Long-term occupancy trends across three insect taxa and their potential drivers in Central Europe

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Disclaimer

Although this thesis represents my original work, the research presented in the following chapters was made possible through productive collaborations, continuous feedback, and developing ideas with my co-authors. Thus, I will use plural formulations to accurately present the results and refer to the research as "our work" or "we conducted this research" throughout the thesis.

AI-based writing tools, namely Grammarly (Grammarly Inc., version 6.8.261), QuillBot (Course Hero Inc.), and ChatGPT-3 (OpenAI) have been used to improve the writing style of this thesis. The content, facts, and opinions presented remain my own.

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Zusammenfassung

Die Systeme der Erde werden zunehmend durch anthropogene Stressfaktoren beeinträchtigt, wobei Veränderungen des Klimas und der Landnutzung erhebliche Auswirkungen auf die biologische Vielfalt haben. Zu diesen Auswirkungen gehören der Rückgang von Populationen, die Verlagerung von Verbreitungsgebieten und Veränderungen in der Zusammensetzung von Lebensgemeinschaften, die zu veränderten biotischen Interaktionen führen.

Insekten sind für die Aufrechterhaltung der Gesundheit und Nachhaltigkeit von Ökosystemen und damit auch von menschlichen Gesellschaften von entscheidender Bedeutung. In mehreren neueren Studien wurde ein weltweiter Rückgang verschiedener Indikatoren für die Insektenvielfalt festgestellt, wie beispielsweise Abundanz, Biomasse und Artenreichtum, wobei einige Studien uneindeutige Trends aufzeigten. Diese Veränderungen sowohl bei der anthropogenen Belastung als auch bei den Insekten wurden vor allem auf dem europäischen Kontinent beobachtet, wo Naturschutzmaßnahmen wie die Europäische Flora-Fauna-Habitat- (FFH-) Richtlinie darauf abzielen, die biologische Vielfalt in der gesamten Europäischen Union vor negativen Auswirkungen zu schützen.

Da es an systematischen Beobachtungsdaten über lange Zeiträume mangelt, gibt es nur wenige artenspezifische Langzeittrends. Außerdem haben die derzeitigen Datenbanken in der Regel eine geringe Auflösung oder einen geringen Erfassungsbereich und sind mit verschiedenen Formen von Verzerrungen (Bias) behaftet. Wenn die Daten Verzerrungen enthalten, kann die Anzahl der Beobachtungen pro Art und Jahr lediglich den Aufwand für die Probenahme widerspiegeln, während die Extrapolation von gut beprobten Standorten auf die gesamte Untersuchungsregion das Vorkommen von Arten überbewerten kann. Dies schränkt die Schlussfolgerungen ein, die aus solchen Daten gezogen werden können, und führt dazu, dass nur wenige Studien Faktoren untersuchen, die langfristige Veränderungen bei Insekten bewirken, insbesondere bei mehreren Taxa.

In dieser Arbeit haben wir anhand eines großen, heterogenen Beobachtungsdatensatzes aus der mitteleuropäischen Region Bayern Vorkommensänderungen bei Schmetterlingen, Heuschrecken und Libellen analysiert. Die Hauptanalyse erstreckt sich über 40 Jahre, von 1980 bis 2019. Zur Ableitung von Vorkommenswahrscheinlichkeiten (Anteil der besetzten Standorte, ‚occupancy') pro Art und Jahr haben wir Bayes'sche ‚occupancy-detection' Modelle verwendet. Bei dieser Methode werden Informationen über das Datenerfassungsverfahren berücksichtigt, indem gekoppelte hierarchische Modelle für die Beobachtungs- und Vorkommenswahrscheinlichkeiten verwendet werden.

Anhand der abgeleiteten Vorkommenswahrscheinlichkeiten analysierten wir die Auswirkungen verschiedener Artmerkmale auf die Vorkommensänderungen der Arten, um potenzielle Triebkräfte für Veränderungen zu ermitteln. Zu diesen Attributen gehören Klima- und Habitatpräferenzen, die Abhängigkeit von Ameisen für die Larvenentwicklung bei Schmetterlingen der Familie der Lycaenidae, sowie der Schutz von Schmetterlingen und Libellen durch die europäische FFH-Richtlinie.

Wir zeigen, dass sich die Artenzusammensetzung im Untersuchungsgebiet in den letzten vier Jahrzehnten deutlich verändert hat. Bei 37 % aller Insektenarten ist ein Rückgang zu verzeichnen, 30 % nahmen zu, und bei 33 % ist kein signifikanter Trend zu erkennen, allerdings stellten wir gravierende Unterschiede zwischen den Taxa fest. Während 52 % der Libellenarten zunahmen und 27 % abnahmen, gingen 41 % der Schmetterlings- und Heuschreckenarten zurück.

Der Klimawandel wirkte sich in den letzten Jahrzehnten bereits konsistent auf das Vorkommen von Insekten aller untersuchten Taxa aus. Die Vorkommen kälteangepasster Arten gingen zurück, während die Vorkommen wärmeangepasster Arten zunahmen. Faktoren, die mit der Bodenbedeckung zusammenhängen, scheinen dagegen unklarer zu sein und nicht mit den einzelnen Lebensraumtypen zusammenzuhängen. Bei den Schmetterlingen nahmen die Habitatspezialisten ab, während es bei Heuschrecken und Libellen keinen Unterschied zwischen Habitatgeneralisten und -spezialisten gab. Die durch Landnutzungsänderungen verursachte geringere Qualität und Ausdehnung von Lebensräumen könnte sich auf die Lebensraumspezialisten unter den Schmetterlingen auswirken, die in hohem Maße auf intakte Lebensräume angewiesen sind. Unseren Ergebnissen zufolge könnte ihre Ameisenabhängigkeit eine stabilisierende Wirkung auf die betroffenen Schmetterlinge gehabt haben. Die Berücksichtigung biotischer Interaktionen ist daher ein wichtiger Aspekt für den Erhalt von Insekten, da solche Wechselwirkungen die Überlebenschancen der Arten sowohl verbessern als auch verschlechtern können.

Wir zeigen, dass sich die Bemühungen zur Dokumentation der Vorkommen von Arten, die unter der Flora-Fauna-Habitat-Richtlinie geschützt werden, nach Verabschiedung der Richtlinie verstärkten, während sich die Bestandsentwicklungen der Arten sowohl verbessert als auch verschlechtert haben. Folglich hat die FFH-Richtlinie entgegen ihrem Hauptzweck eine Verschlechterung des Zustands mancher Arten nicht verhindert.

Die Zuverlässigkeit der Modellierungsergebnisse hängt in hohem Maße von der Qualität der zugrunde liegenden Daten ab, einschließlich der Vertrauenswürdigkeit der Beobachtungsdaten, sowie der räumlichen und zeitlichen Verfügbarkeit sowohl der Beobachtungs- als auch der Treiberdaten. Leider verhindert der Mangel an verfügbaren Daten über Einzelheiten der Landnutzung wissenschaftliche Erkenntnisse über einen der anthropogenen Einflussfaktoren, der als besonders einflussreich für Insekten gilt. Darüber hinaus ergeben sich methodische Herausforderungen aufgrund unterschiedlicher Ansätze zur Bewertung langfristiger Vorkommensänderungen, der Schwierigkeit, eine Ausgangsbasis für Vergleiche zu definieren, sowie unterschiedlicher Methoden zur Bestimmung des sogenannten Status einer Art. Angesichts der großen taxonomischen Vielfalt in der Klasse der Insekten kann die Analyse einer kleinen Anzahl von Gruppen nur ein teilweises Verständnis der komplexen Prozesse und Wechselwirkungen vermitteln, die den beobachteten Mustern zugrunde liegen.

Da eine vollständige Erfassung der biologischen Vielfalt praktisch unmöglich ist, werden in der Biodiversitätsforschung zunehmend Computermodelle eingesetzt, um Ökosysteme zu simulieren und zu untersuchen. Diese Modelle können sich auf historische Daten und Daten aus der Bürgerforschung (citizen science) stützen, die die professionelle Datenerfassung ergänzen. Durch die Anwendung von Modellierungsmethoden können wir die Zusammenhänge zwischen menschlichen Handlungen und ihren Auswirkungen auf die biologische Vielfalt untersuchen und so die Notwendigkeit einer effektiveren Gesetzgebung zu deren Schutz aufzeigen.

Die in dieser Arbeit vorgestellten Studien zeigen mehrere mögliche Richtungen für künftige Forschungsprojekte auf. Zu den weiteren Forschungsarbeiten könnte die Untersuchung zusätzlicher Merkmale gehören, die sich auf die Vorkommen der Arten auswirken könnten, wie beispielsweise ihre Ausbreitungsfähigkeit, Phänologie und benötigten Nahrungsressourcen. Eine weitere Möglichkeit ist die Erweiterung der occupancy-detection Modelle, um ein breiteres Spektrum von Insektentaxa sowie eine räumliche Komponente einzubeziehen, was eine umfassendere Bewertung der Vorkommensänderungen in Zeit und Raum ermöglicht. Schließlich sind explizitere Daten über die mit landwirtschaftlicher Praxis zusammenhängenden Faktoren erforderlich, um deren relativen Beitrag zu Vorkommensänderungen zu ermitteln. Eine Kombination dieser Faktoren könnte Strategien für den Aufbau einer widerstandsfähigeren Umwelt für Insekten und Menschen liefern.

Obwohl einige erste Schritte unternommen wurden, um die entscheidende Rolle der Insekten für das menschliche Wohlergehen und die Verbesserung ihres Schutzes anzuerkennen, gibt es noch viel Raum für Verbesserungen. Um eine nachhaltige Zukunft zu erreichen, muss die Bedeutung von Insekten und der biologischen Vielfalt im Allgemeinen gesellschaftlich stärker anerkannt werden. Um dies zu erreichen, müssen wir unser Verständnis der Werte verbessern, die den unterschiedlichen Ansichten der Beteiligten zugrunde liegen. Wir können das Blatt für Insekten im Anthropozän wenden, wenn wir die Wechselseitigkeit in der Beziehung zwischen Mensch und Natur betonen und gleichzeitig wesentliche Fortschritte bei der Erhaltung und Wiederherstellung der biologischen Vielfalt erzielen.

Summary

The Earth's systems are being increasingly impacted by anthropogenic stressors, with changes in climate and land use significantly affecting biodiversity. These impacts include population declines, range shifts, and changes in community composition with altered biotic interactions.

Insects are vital for maintaining the health and sustainability of ecosystems and, therefore, human societies. Several recent studies have reported a global decline in various measures of insect diversity, such as abundance, biomass, and species richness, although some studies have found more ambiguous trends. These changes, both in anthropogenic pressures and insect change, have been observed especially across the European continent, where conservation policies, such as the European Habitats Directive, aim to protect biodiversity across the European Union from negative impacts.

Species-specific long-term trends are scarce due to a lack of systematic monitoring data over long periods. Moreover, current databases are typical of low resolution or coverage and entail different forms of bias. When data contain biases, the number of observations per species per year may merely reflect the sampling effort, while extrapolation from well-sampled sites to the entire study region may overestimate species' presences. Thus, such biases limit the conclusions that can be drawn from such data, resulting in few studies that examine factors driving long-term insect changes, especially across multiple taxa.

In this thesis, we analysed occupancy changes in butterflies, grasshoppers, and dragonflies using a large, heterogeneous dataset of observations from the central European region of Bavaria. The principal analysis spans 40 years, from 1980 to 2019. To derive occupancy estimates (the proportion of sites occupied) for each species in each year, we used Bayesian occupancy-detection models. This method incorporates information on the data collection procedure by employing joint hierarchical models for observation and occurrence probability.

Using the derived occupancy estimates, we analysed the impacts of various species attributes on species trends to identify potential drivers of change. These attributes include climatic and habitat preferences, the dependence on ants for larval development in Lycaenid butterflies, and protection under the European Habitats Directive.

We show that the species composition in the study area has altered during the last four decades. 37 % of all insect species' occupancies have declined, 30 % have increased, and 33 % have shown no significant trend. We found severe differences in trends between taxa. While 52 % of dragonfly species increased and 27 % decreased, 41 % of butterfly and grasshopper species declined.

Climate change has already impacted insect occurrences across taxa in recent decades and consistently on all examined taxa. Cold-adapted species' occupancies have declined, while warm-adapted species' occupancies have increased. Factors connected to land cover, on the other hand, appear more ambiguous and unrelated to individual habitat types. In butterflies, habitat specialists have decreased, while there was no difference between habitat generalists and specialists in the other taxa. Reduced habitat quality and extent caused by land use change

could affect butterfly habitat specialists, who rely heavily on intact habitats. According to our findings, ant-dependence may have a stabilizing effect on Lycaenid butterflies. Addressing biotic interactions in insect conservation is thus an important consideration, as interactions do not consistently improve or degrade species' chances of survival.

We show that, despite increased monitoring efforts for species listed in the Habitats Directive's annexes, occupancy trends both improved and deteriorated after the adoption of the Directive. As a result, contrary to its primary purpose, the European Habitats Directive did not prevent species' status from deteriorating.

The reliability of modelling results heavily relies on the quality of the underlying data, including the reliability as well as the spatial and temporal availability of both observation and driver data. Unfortunately, the lack of available data on land use practices hinders scientific insights into one of the most influential anthropogenic drivers for insects. Furthermore, methodological challenges arise due to varying approaches to assessing species' long-term trends, difficulty defining a baseline for comparison, and different methods for determining a species' so-called status. Given the high level of taxonomic diversity in the class of insects, analysing a small number of taxa will only provide a partial understanding of the complex processes and interactions underlying observed patterns.

As full coverage of biodiversity is virtually impossible, computer models are increasingly used in biodiversity research to simulate and explore ecosystems. These models can be informed by historical and citizen science data, which complement professional data collection. By applying modelling methods, we can explore the links between human actions and their impact on biodiversity and thus highlight the need for more effective legislation to protect it.

The studies presented in this thesis suggest several possible directions for future research. Further exploration could include investigating additional attributes that may impact species' trends, such as species dispersal ability, phenology, and food resources. Another avenue is the expansion of occupancy-detection models to incorporate a broader range of insect taxa as well as a spatial component, enabling a more comprehensive evaluation of species' occurrence changes over time and space. Lastly, more explicit data on agricultural practices-related drivers are needed to identify their relative contribution to species trends. Combining these factors could inform strategies for building a more resilient environment for insects and people.

Although some initial steps have been taken to recognise insects' vital role in maintaining human well-being and improving their protection, there remains significant room for improvement. Achieving a sustainable future requires greater recognition of the importance of insects and biodiversity in general. To accomplish this, we must improve our understanding of the underlying values that inform stakeholders' divergent views. We may turn the tide for insects in the Anthropocene by emphasizing reciprocity in human-nature relationships while making substantial progress in maintaining and restoring biodiversity.

1 Introduction

1.1 The Era of the Anthropocene

The Earth's systems are progressively impacted by anthropogenic pressures, which are stressors caused or influenced by human activities connected to population growth. The global human population has grown considerably over the past centuries. About 200 years ago, the human population first reached one billion people at the onset of the Industrial Revolution (Roser, Ritchie, Ortiz-Ospina, & Rodés-Guirao, 2013). In mid-November 2022, the global population had grown to eight billion people (United Nations, 2023). Growth rates peaked in the early 1960s, and between 1950 and 1987, the population doubled at the fastest rate in history (Roser et al., 2013). As an intrinsic part of nature, the increasing human population competes with other animals for available resources (Navjot S. Sodhi et al., 2010). Anthropogenic pressures connected to food production, industrialization, and urbanization increased as well, as humans heavily modified the globe to suit our needs.

Based on humanity's exceptional influence on the whole Earth system, the start of a new geological epoch called the Anthropocene has been proposed (Crutzen, 2002; Steffen, Grinevald, Crutzen, & McNeill, 2011). The Anthropocene is defined as a geological epoch by anthropogenic deposits altering geochemical signatures, increased soil nitrogen and phosphorous levels, atmospheric CO_2 and CH_4 concentrations, and rising average global temperatures (Waters et al., 2016). Criticism included that the specific starting point is difficult to define and subject to debate (e.g., S. L. Lewis & Maslin, 2015) and that the Anthropocene

narrative obscures the social and economic structures that drive environmental degradation, such as the role of capitalism, colonialism, and other forms of exploitation (Malm & Hornborg, 2014). However, the Anthropocene is considered a comprehensive framework that is now frequently applied in the social sciences and humanities as it incorporates both the complex inter-human dynamics and their relationships with natural systems (Steffen et al., 2020).

It is irrefutable that human actions have and continuously do shape the Earth's main spheres: the atmosphere, geosphere, hydrosphere, and biosphere. Often the anthropogenic effects affect more than one sphere at once, showing the interconnectedness of the Earth's systems.

The atmosphere is the layer of gases that surrounds the Earth, regulates the Earth's climate, and protects the surface from harmful solar radiation. The Industrial Revolution led to the widespread adoption of fossil fuels, such as coal, oil, and gas, to fulfil the vastly increasing energy demand. While for many people the economic, social, and technological change improved their living conditions, burning fossil fuels releases greenhouse gases into the atmosphere, leading to global warming and climate change. The development of global mean surface temperatures in the past century (see Figure 1 Development of global mean surface temperatures in relation to the time frame of this thesis) has led many to call climate change the most pressing issue of our time. Although the effects of rising CO_2 emissions have already been identified in the 1980s (Hansen et al., 1988) and public awareness of human-caused climate change is ever-increasing, current global efforts to reduce

emissions are not sufficient (IPCC, 2022a). In contrast to other pollutant issues, such as the tackling of acid rain causing large scale forest diebacks in the 1980s, traditional end-of-pipe technologies are currently unavailable for CO2 reduction, implying that structural economic change, more efficient technologies, and new consumption patterns are necessary to tackle climate change (Hey, 2005). Additionally, the required policy changes affect a variety of different sectors, including among else transportation, energy, and agriculture.

The geosphere is the solid part of the Earth, including rocks, minerals, and landforms. Mining and drilling for resources directly impact the geosphere, just like the construction of buildings and infrastructure alters the landforms. At the same time, these actions can also lead to soil erosion.

The hydrosphere includes all water on Earth, including oceans, lakes, rivers, and groundwater. It is tightly linked to both the geosphere and atmosphere through the water cycle, and many human actions alter the components of this cycle. Direct alterations include, for example, the straightening of
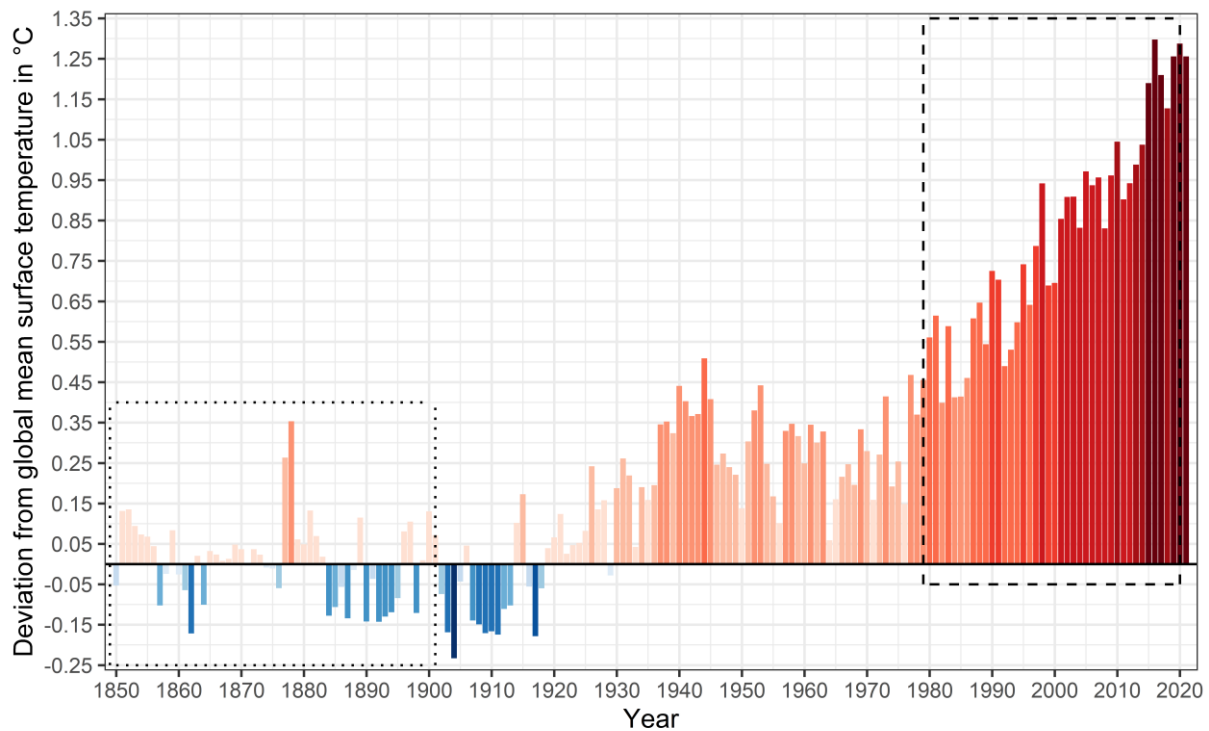
Source: Met Office Hadley Centre, Climate Research Unit; HadCRUT.5.0.1.0 model; median of 200 calculated time series

Figure 1 Development of global mean surface temperatures in relation to the time frame of this thesis. Temperature as deviation from global mean surface temperatures from 1850 to 1900, reference period indicated by the dotted box. The blue colour indicates negative deviations and positive deviations are indicated by the red colour scale, inspired by the 'warming stripes' (Hawkins, 2018). Global surface temperatures were stable during this period (GLM on temperature deviation - lower confidence interval -0.0035, upper CI 0.004). Temperatures as the median of 200 time series modelled using the HadCRUT.5.0.1.0 climate model, received from the Met Office Hadley Centre, Climate Research Unit (accessed on March 9, 2023). During the time frame of our study (1980-2019), indicated by the dashed box, global mean surface temperatures increased (lower CI 0.0167, upper CI 0.02183) significantly more than in the 40 years before (1940-1979), where temperatures remained stable (lower CI -0.0046, upper CI 0.0012), and more than in the period 1900-1939 where first temperature increases occurred (lower CI 0.0071, upper CI 0.0130).

rivers to control the meandering course of natural rivers, and pollution from agricultural or industrial activities can contaminate water bodies.

The biosphere describes all living organisms, including plants, animals, fungi, and microorganisms. The biosphere depends on the geosphere, atmosphere, and hydrosphere to provide liveable conditions for organisms. The other way around, organisms also influence the other spheres, with humans being the best example of a highly influential organism.

Anthropogenic land use has drastically changed all four Earth system components. In the past 300 years, the terrestrial biosphere was transformed from wild and semi-natural to anthropogenic.

Ellis et al. (2010) suggest that nowadays, the Earth's habitats should be classified into 'Anthromes' instead of biomes, which are broad generalizations of global patterns of ecosystem structure and function that mirror the anthropogenic influences on the naturally present biomes. The expansion of pastures, crops, and urban areas was the dominant land use change during the Industrial Revolution, with pastures expanding from 3 % to 26 % of ice-free land, crops rising from 2 % to 12 %, and urban areas increased by a factor of 40 to 0.4 % between 1700 and 2000 globally. The most dramatic transformations occurred in the 20th century.

The European continent was already mostly used in 1700, with relatively few wild and semi-natural habitats remaining (Ellis et al., 2010). With increasing industrialization in the 18th and 19th centuries, however, the growth of cities and towns led to the conversion of both agricultural and natural areas into urban areas and industrial sites, and

thus losses of potential habitats. Today, Europe is one of the most urbanized regions in the world. In parallel, agricultural practices became continually more intensive and expanded into new areas, e.g., due to the straightening of meandering rivers starting in the 19th century. Areas of natural and semi-natural vegetation were lost due to land use change and fragmentation (Krause, Culmsee, Wesche, Bergmeier, & Leuschner, 2011), while eutrophication strongly affected the vegetation composition (Meyer, Wesche, Krause, & Leuschner, 2013; Wesche, Krause, Culmsee, & Leuschner, 2012). Plant species composition changed drastically, with many grassland species in continuing decline over the past century (Jandt et al., 2022). The most substantial recent declines happened between 1960 and 1980 (Eichenberg et al., 2021), and decreases particularly affected insect-pollinated herbs (Wesche et al., 2012). Due to the ongoing multilevel biodiversity decline, the Earth's systems are likely facing a sixth mass extinction crisis (Ceballos, Ehrlich, & Raven, 2020; Cowie, Bouchet, & Fontaine, 2022).

1.2   Insects in the Anthropocene

Insects are essential for the health and sustainability of ecosystems and, thus, human societies. They play an essential part in every terrestrial food web, for example, by serving as food for numerous vertebrate species, controlling pests, recycling nutrients, and pollinating large proportions of vascular plants (Goulson, 2019). 75 % of cultivated plants and up to 94 % of wild plants are pollinated by animals (Ollerton, Winfree, & Tarrant, 2011; Vanbergen et al., 2013), the vast majority of which are insects. Insect pollination of crops accounted for

€14.6 billion annually (1991-2001) across Europe, with increasing economic importance over time (Leonhardt, Gallai, Garibaldi, Kuhlmann, & Klein, 2013). Without insects, both freshwater and terrestrial ecosystems would collapse.

Even though insects are a fascinating, multifaceted, and exceptionally diverse class that is highly important for ecosystem services as well as for the maintenance of functioning ecosystems, our current knowledge of insects is limited. Species data is especially biased toward larger species, with a negative relationship between a taxon's average body size and the estimated percentage of dark taxa (Morinière et al., 2019). A study from Canada on insect barcodes suggests that the global number of gall midges alone could exceed the number of all previously described animal species worldwide (Hebert et al., 2016). Even in countries with extensive taxonomic research throughout history, such as Germany, insects are vastly understudied, especially small-sized groups like parasitic wasps. Between 2011 and 2021, insect collections at about 35 sites across Germany lead to the discovery of 41 pteromalid species previously unknown to occur in Germany (Haas et al., 2021), for most of whom their biology, hosts, and interaction partners are still unknown. Due to their large numbers, these small species probably play an essential role in the functioning of ecosystems globally. Nevertheless, they are barely known and highly likely to be threatened by anthropogenic pressures.

1.2.1 Insect Trends

In recent years, an increasing number of studies revealed a global decline across multiple metrics of insect diversity, including species richness, biomass, and abundance. These declines have been noticeable since the 1950s, but the most severe losses likely occurred in the last two decades (Habel et al., 2016). Burkle et al. (2013) discovered a degradation in both the interaction network function and structure along with the extinction of half the bee species over the past 120 years in Illinois (USA). Insect occurrence data points to reduced diversity of bee species worldwide (Zattara & Aizen, 2021). In Ohio (USA), butterfly abundance declined by a total of one-third over 21 years (Wepprich, Adrion, Ries, Wiedmann, & Haddad, 2019), and in southwest Germany, butterfly and burnet moth abundance declined for two-thirds of the species (Habel, Trusch, Schmitt, Ochse, & Ulrich, 2019). Such abundance declines are tightly linked to biomass declines, as, for example, hoverflies in Germany showed an abundance decline of 89 % in combination with a biomass decline of 82 % (Hallmann, Ssymank, Sorg, de Kroon, & Jongejans, 2021). In Puerto Rico, both the biomass and abundance of arthropods have shown substantial declines since the 1970s, and at the same time, declines in insectivorous lizards, frogs, and birds have been observed (Lister & Garcia, 2018).

Some studies, however, also report more ambiguous insect trends. In the Netherlands, over 20 years, the abundances of moths, beetles, and caddisflies declined at a rate of 3.8 % annually in moths (macro-Lepidoptera), 5 % in beetles (Coleoptera), and 9.2 % in caddisflies (Trichoptera), while lacewings (Neuroptera) showed non-

significant declines. True bugs (Hemiptera: Heteroptera and Auchenorrhyncha) and mayflies (Ephemeroptera) remained stable (Hallmann et al., 2020). Similar ambiguous trends occurred across the US long-term research areas, where the abundance of some taxa, like ants, increased, while others, like bark beetles or butterflies and moths, decreased (Crossley et al., 2020). In the same study, grasshopper abundance increased at two sites but decreased at two others. These ambiguous findings indicate the need for large-scale, multi-taxon analyses on the state of insect diversity.

1.2.2 Drivers of Insect Trends

A threat's impact on species is mediated by a combination of the species' sensitivity and exposure to the threat. While species' sensitivity might be a question of their adaptability, human actions have tremendously increased exposure to multiple threatening factors. In addition, there is a high potential for interactive effects of different drivers.

The causes of insect change are subject to heated debates in the science community and the public. The most important drivers identified vary depending on where the focus is set (Dirzo et al., 2014; Wagner, Grames, Forister, Berenbaum, & Stopak, 2021). However, there is a broad consensus that the observed insect declines are most likely connected to a combination of anthropogenic pressures, including climate change, agricultural intensification along with long-term pesticide exposure and eutrophication, as well as habitat loss and fragmentation (Goulson, 2019; Potts et al., 2010; Scherber, 2015). Often there is no simple cause, but multiple stressors act

together, like land use in combination with climate change. Thus far, the spatial correlations between climate change effects and human pressures are low (Bowler et al., 2020), and discussions emerge over whether the direct effects of rising temperatures will be the most influential driver (Bale et al., 2002), or whether the more pressing causes of biodiversity loss are habitat loss and overexploitation (Caro, Rowe, Berger, Wholey, & Dobson, 2022; Dale, 1997). A broader overview of drivers of insect decline can be found, for example, in Wagner et al. (2021), while the following section focuses on those factors affecting insect trends relevant to this thesis.

Climate Change

The early onsets of climate warming already affect different aspects of insect lives (Boggs, 2016; Wilson & Maclean, 2011). Since insects have short life cycles that are often determined by ambient temperatures, they are likely to be highly susceptible to changing climatic conditions (Crossley et al., 2021; M. L. Forister et al., 2021). Both gradual long-term climatic changes and more frequent extreme events affect individual insect species as well as species interactions (Harvey et al., 2022; Wagner et al., 2021) since a more extreme climate leads to thermal stress (IPCC, 2022b) which results in either extinction, changes in distribution, or physiological or morphological adaptation of the species.

In regions where species are no longer adapted to the changing environmental conditions due to rapid climate change, biodiversity is under threat (Díaz et al., 2019; Goulson, 2019; C. D. Thomas et al., 2004). Higher rates of climatic change foremost affect areas with lower human pressures in terrestrial realms (Bowler et al., 2020), creating another factor of uncertainty where species could so far find refuge from more direct anthropogenic pressures.

Land Use Change

Land use change has been identified as a major source of biodiversity erosion, habitat fragmentation, and habitat loss (Maxwell, Fuller, Brooks, & Watson, 2016). Land use change includes all transformations of natural or semi-natural habitats to anthropogenic structures. These include conversion to agricultural, urban, or industrial areas and infrastructure, but also subsequent transformations of the previous habitat due to the intensification of land use for forestry and agriculture or land abandonment. Land use change also occurs the other way around in forms of renaturation; however, the expenditures allocated to renaturation projects are substantially less compared to expenses on conversions towards anthropogenic structures, as evidenced by a significant disparity between the respective budgetary allocations. For example, in 2019, the German federal government spent €1.7 billion on all types of species and landscape protection, compared to €7.8 billion on road infrastructures (Pro Mobilität, 2022; Statistisches Bundesamt, 2022).

One aspect of land use change is the fragmentation of previously large areas of suitable habitats into smaller subplots, leading to decreasing habitat size and habitat loss. Classic species-area-curves suggest a logarithmic increase of species numbers with increasing patch size (Brückmann, Krauss, & Steffan-Dewenter, 2010; Krauss, Steffan-Dewenter, & Tscharntke, 2003), indicating that smaller habitats inhabit fewer species than larger habitat patches. The size of the remaining habitat patch appears to be more important than overall habitat availability on the landscape level, as larger coherent areas support both butterfly specialists with low dispersal ability (Dapporto & Dennis, 2013) and grasshoppers with increased flight ability as well (König & Krauss, 2019).

Especially specialized species live in island-like ecosystems across central Europe and strongly decline with decreasing patch size (Brückmann et al., 2010; Krauss et al., 2003). Dapporto & Dennis (2013), however, found that both extreme specialists and extreme generalists are able to adapt to highly fragmented habitats. Since specialists monopolize restricted resources while generalists move among patches to use all available resources, the left-over intermediate species might suffer the most from fragmentation.

The ability of species to persist in fragmented landscapes among else depends on their dispersal ability, where good dispersers are better equipped to persevere. The impact of habitat fragmentation on animal movement affects the genetic admixture of the populations of a species. Significant genetic dissimilarity among butterfly individuals (*Phengaris teleius*) appeared at a distance of 1800 km at unfragmented Asian sites, but at only 400 km at European sites, with an atypical genetic structure in the Bavarian region (Śliwińska et al., 2021).

Some conservation efforts focus on creating connecting corridors between habitat patches to enhance dispersal between island-like ecosystems. The habitat quality of these corridors is important for butterflies, especially for specialists, where for example, a high abundance of flowering plants supports species and population persistence (Habel, Ulrich, & Schmitt, 2020). Studies provide great detail on what kind of vegetation is needed to promote biodiversity (for example, Threlfall *et al.* 2017; Mody *et al.* 2020), including extensive lists of garden flowers, for example, suitable for central European pollinators (Nichols, Goulson, & Holland, 2019; Rollings & Goulson, 2019). This knowledge should influence available ready-made seed mixtures (Kuppler et al., 2023) to enhance the quality, especially of urban habitat patches.

Agricultural production increasingly utilizes more intensive production techniques, including large machinery and high amounts of chemicals. These practices put biodiversity under increasing pressure (Henle et al., 2008; Stoate et al., 2009). In areas of intensive agricultural use, the availability and diversity of food resources tend to be low, while pesticide exposure increases (Centrella et al., 2020; Parreño et al., 2022). Pesticide exposure has been shown to negatively affect insect trends (Beketov, Kefford, Schäfer, & Liess, 2013; Ewald et al., 2015), as has exposure to high nitrogen deposition levels (Nijssen, WallisDeVries, & Siepel, 2017). While some specific substances, such as Neonicotinoids, have been specifically criticized (Hallmann, Foppen, Van Turnhout, De Kroon, & Jongejans, 2014), many of the effects of pesticide and nitrogen deposition are indirect (see, for example, Vries *et al.* 2007) and unintended,

often leading to the opposite effects to what the applicants wanted to achieve (Sánchez-Bayo, 2021).

Where agriculture is increasingly intensified, species need other areas to retreat to. Adjacent natural habitats may mitigate declines on agricultural land, especially in low-intensity agricultural systems (Outhwaite, McCann, & Newbold, 2022). Land left fallow is an important factor here; however, it is often viewed more from the perspective of influencing the amounts of goods produced and less from a nature protection point of view (Leopoldina - Nationale Akademie der Wissenschaften, Acatech - Deutsche Akademie der Technikwissenschaften, & Union der deutschen Akademien der Wissenschaften, 2020). Additionally, abandonment of previous land use, especially traditional forms, threatens insect species. As many species rely on specific microclimatic conditions mediated by certain vegetation structures, especially already threatened specialist species suffer from land use abandonment (Modin & Öckinger, 2020; Scherer, Löffler, & Fartmann, 2021). Another option is organic farming, which supports higher biodiversity, including threatened species, than conventional agricultural areas (Hausmann, Segerer, et al., 2020). However, the debate about the effectiveness of organic farming for nature protection is ongoing (e.g., Tscharntke *et al.* 2021; Eichler *et al.* 2022).

Changing Biotic Interactions

Climate and land use change affect species directly, altering their abundance, and spatial or phenological occurrence, which in turn affects all species that interact with each other. Butterfly presence, for example, depends not only on the habitat size itself but also on the area covered by their food plants (Krauss, Schmitt, Seitz, Steffan-Dewenter, & Tscharntke, 2004). Koh et al. (2004) showed the link between local extinctions of butterfly species and the combination of the loss of their larval host plants and direct impacts. Any alterations in biotic dependencies can lead to species declines, including, for example, changes in plant-pollinator networks due to invasions of new plant species (Mathiasson & Rehan, 2020). Thus, a strong dependency on another species could be considered a general risk factor.

Biotic interactions are affected by agricultural practices on agricultural lands and beyond, as both herbicide and nitrogen deposition change the available plant resources and microhabitats. Especially nutrient-poor ecosystems change rapidly under nitrogen deposition, for example, calcareous grasslands, bogs, and heathlands (Habel et al., 2016; Stevens, Dise, Mountford, & Gowing, 2004; Vries et al., 2007). Changes in the available vegetation subsequently affect those species reliant on specific vegetation structures and infertile soil conditions (Filz, Engler, Stoffels, Weitzel, & Schmitt, 2013; Filz, Wiemers, Herrig, Weitzel, & Schmitt, 2013; Stevens et al., 2004; Wenzel, Schmitt, Weitzel, & Seitz, 2006). At the same time, species from more productive environments increase (WallisDeVries & van Swaay, 2017). The subsequent adverse effects on insects have been shown, for example, for wild bees, whose health is highly dependent on biodiverse landscapes (Kaluza et al., 2018; Trinkl et al., 2020). In addition, wild bees face a peak foraging difficulty in the late season due to changes in available flowering plants, which likely affect other insect taxa as well (Garbuzov et al., 2020).

Often, species' ability to adapt to changing climatic conditions depends on their interaction partners and whether they are both able to adapt or disperse into new habitats (HilleRisLambers, Harsch, Ettinger, Ford, & Theobald, 2013; Stewart et al., 2015). Cahill et al. (Cahill et al., 2013) suggest that, so far, more extinctions have occurred as a result of species interactions than as a direct consequence of climate change. Biotic interactions have been found to affect warm limits to species' ranges more than cool limits (Paquette & Hargreaves, 2021) and might lead to faster or slower range shifts than would be anticipated from climate dynamics alone, indicating their specific importance under global warming. Some relationships may be disturbed under changing environmental conditions, while at the same time, chances for new interactions arise (Stewart et al., 2015). Such newly emerging assemblages and dynamics are yet difficult to predict.

Climate change, land use change, and the often unknown interaction network between species present highly complex combinations of risk factors. Even where single species' direct responses to anthropogenic threats would be possible to predict, simply multiplying the outcomes of single-species responses does not fully recognize all the implications for community composition, stability, and ecosystem functioning (Berg et al., 2010). These communities comprise a multitude of species, often still unknown and

undescribed, with unique responses to changing environments.

Protection Efforts

Although nature protection has a long history in human societies, the concept of conservation is a discipline of Western culture (Navjot S. Sodhi et al., 2010). Along with rapid industrialization in the 19th century, the concept of nature conservation gained widespread acceptance across Europe, with Marsh (1865) and Wallace (1863) being recognized as thought leaders. In the early 20th century, many of the problems we face today, such as soil erosion, urban pollution, deforestation, and a decline in wildlife populations, were already known, as well as a general concept of the value of biodiversity. However, only in the mid-1980s did conservation biology emerge as a new interdisciplinary field combining insights from biological sciences with the humanities, social sciences, and ethics.

Insect conservation is a relatively recent phenomenon. Due to growing concerns about the decline of insect populations worldwide, various global efforts have been initiated to protect both insects and their habitats. The United Nations has declared 2020 to 2030 as the "Decade of Ecosystem Restoration" (FAO - Food and Agriculture Organization of the United Nations, 2019), aiming to promote the restoration of ecosystems and enhance biodiversity. The Convention on Biological Diversity (CBD) has also set a target to conserve at least 30 % of the world's land and sea areas by 2030, with a specific focus on protecting insects and other invertebrate groups (Convention on Biological Diversity (CBD), 2022). Various national and international organizations work towards protecting global biodiversity, with an increasing focus on insects.

Although insect declines are often occurring where human density and thus habitat destruction is highest (Conrad, Woiwod, Parsons, Fox, & Warren, 2004; Matthew L. Forister et al., 2010), declines happen in protected areas as well (as shown, for example, by Hallmann *et al.* 2017; Rada *et al.* 2019), suggesting that current protective efforts are not sufficient (Maes et al., 2013). Some claim that, even though we still lack large-scale patterns on the severity of insect trends, existing studies are convincing enough to warrant rapid action to protect insect biodiversity globally (Harvey et al., 2022; Montgomery et al., 2020; Samways et al., 2020).

1.2.3   Research Gaps

Although the research body on insects, their trends, and the drivers of these trends is continually and strongly increasing (compare Figure 2), there remain significant limitations to our current knowledge. Hausmann et al. (2020) point out some common limitations in studies on insect trends. First, some studies only refer to single or few species, thus, inference to an overall trend is impossible. Second, many studies only consider a few time steps (for example, Wenzel *et al.* 2006; Augenstein *et al.* 2012; Filz *et al.* 2013b; Hallmann *et al.* 2017), so that the identified changes may be affected by natural fluctuations in insect numbers, which in some cases are up to one or two orders of magnitude between just two generations (Wagner, 2020). Third, the collected data is often geographically restricted, making it difficult to generalize to other regions (Habel et al., 2016) as small-scale community responses may be disconnected from macroecological trends (Ferrín et al., 2023). Last, available long-term datasets are often of low quality and include data gaps. Many studies combine multiple limitations (McGill, Dornelas, Gotelli, & Magurran, 2015), which need consideration when analysing and discussing insect trends.

1.3   Central Europe: An Anthropogenic Landscape

Central Europe is a relatively densely settled area, and the land is mainly under agricultural use (Hodge, Hauck, & Bonn, 2015). There is essentially no primary forest remaining, although the percentage area covered by forest is not much different from non-European countries. Compared to other
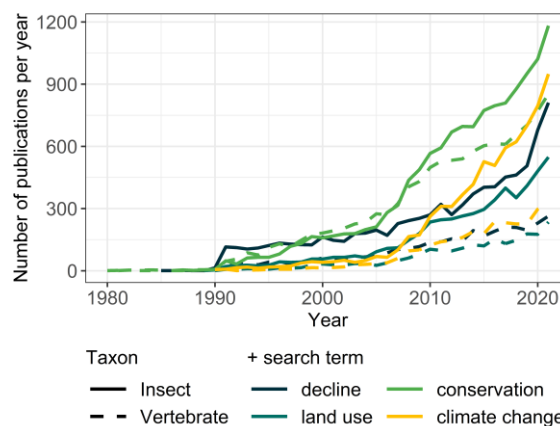
Figure 2 Results of a brief 'Web of Science' search for the number of publications on either insects (solid lines) or vertebrates (dashed lines) in combination with one of the search terms decline (dark green), land use (medium green), conservation (light green), or climate change (yellow), published from 1980 to 2021 [date accessed: 07.09.2022], providing a snapshot view into the growing research body on insect trends and their drivers.

continents, Europe has far fewer remaining natural or semi-natural areas, and the countryside is characterized by high-intensity land use within comparably small agricultural holdings, leading to a mosaic-like landscape structure. While individual protected areas are typically relatively small, the proportion of land under some form of protection tends to be greater in Europe than on other continents.

Europe is among the wealthiest regions globally. The European Union's efforts to protect insects may serve as an example for other regions to follow while striving to improve human living conditions. Thus, identifying the causes of insect decline in Central Europe is essential to preserve ecosystems alongside human livelihoods.

Central Europe is globally the region where the most substantial and most consistent insect declines (e.g., Maes & Van Dyck 2001; Conrad *et al.* 2004; Thomas *et al.* 2004b; Wenzel *et al.* 2006; Fox 2013), as well

as shifts in species composition (for example Habel et al., 2016), have been reported. Hallmann et al. (2017) showed that the biomass of insects across Germany decreased by 75 % in 27 years, bringing widespread attention to the problem (e.g., by the New York Times, Jarvis 2018).

1.3.1 A Brief History of Conservation Efforts in the European Union

In the European Union, many issues regarding nature conservation have a long history (Hey, 2005), which needs consideration when assessing long-term biodiversity trends. Following the increasing industrialization in Europe and elsewhere, the publication of Rachel Carson's "Silent Spring" in the 1960s sparked ecological awareness, as well as more and more concerns about poisonous chemicals in the environment.

In the 1970s, environmental movements gained momentum in Europe, leading to the establishment of several organizations dedicated to protecting nature and advocating for sustainable development. This led to the adoption of the European Union's Environmental Action Program (EAP) in 1973, which set out a framework for environmental policy in Europe (Hodge et al., 2015). This first programme already included many ideas on sustainable development still on the agenda today; however, the ambitious targets had a focus on pollution control rather than conservation. The first conservation target for wild birds, named the Birds Directive (Council Directive 79/409/EEC, 1979), lacked a quantitative side necessary to measure progress.

In the 1980s, the Environmental Action Program changed towards focusing on the effects of environmental policies for the EU's internal market and on 'clean-air' policies, partly resulting from discussions in Germany on the forest dieback caused by acid rain (Hey, 2005).

The early 1990s were characterized by a "roll-back of environmental policies" so that at the end of the decade, the European environmental policies were a patchwork of, in part, contradictory, vague approaches lacking commitment and innovation. Environmental policies were split into sectors, including air, waste, water, and nature. Each sector separately identified common problems and schemes to tackle these. At the same time, actors on the European level managed to establish a system of environmental programmes, including incentives, rights, and duties for member states. They bypassed traditionally vetoing legislators so that European national environmental policy was and still is increasingly driven by the European Union.

The European Habitats Directive was adopted by the European Commission in 1992 (Council Directive 92/43/EEC, 1992) and aimed at extending the protection programs of the Birds Directive (Directive 79/409/EEC). Both Directives combined are the legal foundation of the Natura 2000 protected area network program. The Habitats Directive extends the protection network to a wider variety of both habitats and species to "ensure the long-term survival of Europe's most valuable and threatened species and habitats" (European Commission, 2020a). Annex I of the Directive lists the habitats considered, and Annex II and Annex IV list the species

protected under the Directive (henceforth called annex species).

The Directive imposes numerous obligations on member states. Among else, the European countries are required to install protected areas (Special Areas of Conservation, SACs) for Annex I and II habitats and species. The Directive demands the establishment of management plans for the SACs to restore and sustain optimal conditions, such as adapting mowing periods to support butterfly development (see, e.g., Dolek *et al.* 2017). Species listed in Annex IV should be protected across their entire range. The countries must also submit regular reports on the status of all annex species every six years, starting in 1998.

In 2003 the annexes were amended, among else, by adding more butterfly and dragonfly species to the lists (*Colias myrmidone, Lycaena helle,* and *Coenagrion ornatum* are relevant in the context of this thesis). Currently, 117 insect species are listed in the annexes, but the composition of the annexes is frequently criticized. For example, threatened dragonfly species not covered by the Directive are more likely to have a decreasing population trend than annex species, and the trends of 26% of threatened non-annex species are unknown (Tang & Visconti, 2021).

Another essential legislative feature has been the European Water Framework Directive (Directive 2000/60/EC, 2000). Adopted in 2000, it sets out a framework for the management of water resources to achieve a "good ecological status" for all surface waters by 2015. The Directive includes measurable objectives for water quality and quantity and a monitoring network for water quality. Although

challenges remain, the Directive has led to considerable improvements in the quality of many water bodies across the EU (Termaat, Van Grunsven, Plate, & Van Strien, 2015).

The European Union's 7th Environmental Action Program, which covered the period from 2013 to 2020, identified seven priority areas for action, including climate change mitigation and adaptation, sustainable use and management of natural resources, and protection of biodiversity and ecosystems (European Commission & Directorate-General for Environment, 2014). It emphasized the importance of mainstreaming environmental considerations into other policy areas and developed tools to support this goal, including, for example, environmental impact assessments. Nevertheless, there are substantial gaps in the integration of nature conservation into other policies and in the consistency of policy (Hodge et al., 2015; Scheuer et al., 2005).

Although the Habitats Directive prohibits habitat degradation and requires species' statuses to at least remain stable, the EU's aim of stopping biodiversity loss by 2010 was not met (Butchart et al., 2010; European Environment Agency, 2009). Implementing the Directive into national law is required; however, the implementation details are subject to each nation's interests (Jeanmougin, Dehais, & Meinard, 2017). Member states often insufficiently comply with the requirements set up by the Habitats Directive (López-Bao et al., 2015). Several of the habitat types listed in Annex I are in poor or inadequate condition and continually degrading (in Germany, for example, Adelmann *et al.* 2017). Disputes emerge due to competing land use goals, with conservation programs being underfunded

compared to, for example, the European Common Agricultural Policy (CAP) (Hodge et al., 2015).

1.3.2 The European Union's Common Agricultural Policy

As agricultural land is Central Europe's largest land cover type, the European Union's agricultural policy significantly affects European land use and, thus, insect trends. Development in farming practices linked to accelerating production intensification, structural changes of agricultural holdings, and the abandonment of traditional management practices significantly affected rural environments (Henle et al., 2008; Stoate et al., 2009).

To align environmental policies with agricultural practices, agri-environmental programs have been developed within the Common Agricultural Policy (CAP) framework since the mid-1980s, by now including probably over 355 schemes funded by the European Union (G. Purvis et al., 2009). Due to the considerable influence of agricultural interests, agri-environmental schemes compensate for the voluntary utilization of less harmful practices instead of prohibiting harmful practices (Hodge et al., 2015).

One environmental scheme with strong positive effects on biodiversity was the land left fallow program, established in the 1990s for economic reasons (Leopoldina - Nationale Akademie der Wissenschaften et al., 2020). Fallow lands increasingly enhanced biodiversity the longer they existed (Feng, Arvidsson, Smith, & Birkhofer, 2021), but after the economic situation changed again, the program was stopped in the early 2000s.

Agricultural practices also strongly affect insects in areas not targeted by the actions. In Germany, insects in conservation areas are directly exposed to pesticides (Brühl et al., 2021). Pesticide application is allowed within protected areas, as they are part of the "good agricultural practices" guidelines by the responsible German federal ministry (BMELV, 2010). Some argue that protected areas require a buffer zone of at least 2 km to conventional field sites to protect biodiversity from impacts of pesticide, herbicide, and fertilizer application (Brühl et al., 2021), which, for example, in Germany, would entail one-third of all agricultural areas. Aligning with that suggestion, according to the European Union's 'Farm to Fork Strategy' (European Commission, 2020b), one-third of agricultural areas should become organically managed. However, it is unclear whether organic agriculture works as a buffer for biodiversity (Eichler et al., 2022), and others argue that organic farming is not the ultimate solution for harnessing biodiversity (Tscharntke et al., 2021).

1.3.3 Insect Monitoring in the EU

A lack of sufficient monitoring data is obstructing current efforts in insect conservation. The European Biodiversity Observer Network (EuropaBon) identified the most critical challenges of current biodiversity monitoring in Europe, where a lack of long-term policies for monitoring was the most prominent challenge, followed by, among else, under-representation of taxa, insufficient spatial coverage, and lack of (raw) accessible data (Moersberger et al., 2022). On the other hand, emerging tools such as molecular methods, computer vision,

acoustic monitoring, or radar present immense potential for insect research by enhancing taxonomic, temporal, and spatial coverage (van Klink et al., 2022), especially for wealthy countries. Previously unknown species' interactions have been discovered by applying such new technologies (Hrcek, Miller, Quicke, & Smith, 2011; Thomsen & Sigsgaard, 2019), ecosystem services such as pollination have been quantified (Bjerge, Mann, & Høye, 2022; Ratnayake, Dyer, & Dorin, 2021), and insights into insect migration have been improved (Hu et al., 2016), showing technology's immense potential to enhance biodiversity research.

The European Union aims to start a Pollinators Initiative in the mid-2020s to systematically monitor hoverflies, wild bees, butterflies, and moths. Currently, the EU is running programs like "Taxo-Fly" (basic taxonomy and identification of European hoverflies), ORBIT (wild bee monitoring), and "STiNG" (science and technology for pollinating insects) to create the basis for a large-scale monitoring program. However, these crucial efforts to streamline monitoring programs on the European level should not divert from necessary action for insect protection now.

The European Union is working towards a knowledge centre for biodiversity, with a biodiversity information system for Europe (BISE), a European biodiversity portal (EU BON), and streamlined European biodiversity indicators (SEBI). Many long-term studies on the European continent use data from the UK, where for example, the Biological Records Centre (BRC) and the British Trust for Ornithology (BTO) work on an excellent monitoring network. While different national monitoring schemes across

the European Union are collaborating for some taxa, for example, within the European Butterfly Monitoring Scheme (eBMS), efforts still depend on local contributors. However, until national or European monitoring schemes are implemented, and data are analysed, we argue for the importance of immediate action towards improved insect protection based on the knowledge gained from already available data.

1.4 Aims and Structure of this Thesis

In this thesis, common limitations of studies on insect trends (compare section 1.2.3) are considered, and these challenges were addressed using an exemplary dataset from a Central European model region, the German federal state of Bavaria.

This thesis aimed to analyse high-quality, reliable, but also highly heterogeneous observation data provided by the Bavarian agency for the environment (Bayerisches Landesamt für Umwelt, LfU, see section 2.2.1) to generate reliable occupancy estimates for butterflies (Lepidoptera – Rhopalocera), grasshoppers (Orthoptera), and dragonflies and damselflies (Odonata, henceforth summarized as dragonflies) and connect species' occupancies to different types of attributes possibly affecting their trends (section 2.2.2).

The first objective was to compute annual occupancy estimates using occupancy-detection models (section 2.3.3) to assess trends in species distribution over time while considering the apparent biases in the data (section 2.3.1). The usefulness of computational models to fill research gaps (section 4.1) is discussed, but also the

limitations to consider when interpreting modelling results (section 4.2), deliberating the data basis (section 4.2.1) as well as different approaches to assessing species' long-term trends (section 4.2.2) and the representativeness of the analysed taxa (section 4.2.3).

The second objective was to identify potential drivers of occurrence change and assess how these could affect trends in species occupancy (section 2.3.4, section 2.3.5). The effect the availability of driver data (section 4.2.4) has on our current knowledge about drivers of insect trends is discussed.

The final objective was to evaluate the potential impact of the European Habitats Directive on monitoring efforts (section 2.3.2) and trends (section 2.3.4) in species protected by the Directive's annexes.

Figure 3 Conceptual framework of data analyses and resulting papers presented in this thesis.sketches the conceptual framework of data analyses and resulting papers presented in this thesis.

In **Chapter 1**, we used occupancy-detection models to analyse occurrence records of 300 insect species over 40 years. We assessed species' linear trends and tested several attributes as proxies for drivers of their occurrence change. We identified climate warming as the most influential, consistent driver for all three taxa. Butterflies showed the weakest effects of climate warming but additionally, significant effects of habitat specialization, hinting towards more complex patterns in this group.

In **Chapter 2**, we focused on myrmecophily as another facet of butterfly specialization that could potentially influence species' long-term trends. In contrast to our expectations, obligate myrmecophile Lycaenid butterfly species showed slightly more favourable trends than ant-independent Lycaenids; however, the difference was insignificant.

In **Chapter 3**, we assessed changes in several monitoring metrics as well as species trends before and after the implementation of the European Habitats Directive. While we found increased monitoring efforts after the implementation of the Directive, species trends remained ambiguous, indicating that the current state of nature protection under European law benefits some, but not all, of the target species.

Implications of our findings for insect biodiversity in the model region (section 4.3) are discussed, concluding that species composition is changing (section 4.3.1) probably due to a combination of ambiguous outcomes of conservation efforts (section 4.3.2), a consistent effect of climate warming (section 4.3.3), biotic interactions (section 4.3.4), and complex other factors related to species' habitat characteristics (section 4.3.5). Possible next steps to deepen our understanding of insect biodiversity change with a focus on the study region (section 4.4) are proposed, including analyses on further species' characteristics which might affect their reactions to anthropogenic threats (section 4.4.1), further extending occupancy-detection models (section 4.4.2), and what would be needed to specifically address land use in analyses such as these (section 4.4.3). The discussion summarises in a conclusion (section 5), and I close this thesis with a personal outlook (section 6).
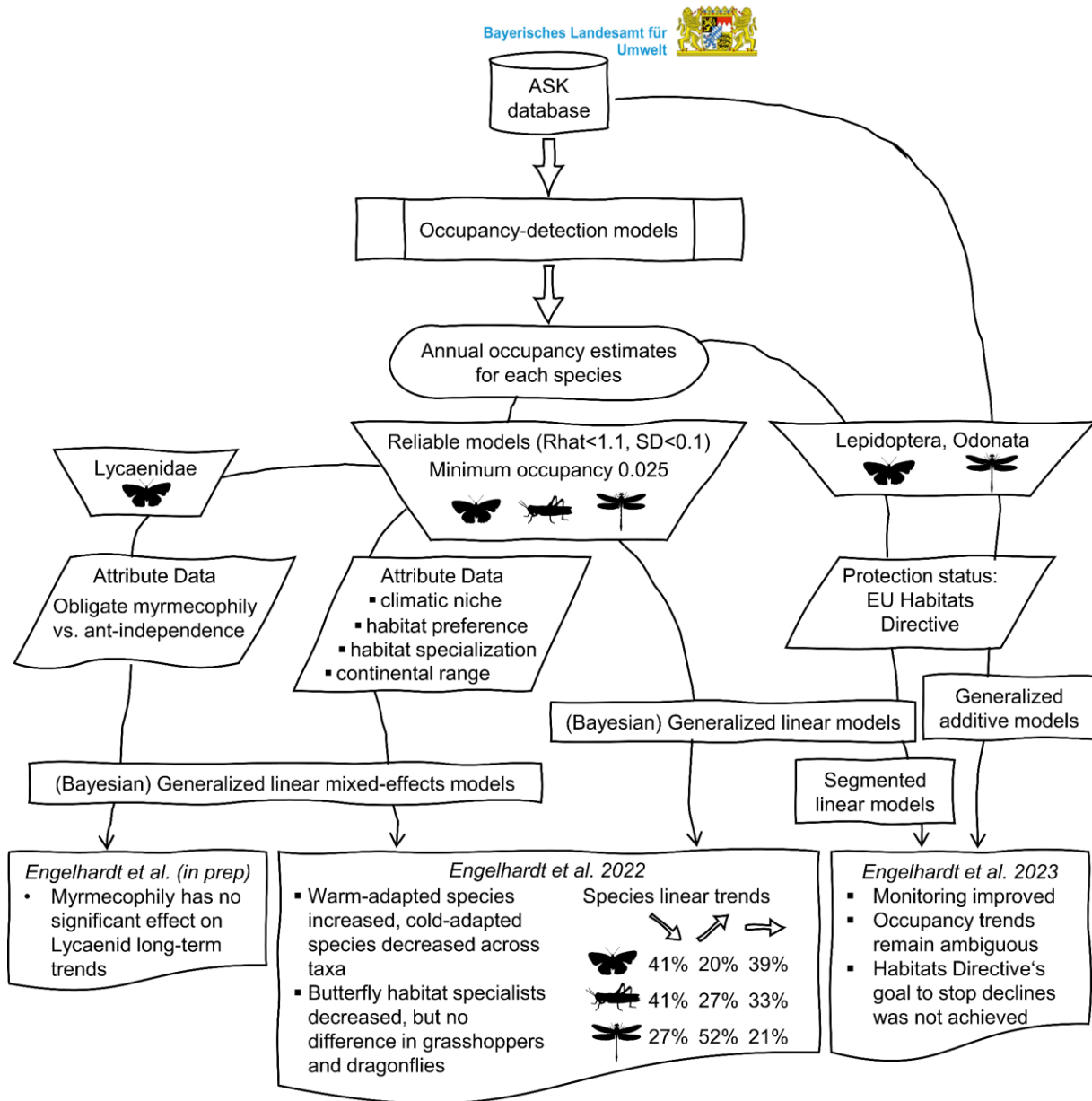
Figure 3 Conceptual framework of data analyses and resulting papers presented in this thesis. Chapter 1: Engelhardt et al. (2022a) bottom center, Chapter 2: Engelhardt et al. (*in prep*) bottom left, and Chapter 3: Engelhardt et al. (2023) bottom right.

2 Methods

For the analyses, we used R version 3.3.3 to version 4.2.0 (R Core Team, 2022) via RStudio version 1.1.4 – version 2022.12.0 (RStudio Team, 2020). Code for graphics and analyses presented in this thesis is given in Appendix D: Code Further, we used Inkscape (Inkscape Project, 2020) for image editing.

2.1 Study Region: The German Federal State of Bavaria

2.1.1 Location, Landscape, and Climate

The German federal state of Bavaria is located right in the centre of the European Union (about 47°-50° North and 8°-14° East, compare Figure 4 A) and features a diverse range of climatic conditions, habitats and land use forms (Dalelane, Früh, Steger, & Walter, 2018; Dou et al., 2021). It covers an area of 70,542 km² (Bayerische Landesanstalt für Landwirtschaft, 2018) and has borders with the Czech Republic, Austria, Switzerland, and the German federal states of Saxony, Thuringia, Hesse, and Baden-Wurttemberg. While the Alps in the south of the state create a barrier, species from southern Europe can migrate via the Rhine-Main River connection in the western and via the Danube River in the eastern direction (see Figure 4 B).

Bavaria is characterized by a mosaic system of different land cover types (Dou et al., 2021). Most of the state is under agricultural use (46 %), 35 % is covered by forest predominantly used for forestry, and almost 12 % of the area is overbuilt (Bayrisches Landesamt für Statistik, 2020). About 12 % of the area is under different

forms of nature protection, including two national parks with the strongest protective power making up about 0.64 % of the state area, and about 11 % Natura 2000 sites (Bayerisches Staatsministerium für Umwelt und Verbraucherschutz, 2021). Bavaria is a highly heterogeneous region (compare Table 1), where both intensification of agriculture, as well as abandonment have significantly altered the land's cover and use.

The climate in Bavaria is continental, with higher temperatures in the northeastern parts and lowest in the south. Overall, the annual mean temperature (1971 to 2000) was 7.8 °C, with more than 100 days per year with a minimum temperature lower than 0 °C and five hot days exceeding 30 °C per year. Mean precipitation was higher during the summer months from May to October, with 533 mm than during the winter months (400 mm) (Danneberg et al., 2012).

Climate change has already affected Bavaria in recent decades. Based on measured data from weather stations covering 1931 to 2010, the annual mean temperature in the region had risen by more than 1°C (Danneberg et al., 2012; Steinbauer et al., 2016). Precipitation increased by 22 % during winter, while summer precipitation decreased by 1 %. Changes in northern parts of Bavaria primarily drive this trend.

Projections of future climate change impacts (2021 - 2050) indicate a further increase in annual mean temperature, an increase in the number of warm (> 25 °C) and hot (> 30 °C) days, and a decrease in cold days (< 0 °C). These changes will likely occur homogeneously across the study region (Danneberg et al., 2012). Already observed precipitation trends were confirmed by model projections and are likely to continue.
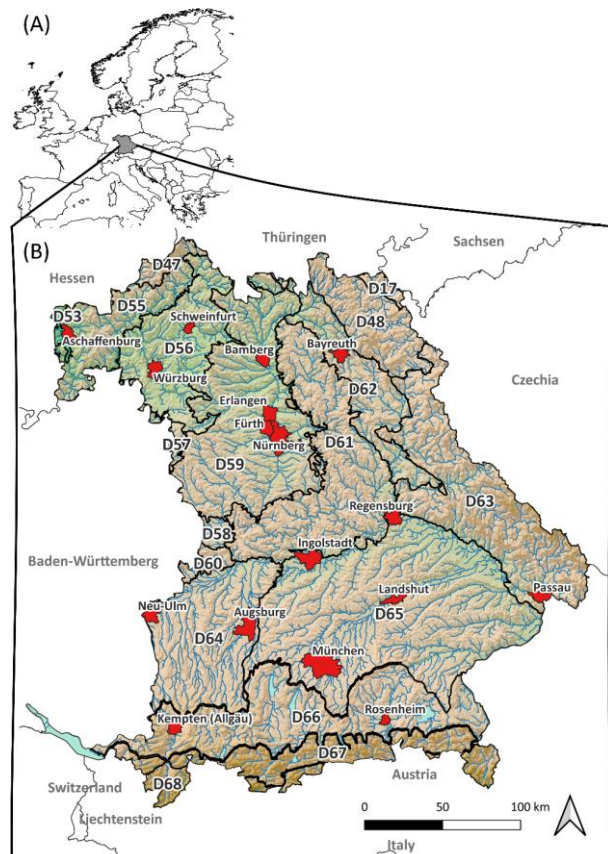
Figure 4 Geographical overview of the study region, the German federal state of Bavaria, indicated by the coloured areas on the European continent (A) and in a close-up in (B). Colouration in (B) indicates the area's geographical relief, rivers, and lakes. Red areas mark large urban areas. Neighbouring German states include, from West to East, Baden-Wurttemberg, Hesse, Thuringia, and Saxony (names in the map given in German). Neighbouring countries are, from East to South-West, Czechia, Austria, and Switzerland at Lake Constance. Scale and arrow pointing North are given at the lower right of the map. Main natural units, as referenced in Table 1, were received from the Bavarian Ministry for the Environment (Bayerisches Landesamt für Umwelt, 2021), borders and cities were received from Eurostat (Eurostat, 2022), and background shaded relief was received from the General Bathymetric Chart of the Oceans (GEBCO Compilation Group, 2022).

Table 1 Main natural units of the German federal state of Bavaria and a rough characterization of prominent ecoregion features. Main natural units, as in Figure 4, and ecoregion descriptions, were received from the Bavarian Ministry for the Environment (Bayerisches Landesamt für Umwelt, 2021).

Code	Region	Rough characterization
D17	Vogtland	low mountain range, little precipitation, strong winds
D47	East Hessian mountains	high precipitation, many streams, upland, and transitional bogs
D48	Thuringian-Franconian low mountains	geologically oldest mountain range, high precipitation, low temperature, forests and meadow valleys, different moor types
D53	Rhein-Main lowland	intensive agriculture
D55	Odenwald, Spessart, Rhön	low mountain ranges, forest, grassland, many wells and streams
D56/57	Neckar-Tauber catchment area, Main-Franconian plates	Mainly agriculture
D58/59	Swabian and Franconian Keuper-Lias-area	frequent floodings, largest pool areas in Bavaria
D60/61	Swabian and Franconian Alb	highland, little precipitation, only small pool areas
D62	Upper Palatinate - Upper Main	hilly landscape, mainly pine forests, and huge pools in south
D63	Upper Palatinate – Bavarian Forests	many streams, pools, high precipitation and low temperatures, lowland, upland, and transitional moors
D64	Danube-Iller-Lech plates	many streams, north with lowland moors but all gone today
D65	Lower Bavaria	hilly landscape, many small rivers, pools, some lowland moors
D65	Isar-Inn-gravel plates	North: lowland moors, South: least water bodies in Bavaria
D66	Alpine foothills and moors	huge lakes, moors, and rivers from lakes and the Alps
D67	Swabian – Upper Bavarian Alpine foothills	many different soil types, upland and transitional moors, many wells, and rivers
D68	Northern limestone high Alps	high mountain region, a third of the area above the tree line, many cold wells, and rivers

In contrast to the projected temperature changes, changes in precipitation patterns will likely occur heterogeneously across Bavaria, and different models come to contrasting results in space. Models agree, however, that dry periods of more than seven days without rain during summer are likely to increase, while local heavy rain events become more and days with snow cover become less likely than during the reference period.

2.1.2   Biodiversity in Bavaria

The Bavarian biodiversity is estimated to contain about 62,000 species of plants, animals, fungi, and lichen, thereby including about half of the species known across Europe (International Union for Conservation of Nature and Natural Resources, 2023). 77 % of these species (about 30,000) are known insect species (Bayerisches Landesamt für Umwelt, 2023). Across Germany, about 33,300 insect species have been described so far, but DNA barcoding projects hint towards thousands of species that have yet to be discovered (Hausmann, Krogmann, Peters, Rduch, & Schmidt, 2020). Especially within the taxa of dipterans and hymenopterans, in particular parasitoid wasps, the suspected number of undescribed species is large, even though the already described species of these taxa account for about two-thirds of Germany's known insects.

2.1.3   Conservation and Monitoring

The preservation of biological diversity is a constitutional goal in Bavaria, according to Art. 141 of the Bavarian Constitution (Bayerische Staatskanzlei, 1998). It is also one of the primary tasks of the state, municipalities, and public corporations to protect and preserve native species and their habitats. The Bavarian State Ministry for Environmental and Consumer Protection claims Bavaria plays a vital part in preserving European biodiversity (Bayerisches Staatsministerium für Umwelt und Verbraucherschutz, 2021). The European Habitats Directive, however, was only incorporated into state legislation in 2016, but in 1998 following the implementation of the Directive in federal law, related state-level conservation initiatives began, and the first Special Areas of Conservation were designated in 2004.

Since 1980, the Bavarian Agency for the Environment (Bayerisches Landesamt für Umwelt, LfU) has coordinated monitoring programs for several animal groups ("Artenschutzkartierungen", roughly translated to species protection mappings), which are still on-going (Bayerisches Landesamt für Umwelt, 2020). While the agency published several atlases based on these observations, for example, for birds (Nitsche & Plachter, 1987; Rödl, Rudolph, Geiersberger, Weixler, & Görgen, 2012), butterflies (Bräu et al., 2013), grasshoppers (Schlumprecht & Waeber, 2003), and dragonflies (Kuhn & Burbach, 1998), the data is highly heterogeneous and could thus far not be used to infer species' trends.

2.2   Data Basis

2.2.1   Species Observation Data

The foundation of this work is the database of the Bavarian agency for the environment (Bayerisches Landesamt für Umwelt, LfU) called "ASK-database", collecting occurrence data for numerous taxa from various sources. We were given access to the datasets of three insect taxa: butterflies (Lepidoptera, Rhopalocera, 205 species) with a total of 575,994 data entries, including 52,914 museum and literature records, 3,242 absence entries and 519,838 field observations; grasshoppers (Orthoptera, 79 species) with a total of 212,500 data entries including 5,098 museum and literature records, 1,887 absence information and 231,450 field observations; and dragonflies (Odonata, 77 species) with a total of 238,435 data entries including 5,382 museum and literature records, 1,359 absence entries and 205,759 field observations (also compare Figure 5). This dataset is a highly valuable resource, as the data collection is ongoing, and all records are being validated by experts, ensuring high data reliability.

2.2.2   Species' Attribute Data

Distribution Attributes

We used the continental distribution of the species to calculate both the distribution and Climate Attributes. We obtained range information for each species (except one butterfly species, *Pyrgus malvoides,* and one grasshopper species, *Miramella alpina*) on a 5 km × 5 km grid for the European continent (10°W, 30°E, 35°N, and 71°N) as digitized atlas range data for butterflies (Kudrna et al., 2011) and dragonflies (Kalkman et al., 2018), as well as polygon range data for grasshoppers (Hochkirch et al., 2016).

We tested different attributes (see also Excursus 3: Collinearity and Predictor Selection) representing the continental range of the species, including the range size in km² as the sum of the area of each occupied grid cell and range size in the number of grid cells occupied. Additionally, we determined the longitudinal centre of each species' continental range as well as the longitudinal centre weighted by the number of available grid cells at each longitude. This data was used both in Chapter 1 and in Chapter 2.
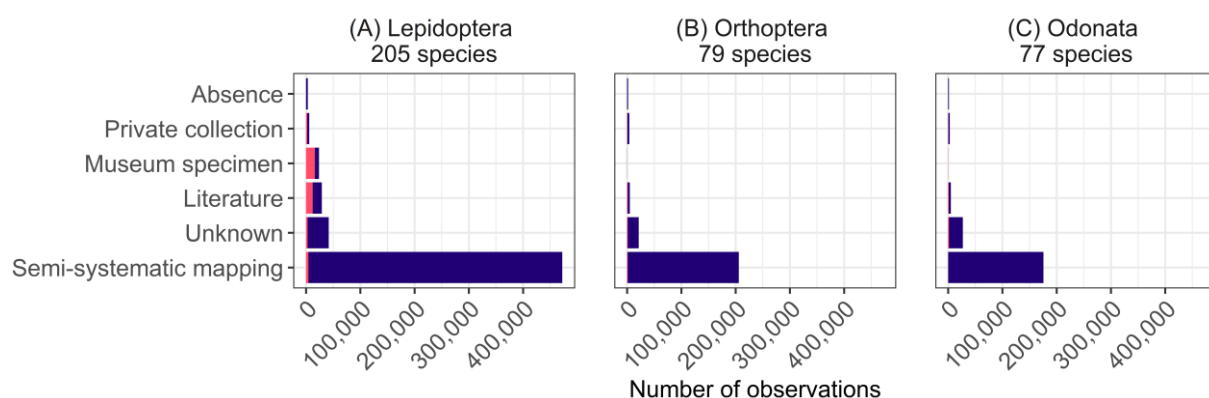
Figure 5 Total number of observations in the ASK database covering the time from 1700 to 2020, split for the data source and each of the three taxa analysed. (A) butterflies (Lepidoptera - Rhopalocera), (B) grasshoppers (Orthoptera), and (C) dragonflies (Odonata). The lighter, red-coloured parts of the bars indicate data from before 1980, and the darker, blue-coloured parts indicate data collected between 1980 and 2020.

Excursus 1: Trait vs Attribute

Following Violle et al. (2007)

Trait: a physiological, morphological, or phenological feature measured at the individual level without referencing their environment in any form.

Functional trait: morpho-physiological traits that affect an individual's growth, reproduction, and survival and, therefore, indirectly determine their fitness.

Demographic parameter: population-wide average of a trait.

Attribute: a value taken by a trait at any place and time at the individual level, which may change through time or along environmental gradients; thus, information on the environment where the trait has been measured is essential for contextualizing the value.

Trait attribute: population-wide average of attributes in space and time, including variance measures and information on the population selected and its environment.

Climate Attributes

We calculated mean bioclimatic variables for each grid cell across the European continent (10°W, 30°E, 35°N, and 71°N) as a basis for the calculation of species' temperature and precipitation preference across their continental ranges. We used monthly bias-adjusted maximum and minimum temperature and precipitation data for a 20-year period (1991-2020) to calculate 19 bioclimatic variables using the DISMO package's BIOVARS function (Hijmans, Phillips, Leathwick, & Elith, 2020). We acquired regional climate model (RCM) simulations for the European realm (EURO-CORDEX, Jacob et al., 2014) at a resolution of 0.11 degrees (~ 12.5 km). We calculated the bioclimatic variables separately for three representative concentration pathways (RCPs; RCP2.6, RCP4.5, and RCP8.5), three RCMs (KNMI-RACMO22E, MPI-CSC-REMO2009, and SMHI-RCA4), three global climate models (IPSL-IPSL-CM5A-MR, ICHEC-EC-EARTH, MPI-M-MPI-ESM-LR), one ensemble (r1i1p1), and one downscaling realization (v1). We then took the mean across climate models and RCPs for

each bioclimatic variable used (see also Appendix A: Chapter 1 Supporting Information S6) for each grid cell.

We derived multiple metrics of each species' temperature and precipitation niche across Europe using each grid cell's bioclimatic variables. We calculated the mean and median annual mean temperature and the mean annual precipitation of all occupied grid cells in Europe to estimate the niche position of each species. We estimated the niche breadth as both the mean and median precipitation and temperature annual range, as well as several measures of upper and lower temperature limits (see also Appendix A: Chapter 1 Supporting Information S7).

This data was used in Chapter 1, Chapter 2, and Supporting Information of Chapter 3.

Habitat Attributes

We assessed species habitat specialization and preference based on the information on habitat types occupied in the Bavarian Atlases for each insect taxon (Lepidoptera: Bräu et al., 2013; Odonata: Kuhn & Burbach, 1998; Orthoptera: Schlumprecht & Waeber, 2003). The habitat information included 11 terrestrial and eight semi-aquatic habitat types: Terrestrial open habitats included 1. dry and poor grasslands, 2. wet grassland, 3. grassland in general, 4. heaths, 5. bogs, 6. gravel banks, bars, and areas, 7. shrubs and ruderal vegetation, 8. buildings, gardens, and railway tracks, and 9. alpine habitats, while forest habitats comprised 10. bushes and hedges, and 11. forests, forest edges, and trees. Semi-aquatic habitats included lotic water bodies such as 1. rivers and creeks, 2. springs, 3. ditches, and 4. oxbow lakes, as well as lentic waterbodies like 5. lakes, 6. ponds and pools, 7. bogs, and 8. quarry lakes, gravel, and sand pits make up the semi-aquatic habitats.

We used a standardized approach to categorize species as habitat specialists or generalists across all three insect taxa. We classified species as habitat specialists if they occur in up to 3 terrestrial or up to 2 semi-aquatic habitats, following Willigalla & Fartmann (2012). Butterflies comprise mostly habitat specialists, with 85.2 % and only 14.8 % habitat generalists, whereas grasshoppers (45.5 % specialists, 54.5 % generalists) and dragonflies (57.7 % specialists, 42.3 % generalists) show an almost even ratio (compare Figure 6 A). To ensure the reliability of our classification approach, we tested whether other classifications based on expert knowledge would lead to different results on the
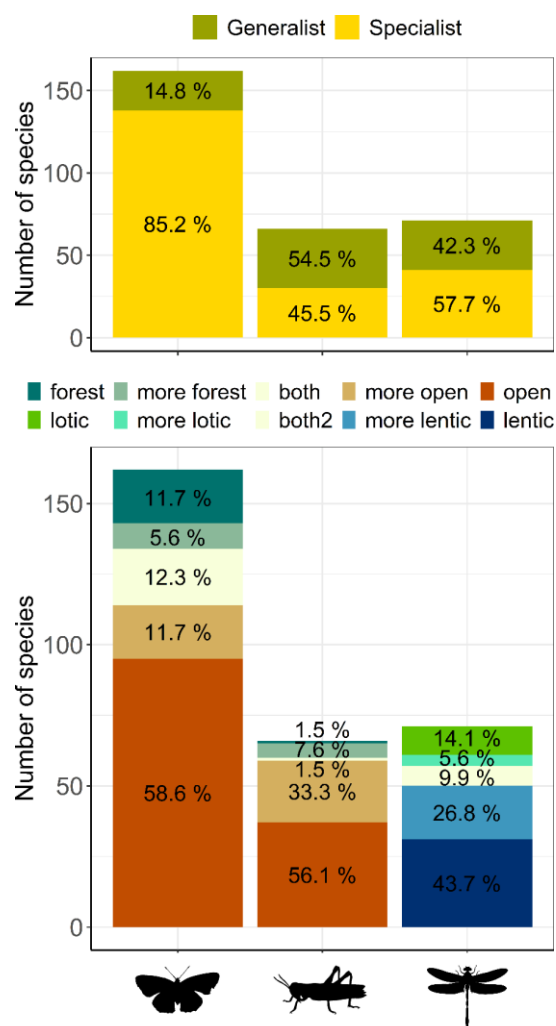
Figure 6 Number of species of each taxon (from left to right: butterflies – Lepidoptera, grasshoppers – Orthoptera, dragonflies – Odonata) classified by (A) habitat specialization and (B) habitat preference, with the corresponding colour legend given on top of each panel and the percentages of each taxon in the respective group written on the bars. (A) Habitat specialization defines species as either habitat generalists (darker green, top) or habitat specialists (lighter yellow, bottom), based on the number of habitat types the species occur in. (B) Habitat preference differentiates between butterfly and grasshopper species inhabiting either forest (dark green), open habitats (dark red), both equally (light yellow) or one more than the other (light green or light red), and dragonflies inhabiting lentic (dark blue), lotic (dark green), both habitat types (light yellow) or one more than the other (light blue or light green). Including all species, a subset of species with reliable model results was used for the driver analysis.

Table 2 Deviating habitat specialization classifications for grasshopper (Orthoptera) species by Engelhardt et al. (2022a), Poniatowski et al. (2020), and Reinhardt et al. (2005). Species with deviating classifications are listed in the 'Species' column, whereas the 'Deviating classification' column indicates the dataset and its species' classification deviating from the classifications of the other two datasets.

Species	Deviating classification
Chorthippus albomarginatus	Engelhardt: Specialist
Chorthippus apricarius	Engelhardt: Specialist
Chorthippus brunneus	Reinhardt: Specialist
Chorthippus pullus	Reinhardt: Generalist
Oedipoda caerulescens	Engelhardt: Generalist
Omocestus rufipes	Reinhardt: Generalist
Tetrix subulata	Engelhardt: Generalist
Gryllus campestris	Poniatowski: Generalist
Gryllotalpa gryllotalpa	Reinhardt: Generalist
Conocephalus fuscus	Reinhardt: Specialist
Isophya kraussii	Engelhardt: Specialist
Metrioptera brachyptera	Poniatowski: Specialist
Polysarcus denticauda	Reinhardt: Generalist
Nemobius sylvestris	Poniatowski: Generalist

example of grasshoppers (Orthoptera). We compared our classification with those of Poniatowski et al. (2020) and Reinhardt et al. (2005) to ensure reliability. Of the 66 orthoptera species in our study region, 34 were classified consistently across the three datasets. In two cases, our method identified a species as habitat generalist and in three cases as habitat specialist, deviating from the classification of the other publications (compare Table 2). For nine species, one of the other datasets deviated from the consensus. We ran the analysis in Chapter 1 with each classification, and all models led to the same results.

We defined the species' habitat preference based on the same data, where we counted the number of habitats of the contrasting categories open vs forest habitats for terrestrial taxa and lentic vs lotic habitats for

dragonflies. We defined the species as belonging to either category, both, or more one or the other (compare Figure 6 (B)). This data was used in Chapter 1 and Chapter 2:

Additionally, we extracted information on whether Lycaenid butterflies prefer rich or poor soil habitats for Chapter 2 from the Bavarian atlas of butterfly species (Bräu et al., 2013).

Biotic Interaction Attributes: Myrmecophily

We obtained information on Lycaenid butterfly–ant interactions from the dataset by Fiedler (2021) and checked its credibility by comparing it to further datasets and background literature (Fiedler, 1991; Kühne et al., 2001; Middleton-Welling et al., 2020; Tartally et al., 2019). Species-specific interactions reported in these datasets are probably preliminary; further interactions could still be unknown. Data for obligate and ant-independent species was consistent across datasets; thus, we focused on comparing these two groups. This data was used in Chapter 2.

2.3   Statistical Analyses

2.3.1   Bias in Observation Data

Species records are becoming increasingly digitally available, often combined into heterogeneous databases such as the one introduced before and used in this work. This data, however, is typically biased, meaning that it does not represent the actual occurrences of the observed taxon over space and time but only a fraction of it. Which part of the actual occurrences is represented in the data is determined by the biases the dataset

entails (Johnston, Matechou, & Dennis, 2022).

The most straightforward bias we find in our dataset is a TEMPORAL BIAS. Here, the number of observations changes strongly over time (Figure 7 A), and the number of species observed follows a related pattern (Figure 7 B). Historical, pre-digitization data often come from literature evaluations and digitized museum specimens (compare also Figure 5). In recent decades, the number of observations from semi-systematic mappings has significantly increased due to growing public interest in biodiversity issues. In the 1980s, the number of records available strongly increased due to increasing efforts by the Bavarian Environment Agency to collect data. In 1992 the European Union implemented the Habitats Directive, which

made regular reporting on annex species mandatory. Additionally, the Bavarian Environment Agency published atlases on the distributions of Bavarian insects, which also increased sampling efforts in preceding years (Bräu et al., 2013; Kuhn & Burbach, 1998; Schlumprecht & Waeber, 2003).

The second type of bias in our dataset is a SPATIAL BIAS. The reported observations are unevenly distributed in space, where for most of the grid cells, only a few observations were reported in the dataset, while few grid cells entail very high numbers of records, for example, up to 1,670 butterfly observations in one grid cell over the past century (Figure 8 G, H, I). The spatial distribution of the observations is linked to human population density with higher numbers of observations
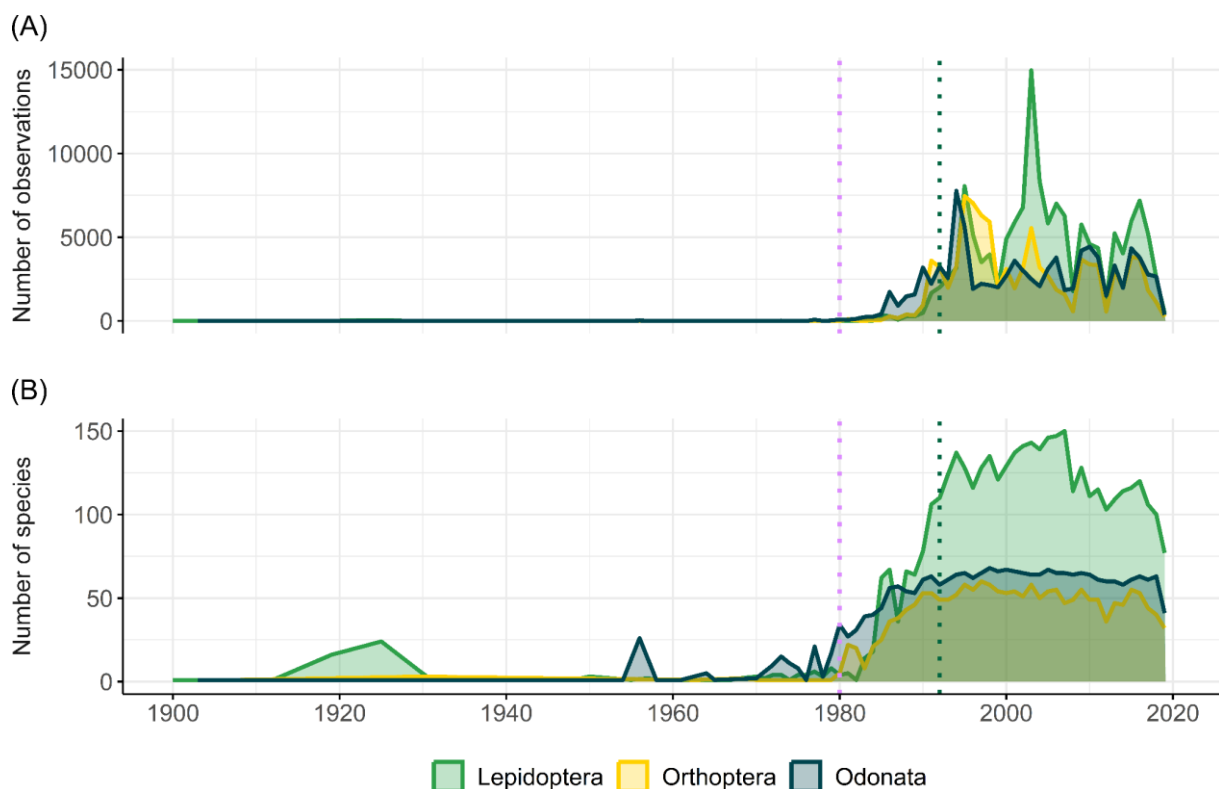
Figure 7 Temporal bias in species observation data between 1900 and 2019. (A) The number of observations, (B) the number of species reported each year. Green: Lepidoptera (Rhopalocera), yellow: Orthoptera, blue: Odonata. The light red dotted line indicates the year 1980, when the Bavarian Environmental Agency started its data collection efforts, dark red dotted line indicates the year 1992 when the European Union implemented the Habitats Directive, which made regular reporting on annex species mandatory.

where more people live (Figure 8 D, E, F), as people tend to observe species closer to their home bases (R L H Dennis & Thomas, 2000). The species number observed in each grid cell (Figure 8 A, B, C) is positively correlated with the number of observations (Pearson-correlation coefficient, Lepidoptera 0.77, Orthoptera 0.68, Odonata 0.72) – or vice versa: species observation data tend to be biased towards areas where more species occur, as observers prefer sampling in those regions (Boakes et al., 2010; Sastre & Lobo, 2009). Spatial and temporal biases could also co-occur if spatial preferences change over time (Boakes et al., 2010) or if more people

report from more urban areas as urbanization increases (Bowler, Callaghan, et al., 2022).

In addition to these relatively straightforward biases, other biases exist, which could also affect the data available but are harder to assess as they depend on the observed species themselves. Species observations underly a VISUAL BIAS, where species that are easier to detect due to larger size, striking colouration, more dynamic behaviour, or higher abundance are observed easier and thus get reported more often (R.L.H. Dennis et al., 2006; Harabiš, Jakubec, & Hronková, 2020). A recent focus on
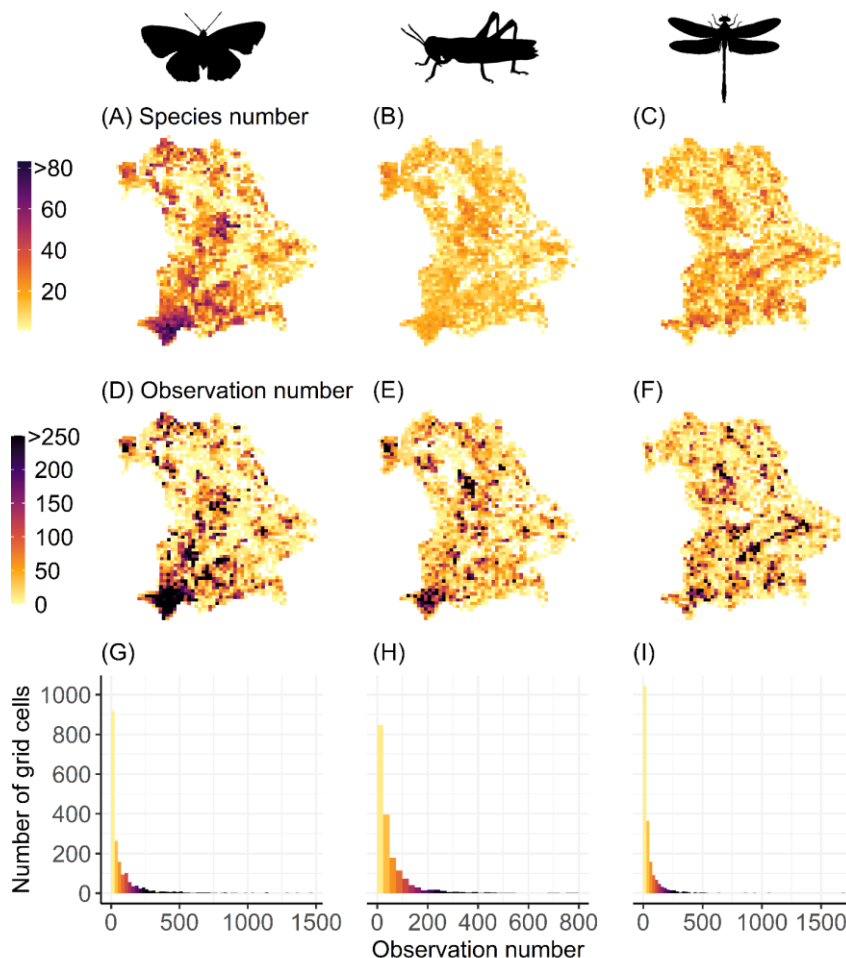
Figure 8 Spatial bias in species observation data between 1900 and 2020. (A), (B), (C) the number of species and (D), (E), (F) the number of observations reported in each grid cell, with darker colours indicating higher numbers (see each respective scale on the left). (G), (H), (I) histogram of the number of grid cells with a certain number of observations reported. The first column (A), (D), (G) represent butterfly (Lepidoptera) data, the middle column (B), (E), (H) grasshopper (Orthoptera), and the right column (C), (F), (I) dragonfly (Odonata) data.

THREATENED AND PROTECTED SPECIES also increased the efforts to detect these species. Increasing their probability of detection might lead to an apparent increase in observations (Boakes et al., 2010); see also Chapter 3.

Due to biases apparent in probably all observation datasets, assessing these is an essential step at the beginning of any data analysis. Newly available packages, such as the OCCASSESS R-package (Boyd, Powney, Carvell, & Pescott, 2021), offer a starting point when screening occurrence data for potential biases. In addition, especially when trying to analyse historical biodiversity records, accessibility maps provide an idea of the spatial and environmental biases that could be present in these records by predicting the sampling efforts undertaken (Monsarrat, Boshoff, & Kerley, 2018).

The usefulness of a dataset depends on the supporting information available describing observer efforts and how systematically and uniformly the data was collected (Roger L. H. Dennis, Sparks, & Hardy, 1999). As complete large-scale mapping schemes are time-consuming and expensive – and only useful for future monitoring of species, but data collected now does not allow inferences about what happened in the past to learn from for the future – reliable, albeit biased and heterogeneous data might be sufficient in combination with sophisticated computational methods such as occupancy-detection models. For future data and citizen-science data collections, available questionnaires help assess the observer's efforts to inform biodiversity models (Bowler, Bhandari, et al., 2022).

2.3.2   Generalized Additive Models

When analysing time series data, such as the development of the number of observations over the years, we want to know whether their number changed over time. A linear model could inform here; however, the data are often not linearly increasing or decreasing. Generalized additive models (GAMs) allow us to model non-linear data with good explainability. In GAMs, the linear form of the predictor is replaced by a sum of smooth functions called a spline (Hastie & Tibshirani, 1986; Wood, 2017). The effective degrees of freedom (edf) is a summary statistic of the GAM and informs about the degree of non-linearity of the curve analysed (Zuur, Ieno, & Elphick, 2009). When edf = 1, the curve is linear; when $2 > \text{edf} > 1$, it is weakly non-linear; and when edf > 2, it is highly non-linear.

In the first part of Chapter 3, we explored the effects the European Habitats Directive (compare section 1.3.1) has had on different aspects of observer effort toward species protected within its annexes (here forth annex species). We calculated four metrics of observer efforts, the annual number of (a) records in total, (b) observed species, (c) sampling days, and (d) projects targeted towards the recording of annex species and compared these for annex with non-annex species. We evaluated the change in the proportion of these metrics dedicated to annex species over time by applying GAMs. We used binomial generalized additive models from the R-package MGCV (Wood, 2011) and applied the smooth function to the year effect by utilizing the Generalized Cross Validation (GCV) criterion, a method to counteract the overfitting of the curve to the data. Based on the models' Akaike

information criterion (Akaike, 1974), we contrasted generalized additive models with generalized linear models that either included or excluded a year effect (see also section 2.3.4). We assumed that evidence of a non-linear increase, as indicated by the GAM presenting as the best-fitting model, suggests a positive effect of the Habitats Directive, whereas a linear increase implies a general, independent increase of monitoring effort. A lack of effect of the year suggests that monitoring effort has remained constant over time.

2.3.3   Occupancy-Detection Models

Statistical modelling techniques enable us to obtain valuable information about species occurrences over time using highly biased, heterogeneous data (Isaac et al. 2014). When data entails different forms of biases, looking at the pure number of observations for each species in a year is a mere reflection of the sampling effort (compare Figure 9), and a simple extrapolation from the well-sampled sites to the whole study region will lead to an overestimation of species' presences. We need to assess whether the absence reported at a site is a true absence, or rather a missing observation.

Occupancy-detection models are hierarchical models working with Bayesian inference (see also Excursus 2: Classical vs Bayesian Statistics) in the form of Markov chain Monte Carlo (MCMC) algorithms. Hierarchical models describe a conditionally related set of models where the probability distribution of one model's variable depends on the state of the variable of another model (see Figure 10 for an overview of model construction). By creating joint hierarchical
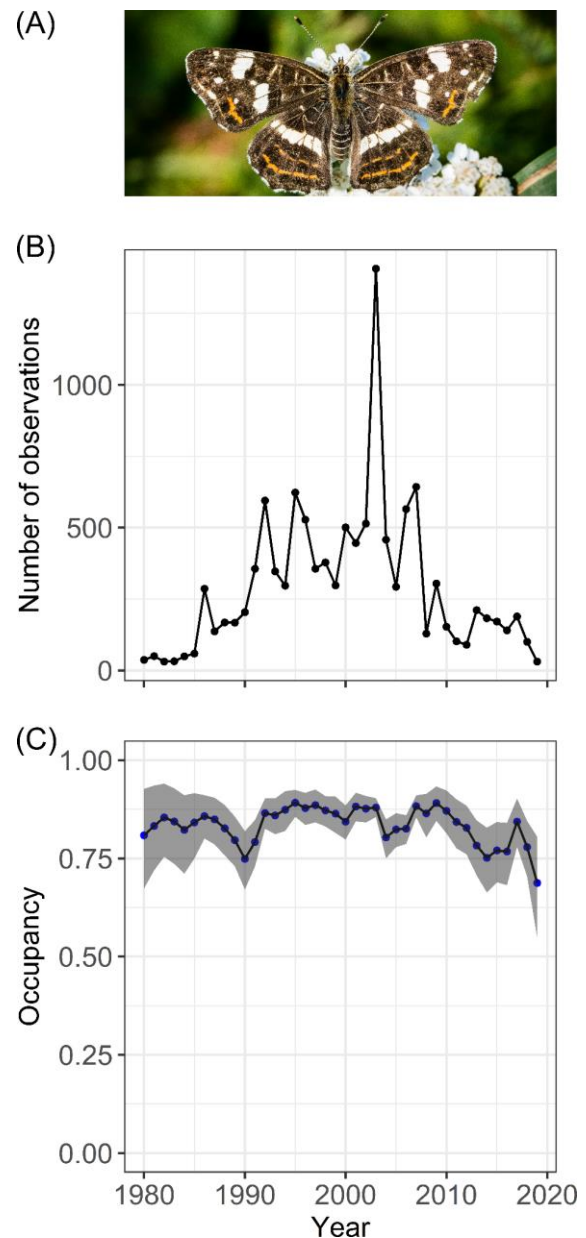
Figure 9 Comparison of the annual number of observations with occupancy estimates over 40 years (1980-2019) for an exemplary butterfly species, *Araschnia levana* (Map, family Nymphalidae). (A) Photograph of the summer form *prorsa* of the Map by E. K. Engelhardt; (B) Annual number of observations (minimum 31, maximum 1,407 observations in a year) based on ASK-database provided by the Bavarian Environment Agency (LfU); (C) annual occupancy estimates, where grey ribbons indicate 95 % credible intervals of the occupancy estimates and blue points indicate reliable model convergence (Rhat < 1.1) as calculated with the Gelman-Rubin statistic, adapted from Engelhardt et al. (Engelhardt et al., 2022b).

Excursus 2: Classical vs Bayesian Statistics

Population parameter: fixed value describing a characteristic of a population whose true value could only be determined by measuring all individuals through time.

Bernoulli distribution: discrete probability distribution for the randomness in a system's initial conditions, modelling a set of possible outcomes of a yes-or-no/ condition, where the variable has a value of one with probability *p* and a value of zero with probability 1-*p*.

CLASSICAL OR FREQUENTIST STATISTICS: the true population parameter is unknown as only a subset is measured; thus, statistics focus on the probability of the data rather than on the probability of the hypothesis.

Null Hypothesis: a mathematical explanation of what could be expected if there was no effect at the population level with entirely random results.

Null Hypothesis Testing: set a Null Hypothesis, then compare it with the experimental results – if they do not match the "nothing special" assumption, they reject the expectation that the results are random and support the idea that something "special" is happening. The rejection threshold (α-rate, often 0.05 %) depends on how often we are prepared to be wrong with our claims, as the threshold determines with which probability the results occur randomly. The cumulative likelihood is the p-value. If the p-value > the threshold, the Null Hypothesis holds true.

Confidence Interval: estimated interval which entails x % of measurements and contains the true population parameter, without giving that exact value, based on the results and the data distribution. Often 95 % confidence interval, where 2.5 % of future measurements are higher and lower than the confidence interval. The narrower the confidence interval, the higher the model's precision.

BAYESIAN STATISTICS: describes population parameters as a probability distribution, thereby expressing a degree of belief of where the true value is. Bayesian approaches tend to produce more precise estimates than classical inference.

Bayes's Theorem: the probability of a hypothesis (*H*) given the data (*D*) with $p(D) > 0$: $p(H|D) = \frac{p(D|H) \times p(H)}{p(D)}$

p(H): prior probability, priors define where each hypothesis starts. Flat or uninformative priors define all hypotheses as equally likely.

p(D|H): likelihood, often a function, conditional probability of observed data based on the hypothesis (the focus of classical inference)

p(D): base rate, a normalizing factor, probability of the data under consideration of the likelihood and the prior, where the sum of all posterior probabilities equals 1.

p(H|D): posterior probability, the result of the analysis, probability of the hypothesis after previous knowledge (prior probability), and new evidence (likelihood) have been taken into account.

Annual mean of the posterior distribution = best estimate of annual occupancy

Credible Interval = Highest Density Interval; the range in which the population parameter is present with x% confidence.

models for the observation data and information about the data collection process, we include a form of observation probability in our assessment of species' occurrence probabilities (Kéry & Royle 2016, 2021, especially chapter 4.11).

Markov chain Monte Carlo (MCMC) algorithms assess missing information by describing a species' occurrence state at timepoint one – the system's baseline state - and then defining a probabilistic rule characterizing the changes from one year to the next by drawing random samples from the posterior distribution. The MCMC algorithm applied here runs in BUGS code using the program JAGS via the R-packages GGMCMC and JAGSUI (Fernández-i-Marín, 2016; Kellner, 2021).

We ran three Markov chains for 20,000 iterations each (Engelhardt et al., 2022b). Markov chains typically take some time to converge to a fixed posterior distribution; thus, we used 10,000 iterations as burn-in, also called warmup. These are discarded from further analysis, where our results were pulled from iteration 10,001 to 20,000 for each of the three chains. A comparison of the chains allows for assessing model reliability by comparing the within-chain variance to the between-chain variance, called the Gelman-Rubin statistic (Rhat, Gelman & Rubin, 1992). These Rhat values should be lower than 1.1 considered the threshold for model convergence (Kéry & Schaub, 2012). Figure 11 illustrates model evaluation plots for two exemplary butterfly species, one with reliable model results (*Araschnia levana*) and one with unreliable model quality (*Limenitis populi*) that lead to its exclusion from further attribute analyses. The density plots (panels (-.2.-)) present the density of the

parameter distribution, which indicates how well the three Markov chains converged in their estimates of the occupancy density function for the year shown. A perfect convergence would be shown as a complete overlap of the three density functions. On the other hand, the trace plots (panels (-.3.-)) give an impression of how well the model iterations within each chain converged. The smaller the oscillations, the better the iterations converged to the same mean of the posterior distribution (here forth estimate of annual occupancy) in that year.

The so-called priors are essential parameters of Bayesian occupancy-detection models. This prior distribution describes "prior beliefs" about a parameter; however, as we usually do not know enough about a parameter to determine it, we often decide on uninformative priors. In the case of our occupancy-detection models, however, where we model species' occupancy estimates over time, it is sensible to use last year's information to inform the priors of the following years in the form of a rolling mean prior, based on Outhwaite et al. (2018). Otherwise, we used vague priors with large variance so that their influence on the posterior distribution is negligible (Kéry & Royle, 2016).

Figure 10 briefly outlines the data preparation steps and the models themselves. The data on observation effort was adapted in an iterative framework, where taxonomic experts for each taxon checked our model results for plausibility and gave feedback for their improvement. For details on the occupancy models used, Chapter 1. The complete code is available via Dryad (Engelhardt et al., 2022b).

Bayerisches Landesamt für Umwelt

ASK database

1980-2019
Observations, no absences
Exact data and species given
>10 observations per species

Closure assumption:
🦋 : March – October
🦗 : May – October
🦗 : Aptil - October

Closure period: Pre-defined time period when a species' occurrence probability ψ should be similar
Closure assumption: repeated visits at one site during the closure period to assess each species' detection probability p

visit j detection (1) and non-detection (0)

Site i	full date year t or α, day $yday$, week	observer	eco-region	Species observation y			
				A	B	C	...
1	01.03.01	X	Type1	1	1	0	...
1	01.08.01	X	Type1	0	1	1	...
1	01.08.02	X	Type1	1	0	1	...
...	...	...	...	...	...	...	...
2	01.03.01	Y	Type2	1	0	0	...
2	01.08.02	Z	Type2	0	1	1	...
...	...	...	...	...	...	...	...

Observation effort:

nuSpecies: total number of observed species per visit

singleList: visits reporting one species

samplInt: total number of records per year

Is the non-detection a true absence?

The observation y depends on the occupancy status z (presence 0 or absence 1) ~ drawn from a Bernoulli distribution (of the occupancy status z and the detection probability p for each visit j, year t and site i)

Hierarchical models: conditionally related

$$y_{j,t,i} \mid z_{t,i} \sim Bernoulli\ (z_{t,i}\ p_{j,t,i})$$

State Submodel describing each species' occupancy status z

$$z_{t,i} \sim Bernoulli\ (\psi_{t,i})$$

$$logit\ (\psi_{t,i}) = year_t + site_i + ecoregion_i$$

Result: each species' occurrence probability ψ for all years t and sites i

Random walk prior on year effect: cross-year information sharing

Observation Submodel describing each species' detection probability p

Univoltine species:

$$logit\ (p_{j,t,i}) =$$
$$\alpha_j + \beta_{yd}\ yday_j + \beta_{yd2}\ yday_j^2 +$$
$$\beta_{sl}\ samplInt_j +$$
$$\beta_{nSpec}\ log(nuSpecies_j) +$$
$$\beta_{sL}\ singleList_j$$

Multivoltine species:

$$logit\ (p_{j,t,i}) =$$
$$\alpha_j + \beta_w\ week_j +$$
$$\beta_{sl}\ samplInt_j +$$
$$\beta_{nSpec}\ log(nuSpecies_j) +$$
$$\beta_{sL}\ singleList_j$$

Figure 10 Sketch of occupancy-detection models and data input applied. The upper half describes the derivation of all relevant parameters from the dataset, and the lower part describes the three parts of the hierarchical model. Adapted from Engelhardt et al. (2022a), based on Kéry & Royle (2016, 2021), Outhwaite et al. (2018), and Bowler et al. (2021).

Most of our models showed high reliability, but for some species, we could not assess overall reliable occupancy estimates. We decided on two criteria to identify models with low reliability, based on model evaluation (40-year mean Rhat $\geq$ 1.1 or mean standard deviation $\geq$ 0.1 following Kéry & Schaub (2012)) and on the minimum occupancy of the species in at least one year exceeding 0.025, assuming that, based on consultation with taxon experts, for species with such low occupancies model reliability is reduced. In the proceeding analyses, we either excluded these species (Chapter 1, Chapter 2) or specifically pointed out the issues arising with the models of these species (Chapter 3).

2.3.4   Generalized Linear Models

Linear trend estimates are an often-utilized tool to represent general trends in species occurrence (e.g., Hallmann *et al.* 2017; Dennis *et al.* 2019a; Seibold *et al.* 2019). Although linear trends have some shortcomings, especially over long periods (see section 4.2.2), they can be utilized to assess whether species' occurrence changed over time in a simplified way.

Generalized linear models (GLMs) can be constructed both in a frequentist and in a Bayesian framework. In contrast to linear models (also called general linear models or abbreviated as LM), generalized linear models allow the residuals of the response distribution to be different than normal (Wood, 2017), which is what we need when analysing single-species linear trends, as the residuals of their occupancies are not normally distributed (compare Figure 12).

Both in Chapter 1 and Chapter 2 we constructed Bayesian generalized linear models, thus consistently using the Bayesian framework. In Chapter 3, however, we crafted frequentist generalized linear models, as some of the applied methods were not implemented in the Bayesian framework at the time.

In Chapter 1 and Chapter 2 we assessed species' linear trends using the R-package BRMS (Bürkner, 2017) fitting Bayesian generalized linear models (see, for example Figure 13 B) in STAN via RSTAN (Stan Development Team, 2022). We based our analysis on species' annual occupancy estimates between 1980 and 2019 and included each annual estimate's standard deviation as a measure of uncertainty.

We ran all models with four chains of 4,000 iterations each, with a burn-in rate of 2,000, an algorithm step of 0.99999, and a tree depth of 12. As each species' occupancy development over time differed, we tested three priors for fixed effects – default uninformative priors, slightly narrower normal (0,10), and narrower normal (0,1) priors. For each species, we selected the model with the best evaluation scores (Rhat closest to 1), although all models showed good convergence (Rhat < 1.1). Additionally, we compared our models to models that run without including the occupancy estimates' uncertainty in the form of their standard deviation (Chapter 1 Supplementary Information). We computed the slope for each species, which showed their linear trends throughout our study period and the corresponding 95 % credible intervals.
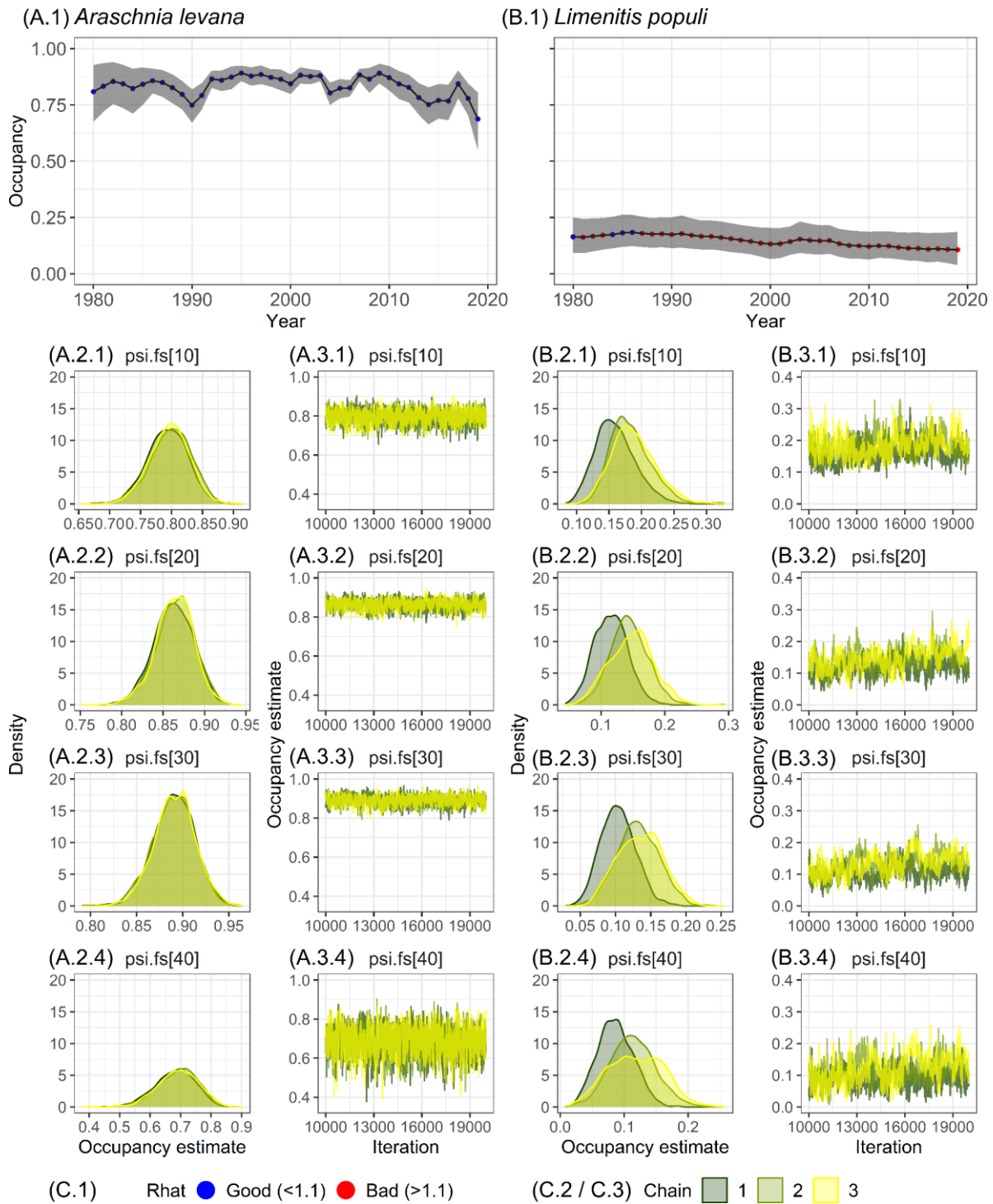
Figure 11 Exemplary model evaluation plots for occupancy-detection models from 1980 to 2019 of two butterfly species, one with reliable model quality (*Araschnia levana* (A)) and one with unreliable model estimates (*Limenitis populi* (B)) with colour legends given in (C). Panels (-.1): mean annual occupancy estimates for both species, where blue points represent reliable (Rhat < 1.1) and red points unreliable (Rhat ≥ 1.1) model estimates (Gelman-Rubin statistic, legend C.1). Grey ribbons represent model estimates' 95 % credible intervals. Panels (-.2.-) and (-.3.-): exemplary model evaluation plots for annual occupancy estimates of four years as estimated by each of the three Markov chains (legend C.2/C.3: dark green- chain 1, medium green – chain 2, light yellow – chain 3). Panels (-.-.1) for year 10 (1989), (-.-.2) for year 20 (1999), (-.-.3) for year 30 (2009) and (-.-.4) for year 40 (2019). Panels (-.2.-) show density plots of the parameter distribution, indicating the between-chain convergence in their estimate of the occupancy density function. Panels (-.3.-) show trace plots where the oscillations indicate the within-chain convergence across model iterations.

In Chapter 2, we additionally used Bayesian generalized linear models to investigate whether the two butterfly groups we compared varied in their levels of habitat specialization and preferred temperatures to determine whether other potential causes may impact their trends. We set the category of myrmecophily (obligate vs ant-independent) as explanatory variable and tested both temperature preference (scaled and centred across all Bavarian butterfly species) and the number of habitats the species occupy (log-transformed) as response variables. Models ran with 2,000 iterations on four chains, with half as warmup. All models showed high convergence.

In Chapter 3, we assessed whether species' linear trends changed before and after the legal implementation of the European Habitats Directive. Thus, we modelled the trends before (1980-1998) and after the implementation (2000-2018) for the same number of years while applying weights of the inverse of the occupancy estimates' standard deviation (*1/SD*) to lessen the effect of outliers on the trend estimates (example in Figure 13 C). We assessed the difference between the linear trends before and after implementation by constructing additional models with an interaction term of a two-level factor for Before versus After on the year effect (*occupancy estimate ~ year*Before-or-After*). We extracted the slopes, and 95 % confidence intervals for each species.

In addition to linear trend estimates, we analysed turning points in species' occupancy curves in Chapter 3 by fitting segmented linear models (Muggeo, 2008). In this method, a standard linear model is fit, and by re-fitting the model with every new step in
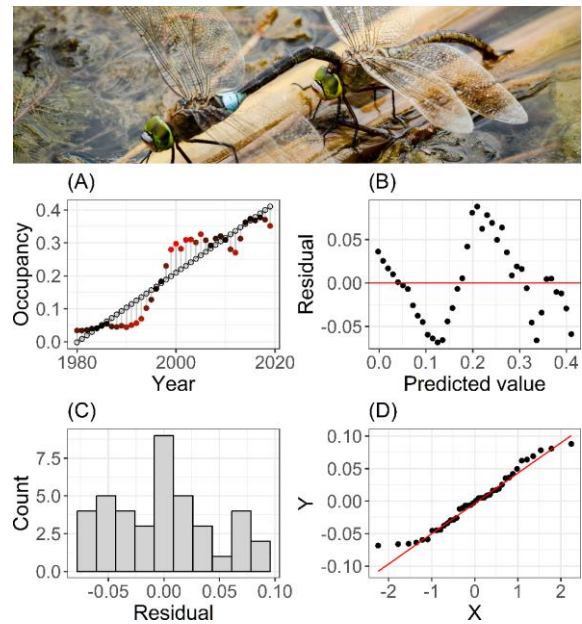
Figure 12 Residual plots of occupancy estimates of *Anax parthenope* (Lesser emperor, family Aeshnidae, pair shown at the top, picture credits E. K. Engelhardt) to test the assumption of normally distributed residuals. (A) Scatterplot of simulated data along the linear regression line (circles) with occupancy estimates (points) where those estimates with larger residuals are coloured brighter red. Residuals are indicated by the line connecting the actual occupancy estimate to the predicted data. (B) Plot of the residuals against the predicted values, where the points should be evenly spread above and below the zero-line shown in red. (C) Histogram of the residuals, where a normal distribution would indicate using a general linear model, whereas non-normal distribution points towards the necessity of applying a generalized model. (D) Quantile plot of residuals, where if the assumption of normality is true, the relationship between X and Y is linear, as indicated by the red line.

our timeline, piecewise linear relationships are added We fit segmented linear models using the SEGMENTED.LM function of the R-package SEGMENTED (Muggeo, 2017). Figure 13 (D) shows the results of such a breakpoint analysis using generalized linear models for comparability to the other generalized linear models. In contrast to other segmented linear models, these models require the segments to join at the estimated breakpoints. Another advantage of the method used here is that it
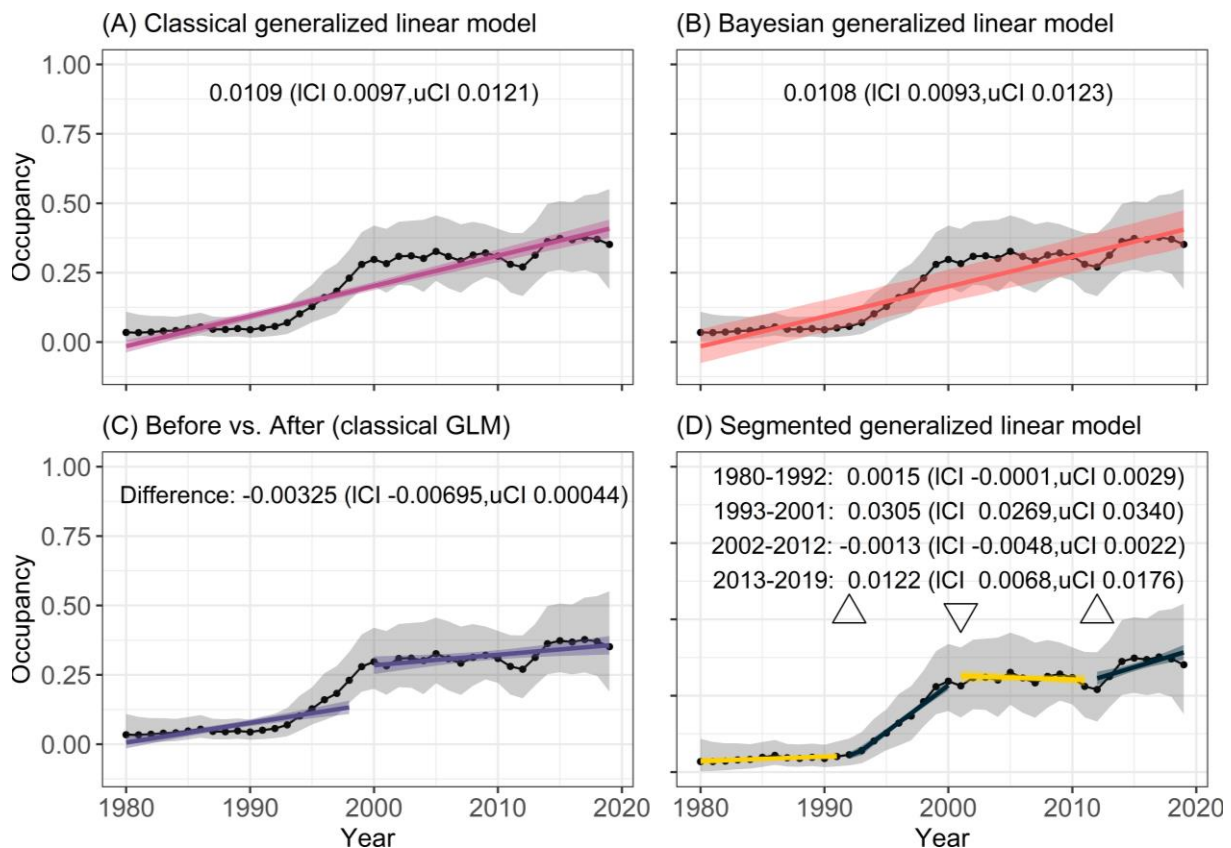
Figure 13 Methods applied to analyse linear trends of long-term annual occupancy estimates on the example of *Anax parthenope* (Lesser emperor, family Aeshnidae). The basis of each plot are mean annual occupancy estimates (points), where grey ribbons represent model estimates' 95 % credible intervals. (A) shows a classical generalized linear model in purple, ribbons indicate a 95 % confidence interval, mean slope and upper (uCI) and lower (lCI) confidence interval given above. (B) shows a Bayesian generalized linear model in red, ribbons indicate a 95 % credible interval, mean slope and upper (uCI) and lower (lCI) credible interval given above. (C) shows a classical generalized linear model in purple, split to compare the time before (1980-1998) and after (2000-2019) implementation of the European Habitats Directive, with ribbons indicating the 95 % confidence interval of both linear models. The difference between the slope before and after with upper (uCI) and lower (lCI) confidence intervals is given above. (D) shows a segmented linear model, where increasing segments are shown in blue and stable segments in yellow, and ribbons indicate 95 % confidence intervals. Triangles indicate years of breakpoints, where triangles pointing up indicate improving trend changes, and the triangle pointing down indicates a deteriorating trend change. The start and end year of each segment, their slopes, and upper (uCI) and lower (lCI) 95 % confidence intervals are given above.

is not necessary to specify in advance how many breakpoints the model should contain in the version of the package used (1.6-2).

2.3.5 Generalized Linear Mixed-Effects Models

Generalized linear mixed-effects models (GLMMs) are extensions of the generalized linear model (GLM) that, in addition to the usual fixed effects, contain random effects of

the linear predictor. These random effects define groups within the data, where the fixed effects are the explanatory variables for the response variable (Wood, 2017). The random effect allows the groups to differ in their slopes, intercepts, or both. We define a variable as a random effect instead of an explanatory variable when we expect it to cause variation in the data, but it is irrelevant for testing the hypothesis.

Excursus 3: Collinearity and Predictor Selection

In a statistical model, collinearity is defined as a linear relationship between two or more predictor variables. The primary issues with collinearity are that variable effects cannot be accurately assigned, and extrapolation is likely incorrect. Therefore, before using a set of predictor variables, these need a check for collinearity.

The most common measure of the direction and the strength of the linear relationship between two variables is the Pearson correlation coefficient (r), which ranges between -1 and 1. It can be applied when both variables are normally distributed without outliers. An effect size $|r| > 0.7$ is considered significant (Dormann et al., 2013); thus, the tested variable combination should not be used in one set of predictor variables. This method is included in the base R-package STATS (R Core Team, 2020) function COR.

Another method to assess collinearity is the variance inflation factor (VIF), which, in contrast to the Pearson correlation coefficient, tests for multi-collinearity between more than two predictors. The VIF does not assess the variables' correlation but instead informs how much of the model's variance is inflated for each coefficient. The minimum value is VIF = 1 and we decided only to consider variable sets where each variable's VIF was lower than three (Tucker et al., 2019; Zuur et al., 2009). We used the R-package PERFORMANCE with the function CHECK_COLLINEARITY to calculate the VIF (Lüdecke, Makowski, Waggoner, & Patil, 2020).

This procedure often results in several uncorrelated variable sets, which all include viable predictors. To decide on one variable set to use for the final analyses and report in the manuscripts, we ran models with each variable set and compared them based on the Bayesian (BIC; Schwarz, 1978) and on Akaike's information criterion (AIC; Akaike, 1974). Both methods are frequently used as model selection criteria, and lower model scores are preferred in both. The AIC is a measure of the goodness of fit of the model tested. It is a frequentist method sensitive to overfitting, tending to give more complex models lower scores. The BIC, however, penalizes higher complexities. It is a Bayesian method whose performance improves with the increasing size of training datasets. Both methods are included in the GLMMTMB function of the R-package GLMMTMB (Brooks et al., 2017), and the AIC and BIC scores are provided with the model results.

In cases where the experimental design affects the interaction we are interested in, correcting for these effects by including them in the model gives us a clearer view of the interaction of interest. In Hallman et al. (2017), for example, their model to estimate linear trends in insect biomass included seasonal effects, a basic effect of habitat type, and a random effect for trap location. Another example is Seibold et al. (2019), whose linear mixed models included weather conditions and land use intensity as covariates.

In our analyses, we were interested in identifying drivers of overall species trends while the species and the years themselves

affect the respective occupancy estimates. Therefore, we allowed the species to affect the intercept of the occupancy estimates in the linear model, as we expected the starting situation to differ between the species, independent of the effects of the environmental drivers we aimed to identify. In addition, we allowed the effect of year to vary among species, as we expected species to develop differently from year to year, independently of the overall trend over the years. That way, for example, a cold spring could have a negative effect on some of the species in a single year, although the other drivers we tested for lead to an overall positive trend.

In Chapter 1 and Chapter 2, we aimed to examine the potential impacts of different insect attributes on the development of their occupancies over the years (see also Excursus 3: Collinearity and Predictor Selection). We used Bayesian generalized linear mixed effects models in both studies via the R-package BRMS (Bürkner, 2017), with the species' annual occupancy estimate as the response variable. We applied models with a beta distribution approach since the occupancies were non-normally distributed and confined between zero and one.

In Chapter 1, we ran the GLMMs separately for each of the three taxa. We ran the models for 4,000 iterations on four chains, half as warmup, with a tree depth of 12 and an increased algorithm step to 0.99999. We used default, weakly informative priors. To ensure the reliability of our results, we compared different sets of models. These included Bayesian models with different priors for fixed effects (narrower normal(0,1), slightly narrower normal(0,10), and the default weakly informative priors), as well as

classical inference models (function GLMMTMB, R- package GLMMTMB, Brooks et al., 2017), and for both Bayesian and classical inference GLMMs we ran models both including and excluding a measure of uncertainty via the annual standard deviation of the occupancy estimate. All model results were reliable (Rhat < 1.1), and similar outcomes were attained across model settings. In the main text, we reported model results for Bayesian models, including uncertainty of the occupancy estimate and slightly narrower normal priors for fixed effects. We defined those attributes as having a significant effect whose 95 % credible intervals are only entirely positive or negative. We assessed the variation explained by the fixed effects of these models by estimating the R^2 (function BAYES_R2, R-package BRMS, Bürkner, 2017). To illustrate the effects over time of those attributes indicated as significant for species' trends, we produced estimated marginal means (R-package EMMEANS, Lenth, 2020). Estimated marginal means model the mean response of the taxon to the attribute of interest while adjusting for the impact of all other attributes in the model. For categorical variables, the estimated marginal means illustrate the response of each group, and for continuous variables, we can define a theoretical value and illustrate the response of the taxon to that value of the attribute, e.g., a temperature preference of 1°C higher than the taxon mean.

In Chapter 2, we compared two categories of butterflies within one family, Lycaenidae, and used Bayesian generalized linear mixed-effects models to test whether the ant-association of the two groups affected their long-term trends. Our models ran with 2,500 iterations on four chains with a warmup of

1,250. The tree depth was 10, and the algorithm step 0.999. As in Chapter 1, we included the annual estimates' standard deviation as model uncertainty and tested three sets of priors for fixed effects (default, weakly informative priors; slightly narrower normal(0,10) priors, which we reported in the main manuscript, and narrower normal(0,1) priors) with default priors for other parameters, which lead to similar results. All models converged well according to Rhat-values (Rhat < 1.1).

3 Chapter Overview

This thesis is divided into three chapters, including two published research papers and one manuscript ready for submission. For each chapter, a summary and description of all co-authors' contributions are provided in this section. Appendices A-C include the full manuscripts.

Chapter 1: Consistent signals of a warming climate in occupancy changes of three insect taxa over 40 years in Central Europe

Eva Katharina Engelhardt, Matthias F. Biber, Matthias Dolek, Thomas Fartmann, Axel Hochkirch, Jan Leidinger, Franz Löffler, Stefan Pinkert, Dominik Poniatowski, Johannes Voith, Michael Winterholler, Dirk Zeuss, Diana E. Bowler, Christian Hof

Background Human well-being depends on intact ecosystems, which are highly dependent on insects. In recent years, climate and land use change have had increasing effects on biodiversity, including dramatic declines in insect abundances and biomasses. Although these declines are widely acknowledged, species-specific long-term trends are scarce, and analyses of driving factors are difficult, especially across taxa, due to a lack of standardized time series data. Poor coverage or low spatial and temporal resolution of existing datasets further limits inferences. New computational methods, however, allow reliable estimates of species' presences from highly heterogeneous datasets, enabling us to analyse past species trends and connect them to possible drivers.

Aim We analysed occupancy changes over 40 years in three insect taxa and linked species' trends to their respective attributes to identify drivers.

Taxa Butterflies (Lepidoptera - Rhopalocera), representing a holometabolous pollinator group; grasshoppers (Orthoptera), an omnivorous, hemimetabolous group; and dragonflies (Odonata), a hemimetabolous, carnivorous, semi-aquatic group.

Methods We used occupancy-detection models to analyse an extensive heterogeneous dataset of species observation data and modelled annual occupancies (the proportion of sites occupied by a species each year) for about 300 species from 1980 to 2019. We calculated each species' linear trend using Bayesian generalized linear models. We assessed the effects of species' attributes on their trends using Bayesian generalized linear mixed models, focussing on attributes regarding temperature and precipitation preference, range size, habitat preference, and habitat specialization.

Results Across taxa, 37 % of all insect species have decreased their occupancies over the past 40 years, 30 % have increased occupancies, and 33 % showed no significant trend. While more than half of the dragonfly species increased (52 %) and 27 % decreased, 41 % of butterfly and grasshopper species declined. We found that temperature preference had a consistent effect across taxa, with warm-adapted species having increased and cold-adapted species having decreased. While butterfly habitat specialists have decreased and habitat generalists have increased, we did not find such a differing effect in grasshoppers and dragonflies.

Main conclusions Climate warming has already affected insect occurrences across taxa during past decades and has consistently affected all taxa. In contrast, landscape-level effects appear more ambiguous and unconnected to specific habitat types. Decreasing habitat quality and area, which are threatened by land use change, could negatively affect butterfly habitat specialists, which are especially dependent on intact habitats. In this study, we showed how species' trends differed across four decades and how these differences could hint towards threats and underestimated effects of human actions. In light of the current biodiversity crisis, these hints could help us to mitigate the detrimental effects of anthropogenic stressors on insects in the future.

See Appendix A for the complete manuscript.

Author contributions

EKE conceptualized the study and defined the data analysis methodology together with DEB and CH. EKE was responsible for data preparation and the formal analysis, working closely with DEB for the occupancy-detection models and with MFB and JL for the attribute analysis. EKE wrote the original draft and generated all figures, with regular feedback from DEB, CH, and MFB. TF, AH, SP, and DZ provided data on species' attributes. MD, TF, FL, DP, JV, and MW gave feedback on species' occupancy estimates and validated the models' results based on their expert knowledge. All authors contributed to the writing by reviewing and editing, and approved the final manuscript.

Chapter 2: Myrmecophily is not a risk factor for long-term occupancy trends of central European Lycaenidae butterflies

Eva Katharina Engelhardt, Diana E. Bowler, Matthias Dolek, Christian Hof

Background Generalist species often fare better than specialist species in a world where anthropogenic stresses are becoming more and more pronounced. Specialization can take numerous forms, for example a reliance on other species through different forms of biotic interactions. Interactions with ants are critical for the survival of several Lycaenid butterflies' larvae, which rely on various types of care supplied by the ant hosts. This reliance may pose a threat to obligate myrmecophile butterflies.

Aim We investigated whether ant-dependency (obligate myrmecophily) affects long-term trends in Lycaenid butterflies.

Taxa Lycaenid butterflies (Lepidoptera – Rhopalocera - Lycaenidae)

Methods We examined 40-year occupancy patterns generated from occupancy-detection models of obligate myrmecophile and ant-independent Lycaenid butterflies.

Results Contrary to what we expected, species of butterflies that are obligate myrmecophiles did not exhibit greater signs of decline than those that are ant-independent. Although five out of eight ant-independent Lycaenids exhibited decreasing trends and five out of seven obligatory myrmecophile species showed increasing

trends, the difference was not statistically significant.

Main conclusions Obligate myrmecophile butterflies interact with various ant species from one or two genera that form long-lived colonies and are found throughout central Europe. These qualities may help the butterflies to adjust to changing conditions. Other Lycaenid species not included in this analysis show varied degrees of affiliation with ants, but our understanding regarding species interactions is limited, making it difficult to identify specific associations that may be under threat. Monitoring changes in the possibilities and intensities of such species interactions is required in our changing environment to prevent the extinction of connected species.

See Appendix B for the full manuscript.

Author contributions EKE developed the study and determined the methodology for data analysis in collaboration with DB and CH. EKE was in charge of data preparation and formal analysis. EKE drafted the initial manuscript, including all figures, with feedback from DB, MD, and CH. Each author reviewed, edited, and approved the written work.

Chapter 3: European Habitats Directive has fostered monitoring but not prevented species declines

Eva Katharina Engelhardt, Diana E. Bowler, Christian Hof

Data from the Bavarian State Agency for the Environment (Bayerisches Landesamt für Umwelt, LfU) were used under license and are subject to limitations. Annual occupancy estimates for the species and the code for occupancy models are accessible via DOI: 10.5061/dryad.4f4qrfjf5, and the code has been published as Supporting Information: Code, respectively.

Background Despite conservation measures like the European Habitats Directive, which tries to stop biodiversity loss across the European Union, there have been widespread reports of significant decreases in biodiversity, particularly in insects.

Aim We evaluated indicators for the Directive's objectives in terms of enhancing monitoring efforts and trends of butterfly and dragonfly annex species in a central European region using 50 years' worth of observational data and 40 years of occupancy patterns.

Taxa Butterflies (Lepidoptera - Rhopalocera), and dragonflies (Odonata), focusing on species listed in the annexes of the European Habitats Directive.

Methods We calculated different metrics of yearly monitoring efforts and compared species trends for 18 years before and after the Directive's legal adoption based on occupancy-detection models.

Results After implementation, monitoring efforts towards annex species intensified while occupancy patterns fluctuated between improving and worsening.

Main conclusions The European Habitats Directive, contrary to its principal purpose, did not prevent the deterioration of all annex species occupancy patterns in the examined region. Even while increased monitoring activities help biodiversity evaluations, more broad-scale conservation actions are required to stop biodiversity loss throughout Europe.

Author contributions EKE conceptualized the study, prepared the data and defined the data analysis methodology together with DB and CH. EKE conducted the analysis and the writing of the original draft with feedback from DB and CH. All authors contributed to the writing by reviewing and editing and approved the final manuscript.

4 Discussion

Occupancy-detection models are valuable tools for assessing past species trends, especially when dealing with highly heterogeneous data where no standardized, long-term time series data is available. We demonstrated that climate warming is a key driver of distribution changes across taxa based on 40 years of occupancy estimates for 300 insect species. Habitat specialization was found to affect butterfly trends but not those of grasshoppers or dragonflies. In contrast to our expectation, the dependence of Lycaenid butterflies on specific ant species for brood care did not negatively affect their trends.

Furthermore, the protection efforts via the European Habitats Directive protection measures had a favourable impact on monitoring efforts toward species listed in its annexes, but species' trends remained ambiguous. Some species showed an increase in their occupancies, while others showed stabilizing or decreasing trends following the implementation of the Directive.

Overall, occupancy-detection models allow the exploration of species trends and offer a solid foundation to understand the drivers of these trends, even in cases where data is limited and heterogeneous. By identifying key drivers of change and understanding the factors that affect different taxa, we can make more informed conservation decisions that effectively protect and manage our natural resources.

4.1 Models as Tools to Fill Research Gaps

In recent years, computer models have become increasingly popular in biodiversity research. They allow us to test assumptions about the natural world where data is unavailable or does not represent the whole truth. A full cover of all biodiversity on Earth is virtually impossible, but models allow us to simulate and explore different scenarios to understand better how ecosystems work.

While large-scale insect monitoring schemes are underway (e.g., Potts *et al.* 2021), current conservation efforts cannot wait for the results of these studies (Harvey et al., 2020; Samways et al., 2020). Therefore, a look into the past using available data is needed. Historical data can help us estimate the potential distribution of threatened species and allow for more effective conservation action (Monsarrat, Novellie, Rushworth, & Kerley, 2019). Occupancy-detection models address biases in available data, providing a higher detection power and lessening data variation (Isaac, van Strien, August, de Zeeuw, & Roy, 2014; Potts et al., 2021; Van Strien, Van Swaay, & Termaat, 2013). They enable us to analyse previously unused data sources, which is especially important where no systematic monitoring took place.

Citizen science offers a complementary approach to professional data collection, which can inform computer models for further inference (Pernat, Kampen, Jeschke, & Werner, 2021). While solely opportunistic citizen science data may not be sufficient for estimating meaningful species trends, our data have the benefit that the Bavarian environmental agency sends qualified experts to resample understudied locations (as recommended by Tulloch, Mustin, Possingham, Szabo, & Wilson, 2013).

Aside from occupancy-detection models, other methods have been proposed to improve estimates of species' occurrence

beyond the available data. For example, Fithian et al. (2015) proposed using species co-occurrence networks to fill gaps in knowledge about species' distributions. By incorporating these methods into biodiversity research, we can better understand the complex relationships between species and their environments and, ultimately, make more informed decisions about the conservation and management of our natural resources.

Models can also be used to test different conservation strategies and assess their effectiveness before implementation. Projections of species occurrences under current and future conditions have received much interest. Species Distribution Modelling (SDMs) has been shown to inform about the location of previously unknown species populations, demonstrating their relevance in directing future field surveys. Incorporating SDMs into environmental impact assessments would improve biodiversity protection prospects in the planning and development of policies (Baker, Maclean, Goodall, & Gaston, 2021). Similarly, occupancy-detection models could be used to fill gaps in long-term surveys, both spatially and temporally.

Computer models also allow calculations of direct links between human actions and on-the-ground impacts on biodiversity. For example, Green et al. (2019) identified Germany's soy consumption at rank four for endangering the Brazilian Cerrado. Proving such direct adverse effects puts more pressure towards improving legislation and its enforcement to improve biodiversity protection globally.

4.2   Limitations to Consider

The quality of the modelling result of any method strongly depends on the quality of the available data used in all modelling steps. Limitations apply and should be considered whenever inferences are drawn from data.

4.2.1   Pitfalls of Species' Observation Data

While occupancy-detection models can make inferences from incomplete observation data, these observations must be species-specific, reliable, and with enough metadata included to inform about the observation process.

Species Identification and Cryptic Species

The first caveat to consider is the reliability of the data at hand, which in the case of observation data centres on the correct identification of the species in the field. Sorting natural items into categories, such as species, families, or classes, is an ability of humans and animals and is essential for survival. The categorization procedure is supported by several processing and representation systems (Smith et al. 2016), which focused on morphological differences between species for a long time but got more fine-scaled up to the molecular level in recent years.

The definition of a species depends on the underlying species concept. The most widely accepted definition is the biological species concept, which defines a species as a group of populations that actually or potentially interbreed and produce viable offspring, and new species are formed where populations are reproductively isolated. Determining reproductive isolation is often challenging,

which has led some to advocate for using more molecular-based, phylogenetic species concepts. These concepts define species based on genetic and evolutionary differences, trying to determine a molecular threshold of differences separating populations into distinct species. However, these populations may still be able to interbreed, and discussions about the best approach to defining a species continue (Bickford et al., 2007; Korshunova et al., 2019; Struck & Cerca, 2019; Talavera, Lukhtanov, Pierce, & Vila, 2013).

Distinguishing between some species can be challenging as it may require a detailed examination of their morphology, behaviour, and genetic makeup (compare Bickford et al., 2007). This process can be particularly challenging in the field, where full coverage of all species is one of the main goals of biodiversity monitoring. Species with minor morphological differences but considerable genetic disparity, resulting in, sometimes partially, inviable offspring where they hybridize, are called cryptic species or sibling species. The terminology used to describe these species is still subject to debate, and improvements in methodology are needed. However, advances in genetic analyses have led to an increase in the number of cryptic species identified (Bickford et al., 2007; Struck & Cerca, 2019). Some argue that the term 'cryptic' is subjective and uncertain and should only be applied when the taxonomy is established (Korshunova et al., 2019).

Cryptic species can have significant implications for biodiversity assessments and the modelling of macroecological processes, analysis of ecological changes, and evolutionary consequences. As a result, it is critical to consider the existence of these

species when making inferences about species development (Struck & Cerca, 2019). In our studies, we identified species that are indistinguishable in the field as cryptic species and aggregated the cryptic species pairs: *Leptidea sinapis* and *L. juvernica* into *Leptidea agg.*, *Polyommatus agestis* and *P. artaxerxes* into *Polyommatus agg.*, and *Colias hyale* and *C. alfacariensis* into *Colias agg.*

Although cryptic species pairs are difficult to distinguish morphologically, they can inhabit vastly different areas across Europe and exhibit distinct environmental preferences. Even if long-term trends show no changes in the occupancy of species aggregates, one species can replace another due to better adaptation to changing environmental conditions. Therefore, we have excluded species aggregates from our driver analyses. Studies have shown that cryptic species often exhibit narrower environmental preferences than their morphospecies counterparts, which could increase their extinction risks (see for example García-Robledo, Kuprewicz, Staines, Erwin, & Kress, 2016), as could be the case for *Polyommatus artaxerxes* in contrast to *P. agestis* (Onay, Hof, Engelhardt *in preparation*).

The accurate identification of species is critical in various aspects of biodiversity research, conservation planning and management, biological pest control, and other areas (Struck & Cerca, 2019). Previous studies have demonstrated that many herbivorous insects previously considered generalists are, in fact, many cryptic host specialists (Berkov, 2002; Blair, Abrahamson, Jackman, & Tyrrell, 2005; Hebert, Penton, Burns, Janzen, & Hallwachs, 2004). Research in tropical regions has revealed that, on the

other hand, herbivorous insects are more generalist in their food plant selection than previously thought due to the emergence of cryptic plant species (Novotny et al., 2002). Without proper species identification, assessing the threat level to a species or identifying factors that could endanger its survival is challenging. Therefore, observation data lacking species-level identification would provide limited information (Potts et al., 2021).

Challenges of Rare Species

Assessments of trends for rare species come with additional challenges due to limited data availability and an increased probability of biases in the sampling (Sastre & Lobo, 2009). In standardized monitoring schemes, rare species are often neglected (Potts et al., 2021), and they require greater monitoring efforts to detect distribution changes (Specht et al., 2017). Trend changes might be obscured by conservative change estimates, such as the use of random walk priors which we applied to our occupancy-detection models (Outhwaite et al., 2018).

Occupancy models may not accurately estimate extinction probabilities for local populations as they are based on average abundance. Extinction risk depends on actual, not average, abundance, which can lead to overconfident extinction probability estimates (Schulz, Vanhatalo, & Saastamoinen, 2020). Rare species are particularly sensitive to increased land use intensity as well as land abandonment (Hilpold et al., 2018; Kleijn et al., 2012).

Especially since rare species could react differently to drivers of change than more common species, considering them adds an important facet to biodiversity assessments. Our inability to assess rare species is an essential constraint in an ecosystem function context, as rare or declining species may play substantial functional roles (Mouillot et al., 2013; Säterberg, Jonsson, Yearsley, Berg, & Ebenman, 2019). Some argue, however, that in terms of ecosystem services, changes in common species' abundances are the driving force (Winfree, Fox, Williams, Reilly, & Cariveau, 2015), and thus rare species could be considered unimportant for human well-being.

Spatial and Temporal Data Availability

The temporal and spatial data availability and its representativeness when inferring to different scales is a crucial aspect to consider, in particular in macroecological settings. The assessment of species' ecological niches is incomplete when only recent distribution records are used (Monsarrat et al., 2019). These erroneous estimates then, in turn, could lead to misguided conservation efforts and affect the forecasting of species' future distributions.

While data for European and North American countries is extensive and continuously growing, global spatial bias is extreme. Sampling effort and gross domestic product (GDP) per capita are positively related, meaning that many areas of the world with limited resources have less available data than more wealthy regions (A. C. Hughes et al., 2021). For instance, the Global Biodiversity Information Facility (GBIF) data only covers 11% of the land surface at a resolution of 5 km. Therefore, drawing inferences solely from European and North American data cannot provide a comprehensive understanding of the

situation in other parts of the world. This is a significant limitation that should always be considered when interpreting results from studies such as ours.

Spatial Scale Dependency

Ecological research often faces the challenge of scale dependence, where ecological patterns and processes can exhibit different behaviours at different spatial scales.

On the one hand, scale dependence is a data issue. When using range maps like the ones we used for our assessments of species' climatic niches, the real-world fine-scale distributions are much patchier than suggested by even the most detailed expert-drawn range maps (Hurlbert & Jetz, 2007). Thus, whenever we use range maps, the parameters derived based on them must be considered rough estimates, which give an impression but not a clear reflection of the truth.

On the other hand, species' responses to environmental drivers depend on the spatial scale considered. Biodiversity changes occur in different forms on different spatial scales. Chase et al. (2019) showed several examples of how species richness can change locally but show opposite patterns on a regional scale. In up to 10 % of analysed studies, biodiversity changes switched their trend directions across scales, indicating frequent and severe scale dependency in the research on drivers of biodiversity change (Chase et al., 2018). Current estimates of ecological responses to climate change, as well as the design of experiments to understand underlying processes, are often focused on broad-scale trends and averages that may have little to do with the sensitivity of animals

and ecosystems at a local level (Helmuth et al., 2014; Nadeau, Urban, & Bridle, 2017). The consideration of spatial scale is an important aspect when interpreting driver effects. Analysing data on a finer or coarser scale can lead to contrasting results, highlighting the need for careful selection of spatial scale in such analyses.

4.2.2   Pitfalls in Analysing Insect Trends

Reliable Long-Term Trend Assessments

Estimating species trends is central to biodiversity research, informing conservation planning, management, and policies. However, different trend estimation methods can yield varying results, highlighting the importance of considering the strengths and limitations of each approach.

A common method for estimating species trends which we also applied here, is through linear trend analyses. This approach assumes a constant rate of change over time. The main shortfall is that linear trend estimates may not account for changes in population dynamics, such as sudden declines or increases.

Breakpoint analyses can identify sudden changes in population dynamics and apply segmented linear models with easily interpretable trend estimates between the breakpoints. When we assessed species trend changes using breakpoint analysis, 15 % of our species showed linear trends without changes in the trend direction over the past 40 years (compare Figure 14). For the majority of species (39.1 %) the models identified two breakpoints over four decades, followed by 26.5 % of species with one breakpoint and 23.5 % with three breakpoints. In contrast, in a recent study Blumgart et al. (2022) compared linear to
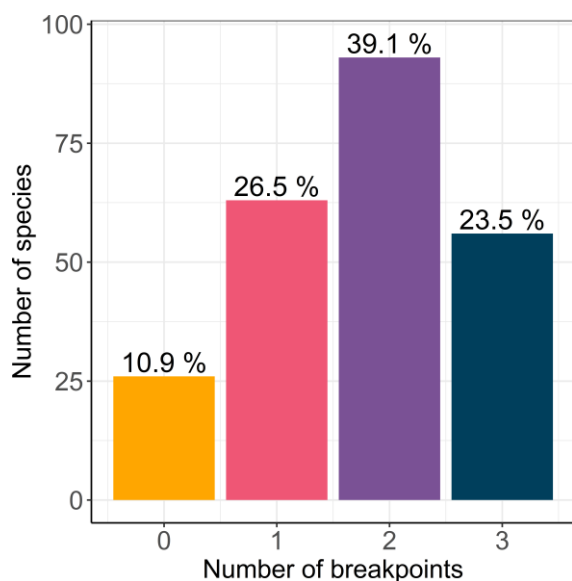
Figure 14 Assessment of the number of breakpoints in the occupancy estimates over 40 years of 238 insect species (butterflies – Lepidoptera, Rhopalocera; grasshoppers – Orthoptera; dragonflies – Odonata) with reliable model results (Rhat < 1.1, SD < 0.1, minimum occupancy of 0.025) using segmented generalized linear models. Percentage of all modelled species with the respective number of breakpoints. See Appendix D for results including all 300 species.

non-linear year effects in moths' total abundance, biomass, and species richness. They found that, except for species richness, the relationship between the variables and time was linear. This suggests that linear trend estimates may be reliable for some aspects of biodiversity assessment; however, more robust, consistent methods for long-term trend estimates need to be discussed for a clear picture of the state of biodiversity.

As an alternative approach to single-species trends, assessments of the trends of entire species communities emerged. These multi-species indicators seek to simplify a complicated reality by identifying the most prominent patterns of change. Metrics such as species richness, evenness, and diversity indices can provide a general sense of community health but may not capture more

subtle changes in species composition or interactions.

A more complex but often utilized method to assess biodiversity trends is the geometric mean (*G*), which can be applied to occupancy estimates (E. B. Dennis, Brereton, et al., 2019; Outhwaite, Gregory, Chandler, Collen, & Isaac, 2020) or relative abundance. It is increasingly used to investigate biological diversity trends and determine if biodiversity objectives are being reached (Buckland, Studeny, Magurran, Illian, & Newson, 2011). One well-known application of the geometric mean of relative abundance indices is the Living Planet Index (Loh et al., 2005), used to monitor progress toward five of the Aichi CBD biodiversity objectives for 2011-2020; see, for example, the Living Planet Index report (WWF, 2022).

While the methodology helps simplify overall trends, the indices should be considered with caution as some weaknesses apply and results are easily misunderstood (Buschke, Hagan, Santini, & Coetzee, 2021; Puurtinen, Elo, & Kotiaho, 2022). Discussions arose about the sensitivity of mean trends to outliers (Leung et al., 2020), where cluster identification was offered as a more suitable approach. A reliable methodology, however, is still under discussion (Loreau et al., 2022).

Bowler et al. (2021) used another time series clustering method, resulting in species assemblies with similar trend dynamics over time. The attribute characteristics of each group hint towards essential drivers of the species trends, while the emerging trend dynamics show more detail than overall trends.

To summarize, whichever approach is used to measure biodiversity changes, we need to

consider results cautiously because all indices are estimates with flaws, and results can be misinterpreted.

Shifting Baselines

Irrespective of which method is applied to assess biodiversity trends, one of the main challenges is the problem of shifting baselines. In theory, an actual 'start' of a species' occurrence is when the species first formed; however, this is a continuous process, usually further in the past than our data entails. Thus, the trend estimate must start at some point, which with linear trend estimates, has substantial effects on the overall species' trend.

Shifting baselines are often discussed in the context of a syndrome affecting conservation, where people are unaware of past biodiversity conditions and thus perceive the changes observed as minor (Loreau et al., 2022; Papworth, Rist, Coad, & Milner-Gulland, 2009). Similarly, the starting point of linear trend estimates affects the results wherever the trend is not continuous over time (see, for example, Figure 15). When the baseline for a species' trend is continually adjusted downward as the population declines over time, this can lead to an underestimation of the severity of declines (Habel et al., 2016; Mehrabi & Naidoo, 2022), altering our perception of conservation success.

Although our models span four decades of species observations and thus are one of the more extended time series available, they are not long enough to represent a state before severe anthropogenic impacts happened. To establish adequate temporal baselines for
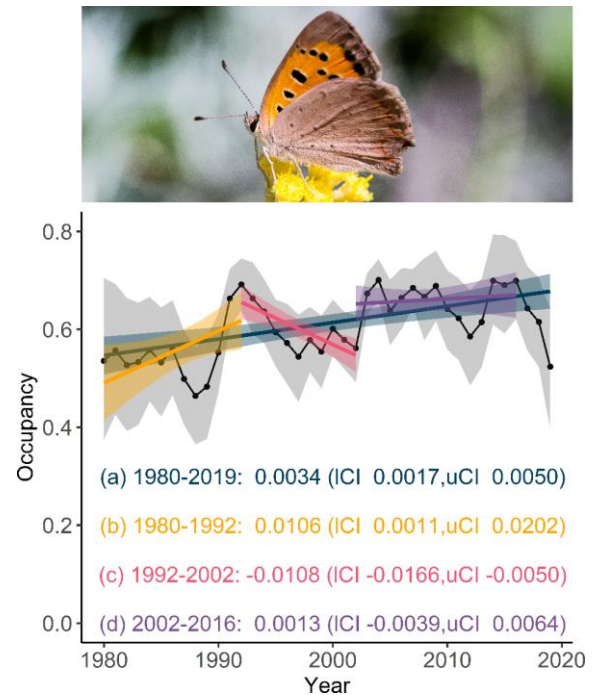
Figure 15 Shifting baselines for linear trend analysis shown on the example of the butterfly *Lycaena phlaeas* (Lepidoptera, Lycaenidae – photograph on top by E. K. Engelhardt) and four exemplary timeframes. Linear trend estimates derived from classical generalized linear models with lower (lCI) and upper (uCI) 95 % confidence intervals given for (a) the entire study period, 1980-2019, in dark blue, showing a slightly increasing trend, (b) a period ending with two years with estimates above the mean trend line, 1980-1992, in light yellow, showing a significant increase (lower and upper CI > 0) (c) a period starting with three years above and ending with several years below the mean trend line, 1992-2002, in medium red, showing a significant decrease (lower and upper CI < 0), and (d) a period with a stable trend (lower CI < 0, upper CI > 0), 2002-2016, in medium purple.

community comparisons, data obtained prior to the onset of the drivers of species trend changes should be included (Habel et al., 2016; Mehrabi & Naidoo, 2022; Papworth et al., 2009). Especially land use-related drivers connected to the industrial revolution in agriculture started in the 17th century already, and in recent decades the most substantial declines in plant diversity occurred between 1960 and 1980 (Eichenberg et al., 2021; Ellis et al., 2010). In contrast, climate change-

induced temperature increases began in the 1970s, and temperatures increased continuously during our study period (compare Figure 1). As a result, identifying rising temperatures as the primary driver of current species trends could be considered self-evident.

Metrics to Estimate Species' Status

Assessments of whether a species is threatened depend on reliable estimates of its status, which is subject to the definition of the underlying metrics. The most commonly used and widely recognized metric is the International Union of Conservation of Nature (IUCN) Red List of Threatened Species, which categorizes the conservation status of species based on a set of criteria (Standards and Petitions Committee of the IUCN Species Survival Commission, 2022). The criteria consider factors such as population size, geographical range, habitat availability, and quality, and the degree of threat from human activities such as hunting, habitat loss, and climate change. Similarly, the European Union assigns a conservation status to each species considered relevant, including different aspects of the species' biology, ecology, genetic diversity, and cultural, social, and economic value. These criteria include population size and trends, distribution and range, habitat quality and trends, threats, and conservation measures (Röschel et al., 2020).

Our analysis focused on distribution rather than abundance changes, two different factors to consider when analysing a species' status. Where both metrics are positively correlated, distribution trends are prone to underestimating abundance trends (Buckley

& Freckleton, 2010; but see Pinkert et al., 2020; Webb, Freckleton, & Gaston, 2012). In some cases where species expand their distribution, their abundance can decrease simultaneously (E. B. Dennis, Morgan, Fox, Roy, & Brereton, 2019).

Clear guidelines for assessing the efficiency of conservation efforts are required to accomplish nature conservation aims, such as the European biodiversity plan for 2030 (European Commission, 2020a). Occupancy-detection models provide valuable insights into a single aspect of a species' status by representing changes in their distribution over time. It is crucial to recognise that an accurate representation of a species' fate can only be achieved by analysing various factors that reflect its occurrence.

4.2.3 Representativeness of the Analysed Taxa

In analysing insect trends and drivers, the representativeness of the taxa included is essential to consider. Among insect taxa, pollinators probably gain most of the attention, research, and monitoring focus (e.g., Potts *et al.* 2021). While pollinators are often considered a group with many commonalities, in a global analysis of pollinator responses to different aspects of land use intensity, Millard et al. (2021) found that while most insect pollinators decreased with increasing fertilizer application, dipterans showed the opposite trend. Crossley et al. (2020) also found differing abundance trends for different insect groups.

The three insect taxa we analysed in our studies, butterflies, grasshoppers, and dragonflies, are frequently used representatives of insects in ecological

research. Data availability is comparably good for all three groups. Especially butterflies and dragonflies are well sampled, well-liked among citizen scientists, and attribute data is accessible as well. The number of species in Germany is comparably low, with 170 butterfly, 87 grasshopper, katydid and cricket, and 81 dragonfly and damselfly species. They are mostly morphologically distinct, have manageable species numbers, and can be readily observed throughout the day. Therefore, these three taxa are recognized as important in nature conservation and frequently used to monitor species diversity (Hausmann, Krogmann, et al., 2020).

In combination, these three groups represent a mix of insect attributes. Butterflies and grasshoppers are predominantly terrestrial, while dragonflies are semi-aquatic. This mix allows for a more comprehensive view of the insect community, and the three taxa have been shortlisted as representatives for open habitats and freshwater conditions, respectively (Samways et al., 2020). Additionally, butterflies are more specialized (compare also Figure 6), relying primarily on flowers for food and larval habitat, while grasshoppers are more generalist, feeding on various plant materials. Dragonflies are carnivorous and feed on other insects, altogether giving them a different ecological role. Another advantage is the different developmental modes of these three groups. Butterflies undergo complete metamorphosis, while grasshoppers and dragonflies are hemimetabolic. This difference in developmental mode represents the broader range of life cycles present in the insect world. In sum, these differences allow a multifaceted look into how insects contribute to

ecosystems and respond to anthropogenic drivers.

However, there are also drawbacks to using these taxa as representatives. As butterflies, grasshoppers, and dragonflies are relatively well-known groups in the highly diverse class of insects, many other insect taxa may be overlooked and react entirely differently to ecological drivers. All three groups tend to include larger, more conspicuous species and may not be representative of most insect species, which are often small and inconspicuous. They represent only a fraction of the insect taxa occurring in central Europe and, thus, likely do not provide a comprehensive picture of the insect community.

Insects are a highly diverse class, and just like we cannot infer from three mammal orders like whales, primates, and lagomorphs to the state of all mammals, we cannot expect all insects to show the same patterns as the few (sub-)orders analysed. Especially since current estimates of global species numbers expect there to be 5,000,000-10,000,000 insect species compared to 5,000-10,000 mammal species, we should be aware that our studies can only provide us with a glimpse into what is happening.

4.2.4   Availability of Driver Data

The availability of data to explore different drivers of biodiversity change can vary widely, depending on the source and the specific variable of interest. While climate-related data, as well as attribute or trait data, is often openly available and provided by scientific institutions, data related to human activities and economic sectors may be harder to obtain due to a range of factors, including

privacy concerns, intellectual property rights, and commercial interests.

Climate Data

The most accessible data in the context of our research is climate-related data. The climate research community has long embraced open science values prioritizing transparency, collaboration, and data sharing. This has led to the development of numerous data repositories and tools for analysing climate data. The choice of meaningful data and scale is an important caveat. The spatial and temporal resolution of the data available is a trade-off between accuracy, detail, and computational resources.

Observational datasets provide high-resolution climate data, such as satellite-based remote sensing data or data from ground-based weather stations. This data can provide more detailed information on the distribution and variability of climate variables in specific regions; however, the timeframe of this data is usually somewhat limited. In addition, weather stations do not cover all regions equally.

Climate models, like the ones we used for our analyses (compare section 2.2.2 Climate Attributes), can simulate past, present, and future climate conditions at various temporal scales, from daily to decadal to century-long simulations, using available historical meteorological data as input. They can be used to simulate climatic conditions under different scenarios for the future, including various scenarios for land use change, greenhouse gas emissions, or population growth. These simulations can provide insights into how climate conditions might change depending on human actions.

However, like all models, they come with some uncertainties, especially in regions with complex terrain or where weather systems interact with the land surface. Model parameterizations are based on simplified representations of complex physical processes and may not accurately represent some physical processes critical for regional climates (Murphy et al., 2004; Rummukainen, 2010).

Attribute Data

Depending on the taxonomic group and the specific trait of interest, the availability of species attribute data can vary widely. Some traits may be well-studied and widely available in existing databases or literature (as, for example, in section 2.2.2 Habitat Attributes), while others may be more difficult to obtain due to a lack of research or data collection. Furthermore, as explained in Excursus 1: Trait vs Attribute, traits often differ under changing environmental conditions (e.g., Prinster *et al.* 2020 on grasshopper dispersal under changing weather conditions), which makes some information more difficult to obtain than others.

In recent years, there has been a growing effort to improve the availability and accessibility of species attribute data by developing new data-sharing platforms and increasingly collaborative research (for example, following the FAIR principles, Wilkinson *et al.* 2016). As open science is on the rise, many data owners publish their data along with their findings, such as the datasets we used for Chapter 2 on myrmecophily (compare section 2.2.2 Biotic Interaction Attributes: Myrmecophily). Specialized groups often focus on studying a particular taxonomic group and accumulate substantial

amounts of data through various methods such as fieldwork (for example König, Krauss, Keller, Bofinger, & Steffan-Dewenter, 2022), measurements of museum specimens, or analysis of photographs (Zeuss, Brandl, Brändle, Rahbek, & Brunzel, 2014). More sophisticated methods for species detection and measuring their traits in the wild are increasingly being developed (Mungee & Athreya, 2020).

These datasets often come with limitations that must be considered when interpreting subsequent analysis results. Collaborative research can provide a valuable means of addressing these limitations and improving the accuracy and reliability of scientific findings. Furthermore, the involvement of taxon experts in the research on a specific group is highly advantageous. Thus, through collaborations more attribute data becomes accessible, providing opportunities for further research, for example, on the effects of larval food sources or dispersal attributes on past species' trends.

In a conservation context, however, this attribute information often serves merely as a proxy for the 'real' drivers, which are mostly land use related and thus connected to agricultural practices.

Data on Pesticide and Fertilizer Application

Despite a changing world regarding data sharing, access, and openness, there are still significant difficulties in compiling datasets that would meet the needs of comprehensive risk assessments for agricultural practices. While multiple databases and tools are available to research specific pesticides (for example, K. A. Lewis, Tzilivakis, Warner, & Green, 2016; Mei et al., 2022), even for

modelling their fate and transport in the environment (Felix, Holst, & Sharp, 2019), by the date of submission of this work it was not possible to receive information of pesticide and fertilizer application on an ecologically meaningful scale for our study region.

The European Union has strict policies on agricultural data, which, among else, require member states to collect and report comprehensive data on pesticide and fertilizer sales and use at the parcel level. This collection includes data on the spatial application of pesticides, specifying the pesticide product used, the quantity applied, and the location of the application. Similarly, member states collect and report data on the use of fertilizers, including their nutrient content and the location of the application. For pesticides, the first EU directive requiring data collection on plant protection products entered into force in 1993 (Council Directive 91/414/EEC, 1991) and was later replaced (Regulation (EC) No 1107/2009, 2009) with more stringent requirements. Additionally, another Directive to develop national action plans for the sustainable use of pesticides (Directive 2009/128/EC, 2009) and further Regulation for the collection and statistical analysis of pesticide production, trade, and use in the EU (Regulation (EC) No 1185/2009, 2009) were implemented. For fertilizers, the EU Fertilizer Regulation entered into force only in 2019 (Regulation (EU) No 2019/1009, 2019). In Germany, pesticide reporting is mandatory under the Plant Protection Act (PflSchG, Bundesministerium der Justiz, 2012) and the Federal Regulation on Integrated Plant Protection. A nationwide reporting system collects data on pesticide use at the farm and parcel levels. Similarly, the fertilizer ordinance

(DüV, Bundesministerium für Ernährung und Landwirtschaft, 2012) sets out rules for using fertilizers and requires farmers to keep records of their applications.

Although the data collection both by the European Union and the state of Germany appears extensive and should be available to the public, especially for research purposes (PflSchG, Bundesministerium der Justiz, 2012; Directive 2009/128/EC, 2009), much of the data is subject to confidentiality or privacy requirements. Under the EU General Data Protection Regulation (GDPR, Regulation (EU) 2016/679, 2016), personal data collected as part of pesticide and fertilizer reporting systems must be protected and processed following data protection principles. Both the German and the EU regulations do not specify the level of public availability of the data collected. The plant protection act stipulates that the data collected should be kept confidential and not disclosed to the public, except in cases where the public interest in disclosure outweighs the interests of the affected parties. Due to these restrictions, we were not able to acquire any information on the amount of fertilizers or pesticides applied in our study region.

Studies investigating the effect of agricultural practices on biodiversity fall back to measuring pesticide exposure in the field. To name just two examples of the extensive literature on pesticide presence in non-agricultural systems, Brühl et al. (2021) found residues of multiple pesticides in insect samples in nature conservation areas close to agricultural areas, with the number of pesticides increasing with the agricultural area in a 2 km radius around the traps. Pesticide runoff from agricultural areas was found to lead to ecologically relevant pesticide

concentrations in small streams across Germany (Szöcs, Brinke, Karaoglan, & Schäfer, 2017), indicating that pesticides affect aquatic as well as terrestrial insect species.

Despite our frequent understanding of how a pesticide works in its intended target species, we have yet to fully grasp the unforeseen consequences it may have on higher levels of biological organization, such as populations, communities, and ecosystems (Köhler & Triebskorn, 2013). The adverse effects of pesticides on different levels of biodiversity are undisputed, and the deposition of nitrogen fundamentally alters previously nitrogen-limited ecosystems with extensive biodiversity (Wagner, 2020).

Although the assessment of possible connections between insect trend changes and fertilizer or pesticide application is crucial to resolve disputes between conservation and agricultural interests (Henle et al., 2008), we were unable to obtain the necessary data for our study. Without these data, informed decision-making by the public, policymakers, and farmers regarding the side effects of pesticide and fertilizer use is not possible. Since the lack of data on the use of pesticides and fertilizers for research purposes deprives the general public of important insights, it would be of great public interest to make such data available.

4.3   Insect Change in the Model Region

While we showed that some limitations apply to our study results and that there are many options to expand our research further, we derived some essential conclusions about

insect change and its drivers in our Central European study region over recent decades.

4.3.1   Species Composition is Changing

During the 40 years our studies covered, we detected considerable changes in species composition with great differences between the three insect taxa. Dragonflies showed a positive mean trend with linear increases in 52 % of the species with reliable model estimates. In contrast, both terrestrial groups were leaning towards the negative. In butterflies, twice as many species decreased than increased (51 species decreased, 25 species increased), and in grasshoppers, 20 species decreased, while 16 species increased.

Increasing trends in dragonflies are likely linked to improved habitat quality of water bodies across Europe, thanks to the Water Framework Directive (Dahl, Patt, Arzet, & Sellheim, 2016; Directive 2000/60/EC, 2000; Karle-Fendt & Stadelmann, 2013; Termaat et al., 2015). Improved habitat quality, combined with dragonflies' strong dispersal capacity (Bowler et al., 2021; Grewe, Hof, Dehling, Brandl, & Brändle, 2013), enables many species to follow their climatic niche (Termaat et al., 2019). Thus, the positive trends of many dragonfly species are most likely associated with successful conservation measures in combination with favourable biological traits.

In contrast, the declines we found in overall butterfly trends might indicate a possible diversity decline and a general decrease in habitat quality across terrestrial butterfly habitats. The diverging trends of grasshopper species might hint towards a possible turnover in community composition, as has been shown in other

places as well (Beketov et al., 2013; Ewald et al., 2015; Outhwaite et al., 2020).

Previous studies observed a spatial homogenisation of biodiversity, where many specialized species were replaced by a few widespread species (Gossner et al., 2016; McGill et al., 2015; McKinney & Lockwood, 1999; Newbold et al., 2018). The relationship between ecosystem functioning and biodiversity changes is still largely unclear. However, we know that the decline of specialized species and the resulting homogenization of biodiversity can have grave consequences for ecosystem functioning and ecosystem services on which humans rely (Newbold et al., 2019). Species extinction risks significantly correlate to cumulative anthropogenic pressures on the environment (Di Marco, Venter, Possingham, & Watson, 2018), which will likely impair ecosystem resilience to future environmental changes.

Attributing species trends to specific, often interacting drivers is difficult. A combination of different indicators could come together; for example, the combination of a preference for low-nitrogen environments and open habitat types led to strong population declines in moths (Fox et al., 2014). Thus, a single attribute is likely not enough to predict the extinction risk of species. Such analyses need to include several ecological characteristics (Mattila, Kaitala, Komonen, Kotiaho, & Päivinen, 2006), and therefore we used combinations of different attributes as proxies for environmental drivers to assess likely causes of species trends.

4.3.2   Ambiguous Outcomes of Protective Efforts

The legal implementation of the European Habitats Directive led to increased monitoring activities toward annex species. First increases occurred after the start of the monitoring activities for the species protection mapping by the Bavarian environmental agency, with peaks in general monitoring efforts in the years preceding the publication of atlases for butterflies and dragonflies (dragonflies: peak in the late 1980s/early 1990s, Kuhn & Burbach 1998; butterflies: peak in the 2000s, Bräu *et al.* 2013). After the publication of the atlases, general monitoring activities decreased again, but not for annex species, which led to an increase in the proportion of observations of annex species. Projects specifically targeting annex species were installed for butterflies even before the Habitats Directive was implemented into national law, and observation numbers for dragonflies increased strongly along with the establishment of monitoring projects after 2006.

We believe that the database accurately reflects the public and institutional commitment to insect monitoring, first intending to publish taxon-specific atlases and later to fulfil the reporting duties required under the Habitats Directive, thus indicating the success of the Habitat Directive's rigorous reporting criteria for species listed in its annexes. It demonstrates the efficacy of quantifiable measures for which governments may be held accountable.

On the other hand, quantifiable measures might be lacking for protective actions, especially for insects. The examination of protected species trends revealed that the implementation of the European Habitats Directive did not succeed in halting the decline of all annex species' occupancy trends (see Chapter 3). While the occupancies of certain annex species continued to decline, some annex species demonstrated improvements or remained stable. These ambiguous results are contrary to the principal objective of the Directive, which aims to prevent any further decline in species' statuses. Legal commitments to species protection may be ineffective if the rule of law is not adequately enforced, especially when conflicting interests are involved (López-Bao et al., 2015).

Only a minor portion of species' trend changes between before and after implementation of the Habitats Directive could be related to local conservation efforts, given that about 11% of the research region is protected within the European framework Natura 2000 (Bayerisches Staatsministerium für Umwelt und Verbraucherschutz, 2021) while our analysis presents species distribution changes across all of Bavaria. Some species, however, such as the butterfly *Coenonympha oedippus*, are only known to occur within protected areas where significant efforts are undertaken to maintain optimal conditions for preserving the species (Dolek et al., 2017). Other species are more common across Bavaria, like *Phengaris nausitous* and *Phengaris teleius*, which are generally protected under the Habitats Directive. About half of the occurrences of these species are located within protected areas with extensive measures to ensure optimal coordination of the mowing time (Dolek et al., 2017). Both these species' trends are among the species with the greatest deteriorating trend changes, driven mainly by significant improvements

prior to the implementation of the Habitats Directive and a later stabilization of their occurrences without further increases. This trend change might indicate that the species already inhabit all available habitats across the study region, but with additional protective efforts they could have the ability to increase their distribution.

The effectiveness of insect conservation efforts, especially for butterflies, depends on conserving, expanding, and connecting the microstructures necessary for larval development (Dolek et al., 2017). This often requires an intensive involvement of landowners and -users, where disputes emerge because of divergent land use objectives. Compared to the agricultural sector represented by the European Common Agricultural Policy (CAP), environmental conservation initiatives are underfunded, and the contract nature conservation program with its compensation offers often seems not attractive enough for farmers (Dolek et al., 2017; Hodge et al., 2015).

Agricultural use interests are often opposed to nature protection interests. Even slight intensifications of land use may cause habitats to become unsuitable for many species. Consequently, many protected habitat types are still degrading and in inadequate or poor condition (Adelmann et al., 2017).

Germany is currently being sued by the European Commission in two cases, referring to inadequate protection of flower-rich meadows and poor general compliance with the Habitats Directive (European Commission, 2021a, 2021b). In addition, previous research has shown that insect biodiversity across Germany is deteriorating

even at protected sites (Hallmann et al., 2017; Rada et al., 2019). Our findings support the hypothesis that the Habitats Directive has provided some, but not enough, protection thus far, and additional conservation work at the landscape level beyond specific conservation areas is needed (Maes et al., 2013).

4.3.3   Consistent Climate Warming Effect

Our analyses showed the consistent effect of climate warming on insect species across three taxa, though the magnitude of the effect differed between groups. Previous studies suggest that, compared to other drivers, climate change has had comparatively small effects in recent decades (Caro et al., 2022; Dale, 1997), but as the strength of the warming increases, so does the effect on species distributions. While warm-adapted species increased their occupancy over the last four decades, cold-adapted species decreased in all three insect taxa (see Chapter 1). Efforts to limit climate change are insufficient to halt the ongoing changes over the next decades (IPCC, 2022b), and thus the disruptive effects are likely to increase further.

We found that butterflies were the least affected by climate warming compared to grasshoppers and dragonflies. The microclimatic conditions required for butterfly larval development might have changed under changing climatic conditions due to higher vegetation growth rates due to a combination of warmer temperatures, sufficient precipitation, and increased nitrogen input (Habel et al., 2016). The increased plant growth may result in a cooler and more humid microclimate near the soil,

subsequent in more negative effects for warm and dry-adapted butterfly species. Thus, butterfly species which, due to their higher temperature preference, should profit from increasing temperatures under climate change may find unfavourable microclimatic conditions, thus lessening the positive effect on species' trends.

In addition to the overarching effects of global warming, a single weather event can significantly impact a population's survival and growth. The butterfly species *Speyeria mormonia* may serve as an example, as the timing of snowmelt affects the availability of floral resources and, subsequently, the per-capita nectar availability for the butterflies. Research has shown that this nectar availability accounts for 84% of the variation in the butterfly's population growth rate (Boggs & Inouye, 2012). Moreover, observations of butterfly populations suggest that wetter and warmer years lead to more butterfly observations (Pardikes, Shapiro, Dyer, & Forister, 2015), likely also linked to higher population numbers, emphasizing the importance of understanding the relationship between weather and population dynamics. Under global warming, the frequency and intensity of extreme weather events are increasing (IPCC, 2022b), which might strongly affect species' trends.

Species respond to environmental changes through local adaptations or changes in distribution. Species' distribution changes in response to climate change not only depend on their temperature preference but also on their ability to shift their ranges into more suitable areas. If all species responded consistently to the changing climatic conditions, habitats would simply move towards the poles, putting 'just' boreal

communities at risk (Berg et al., 2010). However, as more mobile species are predicted to disperse into more favourable environments, while poor dispersers have to adapt to changing conditions in their original range, climate change is expected to have disruptive effects on ecosystems as a whole (IPCC, 2022a). Thus, a serious discussion about the effectiveness of nature protection measures under climate change is necessary (Asamoah, Beaumont, & Maina, 2021; Dobrowski et al., 2021).

Species already shifted their ranges in the past decades, and little is known about their adaptations. During glacial-interglacial cycles, drastically changing regional climates possibly resulted in rapid regional biodiversity turnover over decades and centuries (Fordham, Saltré, Brown, Mellin, & Wigley, 2018). A look into past climate shifts could offer an impression of the amount, location, and timing of physiological stress factors species already faced in the past.

The impact of climate warming on insect species distributions has been significant and ongoing, while the issue has been largely disregarded, underestimated, and deferred to future generations. Numerous studies underscore the imperative to take action against climate change, and the latest 6th IPCC assessment report (IPCC, 2023) stressed that many species might not survive the climate crisis. Our research highlights once more that climate change is not a distant problem but a present-day concern that has had consistent effects over recent decades.

4.3.4 Biotic Interactions are Essential to Consider

Studies that simulate the future ranges of interacting species show how species distribution changes to follow their climatic niche can disrupt biotic interactions (Schweiger, Settele, Kudrna, Klotz, & Kühn, 2008), suggesting a more significant threat to interdependent species. On the other hand, having a widespread and adaptable interaction partner might also increase species' chances of survival under changing conditions (Engelhardt, Neuschulz, & Hof, 2020). Similarly, our studies hint towards a stabilizing effect of ant-dependency on Lycaenid butterflies in the past (see Chapter 2). Host characteristics likely affect the interaction partner's survival, mediated by the hosts' rarity or abundance (Colwell, Dunn, & Harris, 2012). The Lycaenid butterflies we analysed favour ant species that may be more resilient to hazardous environmental change because they build ecologically dominating, long-lived colonies (Fiedler 2021). This could increase the butterflies' resilience, but as ant colonies may also exhibit delayed reactions to stressors, the dependent butterfly species might also experience delayed declines.

Significant gaps remain in our understanding of the complex relationships between organisms, particularly under changing environmental conditions. Therefore, monitoring and further research on interacting species are crucial to improve our understanding of how ecological communities respond to environmental changes and to develop effective conservation strategies (Sutherland, Roy, & Amano, 2015).

4.3.5 Complex Habitat Indicators

The availability of suitable habitats is one of the determinators of species occurrence (J. M. Diamond, 1975). The presence of specialized species is predominantly determined by habitat quality, as well as the available area of the habitat (Löffler & Fartmann, 2017; Poniatowski, Stuhldreher, Löffler, & Fartmann, 2018; C. D. Thomas et al., 2011). Intensification of land use, along with abandonment, reduces habitat quality, particularly for species inhabiting open habitats, and changes in land use can cause certain habitats to become dominant over others (Dou et al., 2021; Stoate et al., 2009).

Our study indicated a negative effect of habitat specialization on butterflies but not on grasshoppers or dragonflies (compare Chapter 1). This difference might be linked to the proportion of species in our study codified as habitat specialists, here classified by the number of habitat types occupied in the research area (compare Figure 6 for all species; thus, percentages differ). In the subset of species with reliable occupancy estimates considered in the driver analysis (compare section 2.3.3 for species selection criteria), 83 % of butterfly species were habitat specialists, compared to 61 % of the grasshopper and 60 % of dragonfly species. As a result, the decline in butterfly specialists may indicate a vulnerability connected with land use, which may impact more butterfly species than species of the other taxa.

A general increase in habitat generalists and a decrease in habitat specialist species has emerged as a typical pattern in the recent past (Habel et al., 2016; N. S. Sodhi, Brook, & Bradshaw, 2009), even when differing definitions of specialization were applied. These trends lead to a homogenisation of

biodiversity (compare section 4.3.1) and a reduced spatial turn-over of species globally (Gossner et al., 2016; McKinney & Lockwood, 1999), where distinct, rare species with narrow distributions get replaced by few widespread generalist species (McGill et al., 2015; Newbold et al., 2018). Rare and specialized species are susceptible to a combination of land use and climate change and are likely less capable of shifting their distributions in response to climate change in landscapes strongly altered by humans (Newbold et al., 2019; Oliver et al., 2017; A. Purvis & Hector, 2000). Increased habitat fragmentation caused foremost by agricultural intensification and urbanization specifically threatens specialized species, as only small, isolated habitat patches of poor quality remain, which are highly sensitive towards low-key disturbances (Krauss et al., 2010; Melbourne & Hastings, 2008; Wenzel et al., 2006). Where habitats are lost to urbanisation and altered by increasing agricultural use, both habitat specialists and generalists decline (Fox et al., 2014).

The preferred habitat type had no significant effect on species trends, although other research has found that grassland butterflies are in considerable decline (van Swaay & Warren, 2006). However, the attributes employed only serve as indirect surrogates for encoded drivers, and the habitat classification is a coarse approximation. Land use intensity indicators have been identified as critical influencers of insect trends (Beketov et al., 2013; Ewald et al., 2015), potentially outweighing the significance of land use per se.

Additionally, although our study covers four decades, landscape changes occurred over longer timescales before.

Habel et al. (2016) link butterfly declines to industrialization and agricultural intensification, which happened over longer timescales than the last few decades; thus, studies covering shorter periods may not catch the initial effects of these drivers. However, in the lack of definite driver data, such as pesticide and fertilizer application rates, it is impossible to rule out any land use characteristics as probable drivers of species occurrence change.

4.4   Next Steps in Understanding Biodiversity Change

Based on the analyses presented here, several options for future research arise. First, further attributes could be considered, such as species dispersal ability, phenology, or food resources. Second, occupancy-detection models could be extended to include more insect taxa as well as a spatial component so that species' occurrence change in space over time could be assessed. Last, more explicit data on drivers related to agricultural practices could be assessed to determine their relative contribution to species trends. Combining these three aspects could inform us about measures necessary to create a resilient environment for insects and people to combat the challenges we are facing under climate change.

4.4.1   Further Attribute Analyses

The main difficulty when assessing attributes of many species covering several taxa is to find coherent data for all. In this thesis, we focused on drivers that we could determine consistently for all three insect groups; however, further analyses might need to focus on single taxa or compromise the

coherence of the used driver data to analyse the effects of additional drivers.

Dispersal

Dispersal ability has been discussed as an important intermediate cause of species' declines or increases in response to climate and land use change. Declines are often linked to weak dispersers, especially in highly agricultural landscapes (Foden et al., 2013; Pacifici et al., 2017; Pearson et al., 2014; Seibold et al., 2019).

Little is known about many insects' dispersal ability, apart from a few iconic species. While movements of larger taxa such as mammals or birds have long been monitored, tracking small insects to determine their dispersal distances is a particular technical challenge, though new technologies might lead to increasingly available data in the future (van Klink et al., 2022). In the lack of real-world dispersal distances, proxies derived from morphological measurements could be used instead.

The ability of a species to disperse can be plastic and evolve (Ronce, 2007). Far-dispersing individuals are likely a subset of the population displaying different physiology or behaviour (Wolf & Weissing, 2012), which may result in selection processes between the sedentary and the dispersing subpopulation (Shine, Brown, & Phillips, 2011). This pattern has been shown, for example, for wing-dimorphic grasshoppers, where more large-winged individuals occur at the expanding front of the species' range, and for butterflies where range-expanding populations have differing wing aspect ratios and more developed flight muscles compared to

sedentary populations (C. L. Hughes, Dytham, & Hill, 2007). Such intraspecific differences cannot yet be considered in trait analyses but should be kept in mind when addressing the effect of dispersal ability, especially when projecting future distributions (Moran, Hartig, & Bell, 2016).

Closely related to dispersal distances are migratory patterns. Little is known about insect migration, although some suggest that many more than the already known species do migrate (Chowdhury, Fuller, Dingle, Chapman, & Zalucki, 2021). Patterns get more complex as some species display partial migration, where parts of the population migrate and others are sedentary. Conservation efforts for sedentary species are relatively straightforward, for example, for the butterfly *Lycaena helle,* which displays a maximum dispersal distance of 600m according to Modin & Öckinger (2020), and thus requires targeted protection efforts within the populations' habitats. In contrast, as our knowledge of migrants' stopover sites and destinations is minimal, protection of migratory species is difficult to achieve.

Phenology

In response to changing climate patterns, species' phenologies change as well. Butterfly species with more advanced overwintering stages, a narrower larval diet breadth, or smaller range sizes have been shown to experience greater phenological advancements (S. E. Diamond, Frame, Martin, & Buckley, 2011). Most grasshopper species in central Europe overwinter in the egg stage and need a cold impulse for their development. If individuals hatch earlier and develop faster, as has been shown to occur by Nufio et al. (2019), the egg-laying date may

also enhance, which could lead to more extended periods where the eggs need to persist in the soil, thus increasing the risk to dry out as well as predation risks.

The effects of phenological aspects on species' long-term trends, such as the number of generations in a year, the time of development from juvenile to adult, the month of first occurrence, or the length of the adult period, have yet to be determined. In addition, such changes in phenology could alter species co-occurrences and, thus, species interactions (e.g. Visser, te Marvelde, & Lof, 2012). Thus, phenological changes have a tremendous disruptive power where much remains unknown.

Food Resources

Over time the average nitrogen values of available host plants for butterfly and moth species increased (Habel et al., 2016), altering microclimatic conditions and phytosociological structures (Vries et al., 2007). Information on species resource plants, their attributes, and distribution could explain why butterflies show more negative overall trends than grasshoppers. In addition, we could gain more detail on the rough habitat type classification we used in our analyses so far.

Analysing the plant resources needed for insects to thrive could inform whether a reduction in food plants caused species declines, which would be especially interesting in combination with occupancy-detection models expanded for a spatial component. Thus, inferences could be drawn to inform conservation action to enhance the availability of plant resources, specifically in

those areas where most insect resources have been lost in the past.

4.4.2 Extending Occupancy-Detection Models

Our studies highlight the value already available species records can have when analysed properly to inform us about past biodiversity changes. We presented first insights for three exemplary insect taxa, but as data for more groups have already been collected and the power of modelling techniques such as occupancy-detection models has been shown, naturally, trend assessments for a broader range of insect groups are more than possible.

An interesting aspect to consider is that data pre-1980 is available as well. While thus far, our taxon experts disagreed with the results of our occupancy models pe-1980, so we discarded those results. A further look into earlier data might be warranted to establish a baseline of species' occurrence to assess current trends. Focusing on species with a sufficient number of observations pre-1980 or adding a factor to relate to the small number of overall samplings might be two possible starting points for further analyses.

Additionally, modelling techniques are increasingly easy to implement, and spatial modelling has become available in recent months (i.e., the SPOCCUPANCY package, Doser *et al.* 2022). Thus, assessments of spatiotemporal trends as a fascinating extension to temporal trends such as the ones assessed here could additionally inform about spatial hotspots of both insect biodiversity and threats.

4.4.3   Investigating Land Use Aspects

Many discussions on insect decline over recent years led to locked-in debates on the importance of pesticide and fertilizer application as drivers of insect trends, with the farmer's lobby claiming that 'sweeping criticism' of plant protection products was unwarranted and caused by a romantic view on wilderness (Krüsken, 2022), especially since farmers adhere to the 'good professional practice' (BMELV, 2010). This discussion could potentially remain ongoing until explicit data on the application of pesticides and fertilizers becomes available.

A combination of data on pesticide and fertilizer application with information on, for example, the percentage of area with organic farming, protected areas, and conventional agricultural areas, surface sealing, and weather data per year on a grid level could combine different drivers of biodiversity change with spatial information from advanced occupancy-detection models. This kind of analysis could inform local decision-makers about the most prevalent threat for insects in their area and foster cross-sectoral discussions about necessary conservation measures. A proactive plan to protect biodiversity is vital in light of the increasing force of climate change, as the combined impacts of climate and land use change increase where more threats collide, and the spatial distribution of threats changes when multiple drivers are taken into account (Mantyka-Pringle et al., 2015).

5 Conclusion

Our work illustrates the potential of underused data sources to expand our knowledge of past insect trends. Occupancy-detection models are effective instruments for analysing occurrence changes over previous decades, even when available data is highly heterogeneous (Isaac et al., 2014; Van Strien et al., 2013), and large-scale trend assessments are mostly anecdotal. Although some limitations apply (compare section 4.2), our modelling technique offers an appropriate compromise between accurate species-specific occupancy estimates and integrating multiple insect taxa in one modelling approach. Most of our model results matched expert expectations, whose feedback is essential in model development (Outhwaite et al., 2019). Future analyses of insect trends could widen the taxonomic scope to include more representatives for the highly diverse class of insects.

We showed that while dragonflies showed a mean increase in occupancies, grasshoppers remained stable, and butterflies showed a slight decline over the past four decades. These three exemplary taxa exhibit considerable species-specific differences in their trends, where each group includes species that are increasing, decreasing, or stable in their distributions.

We tested different attributes as possible drivers of these species' trends across taxa. We found a consistent effect of climate change across all three groups, with a general pattern where warm-adapted species increased, and cold-adapted species decreased. Other drivers lead to more ambiguous changes. Only butterfly habitat specialists declined compared to habitat generalists, and we found no difference in grasshoppers or dragonflies. A reliance on ant species was not a risk factor for Lycaenid butterflies in the past, although we would have expected such dependencies to be unfavourable. Protective efforts under the European Habitats Directive led to trend improvements in some butterfly and dragonfly species but not in others, indicating that current protective efforts are insufficient on the regional scale.

Although nature protection efforts aim to conserve species sustainably, a baseline to define the status to be achieved is often lacking. Collaborative approaches combining the expertise of taxon specialists, quantitative ecologists, and citizen scientists offer the possibility to define such a baseline from heterogeneous data where a coordinated monitoring system has yet to be developed. That way, rapid and focused conservation action can be initiated already.

Increasing monitoring efforts towards annex species due to the implementation of the European Habitats Directive showed the power of strict requirements that are punishable by law. Conservation goals could be defined based on available data from the past without having to wait for current efforts to streamline monitoring systems across the European Union (Potts et al., 2021) or on the national level (Bundesministerium für Umwelt Naturschutz und nukleare Sicherheit (BMU), 2019) to produce results.

In the past, insects in central Europe faced a wide range of anthropogenic stressors. Public awareness, combined with recognition of scientific findings by elected officials, resulted in some cases in effective approaches to addressing the issues. Poor water quality,

for example, has already been addressed by the European Union (Directive 2000/60/EC, 2000), leading to some improvements in habitat quality, resulting in noticeably more positive trends in dragonflies than the two terrestrial taxa in our study region. Nowadays, similarly complex stressors like nitrogen deposition and pesticide use are in the public spotlight, but data acquisition to explicitly analyse these potential drivers of insect change is complicated, thus hampering required actions.

Despite the lingering uncertainty surrounding the precise mechanisms driving ecological disturbances at a micro level (e.g., Nijssen *et al.* 2017 on nitrogen deposition effects), a vast body of compelling evidence implicating the influence of certain factors on the degradation of our ecosystems exists already (Montgomery et al., 2020). Therefore, we must recognize the existing knowledge and undertake a concerted effort to transform our economy in ways that foster biodiversity (Schoof, Luick, & Paech, 2020). Focusing on significant threats such as habitat loss and overexploitation to preserve ecosystems not only safeguards biodiversity but also represents the sole economically feasible global strategy to counteract climate change (Caro et al., 2022). Especially in central Europe, which is strongly affected by industrialization, a high human population density, and few natural habitats left, but with great wealth and theoretically available funding to tackle the challenges before us, we need to increase our efforts to protect and restore biodiversity.

"Insects are in trouble, and we must take conservation actions now,
rather than wait for biologists to provide exhaustive demographic
data, measure all drivers, and attempt to quantify population trends
across thousands of individual lineages."

Montgomery et al. (2020)

6 Outlook

6.1 Recent Developments in Insect Protection

Our analyses on insect change came at a time of increasing public interest in their fates. In 2019, a referendum took place in Bavaria expressing the public expectation to stop the loss of insect diversity (Bayerisches Staatsministerium für Umwelt und Verbraucherschutz, 2023), the "Volksbegehren Artenvielfalt und Naturschönheit in Bayern – Rettet die Bienen". It was based on the findings of Hallmann et al. (2017) on profound insect decline, and with more than 1.7 million votes, it was the most successful referendum in the history of the region. Both the 'Hallmann-paper', the resulting public outcry, and the referendum also pushed the German federal government to work on a program for insect protection, the „Aktionsprogramm Insektenschutz", which was officially adopted in September 2019 (Bundesministerium für Umwelt Naturschutz und nukleare Sicherheit (BMU), 2019).

Both the Bavarian legislation and the federal insect protection program have faced profound criticism. General objections emphasized that the programs are not ambitious enough and do not sufficiently address the root causes of insect decline, such as industrial agriculture and the use of pesticides, and rely too heavily on voluntary measures instead of enforcing stricter regulations needed for adequate insect protection (BUND Naturschutz in Bayern e.V., 2020). Some argue that, although it was about time to establish a national monitoring program, already existing information should first be sufficiently applied to initiate improvements (Schoof et al., 2020).

6.2 The Underappreciation of Insects in the Anthropocene

Despite insect protection being crucial for a sustainable future and thus of significant public interest, the importance of insects (and biodiversity in general) is underappreciated by society and politics. An indicator of our priorities could be the money spent on different causes. The annual costs of running pollinator monitoring schemes are less than 0.02% of the economic value of pollinator services that would be lost after a 30 % decline in pollination service (Breeze et al., 2021), demonstrating that insect conservation and monitoring programs more than pay for themselves. Nevertheless, compared to other areas, insect conservation is vastly underfunded. For example, in 2018, Germany spent around €65.4 billion on environmentally harmful subsidies through tax breaks, direct payments, and other financial support (Burger & Bretschneider, 2022). In comparison, under the „Aktionsprogramm Insektenschutz", the German federal government plans to spend about €100 million annually for insect protection, including about €25 million annually for a nationwide monitoring program and further research on insect conservation.

This asymmetric pattern can be observed in many instances where anthropogenic threats to biodiversity are discussed. Many European policies display a vocabulary of human dominance over nature through technological control, efficiency, and management (Veraart & Blok, 2021). The biosphere is viewed as a source of resources for human consumption, and the need to preserve it is driven primarily by economic considerations. Insect relevance is frequently

justified in terms of their usefulness for humans, described as ecosystem services, and translated into a monetary value. This narrative appeals to a wide range of audiences; yet, because we do not know the precise function and thus the use of many insect species, we do not know what we risk losing and cannot thus inform about their value.

With our current practices in industry, agriculture, and urbanisation, we risk losing large parts of our biodiversity, where insects are one group among many that anthropogenic drivers threaten. Although the dependence of human well-being on biodiversity is by now integrated into the conservation discourse (Mace, 2014), the extent and rate of environmental destruction brought on by human activity are not fully appreciated (Goulson, 2019).

6.3   From Scientific Knowledge to Political Decision-Making

More understanding of ecological facts may be helpful for conservation in cases focusing on specific species in specific environments, but simply increasing the amount of information available would not consequently result in more sustainable actions. Even well-known threats are often ignored, despite being prohibited by existing protection frameworks (e.g., Woods *et al.* 2003 on threats by outdoor cats (*Felis catus*)). While there are no valid legal justifications for the lack of action, Trouwborst & Somsen (2020) list four probable reasons for non-compliance with already established conservation laws, which might also apply to other areas where a lack of effective measures occurs. First, there could be a general lack of

public awareness regarding the threat to biodiversity. Second, disagreements could occur over the exact design and prosecution of the laws that would be necessary for sustainable conservation action. Third, the general perception might be that fulfilling the requirements would be practically impossible, expensive, or otherwise unreasonable. Last, political inconveniences might prevent effective measures, such as a reluctance to prohibit a widely popular practice.

Transforming scientific knowledge into political decision-making may seem like a simple process, yet, scientific facts are often selectively chosen to support the interests and normative frameworks of the involved parties to aid the desired outcome (Sarewitz, 2004). Depending on their social or institutional background, media use, or political context, people may draw differing pictures of reality based on the same scientific facts. Especially where the relationship between cause and effect is still a subject of debate, policy decisions might reflect other stakes (e.g., political or economic) while yet legitimately claiming to be "following the science" (Norberg, Blenckner, Cornell, Petchey, & Hillebrand, 2022). Thus, ecology undermines the importance of research in policymaking by allowing stalled discussions to continue. Scientific uncertainty, often a central issue in such controversies, can also result from competing scientific understandings influenced by different political or ethical positions of the disciplines involved.

To effectively resolve environmental challenges, Sarewitz et al. (2004) argue that the value bases underlying disputes must be determined. The necessity to examine nature through different stakeholder lenses brings with it a variety of viewpoints and competing

interests that must be addressed when informing the public about the importance of biodiversity. Consequently, addressing not only scientific issues but also the underlying value-based political or ethical positions is essential to resolve environmental controversies. Nevertheless, in a democracy, the public may make decisions based on values and priorities that scientists would not agree with (Pielke, Jr, 2007).

6.4 Communicating the Importance of Insect Biodiversity

Prioritization of biodiversity issues is often incomplete and lacks objective information (Underwood & Grace, 2017). Especially concerning insect declines, many people find the thought of fewer insects appealing, as the general perception of insects focuses on their harmful effects on humans and does not appreciate our dependence on the myriad of interactions that make up the ecological systems. As Dave Goulson (2019) stated, we should be "deeply concerned" about the general public's lack of appreciation for insects, especially since significant cross-sectoral transformative action is required to ensure human well-being and end biodiversity reduction (Díaz et al., 2019).

Some people believe that if we learn enough about how ecosystems work and how to replace single elements within them, such as robotic bees for crop pollination, we can substitute natural biodiversity. The development of technology to replace natural systems may seem like a viable solution. However, so far, technology clearly underperforms with regard to ecosystem services provided and supported by insect populations (e.g., in product quality of hand-

pollinated versus insect-pollinated fruit, Leopoldina - Nationale Akademie der Wissenschaften *et al.* 2020). Additionally, this view would reduce the value of nature to something entirely disconnected from its intrinsic worth (Maier, 2012). While it may be possible for humans to survive in a world poor in biodiversity, we should seriously imagine what that world would look like. This biotechnologist option of manipulating natural systems to fit a human-invented design may have unintended consequences which we can neither fully understand nor control.

During recent decades, conservation biology has primarily been problem-focused, with only a quarter of studies dedicated to solution-based research (Fonseca et al., 2021). A shift towards solution-based research could increase the effectiveness of conservation action, providing prospects of what a sustainable future could look like and what practices are needed to forward in our society.

Involving the broader public in conservation and inspiring a sense of the innate value of nature is an important aspect when trying to turn the tide on the fate of biodiversity. Currently, a great focus is put on citizen science, which will likely increase in importance as a data source in the future but requires some investments (Soroye et al., 2022). Additionally, communication, especially about insects, needs to improve. We do not know based on which sources people build their knowledge about insects and how these sources shape public perception of insects' worth (Hart & Sumner, 2020). An interdisciplinary approach involving, for example, sociological, psychological, and economic perspectives, could improve our understanding of how to

promote insect conservation (Leitão et al., 2020).

Promoting biodiversity regularly benefits human-wellbeing. Where areas are under high anthropogenic pressure, for example, in urban habitats, more room for nature would not only serve as habitats and moving corridors for many species (Balbi et al., 2021; Ganser, Albrecht, & Knop, 2021; Plummer, Gillings, & Siriwardena, 2020) but at the same time improve air quality and thus support human health (Abhijith et al., 2017; Pugh, MacKenzie, Whyatt, & Hewitt, 2012). The combination of architectural knowledge with ecology is another example of how interdisciplinary approaches are needed for a sustainable future (Weisser et al., 2022). Green infrastructure and buildings improve the quality of life for both human and animal occupants of the area, lessen environmental impacts of industrialized societies, and improve people's connection to nature (Cole, 2019).

Planet Earth is constantly changing, including the biosphere, where we observe merely a snapshot of the current state (Fordham et al., 2018). Relating conservation goals to a state we perceive as "whole" or "natural" might undervalue the complexity of ecosystems and their adaptability (Rohwer & Marris, 2021). Conserving the remaining intact ecosystems and restoring them to a biodiverse state is an ambitious, important goal, especially in a world under climate change, where our survival as a species depends on the resilience of our natural resources. The potential contribution of remaining ecosystems to net emission reduction is more profound than wind power, and nearly as much as solar, and existing forests are more important than planting new

trees (IPCC, 2023). The importance of ecosystems goes beyond their instrumental value for human well-being. They are an integral part of a life in which humans are not only surviving but flourishing (Jax et al., 2018).

6.5 Utopia: Care for Nature

Interest in insect conservation has spiked in recent years, both in the scientific community and the public, giving reasons for hope. Multiple special issues and review articles have been published, summarizing many of the factors also discussed in this thesis, and ranging from a description of factors threatening insects and driving change (e.g., Leather 2018; Sánchez-Bayo & Wyckhuys 2019; Montgomery *et al.* 2020; Wagner 2020; Harvey *et al.* 2022) to a focus on how to proceed based on this knowledge (Didham et al., 2020; Matthew L. Forister, Pelton, & Black, 2019; Harvey et al., 2020). Samways et al. (2020) boiled the problem down to two necessities: first, making space for insects, and second, promoting a collective political will and concerted effort to protect and restore biodiversity. Many of the named studies conclude that, by now, enough evidence is available providing numerous local-level strategies to preserve insects.

Working together is a central virtue of humanity. More efforts must be undertaken to exchange and understand each other's points of view across disciplines and contrasting perceptions of the same problems and scientific approaches.

Biodiversity is vital for all aspects of life; therefore, conservation practices should focus not only on conservation and restoration but include all societal actions of

production, consumption, and participation. Along this line, feminist theories of care promote the idea that nature should be treated with empathy and compassion rather than as a resource to be exploited for human gain (Jax et al., 2018).

Care for nature emphasizes the importance of relationships between humans and non-human organisms, recognizing that humans are embedded in a web of relations with nature (Chan et al., 2016). Including a relationship approach in the discussion focuses on three main questions: what do people care for, why do they care, and in what way? Defining the value basis underlying our relationship with nature is essential to strengthen the justification, motivation, and focus on actions for nature conservation (Jax et al., 2018). Emphasizing the reciprocity in human-nature relationships is not only relevant for addressing the biodiversity crisis but also for conveying the risks of climate change. By highlighting the importance of care for nature, we may turn the tide for insects in the Anthropocene and make significant progress in conserving and restoring biodiversity.

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Appendix A: Chapter 1

Engelhardt, E. K. et al. (2022) *Consistent signals of a warming climate in occupancy changes of three insect taxa over 40 years in Central Europe.* Global Change Biology, 28/13, 3998-4012, doi:10.1111/gcb.16200

This article is available at https://onlinelibrary.wiley.com/doi/10.1111/gcb.16200

Data and code published as *Dryad Dataset* Annual occupancy estimates for butterflies, grasshoppers and dragonflies in Bavaria (Germany), 1980-2019, DOI: 10.5061/dryad.4f4qrfjf5 and DOI: 10.5281/zenodo.6447332

Appendix B: Chapter 2

Engelhardt, E. K. et al. *Myrmecophily is not a risk factor for long-term occupancy trends of central European Lycaenidae butterflies.*

This article is available upon request, please see orcid.org/0000-0003-0080-8168 for updated contact details.

Appendix C: Chapter 3

Engelhardt, E.K. et al. (2023) *European Habitats Directive has fostered monitoring but not prevented species declines*. Conservation Letters, 1–10, doi: 10.1111/conl.12948

This article is available at https://onlinelibrary.wiley.com/doi/10.1111/conl.12948

Code has been published as Supporting Information: Code.

Long-term occupancy trends across three insect taxa and their potential drivers in Central Europe

E.K. Engelhardt

April, 2023

Appendix D: Code

Data availability statement

The data that support the findings of this thesis are available from the Bavarian State Agency for the Environment (Bayerisches Landesamt für Umwelt,LfU). Restrictions apply to the availability of these data, which were used under license for this thesis. Species' annual occupancy estimates and code for occupancy models are available under doi:10.5061/dryad.4f4qrfjf5. For code and data of the analyses of the chapters,see the respective chapter.

Here I present code for graphics and data presented exclusively in the thesis.

For figure and table descriptions see main text. Graphics formatting is specified for export as PNG graphics file,thus some of the display in this appendix is not optimized.

Preparations

Packages

Session information and literature of packages used here can be found at the end of the file.

```r
# basic packages
library(magrittr) # introduces piping
library(tidyverse) # combination of different packages

# plotting packages
library(ggpmisc) # extensions to ggplot2
library(magick) # read images
library(plotly) # finetune plots
library(patchwork) # combine plots
library(ggimage) # add images to ggplots
library(cowplot) # plot themes,arranging multiple plot,annotations

# Bayesian linear models,generalized,mixed-effect
library(brms)
library(ggmcmc) # analyzing MCMC simulations

# packages needed for segmented linear models
library(segmented)

#
#
#
#
```

Icons, photos, and colours

Icons for taxa

```
butterfly <- image_read("C:/Users/ekath/R_Coding/MINTbio/butterfly_silhouette.png")
dragonfly <- image_read("C:/Users/ekath/R_Coding/MINTbio/dragonfly.jpg")
grasshopper <- image_read("C:/Users/ekath/R_Coding/MINTbio/grasshopper.jpg")

lepi_plot <- image_ggplot(butterfly)
odo_plot <- image_ggplot(dragonfly)
ortho_plot <- image_ggplot(grasshopper)
```

Species photos ((C) E. K. Engelhardt)

```
Alevana <-
  image_read("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/Araschnia_levana1.jpg")
Alevana2 <- image_ggplot(Alevana)
```

Define taxon colour

```
taxon_cols <- c("Lepidoptera"="#2da049","Orthoptera"="#ffd100","Odonata"="#00444e")
taxon_cols1<- c("Butterflies"="#2da049","Grasshoppers"="#ffd100",
                "Dragonflies"="#00444e")
```

Create ggplot2 map theme

```
theme_map <- function(base_size=10,base_family="") {
  theme_classic(base_size=base_size,base_family=base_family) %+replace%
    theme(axis.line=element_blank(),axis.ticks=element_blank(),
          axis.text=element_blank(),axis.title=element_blank(),
          panel.border=element_blank(),
          plot.title=element_text(size=10,face="bold",hjust=0.5),
          strip.background=element_blank(),plot.tag.position=c(0.05,0.9),
          strip.text=element_text(size=10,face="bold"))}
```

Load shapefile of bavaria

```
load("C:/Users/ekath/R_Coding/MINTbio/data/bavaria.rda")

# Re-project shapefile to Northings and Eastings
bavaria <- sp::spTransform(bavaria,sp::CRS("+init=epsg:31468"))
```

Global mean temperatures (Fig. 1)

Temperatures as the median of 200 time series modelled using the HadCRUT.5.0.1.0 climate model, received from the Met Office Hadley Centre, Climate Research Unit, downloaded on March 9 2023.

```
globtemp <- read.csv(
    "C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/LongTermGlobalTemperatures.csv",
    sep=";",dec=",") %>% dplyr::select(1:4) %>% dplyr::rename(temp.deviation=
    Deviation.from.global.mean.surface.temperature.from.the.long.term.average.in..C)

# Define colour scale inspired by the 'warming stripes' (Hawkins 2018)
tempcol <- c("1"="#08306b","2"="#08519c","3"="#2171b5","4"="#4292c6",
             "5"="#6baed6","6"="#9ecae1","7"="#c6dbef","8"="#deebf7",
```

```r
                  "9"="grey90","10"="#fee0d2","11"="#fcbba1","12"="#fc9272",
                  "13"="#fb6a4a","14"="#ef3b2c","15"="#cb181d","16"="#a50f15",
                  "17"="#67000d")

# Define the temperature values for each colour step

min(globtemp$temp.deviation)
## [1] -0.2328947
max(globtemp$temp.deviation)
## [1] 1.297594
```

```r
seq(from=-0.2328947,to=1.297594,length.out=17)
seq(from=-0.2328947,to=0,length.out=9)
seq(from=0,to=1.297594,length.out=9)
```

```r
plot.globtemp <- globtemp %>% dplyr::mutate(cat=
 ifelse(temp.deviation < -0.20378286,1,
 ifelse(temp.deviation >= -0.20378286 & temp.deviation < -0.17467103,2,
 ifelse(temp.deviation >= -0.17467103 & temp.deviation < -0.14555919,3,
 ifelse(temp.deviation >= -0.14555919 & temp.deviation < -0.11644735,4,
 ifelse(temp.deviation >= -0.11644735 & temp.deviation < -0.08733551,5,
 ifelse(temp.deviation >= -0.08733551 & temp.deviation < -0.05822368,6,
 ifelse(temp.deviation >= -0.05822368 & temp.deviation < -0.02911184,7,
 ifelse(temp.deviation >= -0.02911184 & temp.deviation < 0,8,
 ifelse(temp.deviation == 0 ,9,
 ifelse(temp.deviation >= 0 & temp.deviation < 0.1621992,10,
 ifelse(temp.deviation >= 0.1621992 & temp.deviation < 0.3243985,11,
 ifelse(temp.deviation >= 0.3243985 & temp.deviation < 0.4865977,12,
 ifelse(temp.deviation >= 0.4865977 & temp.deviation < 0.6487970,13,
 ifelse(temp.deviation >= 0.6487970 & temp.deviation < 0.8109962,14,
 ifelse(temp.deviation >= 0.8109962 & temp.deviation < 0.9731955,15,
 ifelse(temp.deviation >= 0.9731955 & temp.deviation < 1.1353947,16,
 ifelse(temp.deviation >= 1.1353947,17,NA)))))))))))))))))),
 cat=as.character(cat)) %>%
 ggplot()+ geom_bar(aes(x=Year,y=`temp.deviation`,fill=`cat`),stat="identity")+
 geom_hline(aes(yintercept=0))+
 #draw boxes: reference period
 geom_segment(aes(y=0.4,yend=0.4,x=1850,xend=1900),linetype="dotted",size=0.5)+
 geom_segment(aes(y=-0.25,yend=-0.25,x=1850,xend=1900),linetype="dotted",size=0.5)+
 geom_segment(aes(y=-0.25,yend=0.4,x=1849,xend=1849),linetype="dotted",size=0.5)+
 geom_segment(aes(y=-0.25,yend=0.4,x=1901,xend=1901),linetype="dotted",size=0.5)+
 #draw boxes: study period
 geom_segment(aes(y=1.35,yend=1.35,x=1980,xend=2019),linetype="dashed",size=0.5)+
 geom_segment(aes(y=-0.05,yend=-0.05,x=1980,xend=2019),linetype="dashed",size=0.5)+
 geom_segment(aes(y=-0.05,yend=1.35,x=1979,xend=1979),linetype="dashed",size=0.5)+
 geom_segment(aes(y=-0.05,yend=1.35,x=2020,xend=2020),linetype="dashed",size=0.5)+
 scale_y_continuous(name="Deviation from global mean surface temperature in °C",
                 breaks=c(seq(from=-0.25,to=1.5,0.1)),expand=c(0.005,0.005))+
 scale_x_continuous(breaks=c(seq(from=1850,to=2022,10)),
                 limits=c(1849,2022),expand=c(0.005,0))+
 scale_fill_manual(values=tempcol) + theme_bw() + guides(fill="none")

# Create caption text
capt.globtemp <- globtemp %>% pull(Source) %>% unique()

#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/GlobalTemperatureDeviation.png",
#units="in",width=7,height=4.5,res=1200)
p1 <- plot.globtemp+theme(plot.margin=unit(c(0,0,0,0),"pt")) +
```

```
    plot_annotation(caption=paste("Source: ",capt.globtemp))
#dev.off()
#ggview::ggview(device="png",units="in",width=7,height=4.5)
```
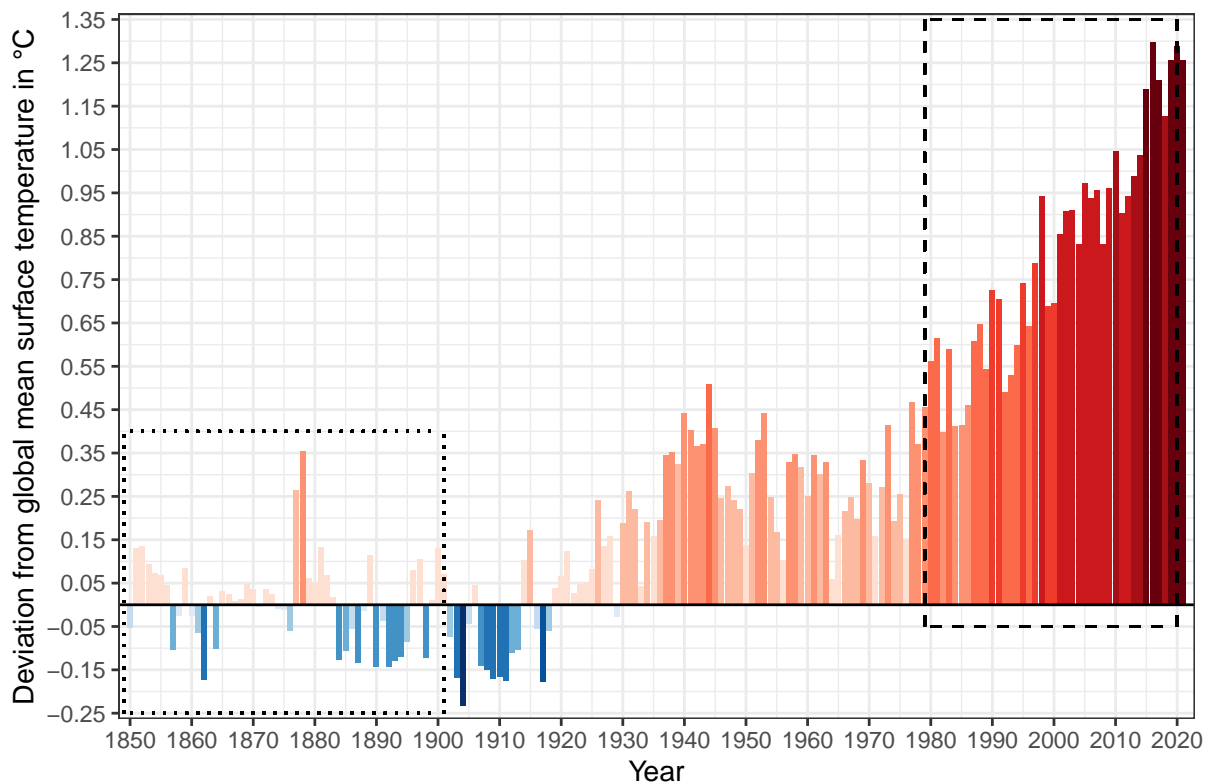

Figure 1 Development of global mean surface temperatures in relation to the time frame of this thesis.

Linear trends of four time periods: 1850-1899 (period 0), 1900-1939 (period1),1940-1979 (period2),1980-2019 (period3 - our study period)

```
globtemp %>% dplyr::mutate(
  timeframe=ifelse(Year>=1850 & Year<1900,0,ifelse(Year>=1900 & Year<1940,1,
  ifelse(Year>=1940 & Year<1980,2,ifelse(Year>=1980 & Year<2020,3,NA))))) %>%
  group_by(timeframe) %>% dplyr::summarise(mean.temp=mean(temp.deviation),
                                           median.temp=median(temp.deviation))
## # A tibble: 5 x 3
##   timeframe mean.temp median.temp
##       <dbl>     <dbl>       <dbl>
## 1         0   0.00572      0.0110
## 2         1   0.0479       0.0497
## 3         2   0.292        0.290
## 4         3   0.799        0.809
## 5        NA   1.27         1.27
glm.temp.0<- globtemp %>% dplyr::mutate(
  timeframe=ifelse(Year>=1850 & Year<1900,0,ifelse(Year>=1900 & Year<1940,1,
  ifelse(Year>=1940 & Year<1980,2,ifelse(Year>=1980 & Year<2020,3,NA))))) %>%
  filter(timeframe ==0) %>% glm(temp.deviation ~ Year,data=.,family=gaussian)

# generalized linear models for each period
glm.temp.1<- globtemp %>% dplyr::mutate(
  timeframe=ifelse(Year>=1850 & Year<1900,0,ifelse(Year>=1900 & Year<1940,1,
  ifelse(Year>=1940 & Year<1980,2,ifelse(Year>=1980 & Year<2020,3,NA))))) %>%
```

```
      filter(timeframe ==1) %>% glm(temp.deviation ~ Year,data=.,family=gaussian)

glm.temp.2<- globtemp %>% dplyr::mutate(
  timeframe=ifelse(Year>=1850 & Year<1900,0,ifelse(Year>=1900 & Year<1940,1,
  ifelse(Year>=1940 & Year<1980,2,ifelse(Year>=1980 & Year<2020,3,NA)))) ) %>%
  filter(timeframe ==2) %>% glm(temp.deviation ~ Year,data=.,family=gaussian)

glm.temp.3<- globtemp %>% dplyr::mutate(
  timeframe=ifelse(Year>=1850 & Year<1900,0,ifelse(Year>=1900 & Year<1940,1,
  ifelse(Year>=1940 & Year<1980,2,ifelse(Year>=1980 & Year<2020,3,NA)))) ) %>%
  filter(timeframe ==3) %>% glm(temp.deviation ~ Year,data=.,family=gaussian)
```

Model summaries and confidence intervals

1850-1899 (period 0),

```
summary(glm.temp.0)
##
## Call:
## glm(formula = temp.deviation ~ Year, family = gaussian, data = .)
##
## Deviance Residuals:
##      Min        1Q    Median        3Q       Max
## -0.19686  -0.08349  -0.00129   0.04912   0.35306
##
## Coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept)  2.915542   1.882540   1.549    0.128
## Year        -0.001552   0.001004  -1.546    0.129
##
## (Dispersion parameter for gaussian family taken to be 0.01050139)
##
##     Null deviance: 0.52916  on 49  degrees of freedom
## Residual deviance: 0.50407  on 48  degrees of freedom
## AIC: -81.96
##
## Number of Fisher Scoring iterations: 2
#
# Confidence intervals
confint(glm.temp.0)
##                  2.5 %        97.5 %
## (Intercept) -0.774169703 6.6052528485
## Year        -0.003520629 0.0004159959
```

1900-1939 (period1)

```
summary(glm.temp.1)
##
## Call:
## glm(formula = temp.deviation ~ Year, family = gaussian, data = .)
##
## Deviance Residuals:
##      Min        1Q    Median        3Q       Max
## -0.20115  -0.08224  -0.01093   0.06593   0.27784
##
## Coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept) -19.198414   2.876619  -6.674 6.81e-08 ***
```

```
## Year            0.010027    0.001499    6.691 6.47e-08 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 0.01197016)
##
##      Null deviance: 0.99072  on 39  degrees of freedom
## Residual deviance: 0.45487  on 38  degrees of freedom
## AIC: -59.55
##
## Number of Fisher Scoring iterations: 2
# Confidence intervals
confint(glm.temp.1)
##                    2.5 %        97.5 %
## (Intercept) -24.836484059 -13.56034470
## Year          0.007089508   0.01296392
```

1940-1979 (period2)

```
summary(glm.temp.2)
##
## Call:
## glm(formula = temp.deviation ~ Year, family = gaussian, data = .)
##
## Deviance Residuals:
##       Min         1Q     Median         3Q        Max
## -0.225868  -0.072976   0.002575   0.061603   0.205453
##
## Coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept)  3.663652   2.886123   1.269    0.212
## Year        -0.001720   0.001473  -1.168    0.250
##
## (Dispersion parameter for gaussian family taken to be 0.01156248)
##
##      Null deviance: 0.45515  on 39  degrees of freedom
## Residual deviance: 0.43937  on 38  degrees of freedom
## AIC: -60.936
##
## Number of Fisher Scoring iterations: 2
# Confidence intervals
confint(glm.temp.2)
##                    2.5 %       97.5 %
## (Intercept) -1.993044100 9.320348803
## Year        -0.004607217 0.001166295
```

1980-2019 (period3 - our study period)

```
summary(glm.temp.3)
##
## Call:
## glm(formula = temp.deviation ~ Year, family = gaussian, data = .)
##
## Deviance Residuals:
##      Min        1Q     Median        3Q        Max
## -0.16483  -0.08834   0.01341   0.06866   0.18142
##
```

```
## Coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept) -37.67404    2.63904  -14.28   <2e-16 ***
## Year          0.01924    0.00132   14.58   <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 0.009284545)
##
##     Null deviance: 2.32610  on 39  degrees of freedom
## Residual deviance: 0.35281  on 38  degrees of freedom
## AIC: -69.713
##
## Number of Fisher Scoring iterations: 2
# Confidence intervals
confint(glm.temp.3)
##                   2.5 %       97.5 %
## (Intercept) -42.84645975 -32.50162782
## Year          0.01665437   0.02182799
```

Web of Science publication numbers (Fig. 2)

```
# Load data of brief 'Web of Science' search (date accessed: 07.09.2022)
dat <- read.delim( # search term "insect+decline"
  "C:/Users/ekath/R_Coding/MINTbio/data/WebofScience_insectdecline.txt")
dat %<>% dplyr::rename(Year=Publication.Years,n_decline=Record.Count) %>%
  dplyr::select(-X..of.8.272)

temp <- read.delim( # search term "insect+climate change"
  "C:/Users/ekath/R_Coding/MINTbio/data/WebofScience_insectclimatechange.txt")
temp %<>% dplyr::rename(Year=Publication.Years,n_climchange=Record.Count) %>%
  dplyr::select(-X..of.7.361)

dat %<>% full_join(temp)
rm(temp)

temp <- read.delim( # search term "insect+land use"
  "C:/Users/ekath/R_Coding/MINTbio/data/WebofScience_insectlanduse.txt")
temp %<>% dplyr::rename(Year=Publication.Years,n_landuse=Record.Count) %>%
  dplyr::select(-X..of.5.377)

dat %<>% full_join(temp)
rm(temp)

temp <- read.delim( # search term "insect+conservation"
  "C:/Users/ekath/R_Coding/MINTbio/data/WebofScience_insectconservation.txt")
temp %<>% dplyr::rename(Year=Publication.Years,n_cons=Record.Count) %>%
  dplyr::select(-X..of.13.038)

dat %<>% full_join(temp)
rm(temp)

temp <- read.delim( # search term "vertebrate+decline"
  "C:/Users/ekath/R_Coding/MINTbio/data/WebofScience_vertebratedecline.txt")
temp %<>% dplyr::rename(Year=Publication.Years,n_vert_decline=Record.Count) %>%
  dplyr::select(-X..of.3.370)
```

```r
dat %<>% full_join(temp)
rm(temp)

temp <- read.delim( # search term "vertebrate+climate change"
  "C:/Users/ekath/R_Coding/MINTbio/data/WebofScience_vertebrateclimatechange.txt")
temp %<>% dplyr::rename(Year=Publication.Years,n_vert_climchange=Record.Count) %>%
  dplyr::select(-X..of.2.997)

dat %<>% full_join(temp)
rm(temp)

temp <- read.delim( # search term "vertebrate+land use"
  "C:/Users/ekath/R_Coding/MINTbio/data/WebofScience_vertebratelanduse.txt")
temp %<>% dplyr::rename(Year=Publication.Years,n_vert_landuse=Record.Count) %>%
  dplyr::select(-X..of.2.205)

dat %<>% full_join(temp)
rm(temp)

temp <- read.delim( # search term "vertebrate+conservation"
  "C:/Users/ekath/R_Coding/MINTbio/data/WebofScience_vertebrateconservation.txt")
temp %<>% dplyr::rename(Year=Publication.Years,n_vert_cons=Record.Count) %>%
  dplyr::select(-X..of.11.212)

dat %<>% full_join(temp)
rm(temp)


dat_simple <- dat %>% filter(Year !=2022 & Year>=1980) %>%
  pivot_longer(.,cols=c(n_vert_decline,n_vert_climchange,n_vert_landuse,n_vert_cons,
                        n_decline,n_climchange,n_landuse,n_cons),
               names_to="data") %>%
  dplyr::mutate(Taxon=ifelse(str_detect(data,"vert"),"Vertebrate","Insect"),
                `+ search term`=str_remove(data,"n_"),
                `+ search term`=str_remove(`+ search term`,"vert_"),
                `+ search term`=str_replace(`+ search term`,"climchange",
                                            "climate change"),
                `+ search term`=str_replace(`+ search term`,"cons","conservation"),
                `+ search term`=str_replace(`+ search term`,"landuse","land use"))

# define colours for categories in data column
cat_col <- c("decline"="#002f3c","climate change"="#ffbf00",
  "land use"="#006f65","conservation"="#50ae4c")

# define linetype for taxon
taxon_lt <- c("Vertebrate"="dashed","Insect"="solid")
dat_simple$`+ search term` <- factor(dat_simple$`+ search term`,
        levels=c("decline","land use","conservation","climate change"))

#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/WebofScience_publications.png",
#units="in",width=4.9,height=3.7,res=1200)
p1 <- dat_simple %>% ggplot() + theme_bw() +
  geom_line(aes(x=Year,y=value,colour=`+ search term`,linetype=Taxon),size=1)+
  scale_y_continuous(name="Number of publications per year")+
  scale_x_continuous(breaks=seq(1950,2021,10),minor_breaks=seq(1950,2021,5))+
  scale_colour_manual(values=cat_col ,na.value="grey50")+
  scale_linetype_manual(values=taxon_lt)+
```

```
theme(axis.text=element_text(size=12),axis.title=element_text(size=12),
    legend.title=element_text(size=12),legend.text=element_text(size=12),
    legend.key.width=unit(c(10),"mm"),
    plot.margin=grid::unit(c(0.1,0.1,1,0.1),"mm"),
    legend.margin=margin(0.1,0.1,0.1,0.1,"mm"),legend.position="bottom",
    legend.justification="left",legend.direction="vertical",
    plot.caption=element_text(size=12),
    panel.grid.minor=element_line())+
guides(colour=guide_legend(order=2,ncol=2),linetype=guide_legend(order=1))
#dev.off()
#ggview::ggview(device="png",units="in",width=4.9,height=3.7)
```
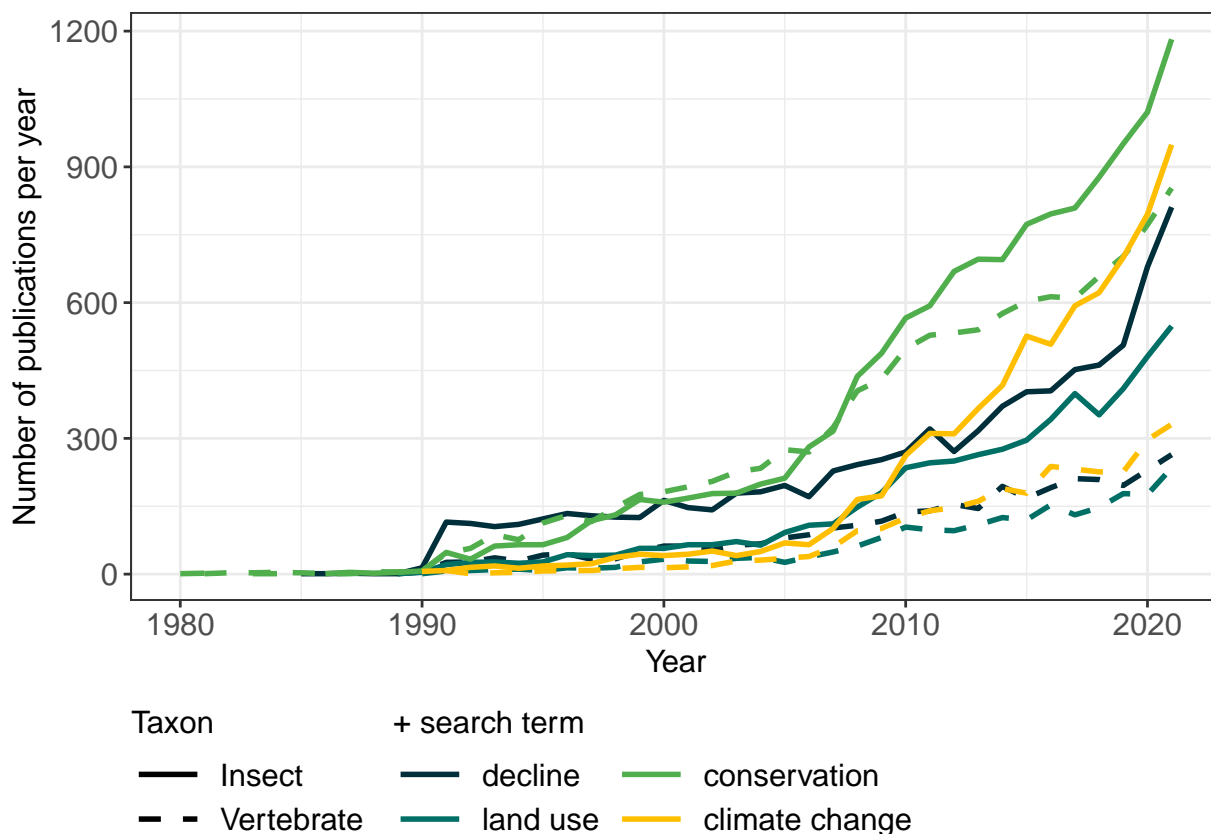

Figure 2 Results of a brief 'Web of Science' search

Data basis (Fig. 5,Fig. 6)

The LfU's ASK database

The data that support the findings of this study are available from the Bavarian State Agency for the Environment (Bayerisches Landesamt für Umwelt,LfU). Restrictions apply to the availability of these data,which were used under license for this study. The code to load the database was created in cooperation with Matthias F. Biber (https://orcid.org/0000-0002-7726-988X).

Load observation data

```
source("R/load_database.R")
ask_art <- load_database(name="ask_art",res="quadrant")
```

Load taxonomy

```
load(file="C:/Users/ekath/R_Coding/MINTbio/data/taxonomyStd.rda")

# Create custom taxon vector (Aves,Lepidoptera,Odonata,Orthoptera)
ask_art %<>% mutate(class_order=ifelse(class =="Aves","Aves",
  ifelse(class =="Insecta" & order =="Lepidoptera","Lepidoptera",
        ifelse(class =="Insecta" & order =="Orthoptera","Orthoptera",
              ifelse(class =="Insecta" & order =="Odonata","Odonata",NA)))))

# filter out moths,take out birds
ask_art %<>% filter(order =="Odonata" | order =="Orthoptera" |
    family =="Papilionidae" | family =="Hesperiidae" | family =="Pieridae" |
      family =="Nymphalidae" | family =="Lycaenidae" | family =="Riodinidae")
```

Overview tables

Table 1: Total number of species reported in the study region for each insect order

order	Number of species
Lepidoptera	205
Odonata	77
Orthoptera	79

Year of the earliest observation:

```
## [1] 1700
```

Year of the latest observation available for this thesis:

```
## [1] 2020
```

Table 2: Total number of observations included in the database per taxon

order	n()
Lepidoptera	575994
Odonata	212500
Orthoptera	238435

Table 3: Number of observations from different sources per taxon reported in the database

order	Source	Number of observations
Lepidoptera	Absence	3242
Lepidoptera	Literature	52914
Lepidoptera	mapping	519838
Odonata	Absence	1359
Odonata	Literature	5382
Odonata	mapping	205759
Orthoptera	Absence	1887
Orthoptera	Literature	5098
Orthoptera	mapping	231450

Occupancy model results

Data published under doi:10.5061/dryad.4f4qrfjf5 including code for occupancy-detection models.

```
dat <- read.delim(
  "C:/Users/ekath/R_Coding/MINTbio/data/Engelhardt_etal_2022_OccupancyEstimates.csv",
  header=TRUE,sep=",")
```

Table 4: Number of species for which occupancy-detection models were calculated

order	Number of species
Lepidoptera	163
Odonata	71
Orthoptera	66

Total number of observations in the ASK-database (Fig. 5)

```
temp <- ask_art %>% dplyr::select(jahr,quelle,order,sta) %>%
 dplyr::mutate(time=ifelse(jahr <1980,"before","after"),Source=quelle,
 Source=str_replace(Source,'keine Angabe',"Unknown"),
 Source=str_replace(Source,'Freilanderfassung',"Semi-systematic mapping"),
 Source=str_replace(Source,'Literaturauswertung',"Literature"),
 Source=str_replace(Source,'Private Aufzeichnung',"Private collection"),
 Source=str_replace(Source,'schriftliche / mündliche Mitteilung',"Private collection"),
 Source=str_replace(Source,'Sammlungsbearbeitung/Herbar',"Museum specimen"),
 Source=str_replace(Source,'LfU-Annahmestelle',"Private collection")) %>%
 ungroup() %>% dplyr::mutate(sta=replace_na(sta,"obs"),
                    sta=ifelse(sta =="XX" | sta =="YY","Absence",Source)) %>%
 group_by(order,sta,time) %>% summarize('Number of observations'=n()) %>%
 dplyr::rename(Source=sta)

# set plot order manually
temp$Source <- factor(temp$Source,
             levels=c("Semi-systematic mapping","Unknown","Literature",
                      "Museum specimen","Private collection","Absence"))
temp %<>% dplyr::mutate(
  order=str_replace(order,"Lepidoptera","(A) Lepidoptera
205 species"),
  order=str_replace(order,"Orthoptera","(B) Orthoptera
79 species"),
  order=str_replace(order,"Odonata","(C) Odonata
77 species"))
temp$order <- factor(temp$order,levels=
     c("(A) Lepidoptera
205 species","(B) Orthoptera
79 species","(C) Odonata
77 species"))


#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/DataSources.png",
#units="in",width=8.5,height=2.8,res=1200)
p1 <- temp %>% ggplot() + facet_wrap(~order) + coord_flip() + theme_bw() +
  geom_bar(aes(x=Source,y=`Number of observations`,fill=as.factor(time)),
           stat="identity",position='stack',show.legend=FALSE) +
```

```
  scale_y_continuous(labels=scales::comma) +
  scale_fill_manual(values=c("#200074","#ff4c69"),na.value="grey50") +
  theme(axis.text=element_text(size=12),axis.text.x=element_text(angle=45,hjust=1),
        axis.title.x=element_text(size=12),axis.title.y=element_blank(),
        strip.text=element_text(size=12),# adapt facet labels
        strip.background=element_blank(),panel.spacing.x=unit(0.7,"cm"),
        plot.margin=grid::unit(c(0.5,0.5,0.5,0.5),"mm"))
#dev.off()
#ggview::ggview(device="png",units="in",width=8.5,height=2.8)
```
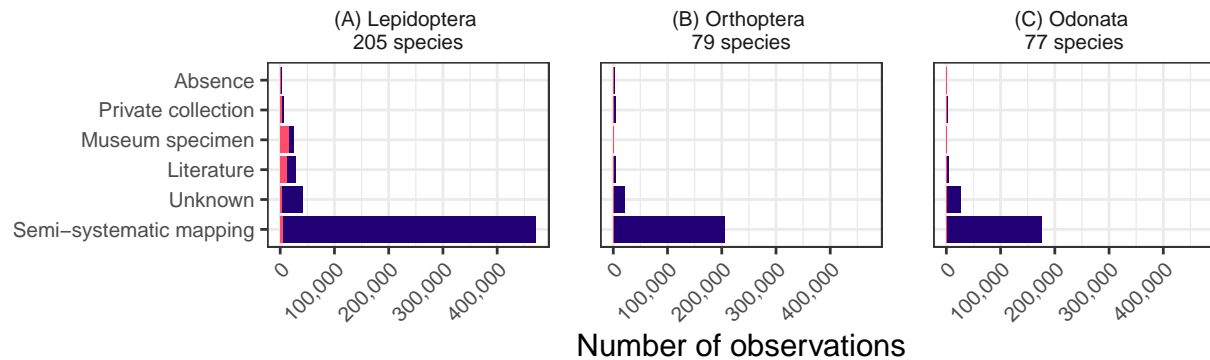

Figure 5 Total number of observations in the ASK-database covering the time from 1700 to 2020, split for the data source and each of the three taxa analysed. Red colour indicates data from before 1980 and blue indicates data collected between 1980 and 2020.

Habitat attributes (Fig. 6)

```
# read data
traits <- read.csv2(
  "C:/Users/ekath/R_Coding/MINTbio/data/Insect_traits_climrangehabitat.csv")

# Generalists vs. specialists
temp <- traits %>% group_by(order,habitat_class) %>%
  dplyr::summarise(nSpec=n_distinct(species)) %>% na.omit() %>% group_by(order) %>%
  dplyr::mutate(total_nspec=sum(nSpec),
                perc_nspec=paste(round((nSpec/total_nspec)*100,1),'%'),
                ytest=ifelse(habitat_class =="Generalist",total_nspec-(nSpec/2),
                            nSpec-(nSpec/2)))
# define plot order
temp$order <- factor(temp$order,levels=c("Lepidoptera","Orthoptera","Odonata"))

#tiff("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/generalistVSspecialist.tiff",
#units="in",width=5,height=5,res=1200)
plot1 <- temp %>% ggplot() + theme_bw() +
 geom_bar(aes(x=order,y=nSpec,fill=habitat_class),stat="identity")+
 geom_text(aes(x=order,y=ytest,label=perc_nspec),size=5)+
 scale_x_discrete(name="Order")+ scale_y_continuous(name="Number of species")+
 scale_fill_manual(name=paste("Habitat class",sep="\n"),values=c("#98a100","#ffd600"))+
 theme(legend.title=element_blank(),legend.box.margin=margin(0,0,0,0,unit="pt"),
       legend.text=element_text(size=14),legend.position="top",
       axis.text.y=element_text(size=16),axis.text.x=element_blank(),
       axis.title.x=element_blank(),axis.title.y=element_text(size=16,angle=90),
       axis.line=element_line(),axis.ticks=element_line())+
 guides(colour="none")
#dev.off()
```

```r
# Habitat type
temp <- traits %>% group_by(order,habitat_type) %>%
  dplyr::summarise(nSpec=n_distinct(species)) %>% na.omit() %>% group_by(order) %>%
  dplyr::mutate(total_nspec=sum(nSpec),
        perc_nspec=paste(round((nSpec/total_nspec)*100,1),'%'),
        habitat_type=ifelse(order=="Odonata"&habitat_type=="both",
                            "both2",habitat_type),
        habitat_type=str_replace(habitat_type,"_"," "))

# Define y-axis position of text
ytest=c(124,152,138,104.5,47.5,53,15.5,67,40.5,60,56,70,63,48,18.5)
temp <- cbind(temp,ytest) %>% dplyr::rename(ytest=`...6`)

# define plot order
temp$order <- factor(temp$order,levels=c("Lepidoptera","Orthoptera","Odonata"))
temp$habitat_type <- factor(temp$habitat_type,levels=c("forest","more forest","both",
              "more open","open","lotic","more lotic","both2","more lentic","lentic"))

# define habitat colours
habcols <- c("both"="#f7ffda","open"="#c14d00","more open"="#d4af5f",
            "more forest"="#8ab899","forest"="#00726d","lentic"="#003172",
            "more lentic"="#3f97be","both2"="#f7ffda","more lotic"="#55e7b0",
            "lotic"="#5dc100")

#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/habitat_types.png",
#units="in",width=5,height=7.5,res=1200)
plot2 <- temp %>% ggplot() + theme_bw() +
  geom_bar(aes(x=order,y=nSpec,fill=habitat_type),stat="identity")+
  geom_text(aes(x=order,y=ytest,label=perc_nspec),size=5)+
  scale_x_discrete(name="Order")+ scale_y_continuous(name="Number of species")+
  scale_fill_manual(name="",values=habcols)+
  theme(legend.title=element_blank(),legend.text=element_text(size=14),
        legend.position="top",legend.box.margin=margin(10,0,0,0,unit="pt"),
        legend.key.size=unit(10,"pt"),legend.justification=c(1,0),
        axis.text.y=element_text(size=16),axis.text.x=element_blank(),
        axis.title.x=element_blank(),axis.title.y=element_text(size=16,angle=90),
        axis.line=element_line(),axis.ticks=element_line())+
  guides(colour="none",fill=guide_legend(ncol=5,byrow=TRUE))
#dev.off()

#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/habitatClassifications.png",
#units="in",width=5,height=9,res=1200)
p1 <- (plot1+theme(plot.margin=unit(c(0,0,7,0),"pt"),
            legend.margin=margin(0,0,0,0,"pt")))/
  (plot2+ theme(plot.margin=unit(c(0,0,0,0),"pt"),
              legend.margin=margin(0,0,0,0,"pt")))/
  ((lepi_plot+theme(plot.margin=unit(c(0,0,0,0),"pt")))+
    (ortho_plot+theme(plot.margin=unit(c(0,50,0,50),"pt")))+
    (odo_plot+theme(plot.margin=unit(c(0,0,0,0),"pt"))))+
  plot_layout(heights=unit(c(0.7,1.2,0.1),"null"))
#dev.off()
#ggview::ggview(device="png",units="in",width=5,height=9)
```
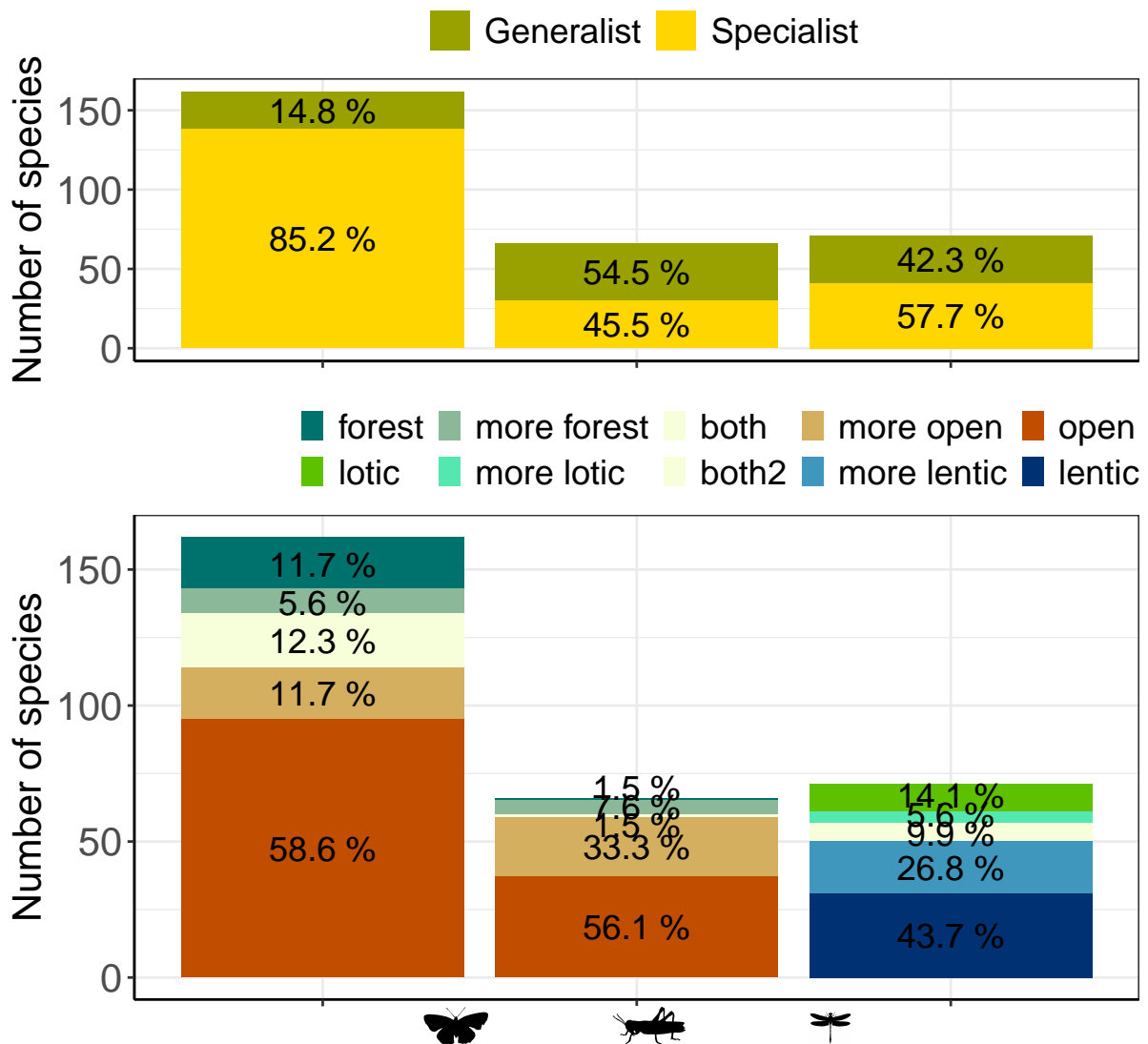
Figure 6 Number of species of each taxon (from left to right: butterflies – Lepidoptera,grasshoppers – Orthoptera, dragonflies – Odonata) classified by (A) habitat specialization and (B) habitat preference

Annotations were added using Inkscape: Inkscape Project,2020. Inkscape,Available at: https://inkscape. org.

Bias in observation data (Fig. 7,Fig. 8,Fig. 9)

Temporal bias in species observation data between 1900 and 2019 (Fig. 7)

```
temp <- ask_art %>% filter(sta !="XX" & sta !="YY") %>%
  dplyr::select(order,art,jahr) %>% group_by(order,jahr) %>%
  dplyr::summarise('Number of species'=n_distinct(art),'Number of observations'=n())

# set plot order manually
temp$order <- factor(temp$order,levels=c("Lepidoptera","Orthoptera","Odonata"))

#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/NumberObsSpec.png",
#units="in",width=8.5,height=5.5,res=1200)
p1 <- temp %>% filter(jahr>=1900) %>%
  pivot_longer(.,cols=c(`Number of species`,`Number of observations`),
```

```
                    names_to="var",values_to="n") %>%
  ggplot() + theme_minimal() + ggtitle("") +
  geom_area(aes(x=jahr,y=n,fill=as.factor(order),colour=as.factor(order)),
            size=1,position=position_identity(),alpha=0.3)+
  geom_vline(aes(xintercept=1980),color="#dd8bff",linetype="dotted",size=1)+
  geom_vline(aes(xintercept=1992),color="#006440",linetype="dotted",size=1)+
  facet_wrap(~var,ncol=1,scales="free_y",strip.position="left") +
  scale_x_continuous(name="",limits=c(1900,2020),
                     breaks=c(1900,1920,1940,1960,1980,2000,2020)) +
  scale_fill_manual(values=taxon_cols,name="")+
  scale_colour_manual(values=taxon_cols,name="")+
  theme(legend.title=element_text(size=12),legend.text=element_text(size=12),
        legend.position="bottom",title=element_text(size=15),
        strip.text=element_text(size=12),strip.placement="outside",
        panel.spacing.y=unit(1.5,"cm"),
        axis.text.y=element_text(size=12),axis.text.x=element_text(size=12),
        axis.title.x=element_blank(),axis.title.y=element_blank(),
        axis.line=element_line(),axis.ticks=element_line(),
        plot.margin=unit(c(0,0,0,0),"cm"))
#dev.off()
#ggview::ggview(device="png",units="in",width=8.5,height=5.7)
```


15
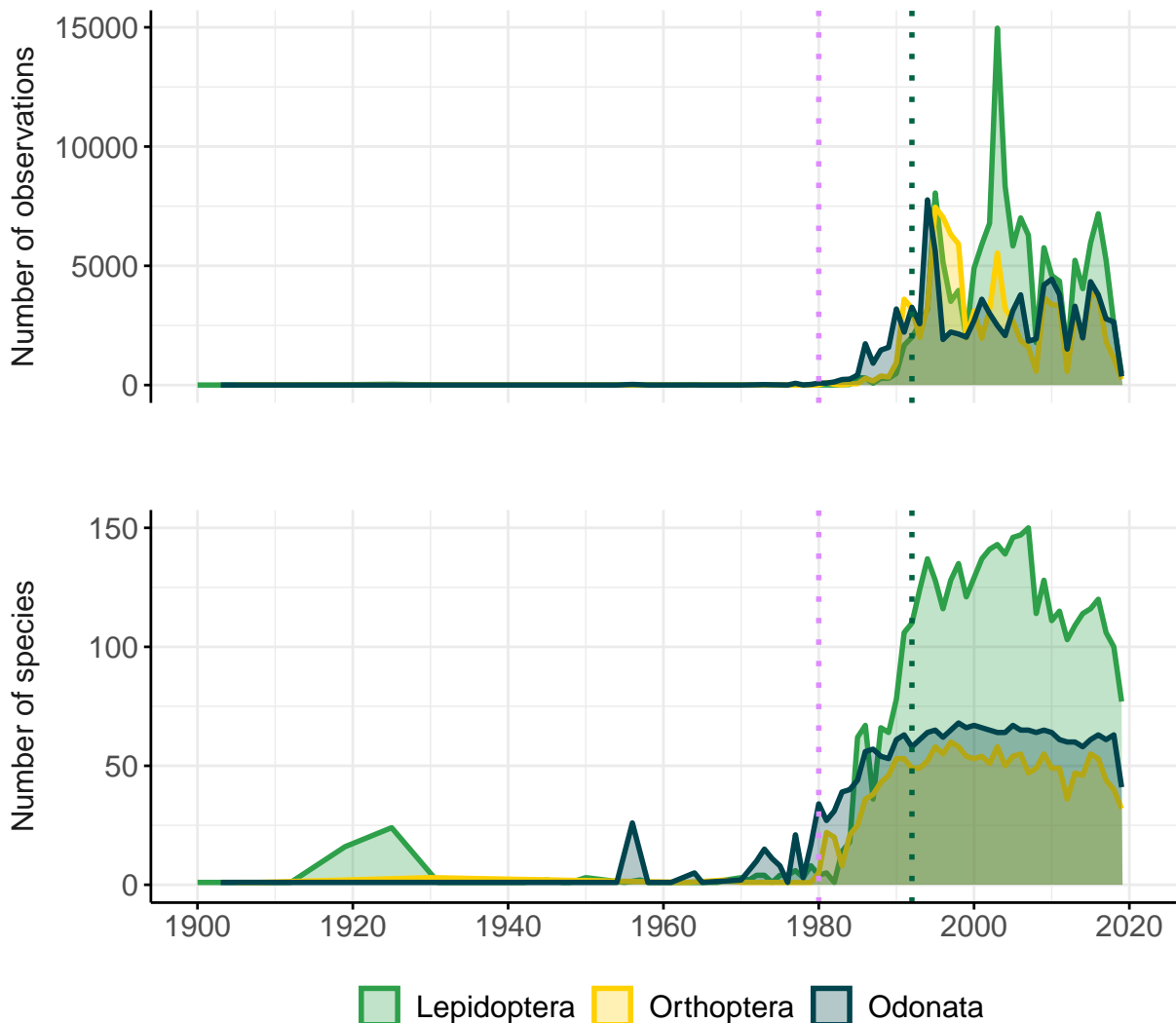
Figure 7 Temporal bias in species observation data between 1900 and 2019.

Annotations were added using Inkscape: Inkscape Project,2020. Inkscape,Available at: https://inkscape.org.

Spatial bias in species observation data between 1900 and 2020 (Fig. 8)

Focus on data collected in the field since 1900

```
temp <- ask_art %>%
  filter(sta !="XX" & sta !="YY") %>% # remove reported absences
  filter(jahr>=1900) %>% # filter the years considered
  dplyr::mutate(quelle=str_replace(quelle,'keine Angabe',"mapping"),
    quelle=str_replace(quelle,'Freilanderfassung',"mapping"),
    quelle=str_replace(quelle,'Literaturauswertung',"Literature"),
    quelle=str_replace(quelle,'Private Aufzeichnung',"mapping"),
    quelle=str_replace(quelle,'schriftliche / mündliche Mitteilung',"mapping"),
    quelle=str_replace(quelle,'Sammlungsbearbeitung/Herbar',"Literature"),
    quelle=str_replace(quelle,'LfU-Annahmestelle',"mapping")) %>%
  filter(quelle =="mapping") %>% # filter the source of the data as field collections
  dplyr::select(order,art,XQMITTE,YQMITTE) %>%
  group_by(order,XQMITTE,YQMITTE) %>% # analyse per order for each grid cell
  dplyr::summarise('Number of species'=n_distinct(art),'Number of observations'=n())
```

Table 5: Pearson correlation coefficient between the number of observations and the number of species observed per grid cell

order	Pearson Correlation Coefficient
Lepidoptera	0.767
Odonata	0.715
Orthoptera	0.684

Table 6: Overview of the number of observations per grid cell between 1900 and 2020

	Lepidoptera	Odonata	Orthoptera
Number of grid cells with observations	1849	1920	1780
Maximum number of observations	1460	1697	784
Minimum number of observations	1	1	1
Mean number of observations	77	50	52
Standard deviation of the number of observations	137	89	76
Maximum number of species	83	48	33
Minimum number of species	1	1	1
Mean number of species	20	14	12
Standard deviation of the number of species	17	10	7

Plot the spatial bias

```
# set plot order manually
temp$order <- factor(temp$order,levels=c("Lepidoptera","Orthoptera","Odonata"))

plot1 <- temp %>% ggplot(aes(x=XQMITTE,y=YQMITTE))+labs(title="(A) Species number")+
  geom_point(aes(colour=`Number of species`),shape=15,size=0.55) +
  scale_colour_viridis_c(option="inferno",direction=-1,begin=0.1,end=1) +
```

```
      facet_wrap(~order,ncol=3) + coord_equal() + theme_map() +
      theme(legend.title=element_blank(),legend.text=element_text(size=12),
            legend.position="left",legend.key.width=unit(0.25,"cm"),
            plot.title=element_text(size=12,face="plain",hjust=0),
            strip.text=element_blank(),strip.placement="outside",
            panel.spacing.x=unit(0.8,"cm"))
plot2 <- temp %>%
  ggplot(aes(x=XQMITTE,y=YQMITTE))+labs(title="(D) Observation number")+
  geom_point(aes(colour=`Number of observations`),shape=15,size=0.55) +
  scale_colour_viridis_c(option="inferno",direction=-1,begin=0,end=1,
   limits=c(0,250),oob=scales::squish,breaks=c(0,50,100,150,200,250)) +
  facet_wrap(~order,ncol=3) + coord_equal() + theme_map() +
  theme(legend.title=element_blank(),legend.text=element_text(size=12),
        legend.position="left",legend.key.width=unit(0.25,"cm"),
        plot.title=element_text(size=12,face="plain",hjust=0),
        strip.text=element_blank(),strip.placement="outside",
        panel.spacing.x=unit(0.8,"cm"))
plot3 <- temp %>% group_by(order) %>%
  mutate(nObs=cut(x=`Number of observations`,
   breaks=hist(`Number of observations`,breaks=0:1700 * 25,plot=FALSE)$breaks,
   labels=hist(`Number of observations`,breaks=0:1700 * 25,plot=FALSE)$mids)) %>%
  group_by(order,nObs) %>%
  summarize(n=n(),`Number of observations`=mean(`Number of observations`)) %>%
  ggplot() + ggtitle("(G)") + theme_bw() +
  geom_col(aes(x=as.numeric(as.character(nObs)),y=n,
               fill=`Number of observations`),width=25) +
  facet_wrap(~order,ncol=3,scales="free_x") +
  scale_x_continuous(name="Observation number") +
  scale_y_continuous(name="Number of grid cells",breaks=c(0,200,400,600,800,1000)) +
  scale_fill_viridis_c(option="inferno",direction=-1,begin=0,end=1,
                       limits=c(0,250),oob=scales::squish,
                       breaks=c(0,50,100,150,200,250))+
  theme(legend.title=element_text(size=12),legend.text=element_text(size=12),
        legend.position="bottom",plot.margin=unit(c(0,0,0,0),"cm"),
        plot.title=element_text(size=12,face="plain",hjust=0),
        strip.text=element_blank(),strip.placement="outside",
        panel.spacing.x=unit(0.8,"cm"),panel.border=element_blank(),
        axis.text=element_text(size=12),axis.title=element_text(size=12),
        axis.line=element_line(),axis.ticks=element_line()) +
  guides(fill="none")

plot0 <- (plot_spacer()|lepi_plot|plot_spacer()|ortho_plot|plot_spacer()|
          odo_plot|plot_spacer()) + theme(plot.margin=unit(c(0,0,0,0),"cm"))


#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/SpacialBias.png",
#units="in",width=7,height=7,res=1200)
p1 <- (plot0 / plot1 / plot2 / plot3  +
  plot_layout(ncol=1,nrow=4,heights=unit(c(1,3,3,3),"null"),
              widths=unit(c(3,3,3,3),"null"))
#dev.off()
#ggview::ggview(device="png",units="in",width=7,height=7)
```
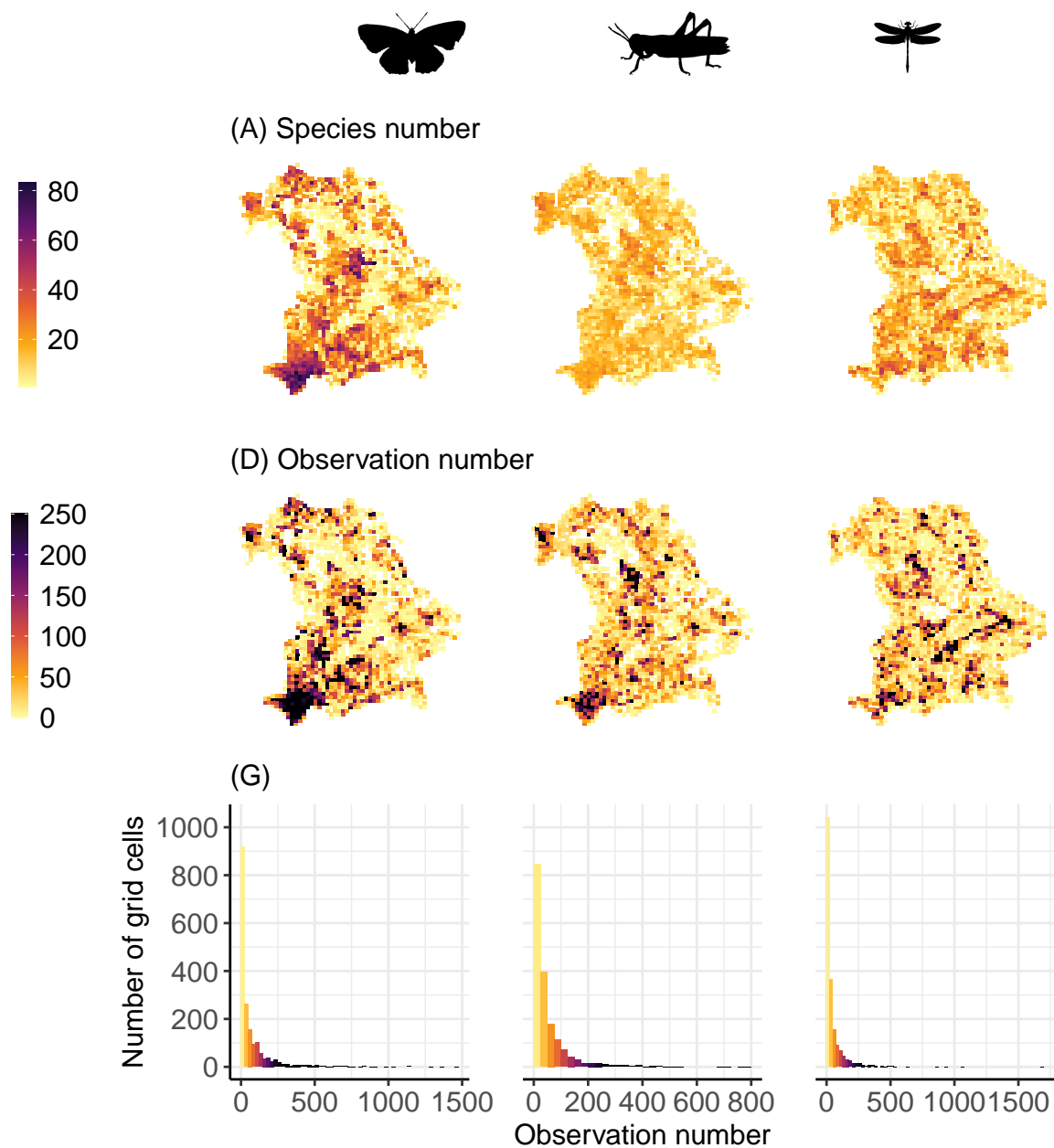
Figure 8 Spatial bias in species observation data between 1900 and 2020.

Annotations were added using Inkscape: Inkscape Project,2020. Inkscape,Available at: https://inkscape.org.

Comparison of observation numbers with occupancy estimates (Fig. 9)

Table 7: Years with minimum an maximum numbers of observation of the exemplary butterfly species,Araschnia levana,since 1980

Year	Number of observations
1982	31
2019	31
2003	1407

Plot the comparison

```r
# plot number of observations
plot_obs <- ask_art %>% filter(jahr>=1980,art =="ARASCHNIA LEVANA") %>%
  group_by(jahr) %>% dplyr::summarise(nObs=n()) %>% ggplot() + theme_bw() +
  geom_point(aes(x=jahr,y=nObs),size=1) + geom_line(aes(x=jahr,y=nObs)) +
  scale_x_continuous(name="Year") + scale_y_continuous(name="Number of observations")+
  theme(plot.margin=unit(c(0.8,0,0,0),"cm"),
        axis.text.x=element_blank(),axis.title.x=element_blank(),
        axis.text.y=element_text(size=12),axis.title.y=element_text(size=12))+
  guides(size=FALSE)

# plot annual occupancy estimates
plot_occ <- dat %>% filter(Species =="ARASCHNIA LEVANA") %>% ggplot() + theme_bw() +
  geom_point(aes(x=Year,y=occupancyMean,
                 color=cut(occupancyRhat,c(-Inf,1.1,Inf))),size=1) +
  geom_line(aes(x=Year,y=occupancyMean))+
  geom_ribbon(aes(x=Year,ymin=occupancyX2.5,ymax=occupancyX97.5),alpha=0.5) +
  scale_color_manual(name="Rhat",values=c("blue","red"),na.value=c("red"),
                     expand=c(-Inf,Inf),limits=c("(-Inf,1.1]","(1.1,Inf]"),
                     labels=c("Good (<1.1)","Bad (>1.1)")) +
  scale_x_continuous(name="Year")+scale_y_continuous(limits=c(0,1),name="Occupancy")+
  theme(axis.text.x=element_text(size=12),axis.text.y=element_text(size=12),
        axis.title=element_text(size=12),plot.margin=unit(c(0.8,0,0,0),"cm"),
        legend.position="bottom",legend.key.size=unit(1.5,"cm"),
        legend.text=element_text(size=12),legend.title=element_text(size=12),
        legend.margin=margin(unit(c(0,0,0,0),"cm")),
        legend.box.margin=margin(unit(c(0,0,0,0),"cm")))+
  guides(size=FALSE,color="none"  )

# combine both plots

#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/obsVSoccmod.png",
#units="in",width=5,height=7.5,res=1200)
p1 <- (Alevana2/plot_obs/plot_occ)
#dev.off()
#ggview::ggview(device="png",units="in",width=5,height=7.5)
```
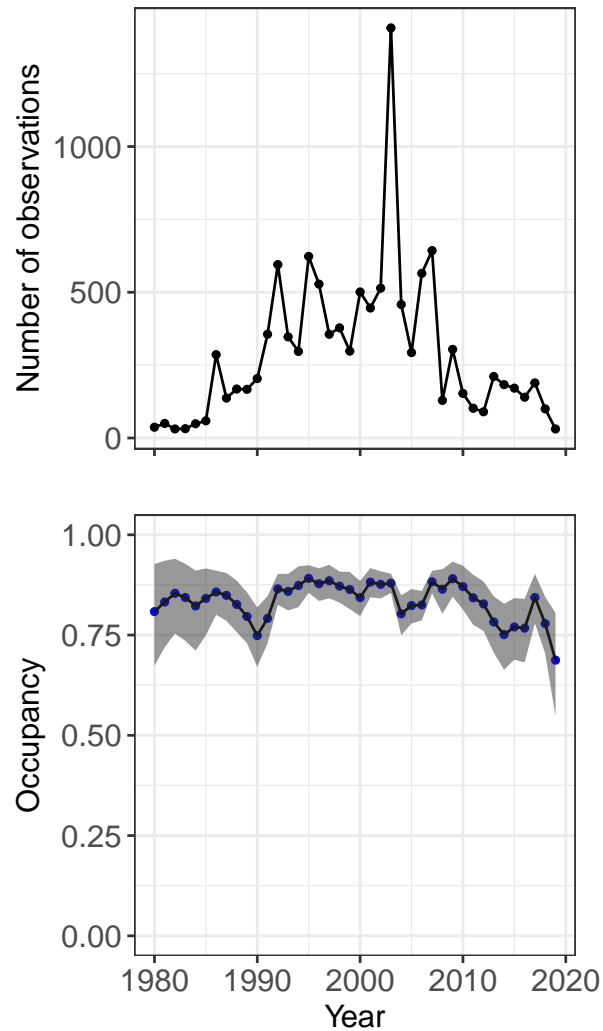
Figure 9 Comparison of annual number of observations with occupancy estimates over 40 years (1980-2019) for an exemplary butterfly species, *Araschnia levana* (Map, family Nymphalidae).

Annotations were added using Inkscape: Inkscape Project, 2020. Inkscape, Available at: https://inkscape.org.

Occupancy-detection models: Model check (Fig. 11, Fig. 12)

Load occupancy-detection models for two exemplary species, *Araschnia levana* and *Limenitis populi*

```
spec_names <- c("ARASCHNIA LEVANA","LIMENITIS POPULI")

filelist <- list.files(
 path="C:/Users/ekath/R_Coding/MINTbio/extdata/occupancy_models/Lepidoptera1980-2019",
 pattern="_occmodel.rds")
filelist <- c(filelist[1],filelist[5])
```

```
Lpopuli <- readRDS(paste(
 "C:/Users/ekath/R_Coding/MINTbio/extdata/occupancy_models/Lepidoptera1980-2019/",
 filelist[2],sep=""))
Alevana <- readRDS(paste(
 "C:/Users/ekath/R_Coding/MINTbio/extdata/occupancy_models/Lepidoptera1980-2019/",
 filelist[1],sep=""))
```

Occupancy-detection model were already plotted before for this species,thus we only add the model quality check here.

Model evaluation (Fig. 11)

Check model quality for *Araschnia levana*

```
bayes.mod.fit.gg <- ggs(Alevana$samples,family="psi.fs")
bayes.mod.fit.gg$ParamNu <- as.numeric(sub(".*\\[(([^][]+)].*","\\1",
                                           bayes.mod.fit.gg$Parameter))

my_attributes<-attributes(bayes.mod.fit.gg)
bayes.mod.fit.gg <- subset(bayes.mod.fit.gg,ParamNu%%10==0) # plot every 5
attributes(bayes.mod.fit.gg)<-c(attributes(bayes.mod.fit.gg),my_attributes[3:8])

Al.bayes.mod.fit.gg <- bayes.mod.fit.gg
```

```
# plots
Al.histo <- ggs_histogram(Al.bayes.mod.fit.gg)
Al.density <- ggs_density(Al.bayes.mod.fit.gg)
Al.traceplot <- ggs_traceplot(Al.bayes.mod.fit.gg)

Al.plot_modeval <-
  (Al.density & aes(colour=as.factor(Chain),fill=as.factor(Chain)) &
    scale_colour_manual(name="Chain",values=c("#194100","#799e08","#fdff00")) &
    scale_fill_manual(name="Chain",values=c("#194100","#799e08","#fdff00")) &
    theme_bw() & scale_y_continuous(name="Density ",limits=c(0,20)) &
    scale_x_continuous(name="Occupancy estimate") &
    theme(legend.position="bottom",legend.text=element_text(size=12),
          legend.title=element_text(size=12),
          axis.text=element_text(size=10),axis.title=element_text(size=12),
          strip.background=element_blank(),strip.text=element_text(size=12))) +
  (Al.traceplot & aes(colour=as.factor(Chain),fill=as.factor(Chain),
                      alpha=as.factor(Chain)) &
    scale_colour_manual(name="Chain",values=c("#194100","#799e08","#fdff00")) &
    scale_fill_manual(name="Chain",values=c("#194100","#799e08","#fdff00")) &
    theme_bw() & scale_y_continuous(name="Occupancy estimate ",limits=c(0.35,1)) &
    theme(legend.position="none",
          legend.text=element_text(size=12),legend.title=element_text(size=12),
          axis.text=element_text(size=10),axis.title=element_text(size=12),
          strip.background=element_blank(),strip.text=element_text(size=12)))
```

Plot occupancy estimates for *Limenitis populi*

```
# plot annual occupancy estimates
Lp.plot_occ <- dat %>% filter(Species =="LIMENITIS POPULI") %>%
  ggplot() + theme_bw() +
  geom_point(aes(x=Year,y=occupancyMean,
                 color=cut(occupancyRhat,c(-Inf,1.1,Inf))),size=1) +
```

```
      geom_line(aes(x=Year,y=occupancyMean))+
      geom_ribbon(aes(x=Year,ymin=occupancyX2.5,ymax=occupancyX97.5),alpha=0.5) +
      scale_color_manual(name="Rhat",values=c("blue","red"),na.value=c("red"),
                         expand=c(-Inf,Inf),limits=c("(-Inf,1.1]","(1.1,Inf]"),
                         labels=c("Good (<1.1)","Bad (>1.1)")) +
      scale_x_continuous(name="Year")+scale_y_continuous(limits=c(0,1),name="Occupancy")+
      theme(axis.text=element_text(size=12),axis.title=element_text(size=12),
           legend.position="bottom",legend.key.size=unit(1.5,"cm"),
           legend.text=element_text(size=12),legend.title=element_text(size=12),
           plot.margin=unit(c(0.8,0,0,0),"cm"),
           legend.margin=margin(unit(c(0,0,0,0),"cm")),
           legend.box.margin=margin(unit(c(0,0,0,0),"cm")))+
      guides(size=FALSE,color="none")


# save legend separately
legend.occ <- dat %>% filter(Species =="LIMENITIS POPULI") %>%
    ggplot()+ geom_point(aes(x=Year,y=occupancyMean,
                          color=cut(occupancyRhat,c(-Inf,1.1,Inf))),size=5) +
     scale_color_manual(name="Rhat",values=c("blue","red"),na.value=c("red"),
                        expand=c(-Inf,Inf),limits=c("(-Inf,1.1]","(1.1,Inf]"),
                        labels=c("Good (<1.1)","Bad (>1.1)")) +
    theme(legend.position="bottom",legend.key.size=unit(0.25,"cm"),
         legend.text=element_text(size=12),legend.title=element_text(size=12),
         plot.margin=unit(c(0.8,0,0,0),"cm"),
         legend.background=element_rect(fill="white",colour="white",linetype=0),
         legend.box.background=element_rect(fill="white",colour="white",linetype=0),
         legend.margin=margin(unit(c(0,0,0,0),"cm")),
         legend.box.margin=margin(unit(c(0,0,0,0),"cm")))+
    guides(size=FALSE)
```

Check model quality for *Limenitis populi*

```
bayes.mod.fit.gg <- ggs(Lpopuli$samples,family="psi.fs")
bayes.mod.fit.gg$ParamNu <-
  as.numeric(sub(".*\\[([^][]+)].*","\\1",bayes.mod.fit.gg$Parameter))

my_attributes<-attributes(bayes.mod.fit.gg)
bayes.mod.fit.gg <- subset(bayes.mod.fit.gg,ParamNu%%10==0) # plot every 5
attributes(bayes.mod.fit.gg)<-c(attributes(bayes.mod.fit.gg),my_attributes[3:8])

Lp.bayes.mod.fit.gg <- bayes.mod.fit.gg
```
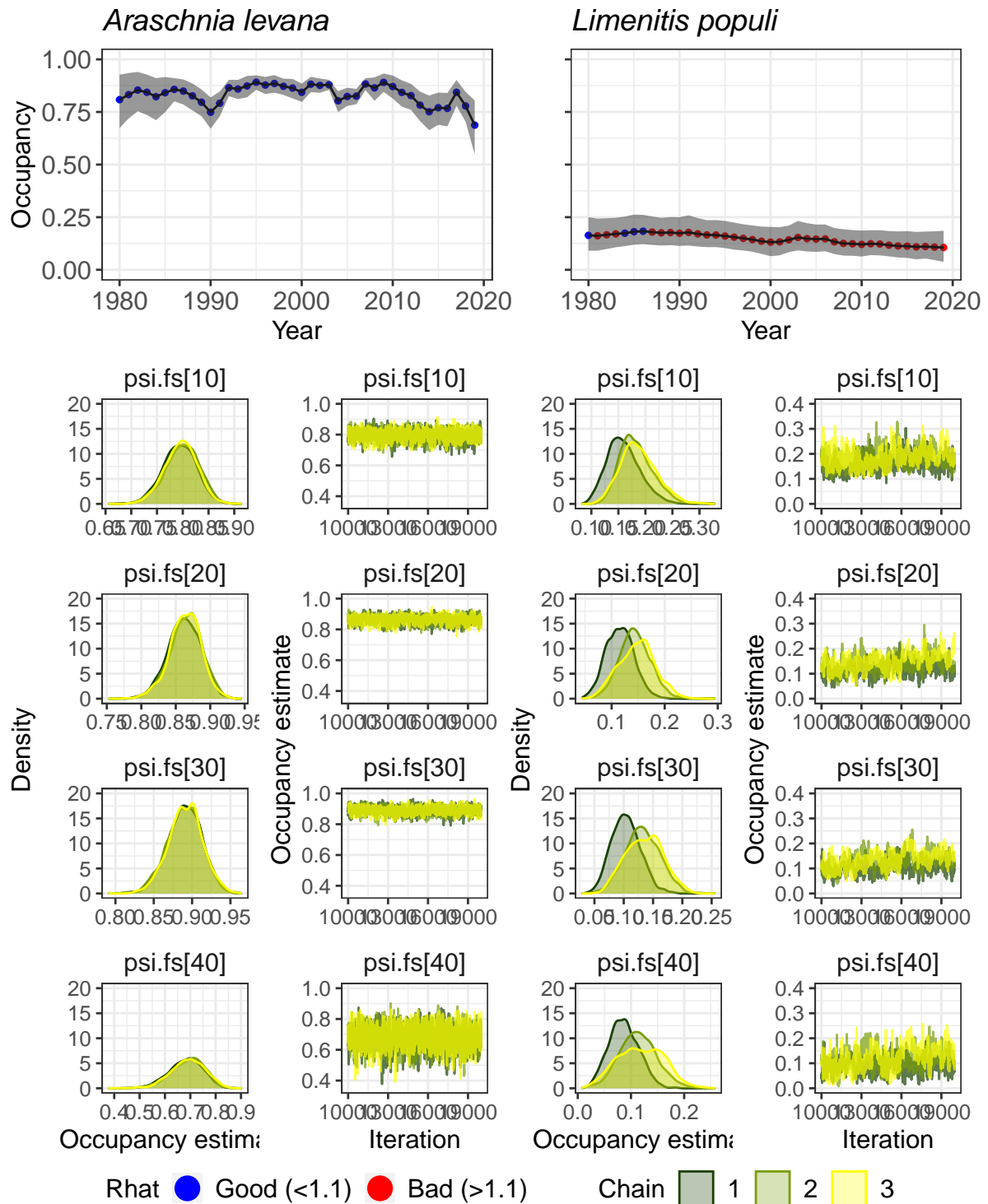
Figure 11 Exemplary model evaluation plots for occupancy-detection models from 1980 to 2019 of two butterfly species one with reliable model quality (Araschnia levana (A)) and one with unreliable model estimates (Limenitis populi (B)) with colour legends given in (C).

Annotations were added using Inkscape: Inkscape Project,2020. Inkscape,Available at: https://inkscape. org.

Residual plots of occupancy estimates (Fig. 12)

```r
temp <- dat %>% filter(Species =="ANAX PARTHENOPE") %>%
  dplyr::mutate(Species=str_to_sentence(Species))

lm.al <- lm(occupancyMean ~ Year,data=temp)
temp$predicted <- predict(lm.al)    # Save the predicted values
temp$residuals <- residuals(lm.al) # Save the residual values

g1 <- ggplot(temp,aes(x=Year,y=occupancyMean)) + theme_bw() +
  geom_smooth(method="lm",se=FALSE,color="lightgrey") + #Plot regression slope
  geom_segment(aes(xend=Year,yend=predicted),alpha=.2) +
  geom_point(aes(color=abs(residuals))) +
  geom_point(aes(y=predicted),shape=1)+  # Add the predicted values
  scale_color_continuous(low="black",high="red") +  # Colors to use here
  scale_x_continuous(breaks=c(1980,2000,2020))+
  labs(x="Year",y="Occupancy",title="(A)")+ # Scatterplot of simulated data
  guides(colour=FALSE)

# Make a scatter plot of residuals against fitted/predicted values
g2 <- ggplot(temp,aes(x=predicted,y=residuals)) + geom_point() + theme_bw() +
  geom_abline(intercept=0,slope=0,colour="red") +
  labs(title="(B)",# Residuals vs. predicted values
       x="Predicted value",y="Residual") + guides(colour=FALSE)

# Make a histogram of the residuals
g3 <- ggplot(temp,aes(x=residuals)) + theme_bw() +
  geom_histogram(bins=10,fill="lightgrey",colour="black")+
  labs(title="(C)",# Histogram of residuals
       x="Residual",y="Count")

# Make a quantile-quantile plot
g4 <- ggplot(temp,aes(sample=residuals)) + geom_qq() + geom_qq_line(colour="red") +
  labs(title="(D)", x="X",y="Y") # Quantile plot of residuals

# Plot the plots
#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/Residuals.png",
#units="in",width=6.5,height=5,res=1200)
ptemp <- (g1+g2)/(g3+g4) & theme_bw() +
  theme(axis.text=element_text(size=14),axis.title=element_text(size=16),
        plot.title=element_text(size=16),strip.background=element_rect(fill="white"),
        strip.text=element_text(size=14,face="italic"),
        legend.position="bottom",legend.key.size=unit(1.5,"cm"),
        legend.text=element_text(size=14),legend.title=element_text(size=14),
        plot.margin=unit(c(0.1,0.4,0.1,0.1),"cm"),
        legend.margin=margin(unit(c(0,0,0,0),"cm")),
        legend.box.margin=margin(unit(c(0,0,0,0),"cm")))
#dev.off()
#ggview::ggview(device="png",units="in",width=8,height=6)
```
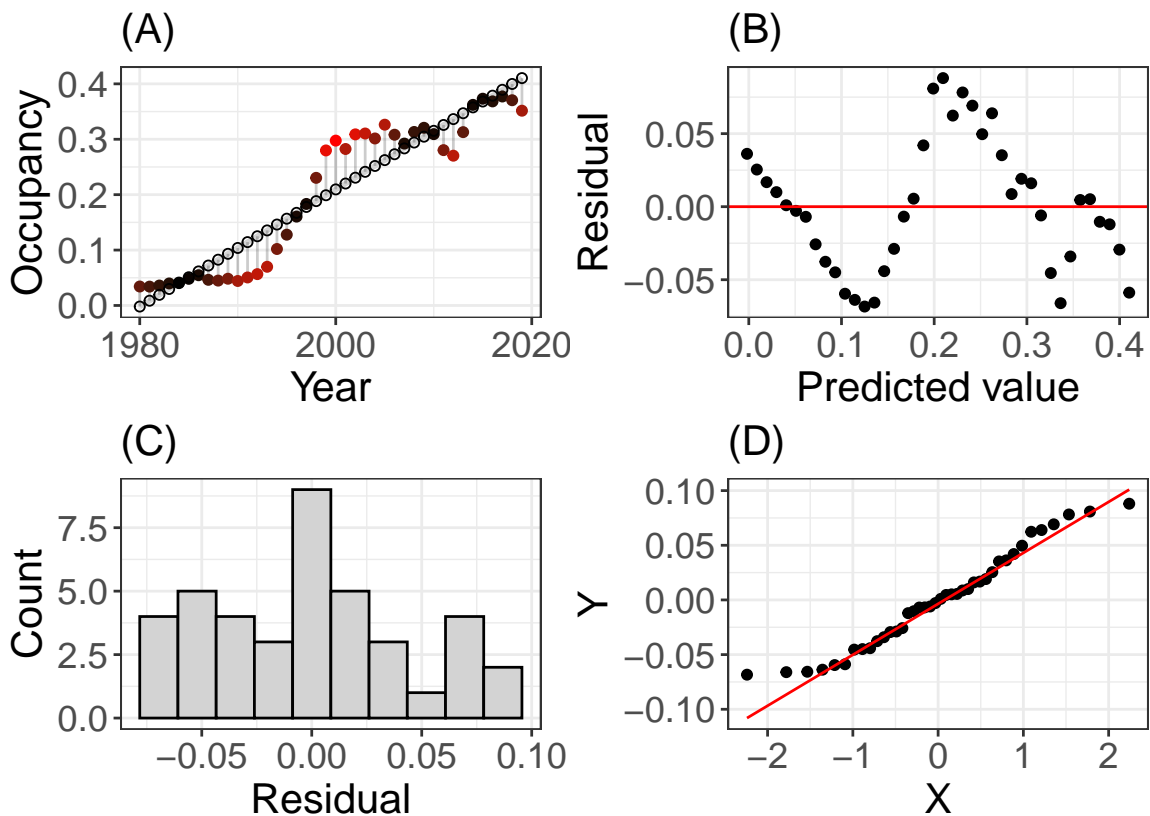
Figure 12 Residual plots of occupancy estimates of *Anax parthenope* (Lesser emperor,family Aeshnidae)

A photograph of the species was added using Inkscape: Inkscape Project,2020. Inkscape,Available at: https://inkscape.org.

Comparison of methods applied to analyse linear trends (Fig. 13,Fig. 14,Fig. 15)

Bayesian GLM

```
Anax_brms <- dat %>% filter(Species =="ANAX PARTHENOPE") %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(Species,occupancyMean,yearIndex,occupancySD) %>%
  brm(occupancyMean | mi(occupancySD) ~ yearIndex,data=.,
      prior=NULL,# default,uniform priors
      control=list(adapt_delta=0.99999,max_treedepth=12),
      chains=4,iter=4000,cores=getOption("mc.cores",4))
```

```
# clean output
Anax_brms2 <- broom.mixed::tidy(Anax_brms,effects="fixed") %>% as.data.frame() %>%
  slice(2) %>% mutate(Species="ANAX PARTHENOPE") %>% dplyr::select(-effect,-component)

Anax_brms_fit <- broom.mixed::tidy(Anax_brms$fit,
                                     rhat=T,conf.int=T,conf.level=.95,ess=T) %>%
  as.data.frame() %>% slice(2) %>% mutate(Species="ANAX PARTHENOPE") %>%
  mutate(term=str_remove(term,"b_")) %>% dplyr::select(-estimate)

Anax_brms2 <- full_join(Anax_brms2,Anax_brms_fit)
rm(Anax_brms_fit)
```

```
Anax_brms2 %<>% dplyr::mutate(model="BRMS")

Anax_brms_pred <- as.data.frame(predict(Anax_brms))
Anax_brms_pred %<>% dplyr::mutate(yearIndex=as.numeric(seq(1:40)))

Anax_brms_pred <- dat %>% filter(Species =="ANAX PARTHENOPE") %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>% full_join(.,Anax_brms_pred)

Anax_brms <- Anax_brms2
rm(Anax_brms2)
```

Classic GLM

```
Anax_classic_glm1 <- dat %>% filter(Species =="ANAX PARTHENOPE") %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(Species,occupancyMean,yearIndex,occupancySD) %>%
  glm(occupancyMean ~ yearIndex,data=.,weights=1/occupancySD)

Anax_classic_glm_ci <- confint(Anax_classic_glm1,level=0.95) %>%
  as.data.frame() %>% tibble::rownames_to_column() %>%
  rename(term=rowname) %>% mutate(Species="ANAX PARTHENOPE")
Anax_classic_glm <- broom::tidy(Anax_classic_glm1) %>% as.data.frame() %>%
  mutate(Species="ANAX PARTHENOPE",model="classic GLM") %>%
  full_join(Anax_classic_glm_ci) %>%
  dplyr::select(model,Species,term,estimate,std.error,p.value,
                '2.5 %','97.5 %',statistic)
rm(Anax_classic_glm_ci)

Anax_classic_glm_pred <-
  dat %>% filter(Species =="ANAX PARTHENOPE") %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(yearIndex) %>%
  predict.glm(Anax_classic_glm1,newdata=.,type="link",se.fit=TRUE)

critval <- 1.96 ### approx 95% CI
upr <- Anax_classic_glm_pred$fit + (critval * Anax_classic_glm_pred$se.fit)
lwr <- Anax_classic_glm_pred$fit - (critval * Anax_classic_glm_pred$se.fit)
fit <- Anax_classic_glm_pred$fit

fit2 <- Anax_classic_glm1$family$linkinv(fit)
upr2 <- Anax_classic_glm1$family$linkinv(upr)
lwr2 <- Anax_classic_glm1$family$linkinv(lwr)

Anax_classic_pred <- dat %>% filter(Species =="ANAX PARTHENOPE") %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::mutate(glm_fit=fit2,glm_uCI=upr2,glm_lCI=lwr2)
```

Classic GLM with before vs. after term

As applied in chapter 2 to compare linear trends before and after implementation of the Habitats Directive in 1998

```
# add before/after as a factor term
dat_temp <- dat %>% filter(Species =="ANAX PARTHENOPE") %>%
```

```r
  dplyr::mutate(period=as.factor(ifelse(Year <=1998,"before",
                                        ifelse(Year>=2000,"after",NA))))

dat_temp$period <- factor(dat_temp$period,levels=c("before","after"))

Anax_BeforeAfter_glm1 <- dat_temp %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(Species,occupancyMean,yearIndex,occupancySD,period) %>%
  glm(occupancyMean ~ yearIndex*period,data=.,weights=1/occupancySD)

Anax_BeforeAfter_glm1_ci <- confint(Anax_BeforeAfter_glm1,level=0.95) %>%
  as.data.frame() %>% tibble::rownames_to_column() %>%
  dplyr::rename(term=rowname) %>% dplyr::mutate(Species="ANAX PARTHENOPE")
Anax_BeforeAfter_glm <- broom::tidy(Anax_BeforeAfter_glm1) %>% as.data.frame() %>%
  dplyr::mutate(Species="ANAX PARTHENOPE") %>% full_join(Anax_BeforeAfter_glm1_ci) %>%
  dplyr::select(Species,term,estimate,std.error,p.value,'2.5 %','97.5 %',statistic)

# prediction
Anax_BeforeAfter_pred <- dat_temp %>% filter(Species =="ANAX PARTHENOPE") %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(yearIndex,period) %>%
  predict.glm(Anax_BeforeAfter_glm1,newdata=.,type="link",se.fit=TRUE)

critval <- 1.96 ### approx 95% CI
upr <- Anax_BeforeAfter_pred$fit + (critval * Anax_BeforeAfter_pred$se.fit)
lwr <- Anax_BeforeAfter_pred$fit - (critval * Anax_BeforeAfter_pred$se.fit)
fit <- Anax_BeforeAfter_pred$fit

fit2 <- Anax_BeforeAfter_glm1$family$linkinv(fit)
upr2 <- Anax_BeforeAfter_glm1$family$linkinv(upr)
lwr2 <- Anax_BeforeAfter_glm1$family$linkinv(lwr)

Anax_BeforeAfter_pred <- dat_temp %>% filter(Species =="ANAX PARTHENOPE") %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::mutate(glm_fit=fit2,glm_uCI=upr2,glm_lCI=lwr2)
```

Segmented linear model

Classic inference GLM including a breakpoint analysis

```r
dat_temp <- dat %>% filter(Species =="ANAX PARTHENOPE") %>%
  dplyr::select(Species,occupancyMean,Year,occupancySD,
                occupancyX2.5,occupancyX97.5,occupancyRhat)

Anax_mod_sg <- dat_temp %>% group_by(Species) %>%
  do(sg_lm=segmented.glm(glm(occupancyMean ~ Year,weights=1/occupancySD,data=.),
                         seg.Z=~Year,psi=list(Year=NA),
                         control=seg.control(fix.npsi=FALSE,n.boot=0,quant=F,h=3,
                                             tol=1e-8,K=3,it.max=20000,display=FALSE)))

# pull linear model occupancy estimate for each year
Anax_mod_fit_sg <- Anax_mod_sg %>% do(data.frame(Species=.$Species,
                yearIndex=as.numeric(sort(unique(dat_temp$Year))),
                fit_sg=predict.glm(.$sg_lm,type="response"),
                se.fit_sg=predict.glm(.$sg_lm,type="response",se.fit=T)$se.fit,
                CI=predict.glm(.$sg_lm,type="response",interval="confidence")))
```

```r
# Combine with occupancy data
Anax_mod_fit_sg <- Anax_mod_fit_sg %>% rename(Year=yearIndex) %>% full_join(.,dat_temp)

# extract slopes with CIs and years of breakpoints
est_sg <- Anax_mod_sg %>% do(data.frame(Species=.$Species,
  var=if(class(.$sg_lm)[[1]]=="segmented"){rownames(data.frame(slope(.$sg_lm)))
    }else{"slope1"},
  # change startyear to 1980 to fit to occupancy models
  Start=c(1980,as.data.frame(summary(.$sg_lm)$psi)$Est.+1),
  # change endyear to 2019 to fit to occupancy models
  End=c(as.data.frame(summary(.$sg_lm)$psi)$Est.,2019),
  if(class(.$sg_lm)[[1]]=="segmented"){slope(.$sg_lm)}else{
    data.frame(Year.Est.=summary(.$sg_lm)$coefficients[2,1],
               Year.St.Err.=summary(.$sg_lm)$coefficients[2,2],
               Year.t.value=summary(.$sg_lm)$coefficients[2,3])}))

# round year of breakpoint
est_sg %<>% dplyr::mutate(Start=round(Start,0),End=round(End,0))

# add confidence intervals to years of breakpoint
est_sg <- Anax_mod_sg %>%
  do(data.frame(Species=.$Species,ci_sg=confint(.$sg_lm,level=0.95))) %>%
  rename(End=ci_sg.Est.,bp_lCI=ci_sg.CI.95...low,bp_uCI=ci_sg.CI.95...up) %>%
  dplyr::mutate(across(where(is.numeric),round,0)) %>%
  dplyr::select(Species,End,bp_lCI,bp_uCI) %>%
  dplyr::mutate(End=
   ifelse(Species =="Lepidoptera,Melitaea britomartis" & End ==1986,1987,
     ifelse(Species =="Lepidoptera,Thymelicus sylvestris" & End ==1994,1993,
       ifelse(Species =="Odonata,Cordulia aenea" & End ==2010,2011,End)))) %>%
  full_join(.,est_sg) %>% filter(!is.na(Start)) %>%
  mutate(bp_lCI=replace_na(bp_lCI,2019),bp_uCI=replace_na(bp_uCI,2019)) %>%
  arrange(Species,Start)

# clean names
est_sg %<>% dplyr::select(-Year.t.value) %>%
  rename(slope=Year.Est.,slope.SD=Year.St.Err.,slope.lCI=Year.CI.95...l,
         slope.uCI=Year.CI.95...u)

# define direction of the slopes,combine information in one table
est_sg %<>% mutate(direction=
             ifelse(slope.lCI <0 & slope.uCI <=0,"decrease",
               ifelse(slope.lCI>=0 & slope.uCI> 0,"increase","stable")))

# filter breakpoints where the estimated startyear equals the end year
# correct breakpoint names so there's no gap
est_sg %<>% group_by(Species) %>% mutate(nbp=row_number(),nbp=nbp-1) %>%
  filter(Start !=End) %>% mutate(nbp2=row_number(),nbp2=nbp2-1) %>%
  mutate(var=ifelse(nbp !=nbp2,paste("slope",nbp,sep=""),var)) %>%
  dplyr::select(-nbp,-nbp2)


# define change (improving/deteriorating) based on upper and lower slope CIs
est_sg_temp <- est_sg %>% dplyr::select(c(Species,var,slope.lCI,slope.uCI)) %>%
  pivot_wider(id_cols=Species,names_from=var,values_from=c(slope.lCI,slope.uCI)) %>%
  mutate(change1=ifelse(
    slope.lCI_slope1 <slope.lCI_slope2 & slope.uCI_slope1 <slope.uCI_slope2,
    "improving",ifelse(
      slope.lCI_slope1> slope.lCI_slope2 & slope.uCI_slope1> slope.uCI_slope2,
```

```r
      "deteriorating",ifelse(
        is.na(slope.lCI_slope2) & is.na(slope.uCI_slope2),NA,"stable"))),
    change2=ifelse(
      slope.lCI_slope2 <slope.lCI_slope3 & slope.uCI_slope2 <slope.uCI_slope3,
      "improving",ifelse(
        slope.lCI_slope2> slope.lCI_slope3 & slope.uCI_slope2> slope.uCI_slope3,
        "deteriorating",ifelse(
          is.na(slope.lCI_slope3) & is.na(slope.uCI_slope3),NA,"stable"))),
    change3=ifelse(
      slope.lCI_slope3 <slope.lCI_slope4 & slope.uCI_slope3 <slope.uCI_slope4,
      "improving",ifelse(
        slope.lCI_slope3> slope.lCI_slope4 & slope.uCI_slope3> slope.uCI_slope4,
        "deteriorating",ifelse(
          is.na(slope.lCI_slope4) & is.na(slope.uCI_slope4),NA,"stable")))) %>%
  dplyr::select(-c(slope.lCI_slope1,slope.lCI_slope2,slope.lCI_slope3,
                   slope.lCI_slope4,slope.uCI_slope1,slope.uCI_slope2,
                   slope.uCI_slope3,slope.uCI_slope4)) %>%
  pivot_longer(cols=c(change1,change2,change3),names_to="bp",
               values_to="change") %>% na.omit()

est_sg %<>% mutate(bp=ifelse(var=="slope2","change1",ifelse(var=="slope3","change2",
                              ifelse(var=="slope4","change3",NA)))) %>%
  full_join(.,est_sg_temp)


# define change (improving/deteriorating) based on direction of previous slopes
est_sg %<>% dplyr::select(c(Species,var,direction)) %>%
  pivot_wider(id_cols=Species,names_from=var,values_from=direction) %>%
  mutate(dir.change1=
           ifelse(slope1=="stable" & slope2=="stable","stable",
                  ifelse(slope1=="stable" & slope2=="increase" |
                           slope1=="decrease" & slope2=="increase" |
                           slope1=="decrease" & slope2=="stable" |
                           slope1=="increase" & slope2=="increase",
                         "improving",
                         ifelse(slope1=="stable" & slope2=="decrease" |
                                  slope1=="increase" & slope2=="decrease" |
                                  slope1=="increase" & slope2=="stable" |
                                  slope1=="decrease" & slope2=="decrease",
                                "deteriorating",NA))),
         dir.change2=
           ifelse(slope2=="stable" & slope3=="stable","stable",
                  ifelse(slope2=="stable" & slope3=="increase" |
                           slope2=="decrease" & slope3=="increase" |
                           slope2=="decrease" & slope3=="stable" |
                           slope2=="increase" & slope3=="increase",
                         "improving",
                         ifelse(slope2=="stable" & slope3=="decrease" |
                                  slope2=="increase" & slope3=="decrease" |
                                  slope2=="increase" & slope3=="stable" |
                                  slope2=="decrease" & slope3=="decrease",
                                "deteriorating",NA))),
         dir.change3=ifelse(slope3=="stable" & slope4=="stable","stable",
                            ifelse(slope3=="stable" & slope4=="increase" |
                                     slope3=="decrease" & slope4=="increase" |
                                     slope3=="decrease" & slope4=="stable" |
                                     slope3=="increase" & slope4=="increase",
                                   "improving",
                                   ifelse(slope3=="stable" & slope4=="decrease" |
```

```
                                        slope3=="increase" & slope4=="decrease" |
                                        slope3=="increase" & slope4=="stable" |
                                        slope3=="decrease" & slope4=="decrease",
                                        "deteriorating",NA)))) %>%
  dplyr::select(-c(slope1,slope2,slope3,slope4)) %>%
  pivot_longer(cols=c(dir.change1,dir.change2,dir.change3),names_to="bp",
               values_to="dir.change") %>%
  na.omit() %>% mutate(bp=str_remove(bp,"dir.")) %>% full_join(est_sg,.)

# combine with occupancy and linear estimate data,
# reformat for sensible plotting
Anax_segmented <-
  est_sg %>% dplyr::select(Start,End,direction,change,bp_lCI,bp_uCI) %>%
  pivot_longer(.,cols=c("Start","End")) %>%
    dplyr::mutate(id=c(1,1,2,2,2,2,2,2),
                  bp_lCI=ifelse(name =="Start",NA,bp_lCI),
                  bp_uCI=ifelse(name =="Start",NA,bp_uCI),
                  change=ifelse(value ==2019,NA,
                         ifelse(value ==1992,"improving",
                           ifelse(value ==2001,"deteriorating",
                             ifelse(value ==2012,"improving",NA)))),
                  direction=ifelse(value ==1992,"increase",
                            ifelse(value ==2001,"stable",
                              ifelse(value ==2012,"increase", direction)))) %>%
  dplyr::select(-name) %>%
    dplyr::mutate(bp_lCI=ifelse(value ==1980,1980,bp_lCI),
                  bp_uCI=ifelse(value ==1980,1980,bp_uCI)) %>%
    filter(!is.na(bp_lCI)) %>%
  unite(col="direction",c("direction","id"),sep="") %>%
  complete(value=seq(min(value),max(value),1L)) %>%
  fill(direction) %>% rename(Year=value) %>% full_join(Anax_mod_fit_sg,.)

# add 95% CI to slope
Anax_segmented %<>%
  mutate(lCI=fit_sg - qt(1 - (0.05 / 2),40 - 1) * se.fit_sg,
         uCI=fit_sg + qt(1 - (0.05 / 2),40 - 1) * se.fit_sg) %>%
  dplyr::select(1:5,lCI,uCI,6:14)

Anax_segmented_glm <- est_sg
rm(est_sg)
```

Plot the different linear model results (Fig. 13)

```
# define colours
Anax_segmented_dir <- c("stable1"="#ffd100","stable2"="#ffd100","increase1"="#002537",
                        "increase2"="#002537","decrease"="#a24381")

# plot segmented linear model
plot_seg <- Anax_segmented %>%
  dplyr::mutate(direction=as.factor(direction),change=as.factor(change)) %>%
  ggplot()+theme_bw()+ggtitle(label="(D) Segmented generalized linear model")+
  geom_point(aes(x=Year,y=occupancyMean),size=1) +
  geom_line(aes(x=Year,y=occupancyMean))+
  geom_ribbon(aes(x=Year,ymin=occupancyX2.5,ymax=occupancyX97.5),alpha=0.25) +
  geom_ribbon(aes(x=Year,ymin=lCI,ymax=uCI,fill=direction,group=direction),alpha=0.4)+
  geom_line(aes(x=Year,y=fit_sg,colour=direction,group=direction),linewidth=1)+
```

```r
  geom_point(aes(x=Year,y=0.52,shape=change),size=5)+
  annotate(geom="text",x=2000,y=0.8,size=3.9,
          label="1980-1992:  0.0015 (lCI -0.0001,uCI 0.0029)
1993-2001:  0.0305 (lCI  0.0269,uCI 0.0340)
2002-2012: -0.0013 (lCI -0.0048,uCI 0.0022)
2013-2019:  0.0122 (lCI  0.0068,uCI 0.0176)") +
  scale_color_manual(name="Trend direction",values=Anax_segmented_dir,drop=FALSE,
                     na.value=c("grey"),labels=c("stable","increase","","")) +
  scale_fill_manual(name="Trend direction",values=Anax_segmented_dir,drop=FALSE,
                    na.value=c("grey"),labels=c("stable","increase","","")) +
  scale_shape_manual(name="Trend change",values=c(24,25),
                     labels=c("improving","deteriorating",""))+
  scale_x_continuous(name="Year") +
  scale_y_continuous(limits=c(0,1),name="Occupancy") +
  theme(axis.text.x=element_text(size=12),axis.text.y=element_blank(),
        axis.title.x=element_text(size=12),axis.title.y=element_blank(),
        title=element_text(size=10),
        legend.position="bottom",legend.key.size=unit(1,"cm"),
        legend.text=element_text(size=12),legend.title=element_text(size=12),
        plot.margin=unit(c(0.2,0.2,0.2,0.3),"cm"),
        legend.margin=margin(unit(c(0,0,0,0),"cm")),
        legend.box.margin=margin(unit(c(0,0,0,0),"cm")))+
  guides(colour="none", fill="none", shape="none")

# plot before vs after model ----
plot_BeforeAfter <- Anax_BeforeAfter_pred %>%
  ggplot() + theme_bw() + ggtitle(label="(C) Before vs. After (classical GLM)") +
  geom_point(aes(x=Year,y=occupancyMean),size=1) +
  geom_line(aes(x=Year,y=occupancyMean))+
  geom_ribbon(aes(x=Year,ymin=occupancyX2.5,ymax=occupancyX97.5),alpha=0.25) +
  geom_ribbon(aes(x=Year,ymin=glm_uCI,ymax=glm_lCI),alpha=0.4,fill="#58508d") +
  geom_line(aes(x=Year,y=glm_fit),linewidth=1,colour="#58508d")+
  annotate(geom="text",x=2000,y=0.9,size=3.9,
          label="Difference: -0.00325 (lCI -0.00695,uCI 0.00044)") +
  scale_x_continuous(name="Year") +
  scale_y_continuous(limits=c(-0.1,1),name="Occupancy") +
  theme(axis.text=element_text(size=12),axis.title=element_text(size=12),
        title=element_text(size=10),
        legend.position="bottom",legend.key.size=unit(1.5,"cm"),
        legend.text=element_text(size=12),legend.title=element_text(size=12),
        plot.margin=unit(c(0.2,0.3,0.2,0.2),"cm"),
        legend.margin=margin(unit(c(0,0,0,0),"cm")),
        legend.box.margin=margin(unit(c(0,0,0,0),"cm")))

# plot brms model ----
plot_brms <- Anax_brms_pred %>%
  ggplot() + theme_bw() + ggtitle(label="(B) Bayesian generalized linear model") +
  geom_point(aes(x=Year,y=occupancyMean),size=1) +
  geom_line(aes(x=Year,y=occupancyMean))+
  geom_ribbon(aes(x=Year,ymin=occupancyX2.5,ymax=occupancyX97.5),alpha=0.25) +
  geom_ribbon(aes(x=Year,ymin=Q2.5,ymax=Q97.5),alpha=0.4,fill="#ff6361") +
  geom_line(aes(x=Year,y=Estimate),linewidth=1,colour="#ff6361")+
  annotate(geom="text",x=2000,y=0.9,size=3.9,label="0.0108 (lCI 0.0093,uCI 0.0123)")+
  scale_x_continuous(name="Year") +
  scale_y_continuous(limits=c(-0.1,1),name="Occupancy") +
  theme(axis.text=element_blank(),axis.title=element_blank(),
        title=element_text(size=10),
        legend.position="bottom",legend.key.size=unit(1.5,"cm"),
```

```r
      legend.text=element_text(size=12),legend.title=element_text(size=12),
      plot.margin=unit(c(0.2,0.2,0.2,0.3),"cm"),
      legend.margin=margin(unit(c(0,0,0,0),"cm")),
      legend.box.margin=margin(unit(c(0,0,0,0),"cm")))

# plot classic model ----
plot_classic <- Anax_classic_pred %>%
  ggplot() + theme_bw() + ggtitle(label="(A) Classical generalized linear model") +
  geom_point(aes(x=Year,y=occupancyMean),size=1) +
  geom_line(aes(x=Year,y=occupancyMean))+
  geom_ribbon(aes(x=Year,ymin=occupancyX2.5,ymax=occupancyX97.5),alpha=0.25) +
  geom_ribbon(aes(x=Year,ymin=glm_lCI,ymax=glm_uCI),alpha=0.4,fill="#bc5090") +
  geom_line(aes(x=Year,y=glm_fit),linewidth=1,colour="#bc5090")+
  annotate(geom="text",x=2000,y=0.9,size=3.9,label="0.0109 (lCI 0.0097,uCI 0.0121)")+
  scale_x_continuous(name="Year") +
  scale_y_continuous(limits=c(-0.1,1),name="Occupancy") +
  theme(axis.text.x=element_blank(),axis.text.y=element_text(size=12),
      axis.title.x=element_blank(),axis.title.y=element_text(size=12),
      title=element_text(size=10),
      legend.position="bottom",legend.key.size=unit(1.5,"cm"),
      legend.text=element_text(size=12),legend.title=element_text(size=12),
      plot.margin=unit(c(0.2,0.3,0.2,0.2),"cm"),
      legend.margin=margin(unit(c(0,0,0,0),"cm")),
      legend.box.margin=margin(unit(c(0,0,0,0),"cm")))


# combine plots
Anax_segmented # segmented glm predictions
Anax_segmented_glm # GLM segmented

Anax_brms_pred # brms glm predictions
Anax_brms # GLM BRMS

Anax_classic_pred # classic glm prediction
Anax_classic_glm # GLM classic

Anax_BeforeAfter_pred # before/after glm prediction
Anax_BeforeAfter_glm # GLM before/after


#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/comparison_GLMs2.png",
#units="in",width=8,height=6.5,res=1200)
ptemp <- (plot_classic + plot_brms) / (plot_BeforeAfter + plot_seg) / guide_area() +
  plot_layout(guides='collect',heights=unit(c(1,1,0.3),"null"),
            widths=unit(c(1,1),"null"))
#dev.off()
#ggview::ggview(device="png",units="in",width=8,height=6.5)
```
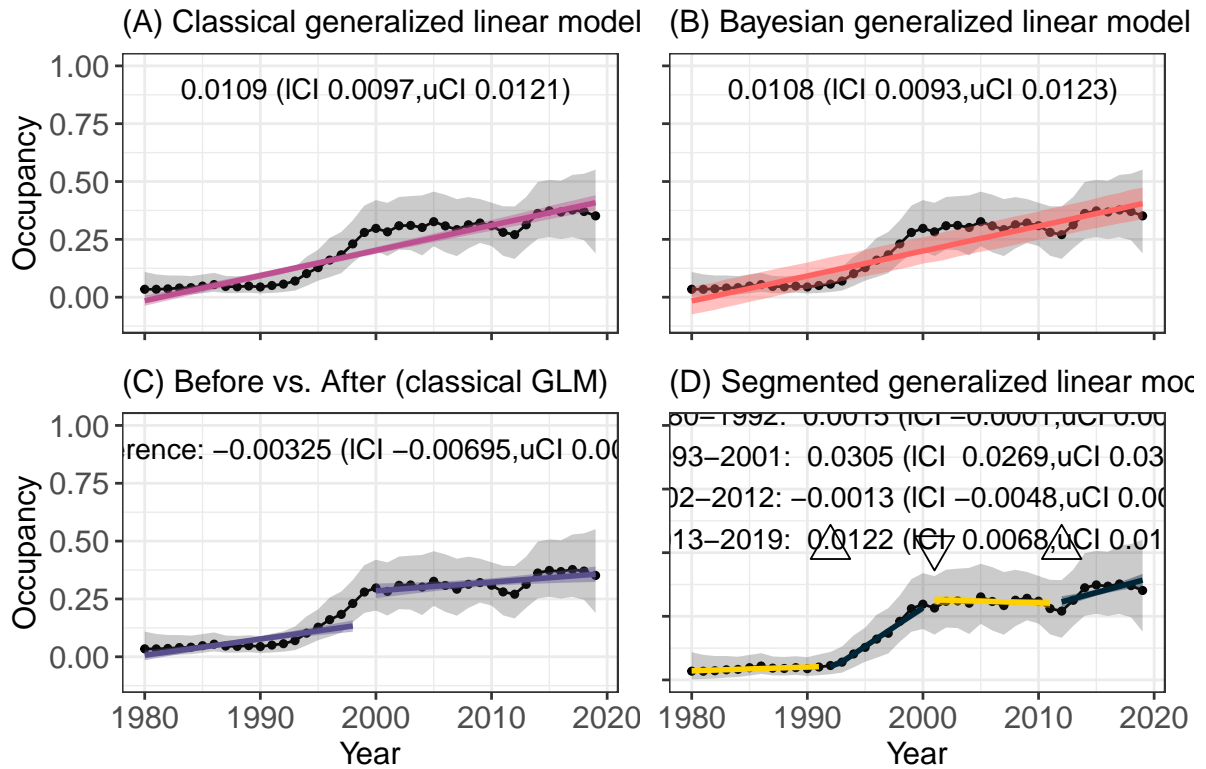
Figure 13 Methods applied to analyse linear trends of long-term annual occupancy estimates on the example of Anax parthenope (Lesser emperor,family Aeshnidae).

Breakpoint Analyses for all species (Fig. 14)

using segmented linear models

```
dat <- read.csv2(
  "C:/Users/ekath/R_Coding/MINTbio/data/Engelhardt_etal_2022_occupancyEstimates.csv",
  sep=",",dec=".")
```

```
# Segmented linear models
dat_sg <- dat
set.seed(3456)
mod_sg <- dat_sg %>% group_by(Species) %>%
  do(sg_lm=segmented.glm
     (glm(occupancyMean ~ Year,weights=occupancyMean/occupancySD,data=.),
      seg.Z=~Year,psi=list(Year=NA),
      # A NA value means that 'K' quantiles
      # (or equally spaced values) are used as
      # starting values; K is fixed via the seg.control
      # auxiliary function
      control=seg.control(fix.npsi=FALSE,
                          # preliminary and tentative approach to deal with an
                          # unknown number of breakpoints
                          n.boot=0,quant=F,h=3,tol=1e-8,K=3,it.max=20000,
                          display=FALSE,
```

```
                               digits=0))) # number of decimal points of breakpoints

mod_fit_sg <- mod_sg %>% do(data.frame(Species=.$Species,
                Year=as.numeric(sort(unique(dat$Year))),
                fit_sg=predict(.$sg_lm,type="response"),
                se.fit_sg=predict(.$sg_lm,type="response",se.fit=T)$se.fit))

est_sg <- mod_sg %>% do(data.frame(Species=.$Species,
                var=if(class(.$sg_lm)[[1]]=="segmented"){
                  rownames(data.frame(slope(.$sg_lm)))}else{"slope1"},
                if(class(.$sg_lm)[[1]]=="segmented"){slope(.$sg_lm)}else{
                  data.frame(Year.Est.=summary(.$sg_lm)$coefficients[2,1],
                          Year.St.Err.=summary(.$sg_lm)$coefficients[2,2],
                          Year.t.value=summary(.$sg_lm)$coefficients[2,3])}))

est_sg %>% group_by(Species) %>%
  summarize(n_seg=n_distinct(var)) %>% arrange(desc(n_seg))
est_sg %>% group_by(Species) %>%
  summarize(n_seg=n_distinct(var)) %>% arrange(desc(n_seg)) %>%
  group_by(n_seg) %>% summarize(n_spec=n_distinct(Species))

coef_sg <- mod_sg %>%
  do(data.frame(Species=.$Species,co_names=names(coef(.$sg_lm)),
                coef(summary(.$sg_lm))))

psi_sg <- est_sg %>% ungroup() %>% group_by(Species,var) %>% group_keys()
psi_sg2 <- mod_sg %>% do(data.frame(
  # change startyear to 1980 to fit to occupancy models
  Start=c(1980,as.data.frame(summary(.$sg_lm)$psi)$Est.+1),
  # change endyear to 2019 to fit to occupancy models
  End=c(as.data.frame(summary(.$sg_lm)$psi)$Est.,2019)))
psi_sg <- bind_cols(psi_sg,psi_sg2); rm(psi_sg2)

colnames(coef_sg)[1:2] <- c("Species","var")
coef_sg <- coef_sg %>% filter(var %in% c("Year",paste0("U",1:3,".Year")))
coef_sg$var <- factor(coef_sg$var,labels=c(paste0("slope",2:4),"slope1"))

sum_dat <- psi_sg %>% left_join(est_sg) %>% left_join(coef_sg) %>%
  mutate(change=case_when(Year.Est.> 0 & Pr...t.. <=0.05 ~ "increase",
                          Year.Est. <0 & Pr...t.. <=0.05 ~ "decrease",
                          TRUE ~ "stable"),
         Start=round(Start,0),End=round(End,0))

# add confidence intervals to years of breakpoint
sum_dat_ci <- mod_sg %>% do(data.frame(Species=.$Species,
                                ci_sg=confint(.$sg_lm,level=0.95))) %>%
  rename(End=ci_sg.Est.,CI5=ci_sg.CI.95...low,CI95=ci_sg.CI.95...up) %>%
  dplyr::mutate(across(where(is.numeric),round,0)) %>%
  dplyr::select(Species,End,CI5,CI95) %>% full_join(.,sum_dat)

# Create classification from breakpoint analysis
class_dat <- sum_dat %>% group_by(Species) %>%
  dplyr::select(c(var,change,Species)) %>% spread(var,change) %>%
  unite("class",paste0("slope",1:4),sep="-",na.rm=T)

# Remove direct duplicates from vector
class_dat <- class_dat %>% rowwise() %>%
  mutate(class=paste(strsplit(class,split="-")[[1]]
```

```
                              [c(TRUE,!strsplit(class,split="-")
                                [[1]][-length(strsplit(class,split="-")[[1]])] ==
                                   strsplit(class,split="-")[[1]][-1])],collapse="-"))

# Combine classification with occupancy data
dat_sg <- dat_sg %>% left_join(class_dat)

# add classification,keep original values for all years
sum_dat2 <- psi_sg %>% group_by(Species,var) %>%
  dplyr::mutate(Start=round(Start,0),End=round(End,0)) %>%
  dplyr::summarize(Year=round(c(Start:End),0)) %>% full_join(sum_dat_ci)

# Combine with occupancy data
sum_dat2 <- sum_dat2 %>% full_join(.,dat_sg) %>% full_join(.,mod_fit_sg)

# Simplify breakpoint information (bp,CI5,CI95,change)
# restructure data so that the breakpoint year is connected to information
# on the direction of the change
bp <- sum_dat2 %>% group_by(Species) %>%
  dplyr::select(Species,var,Start,change,CI5,CI95) %>% unique() %>%
  pivot_wider(names_from=var,values_from=c(change,Start,CI5,CI95)) %>%
  unite(change1,change_slope1:change_slope2,remove=FALSE) %>%
  unite(change2,change_slope2:change_slope3,remove=FALSE) %>%
  unite(change3,change_slope3:change_slope4,remove=FALSE) %>%
  dplyr::select(Species,change1,change2,change3,Start_slope2,CI5_slope1,
                CI95_slope1,Start_slope3,CI5_slope2,CI95_slope2,Start_slope4,
                CI5_slope3,CI95_slope3) %>%
  dplyr::rename(breakpoint1=Start_slope2,CI5_1=CI5_slope1,
                CI95_1=CI95_slope1,breakpoint2=Start_slope3,
                CI5_2=CI5_slope2,CI95_2=CI95_slope2,
                breakpoint3=Start_slope4,CI5_3=CI5_slope3,
                CI95_3=CI95_slope3)

# remove no change information
bp$change1 <- str_replace(bp$change1,"_NA","")
bp$change2 <- str_replace(bp$change2,"_NA","")
bp$change2 <- str_replace(bp$change2,"NA",NA_character_)
bp$change3 <- str_replace(bp$change3,"_NA","")
bp$change3 <- str_replace(bp$change3,"NA",NA_character_)

# add 1980 as breakpoint1 if species shows linear trend without any breakpoint
bp %<>% mutate(breakpoint1=ifelse(is.na(breakpoint1),1980,breakpoint1))

# remove no change information
bp %<>% mutate(change2=ifelse(str_detect(change2,"_"),change2,NA),
               change3=ifelse(str_detect(change3,"_"),change3,NA))

# restructure
bp %<>% tidyr::pivot_longer(c(change1,change2,change3),# columns to change
                    names_to="changepoint",# name of variable created from data
                    values_to="change"     # stored in column names
  ) %>% dplyr::mutate(
    breakpoint=as.numeric(ifelse(changepoint =="change1",breakpoint1,
                          ifelse(changepoint =="change2",breakpoint2,
                                 ifelse(changepoint =="change3",breakpoint3,
                                        changepoint)))),
    CI5=as.numeric(ifelse(changepoint =="change1",CI5_1,
                          ifelse(changepoint =="change2",CI5_2,
```

```r
                                 ifelse(changepoint =="change3",CI5_3,
                                        NA)))),
    CI95=as.numeric(ifelse(changepoint =="change1",CI95_1,
                            ifelse(changepoint =="change2",CI95_2,
                                    ifelse(changepoint =="change3",CI95_3,
                                            NA))))) %>%
  dplyr::select(Species,breakpoint,CI5,CI95,change) %>%
  dplyr::mutate(CI5=ifelse(breakpoint ==1980,1980,CI5),
                CI95=ifelse(breakpoint ==1980,1980,CI95)) %>% na.omit()


# rename
bp %<>% dplyr::mutate(change=
          ifelse(change =="stable_stable","stable",
           ifelse(change =="increase_increase","increase",
            ifelse(change =="decrease_decrease","decrease",change))))

# remove breakpoints where the trend direction doesn't change
bp %<>% distinct(Species,change,.keep_all=TRUE)

bp %<>%
  dplyr::mutate(breakpoint=
                  ifelse(change =="stable" | change =="increase" |
                          change =="decrease",1980,breakpoint),
                CI5=ifelse(change =="stable" | change =="increase" |
                            change =="decrease",1980,CI5),
                CI95=ifelse(change =="stable" | change =="increase" |
                            change =="decrease",1980,CI95)) %>%
  unique() %>% group_by(Species) %>% mutate(n=length(Species)) %>%
  dplyr::mutate(breakpoint=ifelse(change =="stable" & n> 1 |
                                   change =="increase" & n> 1 |
                                   change =="decrease" & n> 1,NA,breakpoint)) %>%
  na.omit() %>% dplyr::select(-n)

# combine with background information on species
bp_full <- dat %>%
  dplyr::select(-c(Year,observed,occupancyMean,occupancySD,occupancyX2.5,
                    occupancyX97.5,occupancyRhat,Suborder)) %>%
  unique() %>% right_join(.,bp,multiple="all")


bpcol <- c("3"="#003f5c","2"="#7a5195","1"="#ef5675","0"="#ffa600")

#png("C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/nBP_all300spec.png",
#units="in",width=5,height=5,res=1200)
ptemp <- bp_full %>% dplyr::group_by(Species) %>%
  dplyr::mutate(id=n(),id=ifelse(breakpoint ==1980,0,id)) %>%
  dplyr::select(Species,id) %>% unique() %>% group_by(id) %>%
  summarize(nspec=n()) %>% dplyr::rename(nbp=id) %>% ungroup() %>%
  mutate(propspec=paste(round((nspec/sum(nspec))*100,1),'%')) %>%

  ggplot() + theme_bw() +
  geom_bar(aes(x=nbp,y=nspec,group=as.factor(nbp),fill=as.factor(nbp)),
            stat="identity") +
  geom_text(aes(x=nbp,y=nspec+3,label=propspec),size=6)+
  scale_x_continuous(name="Number of breakpoints")+
  scale_y_continuous(name="Number of species")+
  scale_fill_manual(name=paste("Number of","breakpoints",sep="\n"),values=bpcol)+
  theme(legend.title=element_text(size=16),legend.text=element_text(size=16),
```

```
        legend.position="right",
        strip.text.x=element_text(size=16),# adapt facet labels
        strip.background=element_blank(),
        panel.spacing.x=unit(0.7,"cm"),
        axis.text=element_text(size=16),axis.title.x=element_text(size=16),
        axis.title.y=element_text(size=16,angle=90),
        axis.line=element_line(),axis.ticks=element_line())+
  guides(fill="none")
#dev.off()
#ggview::ggview(device="png",units="in",width=5,height=5)

bp_full %>% group_by(order) %>% dplyr::summarize(n=n_distinct(Species))
## # A tibble: 3 x 2
##   order            n
##   <chr>        <int>
## 1 Lepidoptera    163
## 2 Odonata         71
## 3 Orthoptera      66
```
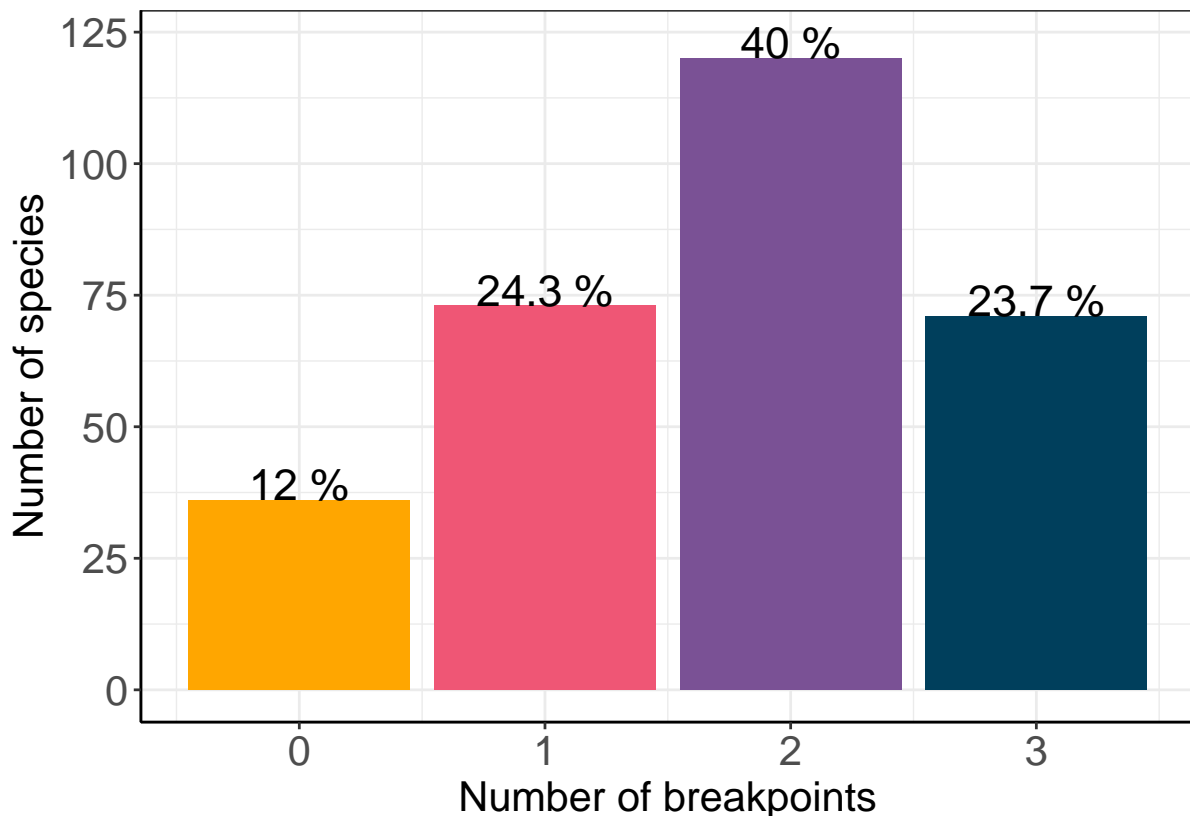

Figure 14.1 all 300 species Assessment of the number of breakpoints in the occupancy estimates over 40 years of all 300 insect species (butterflies – Lepidoptera,Rhopalocera; grasshoppers – Orthoptera; dragonflies – Odonata) using segmented generalized linear models. Percentage of all modelled species with the respective number of breakpoints.

```
#png(
# "C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/nBP_reliable_279spec.png",
# units="in",width=5,height=5,res=1200)
ptemp <- dat %>% dplyr::select(-c(observed,occupancyMean,
                      occupancyX2.5,occupancyX97.5,Suborder)) %>%
  group_by(order,family,Species) %>%
  dplyr::summarise(meanRhat=mean(occupancyRhat),meanSD=mean(occupancySD)) %>%
```

```
  ungroup() %>% unique() %>% right_join(.,bp_full,multiple="all") %>%
  filter(meanRhat <1.1 & meanSD <0.1) %>%  dplyr::group_by(Species) %>%
  dplyr::mutate(id=n(),id=ifelse(breakpoint ==1980,0,id)) %>%
  dplyr::select(Species,id) %>% unique() %>% group_by(id) %>%
  summarize(nspec=n()) %>%  dplyr::rename(nbp=id) %>% ungroup() %>%
  mutate(propspec=paste(round((nspec/sum(nspec))*100,1),'%')) %>%

  ggplot() + theme_bw() +
  geom_bar(aes(x=nbp,y=nspec,group=as.factor(nbp),fill=as.factor(nbp)),
           stat="identity") +
  geom_text(aes(x=nbp,y=nspec+3,label=propspec),size=6)+
  scale_x_continuous(name="Number of breakpoints")+
  scale_y_continuous(name="Number of species")+
  scale_fill_manual(name=paste("Number of","breakpoints",sep="\n"),values=bpcol)+
  theme(legend.title=element_text(size=16),legend.text=element_text(size=16),
        legend.position="right",
        strip.text.x=element_text(size=16),# adapt facet labels
        strip.background=element_blank(),
        panel.spacing.x=unit(0.7,"cm"),
        axis.text=element_text(size=16),axis.title.x=element_text(size=16),
        axis.title.y=element_text(size=16,angle=90),
        axis.line=element_line(),axis.ticks=element_line())+
  guides(fill="none")
#dev.off()
#ggview::ggview(device="png",units="in",width=5,height=5)

dat %>% dplyr::select(-c(observed,occupancyMean,
                        occupancyX2.5,occupancyX97.5,Suborder)) %>%
  group_by(order,family,Species) %>%
  dplyr::summarise(meanRhat=mean(occupancyRhat),meanSD=mean(occupancySD)) %>%
  ungroup() %>% unique() %>% right_join(.,bp_full,multiple="all") %>%
  filter(meanRhat <1.1 & meanSD <0.1) %>%  dplyr::group_by(order) %>%
  dplyr::summarize(n=n_distinct(Species))
## # A tibble: 3 x 2
##   order           n
##   <chr>        <int>
## 1 Lepidoptera    152
## 2 Odonata         67
## 3 Orthoptera      60
```
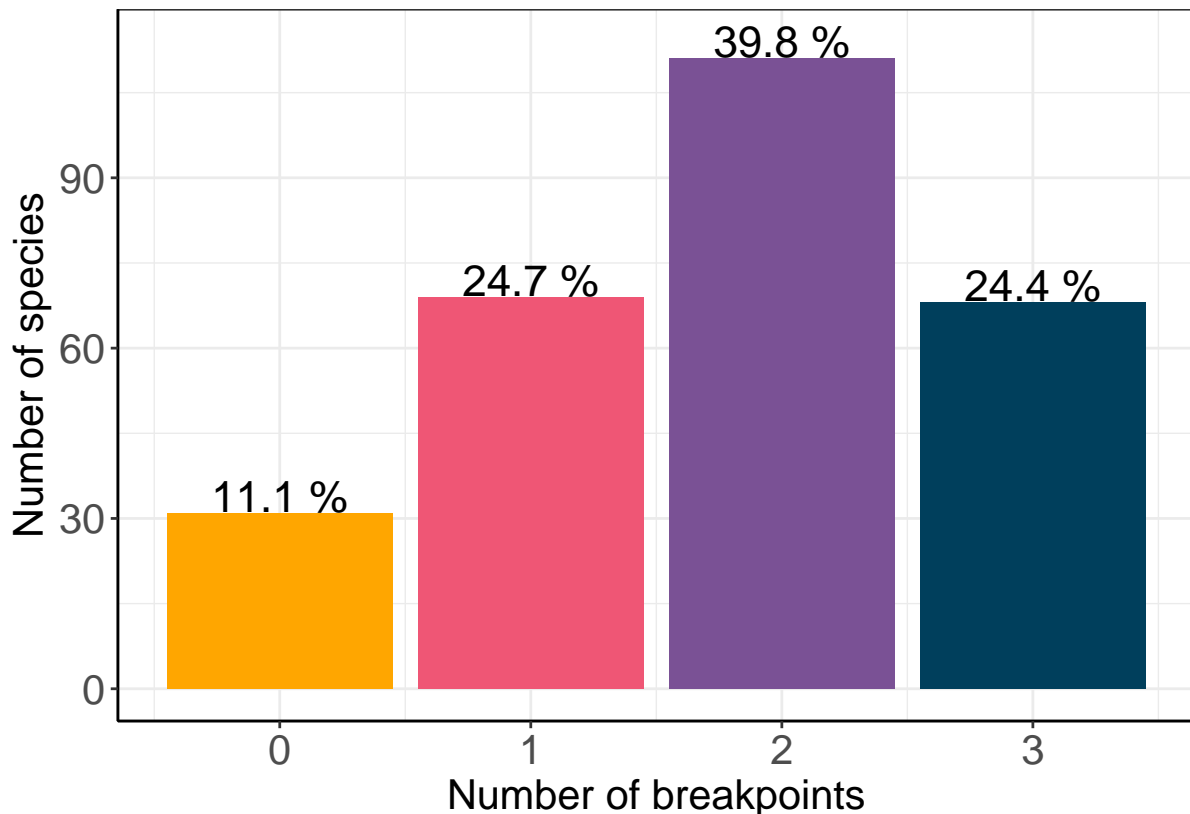
Figure 14.2 279 species (reliable models) Assessment of the number of breakpoints in the occupancy estimates over 40 years of 279 insect species with reliable model results (butterflies – Lepidoptera,Rhopalocera; grasshoppers – Orthoptera; dragonflies – Odonata) using segmented generalized linear models. Percentage of all modelled species with the respective number of breakpoints.

Focus on reliable species

```
temp <- dat %>% dplyr::select(-c(observed,occupancyX2.5,occupancyX97.5,Suborder)) %>%
  group_by(order,family,Species) %>%
  dplyr::summarise(meanRhat=mean(occupancyRhat),meanSD=mean(occupancySD),
                   maxOcc=max(occupancyMean)) %>% ungroup() %>%
  unique() %>% right_join(.,bp_full,multiple="all") %>%
  filter(meanRhat <1.1 & meanSD <0.1 & maxOcc>=0.025) %>%
  filter(!str_detect(Species," AGG. ")) #also filter aggregated species

#png(
#"C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/nBP_reliableMinOcc_238spec.png",
#units="in",width=5,height=5,res=1200)
ptemp <- temp %>%  dplyr::group_by(Species) %>%
  dplyr::mutate(id=n(),id=ifelse(breakpoint ==1980,0,id)) %>%
  dplyr::select(Species,id) %>% unique() %>% group_by(id) %>%
  summarize(nspec=n()) %>% dplyr::rename(nbp=id) %>% ungroup() %>%
  mutate(propspec=paste(round((nspec/sum(nspec))*100,1),'%')) %>%

  ggplot() + theme_bw() +
  geom_bar(aes(x=nbp,y=nspec,group=as.factor(nbp),fill=as.factor(nbp)),
           stat="identity") +
  geom_text(aes(x=nbp,y=nspec+3,label=propspec),size=6)+
  scale_x_continuous(name="Number of breakpoints")+
  scale_y_continuous(name="Number of species")+
  scale_fill_manual(name=paste("Number of","breakpoints",sep="\n"),values=bpcol)+
  theme(legend.title=element_text(size=16),legend.text=element_text(size=16),
```

```
        legend.position="right",
        strip.text.x=element_text(size=16),# adapt facet labels
        strip.background=element_blank(),panel.spacing.x=unit(0.7,"cm"),
        axis.text=element_text(size=16),axis.title.x=element_text(size=16),
        axis.title.y=element_text(size=16,angle=90),
        axis.line=element_line(),axis.ticks=element_line())+
  guides(fill="none")
#dev.off()
#ggview::ggview(device="png",units="in",width=5,height=5)

temp %>% group_by(order) %>% dplyr::summarise(n=n_distinct(Species))
## # A tibble: 3 x 2
##   order         n
##   <chr>       <int>
## 1 Lepidoptera   125
## 2 Odonata        63
## 3 Orthoptera     50
```
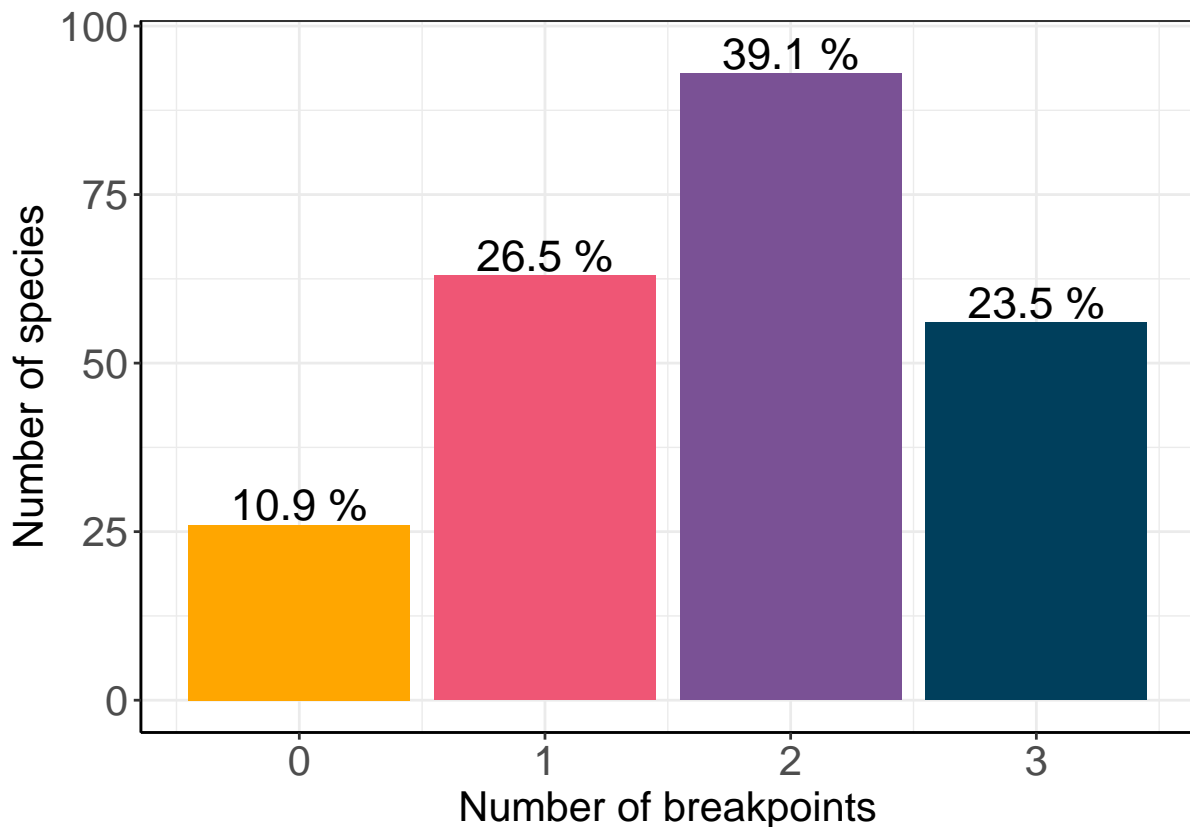

Figure 14.3 238 species (reliable models+minimum occupancy) Assessment of the number of breakpoints in the occupancy estimates over 40 years of 238 insect species with reliable model results and a minimum occupancy of 0.025 (butterflies – Lepidoptera,Rhopalocera; grasshoppers – Orthoptera; dragonflies – Odonata) using segmented generalized linear models. Percentage of all modelled species with the respective number of breakpoints.

This includes one butterfly and one grasshopper species more than were included in the attribute analysis in chapter 1,as for two species we were lacking the required attribute data (compare Supplementary Material of Engelhardt et al. 2022).

Lists of species with the respective number of breakpoints

Table 8: Species with linear trends without breakpoints from 1980
to 2019

Species	change
Aglais urticae	stable
Argynnis aglaja	stable
Colias myrmidone	decrease
Colias phicomone	stable
Cupido minimus	stable
Erebia aethiops	stable
Lycaena hippothoe	stable
Lycaena virgaureae	decrease
Maniola jurtina	increase
Melitaea diamina	stable
Phengaris alcon alcon	stable
Pieris brassicae	stable
Pieris mannii	stable
Polyommatus coridon	stable
Polyommatus damon	decrease
Polyommatus eros	stable
Polyommatus orbitulus	stable
Pontia edusa	increase
Pyrgus armoricanus	stable
Pyrgus serratulae	decrease
Vanessa atalanta	stable
Vanessa cardui	stable
Calliptamus italicus	stable
Leptophyes punctatissima	stable
Metrioptera brachyptera	stable
Aeshna caerulea	stable
Aeshna isoceles	stable
Crocothemis erythraea	stable
Erythromma viridulum	stable
Gomphus flavipes	stable
Ischnura pumilio	stable
Lestes barbarus	stable
Orthetrum albistylum	stable
Sympecma fusca	increase
Sympetrum danae	decrease
Sympetrum sanguineum	stable

ineum & stable* \end{longtable}

Table 9: Species with one breakpoint between 1980 and 2019

Species	breakpoint	CI5	CI95	change
Aglais io	1987	1984	1988	increase_decrease
Araschnia levana	2010	2003	2015	stable_decrease
Boloria aquilonaris	2010	2006	2012	stable_decrease
Boloria pales	2002	2000	2002	stable_decrease
Brenthis ino	2010	2008	2010	increase_decrease
Carcharodus flocciferus	2008	2006	2008	stable_decrease
Coenonympha pamphilus	2015	2012	2016	stable_decrease
Cupido argiades	2017	2015	2017	stable_decrease
Erebia euryale	2006	2002	2008	increase_decrease

(continued ...)

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Table 9: Species with one breakpoint between 1980 and 2019 *(continued)*

Species	breakpoint	CI5	CI95	change
Erebia ligea	1999	1992	2004	decrease_stable
Erebia meolans	2004	2003	2003	increase_decrease
Erebia pandrose	2008	2005	2009	stable_decrease
Erebia pronoe	1985	1979	1989	decrease_stable
Gonepteryx rhamni	1988	1985	1989	increase_decrease
Hesperia comma	2012	2007	2015	stable_decrease
Hipparchia semele	1986	1981	1989	decrease_stable
Issoria lathonia	1988	1982	1992	decrease_stable
Lasiommata petropolitana	2007	2005	2007	stable_decrease
Lycaena dispar	2017	2015	2017	stable_increase
Lycaena tityrus	1993	1988	1996	increase_decrease
Melanargia galathea	2003	1996	2008	increase_stable
Melitaea athalia	1987	1978	1994	decrease_stable
Melitaea aurelia	1995	1992	1996	increase_decrease
Melitaea cinxia	2012	2007	2015	stable_decrease
Melitaea didyma	1996	1994	1996	increase_decrease
Nymphalis antiopa	1986	1982	1988	stable_decrease
Ochlodes sylvanus	2005	2000	2008	increase_stable
Phengaris alcon rebeli	2011	2009	2011	stable_decrease
Pieris napi	1987	1983	1989	stable_decrease
Plebejus argus	2014	2006	2020	decrease_stable
Polygonia c-album	2008	2001	2013	increase_decrease
Polyommatus dorylas	2018	1947	2087	decrease_stable
Polyommatus thersites	2008	2005	2009	stable_decrease
Pyrgus cirsii	1991	1988	1992	decrease_increase
Pyrgus malvae	2008	2003	2011	stable_decrease
Satyrium ilicis	2007	2003	2009	decrease_increase
Thecla betulae	2007	2004	2008	increase_decrease
Thymelicus acteon	1998	1993	2001	increase_decrease
Thymelicus sylvestris	1997	1995	1997	increase_decrease
Barbitistes serricauda	2000	1998	2000	increase_decrease
Chorthippus albomarginatus	1990	1981	1997	increase_stable
Chorthippus biguttulus	1998	1996	1998	stable_decrease
Chorthippus mollis	1999	1995	2001	decrease_stable
Gomphocerippus rufus	2012	2001	2021	decrease_stable
Leptophyes albovittata	1994	1989	1997	decrease_increase
Meconema meridionale	1992	1986	1996	stable_increase
Miramella alpina	1997	1991	2001	stable_decrease
Oecanthus pellucens	1994	1988	1998	stable_increase
Omocestus rufipes	1997	1995	1997	decrease_increase
Platycleis albopunctata	2018	2003	2031	increase_stable
Podisma pedestris	1991	1988	1992	increase_stable
Polysarcus denticauda	2010	2008	2010	stable_decrease
Sphingonotus caerulans	2013	2009	2015	stable_decrease
Tetrix subulata	2002	1999	2003	increase_stable
Tetrix tenuicornis	2010	1994	2024	decrease_stable
Tettigonia viridissima	2008	2003	2011	decrease_increase
Aeshna affinis	2015	2012	2016	stable_increase
Aeshna subarctica	2012	2009	2013	stable_decrease
Anax parthenope	1994	1992	1994	stable_increase
Brachytron pratense	1994	1992	1994	decrease_increase
Calopteryx splendens	2011	2006	2014	increase_decrease
Calopteryx virgo	2006	2004	2006	increase_decrease

(continued ...)

Table 9: Species with one breakpoint between 1980 and 2019 *(continued)*

Species	breakpoint	CI5	CI95	change
Erythromma najas	2014	2005	2021	increase_stable
Leucorrhinia albifrons	2007	2004	2008	stable_decrease
Leucorrhinia caudalis	2009	2005	2011	stable_increase
Leucorrhinia dubia	1987	1983	1989	stable_decrease
Nehalennia speciosa	2007	2003	2009	increase_decrease
Onychogomphus forcipatus	1988	1984	1990	stable_increase
Orthetrum cancellatum	2004	2000	2006	increase_decrease
Orthetrum coerulescens	2013	2010	2014	stable_increase
Platycnemis pennipes	2006	2002	2008	stable_decrease
Pyrrhosoma nymphula	2005	2002	2006	increase_decrease
Sympetrum fonscolombii	2007	2004	2008	stable_decrease

olombii & 2007 & 2004 & 2008 & stable_decrease* \end{longtable}

Table 10: Species with two breakpoints between 1980 and 2019

Species	breakpoint	CI5	CI95	change
Agriades optilete	1991	1988	1992	increase_decrease
Agriades optilete	2001	1998	2002	decrease_increase
Anthocharis cardamines	2004	2001	2005	stable_decrease
Anthocharis cardamines	2018	2000	2034	decrease_stable
Apatura ilia	2004	2001	2005	stable_increase
Apatura ilia	2008	2006	2008	increase_decrease
Apatura iris	2003	1998	2006	decrease_stable
Apatura iris	2007	2004	2008	stable_decrease
Aporia crataegi	1990	1988	1990	decrease_increase
Aporia crataegi	2014	2011	2015	increase_decrease
Argynnis adippe	1987	1984	1988	decrease_increase
Argynnis adippe	2009	2006	2010	increase_decrease
Argynnis niobe	2000	1997	2001	decrease_increase
Argynnis niobe	2004	2001	2005	increase_decrease
Boloria dia	1989	1987	1989	decrease_increase
Boloria dia	2010	2006	2012	increase_decrease
Boloria eunomia	1994	1990	1996	increase_decrease
Boloria eunomia	1998	1991	2003	decrease_stable
Boloria euphrosyne	1990	1987	1991	decrease_increase
Boloria euphrosyne	1997	1994	1998	increase_decrease
Boloria thore	2005	2003	2005	increase_decrease
Boloria thore	2013	2011	2013	decrease_increase
Boloria titania	2000	1997	2001	decrease_increase
Boloria titania	2005	2003	2005	increase_decrease
Callophrys rubi	1994	1992	1994	increase_decrease
Callophrys rubi	2002	1998	2004	decrease_increase
Carcharodus alceae	2004	2002	2004	stable_increase
Carcharodus alceae	2017	2014	2018	increase_decrease
Chazara briseis	1995	1992	1996	stable_decrease
Chazara briseis	1998	1994	2000	decrease_stable
Coenonympha arcania	1988	1986	1988	increase_decrease
Coenonympha arcania	2002	1996	2006	decrease_increase
Coenonympha gardetta	1994	1987	1999	stable_increase
Coenonympha gardetta	2006	2001	2009	increase_decrease

(continued ...)

Species	breakpoint	CI5	CI95	change
Coenonympha glycerion	1991	1988	1992	increase_decrease
Coenonympha glycerion	2018	2007	2027	decrease_stable
Coenonympha hero	1991	1987	1993	increase_decrease
Coenonympha hero	2015	2007	2021	decrease_stable
Coenonympha tullia	1992	1990	1992	increase_decrease
Coenonympha tullia	2000	1998	2000	decrease_increase
Colias agg. Hyale alfacariensis	1991	1985	1995	stable_decrease
Colias agg. Hyale alfacariensis	2004	1991	2015	decrease_stable
Colias croceus	1988	1984	1990	decrease_increase
Colias croceus	1995	1990	1998	increase_stable
Erebia epiphron	1993	1980	2004	decrease_stable
Erebia epiphron	2006	2003	2007	stable_decrease
Erebia eriphyle	1995	1989	1999	decrease_stable
Erebia eriphyle	2009	2006	2010	stable_decrease
Erebia manto	1990	1983	1995	increase_decrease
Erebia manto	2008	2004	2010	decrease_stable
Erebia pharte	1991	1988	1992	stable_increase
Erebia pharte	2008	2004	2010	increase_decrease
Erebia pluto	2010	2007	2011	stable_decrease
Erebia pluto	2017	2009	2023	decrease_stable
Erebia styx	1998	1996	1998	stable_increase
Erebia styx	2005	2003	2005	increase_decrease
Erebia tyndarus	1991	1985	1995	stable_increase
Erebia tyndarus	2006	1987	2023	increase_stable
Erynnis tages	1990	1987	1991	stable_decrease
Erynnis tages	2017	2013	2019	decrease_stable
Euphydryas aurinia	1993	1989	1995	increase_decrease
Euphydryas aurinia	2002	1999	2003	decrease_increase
Favonius quercus	1999	1995	2001	stable_increase
Favonius quercus	2005	2003	2005	increase_decrease
Glaucopsyche alexis	1990	1988	1990	decrease_increase
Glaucopsyche alexis	2002	1998	2004	increase_decrease
Hipparchia alcyone	2006	1998	2012	decrease_increase
Hipparchia alcyone	2018	1858	2176	increase_stable
Lasiommata maera	1991	1988	1992	decrease_stable
Lasiommata maera	1998	1994	2000	stable_decrease
Lasiommata megera	1997	1993	1999	stable_increase
Lasiommata megera	2018	2012	2022	increase_stable
Leptidea agg. Sinapis juvernica	1995	1993	1995	increase_decrease
Leptidea agg. Sinapis juvernica	2007	2005	2007	decrease_increase
Minois dryas	1987	1984	1988	increase_decrease
Minois dryas	2012	2007	2015	decrease_stable
Nymphalis polychloros	2001	1996	2004	stable_increase
Nymphalis polychloros	2008	2005	2009	increase_decrease
Oeneis glacialis	1990	1980	1998	decrease_stable
Oeneis glacialis	2008	2004	2010	stable_decrease
Papilio machaon	1996	1993	1997	increase_stable
Papilio machaon	2008	2004	2010	stable_decrease
Pararge aegeria	2002	1999	2003	stable_decrease
Pararge aegeria	2013	2007	2017	decrease_stable
Parnassius mnemosyne	2001	1999	2001	stable_increase
Parnassius mnemosyne	2009	2007	2009	increase_decrease
Phengaris nausithous	1996	1992	1998	increase_decrease

Species	breakpoint	CI5	CI95	change
Phengaris nausithous	2000	1990	2008	decrease_stable
Phengaris teleius	1997	1991	2001	increase_stable
Phengaris teleius	2006	2003	2007	stable_increase
Plebejus argyrognomon	2005	2003	2005	stable_decrease
Plebejus argyrognomon	2009	2007	2009	decrease_increase
Plebejus idas	1991	1981	1999	decrease_stable
Plebejus idas	1999	1995	2001	stable_increase
Polyommatus amandus	1990	1988	1990	decrease_increase
Polyommatus amandus	1993	1992	1992	increase_decrease
Polyommatus daphnis	1996	1991	1999	decrease_stable
Polyommatus daphnis	2001	1998	2002	stable_decrease
Polyommatus semiargus	1987	1985	1987	decrease_increase
Polyommatus semiargus	2013	2010	2014	increase_stable
Pontia callidice	2005	2003	2005	stable_increase
Pontia callidice	2009	2007	2009	increase_decrease
Pyrgus andromedae	1988	1985	1989	decrease_increase
Pyrgus andromedae	2005	2003	2005	increase_decrease
Pyrgus cacaliae	1994	1991	1995	decrease_increase
Pyrgus cacaliae	2008	2005	2009	increase_decrease
Pyrgus carthami	1987	1983	1989	stable_increase
Pyrgus carthami	2007	2003	2009	increase_decrease
Pyrgus malvoides	2001	1998	2002	stable_increase
Pyrgus malvoides	2005	2003	2005	increase_decrease
Pyrgus warrenensis	1991	1988	1992	decrease_increase
Pyrgus warrenensis	2007	2005	2007	increase_decrease
Satyrium pruni	1988	1985	1989	decrease_stable
Satyrium pruni	1991	1989	1991	stable_increase
Satyrium w-album	2000	1995	2003	stable_increase
Satyrium w-album	2008	2005	2009	increase_decrease
Scolitantides baton	1991	1989	1991	decrease_increase
Scolitantides baton	1996	1991	1999	increase_stable
Scolitantides orion	1990	1987	1991	decrease_increase
Scolitantides orion	2011	1982	2038	increase_stable
Spialia sertorius	1990	1988	1990	decrease_increase
Spialia sertorius	2006	2003	2007	increase_decrease
Thymelicus lineola	1993	1991	1993	increase_decrease
Thymelicus lineola	2000	1996	2002	decrease_increase
Acheta domesticus	1994	1991	1995	increase_decrease
Acheta domesticus	2005	2003	2005	decrease_increase
Arcyptera fusca	1984	1981	1985	decrease_stable
Arcyptera fusca	1992	1990	1992	stable_decrease
Bicolorana bicolor	1986	1983	1987	increase_decrease
Bicolorana bicolor	2003	2000	2004	decrease_increase
Chorthippus apricarius	1988	1985	1989	decrease_increase
Chorthippus apricarius	1997	1995	1997	increase_decrease
Chorthippus dorsatus	2002	1998	2004	stable_increase
Chorthippus dorsatus	2017	2013	2019	increase_stable
Chorthippus pullus	1996	1992	1998	decrease_increase
Chorthippus pullus	2002	1999	2003	increase_decrease
Chrysochraon dispar	2001	1998	2002	decrease_increase
Chrysochraon dispar	2012	2010	2012	increase_decrease
Conocephalus dorsalis	1990	1987	1991	stable_decrease
Conocephalus dorsalis	2000	1998	2000	decrease_increase

Table 10: Species with two breakpoints between 1980 and 2019 *(continued)*

Species	breakpoint	CI5	CI95	change
Conocephalus fuscus	1990	1987	1991	increase_decrease
Conocephalus fuscus	2002	1999	2003	decrease_stable
Euthystira brachyptera	2004	1999	2007	stable_increase
Euthystira brachyptera	2014	2011	2015	increase_decrease
Gomphocerus sibiricus	2006	2003	2007	increase_decrease
Gomphocerus sibiricus	2014	2010	2016	decrease_increase
Gryllotalpa gryllotalpa	1991	1985	1995	decrease_stable
Gryllotalpa gryllotalpa	2010	2008	2010	stable_decrease
Gryllus campestris	1987	1983	1989	stable_increase
Gryllus campestris	1993	1988	1996	increase_stable
Isophya kraussii	1993	1990	1994	decrease_increase
Isophya kraussii	2001	1999	2001	increase_decrease
Meconema thalassinum	1996	1994	1996	decrease_increase
Meconema thalassinum	1999	1998	1998	increase_decrease
Mecostethus parapleurus	2001	1998	2002	stable_increase
Mecostethus parapleurus	2010	2007	2011	increase_decrease
Nemobius sylvestris	1995	1992	1996	decrease_increase
Nemobius sylvestris	1999	1997	1999	increase_decrease
Oedipoda caerulescens	1998	1996	1998	stable_increase
Oedipoda caerulescens	2008	2001	2013	increase_stable
Oedipoda germanica	1995	1990	1998	decrease_stable
Oedipoda germanica	1999	1996	2000	stable_increase
Phaneroptera falcata	2005	2002	2006	stable_increase
Phaneroptera falcata	2015	2008	2020	increase_stable
Pseudochorthippus montanus	1991	1989	1991	increase_decrease
Pseudochorthippus montanus	2008	2004	2010	decrease_increase
Pseudochorthippus parallelus	1994	1989	1997	increase_decrease
Pseudochorthippus parallelus	2003	1997	2007	decrease_stable
Psophus stridulus	1997	1995	1997	decrease_increase
Psophus stridulus	2002	1999	2003	increase_decrease
Roeseliana roeselii	1996	1989	2001	increase_stable
Roeseliana roeselii	2009	2004	2012	stable_decrease
Ruspolia nitidula	1989	1984	1992	stable_increase
Ruspolia nitidula	2001	1997	2003	increase_stable
Stenobothrus lineatus	1991	1975	2005	decrease_stable
Stenobothrus lineatus	2010	2005	2013	stable_decrease
Stenobothrus nigromaculatus	2003	1998	2006	increase_decrease
Stenobothrus nigromaculatus	2012	1979	2043	decrease_stable
Stenobothrus stigmaticus	2001	1999	2001	stable_increase
Stenobothrus stigmaticus	2014	2012	2014	increase_decrease
Stethophyma grossum	1993	1990	1994	increase_decrease
Stethophyma grossum	2001	1997	2003	decrease_increase
Tetrix bipunctata	1994	1991	1995	decrease_stable
Tetrix bipunctata	2004	2000	2006	stable_increase
Tetrix ceperoi	1991	1988	1992	decrease_increase
Tetrix ceperoi	2005	2002	2006	increase_decrease
Tettigonia cantans	1989	1985	1991	stable_increase
Tettigonia cantans	2003	1999	2005	increase_decrease
Aeshna cyanea	1994	1991	1995	increase_decrease
Aeshna cyanea	2012	2009	2013	decrease_stable
Aeshna grandis	1989	1986	1990	increase_decrease
Aeshna grandis	2004	2001	2005	decrease_increase
Aeshna mixta	1998	1992	2002	stable_decrease

(continued . . .)

Table 10: Species with two breakpoints between 1980 and 2019 *(continued)*

Species	breakpoint	CI5	CI95	change
Aeshna mixta	2017	2012	2020	decrease_stable
Anax ephippiger	1992	1989	1993	stable_increase
Anax ephippiger	1996	1994	1996	increase_decrease
Anax imperator	1995	1992	1996	increase_stable
Anax imperator	2008	2004	2010	stable_decrease
Chalcolestes viridis	1989	1986	1990	decrease_increase
Chalcolestes viridis	2007	2004	2008	increase_decrease
Coenagrion mercuriale	1994	1991	1995	increase_decrease
Coenagrion mercuriale	2018	2015	2019	decrease_stable
Coenagrion puella	1994	1989	1997	stable_decrease
Coenagrion puella	2004	1986	2020	decrease_stable
Cordulegaster bidentata	1993	1989	1995	increase_decrease
Cordulegaster bidentata	2003	1999	2005	decrease_stable
Cordulegaster boltonii	1993	1990	1994	increase_decrease
Cordulegaster boltonii	2000	1997	2001	decrease_increase
Enallagma cyathigerum	1995	1988	2000	stable_decrease
Enallagma cyathigerum	2013	1999	2025	decrease_stable
Gomphus pulchellus	2001	1999	2001	stable_increase
Gomphus pulchellus	2010	2008	2010	increase_decrease
Ischnura elegans	1987	1984	1988	stable_increase
Ischnura elegans	2007	1994	2018	increase_stable
Lestes sponsa	1999	1997	1999	decrease_increase
Lestes sponsa	2013	2011	2013	increase_decrease
Libellula fulva	1988	1984	1990	stable_increase
Libellula fulva	2014	2012	2014	increase_decrease
Libellula quadrimaculata	1988	1985	1989	increase_decrease
Libellula quadrimaculata	2003	1996	2008	decrease_increase
Ophiogomphus cecilia	2001	1996	2004	stable_increase
Ophiogomphus cecilia	2013	2011	2013	increase_decrease
Orthetrum brunneum	1995	1990	1998	increase_stable
Orthetrum brunneum	2001	1998	2002	stable_increase
Somatochlora alpestris	1992	1989	1993	increase_decrease
Somatochlora alpestris	1999	1997	1999	decrease_increase
Somatochlora arctica	1987	1984	1988	increase_decrease
Somatochlora arctica	1995	1992	1996	decrease_increase
Somatochlora metallica	2003	2001	2003	increase_decrease
Somatochlora metallica	2017	2012	2020	decrease_stable
Sympecma paedisca	2001	1999	2001	decrease_increase
Sympecma paedisca	2013	2010	2014	increase_decrease
Sympetrum flaveolum	1994	1992	1994	stable_increase
Sympetrum flaveolum	1996	1994	1996	increase_decrease
Sympetrum meridionale	1990	1984	1994	stable_increase
Sympetrum meridionale	2002	1997	2005	increase_stable
Sympetrum pedemontanum	2000	1997	2001	decrease_increase
Sympetrum pedemontanum	2012	2009	2013	increase_decrease
Sympetrum vulgatum	2003	2001	2003	stable_decrease
Sympetrum vulgatum	2010	2007	2011	decrease_increase

tum & 2010 & 2007 & 2011 & decrease_increase* \end{longtable}

Table 11: Species with three breakpoints between 1980 and 2019

Species	breakpoint	CI5	CI95	change
Aphantopus hyperantus	1991	1988	1992	increase_decrease
Aphantopus hyperantus	1996	1991	1999	decrease_stable
Aphantopus hyperantus	2011	2006	2014	stable_decrease
Argynnis paphia	1996	1993	1997	stable_decrease
Argynnis paphia	2000	1998	2000	decrease_increase
Argynnis paphia	2004	2002	2004	increase_decrease
Boloria napaea	1991	1984	1996	decrease_stable
Boloria napaea	2002	1999	2003	stable_increase
Boloria napaea	2008	2006	2008	increase_decrease
Boloria selene	1988	1981	1993	decrease_stable
Boloria selene	2003	2000	2004	stable_increase
Boloria selene	2010	2008	2010	increase_decrease
Brintesia circe	1990	1982	1996	decrease_stable
Brintesia circe	1996	1993	1997	stable_increase
Brintesia circe	2008	2006	2008	increase_decrease
Carterocephalus palaemon	1993	1978	2006	increase_stable
Carterocephalus palaemon	2003	2000	2004	stable_decrease
Carterocephalus palaemon	2010	2007	2011	decrease_increase
Celastrina argiolus	1989	1983	1993	stable_increase
Celastrina argiolus	2005	2000	2008	increase_decrease
Celastrina argiolus	2018	2010	2024	decrease_stable
Coenonympha oedippus	1993	1989	1995	stable_increase
Coenonympha oedippus	1999	1996	2000	increase_decrease
Coenonympha oedippus	2012	2005	2017	decrease_stable
Colias palaeno	1993	1990	1994	increase_decrease
Colias palaeno	2000	1996	2002	decrease_increase
Colias palaeno	2007	2001	2011	increase_stable
Erebia gorge	1991	1988	1992	stable_increase
Erebia gorge	2002	2000	2002	increase_decrease
Erebia gorge	2017	2011	2021	decrease_stable
Erebia medusa	1994	1991	1995	stable_decrease
Erebia medusa	2007	2003	2009	decrease_increase
Erebia medusa	2014	2011	2015	increase_decrease
Erebia melampus	1991	1986	1994	stable_increase
Erebia melampus	2004	2001	2005	increase_stable
Erebia melampus	2006	2004	2006	stable_decrease
Erebia oeme	1993	1990	1994	decrease_increase
Erebia oeme	1996	1993	1997	increase_stable
Erebia oeme	2005	2002	2006	stable_decrease
Euphydryas cynthia	1990	1987	1991	decrease_increase
Euphydryas cynthia	2005	2001	2007	increase_decrease
Euphydryas cynthia	2009	1963	2053	decrease_stable
Euphydryas maturna	1986	1983	1987	stable_decrease
Euphydryas maturna	1999	1996	2000	decrease_increase
Euphydryas maturna	2015	2012	2016	increase_decrease
Hamearis lucina	1985	1979	1989	decrease_stable
Hamearis lucina	2002	1999	2003	stable_increase
Hamearis lucina	2009	2005	2011	increase_decrease
Iphiclides podalirius	1989	1983	1993	decrease_stable
Iphiclides podalirius	1999	1995	2001	stable_decrease
Iphiclides podalirius	2008	2004	2010	decrease_increase
Limenitis camilla	1990	1983	1995	stable_increase
Limenitis camilla	2003	1998	2006	increase_stable

Table 11: Species with three breakpoints between 1980 and 2019
(continued)

Species	breakpoint	CI5	CI95	change
Limenitis camilla	2007	2004	2008	stable_decrease
Limenitis populi	1990	1988	1990	increase_decrease
Limenitis populi	2002	1999	2003	decrease_increase
Limenitis populi	2004	2002	2004	increase_stable
Lopinga achine	1991	1988	1992	stable_decrease
Lopinga achine	2001	1998	2002	decrease_increase
Lopinga achine	2004	1997	2009	increase_stable
Lycaena alciphron	1994	1991	1995	increase_decrease
Lycaena alciphron	2002	1999	2003	decrease_increase
Lycaena alciphron	2018	2003	2031	increase_stable
Lycaena helle	1992	1988	1994	stable_increase
Lycaena helle	1998	1983	2011	increase_stable
Lycaena helle	2013	2010	2014	stable_decrease
Lycaena phlaeas	1994	1990	1996	increase_stable
Lycaena phlaeas	1998	1995	1999	stable_increase
Lycaena phlaeas	2005	2001	2007	increase_decrease
Melitaea britomartis	1986	1983	1987	decrease_increase
Melitaea britomartis	2007	2005	2007	increase_decrease
Melitaea britomartis	2015	2010	2018	decrease_stable
Melitaea parthenoides	1992	1989	1993	increase_decrease
Melitaea parthenoides	2001	1998	2002	decrease_increase
Melitaea parthenoides	2007	2002	2010	increase_stable
Melitaea phoebe	1987	1985	1987	decrease_increase
Melitaea phoebe	1995	1993	1995	increase_decrease
Melitaea phoebe	1998	1995	1999	decrease_stable
Parnassius apollo	1990	1988	1990	increase_decrease
Parnassius apollo	1997	1994	1998	decrease_increase
Parnassius apollo	2013	2006	2018	increase_stable
Phengaris arion	1987	1984	1988	stable_increase
Phengaris arion	1997	1995	1997	increase_decrease
Phengaris arion	2010	2008	2010	decrease_increase
Pieris bryoniae	1990	1985	1993	decrease_increase
Pieris bryoniae	1996	1983	2007	increase_stable
Pieris bryoniae	2002	1998	2004	stable_decrease
Pieris rapae	1990	1986	1992	increase_decrease
Pieris rapae	1994	1990	1996	decrease_stable
Pieris rapae	2006	2002	2008	stable_decrease
Polyommatus agg. Agestis artaxerxes	1987	1984	1988	decrease_increase
Polyommatus agg. Agestis artaxerxes	2004	2001	2005	increase_decrease
Polyommatus agg. Agestis artaxerxes	2018	1981	2053	decrease_stable
Polyommatus bellargus	1995	1991	1997	stable_decrease
Polyommatus bellargus	1999	1996	2000	decrease_increase
Polyommatus bellargus	2008	2005	2009	increase_decrease
Polyommatus eumedon	1986	1982	1988	stable_increase
Polyommatus eumedon	1998	1995	1999	increase_decrease
Polyommatus eumedon	2011	2006	2014	decrease_increase
Polyommatus glandon	1993	1990	1994	stable_increase
Polyommatus glandon	2004	2002	2004	increase_decrease
Polyommatus glandon	2006	2004	2006	decrease_increase
Polyommatus icarus	1991	1987	1993	increase_decrease
Polyommatus icarus	1997	1991	2001	decrease_stable
Polyommatus icarus	2011	2008	2012	stable_decrease
Pyrgus alveus	1993	1990	1994	stable_decrease

(continued . . .)

Table 11: Species with three breakpoints between 1980 and 2019
(continued)

Species	breakpoint	CI5	CI95	change
Pyrgus alveus	1999	1996	2000	decrease_increase
Pyrgus alveus	2009	2005	2011	increase_decrease
Pyrgus trebevicensis	1987	1985	1987	decrease_increase
Pyrgus trebevicensis	2005	2002	2006	increase_decrease
Pyrgus trebevicensis	2013	2008	2016	decrease_stable
Pyronia tithonus	1996	1993	1997	stable_increase
Pyronia tithonus	2002	2000	2002	increase_decrease
Pyronia tithonus	2004	2002	2004	decrease_increase
Satyrium acaciae	1990	1984	1994	stable_increase
Satyrium acaciae	2006	2003	2007	increase_decrease
Satyrium acaciae	2013	2010	2014	decrease_increase
Satyrium spini	1989	1986	1990	decrease_increase
Satyrium spini	2010	2007	2011	increase_decrease
Satyrium spini	2014	2010	2016	decrease_stable
Barbitistes constrictus	1992	1988	1994	stable_increase
Barbitistes constrictus	1999	1997	1999	increase_decrease
Barbitistes constrictus	2011	2008	2012	decrease_increase
Bryodemella tuberculata	1991	1986	1994	stable_increase
Bryodemella tuberculata	2001	1998	2002	increase_decrease
Bryodemella tuberculata	2011	2008	2012	decrease_increase
Chorthippus brunneus	1987	1983	1989	stable_increase
Chorthippus brunneus	2005	2002	2006	increase_decrease
Chorthippus brunneus	2009	2006	2010	decrease_increase
Chorthippus vagans	1991	1987	1993	stable_decrease
Chorthippus vagans	2000	1996	2002	decrease_increase
Chorthippus vagans	2012	2008	2014	increase_decrease
Decticus verrucivorus	1989	1984	1992	stable_decrease
Decticus verrucivorus	2001	1998	2002	decrease_increase
Decticus verrucivorus	2012	2010	2012	increase_decrease
Myrmecophilus acervorum	1991	1988	1992	stable_increase
Myrmecophilus acervorum	2000	1998	2000	increase_decrease
Myrmecophilus acervorum	2016	2008	2022	decrease_stable
Myrmeleotettix maculatus	1996	1993	1997	stable_decrease
Myrmeleotettix maculatus	2006	2004	2006	decrease_increase
Myrmeleotettix maculatus	2011	2009	2011	increase_decrease
Omocestus haemorrhoidalis	1992	1985	1997	decrease_stable
Omocestus haemorrhoidalis	2000	1998	2000	stable_increase
Omocestus haemorrhoidalis	2011	2008	2012	increase_decrease
Omocestus viridulus	1992	1987	1995	increase_decrease
Omocestus viridulus	2000	1992	2006	decrease_stable
Omocestus viridulus	2016	2013	2017	stable_decrease
Pholidoptera aptera	1997	1994	1998	stable_increase
Pholidoptera aptera	2001	1999	2001	increase_decrease
Pholidoptera aptera	2016	2011	2019	decrease_stable
Pholidoptera griseoaptera	1990	1986	1992	stable_increase
Pholidoptera griseoaptera	1998	1996	1998	increase_decrease
Pholidoptera griseoaptera	2006	2004	2006	decrease_increase
Pteronemobius heydenii	1995	1991	1997	stable_increase
Pteronemobius heydenii	2006	2004	2006	increase_decrease
Pteronemobius heydenii	2013	2010	2014	decrease_increase
Tetrix tuerki	1991	1984	1996	stable_increase
Tetrix tuerki	2005	2002	2006	increase_decrease
Tetrix tuerki	2011	2008	2012	decrease_increase

Table 11: Species with three breakpoints between 1980 and 2019
(continued)

Species	breakpoint	CI5	CI95	change
Tetrix undulata	1992	1990	1992	stable_increase
Tetrix undulata	1998	1996	1998	increase_decrease
Tetrix undulata	2013	2010	2014	decrease_increase
Aeshna juncea	1990	1988	1990	increase_decrease
Aeshna juncea	1992	1990	1992	decrease_stable
Aeshna juncea	2013	2009	2015	stable_increase
Coenagrion hastulatum	1990	1987	1991	stable_decrease
Coenagrion hastulatum	1998	1996	1998	decrease_increase
Coenagrion hastulatum	2004	2002	2004	increase_decrease
Coenagrion lunulatum	1987	1984	1988	stable_decrease
Coenagrion lunulatum	1996	1993	1997	decrease_increase
Coenagrion lunulatum	2013	1982	2042	increase_stable
Coenagrion ornatum	1990	1985	1993	stable_increase
Coenagrion ornatum	1997	1993	1999	increase_decrease
Coenagrion ornatum	2013	2007	2017	decrease_stable
Coenagrion pulchellum	1993	1985	1999	decrease_stable
Coenagrion pulchellum	2000	1996	2002	stable_increase
Coenagrion pulchellum	2006	1999	2011	increase_stable
Cordulia aenea	1988	1984	1990	stable_decrease
Cordulia aenea	1995	1992	1996	decrease_increase
Cordulia aenea	2012	2010	2012	increase_decrease
Epitheca bimaculata	1995	1991	1997	stable_increase
Epitheca bimaculata	2006	2001	2009	increase_stable
Epitheca bimaculata	2010	2008	2010	stable_decrease
Erythromma lindenii	1995	1990	1998	increase_decrease
Erythromma lindenii	2003	1995	2009	decrease_stable
Erythromma lindenii	2009	2006	2010	stable_increase
Gomphus vulgatissimus	2001	1997	2003	increase_stable
Gomphus vulgatissimus	2003	2001	2003	stable_decrease
Gomphus vulgatissimus	2010	2007	2011	decrease_increase
Lestes dryas	1991	1981	1999	decrease_stable
Lestes dryas	2004	2001	2005	stable_increase
Lestes dryas	2011	2008	2012	increase_decrease
Lestes virens	2003	2000	2004	decrease_increase
Lestes virens	2007	2005	2007	increase_decrease
Lestes virens	2010	2006	2012	decrease_stable
Leucorrhinia pectoralis	1985	1982	1986	stable_decrease
Leucorrhinia pectoralis	1994	1991	1995	decrease_increase
Leucorrhinia pectoralis	2010	2003	2015	increase_decrease
Leucorrhinia rubicunda	1991	1988	1992	stable_increase
Leucorrhinia rubicunda	2000	1997	2001	increase_decrease
Leucorrhinia rubicunda	2013	2006	2018	decrease_stable
Libellula depressa	1995	1992	1996	increase_decrease
Libellula depressa	1999	1996	2000	decrease_increase
Libellula depressa	2018	1957	2077	increase_stable
Somatochlora flavomaculata	1994	1991	1995	increase_decrease
Somatochlora flavomaculata	1999	1995	2001	decrease_increase
Somatochlora flavomaculata	2015	2005	2023	increase_stable
Sympetrum depressiusculum	1992	1989	1993	stable_decrease
Sympetrum depressiusculum	2001	1999	2001	decrease_increase
Sympetrum depressiusculum	2013	2011	2013	increase_decrease
Sympetrum striolatum	1990	1988	1990	decrease_increase
Sympetrum striolatum	1995	1993	1995	increase_decrease

(continued . . .)

Table 11: Species with three breakpoints between 1980 and 2019
(continued)

Species	breakpoint	CI5	CI95	change
Sympetrum striolatum	1997	1995	1997	decrease_stable

latum & 1997 & 1995 & 1997 & decrease_stable* \end{longtable}

Shifting baselines (Fig. 15)

```r
# load species photo
Lphlaeas <- image_read(
  "C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/Lycaena_phlaeas.jpg")


Lphlaeas2 <- image_ggplot(Lphlaeas)

LP_glm_full <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(Species,occupancyMean,yearIndex,occupancySD) %>%
  glm(occupancyMean ~ yearIndex,data=.,weights=1/occupancySD)

LP_glm_full_ci <- confint(LP_glm_full,level=0.95) %>% as.data.frame() %>%
  tibble::rownames_to_column() %>% rename(term=rowname) %>%
  mutate(Species="LYCAENA PHLAEAS")

LP_glm_full1 <- broom::tidy(LP_glm_full) %>% as.data.frame() %>%
  mutate(Species="LYCAENA PHLAEAS",model="full GLM") %>%
  full_join(LP_glm_full_ci) %>%
  dplyr::select(model,Species,term,estimate,std.error,p.value,
                '2.5 %','97.5 %',statistic)

rm(LP_glm_full_ci)

LP_glm_full_pred <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(yearIndex) %>%
  predict.glm(LP_glm_full,newdata=.,type="link",se.fit=TRUE)

critval <- 1.96 ### approx 95% CI
upr <- LP_glm_full_pred$fit + (critval * LP_glm_full_pred$se.fit)
lwr <- LP_glm_full_pred$fit - (critval * LP_glm_full_pred$se.fit)
fit <- LP_glm_full_pred$fit

fit2 <- LP_glm_full$family$linkinv(fit)
upr2 <- LP_glm_full$family$linkinv(upr)
lwr2 <- LP_glm_full$family$linkinv(lwr)

LP_full_pred <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::mutate(glm_fit=fit2,glm_uCI=upr2,glm_lCI=lwr2)

# shifted baseline 1
LP_glm_1 <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  filter(Year>=1980 & Year <=1992) %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
```

```r
  dplyr::select(Species,occupancyMean,yearIndex,occupancySD) %>%
  glm(occupancyMean ~ yearIndex,data=.,weights=1/occupancySD)

LP_glm_1_ci <- confint(LP_glm_1,level=0.95) %>% as.data.frame() %>%
  tibble::rownames_to_column() %>% rename(term=rowname) %>%
  mutate(Species="LYCAENA PHLAEAS")

LP_glm_11 <- broom::tidy(LP_glm_1) %>% as.data.frame() %>%
  mutate(Species="LYCAENA PHLAEAS",model="1 GLM") %>% full_join(LP_glm_1_ci) %>%
  dplyr::select(model,Species,term,estimate,std.error,p.value,
                '2.5 %','97.5 %',statistic)

rm(LP_glm_1_ci)

LP_glm_1_pred <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  filter(Year>=1980 & Year <=1992) %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(yearIndex) %>%
  predict.glm(LP_glm_1,newdata=.,type="link",se.fit=TRUE)

critval <- 1.96 # approx 95% CI
upr <- LP_glm_1_pred$fit + (critval * LP_glm_1_pred$se.fit)
lwr <- LP_glm_1_pred$fit - (critval * LP_glm_1_pred$se.fit)
fit <- LP_glm_1_pred$fit

fit2 <- LP_glm_1$family$linkinv(fit)
upr2 <- LP_glm_1$family$linkinv(upr)
lwr2 <- LP_glm_1$family$linkinv(lwr)

LP_1_pred <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  filter(Year>=1980 & Year <=1992) %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::mutate(glm_1_fit=fit2,glm_1_uCI=upr2,glm_1_lCI=lwr2) %>%
  dplyr::select(Species,yearIndex,glm_1_fit,glm_1_uCI,glm_1_lCI)

LP_full_pred %<>% full_join(.,LP_1_pred)

# shifted baseline 2
LP_glm_2 <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  filter(Year>=1992 & Year <=2002) %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(Species,occupancyMean,yearIndex,occupancySD) %>%
  glm(occupancyMean ~ yearIndex,data=.,weights=1/occupancySD)

LP_glm_2_ci <- confint(LP_glm_2,level=0.95) %>% as.data.frame() %>%
  tibble::rownames_to_column() %>% rename(term=rowname) %>%
  mutate(Species="LYCAENA PHLAEAS")

LP_glm_21 <- broom::tidy(LP_glm_2) %>% as.data.frame() %>%
  mutate(Species="LYCAENA PHLAEAS",model="1 GLM") %>%
  full_join(LP_glm_2_ci) %>%
  dplyr::select(model,Species,term,estimate,std.error,p.value,
                '2.5 %','97.5 %',statistic)

rm(LP_glm_2_ci)

LP_glm_2_pred <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  filter(Year>=1992 & Year <=2002) %>%
```

```
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(yearIndex) %>%
  predict.glm(LP_glm_2,newdata=.,type="link",se.fit=TRUE)

critval <- 1.96 # approx 95% CI
upr <- LP_glm_2_pred$fit + (critval * LP_glm_2_pred$se.fit)
lwr <- LP_glm_2_pred$fit - (critval * LP_glm_2_pred$se.fit)
fit <- LP_glm_2_pred$fit

fit2 <- LP_glm_2$family$linkinv(fit)
upr2 <- LP_glm_2$family$linkinv(upr)
lwr2 <- LP_glm_2$family$linkinv(lwr)

LP_2_pred <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  filter(Year>=1992 & Year <=2002) %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))+12) %>%
  dplyr::mutate(glm_2_fit=fit2,glm_2_uCI=upr2,glm_2_lCI=lwr2) %>%
  dplyr::select(Species,yearIndex,glm_2_fit,glm_2_uCI,glm_2_lCI)

LP_full_pred %<>% full_join(.,LP_2_pred)

# shifted baseline 3
LP_glm_3 <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  filter(Year>=2002 & Year <=2016) %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(Species,occupancyMean,yearIndex,occupancySD) %>%
  glm(occupancyMean ~ yearIndex,data=.,weights=1/occupancySD)

LP_glm_3_ci <- confint(LP_glm_3,level=0.95) %>% as.data.frame() %>%
  tibble::rownames_to_column() %>% rename(term=rowname) %>%
  mutate(Species="LYCAENA PHLAEAS")

LP_glm_31 <- broom::tidy(LP_glm_3) %>% as.data.frame() %>%
  mutate(Species="LYCAENA PHLAEAS",model="1 GLM") %>% full_join(LP_glm_3_ci) %>%
  dplyr::select(model,Species,term,estimate,std.error,p.value,
                '2.5 %','97.5 %',statistic)

rm(LP_glm_3_ci)

LP_glm_3_pred <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  filter(Year>=2002 & Year <=2016) %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))) %>%
  dplyr::select(yearIndex) %>%
  predict.glm(LP_glm_3,newdata=.,type="link",se.fit=TRUE)

critval <- 1.96 # approx 95% CI
upr <- LP_glm_3_pred$fit + (critval * LP_glm_3_pred$se.fit)
lwr <- LP_glm_3_pred$fit - (critval * LP_glm_3_pred$se.fit)
fit <- LP_glm_3_pred$fit

fit2 <- LP_glm_3$family$linkinv(fit)
upr2 <- LP_glm_3$family$linkinv(upr)
lwr2 <- LP_glm_3$family$linkinv(lwr)

LP_3_pred <- dat %>% filter(Species =="LYCAENA PHLAEAS") %>%
  filter(Year>=2002 & Year <=2016) %>%
  dplyr::mutate(yearIndex=as.numeric(as.factor(Year))+22) %>%
  dplyr::mutate(glm_3_fit=fit2,glm_3_uCI=upr2,glm_3_lCI=lwr2) %>%
```

```r
  dplyr::select(Species,yearIndex,glm_3_fit,glm_3_uCI,glm_3_lCI)

LP_full_pred %<>% full_join(.,LP_3_pred)

# plot
baseline_plot <- LP_full_pred %>% ggplot() + theme_classic() +
  geom_point(aes(x=Year,y=occupancyMean),size=1) +
  geom_line(aes(x=Year,y=occupancyMean))+
  geom_ribbon(aes(x=Year,ymin=occupancyX2.5,ymax=occupancyX97.5),alpha=0.25) +
  geom_ribbon(aes(x=Year,ymin=glm_lCI,ymax=glm_uCI),alpha=0.4,fill="#003f5c") +
  geom_line(aes(x=Year,y=glm_fit),linewidth=1,colour="#003f5c")+
  annotate(geom="text",x=2000,y=0.3,size=4.2,colour="#003f5c",
           label="(a) 1980-2019:  0.0034 (lCI  0.0017,uCI  0.0050)") +
  geom_ribbon(aes(x=Year,ymin=glm_1_lCI,ymax=glm_1_uCI),alpha=0.4,fill="#ffa600") +
  geom_line(aes(x=Year,y=glm_1_fit),linewidth=1,colour="#ffa600")+
  annotate(geom="text",x=2000,y=0.2,size=4.2,colour="#ffa600",
           label="(b) 1980-1992:  0.0106 (lCI  0.0011,uCI  0.0202)") +
  geom_ribbon(aes(x=Year,ymin=glm_2_lCI,ymax=glm_2_uCI),alpha=0.4,fill="#ef5675") +
  geom_line(aes(x=Year,y=glm_2_fit),linewidth=1,colour="#ef5675")+
  annotate(geom="text",x=2000,y=0.1,size=4.2,colour="#ef5675",
           label="(c) 1992-2002: -0.0108 (lCI -0.0166,uCI -0.0050)") +
  geom_ribbon(aes(x=Year,ymin=glm_3_lCI,ymax=glm_3_uCI),alpha=0.4,fill="#7a5195") +
  geom_line(aes(x=Year,y=glm_3_fit),linewidth=1,colour="#7a5195")+
  annotate(geom="text",x=2000,y=0,size=4.2,colour="#7a5195",
           label="(d) 2002-2016:  0.0013 (lCI -0.0039,uCI  0.0064)") +
  scale_x_continuous(name="Year") +
  scale_y_continuous(limits=c(0,0.8),name="Occupancy") +
  theme(axis.text=element_text(size=12),axis.title=element_text(size=12),
        title=element_text(size=10),
        legend.position="bottom",legend.key.size=unit(1.5,"cm"),
        legend.text=element_text(size=12),legend.title=element_text(size=12),
        plot.margin=unit(c(0.2,0.3,0.2,0.2),"cm"),
        legend.margin=margin(unit(c(0,0,0,0),"cm")),
        legend.box.margin=margin(unit(c(0,0,0,0),"cm")))
#png(
#"C:/Users/ekath/R_Coding/MINTbio/Thesis_figures/shiftingBaselines_LycaenaPhlaeas.png",
#units="in",width=4.5,height=5.5,res=1200)
ptemp <- ((Lphlaeas2+theme(plot.margin=unit(c(0,0,0,0),"pt"))))/
    (baseline_plot+theme(plot.margin=unit(c(0,8,0,0),"pt")))+
  plot_layout(heights=unit(c(4,8),"null")))
#dev.off()
#ggview::ggview(device="png",units="in",width=4.5,height=5.5)
```
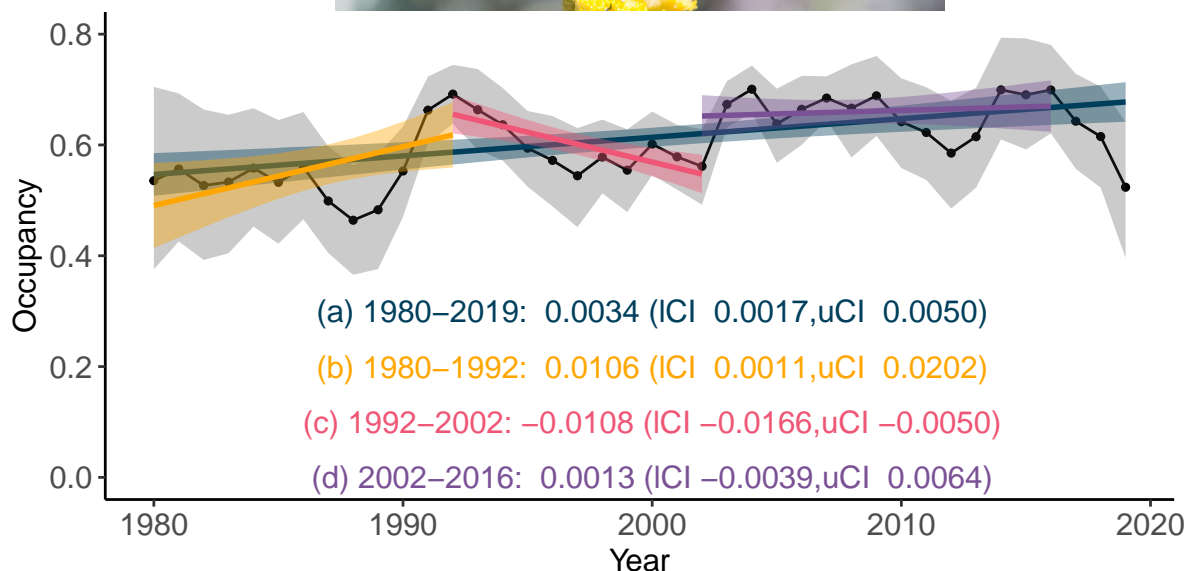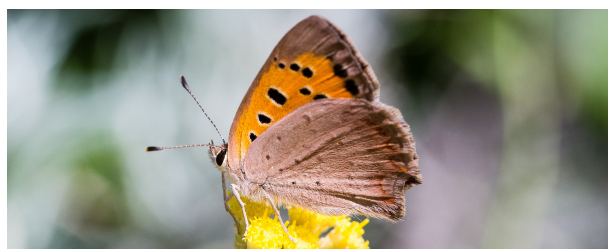
Figure 15 Shifting baselines for linear trend analysis shown on the example of the butterfly Lycaena phlaeas (Lepidoptera,Lycaenidae – photograph on top by E. K. Engelhardt) and four exemplary time-frames.

Did species disappear or immigrate during our study period?

Based on minimum occupancy,roughly relating to high occurrence probability in up to 5 grid cells

```
ptemp <- dat %>% dplyr::select(Species,order,Year,occupancyMean,
                occupancyX2.5,occupancyX97.5,occupancyRhat,observed) %>%
  group_by(order,Species) %>%
  dplyr::mutate(min_occMean=min(occupancyMean),min_occX2.5=min(occupancyX2.5),
                Species=str_to_sentence(Species)) %>%
  # filter for species with occurrences in
  # up to 5 grid cells (~ occupancy of 0.002256)
  filter(min_occMean <=0.002256) %>%
  ggplot() + theme_bw() + facet_wrap(order~Species) +
  ggtitle(label="Species occurring in ~ 5 grid cells in at least one year") +
  geom_point(aes(x=Year,y=occupancyMean,shape=factor(observed),
                color=cut(occupancyRhat,c(-Inf,1.1,Inf))),size=0.5) +
  geom_line(aes(x=Year,y=occupancyMean)) +
  geom_ribbon(aes(x=Year,ymin=occupancyX2.5,ymax=occupancyX97.5),alpha=0.5) +
  scale_color_manual(name="Rhat",values=c("blue","red"),na.value=c("red"),
                expand=c(-Inf,Inf),limits=c("(-Inf,1.1]","(1.1,Inf]"),
                labels=c("Good (<1.1)","Bad (>1.1)")) +
  scale_shape_manual(name="observed",values=c(1,19),limits=c(0,1),
                labels=c("FALSE","TRUE")) +
  scale_x_continuous(name="Year") +
  scale_y_continuous(limits=c(0,1),name="Occupancy") +
  theme(axis.text=element_text(size=7),axis.title=element_text(size=12),
        strip.text=element_text(size=7,face="italic"),title=element_text(size=12),
```
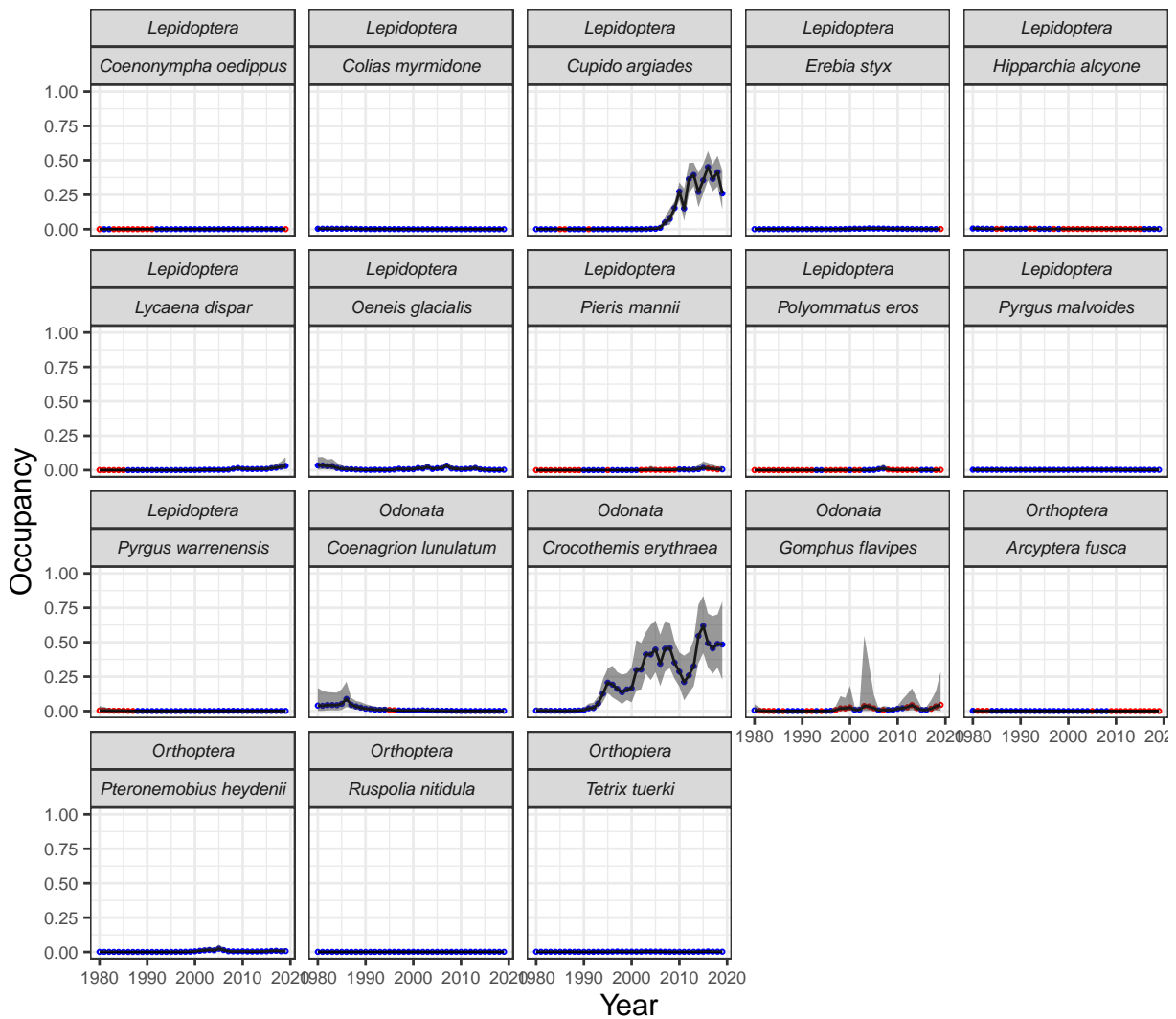
```
        legend.position="bottom",legend.key.size=unit(1.5,"cm"),
        legend.text=element_text(size=12),legend.title=element_text(size=12),
        plot.margin=unit(c(0.8,0,0,0),"cm"),
        legend.margin=margin(unit(c(0,0,0,0),"cm")),
        legend.box.margin=margin(unit(c(0,0,0,0),"cm")))+
  guides(size=FALSE)
```

```
ptemp
```


Species occurring in ~ 5 grid cells in at least one year

Based on observations,species not observed in at least 5 years

```
speclist <- dat %>% ungroup() %>% dplyr::select(Species,order,Year,observed) %>%
  filter(observed ==0) %>% group_by(order,Species) %>%
  dplyr::summarise(cons_years=rle(diff(Year) ==1)$lengths) %>% ungroup() %>%
  filter(cons_years>=5) %>% dplyr::select(order,Species) %>%
  unique() %>% pull(Species)
```
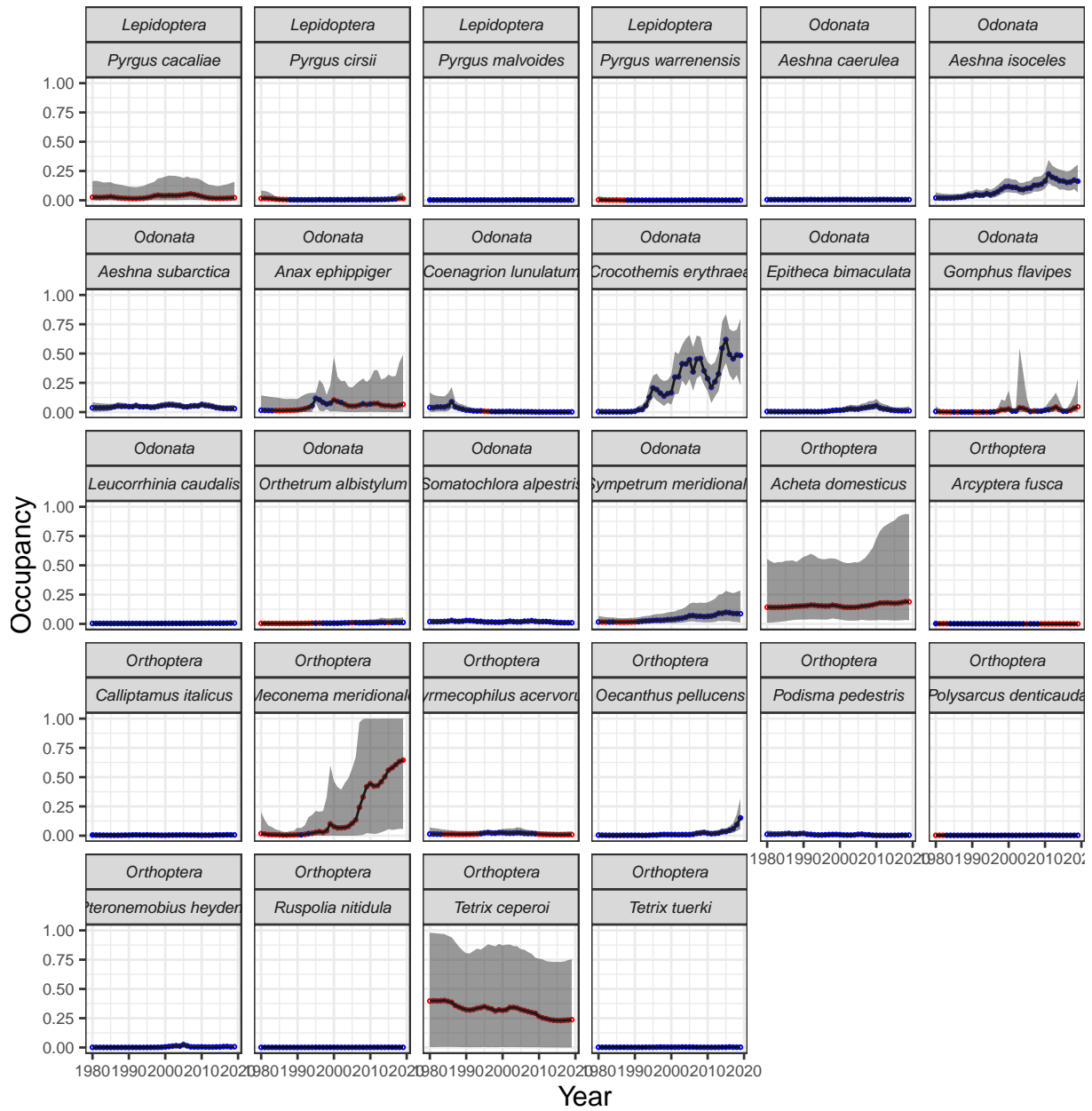
Species without observations in at least 5 years
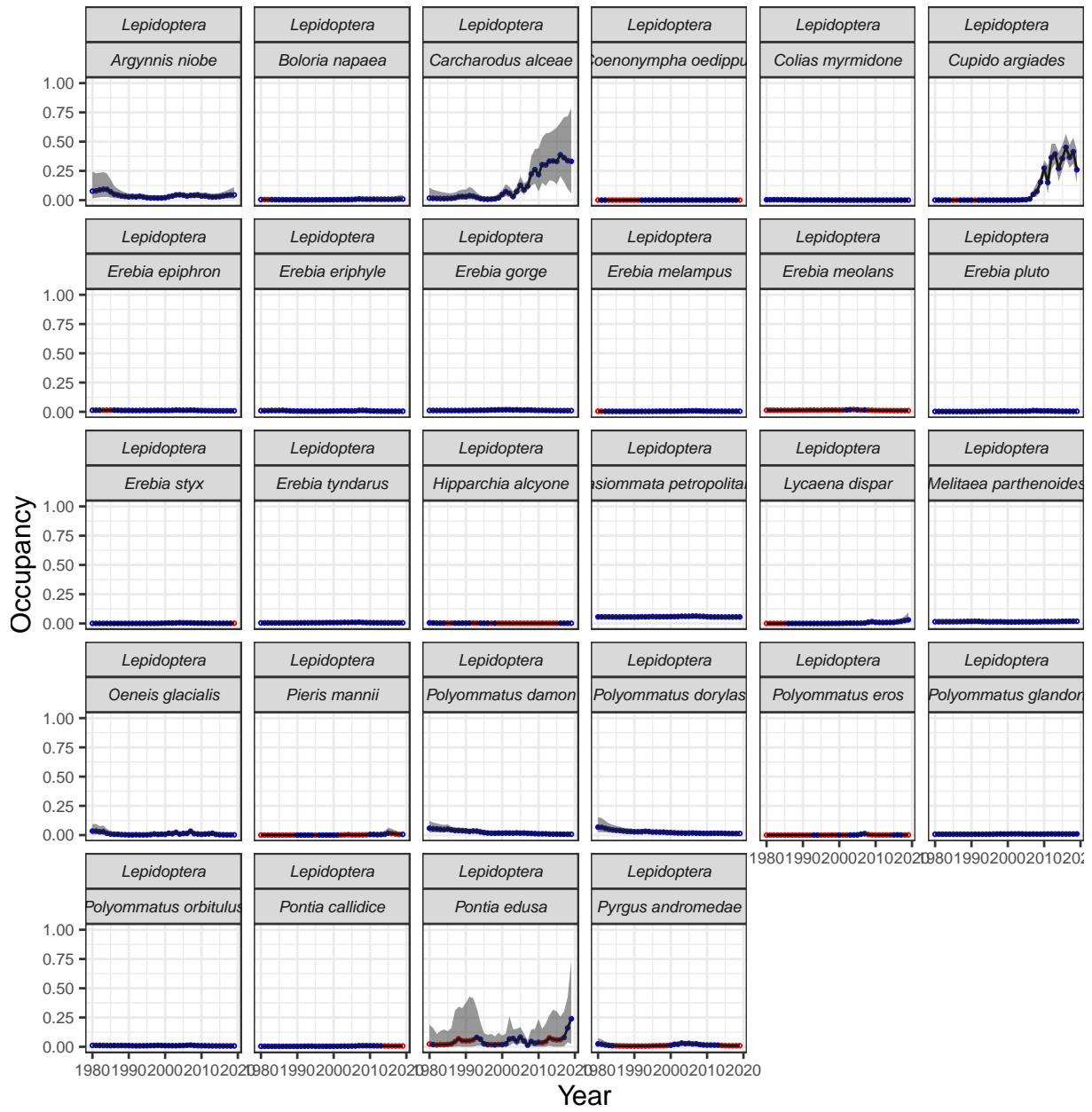
Species without observations in at least 5 years (continued)

Packages and Session Information

```
library("purrr")

temp <- devtools::session_info()
temp$platform
##  setting  value
##  version  R version 4.2.0 (2022-04-22 ucrt)
##  os       Windows 10 x64 (build 22621)
```

```
##   system    x86_64, mingw32
##   ui        RTerm
##   language (EN)
##   collate   German_Germany.utf8
##   ctype     German_Germany.utf8
##   tz        Europe/Berlin
##   date      2023-05-29
##   pandoc    2.19.2 @ C:/Program Files/RStudio/resources/app/bin/quarto/bin/tools/ (via rmarkdown)
temp <- temp$packages
temp <- temp %>% as.data.frame() %>% filter(attached =="TRUE") %>% pull(package)

temp %>%
  map(citation) %>%
  print(style="text")
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