AICcWt**	**LL**	**Cum.Wt**
(1|Year/Date)+ (Year/Date|Farm)	23	-85,103.97	0.00	1.00	0.49	42,575.02	0.49
(1|Year/Date)+ (1|Farm)	14	-84,680.95	423.03	0.00	0.00	42,354.49	1.00
(1|Year)+ (Year/Date|Farm)	22	-83,627.54	1,476.43	0.00	0.00	41,835.80	1.00
(1|Date)+ (Date|Farm)	18	-83,297.29	1,806.69	0.00	0.00	41,666.66	1.00
(Year/Date|Farm)	21	-83,273.65	1,830.33	0.00	0.00	41,657.85	1.00

(b)

Modnames	**K**	**AICc**	**Delta_AICc**	**ModelLik**	**AICcWt**	**LL**	**Cum.Wt**
(1|Year/Date)+ (Year/Date|Farm)	23	41,544.48	0.00	1.00	0.50	-20,749.20	0.50
(1|Year/Date)+ (1|Farm)	14	42,012.70	468.22	0.00	0.00	-20,992.33	1.00
(1|Year)+ (Year/Date|Farm)	22	43,935.41	2,390.93	0.00	0.00	-21,945.67	1.00
(1|Date)+ (Date|Farm)	18	45,939.04	4,394.56	0.00	0.00	-22,951.50	1.00

Table S3. Coefficients and p values from the top two models and the temporal model selected to model Diptera biomass (from Model Set 1, model selection through AICc comparison shown in Table 2 of main text).

Mod	Parameter	Coef.	SE	Conf.low	Conf.high	Statistic	P.Value
Spatio-Temporal3	(Intercept)	-3.666	0.094	-3.850	-3.482	-39.113	< 0.001
Spatio-Temporal3	poly(JJ, 2)1	13.732	2.450	8.930	18.534	5.605	< 0.001
Spatio-Temporal3	poly(JJ, 2)2	-11.865	2.451	-16.668	-7.061	-4.841	< 0.001
Spatio-Temporal3	s.Year	-0.091	0.058	-0.205	0.024	-1.556	0.120
Spatio-Temporal3	Comp.1	-0.062	0.031	-0.123	-0.001	-1.997	0.046
Spatio-Temporal3	Comp.2	0.042	0.034	-0.025	0.109	1.224	0.221
Spatio-Temporal3	s.Long	-0.107	0.086	-0.274	0.061	-1.245	0.213
Spatio-Temporal3	Comp.1: Comp.2	-0.007	0.015	-0.037	0.024	-0.426	0.670
Spatio-Temporal3	s.Year: Comp.1	-0.013	0.016	-0.044	0.018	-0.799	0.424
Spatio-Temporal3	s.Year: Comp.2	-0.028	0.023	-0.073	0.017	-1.210	0.226
Spatio-Temporal3	s.Year:Comp.1 :Comp.2	-0.035	0.012	-0.059	-0.011	-2.864	0.004
Spatio-Temporal2	(Intercept)	-3.661	0.094	-3.845	-3.477	-39.080	< 0.001
Spatio-Temporal2	poly(JJ, 2)1	13.676	2.450	8.873	18.479	5.581	< 0.001
Spatio-Temporal2	poly(JJ, 2)2	-11.864	2.451	-16.668	-7.060	-4.840	< 0.001
Spatio-Temporal2	s.Year	-0.095	0.058	-0.209	0.018	-1.642	0.100
Spatio-Temporal2	Comp.1	-0.069	0.031	-0.130	-0.008	-2.212	0.027
Spatio-Temporal2	Comp.2	0.039	0.035	-0.029	0.107	1.129	0.259
Spatio-Temporal2	s.Long	-0.099	0.086	-0.266	0.069	-1.155	0.248
Spatio-Temporal2	Comp.1: Comp.2	-0.005	0.015	-0.036	0.025	-0.345	0.730
Spatio-Temporal2	s.Year: Comp.1	0.003	0.015	-0.028	0.033	0.166	0.868
Spatio-Temporal2	s.Year: Comp.2	-0.065	0.019	-0.102	-0.027	-3.391	0.001
Temporal	(Intercept)	-3.712	0.087	-3.883	-3.541	-42.581	< 0.001
Temporal	poly(JJ, 2)1	13.627	2.450	8.826	18.428	5.563	< 0.001
Temporal	poly(JJ, 2)2	-11.827	2.451	-16.630	-7.023	-4.826	< 0.001
Temporal	s.Year	-0.075	0.058	-0.190	0.040	-1.282	0.200

Table S4. Coefficients and p values from the top two models and the temporal model selected for modelling Diptera abundance (from Model Set 2, model selection through AICc comparison shown in Table 3 of main text).

Mod	Parameter	Coef.	SE	Conf.low	Conf.high	Statistic	P.Value
Spatio-Temporal3	(Intercept)	3.391	0.141	3.115	3.668	24.040	< 0.001
Spatio-Temporal3	poly(JJ, 2)1	-2.896	2.715	-8.219	2.426	-1.067	0.286
Spatio-Temporal3	poly(JJ, 2)2	-8.782	2.716	-14.105	-3.458	-3.233	0.001
Spatio-Temporal3	s.Year	0.131	0.120	-0.104	0.365	1.094	0.274
Spatio-Temporal3	Comp.1	0.068	0.028	0.013	0.124	2.421	0.015
Spatio-Temporal3	Comp.2	-0.058	0.031	-0.119	0.002	-1.901	0.057
Spatio-Temporal3	s.Long	-0.056	0.079	-0.210	0.097	-0.718	0.473
Spatio-Temporal3	Comp.1:Comp.2	-0.013	0.014	-0.040	0.013	-0.981	0.326
Spatio-Temporal3	s.Year:Comp.1	0.052	0.017	0.019	0.085	3.128	0.002
Spatio-Temporal3	s.Year:Comp.2	-0.040	0.022	-0.084	0.004	-1.796	0.073
Spatio-Temporal3	s.Year:Comp.1:Comp.2	-0.024	0.011	-0.046	-0.002	-2.142	0.032
Spatio-Temporal2	(Intercept)	3.393	0.141	3.117	3.668	24.113	< 0.001
Spatio-Temporal2	poly(JJ, 2)1	-2.916	2.717	-8.241	2.409	-1.073	0.283
Spatio-Temporal2	poly(JJ, 2)2	-8.798	2.718	-14.125	-3.471	-3.237	0.001
Spatio-Temporal2	s.Year	0.127	0.119	-0.107	0.361	1.062	0.288
Spatio-Temporal2	Comp.1	0.066	0.028	0.011	0.122	2.331	0.020
Spatio-Temporal2	Comp.2	-0.061	0.031	-0.122	-0.001	-1.980	0.048
Spatio-Temporal2	s.Long	-0.051	0.078	-0.205	0.102	-0.657	0.511
Spatio-Temporal2	Comp.1:Comp.2	-0.012	0.014	-0.039	0.015	-0.876	0.381
Spatio-Temporal2	s.Year:Comp.1	0.061	0.017	0.028	0.094	3.633	< 0.001
Spatio-Temporal2	s.Year:Comp.2	-0.066	0.020	-0.104	-0.027	-3.347	0.001
Temporal	(Intercept)	3.474	0.142	3.196	3.752	24.478	< 0.001
Temporal	poly(JJ, 2)1	-2.874	2.718	-8.201	2.454	-1.057	0.290
Temporal	poly(JJ, 2)2	-8.721	2.719	-14.051	-3.392	-3.208	0.001
Temporal	s.Year	0.190	0.118	-0.041	0.421	1.610	0.108

Table S5. Coefficients and p values from the top two models and the temporal model selected for Diptera biomass offset by abundance (from Model Set 3, model selection through AICc comparison shown in Table 4 of main text).

Mod	Parameter	Coef.	SE	Conf.low	Conf.high	Statistic	P.Value
Spatio-Temporal3	(Intercept)	-7.347	0.084	-7.511	-7.184	-87.887	< 0.001
Spatio-Temporal3	poly(JJ, 2)1	12.537	2.057	8.506	16.568	6.096	< 0.001
Spatio-Temporal3	poly(JJ, 2)2	-3.494	2.058	-7.528	0.539	-1.698	0.090
Spatio-Temporal3	s.Year	-0.248	0.080	-0.404	-0.092	-3.118	0.002
Spatio-Temporal3	Comp.1	-0.077	0.021	-0.118	-0.035	-3.628	< 0.001
Spatio-Temporal3	Comp.2	0.051	0.025	0.002	0.099	2.059	0.039
Spatio-Temporal3	s.Long	-0.046	0.043	-0.129	0.037	-1.079	0.280
Spatio-Temporal3	Comp.1: Comp.2	0.022	0.012	-0.001	0.045	1.849	0.064
Spatio-Temporal3	s.Year:Comp.1	-0.060	0.010	-0.080	-0.039	-5.728	< 0.001
Spatio-Temporal3	s.Year:Comp.2	-0.010	0.018	-0.045	0.026	-0.532	0.595
Spatio-Temporal3	s.Year:Comp.1 :Comp.2	-0.005	0.009	-0.024	0.013	-0.576	0.565
Spatio-Temporal2	(Intercept)	-7.347	0.084	-7.511	-7.183	-87.845	< 0.001
Spatio-Temporal2	poly(JJ, 2)1	12.533	2.056	8.503	16.563	6.095	< 0.001
Spatio-Temporal2	poly(JJ, 2)2	-3.499	2.058	-7.533	0.534	-1.701	0.089
Spatio-Temporal2	s.Year	-0.249	0.080	-0.405	-0.093	-3.132	0.002
Spatio-Temporal2	Comp.1	-0.078	0.021	-0.119	-0.037	-3.710	< 0.001
Spatio-Temporal2	Comp.2	0.050	0.025	0.002	0.099	2.052	0.040
Spatio-Temporal2	s.Long	-0.047	0.042	-0.130	0.036	-1.100	0.271
Spatio-Temporal2	Comp.1: Comp.2	0.022	0.012	-0.001	0.045	1.842	0.065
Spatio-Temporal2	s.Year:Comp.1	-0.057	0.010	-0.076	-0.039	-5.987	< 0.001
Spatio-Temporal2	s.Year:Comp.2	-0.015	0.015	-0.045	0.015	-0.993	0.321
Temporal	(Intercept)	-7.408	0.082	-7.569	-7.247	-90.327	< 0.001
Temporal	poly(JJ, 2)1	12.616	2.085	8.529	16.703	6.051	< 0.001
Temporal	poly(JJ, 2)2	-3.635	2.082	-7.716	0.445	-1.746	0.081
Temporal	s.Year	-0.267	0.079	-0.422	-0.112	-3.375	0.001

Figures

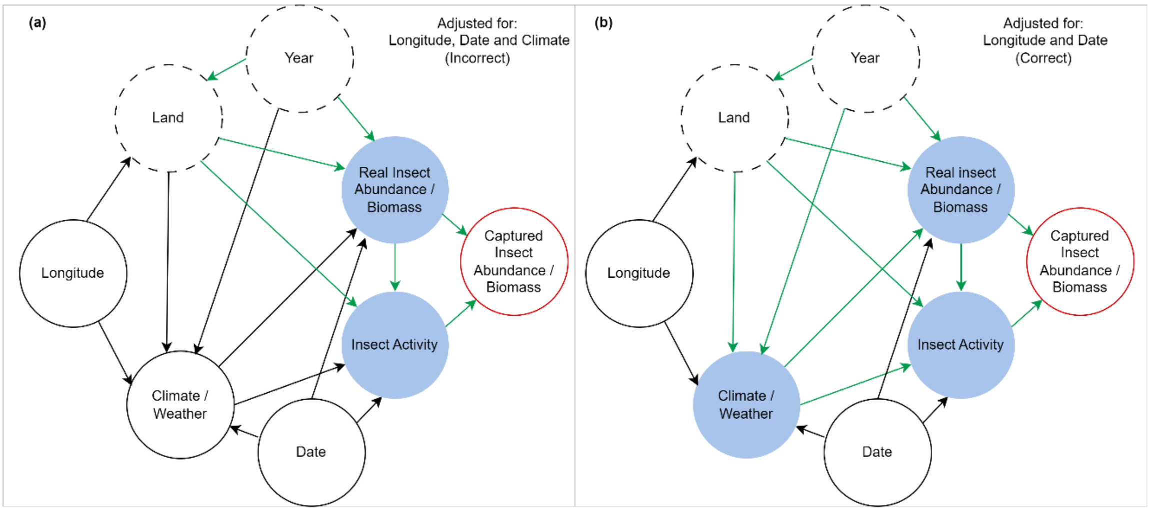


Figure S1. Two alternative Directed Acyclic Graphs (DAGs) that show how including climatic/weather variables in Model Sets 1-3 biases the estimation of the total effect of Year and Land (Comp1 and 2) on the captured abundance / biomass (e.g., for trapping or for their predators, parasitoids, or plant hosts). The dashed circles (Land and Year) represent the independent variables of interest ('exposure' variables); the black solid circles represent the variables adjusted (or controlled) for; the blue-filled circles represent 'unobserved' variables; and the red circle (Insect Availability) represents the outcome – or response variable. Arrows represent putative causal effects of one variable on another, the green showing causal effects flowing from the variables of interest. In (a), the models include climatic variables as a control, and are shown to be incorrectly adjusted due to the interdependencies between climate and other variables of interest in the model. In (b), climate is removed and becomes 'unobserved', with longitude and data alone controlled for, and shows the DAG to be correctly adjusted. DAG analysis was carried out using 'DAGgity' software for analysing causal effect identification.

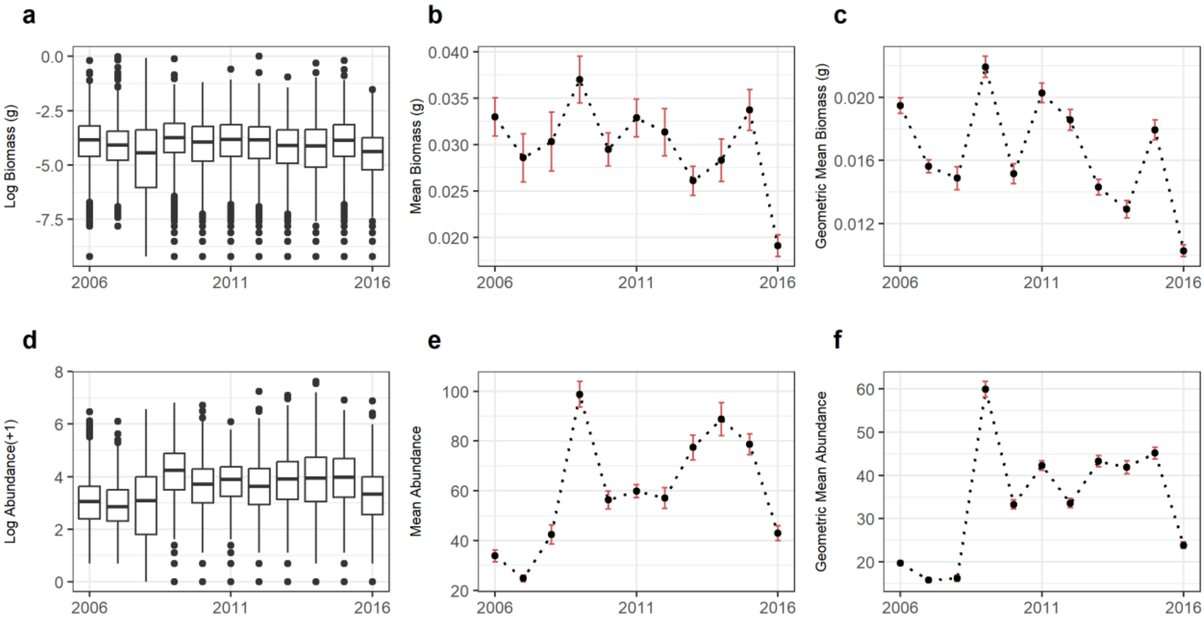


Figure S2. Plots on the left ((a) and (d)) show the spread of the data for Log biomass and abundance of Diptera, with boxes representing the median and interquartile ranges on either side. Also shown are the arithmetic means ((b) and (e)) and geometric means ((c) and (f)) per year for the biomass (top) and abundance (bottom) of Diptera from traps, across all farms, with error bars showing the 95% confidence intervals.

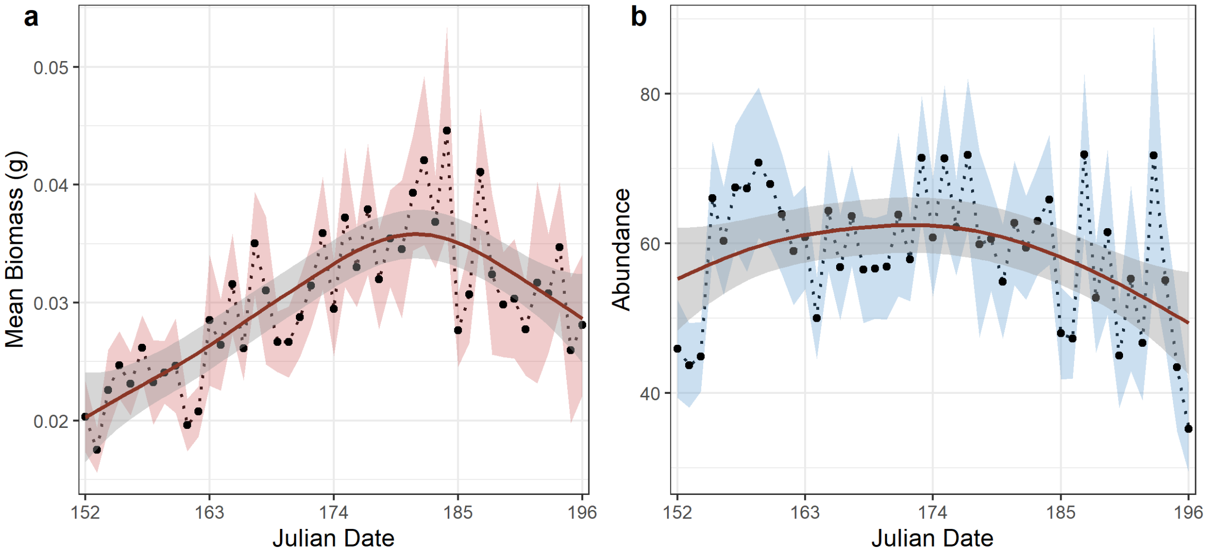


Figure S3. (a) Mean biomass and (b) mean abundance of Diptera caught in samples according to ordinal date. Pink and blue shaded envelopes represent the 95% confidence intervals around the mean for each date. Dark red lines show the smoothed trend (y ~ s(x, bs = "cs")) of the means using “mgcv” package in R, with their 95% confidence intervals represented by the grey shaded envelopes.

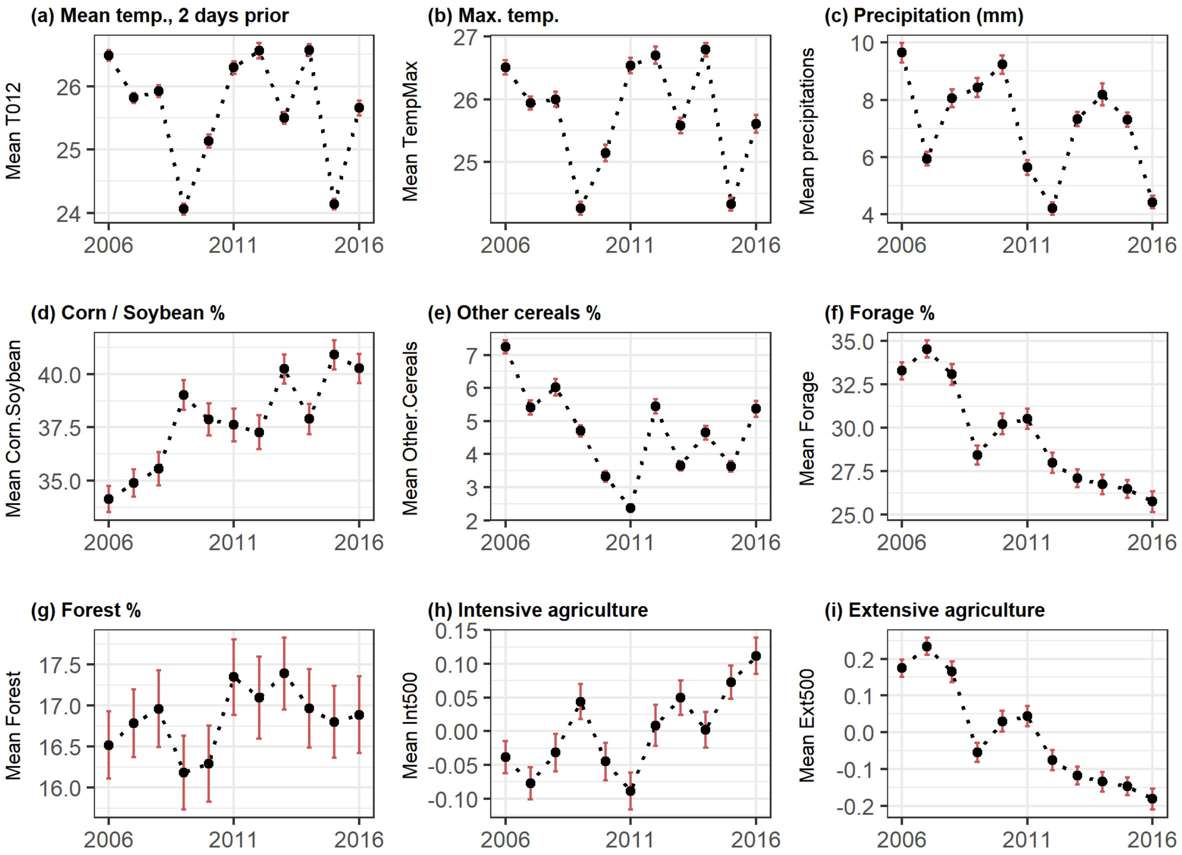


Figure S4. Mean values of weather and landscape variables for the 40 sampling farms for each year from 2006-2016, ± standard errors. The top left panel represents means of temperatures recorded on sampling days, the day before sampling, and two days before sampling. ‘Intensive agriculture’ refers to the sum of the percentage cover of corn, soybean and other cereals; ‘extensive agriculture’ refers to percentage forage and pastures combined. These two latter panels are represented by rescaled values to give a mean value of 0 and a standard deviation of 1.

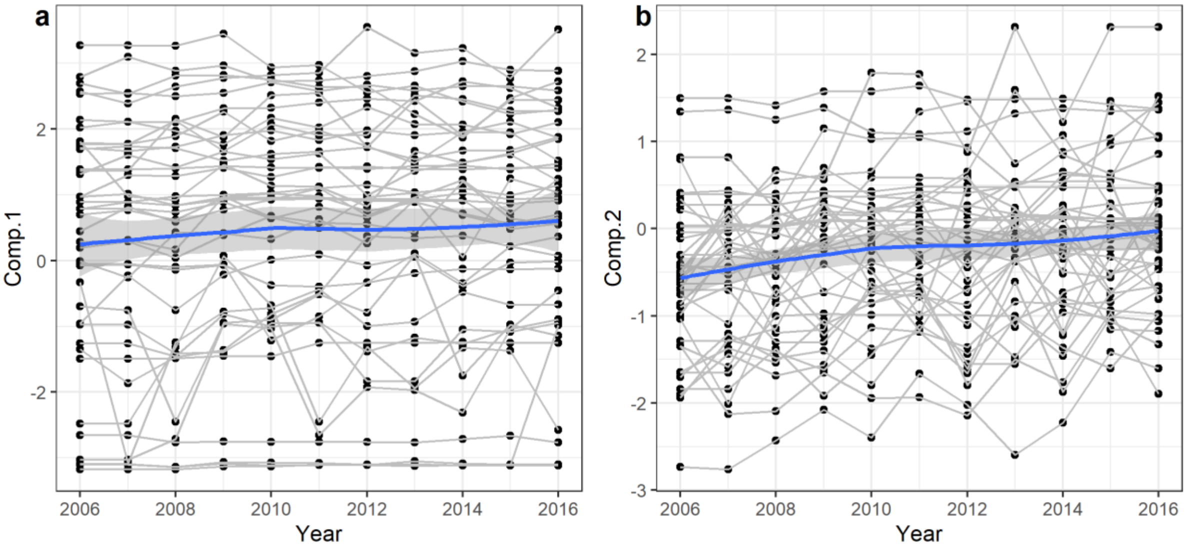


Figure S5. The landscape compositions, axes 1 (a) and 2 (b), for each Farm-Year datapoint from the years 2006-2016. Grey lines link the data points for each of the 40 farms across years; blue lines show a loess smoothed curve of y ~ x, with 95% confidence intervals represented by the shaded envelope.

Chapter 4

Chapter 4

Diptera communities lose larger species and homogenise under agricultural intensification

Abstract

Land use change, especially agricultural intensification, can negatively impact ecological communities and the ecosystem functions they provide. In a previous study, we found that row-cropping altered farmland Diptera (true fly) community biomass negatively over time, while abundance increased concurrently. This suggests that the community of Diptera species is subject to mass-specific selection pressures, resulting in species becoming smaller on average, or variation in the response of species' population sizes depending on their mass. Here, we explore these hypotheses using macroecological principles to predict how relationships between abundance, the number of species, and their body mass change in Diptera communities over time and under increasing agricultural intensity. Our models predict fewer large-bodied species and more small and medium-bodied species in Diptera communities over time, as well as increasing population sizes of small species and declining population sizes of large species in our study area. We also predict homogenisation of body mass in Diptera communities. By comparing areas of low and high intensity agriculture, we find that these community transformations occur much more rapidly and to a much greater extent in areas of high cover of arable land, compared with areas of low intensity land use. Given our predictions, we suggest that agricultural intensification has profound consequences for ecosystem function delivery mediated by Diptera, including the possible disruption of trophic relationships.

Keywords: ecosystem function, Canada, agriculture, insect decline, community turnover, functional traits

Introduction

The intensification of agriculture, aimed at increasing the amount of food produced per unit area, is one of the most important drivers of biodiversity decline due to the damaging practices that occur under such production systems (IPBES, 2019; Tscharntke et al., 2005). These include the high use of pesticides and fertilisers that pollute both terrestrial and aquatic ecosystems, degradation of soil and above-ground habitat structure, and the monoculturalisation of crops and consequential landscape homogenisation (IPBES, 2019; Raven & Wagner, 2021).

Agricultural intensification can affect biodiversity by favouring species with traits that allow them to exploit intensive production systems (Gámez-Virués et al., 2015). The types of traits that tend to be favoured by agricultural intensification are those that prioritise resource acquisition, and faster growth and reproduction – known as 'fast' or 'r-selected' traits (Parry, 1981). Species with these traits tend to have high dispersal (Reich, 2014), and broad niche requirements (Rader et al., 2014). In contrast, traits that tend to be filtered out of communities under these environmental pressures include those that support slower population growth, greater longevity and lower fecundity ('slow' or 'K-selected' traits; Parry, 1981; Reich, 2014), and more specialist niche requirements (Clavel et al., 2011). Hence, agricultural intensification can act as an ecological filter that homogenises communities according to their traits (Tscharntke et al., 2005).

Traits play important roles in ecosystem functions and services, from both the perspective of the types of traits present – which may be linked to the ability to perform a particular function – as well as the diversity of traits in communities, known as 'functional diversity' (Díaz et al., 2013; Mason et al., 2005; Tilman, 2001). Therefore, it is expected that the filtering and homogenisation of traits under processes such as agricultural intensification can dramatically undermine both the provision and the long-term resilience of ecosystem functions (Carmona et al., 2021; Gámez-Virués et al., 2015; Oliver, Isaac, et al., 2015).

As agricultural intensification continues across the world, it is important to document and understand the ecological and functional changes under the associated environmental pressures. In a previous study, we showed that Diptera (true fly) community abundance and biomass change at different rates over 11 years along a gradient of agricultural intensity in Québec, Canada (Powell et al., 2023). Given that community biomass is simply the product of community abundance and mean body size, the discrepancy between biomass and abundance trends was likely due to the average body size declining more rapidly in areas of higher agricultural intensity. This discrepancy can only arise from one of three scenarios: 1) a change in the species body size distribution; 2) a change in the size density relationship; or 3) change in size of individuals within species. Any of these phenomena could potentially support the hypothesis of a switch from ‘slow’ to ‘fast’ traits – such as smaller body mass – dominating in communities under high disturbance conditions, if the associated changes result in Diptera generally becoming smaller. We also expect that there would be a narrower range of body mass under the homogenising effects of agricultural intensification. Indeed, previous studies have found that Diptera differed along the spatial gradient of our study area during a single year, with more smaller species and greater dominance of smaller species as agricultural intensity increased (Laplante, 2013). However, as is the case of many ecological study systems, there are no empirical data of individual body mass, or abundance at the species or family-level to demonstrate the *temporal* changes in Diptera and their traits in the community.

In this study, we use macroecological theory of species body size distributions - which typically follow a log-normal curve and thus state that ecological communities are generally composed of more small species than large ones (Kozłowski & Gawelczyk, 2002; McGill, 2011) - and size density relationships, whereby species population sizes decline with increasing body mass under a power-law function (Isaac, Storch, et al., 2011; McGill, 2011), to build theory to test competing explanations for the divergent trends in biomass and abundance. We then use this theory to predict how Diptera communities are being transformed by agricultural practices over time in our study area. We do this by working under two different scenarios that we hypothesise may occur either alone or concurrently – that is, a change in the number of species of different sizes due to either intraspecific body mass change and/or species turnover, or changes in the relative abundance of species of different body masses. We use data from previous model predictions from Powell et al. (2023) to propose how Diptera communities in our study region have been transformed under these alternative conditions.

Methods

Using macroecological principles, we assume that species within a Diptera community follow specific mass-abundance relationships. We then create alternative mathematical constraints for each relationship – the species body size distribution and the size density relationship - based on the idea that they can be used in conjunction to estimate the total biomass and abundance of individuals in an ecological community. We then use predictions from our own models in Powell et al. (2023) to estimate change in each of these relationships in Diptera communities over time and with increasing agricultural intensity, under these mathematical constraints.

The species body size relationship

Consider a hypothetical ecological community composed of a number of different species (s), which span a range of different body sizes - or masses. The number of species of a certain body mass, M, in this community is assumed to follow a right-skewed lognormal distribution, i.e., there are more smaller species than larger species in a community (Kozłowski & Gawelczyk, 2002; McGill, 2011). The mean species' mass, $\bar{M}$, can be expressed as

$$\bar{M} = \mathrm{e}^{\phi + \frac{\sigma^2}{2}}, \qquad [1]$$

where ϕ denotes the mean of the natural log of M – i.e., the median species mass, and σ denotes the standard deviation of the natural log of M, and so can be thought of as controlling the degree of 'skew' in the relationship, and the variance around the log mean body mass (see Weisstein, 2023, for details).

The size density relationship

We also assume that in this community, for any species (i), its abundance (n) can be predicted as a function of its mass (M) (Isaac, Storch, et al., 2011; McGill, 2011), using the power law equation

$$ln(n_i) = a + b\, ln(M_i), \qquad [2]$$

where $b < 0$. Therefore, species populations decline as a function of their mass.

In the ecological community, observations of the total abundance and biomass of individuals are made at various time points (between 2006 and 2016). If we consider 2006 to be time point 1, and the end of the time series, 2016, to be time point 2, then we can express the total biomass at time point 1 as B_1, and at time point 2 as B_2, whilst the total abundance at time points 1 and 2 can be expressed as N_1 and N_2 *respectively.* The abundance and biomass of Diptera in the community have undergone change over time so that

$$N_2 = xN_1, \tag{3}$$

and

$$B_2 = yB_1, \tag{4}$$

i.e., the 'new' abundance and biomass at time 2 can be calculated as some multiplier 'x' and 'y'. For example, if the abundance declines by 10% but the biomass by 50%, then $x = 0.9$ and $y = 0.5$.

We assume that the incongruence between change in abundance and biomass in Diptera communities over time could be because either: 1) the species body size relationship (equation [1]) is changing, what we refer to throughout as 'scenario 1', or 2) the size density relationship is changing (equation [2]); we refer to this situation as 'scenario 2'. We examine these two scenarios and how differences between x and y can be explained by these relationships.

Scenario 1

In this scenario, we assume there is no change in the relationship between body mass and the population size of a species, i.e., the size density relationship [2] for species is constant across time and space in Diptera communities. For there to be a different relationship between the *total* abundance and the *total* biomass of the Diptera community at times 1 and 2, our underlying assumptions mean that the community must be **a)** comprised of different species (there is 'species turnover', with local extinctions and / or colonisations of species), and / or **b)** body mass undergoes evolutionary processes that reduce the average size of individuals *within species.* Although these are two very different processes, they would both result in a change in shape of the species body size distribution [1]. The following logic shows how the species body size distribution changes in communities under these assumptions.

The total biomass B of individuals in a community can be expressed as a product of the total number of individuals N and the mean mass of all individuals in the community, which we shall call 'μ'. Therefore, we can express B_1 and B_2 as $B_1 = u_1N_1$, and $B_2 = u_2N_2$. Given equations [3] and [4], we can therefore say $B_2 = u_2xN_1$, $yB_1 = u_2xN_1$, $yu_1N_1 = u_2xN_1$, and, therefore,

$$\frac{y}{x} = \frac{u_2}{u_1}. \qquad [5]$$

The total biomass B can also be expressed as the sum of each species (i) abundance multiplied by their masses, or, alternatively, as the product of the mean abundance of species ($\bar{n}$) and the mean mass of all species ($\bar{M}$), multiplied by the total number of species (s) in the community:

$$B = \bar{n}\bar{M}s, \qquad [6]$$

and, following the same logic,

$$N = \bar{n}s. \qquad [7]$$

Given [6], this means that the mean mass of all individuals μ can be expressed as $\mu = \frac{\bar{n}\bar{M}s}{N}$,

or, given equation [1],

$$\mu = \frac{\bar{n}e^{\phi+\frac{\sigma^2}{2}}s}{N}.$$

If we consider equation [5] and [7], we can therefore express the ratio between y and x by

$$\frac{y}{x} = e^{\phi_2+\frac{\sigma_2^2}{2}-\phi_1-\frac{\sigma_1^2}{2}} \qquad [8]$$

(see Appendix S1 for derivation). To understand change in ϕ and σ, i.e., to understand how the species body size relationship [1] has changed between time 1 and 2, we hold each parameter constant and calculate how the other must have changed. If we first hold ϕ constant, then $\phi_1 = \phi_2$, and so we assume that the *median* species size does not change. Therefore, if we consider that biomass and abundance change at the same rate between times 1 and 2, then $y = x$, therefore $\frac{y}{x} = 1$, and so $\sigma_2 = \sigma_1$. Therefore the distribution of the number of species over mass remains the same. If, however, we have a situation where the biomass is found to decline at a greater rate than abundance between times 1 and 2, then $y < x$, $\frac{y}{x} < 1$, and so $\sigma_2 < \sigma_1$. This means there is a reduction in the standard deviation / variance around the mean of the log of the species body size distribution, and hence a reduced skew of the distribution between time points, generally meaning that there are fewer large species and more medium-small species with less variation in body mass (Figure 1a). If, on the other hand, we have a situation where the abundance declines more rapidly than the biomass between

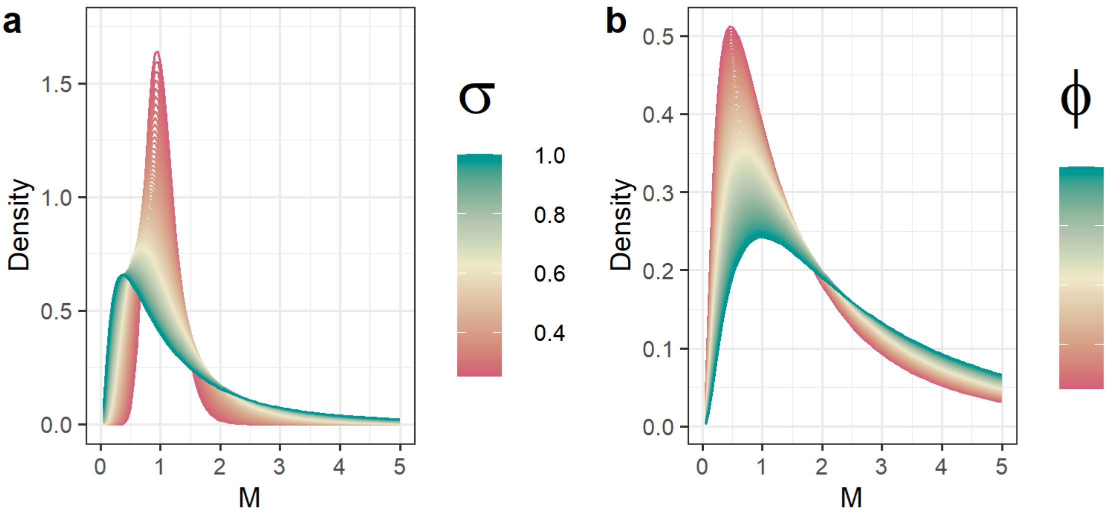


Figure 1. A demonstration of how the species body size distribution – the density of species with mass or body size 'M' (here arbitrary numbers) - changes when the two parameters ϕ and σ are kept constant between time points alternately. In a) the ϕ (median mass) is kept constant, and the σ allowed to vary over time under biomass and / or abundance changes, and in *b*) σ is kept constant, and ϕ allowed to vary over time under community change. In both examples, as the parameter declines, there are fewer large species and more homogenous communities.

time points, then $y > x$, $\frac{y}{x} > 1$, and so $\sigma_2 > \sigma_1$. This means there is an increase in the skew of the species body size distribution (Figure 1a), meaning more large species, a reduction in the number of average-sized species, and greater variation in body mass due to an increased variance around the mean.

On the other hand, we could keep σ constant, meaning the skew of the relationship is not changing over time. Therefore, if we follow the same ideas as in the previous example where biomass and abundance changed either at either the same or different rates, then we can say if $y = x$, then $e^{\phi_2 - \phi_1} = 1$ or $e^{\phi_2} = e^{\phi_1}$, so $\phi_2 = \phi_1$; if $y < x$, then $e^{\phi_2 - \phi_1} < 1$ or $e^{\phi_2} < e^{\phi_1}$, so $\phi_2 < \phi_1$; and finally, if $y > x$, then $e^{\phi_2 - \phi_1} > 1$ or $e^{\phi_2} > e^{\phi_1}$, so $\phi_2 > \phi_1$. In the situation where $\phi_2 < \phi_1$, the median species mass declines, and the abundance distribution again changes shape so that there are fewer larger species, and there are more smaller species (Figure 1b). When $\phi_2 > \phi_1$, the median increases, resulting in the opposite changes occurring to the species body size distribution (Figure 1b).

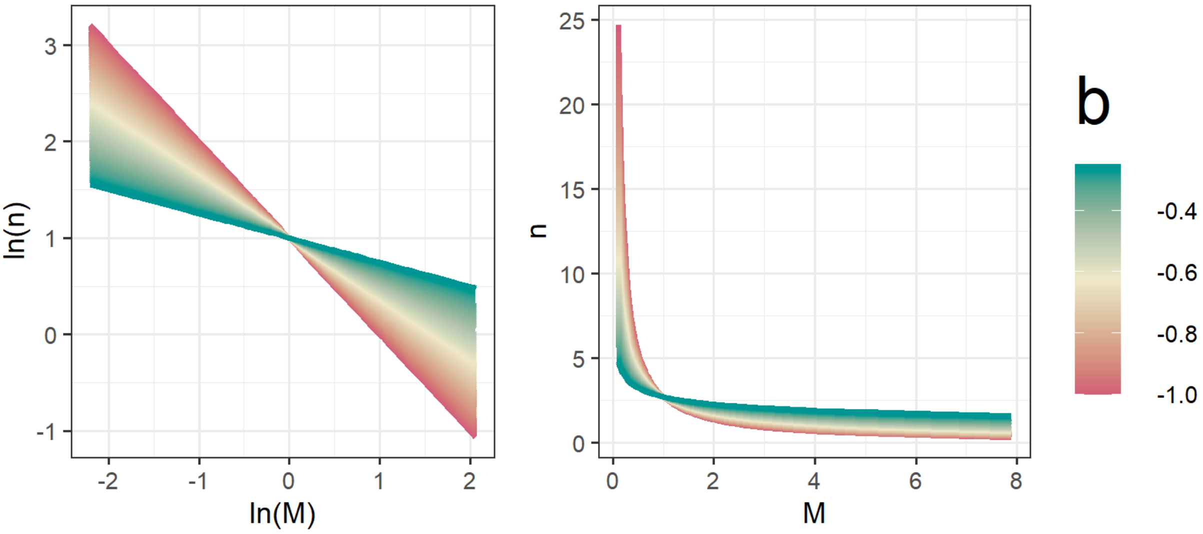


Figure 2. A demonstration of how the size density distribution of Diptera is changing under scenario 2. Population size or abundance (n) of a species varies over a range of body masses (M) and by varying values of 'b'.

Scenario 2

In this scenario, we now assume that there is no intraspecific body mass change between time points, and there are no local colonisations or extinctions of species (i.e., there is no species turnover). This means that, for there to be a changing relationship between the total abundance and total biomass of Diptera communities, there must be a change in the relationship between body mass and the population size of species in a community (the size density relationship).

Under the assumptions of scenario 2, we assume that the mass of species (M_i) does not change between time points 1 and 2, but that the abundance (n_i) of the species changes. This means that parameters 'a' and 'b' of the size density relationship may change between time points 1 and 2. We can therefore express for species (i) with mass M_i it's abundance at time point 1, n_{1i}, by

$$\ln\left(n_{(1i)}\right) = a_1 + b_1\, ln(M_i), \qquad [9]$$

and at time point 2 as

$$ln\left(n_{(2i)}\right) = a_2 + b_2\, ln(M_i). \qquad [10]$$

The total abundance of all individuals in the community, N, can be defined as the sum of the abundance of each species present in the community, and the total biomass B as the sum of the product of the abundance of each species and its mass; therefore $N = \sum_{i=1} n_i$, and $B = \sum_{i=1} n_i M_i$. It follows that, given equations [3] and [4],

$$x \sum_{i=1} n_{(1i)} = \sum_{i=1} n_{(2i)},$$

or

$$x = \frac{\sum_{i=1} n_{(2i)}}{\sum_{i=1} n_{(1i)}},$$

and

$$y \sum_{i=1} n_{(1i)} M_i = \sum_{i=1} n_{(2i)}\, M_i,$$

or

$$y = \frac{\sum_{i=1} n_{(2i)} M_i}{\sum_{i=1} n_{(1i)} M_i}.$$

To understand how *x* and *y* relate to each other, in the same way as we do in scenario 1, we can express the relationship between them as

$$\frac{y}{x} = \frac{\left(\sum_{i=1} n_{(2i)} M_i\right) \sum_{i=1} n_{(1i)}}{\left(\sum_{i=1} n_{(1i)} M_i\right) \sum_{i=1} n_{(2i)}}.$$

Using [9] and [10] we can also express this as

$$\frac{y}{x} = \frac{\left(\sum_{i=1} \mathrm{e}^{a_2 + b_2\, ln(M_i)} M_i\right) \sum_{i=1} \mathrm{e}^{a_1 + b_1\, ln(M_i)}}{\left(\sum_{i=1} \mathrm{e}^{a_1 + b_1\, ln(M_i)} M_i\right) \sum_{i=1} \mathrm{e}^{a_2 + b_2\, ln(M_i)}}. \qquad [11]$$

Following this through, we get the following equation:

$$\frac{y}{x} \frac{\sum_{i=1} M_i^{b_1+1}}{\sum_{i=1} M_i^{b_1}} = \frac{\sum_{i=1} M_i^{b_2+1}}{\sum_{i=1} M_i^{b_2}} \qquad [12]$$

(see Appendix S1 for the derivation of this result). To understand what this means for the size density relationship, consider an example where we have the biomass B declining at a faster rate than the abundance N. In this example *y* must be smaller than *x* as there has been a larger change between B_1 and B_2 than between N_1 and N_2, so $y < x$. If $y < x$, then $\frac{y}{x} < 1$, and, therefore $\frac{\sum_{i=1} M_i^{b_1+1}}{\sum_{i=1} M_i^{b_1}} > \frac{\sum_{i=1} M_i^{b_2+1}}{\sum_{i=1} M_i^{b_2}}$, meaning $b_1 > b_2$. We find this by simulating multiple Diptera communities of 100 species where the mean of $ln(M) = 0$ and standard deviation of $ln(M) = 1$, and by inputting values of b_1 and b_2 (Appendix S2). We find b declines over time when $y < x$, so $b_1 > b_2$, meaning the slope of the power law relationship is steeper at time 2 (see Appendix S2). By examining the relationship of n on M at times 1 and 2, a reduction in b_2 - a steepening of the slope - results in a change in the size density relationship such that the abundance, or population size, of small species at time 2 increases relative to time 1, whilst it shrinks for larger species at time 2 relative to time 1. This can be visualised in Figure 2, in the way the y axis responds with a change in 'b' values. In a similar fashion to scenario 1, if we were to find that the abundance declined faster than biomass, then we can state that $y > x$, then $\frac{y}{x} > 1$, and, therefore $\frac{\sum_{i=1} {M_i}^{b_1+1}}{\sum_{i=1} {M_i}^{b_1}} < \frac{\sum_{i=1} {M_i}^{b_2+1}}{\sum_{i=1} {M_i}^{b_2}}$. Therefore, the opposite is true, and for all values of $b < 0$, $b_1 < b_2$. This results in an increase of the power law exponent, meaning a shallower gradient and inherently a reduced effect of size on the populations of larger species (Figure 2). Hence, we get a decrease in the population sizes of smaller species, and an increase in populations of larger species.

Estimating change in species body size and size density relationships

We use predictions of abundance and biomass values from the 'temporal models' from Powell et al. (2023) to calculate values for 'x' and 'y' on average for Diptera samples across our study system. The temporal models are generalised linear mixed effect models (GLMMs) that predict the change in total abundance and biomass of Diptera caught in traps on 40 farms between 2006-2016 as a function of 'Year' and 'Date' (the fixed effects), and controlling for random effects of 'Year', 'Date', and 'Farm'. We use the 'ggpredict()' function from the 'ggeffects' package in R (Lüdecke, 2018) to predict the abundance of Diptera in the first and last years of the study (N_1, N_2), and the biomass of Diptera in the first and last years of the study (B_1, B_2). We use equations [3] and [4] to calculate 'x' and 'y' from these predictions. We then use the Spatio-temporal models from Powell et al. (2023), which add interactive effects of 'land use variables' ('Comp1' and 'Comp2') with 'Year' to the temporal models earlier described, to understand how 'x' and 'y' change under increasing values of Comp1 (the variable along which agricultural intensification, in terms of the percentage cover of land use types on farms, varies). See Powell et al. (2023) for further information on how these landscape variables were calculated and for more information on the study sites. We extract predictions of N_1, N_2, B_1 and B_2 using the same package and function as described for temporal models, but with predictions conditional on 1) the minimum and 2) the maximum Comp1 values present across farms – i.e., for the lowest and highest levels of agricultural intensity in our study region. For more information on the study area, the Diptera sampling protocol and the models of Diptera abundance and biomass over space and time, see Powell et al. (2023).

We then use the calculated values of 'x' and 'y' from each of these predictions to determine how σ, ϕ and b change under scenarios 1 and 2 outlined above. In the case of scenario 2 where we aim to understand changes in b, we simulate 1000 hypothetical Diptera

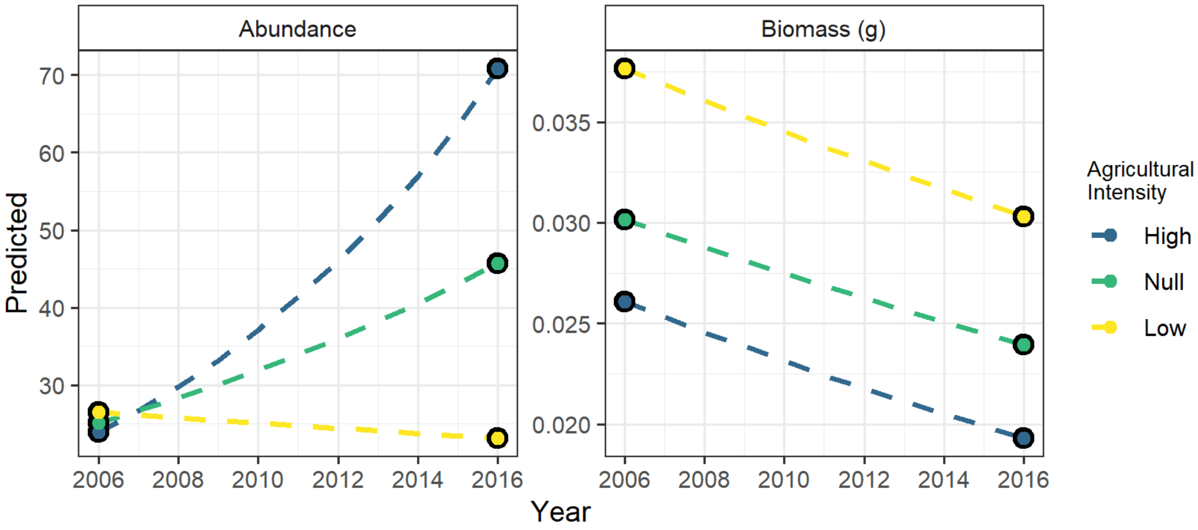


Figure 3. Predictions of total Diptera abundance (left panel) and biomass (right panel) for each year of sampling, at varying levels of agricultural intensity, extracted from models in Powell et al. (2023). On the left panel, the points highlighted for years 2006 and 2016 represent the N_1 and N_2 values respectively, that were used to calculate 'x' (change in abundance over 11 years) for each level of agricultural intensification. On the right panel, the points highlighted for years 2006 and 2016 represent the B_1 and B_2 values respectively, that were used to calculate 'y' (change in biomass over 11 years) for each level of agricultural intensification. 'Null' agricultural intensification signifies predictions extracted from the 'Temporal Model' in Powell et al. (2023), which does not contain agricultural intensity as an effect.

communities, each of 100 species, where the natural log of the mean mass within each community (M) = 0 and of the standard deviation = 1. We propose sensible values of b_1 to understand relative changes in b_2, using trial and improvement of experimental b_2 values (see Appendix S2). The purpose of this is to demonstrate what happens to size density relationships or mean body mass of species under our study system over time and under changing landscape contexts. We use this to draw conclusions on the impact of agricultural intensity on Diptera of different sizes in the community.

Results

Change in Diptera communities over time

Using predictions from the 'Temporal' models from Powell et al. (2023), we estimate that in 2006, abundance of Diptera per flight intercept trap sample (N_1) is approximately 25 individuals on average, with a total biomass (B_1) of 0.0301g. In 2016, this changed to 46 individuals (N_2) at 0.024g (B_2) (Figure 3). Our change in abundance (x) and biomass (y) are therefore approximately $x = \frac{46}{25} = 1.82$, and $y = \frac{0.024}{0.0301} = 0.795$. Therefore, $y < x \, (0.795 < 1.82)$, because abundance increases whilst biomass declines.

<u>Scenario 1</u>

In this scenario we assumed that the size density relationship is kept constant, and so explored how the species body size distribution changes by varying parameters ϕ and σ. Given $y < x$, we find that, if we keep ϕ constant, $\sigma_2 < \sigma_1$(Figure 1a), or, if we keep σ constant, $\phi_2 < \phi_1$ (Figure 1b), meaning communities become more homogenous in size and have fewer large species. By putting the results of x and y into equation [8], we get $\frac{y}{x} = \frac{0.795}{1.82} = 0.437 = e^{\frac{\sigma_2^2 - \sigma_1^2}{2}}$, and, therefore, ${\sigma_1}^2 - 1.66 = \sigma_2^2$. So, there is a reduction in the skew of the relationship, and the variance of body mass over time. Alternatively, we also get $0.437 =$

$e^{\phi_2 - \phi_1}$, meaning $0.437\,e^{\Phi_1} = e^{\phi_2}$, when holding σ constant, and there is therefore a reduction in the mean species' mass.

Scenario 2

Under scenario 2, we assumed that the species body size relationship is kept constant, and so explored how the size density distribution changes by varying parameter b. Given $y < x$, we find therefore that $b_2 < b_1$. Specifically, using equation [12], $0.437\,\frac{\sum_{i=1} M_i^{b_1+1}}{\sum_{i=1} M_i^{b_1}} = \frac{\sum_{i=1} M_i^{b_2+1}}{\sum_{i=1} M_i^{b_2}}$. By setting $b_1 = -0.2$ and using our simulated communities of Diptera with masses M_i we find a value of $b_2 \sim -1.055 \pm 0.004$; at the lowest value of b_1 that we tested, -0.8, we found $b_2 \sim -1.734 \pm 0.007$ (for the results of all b_2 for all b_1 values between -0.2 and -0.8, see Appendix S2). Therefore, we find a reduction in the population size of large species and increase in population sizes of small species (Figure 2), according to the reduction in b and steeper exponent of the size density relationship.

Change in Diptera communities under increasing agricultural intensity

The lowest Comp1 value, the measure of agricultural intensification in our dataset, was -3.175, and the greatest Comp1 value was 3.544. Where we use the Comp1 value of -3.175 to make predictions of abundance and biomass, we refer to this as 'low agricultural intensity', and where we use the Comp1 value of '3.544', we refer to this as 'high agricultural intensity'.

Low agricultural intensity

Using the lowest Comp1 value of -3.175, we predicted from the spatio-temporal models in Powell et al. (2023) that abundance of Diptera (N_1) per sample went from approximately 27 individuals in 2006 to 23 individuals (N_2) in 2016, whereas biomass is predicted to go from 0.0376g (B_1) to 0.0303g (B_2) over the same period (Figure 3). These values give us $y =$

$\frac{0.0303}{0.0376} = 0.805$, and $x = \frac{23}{27} = 0.873$. Therefore, biomass declines more rapidly than abundance, i.e., $y < x$, $(0.805 < 0.873)$.

Scenario 1

Given $y < x$, we find that, if we keep ϕ constant, $\sigma_2 < \sigma_1$(Figure 1a), or, if we keep σ constant, $\phi_2 < \phi_1$ (Figure 1b), meaning communities become more homogenous in size and have fewer large species. By putting the results of x and y into equation [8], we get $\frac{y}{x} = \frac{0.805}{0.873} = 0.922 = \mathrm{e}^{\frac{\sigma_2^2 - \sigma_1^2}{2}}$, and, therefore, ${\sigma_1}^2 - 0.16 = \sigma_2^2$. So, there is a slight reduction in the skew of the relationship, and the variance of body mass over time. Alternatively, we also get $0.922 = \mathrm{e}^{\phi_2 - \phi_1}$, meaning $0.922\ \mathrm{e}^{\phi_1} = \mathrm{e}^{\phi_2}$, when holding σ constant, and there is therefore a small reduction in the mean species' mass.

Scenario 2

Given $y < x$, we find therefore that $b_2 < b_1$. Specifically, using equation [12], $0.922 \frac{\sum_{i=1} {M_i}^{b_1+1}}{\sum_{i=1} {M_i}^{b_1}} = \frac{\sum_{i=1} {M_i}^{b_2+1}}{\sum_{i=1} {M_i}^{b_2}}$. By setting $b_1 =$ -0.2 and using our simulated communities of masses M_i, we find a value of $b_2 \sim$ -0.285 $\pm < 0.001$, and, for $b_1 =$ -0.8, $b2 \sim$ -0.884 $\pm < 0.001$ (see Appendix S2 for b_2 values in between). Therefore, we find a very slight reduction in the population sizes of large species and increase in population size of small species (Figure 2), according to the small reduction in b and steeper exponent of the size density relationship.

High agricultural intensity

At the other end of the agricultural intensity spectrum, using the highest Comp1 value of 3.544, we predicted abundance per sample to increase from approximately 24 (N_1) to 71 (N_2) individuals between 2006 and 2016, whilst biomass declined from 0.0261g (B_1) to 0.0193g (B_2) approximately (Figure 3). Therefore $y = \frac{0.0193}{0.0261} = 0.739$ and $x = \frac{71}{24} = 2.95$. Hence,

$y < x$, $(2.95 > 0.739)$, and this difference between y and x is much greater than at low intensity agriculture.

Scenario 1

Given $y < x$, we find that, if we keep ϕ constant, $\sigma_2 < \sigma_1$(Figure 1a), or, if we keep σ constant, $\phi_2 < \phi_1$ (Figure 1b), meaning that again communities become more homogenous in size and have fewer large species. By putting the results of x and y into equation [8], we get $\frac{y}{x} = \frac{0.739}{2.95} = 0.251 = \mathrm{e}^{\frac{\sigma_2^2-\sigma_1^2}{2}}$, and, therefore, ${\sigma_1}^2 - 2.77 = \sigma_2^2$. So, there is a much larger reduction in the skew of the relationship and the variance of body mass under high intensity agriculture than under low intensity agriculture over time. Alternatively, we also get $0.251 = \mathrm{e}^{\phi_2 - \phi_1}$, meaning $0.251\ \mathrm{e}^{\phi_1} = \mathrm{e}^{\phi_2}$, when holding σ constant, and there is therefore a large reduction in the mean species' mass.

Scenario 2

Given $y < x$, we find that $b_2 < b_1$ again. Specifically, using equation [12], $0.251 \frac{\sum_{i=1} {M_i}^{b_1+1}}{\sum_{i=1} {M_i}^{b_1}} = \frac{\sum_{i=1} {M_i}^{b_2+1}}{\sum_{i=1} {M_i}^{b_2}}$. By setting $b_1 =$ -0.2, our simulations result in a value of $b_2 \sim$ -1.703 $\pm$ 0.01, and for $b_1 =$ -0.8, $b_2 =$ -2.775 $\pm$ 0.048 (again, for the results of b_2 for all b_1 values between -0.2 and -0.8, see Appendix S2). Therefore, we find a significantly larger reduction in the population sizes of large species and increase in the population sizes of small species (Figure 2), compared to communities under low intensity agriculture, according to the large reduction in b and steeper exponent of the size density relationship under this degree of agricultural intensity.

At both ends of the agricultural intensity spectrum, for scenario 1 there is a reduction of skewness ($\sigma_2 < \sigma_1$) and / or a reduction in the mean ($\phi_2 < \phi_1$), and there is a reduction in b for scenario 2. However, if we focus on scenario 1, then the difference in parameters σ and ϕ are much greater under high intensity agriculture, meaning the changes in species body size distribution that we predict, the reduction in numbers of large species and a decrease in the variation of species' body mass, happens more rapidly and to a much greater degree under high intensity agriculture. If we consider scenario 2, then the difference in b, the scaling exponential of the size density distribution, is again much greater under high agricultural intensity, resulting in greater declines in the abundance of large species and greater increases in the abundance of small species under increasing intensification of agricultural practices.

Discussion

We use established macroecological relationships to gain greater insight into how Diptera communities might have changed over time and under increasing agricultural intensity across the study site in Powell et al. (2023). In the alternative scenarios, we find fewer large species, more smaller species; individuals are getting smaller on average; there is a reduction in the heterogeneity of body mass; and /or the population sizes of larger species declines whilst that of small species increases significantly. These conclusions can be visualised in the way the species body size distributions change under a decline in σ and ϕ in Figure 1, and how the size density relationship changes under declining b values in Figure 2. We find that both patterns of community change occur at a much greater rate in Diptera communities under the most intensive agricultural systems in our study area, as opposed to the least intensive ones, shown by the greater difference in the distribution of both types of relationship under increased levels of agricultural intensity.

It is most likely that both scenarios that we explore here are occurring simultaneously and to varying degrees in our study system, given the expected effect that anthropogenic pressures have on insect community assembly and evolutionary processes. This is because of selection of smaller body mass as part of a suite of 'fast traits' that make individuals more resilient to the negative impacts of agricultural intensification, affecting both population size and presence of species (Outhwaite et al., 2022; Wonglersak et al., 2021). For example, there may be significant microclimatic effects that we were unable to unpick here, with much warmer temperatures in a more harsh and exposed intensively cultivated landscape leading to smaller body sizes due to physiological (metabolic) constraints (Davies, 2019; Ewers & Banks-Leite, 2013; Gardner et al., 2011; Wonglersak et al., 2021). Warming may result in scenario 1 through creating niches more suitable for some species that then colonise the area and replace others, or through species adapting to the warmer climate, or could result in scenario 2 by limiting the population size of larger species due to negative effects on their reproduction or longevity, whilst smaller species' reproduction would be accelerated (e.g., Fryxell et al., 2020).

What we imply with this study is the filtering out of certain traits at the individual and / or species level, by the pressures exerted on Diptera communities under agricultural intensification. In scenario 1, the evenness, range, and diversity of body mass in Diptera declines, and, therefore, the range of niches occupied by different species may also be 'compressed', leading to negative functional consequences (Burdon et al., 2020). This is because the reduction of both larger and, if we witness a change in skew alone (Figure 1a), smallest species, may have significant consequences for the diversity of the range of functions provided by species of these sizes. For example, very small-bodied flies such as chironomids tend to be important for decomposition and nutrient cycling, providing the bulk of diet for many aquatic species (Einarsson et al., 2002; Macadam & Stockan, 2015). Meanwhile, larger species tend to be important for pollination and as prey species for aerial insectivores in this region of Québec, such as the red-listed and declining Tree Swallow (Bellavance et al., 2018). The functions provided by Diptera on both ends of the size spectrum may therefore be under threat from agricultural intensification.

In scenario 2, where we assume the number of species of different body masses remains the same over time over the agricultural gradient, we witness a large difference in the size density relationship, meaning the relative abundance within species undergoes a sizeable shift towards smaller species that is exacerbated with agricultural intensification. The consequences of this pattern are similar to our suggestions of functional change taking place under scenario 1; we have fewer large individuals and more small individuals, though here due to a change in the relative abundance of species of different sizes, meaning functions that rely on healthy and resilient populations of larger species may be under threat by agricultural intensification. We find that the variation in the exponent of this relationship for Diptera communities between time points, calculated by simulating initial *b* values, exceeds that calculated in Isaac et al. (2011), which examined variation in the average size density relationship across different orders of mammal and bird. Here, we explore change within one single order – Diptera, in one region of Québec, Canada. Hence, we suggest that the size density relationship may be more diverse within taxonomic groupings than between.

Communities appear to become more homogenous under both scenarios we tested (Figure 1), meaning the diversity of body mass – a functional trait – declines. The diversity of functional traits in communities is linked not only to multifunctionality and the provision of functions itself but the long-term resilience of function (Oliver, Heard, et al., 2015). For example, diversity of traits such as body mass can increase the ability of communities to be able to withstand environmental perturbations, through increasing the likelihood that some species will be more resistant to an emerging environmental stressor or be able to recover from a perturbation more rapidly (Elmqvist et al., 2003; Oliver, Heard, et al., 2015). The reduction in trait diversity that we predict occurs in Diptera communities over time and under increasing agricultural intensity may therefore suggest that these communities are both more limited in their ability to provide functions, and may be less functionally resilient (Mori et al., 2013; Vandewalle et al., 2010). On the other hand, if a large part of the community change we predict is due to mechanisms under scenario 1, there's also a possibility that a turnover in species under intensive agricultural systems results in a community of species that are in and of themselves more 'hardy' and resilient than the average species, due to the environmental filtering of the more sensitive species under agricultural intensification (Redhead et al., 2018). We find that these changes are limited on farms that have lower intensity agriculture and a greater percentage of forest cover, and so Diptera communities are likely more resilient and functionally diverse in those regions. Land strategies that can incorporate more extensive, less intensive agricultural practices could therefore potentially help conserve Diptera and other insect communities and their functions in the long term (e.g., Bellamy et al., 2018; Redhead et al., 2022).

We show that measuring abundance or biomass alone is not necessarily a good indicator of community or biodiversity change occurring over time and under increasing anthropogenic environmental pressures, due to the impact of these pressures on traits within and amongst species' populations (Brass et al., 2021; Violle et al., 2012). Whilst many monitoring programmes do not monitor at the species-level due to constraints on time and resources, important information pertaining to ecosystem functions can be missed by such approaches. However, our study could potentially provide a way in which more detailed information could be grasped about community-level change where species data is not available, through using abundance and biomass estimates in conjunction to predict how the species body size and size density distributions are affected by environmental pressures and, therefore, predict the relative impact on species of different body mass.

Finally, we recommend further work could focus on corroborating our results through examining the true size density and species body size distributions in insect communities captured by monitoring programmes, by identifying insects down to the species-level and potentially recording more detailed information about individual body mass under increasing agricultural intensification.

Supporting Information

Appendix S1

The derivation of equations [8] and [12]

Equation [8]

In scenario 1, we end up with the equation:

$$\mu = \frac{\bar{n}\mathrm{e}^{\phi+\frac{\sigma^2}{2}}s}{N}.$$

We use this equation, along with equation [5] and [7], which are defined as

$$\frac{y}{x} = \frac{u_2}{u_1}. \qquad [5]$$

and

$$N = \bar{n}s. \qquad [7]$$

to derive the following:

$$\frac{y}{x} = \frac{u_2}{u_1} = \frac{N_1\bar{n}_2\mathrm{e}^{\phi_2+\frac{\sigma_2^2}{2}}s_2}{N_2\bar{n}_1\mathrm{e}^{\phi_1+\frac{\sigma_1^2}{2}}s_1},$$

and, by substituting N using equation [7],

$$\frac{y}{x} = \frac{\bar{n}_1s_1\bar{n}_2\mathrm{e}^{\phi_2+\frac{\sigma_2^2}{2}}s_2}{\bar{n}_2s_2\bar{n}_1\mathrm{e}^{\phi_1+\frac{\sigma_1^2}{2}}s_1}.$$

This can then be simplified down to

$$\frac{y}{x} = \frac{\mathrm{e}^{\phi_2+\frac{\sigma_2^2}{2}}}{\mathrm{e}^{\phi_1+\frac{\sigma_1^2}{2}}},$$

which is equivalent to our equation [8],

$$\frac{y}{x} = \mathrm{e}^{\phi_2+\frac{\sigma_2^2}{2}-\phi_1-\frac{\sigma_1^2}{2}} \qquad [8]$$

Equation [12]

In scenario 2, we end up with equation [11]:

$$\frac{y}{x} = \frac{\left(\sum_{i\,=\,1} \mathrm{e}^{a_2+b_2\, ln\left(M_i\right)} M_i\right) \sum_{i\,=\,1} \mathrm{e}^{a_1+b_1\, ln\left(M_i\right)}}{\left(\sum_{i\,=\,1} \mathrm{e}^{a_1+b_1\, ln\left(M_i\right)} M_i\right) \sum_{i\,=\,1} \mathrm{e}^{a_2+b_2\, ln\left(M_i\right)}}. \qquad [11]$$

To simplify this equation, we consider that

$$e^{a+b\, ln\left(M_i\right)} = e^{a} e^{ln\left(M_i\right)^{b}};$$

then we can write equation [11] as

$$\frac{y}{x} = \frac{\left(\sum_{i\,=\,1} e^{a_2} e^{\ln\left(M_i\right)^{b_2}} M_i\right) \sum_{i\,=\,1} e^{a_1} e^{\ln\left(M_i\right)^{b_1}}}{\left(\sum_{i\,=\,1} e^{a_1} e^{\ln\left(M_i\right)^{b_1}} M_i\right) \sum_{i\,=\,1} e^{a_2} e^{\ln\left(M_i\right)^{b_2}}},$$

or

$$\frac{y}{x} = \frac{\left(e^{a_2} e^{a_1} \sum_{i\,=\,1} e^{\ln\left(M_i\right)^{b_2}} M_i\right) \sum_{i\,=\,1} e^{\ln\left(M_i\right)^{b_1}}}{\left(e^{a_1} e^{a_2} \sum_{i\,=\,1} e^{\ln\left(M_i\right)^{b_1}} M_i\right) \sum_{i\,=\,1} e^{\ln\left(M_i\right)^{b_2}}},$$

$$\frac{y}{x} = \frac{\left(\sum_{i\,=\,1} e^{\ln\left(M_i\right)^{b_2}} M_i\right) \sum_{i\,=\,1} e^{\ln\left(M_i\right)^{b_1}}}{\left(\sum_{i\,=\,1} e^{\ln\left(M_i\right)^{b_1}} M_i\right) \sum_{i\,=\,1} e^{\ln\left(M_i\right)^{b_2}}},$$

$$\frac{y}{x} = \frac{\left(\sum_{i\,=\,1} {M_i}^{b_2} M_i\right) \sum_{i\,=\,1} {M_i}^{b_1}}{\left(\sum_{i\,=\,1} {M_i}^{b_2}\right) \sum_{i\,=\,1} {M_i}^{b_1} M_i},$$

$$\frac{y}{x} = \frac{\left(\sum_{i\,=\,1} {M_i}^{b_2+1}\right) \sum_{i\,=\,1} {M_i}^{b_1}}{\left(\sum_{i\,=\,1} {M_i}^{b_2}\right) \sum_{i\,=\,1} {M_i}^{b_1+1}}.$$

and, therefore, finally as equation [12] as such:

$$\frac{y}{x} \frac{\sum_{i\,=\,1} {M_i}^{b_1+1}}{\sum_{i\,=\,1} {M_i}^{b_1}} = \frac{\sum_{i\,=\,1} {M_i}^{b_2+1}}{\sum_{i\,=\,1} {M_i}^{b_2}}. \qquad [12]$$

Appendix S2

Simulated Diptera communities, and the results of trial and improvement to solve b_2

To explore how the size-density relationship changes under scenario 2, we simulated 1000 Diptera communities, each containing 100 species, with a log-normal species body size distribution for mass M where the mean of $ln(M) = 0$ and standard deviation of $ln(M) = 1$. The density of species of each body size in the communities is shown in Figure S1. We then used equation [12] to calculate the left-hand side (LHS) of the equation by entering our predicted values of y and x at each level of agricultural intensity (or no agricultural intensity – 'temporal' only models) with values of $b_1 =$ -0.2 to -0.8, a sensible range of values given the range of b from results in Isaac et al. (2011). We then used a process of 'trial and improvement', trying different values of b_2 in the right-hand side (RHS) of eqn [12], and selecting the b_2 value whose given RHS output came within 2 decimal places of the LHS output for the given b_1 value. The results of this process are highlighted in Table S1.

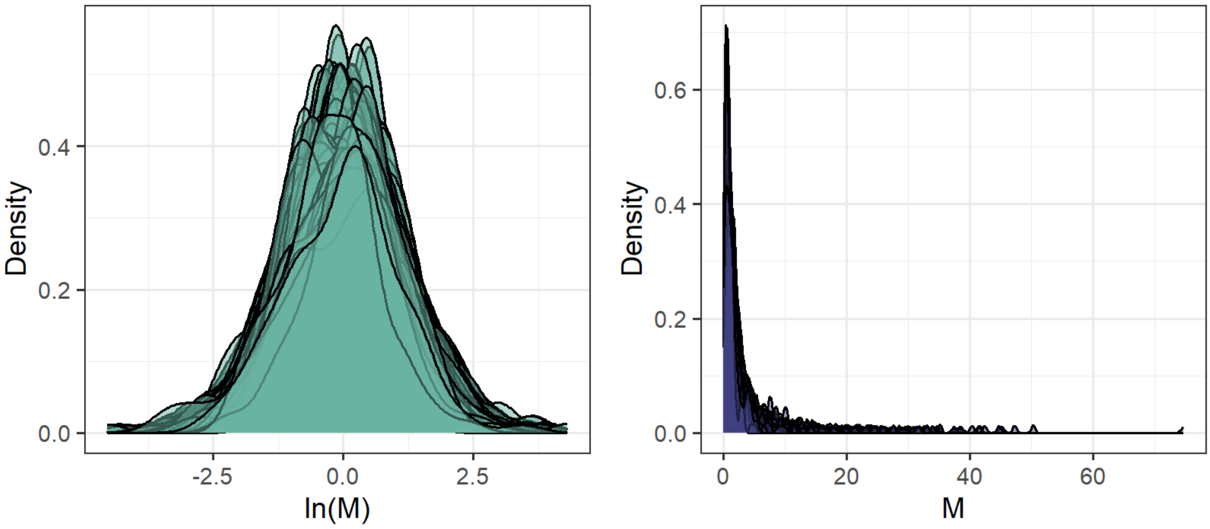


Figure S1. Density plots for the 1000 simulated Diptera communities, showing species in each community distributed by mass M.

Table S1. The results of trial and improvement to solve approximate b_2 values, given the predicted x and y values at each state of agricultural intensity that we tested, for $b_1 = -0.2$ to -0.8. The b_2 values given are a mean (and standard errors, SE) of the 1000 b_2 values settled on for the simulated Diptera communities. 'Null' agricultural intensification signifies where we have used predictions from the 'temporal' models from Powell et al. (2023), where agricultural intensification was not included in the model.

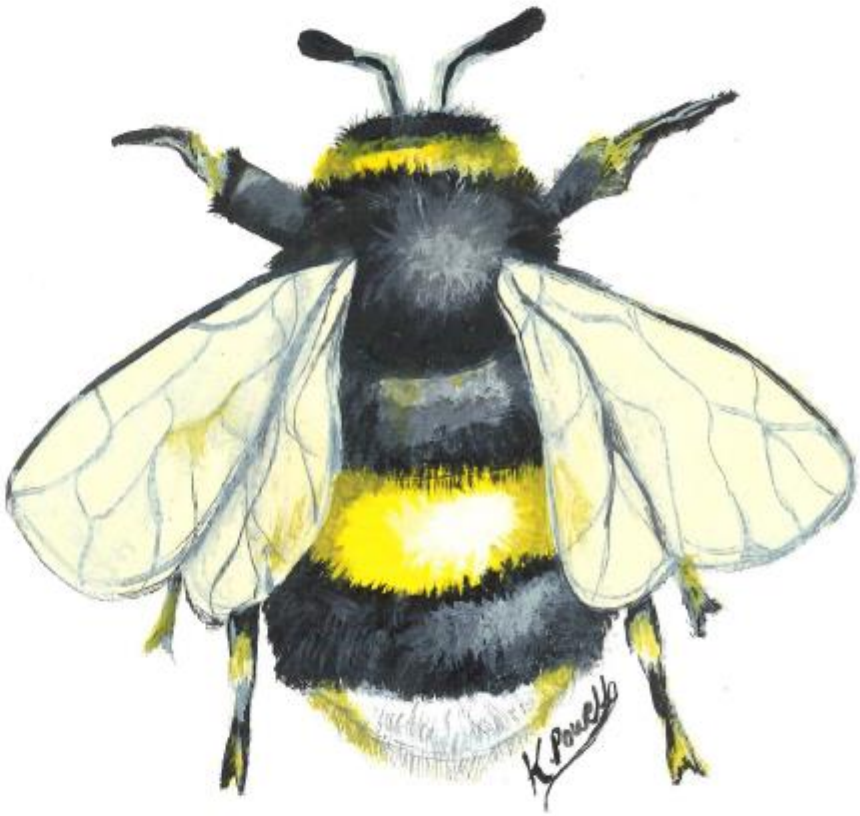
b_1 value	Agricultural Intensification	b_2 mean	b_2 SE
-0.2	Null	-1.055	0.004
	Low	-0.285	< 0.001
	High	-1.703	0.01
-0.3	Null	-1.161	0.004
	Low	-0.385	< 0.001
	High	-1.835	0.011
-0.4	Null	-1.269	0.005
	Low	-0.484	< 0.001
	High	-1.979	0.013
-0.5	Null	-1.379	0.005
	Low	-0.583	< 0.001
	High	-2.132	0.015
-0.6	Null	-1.494	0.006
	Low	-0.683	< 0.001
	High	-2.304	0.018
-0.7	Null	-1.612	0.006
	Low	-0.783	< 0.001
	High	-2.509	0.025
-0.8	Null	-1.734	0.007
	Low	-0.884	< 0.001
	High	-2.775	0.048

Equation [12]:

$$\left\{\frac{y}{x}\frac{\sum_{i=1} M_i^{b_1+1}}{\sum_{i=1} M_i^{b_1}}\right\} = \left[\frac{\sum_{i=1} M_i^{b_2+1}}{\sum_{i=1} M_i^{b_2}}\right]. \quad [12]$$

The Left-Hand Side (LHS) is indicated by { }, and the RHS by [ ].

Chapter 5



Chapter 5

Asynchrony in terrestrial insect abundance corresponds with species' traits mediating exposure and sensitivity to environmental perturbations

Abstract

Asynchrony in population abundance can buffer the effects of environmental change leading to greater community and ecosystem stability. Both environmental (abiotic) drivers and species functional (biotic) traits can influence population dynamics leading to asynchrony. However, empirical evidence linking variation in species traits to abundance asynchrony is limited, especially for understudied taxa such as insects. To fill this knowledge gap, we explored the relationship between trait variation (dissimilarity) and asynchrony in interannual abundance dynamics for 422 moth, butterfly, and bumblebee species in Great Britain. We also explored patterns differentiating traits that capture 'sensitivity to environmental variables' (such as body mass), and traits that reflect 'diversity in exposure' to environmental conditions and lead to niche partitioning (for example, habitat preferences, and intra-annual emergence periods). As expected, trait dissimilarity calculated overall and for many individual traits representing response and exposure was positively correlated with asynchrony in all three insect groups. We found that 'exposure' traits, especially those relating to the phenology of species, had the strongest relationship with abundance asynchrony from all tested traits. Positive relationships between trait dissimilarity and asynchrony were not simply due to shared evolutionary history leading to similar life-history strategies: detected effects remained significant for most traits after accounting for phylogenetic relationships within models. Our results provide empirical support that dissimilarity in both the exposure and sensitivity to the environment influences temporal variation in insect abundance. Hence, we suggest that general trait diversity, but especially diversity in 'exposure' traits, plays a significant role in the resilience of insect communities to short-term environmental perturbations through driving asynchrony between species abundances.

Keywords: asynchrony, stability, functional traits, trait diversity, Lepidoptera, Bombus

Introduction

With biodiversity rapidly changing across the globe, it is important to understand what makes communities more vulnerable to the abiotic anthropogenic environmental drivers widely causing this change, and what leads to greater resilience (Oliver, Heard, et al., 2015). Interspecific asynchrony – i.e., negative temporal correlation between species population sizes (Caruso et al., 2020) - is increasingly recognised to underpin stability, and therefore the resilience, of community and ecosystem-level dynamics in nature (Craven et al., 2018; Lepš et al., 2018; Valencia et al., 2020; although see Caruso et al., 2020;). Asynchronous temporal fluctuations between species can be detectable in time-series abundance data (Loreau & De Mazancourt, 2008).

Variation in abundance dynamics is likely driven by a complex range of interacting biotic and abiotic factors, including genetic drift or stochastic processes, intra- and interspecific density dependence, environmental conditions and the functional properties of species and their realised niches (Loreau & De Mazancourt, 2008). These functional properties are referred to as “functional traits”. Although there are several definitions across the literature, generally, functional traits consist of measurable morphological, physiological, behavioural, phenological or cultural characteristics which affect how individuals interact with the surrounding environment (Dawson et al., 2021; Luck et al., 2012; Schneider et al., 2019). In general, traits which affect how an individual or species responds to deviations in an environmental pressure such as short-term climatic perturbations are referred to as ‘functional response’ traits, and those that affect how an individual or species impacts the environment around them through a functional role – such as pollination proficiency – are often referred to as “functional effects” traits (Bruelheide et al., 2018; Díaz et al., 2013; Oliver, Heard, et al., 2015). Some complexity arises, seeing as response and effects traits are by no means mutually exclusive – that is to say, there is overlap and correlation between response and effects traits, which can undermine the resilience of function to environmental change (Díaz et al., 2013; Greenwell et al., 2019).

Species with different traits can vary in their sensitivity to certain environmental conditions, leading to variable population-level responses (Craven et al., 2018; Li et al., 2021; Mumme et al., 2015; van Klink et al., 2019). The ‘dissimilarity’ between traits, using metrics such as Gower distance between species trait values, is one way of measuring how widely traits vary between species (de Bello et al., 2016), and this dissimilarity between traits can result in asynchronous abundance dynamics through the variation in their population-level responses to the environment (Craven et al., 2018; Li et al., 2021; Mumme et al., 2015; van Klink et al., 2019). For example, physiological differences associated with variation in body size can lead to divergence in thermal tolerances and thus, in the response to climatic fluctuations (Stevenson, 1985). Species with larger body size generally lose heat less quickly which allows them to tolerate a cold snap and maintain or increase their abundance, whilst smaller species tend to be more vulnerable to cold snaps and decrease in abundance, resulting in temporal asynchrony between species (Stevenson, 1985; Verdú et al., 2006).

Although often excluded in the definition of a true “response trait”, some of these traits may also be linked to either spatial or temporal niche partitioning between different species, meaning that species vary in their exploitation of resources, as well as exposure to an environmental driver of abundance change in space or time (MacArthur, 1958; Turnbull et al., 2013). For example, considering mobility, a species which can disperse over a wider range may be able to escape the effects of drivers such as localised extreme climate conditions - for example, drought - as opposed to a smaller and less mobile species (Gámez-Virués et al., 2015). Two species, each with different habitat preferences, can also be subject to fairly extreme differences in microclimatic pressures at any one point in time due to the influence of habitat structure on microclimate (Suggitt et al., 2011); therefore, although their physiological sensitivity to an environmental extreme may not vary per se, species abundances may cycle asynchronously due to the spatial partitioning in their exposure to these variables (Turnbull et al., 2013). Similarly, different species can have different emergence times and lengths of life stages, or their breeding patterns may be exposed to temporal variation in the environment, potentially leading to annual differences in abundance change if one species is subject to worse environmental conditions than the other (Usinowicz et al., 2012). These traits, that can determine the spatial and/or temporal niche partitioning between species, and therefore their exposure to the environment, are not typically thought of as pure “functional traits” due to the lack of measurability from a single individual and the determination of sensitivity to a level of one variable (Dawson et al., 2021). They instead reflect - what we will refer to here as – “diversity in exposure”. Nevertheless, they may be inherently important for mediating temporal asynchrony and community stability through their variable effects on species abundance. Dawson et al. (2021) considers the broadening of the definition of functional traits to incorporate aspects of organisms such as these diversity in exposure traits, due to the idea that most traits are to some degree “functional” due to their association with the interaction between individuals and/or species and their environment.

Here, we explore the association of trait dissimilarity with abundance asynchrony across a range of terrestrial insect taxa in Great Britain. Insects play important functional roles in ecosystems, and have found to be declining in diversity, abundance and biomass in several studies; although there is debate on the extent to which this constitutes a general pattern (Wagner, 2020). At the same time, insects are generally understudied taxa when it comes to understanding the role of functional traits, and trait-based mechanisms in ecology; and most understanding of how traits relate to the environment come from studies of plants (Brousseau et al., 2018; Noriega et al., 2018b).

We analyse asynchrony in abundance and trait dissimilarity from pairwise species relationships using long-term citizen science and standard abundance monitoring datasets in combination with recently published novel functional trait data for 422 species of macro-moths, butterflies, and bumblebees. We explore the relative role of individual traits in contributing to abundance asynchrony. We compare traits deemed to be: 1) “sensitivity traits” that determine species sensitivities to the environment through a link to a direct physiological response to a perturbation, and are therefore functional response traits (in our study: minimum and maximum forewing lengths, estimated dry mass, voltinism and diet breadth and specialisation); as well as 2) “exposure traits”: traits in the broader sense which come under the definition given by Dawson et al. (2021) (hostplant and dietary specialisation, habitat preference, nesting habits, emergence periods, overwintering stages, and voltinism; some traits could be classified as both categories). Variation in the exploitation of food plants, nesting quarters and habitat preference represents spatial niche partitioning, whilst voltinism, overwintering stage and emergence period represent temporal niche partitioning and so they may determine varying responses amongst species to environmental perturbations. Therefore, we hypothesised that the more these traits differed amongst species, the greater the annual abundance asynchrony between species would be (i.e., a positive correlation between trait dissimilarity and abundance asynchrony). Through this study we aim to shed light on possible underlying mechanisms that drive asynchrony between species populations and hence which contribute to more stable functional communities in terrestrial insects.

Methods

Abundance Dynamics

We used three different insect abundance time series datasets taken from standardised monitoring projects to calculate relative abundance changes from year-to-year for three main insect taxa in Great Britain: i) macro-moths, using the ‘Rothamsted Insect Survey’ light trap data (RIS; Woiwod & Harrington, 1994); ii) butterflies, using the ‘UK Butterfly Monitoring Scheme’ (UKBMS; Botham et al., 2020); and iii) bumblebees, using the Bumblebee Conservation Trust’s BeeWalk survey (Comont & Dickinson, 2020). For each dataset, the ‘Generalised Abundance Index (GAI)’ approach was used to calculate ‘collated abundance indices’ that account for missing count data and the variability in seasonal patterns for species in the three taxonomic groups (Dennis et al., 2013). These indices are an estimate of the expected number of individuals observed on a standardised transect walk (BeeWalk and UKBMS) or trapping event (RIS) during that year. We used collated indices for macro-moths and butterflies reported by the NERC Environment Information Data Centre. To align methodology for predicting bumblebee annual abundance indices with the GAI methods used for the UKBMS and RIS data, we used the ‘rbms’ package in R to fit the required GAI models to each bumblebee species recorded with a sufficient number of observations from the BeeWalk data (Schmucki et al., 2022). We then calculated relative interannual abundance change values for each species by subtracting the collated annual abundance index for each

Table 1. List of traits used for building functional trait dissimilarity matrices.

Trait Group	Trait	Description	Functional Association	Combined Traits Dissimilarity Weighting	Relevant Taxa		
							
Nesting Habits	Pupal Nesting Habit (PH)	Location for the pupal and/or nesting stages (underground, soil surface, on hostplant, within hostplant, on other vegetation, within stone walls, and dead wood)	Links to extinction risk and distribution; exposure to different microhabitats, microclimates, and disturbance (Exposure)	0.167	✓	✓	✓
Body Size	Forewing Minimum (FMI)	Minimum forewing length (mm)	Predictor of dispersal and population declines, linked to physiological sensitivity (Sensitivity)	0.0556	✓	✓	
Body Size	Forewing Maximum (FMA)	Maximum forewing length (mm)	Predictor of dispersal and population declines, linked to physiological sensitivity (Sensitivity)	0.0556	✓	✓	✓
Body Size	Estimated Body Mass (EDM)	Dry mass estimate (mg), calculated using models from Kinsella et al. (2020) for moths and Cane, (1987) for bumblebees	Predictor of dispersal and population declines, linked to physiological sensitivity (Sensitivity)	0.0556	✓		✓
Phenology	Voltinism (V)	Number of broods per year (univoltine: 1 brood; multivoltine: 2 or more broods)	Links to recovery from disturbance, exposure to different drivers of change temporally (Sensitivity and Exposure)	0.0278	✓	✓	✓
Phenology	Egg Stage (ES)	Months during which individuals are eggs (Jan-Dec)	Associated with extinction risk and distribution, exposure to different drivers of change temporally (Exposure)	0.0278	✓	✓	
Phenology	Pupal Stage (PS)	Months during which individuals are pupae (Jan-Dec)	Associated with extinction risk and distribution, exposure to different drivers of change temporally (Exposure)	0.0278	✓	✓	
Phenology	Larval Stage (LS)	Months during which individuals are larvae (Jan-Dec)	Associated with extinction risk and distribution, exposure to different drivers of change temporally (Exposure)	0.0278	✓	✓	

Trait Group	**Trait**	**Description**	**Functional Association**	**Combined Traits Dissimilarity Weighting**	**Relevant Taxa** 		
Phenology	Adult Stage (AS)	Months during which individuals are adults and actively flying (Jan-Dec)	Associated with extinction risk and distribution, exposure to different drivers of change temporally (Exposure)	0.0278	✓	✓	✓
Phenology	Overwinter Stage (OS)	The life stage that species overwinter in (egg, larva, pupa or adult)	Correlated with both distribution, extinction risk and abundance trend, exposure to different drivers of change temporally (Exposure)	0.0278	✓	✓	✓
Diet	Hostplant Number (HN)	The number of host plant species used by larvae	Correlated with dispersal and range size (Exposure)	0.0556	✓	✓	
Diet	Hostplant (or diet) Specificity (HS)	Whether species are monophagous, oligophagous, or polyphagous	Correlated with dispersal and range size (Exposure)	0.0556	✓	✓	✓
Diet	Hostplant Category (HC)	Plant category that host-plants come under (e.g., trees, grasses, sedges, mosses, etc.)	Correlated with both increases and decreases in abundance trends; exposure to different drivers of change spatially and temporally (Exposure)	0.0556	✓	✓	
Habitat	Habitat (H)	Habitat preferences (Woodland, heathland, moorland, grassland, wetland, coastal, montane, urban / agricultural)	Preference and specificity can predict population declines; exposure to different drivers of change spatially and temporally (Exposure)	0.167	✓	✓	✓

year from the following year's value, creating a dataset of the annual changes in each species standardised log abundance, following the methodology for calculating relative interannual abundance change outlined in Greenwell et al. (2019).

We then examined interannual abundance dynamic asynchrony between pairs of species using distance matrices. Pairwise distance values were calculated to produce the matrix M_b such that:

$$\boldsymbol{M_b = (1- K) / 2}$$

where K is a matrix of pairwise Pearson’s correlation coefficients calculated from inter-annual abundance change values using the corr() function in R (version 4.0.3). This produced values between 1 (completely asynchronous) and 0 (completely synchronous; see Figure 1 for an example of different levels of asynchrony between species from the RIS dataset). We produced matrices for butterfly, moth and bumblebee abundance. It should be noted that in the BeeWalk dataset, species recorded as *Bombus quorum, Bombus magnus, Bombus cryptarum* and *Bombus terrestris* had to be combined into one species complex (which we call *Bombus lucorum/terrestris*), due to taxonomic identification difficulties of the worker castes in the field (Carolan et al., 2012).

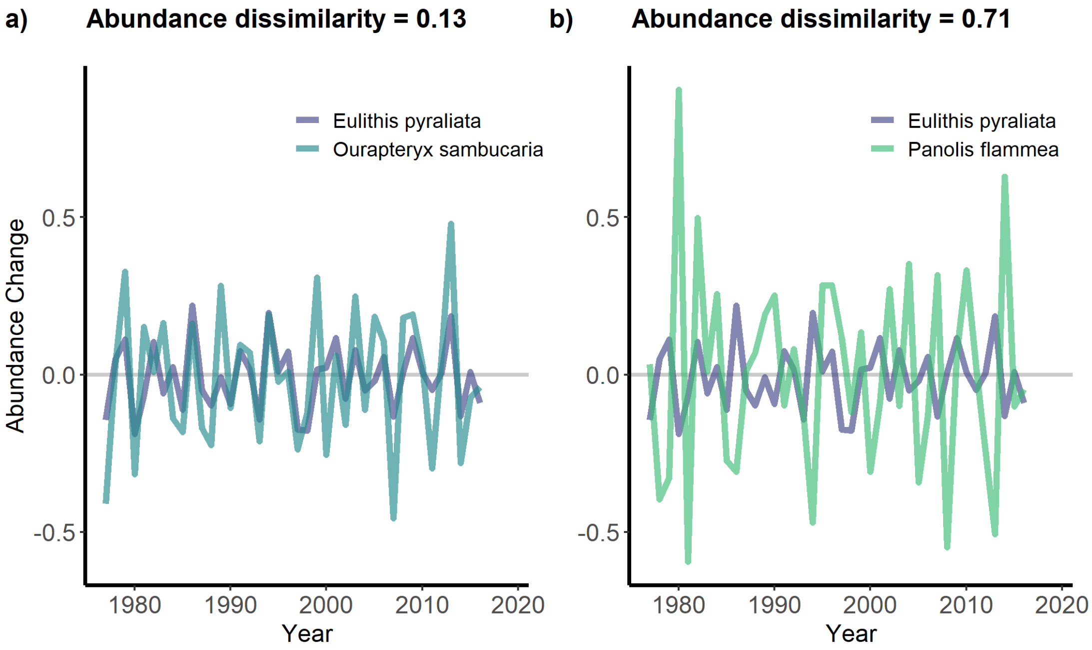


Figure 1. Examples of variation in asynchrony between interannual abundance dynamics of two pairs of macro-moth species; (a) *Eulithis pyraliata* (barred straw moth) and *Ourapteryx sambucaria* (swallow-tailed moth); and (b) *Eulithis pyraliata* and *Panos flammea* (pine beauty moth). In example (a), the high correlation between the species interannual abundance change values results in a calculated abundance asynchrony value of 0.13 (where asynchrony lies between 0 and 1, with 0 being completely synchronous and 1 being completely asynchronous); in example (b), the two species cycle more asynchronously in abundance, with lower correlation between their abundance dynamics, resulting in a calculated asynchrony value which is closer to 1 (0.71).

Functional Traits

We collated and compiled functional trait data for all species using guidebooks for bumblebee species (Falk, 2015) and a compiled Lepidoptera trait dataset for macro-moths and butterflies (Cook et al., 2021). We focused on traits reported in the literature as showing correlation with abundance, distribution, or extinction risk in response to environmental drivers for any of the three taxa, which we considered to be appropriate traits under the definition outlined in the introduction. A full list of traits used in the analysis are outlined in Table 1. For bumblebees, as we collated these data ourselves, we coded traits in line with the values used in the published lepidopteran data to keep this as standardised as possible, i.e., trait values were mostly categorical and coded in binary (1 or 0, depending on presence of trait in species) with multiple columns for each trait category (e.g., monophagous, oligophagous, or polyphagous categories for the Hostplant or diet Specialism trait; species can be coded as ‘1’ for multiple columns within traits if traits were not mutually exclusive, e.g., for Hostplant Category, when multiple types of hostplant are used by the species), unless the trait was a continuous variable such as body mass estimates. As eusocial bumblebee species castes vary widely in their body size and forewing lengths, e.g., between queens and workers, size and mass measurements relating to queens was used in trait matrices to be comparable with cuckoo bumblebee species which do not have workers. We assumed this would not change directions of relationships between species in our analyses as bumblebee species with larger queens have larger workers, and vice versa.

We used the gawdis() function of the ‘Gawdis’ package in R (de Bello et al., 2020) to calculate Gower distances for functional trait values between each pair of species across butterflies, macro-moths and bumblebees. We constructed trait distance matrices for each individual trait, as well as a ‘combined traits’ distance matrix for each taxonomic group and combination of groups. For this combined traits matrix, as there was correlation between a number of traits which described similar aspects of species ecologies, as well as the challenge of addressing and combining both categorical and continuous traits, we used the grouping argument of the gawdis() function to combine traits that we considered to come together to describe one functional aspect (a ‘trait group’). This methodology alters the weighting of each individual ‘raw’ trait within trait groups so that each final trait group contributes equally to the resulting final combined traits dissimilarity matrix, in line with methods described in de Bello et al. (2020). Using this function to combine and condense traits allowed us to reduce bias given to certain traits that were closely correlated to others in the dataset, whilst avoiding removing traits from the analysis, which may have otherwise reduced the accuracy of the Gower distances calculated between species pairs. The grouping argument identified five trait groups which can broadly be described as: nesting habits, body size, phenology, diet, and habitat (Table 1).

Phylogenetic Distance

Phylogenetically related species are more likely to show similar trait values due to their shared evolutionary history, thus, trait distance between species may be phylogenetically patterned. We wanted to test, therefore, for evidence of phylogenetic signal in pairwise trait distances, and to examine whether temporal asynchrony of abundance dynamics could still be explained by trait distances regardless of phylogenetic constraints. We use the lepidopteran phylogenetic tree in Pöyry et al. (2017) for macro-moths and butterflies, and the bumblebee phylogenetic tree from Cameron et al. (2007). We then calculated distance matrices between each pair of species within taxonomic groups from the branch lengths of the phylogenies using the cophenetic.phylo() function in the ‘ape’ package in R (Paradis & Schliep, 2019). For bumblebee species we calculated average branch lengths between each species and the *B. lucorum/terrestris* species complex by taking the mean of the branch lengths between each species and *B. cryptarum, B. magnus, B. lucorum* and *B. terrestris.*

Testing correlative relationships between distance matrices

For each of the following statistical analyses, only species for which we could obtain data for all three datasets (i.e., abundance dynamics, traits and phylogenetics datasets for each taxonomic group), were included in pairwise distance matrices. We created Mantel tests using the Mantel() function with 10,000 permutations in the ‘ecodist’ package in R (Goslee & Urban, 2007) to test whether there was correlation between pairwise temporal abundance asynchrony and functional trait dissimilarity matrices. 95% confidence limits and p values were constructed using bootstrap resampling for 10,000 repeats. We deemed Mantel r values to be significant based on the ‘p value 1’ output from Mantel tests which tests the null hypothesis that Mantel r value < 0, based on a one-tailed t-test.

Using the same method for Mantel tests above, we tested both trait dissimilarity and abundance asynchrony matrices in macro-moths, butterflies, and bumblebees against phylogenetic distance matrices. Seeing as phylogenetic distance was found in all cases to be significantly positively correlated with abundance asynchrony, we also tested the relationship between trait distance and abundance asynchronies once the correlation between phylogeny and abundance was removed, i.e., accounting for phylogenetic differences between species, through partial Mantel tests. This allowed us to explore whether traits alone could explain abundance asynchrony beyond the effects of phylogenetics.

Partial tests to estimate the similarity between trait distance and abundance asynchrony were structured as follows:

Abundance asynchrony ~ Trait dissimilarity + Phylogenetic distance

where each of the three elements is a distance matrix constructed according to the methodology outlined above.

Results

Sample sizes in terms of numbers of species for each pairwise asynchrony, trait dissimilarity and phylogenetic distance matrix construction were as follows: macro-moths, n = 358 species; butterflies, n = 48; and bumblebees, n = 16.

Overall functional dissimilarity: Combined Traits analyses

In all three species groups, functional trait dissimilarity was significantly positively correlated with abundance asynchrony (Moths: Mantel r = 0.13, p < 0.001, n = 358; Butterflies: Mantel r = 0.103, p < 0.05, n = 48; and Bumblebees: Mantel r = 0.15, p < 0.05, n = 16; Figure 2). Hence,

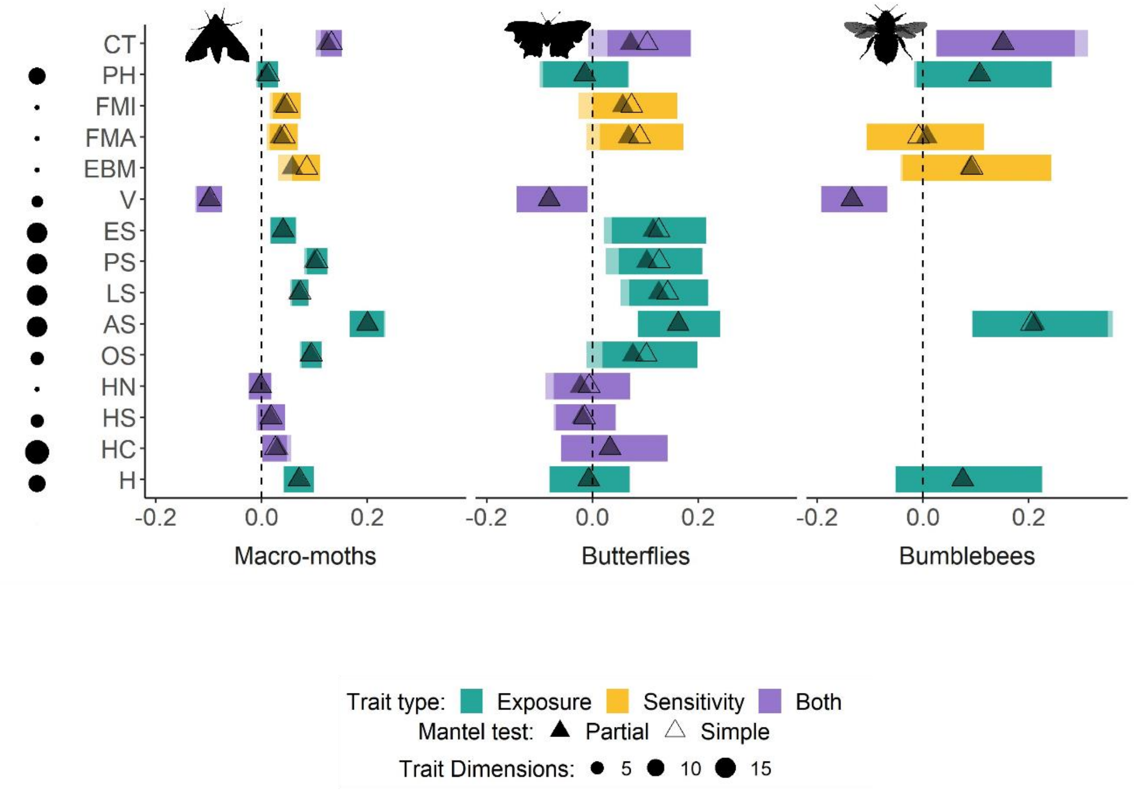


Figure 2. Mantel R values extracted from both simple and partial Mantel tests for macro-moths (n = 358), butterflies (n = 48), and bumblebees (n = 16). The width of the bars represents the 95% confidence intervals around each Mantel value. The initials on the y axis refer to the combined traits and the individual traits tested from Table 1, alongside a visual representation of the number of dimensions used to code each trait within trait databases, and are ordered from top to bottom as the following: CT = Combined Traits, PH = Pupal Nesting Habit (n dimensions [hereon referred to as 'n'] = 8), FMI = Forewing Minimum (n = 1) , FMA = Forewing Maximum (n = 1), EBM = Estimated Body Mass (n = 1), V = Voltinism (n = 3), ES = Egg Stage (n = 12), PS = Pupal Stage (n = 12), LS = Larval Stage (n = 12), AS = Adult Stage (n = 12), OS = Overwintering Stage (n = 4), HN = Hostplant Number (n = 1), HS = Hostplant (or diet) Specificity (n = 4), HC = Hostplant Category (n = 18), and H = Habitat (n = 8).

when two species of moth, butterfly or bumblebee are less similar in terms of their overall trait profiles, then those two species will tend to have divergent abundance changes.

When accounting for the correlation between phylogenetic distance and abundance asynchrony using partial Mantel tests, this relationship between functional trait distance and abundance asynchrony remained significant in all groups except butterflies (partial Mantel;

Macro-moths: Mantel $r = 0.12$, $p < 0.001$, $n = 358$; Butterflies: Mantel $r = 0.07$, $p = 0.12$, $n = 48$; and Bumblebees: $r = 0.15$, $p < 0.05$, $n = 16$; Figure 2).

Separate trait analyses

We found variation in the association between individual functional response traits and abundance asynchrony across species groups.

For macro-moths, dissimilarity in habitat preference, life stage periods (egg, larval, pupal and adult), overwintering stage, minimum and maximum forewing lengths, estimated body mass were all significantly positively correlated with abundance asynchrony (both simple and partial Mantel, Figure 2; partial Mantel presented in Appendix S1). However, number, type, and specificity of hostplants; and pupal habit were not significantly correlated with abundance asynchrony, whilst voltinism was negatively correlated with abundance asynchrony (both simple and partial Mantel, Figure 2; partial Mantel presented in Appendix S1).

For butterflies only dissimilarity in the life stage periods remained positively significant when the association between phylogenetic relatedness and abundance asynchrony was accounted for in partial Mantel tests (Figure 2 and Appendix S1). For simple Mantel tests, dissimilarity in overwintering stage and maximum forewing lengths were also marginally positively associated with abundance asynchrony amongst butterflies, their credible intervals overlapping with zero once phylogenetic patterns were included in models (Figure 2).

For bumblebees, data for fewer functional traits were available. Adult period (or flight window) dissimilarity was significantly positively correlated with abundance asynchrony, while voltinism dissimilarity was significantly negatively correlated (Figure 2 and Appendix S1). Other explored traits (forewing length, pupal (nesting) habit, estimated body mass and habitat preference) were not significantly correlated with abundance asynchrony (Figure 2 and Appendix S1).

Discussion

In line with our hypothesis, we found trait dissimilarity to be generally positively associated with abundance asynchrony across different species of macro-moths, butterflies, and bumblebees (i.e., species with different traits tend to have asynchronous population dynamics).

Phylogenetic distance was also positively associated with abundance asynchrony, possibly because there is phylogenetic signal amongst functional traits that we tested and/or additional traits that we did not include that have an influence on asynchrony (Díaz et al., 2013). However, our traits could still explain a significant amount of abundance asynchrony even when taking phylogenetic relationships into account (Figure 2).

There was variation across the relationships between functional traits and abundance dynamics for different taxonomic groups, and for different functional traits. For example, traits such as habitat preference and annual timings of life history stages were the most strongly associated with asynchrony, with adult stage consistently having the strongest association across all groups (although for bumblebees, fewer traits were able to be tested due to data gaps). This suggests species with similar adult emergence have more similar population dynamics than those emerging in different months, which might be expected as they are exposed to more similar weather conditions (e.g. a spring drought could affect all species in early-larval stages similarly) (Zhang, Bao, et al., 2022). Intra-annual variation in environmental factors, such as seasonal weather change in the UK, mean that species emerging at different times will vary in their exposure to these factors (Zhang, Hautier, et al., 2022). Intra-annual asynchrony has been found to increase intra-annual stability and support co-existence of species in plant communities (Usinowicz et al., 2012; Zhang, Bao, et al., 2022); our results suggest that such factors may be important for asynchrony in insect communities, and for variation in inter-annual abundance dynamics between species. Drivers of phenological shifts and intra-annual abundance dynamics of these insect taxa, such as climate change (Davies, 2019; McCauley & Mabry, 2011; Stemkovski et al., 2020; Visser & Holleman, 2001; Wuethrich, 2000), may result in greater overlap in adult emergence as springs generally become warmer and species that usually emerge in late spring or early summer begin to emerge earlier in the year (O’Neill et al., 2012). Given our results, there is a possible risk that such phenological shift and overlap may decrease inter-annual asynchrony (and therefore stability) between species, although this effect could also potentially be offset by increasing the number of broods per year during warmer years where there is a longer time period of reproduction (Altermatt, 2009; Zografou et al., 2021).

Dissimilarity in species habitat preference was also significantly correlated with abundance asynchrony in macro-moths. This trait was not significant for butterflies or bumblebees in our study; however, this result may be an artefact of limited species pools for these taxa, resulting in a larger proportional overlap in habitat preference for the species considered in the study. Variation in habitat preference leads to pairs of species being more likely to exploit different resources as well as experience different local environmental conditions – such as microclimatic extremes - and pressures at any one time point (Gilbert et al., 2020; Suggitt et al., 2011; Van Ruijven & Berendse, 2005). We suggest that not only 'response diversity' - in the sense that species vary in their *sensitivity* to environmental pressures - drives asynchronous abundance dynamics, but that variation in *exposure* to different environmental drivers over time and space, both through phenological dissimilarity and difference in habitat preference, is an important aspect of inter-annual asynchrony amongst these taxa (Albrecht & Gotelli, 2001).

In contrast, dissimilarity in other traits such as those linked to diet, specialism and pupal habits were generally not correlated with abundance asynchrony. We also found dissimilarity in voltinism to have negative correlation with abundance asynchrony (i.e., species with different voltinism were *more* similar in population dynamics). This may be because, in Lepidoptera for example, the first generations of most multivoltine species tend to coincide with the flight periods of early flying species and the second generation with late flying species, reducing variation between multivoltine and univoltine species pairs. As our analysis shows, variation in species adult emergence throughout the year increases population asynchrony, so perhaps this is more important than being univoltine or multivoltine per se. It is expected that having species with more than one generation in a year would increase resilience within a population because a subset will be less exposed to an extreme event that strongly negatively affects a species at a given time (Knell & Thackeray, 2016). Thus, their annual abundance could still be high while the univoltine species emerging at the same time will be low. Our negative result for voltinism is interesting as it suggests this may not be the case for stabilisation of community abundance. To examine this phenomenon from another angle, we may see this pattern because species with one brood are less likely to have them at the same time during the year as other univoltine species, or reach adult stages at different times, and so have differential exposure to environmental perturbations, leading to decoupling of abundance dynamics. Within the macro-moths, many species fly at times of year when other insects are inactive, in late autumn, winter and early spring (Soszyńska-Maj, 2015). These are generally univoltine, and are adapted to cooler temperatures (Heinrich, 1987). Univoltine moth species generally show much greater variation amongst their flight periods and brood period timing than multivoltine species, where species are active across the entire calendar year and overlap. However, this is less likely to be the case for bumblebees and butterflies whose brood timings are more seasonally restricted.

For traits that we deemed to be linked to species sensitivity to the environment, we found body size metrics – including forewing length and estimated dry mass, to be positively associated with abundance asynchrony in macro-moths. However, although we had no data on estimated body mass for butterflies, the effect for forewing length – which likely strongly associates with body mass - was lower (closer to 0) in butterflies, which corresponds with similar results in Greenwell et al., (2019). We found no effect of forewing length or body mass in bumblebees. Body size is frequently described as a functional response trait, as larger body size is predicted to make species more vulnerable to environmental stressors and increase extinction risk (Coulthard et al., 2019), although this may sometimes be offset by the ability of larger species to generally disperse more quickly to reach more favourable environments (Sekar, 2012). This complexity of how traits result in varying individual and population responses to environmental drivers – over short and long-term timescales and over different spatial scales – has been noted in recent studies linking moth traits to trends (Tordoff et al., 2022). For example, from the results of our study, it’s possible that temperature fluctuations between years favour a particular minimum or maximum body size, resulting in varied species-level responses and resulting in asynchronous dynamics between species of different size (Mattila et al., 2011).

We found some phylogenetic signal amongst functional traits across macro-moth and butterfly taxa, with more phylogenetically distant pairs of species having less similar functional response trait complexes (Appendix S1). This is expected given that traits evolve over time and species diverge genetically and phenotypically as they adapt to new environmental challenges (Díaz et al., 2013). In butterflies, this has been found to extend to the 'exposure traits' that we test here such as adult emergence, the date of which shows evidence of local adaption in response to climate (Roy et al., 2015). Hence, as we hypothesised trait dissimilarity to also be positively associated with population asynchronies between species, we would expect that phylogenetic distance also correlates with abundance asynchrony, which our results supported (Appendix S1). This phylogenetic 'signal' may help explain why some traits become decoupled from population asynchronies when accounting for phylogenetic relatedness amongst species, and for most traits shifts the Mantel R value closer to 0.

An important limitation to our analysis is that the features of the datasets we use here only allowed us to explore abundance asynchrony and traits at large scales – spatially, using annual abundance indices at a national level; and taxonomically, using mean values for species traits when there is ample evidence that the traits we use in this analysis can vary intraspecifically (Wong & Carmona, 2021). For example, some traits such as habitat preference or host plant use are likely to be important for species on different spatial scales than our analysis considered. Whilst the coarseness of the available data did not allow us to look at this, or further into more nuanced traits – for example, floristic richness and microhabitat preference, which may play a more significant role in bumblebee niches (e.g., Scriven et al., 2015) - our results still support a temporal and spatial niche-partitioning hypothesis for stabilising lepidopteran and bumblebee communities at the wider spatial scale (Isbell et al., 2009).

Although our analysis suggests that there are positive associations between functional trait dissimilarity, phylogenetic distance and abundance asynchrony, several factors may have reduced the power of our results in explaining the role of functional traits in abundance asynchrony and may help explain some of the variation between different taxonomic groups. For each dataset, the length of population time series varied. Additional analyses found that there was a significant positive effect of time series length on the strength of the correlation between functional trait dissimilarity and abundance asynchrony in butterflies and macro-moths, as well as the likelihood of detecting significance in this relationship (Appendix S2). The number of species included in each dataset and for each taxonomic group also varies markedly. One of the reasons that lower species numbers may result in a lack of signal between traits and asynchrony may be that the variability in traits amongst species within these taxa may be lower. We explored the spread of the trait dissimilarity data however and found a normal distribution across similar ranges of trait dissimilarity in the standardised matrices used for analyses (Appendix S3). For bumblebees, however, there was a right-hand skew in the spread of abundance asynchrony values, with more pairs having lower asynchrony; this may go some way to explain a lack of correlation between traits and asynchrony in this group. Another reason for the lack of signal may be the reduced power afforded to significance testing with a smaller dataset, when there are weaker correlations between trait dissimilarity and asynchrony. Testing the effect of increasing the number of species included in the analysis didn't change the overall average correlation between trait distance and abundance asynchrony, although using low numbers of species (< 50) resulted in large variation in the results as well as high confidence intervals which lead to less chance of a signification correlation. Although we could only investigate this issue in lepidopteran time series, we suggest that it may generally explain why we found fewer butterfly traits and only one bumblebee trait to be significant.

Our findings that dissimilarity in traits – both when traits are associated with sensitivity to environmental variables and when traits are associated with spatial and temporal niche partitioning – are linked to interspecific asynchrony in insect communities, could have wider implications for understanding the functional mechanisms behind long-term stability and resilience (Oliver, Heard, et al., 2015). As asynchrony is frequently found to be one of the most important drivers of stability within biological communities, our results support the view that communities with diverse traits can maintain functional resilience to environmental perturbations (Craven et al., 2018; Loreau & de Mazancourt, 2013; Sasaki et al., 2019).

Beyond our understanding that asynchrony can emerge from variation in pure ‘functional response trait’ values and *sensitivity* to environmental drivers, we show that traits relating to aspects of species and their spatial and temporal niche partitioning (i.e. their *exposure* to particular environmental conditions) may be important for mediating between-year asynchrony (Dawson et al., 2021). This may be important in the context of future environmental change, given these ‘traits’, such as flight period, are usually more plastic; for example, shifting phenology with climate change may result in species advancing their emergence times to earlier in the year and decreasing variation in their flight periods, with potential negative effects on between-year asynchrony between species, and stability of these communities (Stewart et al., 2020).

A greater understanding of the relationship between both perturbations and long-term environmental change, intra-annual abundance dynamics and inter-annual asynchrony in these species may help us further understand how resilient communities are under anthropogenic drivers such as climate and land use change (Bellard et al., 2012; He et al., 2019; Oliver, Isaac, et al., 2015).

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Supporting Information

Appendix S1

Table S1. Mantel r values calculated for all partial mantel tests conducted between abundance asynchrony and trait dissimilarity matrices

Taxa	Matrix_2	Mantel R	Lower CI (95%)	Upper CI (95%)	P value
Macro-moths	All traits	0.123	0.102	0.143	< 0.001
	Adult Stage	0.201	0.168	0.234	< 0.001
	Pupal Stage	0.100	0.080	0.119	< 0.001
	Overwintering Stage	0.091	0.072	0.111	< 0.001
	Larval Stage	0.070	0.055	0.086	< 0.001
	Habitat	0.069	0.041	0.097	< 0.001
	Estimated Body Mass	0.058	0.031	0.083	< 0.001
	Forewing Minimum	0.041	0.015	0.067	0.03
	Egg Stage	0.041	0.017	0.065	0.03
	Forewing Maximum	0.035	0.009	0.061	0.05
	Hostplant Category	0.029	0.002	0.056	0.10
	Photoperiod	0.027	-0.004	0.059	0.16
	Hostplant Specificity	0.015	-0.010	0.042	0.23
	Pupal Habit	0.008	-0.011	0.027	0.31
	Hostplant Number	-0.004	-0.025	0.017	0.58
	Voltinism	-0.101	-0.126	-0.077	1.00
Butterflies	All traits	0.072	-0.008	0.166	0.13
	Adult Stage	0.162	0.087	0.242	< 0.001
	Larval Stage	0.125	0.053	0.203	< 0.001
	Egg Stage	0.115	0.022	0.206	0.04
	Pupal Stage	0.103	0.026	0.187	0.03
	Overwintering Stage	0.076	-0.011	0.178	0.08
	Forewing Maximum	0.068	-0.012	0.160	0.12
	Forewing Minimum	0.057	-0.027	0.148	0.17
	Hostplant Category	0.033	-0.054	0.140	0.34
	Habitat	-0.006	-0.079	0.071	0.51
	Pupal Habit	-0.016	-0.100	0.069	0.60
	Hostplant Specificity	-0.020	-0.074	0.042	0.67
	Hostplant Number	-0.023	-0.089	0.054	0.62

	Voltinism	-0.082	-0.142	-0.011	0.91
Bumblebees	All traits	0.149	0.024	0.312	0.07
	Adult Stage	0.211	0.094	0.359	0.03
	Pupal Habit	0.105	-0.017	0.244	0.19
	Estimated Body Mass	0.089	-0.043	0.235	0.24
	Habitat	0.074	-0.050	0.226	0.25
	Forewing Maximum	0.006	-0.087	0.102	0.44
	Voltinism	-0.135	-0.193	-0.068	0.92

Table S1a. Results of Mantel tests conducted between phylogenetic distance and abundance asynchrony for each taxon, along with 95% confidence intervals.

Taxa	**Mantel R**	**P Value**	**Lower CI**	**Upper CI**
Lepidoptera	0.0304	0.01	0.0204	0.0412
Macro-moths	0.057	< 0.001	0.0477	0.0691
Butterflies	0.137	0.01	0.0876	0.189
Bumblebees	-0.0503	0.702	-0.144	0.0305

Appendix S2

The role of time series length and matrix size in the sign and strength of relationship between trait distance and abundance asynchrony

As the population time series were of different lengths depending on datasets, and our Mantel tests were carried out on matrices of varying sizes, we wanted to test the effect of both time series length and matrix size on the outcome of mantel tests, in terms of the strength of the correlation between matrices (mantel r) and the detection of significant values (p values). To do this, we resampled the lepidopteran (macro-moth and butterfly) population time series 1000 times using randomised start and end years, thus allowing us to create 1000 different matrices of pairwise population asynchrony values for all 470 lepidopteran species, using time series of varying lengths (between 5 and 42 years). We then carried out mantel tests between each of these population matrices and the trait and phylogenetic matrices. We also resampled lepidopteran time series another 1000 times, using the full time series length (42 years) but included different numbers of species using randomized species selection in the final matrices (between 5 and 470 species). Mantel tests were then carried out between each of these matrices and the trait / phylogenetic matrices (which were trimmed down to the relevant species included from time series), as well as to test for phylogenetic signal in traits when matrices were of different size. We used generalized linear models with a binomial error to test the effects of time series length and matrix size on the outcome of mantel tests (mantel r value and p values). Resampling the macro-moth and butterfly time series data revealed there to be a significant positive effect of time series length on the mantel r values produced when testing for multi-trait and phylogenetic signal in population dynamics, as well as on the detection of significance. We found no effect of matrix size in general on the mantel r value, but significant effects on the p values produced in mantel tests, for all three comparisons between population asynchrony, functional trait dissimilarity and phylogenetic distance.

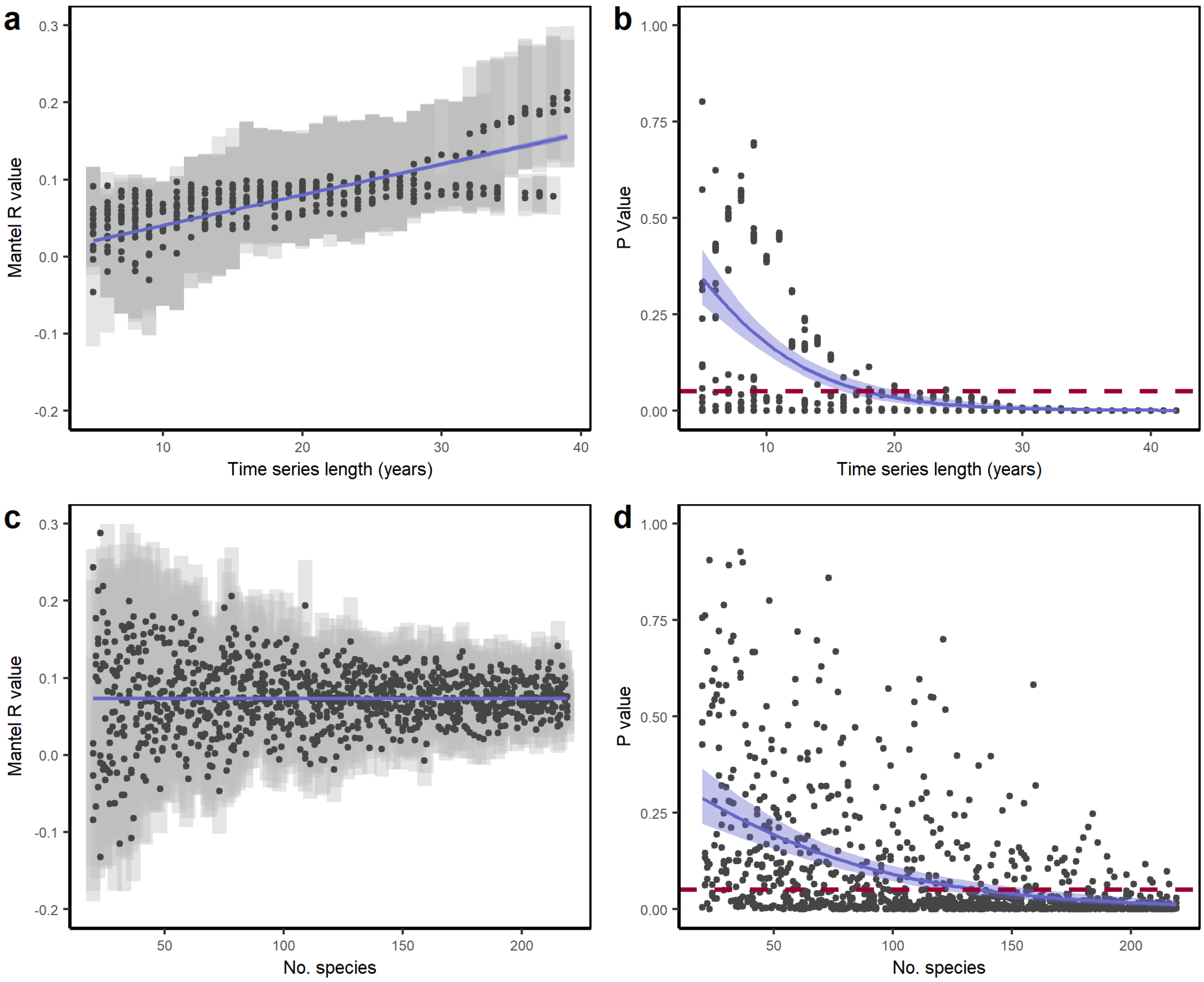


Figure S1. The outcome of mantel tests comparing population asynchrony with functional trait dissimilarity in Lepidoptera when resampled 1000 times. Panels a) and b) show the mantel r values and p values for tests conducted in communities resampled with increasing length of time series data respectively. Panels c) and d) show the mantel r values and p values for tests conducted in communities resampled with an increasing number of species included in the analysis.

Appendix S3

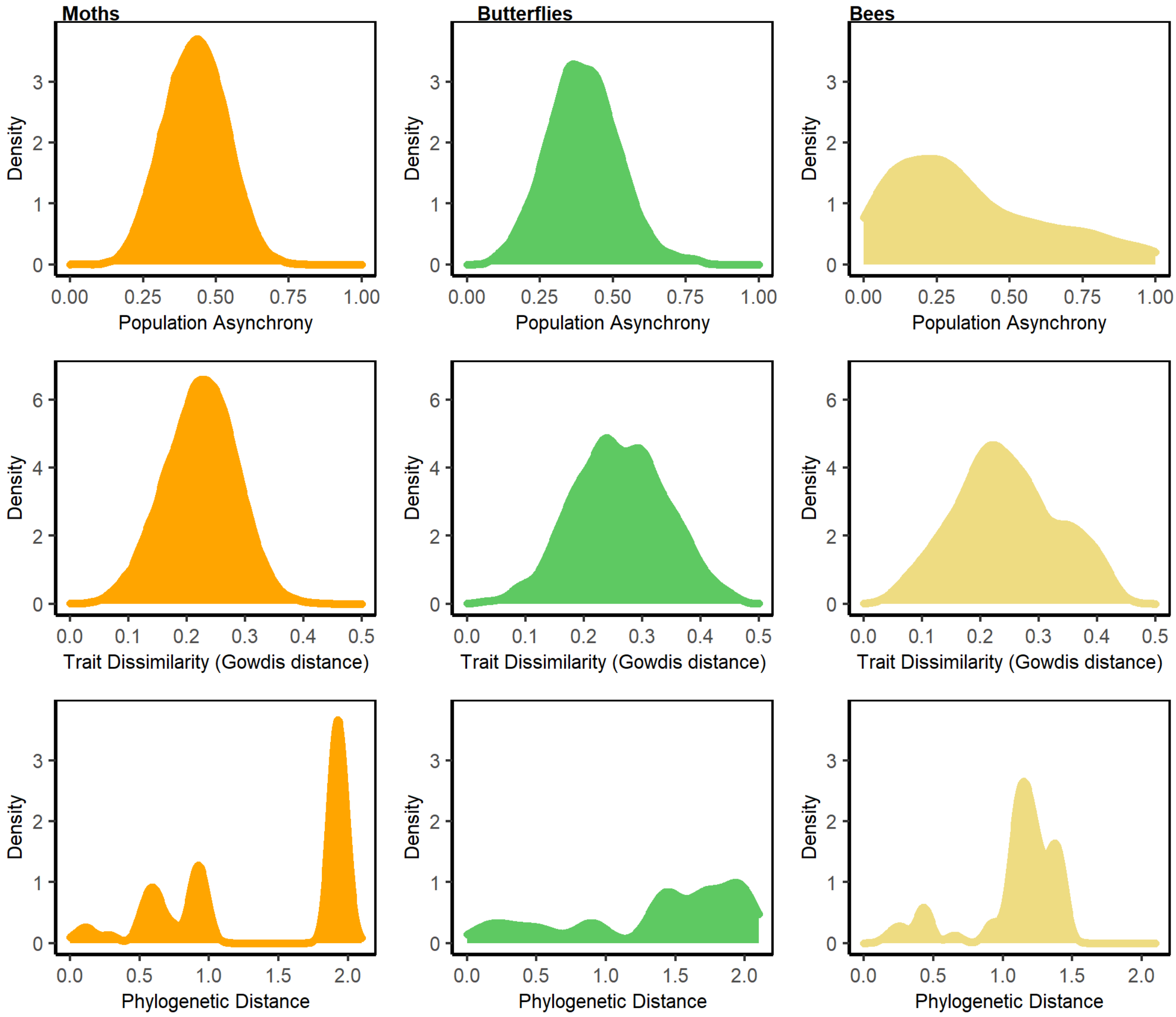
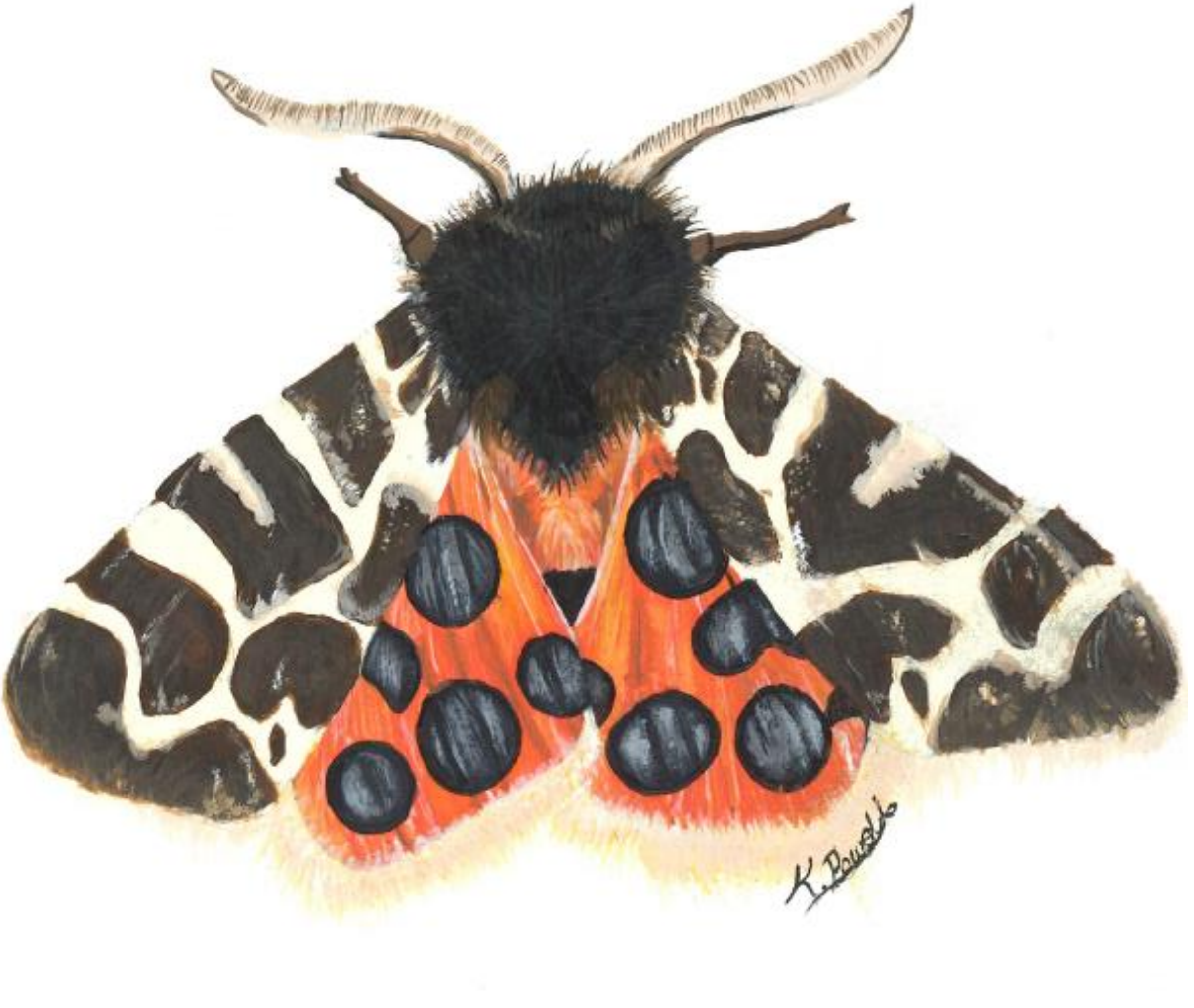


Figure S3. Distribution of pairwise interspecific dissimilarity values produced for matrices for interannual population changes (top), functional traits (middle), and phylogeny (bottom) across macro-moths (left), butterflies (middle) and bumblebees (right).

Chapter 6



Chapter 6

Predicting trends in ecosystem function provided by lepidopteran and freshwater insect communities

Abstract

There is growing concern that declines in biodiversity will result in loss of associated ecosystem functions and services. The diversity of functional traits in communities has been shown to capture the provision of ecosystem functions, although this concept has rarely been used to predict the temporal change in function provided by communities. Here, we use a functional trait-based approach using n-dimensional hypervolumes to predict temporal trends in functional indices of butterfly, moth, and freshwater insect communities, and compare these with other measures of biodiversity change – abundance and taxonomic diversity. We find that, at the national scale, despite some significant declines in abundance and/or taxonomic diversity, the abundance-weighted functional indices show little change over the time series, and so may show a level of resilience to environmental pressures. However, trends in abundance, taxonomic and functional indicators were found when habitats were analysed separately (agricultural, semi-natural, urban, and woodland). Moths showed the steepest declines in taxonomic and functional diversity indices, especially in semi-natural habitat systems, whilst freshwater community diversity indices declined in urban habitat. The trends that we present here shed light on predicted functional changes of lepidopteran and freshwater communities in the UK, highlighting increasing vulnerability of communities and ecosystem functions. Our approach to understanding functional changes in communities could be expanded across regions where there are comparable standardised monitoring schemes.

Keywords: Lepidoptera, Ephemeroptera, Plecoptera, Trichoptera, biodiversity change, abundance change, ecosystem function, functional change.

Introduction

The global biodiversity crisis, sometimes described as the 6th mass extinction, has been characterised as the accelerating loss of species and the consequential erosion of ecosystems and their important functions and services (Barnosky et al., 2011; Ceballos et al., 2015b; Valiente-Banuet et al., 2015). In recent years, despite a relative lack of research due to their sheer number and diversity (Cardoso et al., 2011), have come under the spotlight due to increased evidence of declines in abundance, biomass and richness at sites across multiple continents (Didham, Barbero, et al., 2020; Hallmann et al., 2017; Lister & Garcia, 2018; van Klink et al., 2020; Wagner, 2020). Much of this decline – and general transformation of insect community biodiversity - has been found to be caused by land use change and the associated habitat loss, largely through replacement of semi-natural habitat and more extensive land uses with agriculture (Outhwaite et al., 2022; Powell et al., 2023; Raven & Wagner, 2021). For example, in the UK, a recent study found that invertebrate species were disappearing considerably more rapidly from agricultural land, especially in intensive cropland production systems (Mancini et al., 2023).

Insects underpin the functioning of almost every terrestrial ecosystem on earth, through constituting the diets of multiple trophic levels (vertebrates and other invertebrates), engineering complex habitats and microhabitats, pollinating crops and wild plants, recycling nutrients and more (Cardoso et al., 2011; Schowalter et al., 2018). Insect declines are predicted to have significant, negative consequences for ecosystems, given their enormous contribution to ecosystem functioning (Cardoso & Leather, 2019; Goulson, 2019). For example, local extinction of rarer insect species is thought to reduce the resilience of communities to environmental perturbations due to the destabilising effect of lost redundancy (Oliver, Heard, et al., 2015), whilst abundance declines of more common species – even if extinction does not occur – could severely impact on the delivery of specific ecosystem functions performed by dominant species (Winfree et al., 2015).

Knowledge of insect biodiversity change and the role of insects in ecosystem function is increasing, and yet we still have little understanding of the wider impact of insect declines on ecosystems in the long-term beyond assumption and hypothesis (Noriega et al., 2018a). This is largely because the ‘function’ of ecosystems is itself a difficult concept, and to measure specific functional changes over time and space requires considerable resources to collect data in the field or through experimentation. Further, the impact of the decline or absence of a species is often equated to the opposite effect of the presence or increase of a species, when in reality, under biodiversity decline, further processes that influence ecosystem resilience may come into play (Oliver, Heard, et al., 2015).

As a result, proxies for the influence of species and individuals on ecosystem function are much more commonly used to understand functional change under species gain / loss, such as species' 'functional traits' (Noriega et al., 2018a). Functional traits are aspects of an individual that are connected to how an organism impacts the environment ('effects traits') or how they are affected by the environment ('response traits'; Díaz et al., 2013). However, these two aspects often coincide, and what constitutes a functional trait is increasingly being widened to include previously excluded aspects of organisms (Dawson et al., 2021; Sobral, 2021; Streit & Bellwood, 2022). Although the study of functional traits is most advanced in the plant sciences (e.g., Grime, 1998; Kraft et al., 2015), with a burgeoning interest in insect biodiversity and insect declines there is a growing number of trait-based approaches being taken – accompanied by the publishing of novel species trait data – to understand the processes shaping invertebrate communities over time and space (Wong et al., 2019). For example, insect functional diversity – in terms of both richness of traits and the relative distribution of those traits in trait space – has been found to be important for both the provision and resilience of ecosystem functioning (Auber et al., 2022; Deraison et al., 2015; Greenop et al., 2018; Woodcock et al., 2019), stabilising communities and their functional roles through mediating complementary abundance dynamics (Bird et al., 2021; Lasky et al., 2016; Schnabel et al., 2021; and see Chapter 5).

Despite advances in our understanding of the relationship between functional diversity and the provision and stability of ecosystem function, and demonstration of this relationship amongst insects and other invertebrates, knowledge gaps remain for trends in insect-mediated ecosystem function through time. Most studies that predict change in biodiversity indices – including ecosystem functioning or functional diversity of communities – under environmental

Table 1. Datasets used to create abundance, taxonomic and functional diversity indices.

Dataset Origins	Taxa	Indices	Time scale	Spatial Scale	Data and sample type	Data filtering process	Reference
UK Butterfly Monitoring Scheme (UKBMS)	Butterflies	All	1977 - 2019	Great Britain	Site-level abundance indices; transect walks	Data only from 1977 onwards (previous years had too few sites sampled). Density per 2km of transect calculated.	(Botham et al., 2020)
Rothamsted Insect Survey Light Trap (RIS)	Moths	All	1978 – 2016	Great Britain	Site-level abundance indices; light traps	Data only from 1978 onwards (uncertainty around abundance of numerous moth species in previous year)	(Woiwod & Harrington, 1994)
Environment Agency Biosys (EA)	EPT	All	2009 - 2019	England	Raw abundance data; kick samples	Species-level counts, Ephemeroptera, Trichoptera and Plecoptera only, sites sampled at least in spring and autumn over at least 3 years between 2009 and 2019 (species not recorded consistently prior to 2009)	(EA, 2020)
European Freshwater Macroinverte	EPT	Functional richness, Functional dispersion	-	-	Fuzzy trait data	Only species represented in the Biosys sites	(Tachet et al., 2010)

brate Traits Dataset						(Ephemeroptera, Trichoptera and Plecoptera only)	
Traits data for the butterflies and macro-moths of Great Britain and Ireland	Butterflies, Moths	Functional richness, Functional dispersion	-	-	Binomial trait data	Only species represented in the UKBMS and RIS data	(Cook et al., 2021)
Land Cover Map 2000	Butterflies, Moths	All (habitat-level only)	2000	Great Britain	Raster spatial data	500m buffers around all sites included in UKBMS and RIS monitoring data	(Fuller et al., 2002)
Land Cover Map 2015	EPT	All (habitat-level only)	2015	Great Britain	Raster spatial data	Catchment areas upstream of EA Biosys sites	(Rowland et al., 2017)

change do so over space and assume a space-for-time substitution. However, the complexity of mechanisms driving diversity change mean such assumptions may not be suitable for understanding biodiversity in temporal dimensions (Blüthgen et al., 2022; Isaac, Girardello, et al., 2011). In one study, Greenop et al. (2021) quantifies temporal change in insect-mediated function using functional diversity indices, although this study was based on opportunistically-collected occupancy data of insects, and was unable therefore to capture the presumably important impact of species' abundance change on function (Winfree et al., 2015). Utilising long-term species-level abundance data from standardised monitoring schemes would therefore improve our understanding of temporal functional diversity change.

Here, we aim to understand long-term change in abundance-weighted functional diversity, as a proxy of ecosystem functioning mediated by insect communities, over time. We bring together standardised monitoring scheme abundance data for butterfly, moth, and freshwater insects across the UK with recently published trait data for these insect species and use a trait-space dimensionality approach to calculate change in the functional diversity, comparing this with abundance and taxonomic diversity. We use these groups of insects as they are both well-surveyed over time and space using standardised sampling methods in the UK and represent both terrestrial and aquatic environments. Butterflies, moths and freshwater insects provide and support a wide range of important functions in ecosystems, including as food sources for higher trophic levels, pollinators (moths and butterflies), and as regulators of water purification processes through nutrient cycling (Anderson et al., 2023; Holland et al., 2012; Macadam & Stockan, 2015). We aim to understand: 1) How has the functional diversity of lepidopteran and freshwater insect communities – as a proxy of ecosystem functions delivered by these communities – changed over time? 2) How does this compare to other indices for biodiversity, including abundance and taxonomic diversity? And, to help understand the effects of different land use types including agricultural and semi-natural habitat on temporal biodiversity trends, 3) How do the temporal changes in biodiversity indices vary across different habitat types?

Methods

To compare national trends in moth, butterfly, and freshwater communities over time, we used several types of biodiversity indices: abundance, taxonomic diversity, and two different indices that represent functional diversity – ‘functional richness’ and ‘functional dispersion’. We brought together established long-term monitoring schemes and recently published trait datasets for these taxa to calculate yearly abundance, taxonomic and functional diversity indices and describe their temporal trends (Table 1). We studied trends over the entire UK and compared trends across different high-level habitat categories, by classifying land cover around sites as agricultural areas, urban environments, open semi-natural habitats, or broad-leaved woodland. We used both linear and non-linear models to explore trends; we used linear models to statistically compare the directional change over time amongst different indices, taxa and habitats, whilst non-linear models enabled us to examine important non-linear changes in individual trends, and to compare shorter-term temporal fluctuations between groups to identify patterns of change.

Biodiversity Index Calculation

Abundance

We calculated an annual abundance index at greatest spatial scale for each dataset – the entire UK for each species of Lepidoptera, and England for freshwater taxa - for each year of the time series using abundance monitoring schemes (Table 1; Butterflies: No. Species = 58, No. years = 45 [1976-2020]; Moths: No. Species = 425, No. years = 40 [1977-2016]; and freshwater taxa, Ephemeroptera/Plecoptera/Trichoptera [hereon referred to as 'EPT']: No. Species = 188, No. years = 11 [2009-2019]). We took two main steps to create the indices; 1) the calculation of site-level indices from monitoring scheme abundance data; and 2) the collation of site-level indices to create national abundance indices, which represented the average total abundance for each species found at sampling sites.

For butterflies and moths, site-level and national indices were created according to the Generalised Abundance Index approach laid out in Dennis et al. (2016), using the 'rbms' package in R (Schmucki et al., 2022). This approach models 'flight curves' using GAMs from the abundance data to impute missing counts within years from seasonally abundant insects (Dennis et al., 2016). Site-level indices could then be calculated from the imputations using the site_index() function in the 'rbms' package. For the butterfly abundance data, as transect lengths varied across sites, we standardised site-level abundance indices by the recorded transect lengths to produce a 'site-level density' for each butterfly species; this was not necessary for moths which were recorded at points rather than on transects.

For freshwater macroinvertebrates, a different approach was required for the preparation of site-level indices, as only 2 samples were typically taken per year at sites by the Environment Agency: 1 in Spring and 1 in Autumn. Therefore, annual mean abundances per site were calculated where possible for each species of Ephemeroptera, Plecoptera and Trichoptera (hereon referred to as EPT), where data was available (see Table 1). Site-level indices for years where sites were not sampled were then imputed using the trim() function from the 'rtrim' package (Bogaart et al., 2020). This function used a log-linear switching-trend model for abundance that included both site and time effects, allowing the slope of the time effect to switch from time-point to time-point (i.e., capturing non-linear temporal trends in abundance). Predictions of abundance were then calculated for site-year combinations where sites had been inconsistently sampled and there were missing data for that period. The model accounted for overdispersion as well as serial autocorrelation between years, by relaxing assumptions about independence between consecutive time points.

We then used the ‘collated_index()’ function from the ‘rbms’ package to create a collated abundance index from these site-level indices for all taxa, to represent the average site’s sum of the abundance counts expected over the annual sampling effort, for each species. Here, abundance is predicted from GLMs that model site and year effects – but weighted by the relative proportion of site visitations – and are averaged over sites. The collated abundance index approach resulted in the following number of abundance observations for each group of taxa: butterflies, n = 2610; moths, n = 17000; and EPT, n = 2068.

Taxonomic Diversity

Abundance-weighted taxonomic diversity – Shannon-Weiner Indices – were calculated for each taxonomic group (butterflies, moths and EPT) from the collated abundance indices detailed in the previous section (Ortiz-Burgos, 2016). This was carried out using the diversity() function in the ‘Vegan’ package in R (Dixon, 2003).

Functional Diversity

For functional diversity, we measured two aspects of n-dimensional hypervolumes representing functional-trait space, which we created using published trait data for each taxonomic group (Table 1).

Trait data preparation

For each group we selected a set of traits based on their association with population-level responses to abiotic factors through changes in abundance, biomass, range size, dispersal, or

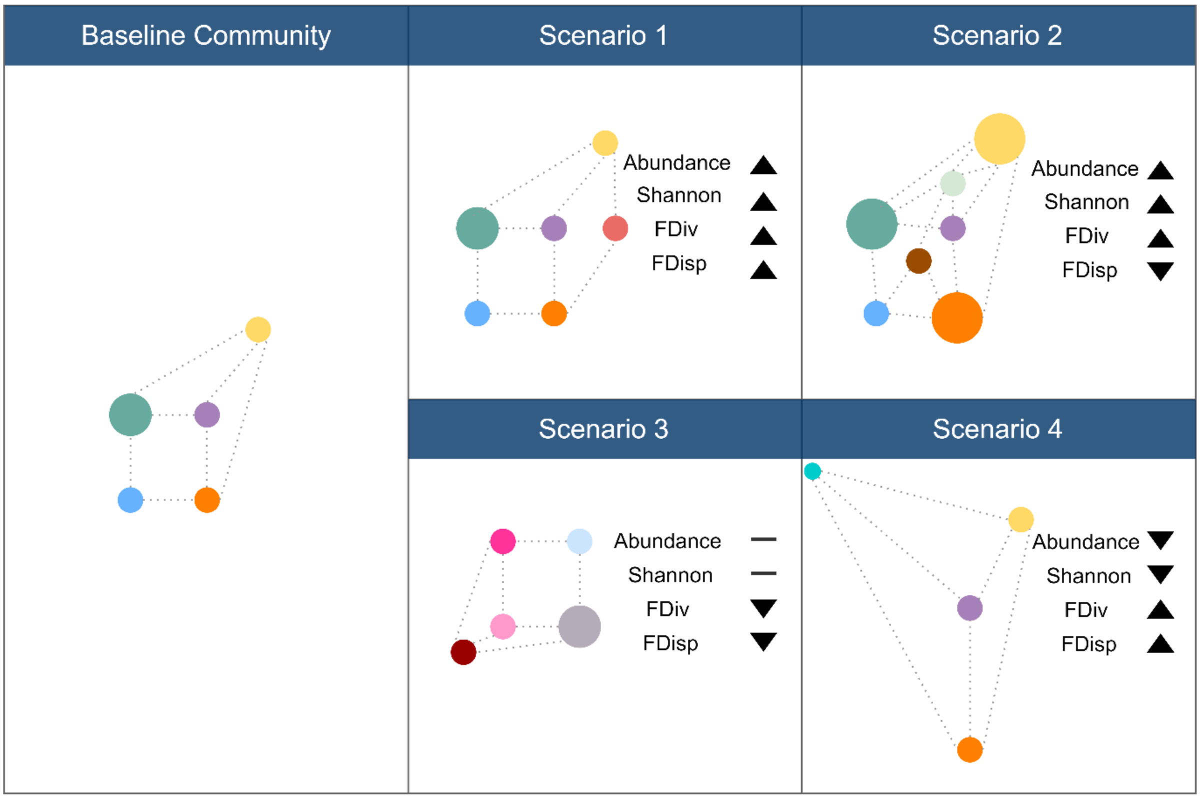


Figure 1. Conceptual representation of species (shown as circles), weighted by the abundance of individuals / population sizes, in trait-based n-dimensional hypervolumes. Here the hypervolumes are shown in 3-dimensions for visual purposes, and represent a community of insects (macro-moths, butterflies, or freshwater communities – Ephemeroptera, Trichoptera and Plecoptera / EPT). Each scenario represents some different ways in which the change in community index from the baseline community may differ between different types of indices; arrows pointing upwards indicate an increase in the index, arrows pointing downward indicate a decrease, and the straight lines indicate no change in the index. 'Shannon' = taxonomic diversity; 'FDiv' = functional richness, a measure relating to the volume of the hypervolume; and 'FDisp' = functional dispersion, the mean distance between pairs of points in the hypervolume.

extinction risk (Table 1 in Chapter 5), and so relate to species' diversity in exposure and sensitivity to environmental drivers (Chapter 5). We used the 'Gawdis' package in R to create pairwise Gower distance matrices between species within each taxonomic group, according to Chapter 5 (Bello et al., 2023). The package allows for the creation of Gower distances with continuous, categorical, binary, and fuzzy-coded trait data, and enables weighting and grouping of traits that are closely correlated due to non-independence. Therefore, we grouped more related traits (Spearman's Rank Correlation Coefficient r > |0.5|). We then used Principle

Coordinate Analyses (PCoA) through the pco() function in the ‘ade4’ package in R to create ‘synthetic traits’ (a representation of functional response trait profiles) for each species, of a reduced number of dimensions compared to the original trait datasets (Dray et al., 2023; Greenop et al., 2021). For each taxonomic group, we chose the number of dimensions for synthetic traits that accounted for ≥ 80% variation amongst species; for butterflies: 5, moths: 5, EPT: 9. These synthetic traits were then used in functional hypervolume construction.

Functional hypervolume construction

We used the ‘hypervolume’ package in R to construct n-dimensional hypervolumes for each year representing the synthetic trait space of the species present that year and whose abundance was used to estimate the collated abundance index (Blonder et al., 2014, 2023). We multiplied the number of rows in the synthetic trait datasets by species’ total abundance estimates (the abundance indices earlier described), so that hypervolume construction was based on the abundance of individuals within the average community for each year rather than species’ presence alone (Figure 1). Hypervolume construction requires the estimation of a ‘kernel density bandwidth’ (*b*), which we calculated for each initial year of the time series for each taxonomic group using the Silverman method (Blonder et al., 2023). We used this bandwidth value for all following hypervolume constructions within each time series, along with the set.seed() function preceding the hypervolume() function in order to standardise the random numbers used for probability density estimation and to create reproduceable results. See Greenop et al. (2021) for further details on how hypervolumes were constructed.

Functional richness and dispersion were then estimated from each hypervolume using the ‘BAT’ package in R (Cardoso et al., 2022). Functional richness is a measure of the volume of the hypervolume itself, and dispersion describes the average distance between pairs of points within the hypervolume. For simplified visual representations of functional indices measured from hypervolumes, see Figure 1.

Habitat-level indices

We then produced habitat-specific indices by grouping sites from each taxonomic groups' monitoring scheme into agricultural, urban, semi-natural habitat and broad-leaved woodland sites. For butterflies and moths, we used the UKCEH Land Cover Map 2000 (Fuller et al., 2002) to calculate the proportion of $25m^2$ pixels of each type of habitat within 500m circular buffers around UKBMS and RIS sites, and allocated sites to the dominant habitat type (i.e., the habitat occupying > 50% of the buffer zone; we only retained sites where the dominant habitat was >50% of the land cover within buffers, resulting in a final dataset of 190 sites for butterfly trends, 229 for moths, and 2143 for EPT). We also explored 3km, 2km and 1km buffers around sites; however, all these buffer types resulted in an inadequate number of woodland sites for rigorous statistical analysis, due to the relatively low amount of continuous woodland area in the UK. However, 500m buffers were previously found to be the scale which best links landscape composition to population dynamics, at least for butterflies (Oliver et al., 2010), and is in line with the methods of Blumgart et al. (2022) which explored moth population change in woodland sites in the UK using the RIS and LCM2000 data.

For the EA Biosys dataset, which was used to assess the EPT group, we used the Land Cover Map 2015 (Rowland et al., 2017) and calculated the proportion of habitat in catchments upstream of sites, and then allocated habitat labels to sites where each habitat comprised > 50% of the catchment area and so was the dominant habitat type. We took this approach due to the complexity of drivers in freshwater systems in comparison to terrestrial systems, with freshwater systems generally being affected by the pressures exerted upstream of sites due to the linear nature of river flow. As the period differed between different abundance datasets (Table 1), we chose the land cover map version that was closest to the middle date of each time series. As we did not statistically compare results between taxa, and our analyses examines the relative change in index under different habitat types from year to year, this should not affect our inferences.

We then used the methodology outlined for all collated indices above to calculate habitat-specific abundance, taxonomic and functional diversity indices for butterflies, moths, and EPT through segregating sites into one of the four habitat types and re-calculating each index using these site selections.

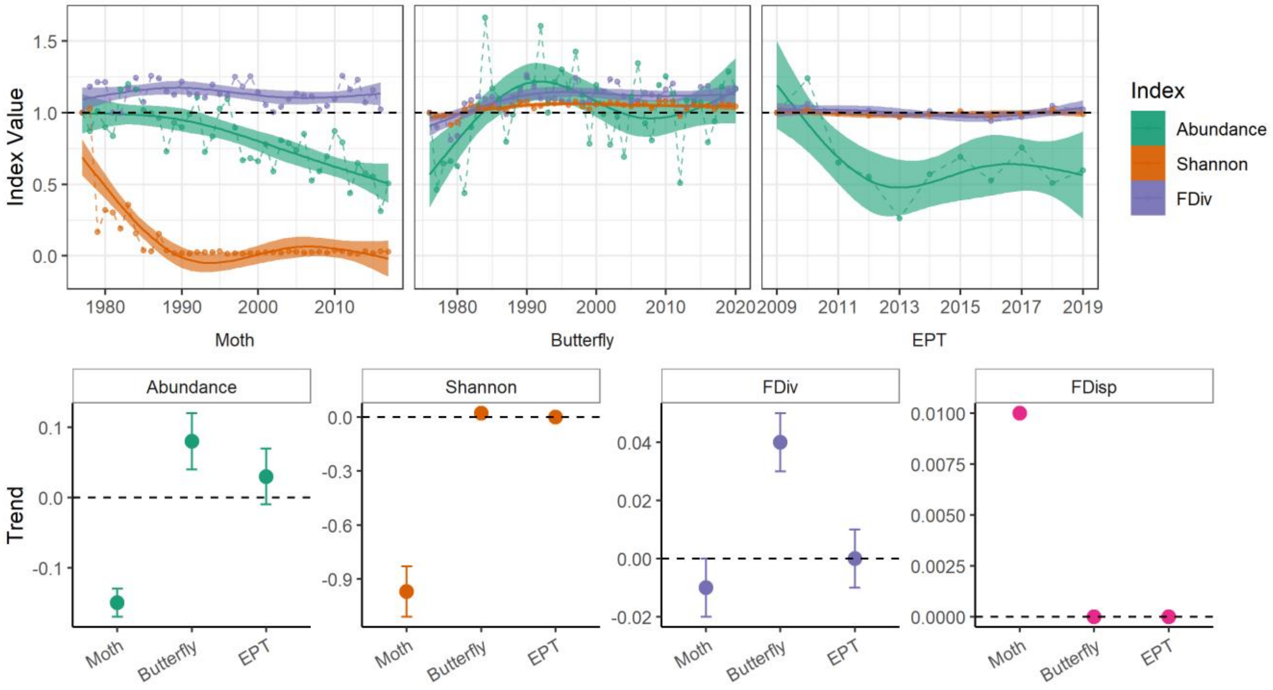


Figure 2. Temporal trends in the abundance, taxonomic diversity (“Shannon”), and functional richness (“FDiv”) for each insect group (macro-moths, butterflies and freshwater EPT). The top row shows the annual collated indices for national-scale data, relative to the first index value of the time series, calculated for each index type as points connected by the dashed lines. The abundance is represented by the relative geometric mean of all species’ collated abundance indices. Functional Dispersion (“FDisp”) is excluded here due to the difficulty of discerning FDisp from other trends when included together on the same plot, as change in FDisp from year-to-year is close to 0 (see Supporting Information, Figure S1, for these non-linear trends in FDisp). The non-linear smoothed trend is shown with a solid line (gam; y ~ s(x, bs = "cs") calculated using k = 4) and 95% credible intervals shown as shaded envelopes. The bottom row shows the linear trend (slope estimates and standard errors) for the same set of collated indices plus FDisp.

Modelling trends

Both linear and non-linear temporal trends across all indices and taxa were examined. To explore non-linearity in national trends, we fit Generalised Additive Models (GAMs) for each taxonomic group – index combination, using the 'mgcv' package in R (Wood, 2022). These models were constructed using cubic regression splines and the following formula:

$$Index \sim s\,(year,\ bs = \text{'cs'}) \qquad [1]$$

Where s = smooth term and 'cs' denotes the cubic spline. The basis dimension term (k) was set to k = 4. We used the same GAM formula ***[1]*** across all indices. All linear models were fit using the glmmTMB() function in the 'glmmTMB' package in R (Brooks et al., 2017). For all maximal linear models in formulae ***[2] – [5]***, the AICs of a set of nested models were compared in a model-selection process. To test the relevance of fixed effects, null models (no fixed effects), temporal models (with year effects) and, for habitat-level indices, models with year *and* habitat effects (both additive and interactive) were constructed and the AICs compared. Where relevant (i.e., for abundance indices), random effects were tested using another set of models that varied in random-effects structure and through further AIC comparison. Here, GLMs (no random effects), and GLMMs with temporal random effects and then both temporal and species-level random effects were constructed and compared. Error distributions for all models were tested in the same way, through constructing alternative models with different error distributions and comparing AICs, as well as visual examination of data density distribution.

The linear trends of national abundance indices were modelled using Generalised Linear Mixed-effect Models (GLMMs) in the following format:

$$Index \sim year + (1 \mid year) + (1 \mid species) \qquad [2]$$

where the index itself was used as the response variable with a Gamma error distribution and loge link function for moths and EPT, and where the log(index+1) was used with a Gaussian error distribution for butterflies, according to the best fit using model selection processes and model checking (see supporting information, Tables S1-4). Habitat-level abundance indices were modelled as:

$$\mathit{Index} \sim \mathit{year} * \mathit{habitat} + (1 \mid \mathit{year}) + (1 \mid \mathit{species}) \qquad [3]$$

Using the same error distributions for each taxonomic group as outlined above.

Taxonomic and functional diversity collated indices were modelled using the following formula:

$$\mathit{Index} \sim \mathit{year} \qquad [4]$$

Where the log(index+1) was used as a response with a Gaussian error distribution for butterflies and EPT, and a Gamma error distribution for moths due to the outcome of model selection and model checking processes (see supporting information, Tables S1-4). The habitat-level indices for taxonomic and functional diversity were modelled in the following way:

$$\mathit{Index} \sim \mathit{year} * \mathit{habitat} \qquad [5]$$

Using the same error distributions for each taxonomic group as outlined above for taxonomic and functional indices.

Model performance checks for linear models (linearity, normality of residuals, homogeneity of variance, variance inflation factors, and overdispersion) were carried out using the ‘performance’ package in R (Lüdecke, 2021). Model predictions for purposes of visualizing and comparing effect sizes were calculated for collated indices using the ggpredict() function from the ‘ggeffects’ package in R (Lüdecke, 2018), and the trends and credible intervals for habitat level indices using the emtrends() function from the ‘emmeans’ package (Lenth et al., 2023).

Results

Abundance, taxonomic and functional indices show different trends over time with variation across taxonomic groups and habitats.

Table 2. Fixed effect coefficients for each linear model performed on the collated (national) annual biodiversity indices for each taxon. ‘Shannon’ = taxonomic diversity; ‘FDiv’ = functional richness, a measure relating to the volume of the hypervolume; and ‘F Disp’ = functional dispersion, the mean distance between pairs of points in the hypervolume. Only abundance models were carried out using mixed-effects models, whilst GLMs were used for other indices. The random effect coefficients (θ, or variance) for each of the abundance models are as follows; Moths: Year = 0.0205 (n = 42), Species = 1.37 (n = 425); Butterflies: Year = 0.0455 (n = 45), Species = 2.26 (n = 58); EPT taxa: Year = 0.00 (n = 11), Species = 14.96 (n = 188). Bold text and * indicate a trend significant at the $p < 0.05$ level.

Taxon	Index	Intercept		Year			
		Estimate	SE	Estimate	SE	Statistic	P value
Moth	Abundance	0.89	0.06	-0.15*	0.02	-6.55	< 0.001
	Shannon	-1.15	0.14	-0.97*	0.14	-7.03	< 0.001
	FDiv	0.12	0.01	-0.01	0.01	-0.76	0.45
	FDisp	1.01	0.00	0.01*	0.00	10.52	< 0.001
Butterfly	Abundance	3.04	0.20	0.08	0.04	1.82	0.07
	Shannon	1.21	0.00	0.02*	0.00	3.24	< 0.001
	FDiv	0.09	0.01	0.04*	0.01	3.50	< 0.001
	FDisp	0.98	0.00	0.00	0.00	1.07	0.29
EPT	Abundance	-0.13	0.29	0.03	0.04	0.77	0.44
	Shannon	1.43	0.01	0.00	0.01	-0.07	0.95
	FDiv	0.00	0.01	0.00	0.01	-0.44	0.67
	FDisp	0.00	0.00	0.00	0.00	0.00	1.00

Collated Indices

When modelled linearly, macro-moth abundance and taxonomic diversity declined significantly from the baseline year, whilst functional richness remained fairly stable and functional dispersion showed a minor but statistically significant increase (Table 2). On the other hand, against our assumptions, butterflies showed a slight increase in both taxonomic diversity and functional richness indices and remained stable for other biodiversity indices (Table 2). EPT

Table 3. Summary of all indicators and significance of predictors from the models that included habitat. A tick or arrow indicates whether a predictor was found to be significant at the level of $p \leq 0.05$. ‘Shannon’ = taxonomic diversity; ‘FDiv’ = functional richness, a measure relating to the volume of the hypervolume; and ‘FDisp’ = functional dispersion, the mean distance between pairs of points in the hypervolume. Arrows in the ‘time’ column represent the direction of change in the indicator over time, with upward pointing arrows suggesting an increase and downward pointing arrows a decrease.

Index	**Moths**			**Butterflies**			**EPT**		
	Time	**Habitat**	**Time: Habitat**	**Time**	**Habitat**	**Time: Habitat**	**Time**	**Habitat**	**Time: Habitat**
Abundance	↘	✓	✓		✓	✓		✓	
Shannon		✓		↗	✓	✓		✓	✓
FDiv		✓	✓	↗	✓				✓
FDisp	↗	✓	✓		✓	✓			

showed no significant change over time in any index since their baseline year (Table 2). Both linear and non-linear trends for all collated indices are shown in Figure 2, and we summarise model outputs (coefficients) from linear models [2-5] in Table 2, which corresponds with Figure 2b. Visualisation of non-linear trends tend to show that, even when the linear trend may not be significant, there is some temporal fluctuation in some of the indices between years (such as a steep decline in abundance at the start of the EPT time series, or a rapid change in abundance at the start of the butterfly time series, followed by a levelling-off period).

Habitat-level indices

Temporal trends differed significantly between habitat types for several taxa and indices used. Results outlined in Table 4, show that there were significant declines in the abundance of moths in both agricultural and urban sites, whilst at semi-natural sites, all taxonomic and functional diversity indices declined over time. For butterflies, functional dispersion declined significantly at woodland sites, but other habitats appeared to support either stable or increasing values for other indices. Finally, for EPT, whilst abundance remained stable across all habitats, urban areas showed significant declines in both taxonomic diversity and functional richness indices. Linear trends for indices at the habitat level can be found in Figure 3 and Table 4. Non-linear trends for all taxonomic groups at the habitat level can be found in the supporting information (Figure S2-4).

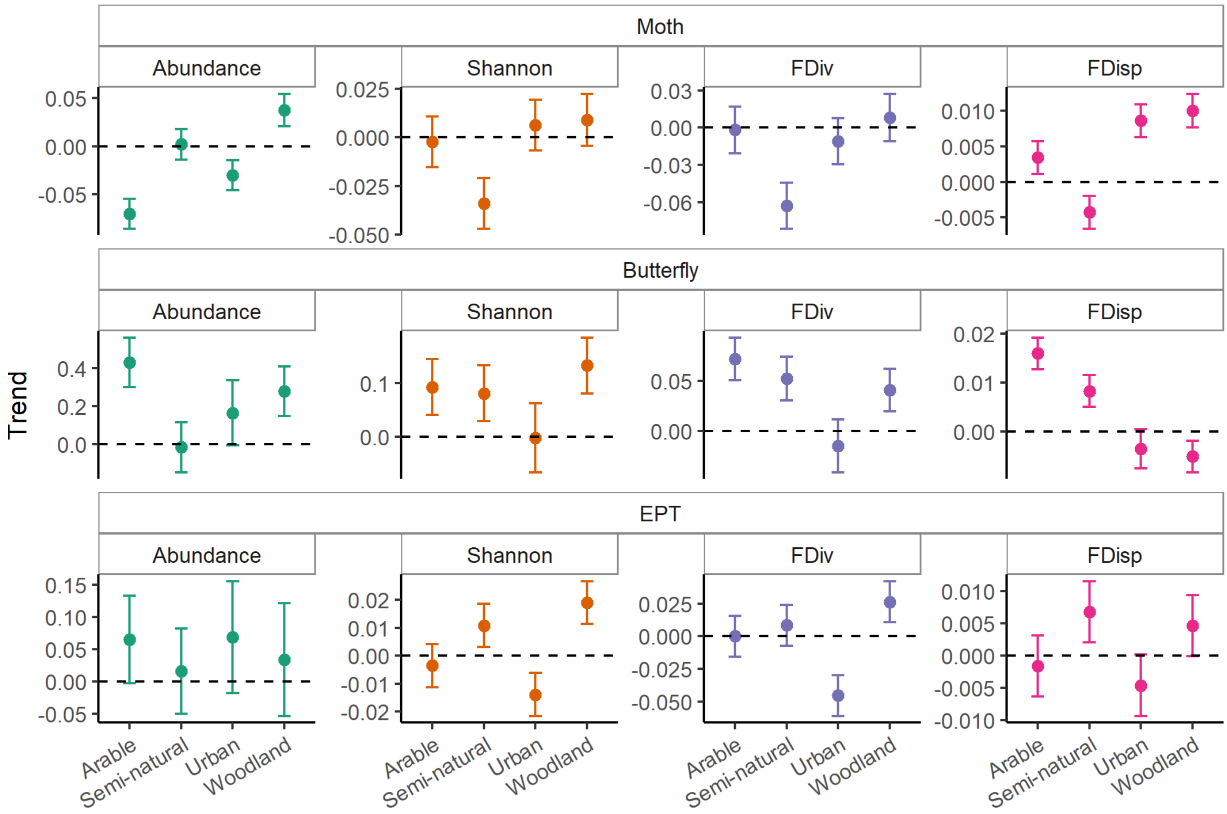


Figure 3. Temporal trends from linear models of abundance, taxonomic diversity (“Shannon”), functional richness (“FDiv”) and functional dispersion (“FDisp”) indices for each taxonomic group (macro-moths, butterflies and freshwater EPT taxa), for each major habitat type – arable, semi-natural habitat, urban and woodland. The slope (year: habitat estimates) from models are shown +/- standard errors. The scaling of the y axis varies to allow for examination of trends which differ between taxonomic groups and index type.

Table 4. Trend slopes (year on index) and their standard errors (SE) obtained from linear models of biodiversity indices for each taxon in different habitat types. Bold text and * indicate a trend significant at the $p < 0.05$ level. ‘Shannon’ = taxonomic diversity; ‘FDiv’ = functional richness, a measure relating to the volume of the hypervolume; and ‘F Disp’ = functional dispersion, the mean distance between pairs of points in the hypervolume

Taxon	**Index**	**Arable**			**Semi-natural habitat**			**Urban**			**Woodland**		
		Trend	**SE**	**P value**	**Trend**	**SE**	**P value**	**Trend**	**SE**	**P value**	**Trend**	**SE**	**P value**
Butterfly	Abundance	0.43*	0.13	< 0.001	-0.02	0.13	0.91	0.16	0.17	0.33	0.28*	0.13	0.03
	Shannon	0.09	0.05	0.08	0.08	0.05	0.12	0.00	0.06	0.97	0.13*	0.05	0.01
	FDiv	0.07*	0.02	< 0.001	0.05*	0.02	0.02	-0.01	0.03	0.58	0.04	0.02	0.06
	FDisp	0.02*	0.00	< 0.001	0.01*	0.00	0.01	0.00	0.00	0.38	-0.01	0.00	0.12
EPT	Abundance	0.07	0.07	0.34	0.02	0.07	0.81	0.07	0.09	0.43	0.03	0.09	0.70
	Shannon	0.00	0.01	0.65	0.01	0.01	0.16	-0.01	0.01	0.08	0.02*	0.01	0.02
	FDiv	0.00	0.02	1.00	0.01	0.02	0.59	-0.05*	0.02	< 0.001	0.03	0.02	0.09
	FDisp	0.00	0.00	0.73	0.01	0.00	0.16	0.00	0.00	0.33	0.00	0.00	0.33
Moth	Abundance	-0.07*	0.02	< 0.001	0.00	0.02	0.90	-0.03*	0.02	0.05	0.04*	0.02	0.03
	Shannon	0.00	0.01	0.86	-0.03*	0.01	0.01	0.01	0.01	0.63	0.01	0.01	0.50
	FDiv	0.00	0.02	0.92	-0.06*	0.02	< 0.001	-0.01	0.02	0.55	0.01	0.02	0.67
	FDisp	0.00	0.00	0.14	0.00	0.00	0.06	0.01*	0.00	< 0.001	0.01*	0.00	< 0.001

Discussion

Here, we show that temporal trends in biodiversity indices vary widely between different insect groups in the UK, and that the picture of change may depend on the type of index used. We find that, on a national scale, although there are some temporal fluctuations in functional richness and dispersion indices in our non-linear models, there were no declines in these functional diversity indices over the long-term. Unexpectedly, we found an increase in the functional richness of butterfly communities at the national scale, and a slight increase in the functional dispersion index for macro-moths (Figure 2).

These findings, especially for macro-moths, may appear to contrast with other national-scale indices that we analysed, but may support them. A greater value for the functional dispersion index means the average functional distance between species has increased. Therefore, this signifies that we are losing species weight in the middle of the functional trait space, expanding the space between those that remain. That is consistent with a loss of diversity, but a loss that does not necessarily reduce the overall trait volume (considering functional richness is not changing in the same manner). In our case, this could represent loss of non-functionally unique species and a loss of redundance, due to having fewer species with similar traits, which then increases their distance in trait space. We found a significant decline in taxonomic diversity and abundance indices in moth communities, evident from the results of both non-linear and linear models (Figure 2), which would support this hypothesis. It is possible that the functional diversity of insect communities in our case is relatively robust to declines in abundance and richness (for example, as is shown in Fig1, Scenario 4). In this case, moth communities may be experiencing loss in the abundance of some species, however, there may be gains in others that are more functionally distinct, resulting in a temporal compensatory effect in functional diversity at the national level. Indeed, both gains and losses of lepidopteran species have been recorded widely in the UK (Boyes et al., 2019; Lamarre et al., 2022).

Through examining trends at the habitat-scale, we detected declines in functional indices that were masked at the national-level, and which could point toward vulnerability of the resilience and provision of functions by certain taxa. For macro-moths, taxonomic diversity, and functional diversity (both functional richness and dispersion) declined over time in semi-natural habitats. This went against our assumptions for how insect taxa would fair across different habitats; given the greater disturbance and anthropogenic pressures associated with agricultural and urban areas, we assumed that insect taxa in these areas would be facing steeper declines than in semi-natural and broad-leaved woodland habitats (Flick et al., 2012; Fox, 2013; Hayhow et al., 2019). However, recent studies have found declines in Lepidoptera in woodland despite increased woodland area in recent years in the UK (Blumgart et al., 2022), and, similarly, flying insect biomass was found to severely decrease in protected areas in Germany (Hallmann et al., 2017). We suggest it is possible that, due to the disturbance regimes inflicted on these communities throughout the development of agricultural practices and intensification of arable habitat in decades passed, the filtering out of more vulnerable species within these communities has taken place prior to the baseline chosen for this study, leaving behind resistant communities that are better adapted to the pressures of agricultural practices (Redhead et al., 2018). Meanwhile, communities in semi-natural habitat may support species which are more susceptible to the continued pressures of neighbouring agricultural habitat, especially given such habitat is never far away in the UK where 72% of land is farmed (Hayhow et al., 2019).

For freshwater taxa (Ephemeroptera, Plecoptera and Trichoptera) biodiversity indices were most negatively affected in urban areas (Figure 3), especially for taxonomic and functional richness. Whilst abundance and diversity trends for freshwater taxa have generally been recovering from the negative effects of gross pollution suffered by riverine habitats in much of the 20th Century in the UK (Outhwaite et al., 2020; Vaughan & Gotelli, 2019), urban expansion and densification continues to exert pressure on these communities through sewage discharge, channel modification and riparian habitat removal and degradation (Windsor et al., 2019), the effects of which may be evident in our results.

In this study, we used functional diversity indices as a proxy of ‘ecosystem functioning’, assuming a decline in functional diversity will cause a drop in the functional provision and resilience mediated by the insect taxa in question. This is based on previous studies that find a positive relationship between functional diversity and the provision and resilience of ecosystem functions and services (e.g., Greenop et al., 2018, 2021; Oliver et al., 2015; Woodcock et al., 2014, 2019). However, it is important to note that we did not measure ecosystem functions directly, and so caution should be taken when interpreting the trends from our results. For example, where we find that functional diversity did not decline significantly from the results of linear models, we cannot assume that ecosystem functions provided by these insect taxa are healthy and resilient. The types of traits and the species that we used to construct functional hypervolumes were, ultimately, limited to those with published and accessible data (Cook et al., 2021; Tachet et al., 2010). It is possible that other traits might be especially important for determining function, and our data limitations may conceal potential temporal changes in hypervolume structure and consequential index values that may occur with the inclusion of other traits in the analysis. Indeed, some species that were not able to be included in datasets due to the absence of trait data, or difficulty with modelling abundance change in those species, may have been especially important contributors of function through their abundance or could have contributed to greater functional diversity in insect communities, again concealing any potential hypervolume changes occurring as a result. It is not known how robust our analyses are to missing trait and species data, but the hypervolume method for calculating functional diversity using convex hulls may be sensitive to missing data, as has been found for a study which tested different methods of calculating functional diversity in birds (Stewart et al., 2023). Future research could focus on efforts to impute missing trait data for species present in invertebrate communities in the UK and comparison with our findings, given that imputation of traits has been found to improve functional diversity estimates (Stewart et al., 2023).

The trends that we present here shed light on predicted change in the functional diversity of lepidopteran and freshwater communities in the UK, highlighting increasing vulnerability of communities and ecosystem functions in particular habitats over time whilst suggesting there may be greater resilience in diversity of the traits included in our analyses at the wider spatial scale. Our approach to understanding functional changes in communities could be expanded across regions where there are standardised monitoring schemes already in place to predict temporal functional change in other areas, and for comparison against the trends we find here for lepidopteran and freshwater communities in the UK.

Supporting Information

Figures

Figure S1. Non-linear temporal trends in the functional richness (“FDiv”) and functional dispersion (“FDisp”) for each insect group (macro-moths, butterflies and freshwater EPT). The plot shows the annual collated indices for national-scale data, relative to the first index value of the time series, calculated for each index type as points connected by the dashed lines. The abundance is represented by the relative geometric mean of all species’ collated abundance indices.

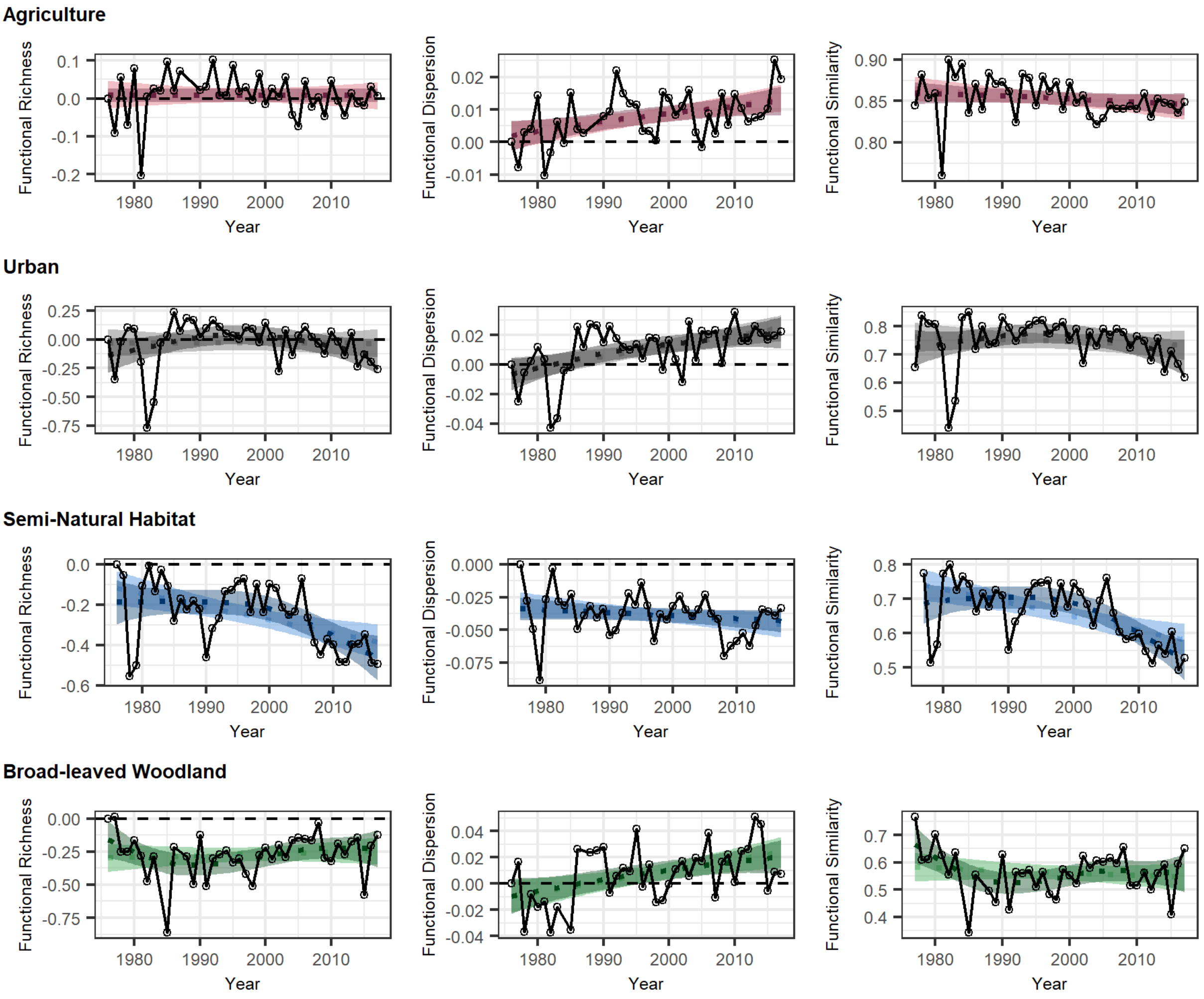


Figure S2. Linear and Non-linear trends and 95% credible intervals for butterfly functional diversity indices (Ephemeroptera, Plecoptera and Trichoptera) in agricultural, urban, semi-natural and woodland habitats. Linear trends are represented by lighter / more transparent colour trends and envelopes. The functional indices on the y axes for functional richness and dispersion are log-relative values – i.e., relative to the first value of the first time point.

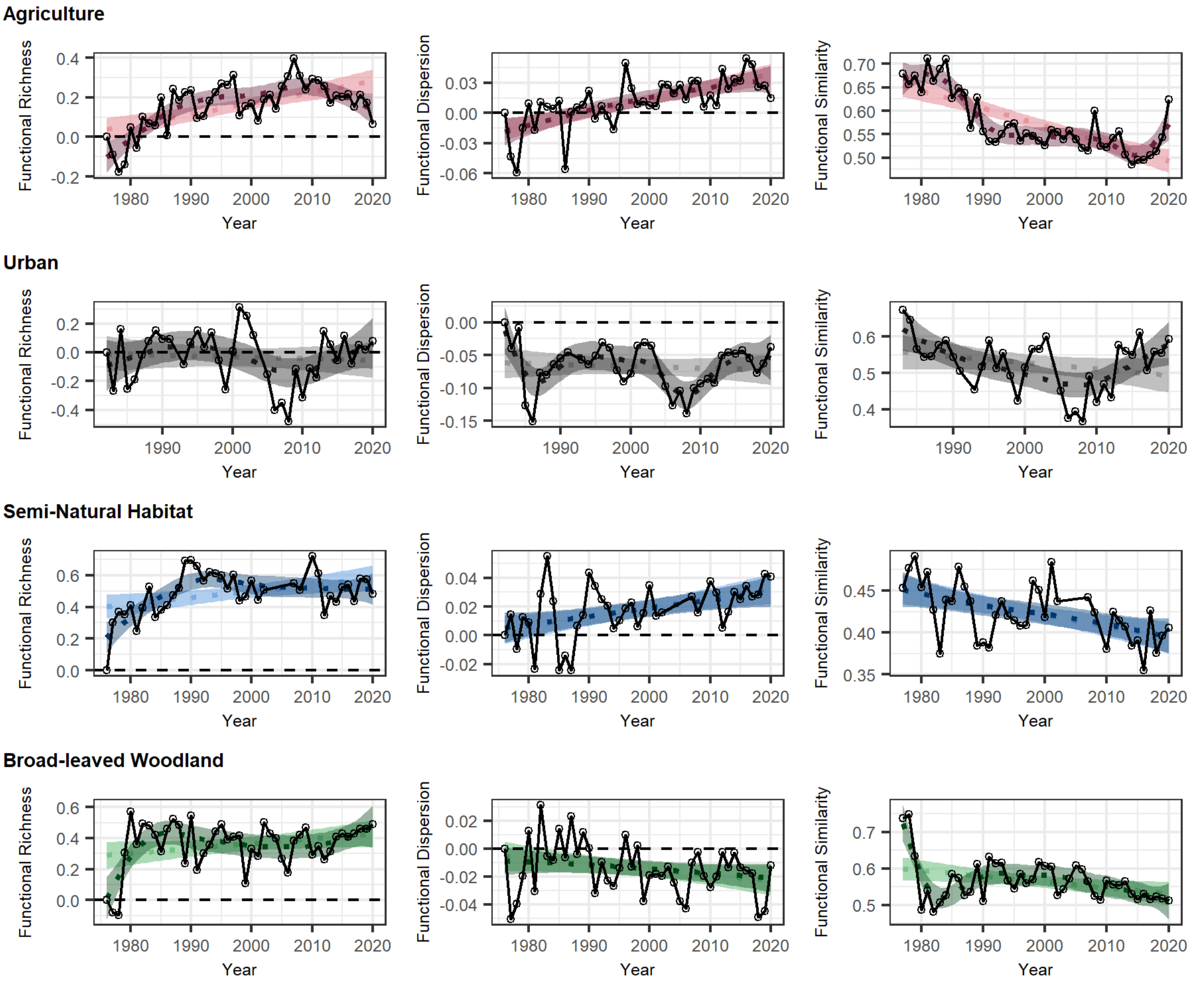


Figure S3. Linear and Non-linear trends and 95% credible intervals for moth functional diversity indices (Ephemeroptera, Plecoptera and Trichoptera) in agricultural, urban, semi-natural and woodland habitats. Linear trends are represented by lighter / more transparent colour trends and envelopes. The functional indices on the y axes for functional richness and dispersion are log-relative values – i.e., relative to the first value of the first time point.

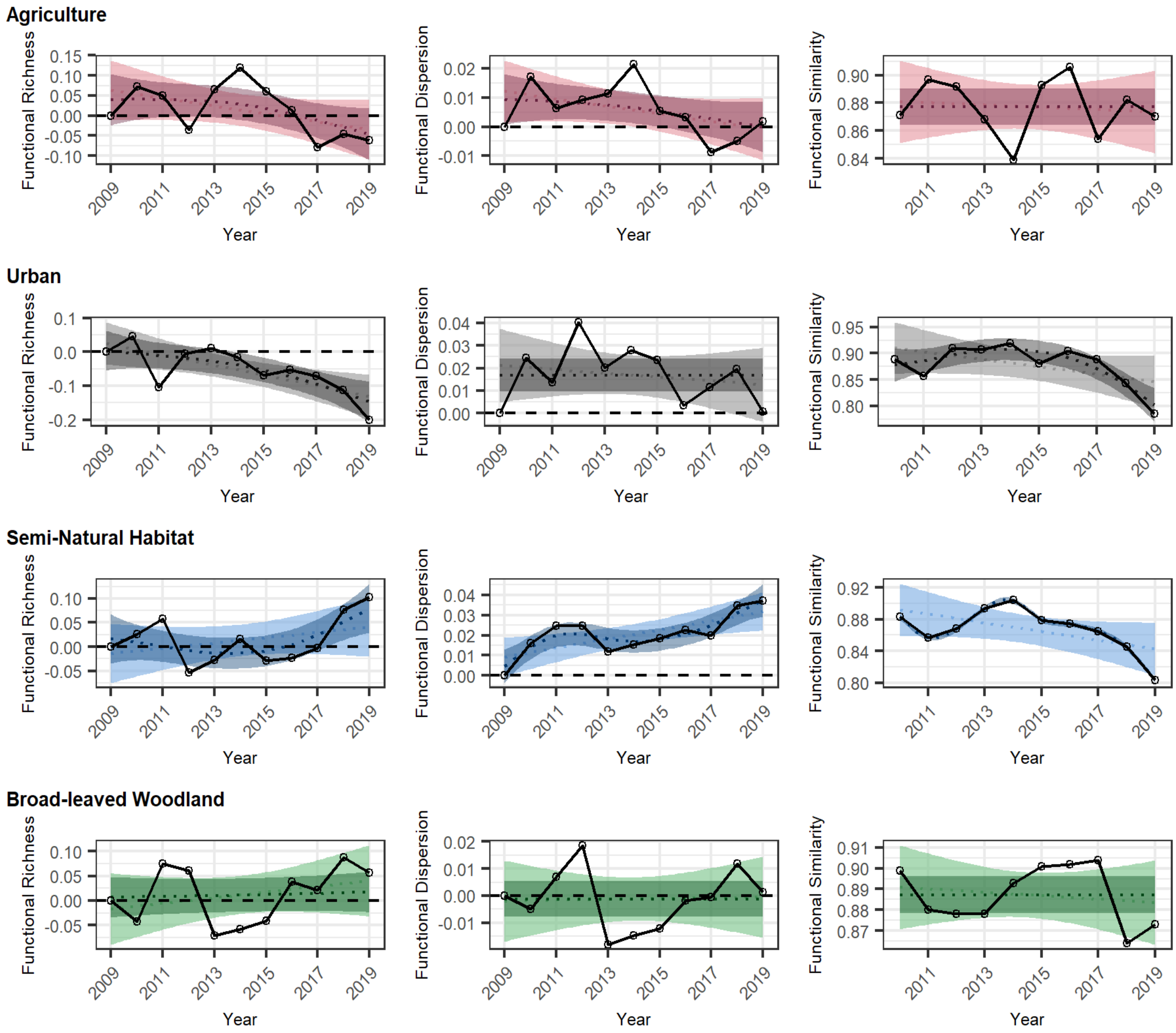


Figure S4. Linear and Non-linear trends and 95% credible intervals for EPT functional diversity indices (Ephemeroptera, Plecoptera and Trichoptera) in agricultural, urban, semi-natural and woodland habitats. Linear trends are represented by lighter / more transparent colour trends and envelopes. The functional indices on the y axes for functional richness and dispersion are log-relative values – i.e., relative to the first value of the first time point.

Tables

Table S1. Abundance Model Comparisons

Group	Modnames	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Butterfly	Year * Habitat	11	56,140.507	0.00	0.8	0.8
	Year + Habitat	8	56,143.220	2.71	0.2	1.0
	Year (Habitat Indices)	5	56,316.890	176.38	0.0	1.0
	Null model (Habitat Indices)	4	56,318.303	177.80	0.0	1.0
	Year * Species (Collated Indices)	119	9,253.946	0.00	1.0	1.0
	Year (Collated Indices)	5	9,576.026	322.08	0.0	1.0
	Null model (Collated Indices)	4	9,577.232	323.29	0.0	1.0
Moth	Year * Habitat	11	269,654.46	0.00	1	1
	Year + Habitat	8	269,800.41	145.95	0	1
	Year (Habitat Indices)	5	270,104.14	449.68	0	1
	Null model (Habitat Indices)	4	270,104.87	450.41	0	1
	Year * Species (Collated Indices)	853	58,577.61	0.00	1	1
	Year (Collated Indices)	5	65,287.39	6,709.78	0	1
	Null model (Collated Indices)	4	65,314.88	6,737.27	0	1
EPT	Year + Habitat	8	-37,574.656	0.00	0.94	0.94
	Year * Habitat	11	-37,569.018	5.64	0.06	1.00
	Null model (Habitat Indices)	4	-37,556.763	17.89	0.00	1.00
	Year (Habitat Indices)	5	-37,556.083	18.57	0.00	1.00
	Year * Species (Collated Indices	379	1,339.417	0.00	1.00	1.00
	Null model (Collated Indices)	4	1,705.922	366.51	0.00	1.00
	Year (Collated Indices)	5	1,707.336	367.92	0.00	1.00

Table S2. Taxonomic Diversity (Shannon index) Model Comparisons

Group	Modnames	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Butterfly	Year + Habitat	6	142.5113	0.00	0.87	0.87
	Year * Habitat	9	146.3204	3.81	0.13	1.00
	Year (Habitat Indices)	3	210.2407	67.73	0.00	1.00
	Null model (Habitat Indices)	2	211.2250	68.71	0.00	1.00
	Year (Collated Indices)	3	-175.8082	0.00	0.98	0.98
	Null model (Collated Indices)	2	-168.3028	7.51	0.02	1.00
Moth	Year * Habitat	9	-340.41523	0.00	0.55	0.55
	Year + Habitat	6	-340.02186	0.39	0.45	1.00
	Null model (Habitat Indices)	2	-165.78403	174.63	0.00	1.00
	Year (Habitat Indices)	3	-164.13002	176.29	0.00	1.00
	Null model (Collated Indices)	2	-38.98472	0.00	0.64	0.64
	Year (Collated Indices)	3	-37.83410	1.15	0.36	1.00
EPT	Year * Habitat	9	-184.72526	0.00	0.79	0.79
	Year + Habitat	6	-182.04791	2.68	0.21	1.00
	Null model (Habitat Indices)	2	-81.61133	103.11	0.00	1.00
	Year (Habitat Indices)	3	-79.35435	105.37	0.00	1.00
	Null model (Collated Indices)	2	-53.07165	0.00	0.88	0.88
	Year (Collated Indices)	3	-49.14899	3.92	0.12	1.00

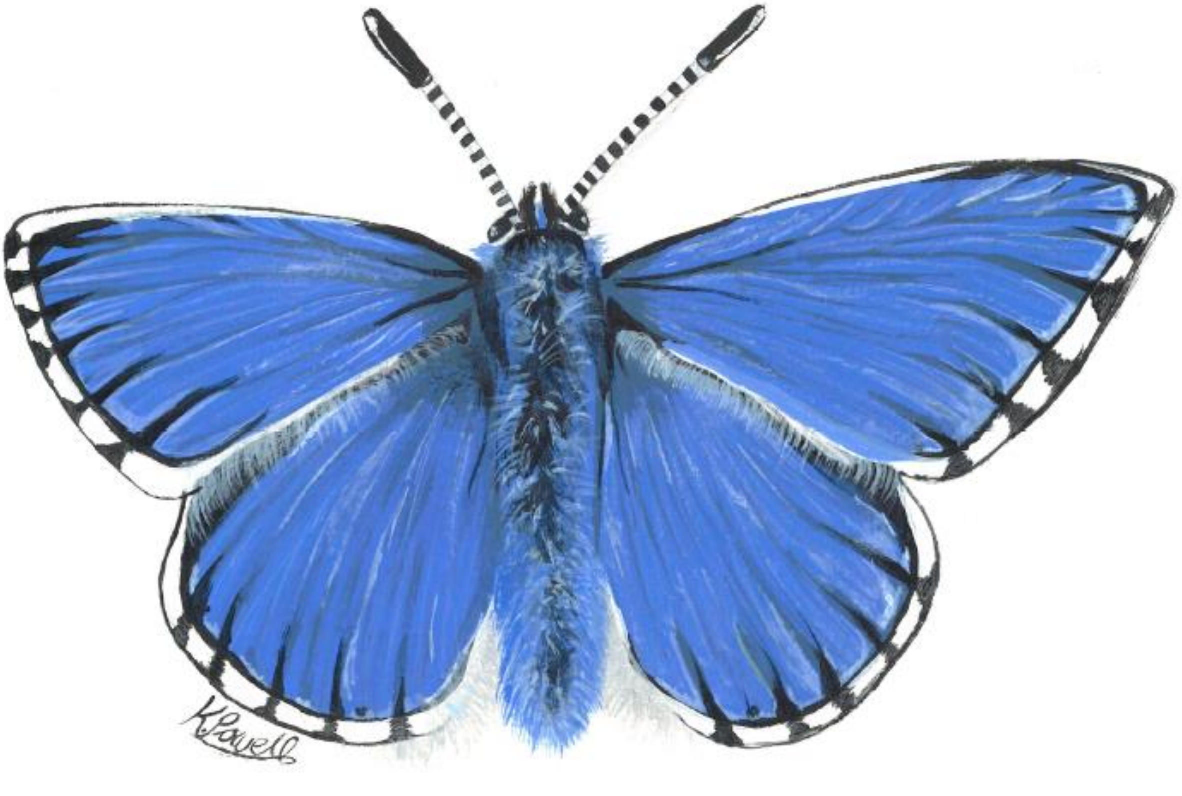
Table S3. Functional Richness (FDiv) model comparison.

Group	Modnames	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Butterfly	Year * Habitat	9	-166.449460	0.00	0.55	0.55
	Year + Habitat	6	-166.057470	0.39	0.45	1.00
	Null model (Habitat Indices)	2	3.801090	170.25	0.00	1.00
	Year (Habitat Indices)	3	4.448601	170.90	0.00	1.00
	Year (Collated Indices)	3	-94.100032	0.00	0.99	0.99
	Null model (Collated Indices)	2	-85.095679	9.00	0.01	1.00
Moth	Year * Habitat	9	-220.11848	0.00	0.74	0.74
	Year + Habitat	6	-218.00224	2.12	0.26	1.00
	Null model (Habitat Indices)	2	-125.88631	94.23	0.00	1.00
	Year (Habitat Indices)	3	-125.72576	94.39	0.00	1.00
	Null model (Collated Indices)	2	-93.99785	0.00	0.70	0.70
	Year (Collated Indices)	3	-92.25874	1.74	0.30	1.00
EPT	Year * Habitat	9	-287.69891	0.00	0.88	0.88
	Year + Habitat	6	-282.72629	4.97	0.07	0.96
	Null model (Habitat Indices)	2	-281.07817	6.62	0.03	0.99
	Year (Habitat Indices)	3	-279.11438	8.58	0.01	1.00
	Null model (Collated Indices)	2	-38.83661	0.00	0.86	0.86
	Year (Collated Indices)	3	-35.13715	3.70	0.14	1.00

Table S4. Functional Dispersion (FDisp) model comparison.

Group	Modnames	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Butterfly	Year * Habitat	9	-795.7103	0.00	1.00	1.00
	Year + Habitat	6	-776.0237	19.69	0.00	1.00
	Null model (Habitat Indices)	2	-606.3543	189.36	0.00	1.00
	Year (Habitat Indices)	3	-604.4242	191.29	0.00	1.00
	Null model (Collated Indices)	2	-267.6593	0.00	0.64	0.64
	Year (Collated Indices)	3	-266.5361	1.12	0.36	1.00
Moth	Year * Habitat	9	-906.0700	0.00	1	1
	Year + Habitat	6	-889.5274	16.54	0	1
	Year (Habitat Indices)	3	-733.2319	172.84	0	1
	Null model (Habitat Indices)	2	-730.0417	176.03	0	1
	Year (Collated Indices)	3	-335.1007	0.00	1	1
	Null model (Collated Indices)	2	-282.8653	52.24	0	1
EPT	Null model (Habitat Indices)	2	-716.28525	0.00	0.66	0.66
	Year (Habitat Indices)	3	-714.51027	1.77	0.27	0.94
	Year + Habitat	6	-711.12755	5.16	0.05	0.99
	Year * Habitat	9	-708.41524	7.87	0.01	1.00
	Null model (Collated Indices)	2	-63.47375	0.00	0.88	0.88
	Year (Collated Indices)	3	-59.54518	3.93	0.12	1.00

Chapter 7



Chapter 7

Discussion

There is a growing body of evidence for trends in insect diversity and abundance around the world, but a lack of focus on how insect declines will impact ecosystem functions in the long term (Didham, Barbero, et al., 2020; Powney et al., 2019). With this thesis, I refocus research efforts on this important element of insect declines to help fill knowledge gaps around the relationship between insect abundance, diversity, and function (Figure 1). I brought together the most comprehensive time series datasets we have in the UK for monitoring change in insect populations and used novel trait data – compiling my own in some cases – to delve into the relationship between functional traits and abundance and diversity of this fascinating group

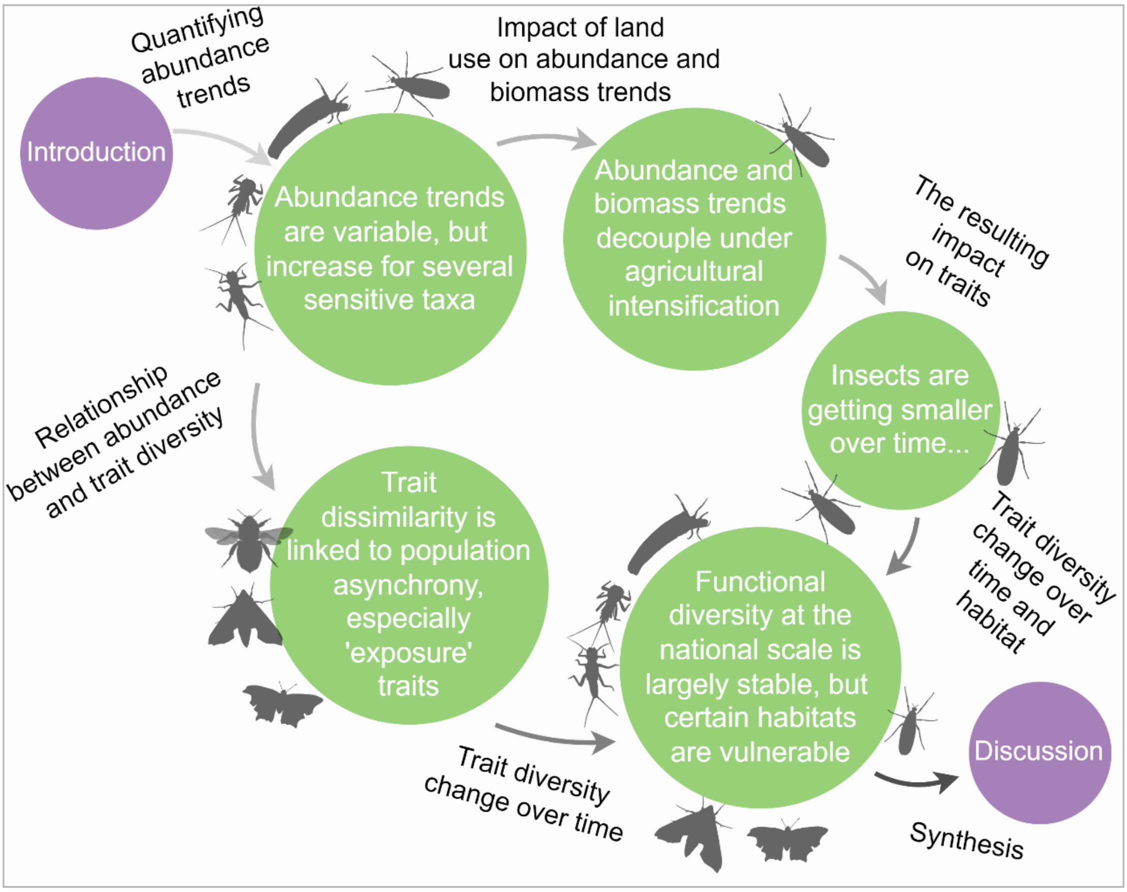


Figure 1. Visual representation of the flow of knowledge gained throughout the thesis, with circles representing the main message from each chapter of the thesis. Figure is an adaptation of Chapter 1 Figure 1.

of arthropods. By focusing on insects, I address the call for more rigorous studies using long-term data to understand the causes and consequences of insect decline (Didham, Basset, et al., 2020). However, I argue that some of the important findings of this thesis could help address questions about wider biodiversity change. For example, given generalised macroecological principles, I show how environmental impacts can alter the distribution of functional traits (Chapter 4), as well as furthering our understanding of how species' trait diversity links to resilience effects (Chapter 5) and how it changes over time (Chapter 6). Hence, I provide evidence that links environmental drivers of biodiversity change through to the undermining of functional resilience in ecological communities. I hope that some of my findings can help stimulate further research on insects, their traits, and threats to their diversity, abundance, and ecosystem functions.

Thesis overview

I first consider the idea that we do not have enough information about insect populations to make confident statements that all insects are declining everywhere around the world. To help contribute toward a more complete picture of change in temporal insect abundance and biodiversity, the reuse of data originally collected for purposes other than monitoring biodiversity have been advocated (Didham, Basset, et al., 2020). I attempt to tackle this in "Chapter 2: Abundance trends for river macroinvertebrates vary across taxa, trophic group, and river typology", through making use of the extensive Environment Agency water quality monitoring datasets to understand how the abundance of freshwater invertebrates has changed over time. The strongest messages I would like to emphasise from this chapter are that functional changes may be underway where the decomposition of organic matter is concerned; and that there is strong heterogeneity in temporal trends, including between different trophic groups and different types of rivers in England. The scale at which the data are recorded – and / or pooled during analysis – can be fundamental in determining the outcome of trend analyses, demonstrated by the fact that I found significant turnover in the relative abundance of families within insect groups that were stable overall when considered at a different taxonomic level. I emphasise that the taxonomic and spatial scale is therefore incredibly important to consider in the interpretation of biodiversity trends.

In “Chapter 3: Complex temporal trends in biomass and abundance of Diptera driven by the impact of agricultural intensity on community-level turnover”, I again point to this phenomenon of stability at one taxonomic level concealing underlying heterogeneity in trends between different taxa. In this chapter, I wanted to understand how land use change, which is often cited as one of the main drivers of insect declines, affected Diptera communities – specifically looking across a gradient of agricultural intensification in space and time (Outhwaite et al., 2022; Raven & Wagner, 2021). What I found was surprising to me. Previous work by a co-author had shown that biomass of total Diptera caught in traps was negatively impacted by agricultural intensification (Garrett et al., 2022), and my work showed that this effect intensified temporal decline in biomass. However, the abundance trends did not follow the same pattern and largely increased with agricultural intensification. This work led me to hypothesise that there must be a relatively greater negative effect of agriculture on larger dipteran species, resulting in heterogeneity in trends within the community and driving the observed incongruence between biomass and abundance trends.

In “Chapter 4: Diptera communities lose larger species and homogenise under agricultural intensification”, I used a theoretical approach to address the hypotheses generated by Chapter 3, showing that community change in our study area could occur under two alternative mechanisms – change in the species body size distribution, or a changing size density relationship amongst species. Unfortunately, I did not have access to species or family-level empirical data that could confirm what I was able to show in the theoretical approach. Nevertheless, I show the distribution of species’ functional traits (here, body size) in communities is altered by land use change in space and time, leading to fewer large species, declining populations of large species and booming populations of small species, suggesting insect communities and their functions are being re-shaped over time by this environmental pressure.

By beginning to probe into our understanding of how traits change under environmental drivers in my Canadian study, I was left with questions around how insect traits relate to longer term resilience in insect communities. Asynchrony between species' abundances supports resilience at the community-level through complementarity and portfolio effects (Thibaut & Connolly, 2013; introduced in Chapter 1). In "Chapter 5: Asynchrony in terrestrial insect abundance corresponds with diversity in exposure and sensitivity to environmental perturbations", I explore the relationship between traits and abundance change across taxa, finding that many traits that are associated with species' diversity in exposure to environmental perturbations – through temporal and / or spatial niche partitioning – are especially important for asynchrony. Many questions remain that I was unable to explore further – including how such relationships play out on smaller spatial scales that are more relevant for ecosystem functioning and quantifying the relationship between asynchrony and the resistance of community mean abundance to environmental perturbations. Regardless, I hint at the importance of trait diversity as a mechanism in functional resilience in insect communities and make contributions to insect functional ecology literature through the compilation of species' traits in a new dataset.

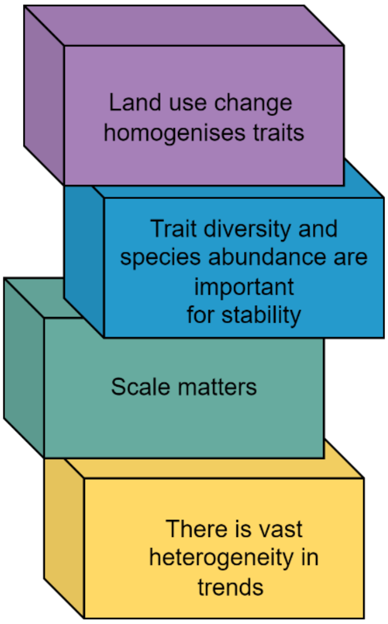


Figure 2. Some of the overlapping and important themes from the thesis.

Finally, after finding out more about the relationship between traits and long-term abundance change (and asynchrony), I wanted to understand how trait diversity has changed over time in insect communities, which I explored in “Chapter 6: Predicting long-term trends in ecosystem function provided by lepidopteran and freshwater insect communities”. Overall, this chapter suggests that at the national-scale, functional diversity has remained fairly stable in these communities, but varied in different habitats. Particularly, semi-natural and urban habitats had larger functional decline than agricultural and woodland habitats, especially with regards to moths and freshwater insects. Again, this difference in trends between large and then smaller spatial scales (national versus habitat-level) reveals the importance of scale and context when interpreting biodiversity trends and their functional impact. The interpretation from this chapter that both taxonomic diversity and abundance are important for determining trends in functional richness in insect communities, with perturbations in abundance being reflected in interannual fluctuations in functional richness, harks back to our understanding that abundance and traits are intrinsically linked and that this relationship can destabilise communities under environmental perturbation.

Some important and consistent messages emerge from the thesis, outlined in Figure 2. My chapters come together to show that heterogeneity amongst trends is the norm, whether this is across spatial scales (Chapters 2, 3 and 6), taxonomic groupings (Chapters 2, 4, and 6), or different facets of biodiversity (Chapters 3 and 6), and, therefore, considering these different scales is core to our interpretation of trends. Heterogeneity may lead to functional consequences when such variation in trends is tied to species’ traits and, therefore, likely has consequences for ecosystem function. For example, in Chapter 4 we use macroecological theory to show that there must be variation in the long-term temporal abundance trends of different species, and / or variation in the presence / absence of species, according to their size - which is an important functional trait. This is also found in Chapter 2 where we show some families of freshwater macroinvertebrate increase and some decline over time; functional traits associated with these families may well underpin these trends, and although the overall abundance of an order of insects may not change considerably over time, a turnover in the dominance of traits could alter the functional capacity of these insect communities. On the other hand, short term divergence of trends (e.g., interannual abundance change) driven by different responses to environmental pressures under trait variation is an important stabiliser of community abundance and long-term resilience (Chapter 5, Figure 2). My thesis highlights that, therefore, the diversity of traits is an important concept for community resilience through the mediation of heterogenous population trends (Chapter 5), but that this trait diversity is under threat in many systems due to the impact of anthropogenic drivers, such as land use change (Chapters 3, 4, 6).

Limitations of the thesis

Future research could begin by focusing on the gaps that are left by my thesis. For example, intraspecific variation or diversity in traits is not considered outright in my analyses. There is limited data for intraspecific variation in traits for insects. This is flagged up as a major issue for trait-based studies of arthropods by Wong et al. (2019). Although the methods I used in Chapter 6 accounted for some expected variation around trait values amongst individuals, as n-dimensional hypervolumes are based on probability density functions for trait values, this method does not account for the case where intraspecific trait variation is greater than variation amongst species. If this is a commonplace phenomenon amongst the taxa and traits that I have chosen in this study, then my findings of relationships between traits and abundance are likely biased. As functional ecology progresses to be more inclusive of insects and other invertebrates, trait datasets that account for intraspecific variation could become more common. However, for this to take place, significant effort into measuring and modelling trait variation within insect species needs to occur, requiring a large amount of replicates to capture variation in multidimensional trait space (Wong et al., 2019). Some analytical tools exist that can then incorporate this intraspecific trait variation into estimates of community-level functional trait space (de Bello et al., 2011; Wong & Carmona, 2021).

The focus of my analyses was spatially, taxonomically, and temporally limited; this is partly because I made the decision to work with structured data taken from standardised monitoring schemes, to avoid the statistical issues and biases that are inherent within unstructured and opportunistic data. Taking this approach meant that I was able to use abundance data, which reveals significantly more information about population change than presence or presence-absence data, and, considering abundance is closely tied to ecosystem functions, it meant I could explore hypotheses about change in function (e.g., Winfree et al., 2015). However, that is not to say that the data I used was unbiased in any way; on the contrary I expect that the site selection in some of the datasets, such as both Lepidoptera and the bumblebee dataset, would have been biased toward sites where there is a better chance of recording the presence of insects from these taxa (Defra, 2023). If I had included structured data from the 'wider countryside', perhaps changes in functional diversity that I was not able to capture at the national scale from these datasets would have been more obvious.

What's more, the methods used to impute data where there are gaps mean there were inherent issues with applying models to test environmental drivers at the site-level, for species-level data. This is because of the 'borrowing' that the imputation process conducts by modelling data gaps from other sites which are under different degrees of ecological disturbance. Whilst national and collated trends are invaluable for getting an overview of the state of change in the system and are useful for informing biodiversity policy, it should not be forgotten that ecosystem functions are carried out at multiple spatial scales, and that such broad approaches to analysis of trends can miss important localised effects (Bond & Chase, 2002).

The UK is a particularly good source of structured data from insect monitoring schemes, perhaps due to its long history of species recording and natural history research. There are, however, similar datasets of perhaps slightly shorter temporal breadth that cover elsewhere in Europe – for example, data from the European Butterfly Monitoring Schemes (eBMS e.g., European Environment Agency., 2013), which I could have utilised. Given more time, I would have loved to have been able to explore my ideas using these data; as it stands, I chose to focus on including more taxonomic groups in my analyses instead, to enable cross-taxonomic comparisons to be made. Future research would benefit from widening the scope to include further data such as that from the eBMS to investigate whether the patterns I've found throughout the thesis can be generalised across other datasets.

Most importantly, whilst I have been able to show various patterns in the data and test hypotheses relating to the functional diversity and trait spaces of insect communities, it should be reiterated that these trait-based methods remain proxies only of ecosystem functioning itself (Flynn et al., 2011). Therefore, I am limited in my ability to provide a direct causal link between loss of insect abundance and diversity and actual ecosystem functioning without further data that directly captures an ecosystem function, or a suite of functions. This kind of data would be incredibly cumbersome to collect on a wide scale, and therefore is very rare, leading to the use of proxies in most studies on insect effects on ecosystem functions and services (Noriega et al., 2018a). Some examples of hypothetical ecosystem function data that could provide more direct links between abundance change and functional changes include pollination rate or food provisioning rate linked to the insect communities for which we have temporal abundance and diversity data.

Knowledge gaps remain

It remains that we know little about insect population change and the functional consequences for most ecosystems across the biogeographical regions of the world. This is due to an absence of long-term insect monitoring taking place beyond Europe, North America, and parts of Australasia. Large areas of Asia, Africa, and South America are consistently missed from insect decline studies, even those that refer to ‘worldwide’ insect declines (Simmons et al., 2019; Wagner, 2020). Given the lack of data on baseline insect communities and functional diversity in these regions, not least the geographical data bias in evidence of insect population changes, we still have little understanding of the functional resilience of insect communities under environmental change across the globe. The dominant anthropogenic pressures of biodiversity change also vary to some extent biogeographically, making it even harder to speculate on the resilience of insect communities in understudied regions (Bowler et al., 2020).

Clearly, future efforts to understand the extent of insect declines and their impact on ecosystem functioning should focus on filling data gaps from these understudied biogeographical regions. Citizen Science data such as opportunistic insect records from around the world could provide a useful source of untapped knowledge (Johnston et al., 2022; Theobald et al., 2015). Such data is more difficult to extract trends from due to the inherent issues with their unstructured nature (Bowler et al., 2022); therefore, a focus on developing methods to integrate datasets with minimal bias, to understand better how unstructured citizen science data can be used to estimate population and functional change, could help move research forward (Pagel et al., 2014). Exciting progress is already beginning to be made in this area, along with the development of new technologies such as automated monitoring systems for biodiversity, using artificial intelligence to identify species (Miller et al., 2019; van Klink et al., 2022). New technologies like this could potentially bring the dawn of standardised monitoring of insects to areas of the globe where we know little about their population trends, but that could be suffering the greatest losses, such as areas of the tropics (Bradshaw et al., 2009; Newbold et al., 2020).

Despite a continually expanding body of research on past and present insect declines, there is a large knowledge gap around the future of insect biodiversity, and the resulting change in ecosystem functioning. Future projections of insect and other species' trends remains highly challenging due to the level of uncertainty around current trends, as well as uncertainty around the future trajectory of environmental pressures on biodiversity and the complexity of interactions between different effects (Rosa et al., 2020). The future path taken by environmental pressures such as climate and land use change, along with the future of biodiversity conservation, is dependent to a large degree on the socioeconomic climate and political decisions, relying on our global political trajectory and so contributing another source of great uncertainty (Mikkelson et al., 2007). Progress should be made to model future biodiversity projections under a range of environmental, socioeconomic, and political scenarios, making use of emerging tools in network theory and AI development, in order to inform the public and policymakers on decisions that could be made to best conserve ecosystems (e.g., Silvestro et al., 2022). This will also require improvement in translating research into something impactful for decision makers, commanding better communication skills from researchers (Hertog & Zuercher, 2014). Collaborating across sectors in future research projects, and becoming more interdisciplinary ourselves as individual researchers, is a vital first step in stimulating more impactful and meaningful research along these lines (Craven et al., 2019; Liu et al., 2007).

Concluding remarks

Insects are not the most beloved creatures, but they are incredibly important. Their sheer diversity relative to all other living organisms makes it particularly challenging to understand the extent of declines in their abundance and the resulting impact on ecosystem function. Yet, by studying the relationships between biodiversity, traits, abundance, and function in this thesis, I progress our knowledge of the expected negative impact that population changes under environmental pressures can have on trait diversity, and the negative consequences of this for long term functional resilience. Whilst I focus on insects here, trait-based frameworks used in this thesis make the main messages pulled out in Figure 2 applicable to biodiversity in general. I join others in understanding more about how important biodiversity is for the healthy functioning of ecosystems on our planet, and how this is undermined by the anthropogenic destruction of life on earth. I hope that this will lead to greater awareness and conservation of this fascinating group of arthropods, so that they can bless us with their continued bountiful presence into the future.

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