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Climate change drives re-arrangement of distribution ranges among Noctuidae moths in Central Europe

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ABSTRACT

The study at hand investigates the distributional changes of 24 Noctuidae species within the geographical confines of Central Europe from 1970 to 2023, focusing on shifts in their geographic range. As climate change increasingly impacts ecosystems and biodiversity, understanding species' responses is crucial. By analysing publicly available records from the portal GBIF, this thesis aimed to identify observable changes in latitude and distribution patterns and explore their associations with certain ecological species traits. Statistical analysis was conducted using Kruskal-Wallis ANOVA to assess differences across decades, with results further validated through Fligner-Killeen tests to account for variance discrepancies. LOESS regressions were employed to visualize the direction of range changes. The analysis revealed statistically significant alterations of their distributions in Central Europe for all 24 species, with 14 exhibiting notable distribution changes and range expansion also visible in the LOESS regressions. Specifically, two species, *Caradrina kadenii* and *Caradrina gilva*, exhibited northward shifts, while nine species demonstrated southward latitudinal shifts, with the most pronounced being *Athetis hospes*, *Hadena magnolii*, *Trigonophora flammea*, and *Callopistria latreillei*. *Aedia leucomelas*, *Cucullia verbasci*, and *Polyphaenis sericata* showed range expansions without a clear directional trend. Species that successfully expanded their ranges or shifted latitudes often shared traits such as polyphagy, adaption to warm climate, generalist habitat requirements, and the ability to utilize potentially invasive, human-introduced, or climate-resilient host plants. These characters likely facilitate their ability to efficiently track shifting climate zones and colonize new areas. Conversely, traits such as affiliation with cold habitats, habitat specialization, larval monophagy (i.e. reliance on specific host plants), and restricted altitudinal ranges, were more prevalent among the ten species without a visible trend displayed. Characteristics like those may limit their ability to respond effectively to recent climate change and habitat loss.

ZUSAMMENFASSUNG

Die vorliegende Studie untersucht die Verbreitungsänderungen von 24 Noctuidae-Arten innerhalb der geografischen Grenzen Zentraleuropas im Zeitraum von 1970 bis 2023, mit einem Fokus auf Verschiebungen ihrer geografischenVerbreitung. Da der Klimawandel zunehmend Ökosysteme und die Biodiversität beeinflusst, ist es entscheidend, die Reaktionen von verschiedenen Arten zu verstehen. Durch die Analyse öffentlich verfügbarer Daten vom Portal GBIF verfolgte diese Arbeit das Ziel, beobachtbare Änderungen im Breitengrad der Nachweise und in den Verbreitungsmustern aller 24 Arten zu identifizieren und deren potenzielle Zusammenhänge mit spezifischen ökologischen Merkmalen zu erforschen. Zur statistischen Analyse wurden Kruskal-Wallis-ANOVAs durchgeführt, um Unterschiede zwischen den Jahrzehnten zu bewerten, und die Ergebnisse wurden durch Fligner-Killeen-Tests weiter validiert, um Unterschiede in der Varianz der Nachweisdaten zu berücksichtigen. LOESS-Regressionen wurden angewandt, um die Himmelsrichtung der Veränderungen im Verbreitungsbereich für jede Art zu visualisieren. Die Ergebnisse zeigten statistisch signifikante Verteilungsverschiebungen der Nachweise bei allen 24 Arten, wobei bei 14 Arten solche Veränderungen auch in der LOESS-Regression sichtbar waren. Konkret wiesen zwei Arten, *Caradrina kadenii* und *Caradrina gilva,* eine Arealerweiterung nach Norden auf, während neun Arten eine Verschiebung ihrer mitteleuropäischen Verbreitung nach Süden zeigten, wobei die ausgeprägtesten Verschiebungen bei *Athetis hospes, Hadena magnolii, Trigonophora flammea* und *Callopistria latreille*i beobachtet wurden. *Aedia leucomelas, Cucullia verbasci* und *Polyphaenis sericata* zeigten Erweiterungen des Verbreitungsbereichs, jedoch ohne einen klaren Richtungstrend. Arten, die erfolgreich ihre Verbreitungsbereiche ausgedehnt oder verschoben haben, teilen häufig Merkmale wie Polyphagie der Larven, Bevorzugung wärmebegünstigter Habitate, generalistische Habitatanforderungen und das Nutzen von potenziell invasiven, kultivierten oder widerstandfähigeren Wirtspflanzen. Diese Eigenschaften erleichtern es ihnen vermutlich, sich effektiv an sich verschiebende Klimazonen anzupassen und neue Gebiete zu besiedeln. Im Gegensatz dazu waren Merkmale wie Bindung an kühle Lebensräume, hohe Habitatspezialisierung, Monophagie der Larven, die Abhängigkeit von spezifischen Wirtspflanzen und eine Verbreitung nur in eingeschränkten Höhenlagen bei den zehn Arten ohne sichtbare Trends häufiger. Diese Eigenschaften könnten ihre Fähigkeit einschränken, effektiv auf den Klimawandel zu reagieren.

1. INTRODUCTION

1.1 CLIMATE CHANGE

The term “climate” is used to describe regional or global averages of temperature, precipitation, and humidity over a longer timeframe (seasons, years, or decades). Climate change refers to a significant variation of average weather conditions over several decades or longer, for differentiating from short-term weather variability (Ummenhofer and Meehl, 2017). In 1896, a developed conjecture emerged that human activities, particularly carbon dioxide emissions, could impact the global climate. However, this hypothesis was initially dismissed and only regained attention in the mid-20th century (Weart, 2010).

Global warming is primarily depending on the accumulation of greenhouse gases (the most potent ones being CO_2 and CH_4) in the atmosphere and will continue to increase in the near future (2021–2040) with current trends showing that we are likely going to exceed the 1.5°C mark globally by 2030 (Calvin *et al.*, 2023) potentially causing further and more severe impacts on local, regional, and global natural ecosystems (Ummenhofer and Meehl, 2017).

It is important to emphasize that currently, climate change is not the leading cause of recent biodiversity loss worldwide. Land and sea use change are identified as the primary drivers, followed by resource exploitation and pollution. Climate change and invasive species have lesser impacts. The hierarchy of these drivers varies across different ecosystems and biodiversity indicators. All of these drivers threaten marine, terrestrial, and freshwater ecosystems around the world, potentially exacerbating the loss of local species, causing mass mortality of plants and animals, and increasing disease prevalence, ultimately resulting in the first climate-driven extinctions (Engelhardt *et al.*, 2022; Jaureguiberry *et al.*, 2022).

Predicting the full consequences of climate change is challenging and complex, requiring a deeper understanding of how species, and in some cases their required host plants, adapt to shifting climatic conditions within their niches. Studies reveal significant shifts in species' niche positions in response to climate variables, predominantly temperature. However, making accurate predictions could become even more complicated, considering the heightened probability of local species extinction and the potential reopening of local niches (Schweiger *et al.*, 2012; Antão *et al.*, 2022). In this context, considering herbivore insects and potential specialization to host plants is crucial. Climate acts as the primary constraint for butterfly species, with those inhabiting warmer regions and displaying tolerance to moisture variations faring better. Nevertheless, a discernible gradient from climate-driven to host plant-driven control was evident, affecting butterflies with range restricted host plants the most. Future projections suggest a rise in mismatches between butterflies and their hosts, exacerbating with the severity of scenarios. This underscores the significance of understanding ecological species traits in predicting future biodiversity outcomes and in mitigating negative impacts on ecosystem functions (Schweiger *et al.*, 2012).

Conservation biology’s primary goal is to preserve and restore biodiversity and ecosystem function, as well as mitigate the ongoing loss of species and further seeks to address the urgent global environmental challenges. Popularized by Wilson in 1988, scientists in this multidisciplinary field work towards assessing, understanding, preserving, and restoring biodiversity (Wilson *et al.*, 1988).

1.2 CLIMATE CHANGE EFFECTS ON THE BIODIVERSITY OF INSECTS

The term “biodiversity” describes the heterogeneity of life on Earth and fundamental aspects for measuring it are species richness and evenness, genetic variability, and ecosystem diversity (Haila and Kouki, 1994; Sarkar and Margules, 2002) as well as phylogenetic diversity which represents the combined evolutionary heritage of a group of species and functional diversity which encompasses the variety and arrangement of functional traits within a set of species (Hughes *et al.*, 2023).

The consequences of global climate change and land-use alteration on biodiversity are likely to be substantial and are already evident (Bellard *et al.*, 2012; Engelhardt *et al.*, 2022). In the face of recent rapid climate alternations, plant and animal species respond to it through phenotypic plasticity, evolutionary changes or have exhibited shifts in their geographic distributions, both in latitude and altitude (Schai-Braun *et al.*, 2021).

Insects specifically being poikilothermic animals, are highly influenced by environmental conditions, predominantly temperature, annual rainfall, and the aridity index, which significantly affect their biology, phenology, and ecology. The direct impacts of climate change on insects encompass changes in population dynamics, diurnal activity rhythms, growth rate, and diapause cycles. Altered precipitation patterns and more frequent disturbances such as droughts and floods also affect insect survival and diapause, thereby influencing their population size for years to come after the event of disturbance (Stefanescu, Carnicer and Peñuelas, 2011; Chandrakumara *et al.*, 2023).

Furthermore, climate-induced modifications in host plants and competitors can further complicate the effects on insect biology and phenology. Through climate change elevated CO_2 levels, host plant growth rates could change further affecting insect fecundity and population densities. Overall, climate change exerts multifaceted effects on insect populations, influencing their behaviour, development, and interactions with their environment (Chandrakumara *et al.*, 2023).

Butterflies and moths, being highly mobile with short generation times and high fecundity, are particularly suitable for exploring how species distributions change in response to altered climate and habitat conditions (Sunde *et al.*, 2023). Monitoring data shows an overall decline in cold-adapted species whereas warm-adapted species show an overall increase in numbers and broadening of their distribution range (Antão *et al.*, 2022).

Studies like Chen *et al.`s* and Fält-Nardmann *et al.`s* suggest that these distribution pattern changes as well as further indicated that latitudinal shifts have been more conspicuous than elevational shifts (Chen *et al.*, 2011; Fält-Nardmann *et al.*, 2018). This implies that northern range edge margins could have a greater capability to keep up with warming compared to those at higher elevations (Bellard *et al.*, 2012). However, recent evidence from the Alps shows that elevational shifts are indeed occurring in some species and seem to be becoming more common, which could be further intensified by the increasing land use intensity and habitat loss in the valleys potentially driving species to higher elevations (Habel *et al.*, 2021; Rödder *et al.*, 2021).

In contrast, southern range edge populations of insects are particularly vulnerable to the impacts of climate change. Even widely distributed and warm-adapted species have been shown to be constrained by extreme drought and other harsh environmental conditions, which are expected to intensify with continued warming, making habitat loss particularly severe (Gil-Tapetado *et al.*, 2023).

1.3 CLIMATE CHANGE EFFECTS ON SPECIALIST VERSUS GENERALIST'S SPECIES

Climate change has shown to affect specialist and generalist species differently due to their distinct ecological traits and is anticipated to place habitat specialists at a disadvantage compared to their generalist counterparts (Bellard *et al.*, 2012).

Studies across various taxa, including fungi, plants, birds, mammals, and insects, have consistently shown that generalist species, which have the ability to cope with a wider range of environments and resources, generally seem to possess better resilience to the rapidly changing conditions induced by climate change (Colles, Liow and Prinzing, 2009; Bellard *et al.*, 2012; Antão *et al.*, 2022). Generalists typically have less stringent environmental requirements within a specific geographic range, utilizing a wide array of resources available. Their ability to outcompete other species in various regions provides them with an advantage in locating new habitats and adapting to recently altered environments. In contrast, habitat specialists, characterized by their association with specific habitats and narrow range of resource usage, have evolved to occupy very specific niches. They rely on stability and have shown to be more vulnerable to the impacts of climate change (Van Dyke and Lamb, 2020).

For butterflies and moths, it is essential to further differentiate between habitat and host specialists. Host specialists exhibit clear preferences during host selection for their larvae to feed on, and host plant availability is key for potential population establishment. These species often show greater tolerance for other varying environmental factors, allowing them to inhabit diverse habitats, provided that the larval food source is available. In contrast, habitat specialists are much more selective about their living conditions with their primary occurrence factors being specific habitat structures and conditions, such as low vegetation cover, sufficient sunlight, and microhabitat features. (Stilmant *et al.*, 2008) Habitat loss, land-use, temperature changes, and alterations in resource availability pose significant threats to both host and habitat specialist species, leading to more frequent population declines and increased extinction risks (Engelhardt *et al.*, 2022).

Frequently, an observed decline in lepidoptera specialists' is contrasted by a stable or even increasing generalist population, emphasizing the potential risk to biodiversity resulting from the increased loss of specialist species (Engelhardt *et al.*, 2022).

Especially alpine ecosystems are particularly sensitive to temperature fluctuations, with limiting migration options for species available and overall simpler trophic interactions, potentially resulting in significant biodiversity losses. Climate warming directly exerts selective pressures disadvantaging cold-adapted species while favouring the proliferation of warm-adapted counterparts (Neff *et al.*, 2022). For instance, in the north-west Mediterranean Basin, butterfly specialists confined to montane habitats have experienced population declines attributable to habitat degradation and heightened temperatures (Stefanescu, Carnicer and Peñuelas, 2011; Bellard *et al.*, 2012).

Furthermore, alterations in host-plant distributions indirectly induced by climate change can lead to diminished suitable habitats, thereby further constricting species' distribution ranges (Filazzola, Matter and Roland, 2020).

1.4 CLIMATE CHANGE AND LAND-USE EFFECTS ON HOST PLANTS

Notably, some lepidoptera species, especially butterfly species exhibit specialization by associating themselves with one or a few closely related host plants (Hausharter *et al.*, 2023). Even polyphagous butterfly species, constituting less than 10% of the population, still demonstrate a preference for specific host plants during oviposition (Friberg *et al.*, 2008). On the contrary, studies have shown that larvae would still thrive on other host plants, females rarely oviposit on. Significant factors for driving shifts in insect host-plant preferences could be the ongoing co-evolutionary struggle with parasites and predators, as well as the important concept of securing an enemy-free space (Friberg *et al.*, 2008). Butterflies heavily rely on their host plants for survival and reproduction, making them vulnerable to changes in host plant availability induced by climate change. This can lead to mismatches between butterfly phenology and host plant phenology, threatening population persistence (Zhang, 2023).

In contrast, the more often-polyphagous nature of Noctuid moths makes them less vulnerable to changes in host plant availability induced by climate change. While butterflies may experience mismatches between their phenology and that of their host plants, threatening their population persistence, Noctuid moths are more resilient due to their broader diet providing higher food availability (Mattila *et al.*, 2009; Végvári *et al.*, 2015).

Polyphagous moths have been shown to perform well regardless of host plant type, unlike monophagous species, especially those feeding on herbs, which have experienced significant declines. This vulnerability is likely not only contributed to by climate change but also attributed to land use changes that disproportionately affect herbs, making monophagous species more vulnerable to extinction due to their reliance on a single, potentially unstable food source (Mattila *et al.*, 2009; Végvári *et al.*, 2015).

1.5 CLIMATE CHANGE IMPACTS ON THE RANGE EXPANSION OF LEPIDOPTERA SPECIES

Species and populations respond dynamically to altered environmental conditions caused by climate and land-use change, either by migrating to more suitable areas, adapting, or, in severe cases, facing extinction. These responses often result in range shifts, documented across various taxonomic groups, which can significantly impact species richness, community composition, ecosystem functioning, and resilience. In Lepidoptera, key drivers of range expansion and environmental adaptation include climate change, land-use patterns, habitat quality, and species-specific traits such as dispersal capacity, colour pattern variation (which influences predation risk), physiology, behaviour, flight performance, and temperature sensitivity and regulation. Additionally, range expansions are influenced by species richness and trait distribution within recipient communities, impacting the assembly of communities via ecological filtering (Sunde *et al.,* 2023).

Butterflies and moths, with their fast reproduction, high mobility, and short generation times, offer clear insights into responses to changing environmental conditions. Nevertheless, while they often track changing climates effectively, it is important to consider that some species exhibit a lag in response to temperature shifts or expand their ranges in unexpected ways (Sunde *et al.,* 2023).

1.6 POTENTIALLY ADVANTAGEOUS SPECIES TRAITS FOR EXPANDING SPECIES

The association between latitude and the limited effect of host plant niche width suggests that environmental factors in general play a more significant role than species interactions in driving expansions from biologically diverse southern regions to depauperate northern areas, for example Sweden and Finland. This indicates that the unique conditions found at different latitudes are key drivers of these species' distribution patterns (Forsman, Betzholtz and Franzén, 2016).

In Sweden and Finland, the observed increase in butterfly and moth species richness over the past 120 years highlighted the importance certain species traits in colonizing and establishing in emerging climates. Notably, butterfly and moth species with larger range sizes, broader thermal niches, wider larval diet ranges, and diverse habitat use exhibit enhanced abilities to colonize new areas, facilitating the development of more generalized and species-rich communities (Sunde *et al.*, 2023; Hällfors *et al.*, 2024).

Additionally, the availability of resources has shown significant impact on butterfly condition and flight performance. Elevated temperatures have also been found to augment flight performance and mobility, underscoring the influence of environmental conditions on dispersal (Reim, 2018).

The investment in morphological traits that enhance dispersal capacity varies among species, with some demonstrating a stronger correlation between wing length and mobility than others. Notably, individuals from recently colonized sites frequently display increased dispersal capacity compared to those in long-established populations, possibly due to traits associated with enhanced dispersal ability (Kallioniemi, 2013).

With the focus on Noctuidae in particular, species with more heterogenic coloration have been shown to shift their geographic distribution faster, supporting the assumption that trait diversity grants more options for reducing vulnerability to rapidly changing environments. Furthermore, moth species with higher average abundances and more stable populations over the years tend to shift their leading-edge margins further northward, underscoring that not only genetic diversity, but also the production of dispersers in sufficient numbers within a population and the species' ability to tolerate environmental changes play key roles in shaping these dynamics (Forsman, Betzholtz and Franzén, 2016).

The distributional range of species considered has significant implications for their survival and expansion probability. Species with a more widespread distribution pattern have better changes of persisting (regionally and globally), even if individual populations face environmental disruptions possibly causing localized extinctions. The key to their resilience lies in their capacity to disperse, allowing recolonizing of areas affected by local extinctions. Understandably, species with a more restricted distribution range are more prone to the impacts of human land-use and shifts in climate patterns (Forsman, Betzholtz and Franzén, 2016).

Effective overwintering strategies and cold adaptations of ectothermic species have proven beneficial for maintaining current populations dynamics, establishing larger distribution ranges, colonizing unfavourable environmental conditions and harsher temperate regions. These strategies include physiological and biochemical changes like the accumulation of cryoprotectants such as glycerol, which lower the freezing point of bodily fluids and protect cells against freezing, as well as Rapid Cold Hardening (RCH), which enables insects to quickly acclimate to sudden cold exposure, enhancing their temporary cold tolerance (Stanic *et al.*, 2004; Teets, Gantz and Kawarasaki, 2020).

Cryoprotectants are substances like glycerol, that insects biosynthesize and accumulate during periods of low metabolism as temperatures gradually fall. These low molecular weight organic solutes act to prevent freezing by lowering the freezing point of bodily fluids, thereby avoiding ice formation, and preventing cellular damage. An example of a studied species exhibiting this exact ability is *Spodoptera frugiperda* (J. E. Smith, 1797), which aids in its survival in low temperatures (Vatanparast and Park, 2022).

Cold acclimation often occurs over days to weeks, whereas RCH is a nearly instantaneous short-term protection against acute cold stress. RCH is the fastest acclimatory response to low temperature known in insects and describes a type of phenotypic plasticity that allows ectotherms to undergo biochemical changes in the hemolymph, increasing polyols like glycerol, which is key for coping with thermal variability. For instance, in the Noctuidae species *Spodoptera exigua* (Hübner, 1808), exposure to low temperatures (5°C for 6 hours) triggered a major RCH in all developmental stages, accompanied by a substantial increase in glycerol, enhancing survival across various stages (Teets, Gantz and Kawarasaki, 2020; Vatanparast and Park, 2022).

These overwintering strategies not only help insects withstand harsh winters but also facilitate their ability to expand their range and enhance their invasive potential, allowing them to colonize new areas with diverse climatic conditions, posing significant challenges for pest management and ecological balance. An example of this is *Spodoptera frugiperda*, a polyphagous species that feeds on tropical annual crops. Originally native to the Americas, it has rapidly invaded Africa and Asia, utilizing cryoprotectants among other strategies to survive in regions with colder climates, thus aiding its spread to new territories (Stanic *et al.*, 2004; Teets, Gantz and Kawarasaki, 2020; Vatanparast and Park, 2022).

Additionally, other Lepidopteran families demonstrate significant overwintering strategies as well. For example, *Ostrinia nubilalis* (Hübner, 1796) a moth of the family Crambidae synthesizes glycerol and activates its antioxidative defense system during diapause to withstand cold temperatures, while *Danaus plexippus (*Linnaeus, 1758) a butterfly of the Nymphalidae family benefits from Rapid Cold Hardening (RCH), which preserves their flight capability after exposure to cold conditions, crucial for their extensive migratory journeys (Stanic *et al.*, 2004; Teets, Gantz and Kawarasaki, 2020; Vatanparast and Park, 2022).

1.7 OBJECTIVES & RESEARCH QUESTIONS

This study aims to elucidate the changes in the distribution patterns of owlet moths statistically and visually through mapping, with a focus on the Noctuidae family, within the geographic confines of Central Europe over the past four to five decades. While the northward range expansion of numerous butterfly and moth species in Finland and Scandinavia has been well documented over the past decades (Fält-Nardmann *et al.*, 2018; Antão *et al.*, 2022; Sunde *et al.*, 2023; Hällfors *et al.*, 2024), surprisingly, there is a notable lack of comprehensive studies on the potential areal expansion and changing distribution patterns of species native to Central Europe. Through a comprehensive analysis of publicly available data from GBIF on 24 Noctuidae species, this study aims to provide an overview of potential alterations in distribution patterns, offering valuable insights into the extent and nature of these shifts. Specifically, the following research questions were formulated:

1. Is a notable alteration in the distribution range observable, and since when has this been apparent in the data?
2. In which direction is the visible expansion going: northward or southward?
3. What common characteristics do these range shifting and potentially even expanding species share?
4. Which species do not show any evidence for a range shift, and do they share any traits?

2. METHODS

2.1 DATA RETRIEVAL, PROCESSING, AND DATASET CONSTRUCTION

The present study centres on the distribution and occurrence data of 24 moth species, specifically from the monophyletic group Noctuidae sensu stricto within the geographical confines of Europe, spanning from 1970 to 2023. My study area includes occurrence data from the following countries and islands: Austria (AT), Albania (AL), Åland Islands (AX), Bosnia and Herzegovina (BA), Belgium (BE), Bulgaria (BG), Switzerland (CH), Czech Republic (CZ), Germany (DE), Denmark (DK), Estonia (EE), Spain (ES), Finland (FI), France (FR), United Kingdom (GB), Greece (GR), Croatia (HR), Hungary (HU), Isle of Man (IM), Ireland (IR), Italy (IT), Jersey (JE), Liechtenstein (LI), Latvia (LV), Lithuania (LT), Luxembourg (LU), Montenegro (ME), North Macedonia (MK), Netherlands (NL), Norway (NO), Poland (PL), Portugal (PT), Romania (RO), Sweden (SE), Slovakia (SK), and Slovenia (SI). I excluded Belarus (BY), Moldova (MD), Ukraine (UA), Russia (RU), Malta (MT), Cyprus (CY), and Turkey (TR) because of insufficient data or their climates differing significantly from the typical Central European climate. I utilized open-access data, primarily sourced from GBIF (Global Biodiversity Information Facility), an international network that aggregates biodiversity information from various databases into a centralized portal (GBIF.org, 2024). The data was downloaded on November 11, 2023.

The selection process of the final 24 Noctuidae species was determined through careful consideration and was performed as follows:

- Initially, out of the total 500 Noctuidae species that are confirmed to occur or have occurred in Austria (excluding rare migrants and those found exclusively in alpine regions), 125 species have their northern range boundaries within Central Europe. This criterion ensured that the selected species are not sporadic migrants but are consistently found within the focal region.
- The focus was specifically on species within Central Europe whose current northern distribution boundaries lie between 45 and 56 degrees northern latitude, up to the coasts of the North and Baltic Seas. These species were chosen because they have not yet expanded significantly into Northern Europe, such as Scandinavia, Finland, or the Baltic states. Species primarily distributed southward in Europe, classified as sub-Mediterranean or Mediterranean and occurring mainly south of 45 degrees north, were excluded. Additionally, species with ranges already covering large parts of Northern Europe were not considered, as comprehensive analyses for Scandinavia and Finland already exist.
- Additionally, species strictly limited to high mountain regions were excluded based on biogeographical reasoning. Such species are more likely to shift to higher elevations in response to changing environmental conditions, and their potential for northward range expansion is relatively limited.
- To ensure the best possible accuracy in identification and to further minimize potential misidentifications in the online data, only moth species were selected which are relatively easy

to identify. For example, no complexes of sibling species were considered where correct species identification requires the study of anatomical and/or genetic characters.

- Lastly, to ensure robust statistical analysis, an exclusion criterion based on data sufficiency was applied: 100 species were excluded due to insufficient data, specifically those with fewer than 700 recorded georeferenced occurrence data points in the Global Biodiversity Information Facility (GBIF) between 1970 and 2023. These presence data must also contain crucial information, including the year of observation and a precise location, specifying northern latitude and eastern longitude with coordinates.

After a thorough re-examination of the downloaded datasets and the creation of species-specific maps in QGIS, *Mythimna anderreggii* (Boisduval, 1840) was also removed from the list. This decision was based on the realization that most GBIF records for this mountain species were likely misidentifications or confusions with either *Mythimna l-album* (Linnaeus, 1767) and *Leucania comma* (Linnaeus, 1761), rendering the dataset unreliable. This left me with a refined list of 24 species for detailed study. An exception was made for *Aedia leucomelas* (Linnaeus, 1758), which was retained in the dataset despite having only 265 data points due to its particularly interesting occurrences in the last 25 years. This thermophilic species is typically found in Mediterranean to subtropical regions. However, in recent years, there have been increasing individual records of this species north of the Alps.

The GBIF datasets for each species were organized chronologically from 1970 to 2023 and cleaned by removing outliers, specifically records without scientifically confirmed evidence of the species in the respective country, and where the data was limited to a maximum of three sightings over the 50-year period.

I further incorporated data from GBIF stored under synonymic names for the following species:

- *Cucullia verbasci* (Linnaeus, 1758*)* – including records under *Shargacucullia verbasci* (Linnaeus, 1758).
- *Ochropleura musiva* (Hübner, 1803) – including records under *Dichagyris musiva* (Hübner, 1803)
- *Caradrina gilva* (Donzel, 1837) – including records under *Eremodrina gilva* (Donzel, 1837)
- *Athetis hospes* (Freyer, 1831) – including records under *Proxenus hospes* (Freyer, 1831)

The visualization of potential species expansion and further validation of dataset integrity were conducted in the QGIS 3.34.2-Prizren mapping software. To ensure precision and authenticity, distribution areas were visually assessed separately for each candidate species. Subsequently, a spatial representation illustrating species occurrences was generated, incorporating both the year of sightings and latitude coordinates.

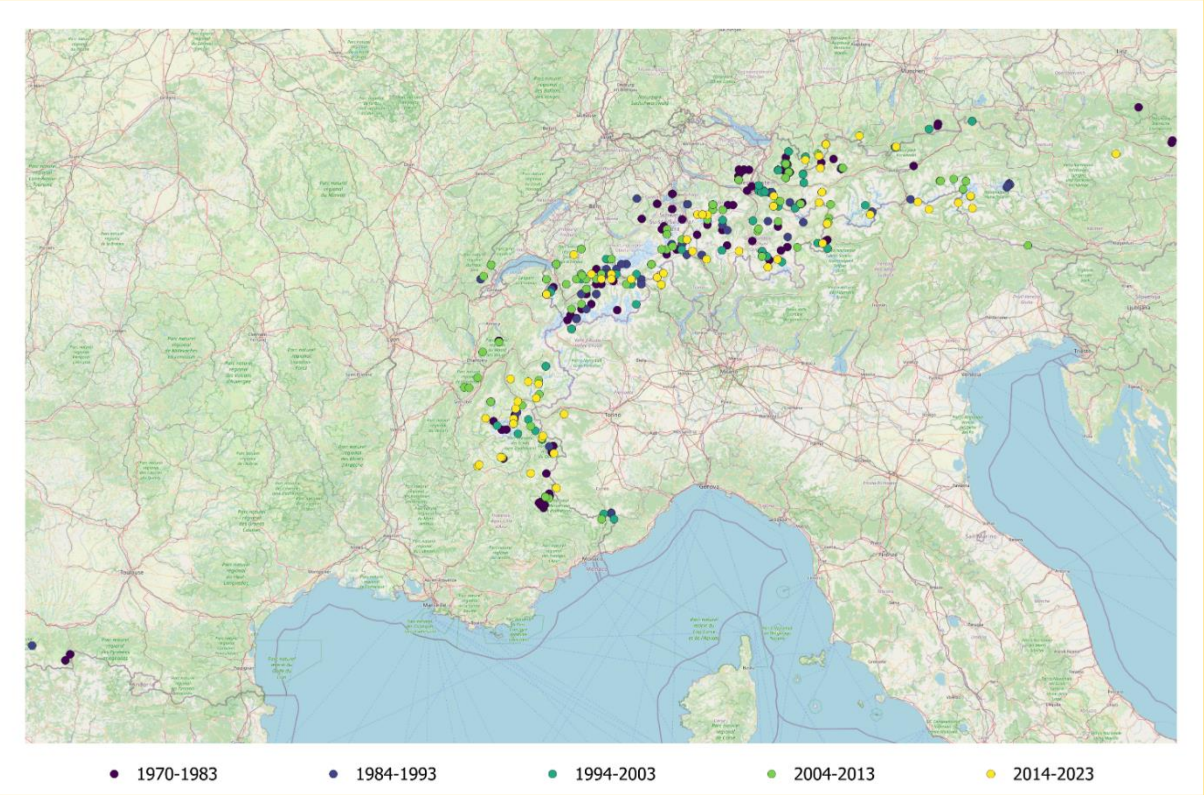

Figure 1: *Autographa aemula* (Grote, 1864) recorded occurrences in Europe from 1970-2023. 1059 data points visualized in color-coded decade intervals: purple = 1970-1983, blue = 1984-1993, turquoise = 1994-2003, yellow = 2004-2013, orange = 2014-2023

These maps were used as a pre-test to visually detect outliers and irregularities and to further visualize any potential species expansion. An example is shown in Figure 1. Subsequently the data was subjected to statistical analysis for further validation.

2.2 VISUAL DATA ANALYSIS

I visualized the dataset for each selected species in a table detailing the number of data points (occurrences) across the decade intervals from 1970 to 2023. Additionally, a bar chart was created in Microsoft Excel 365 that summarizes the total data available across all species per decade, providing a clearer understanding of the dataset's size and its size changes over time. These intervals were chosen as follows: 1970-1983, 1984-1993, 1994-2003, 2004-2013, and 2014-2023. This decade-based interval division is consistently applied throughout the majority of the statistical analyses performed.

To further analyse potential long-term trends in species distribution, I employed box-and-whisker plots using JAMOVI 2.4.14, again utilizing the aforementioned decade intervals.

The generated box and-whisker plots have the X-axis representing time intervals (decades) and the Y-axis depicting the northern latitudes of species occurrences. My objective was to discern temporal change in species distribution, particularly investigating whether the median latitude shifted northward over time. By systematically analysing species distributions across temporal and spatial dimensions, I looked for evidence of range expansion or contraction.

2.3 STATISTICAL ANALYSIS

Subsequent to confirming a non-normal distribution of the data via Shapiro-Wilk tests ($p \leq 0.05$) across all 24 datasets, statistical significance of differences between decades was evaluated using a Kruskal-Wallis ANOVA, with the latitude coordinate data as the response variable. It is important to note that the Kruskal-Wallis test does not solely respond to differences in the central tendency of the sub-samples (medians) but can also yield significant results if the shape (e.g., dispersion = variance) between the sub-samples (decades) differs markedly. Therefore, it would be incorrect to infer range shifts solely from a significance finding without further analysis when there are substantial differences in dispersion.

To address this issue, I performed a Fligner-Killeen test for each species to examine whether the decadal data also differ significantly in their spread. This test, suitable for assessing the homogeneity of variances in non-parametric data, was conducted using RStudio 2021.09.2 Build 382. The results of the Fligner-Killeen tests are presented in two additional columns, detailing the p-values and test statistics for each species.

Subsequently, I opted for LOESS regressions to visualize the direction (north or south) of potential range changes for each species. Specifically, I examined the correlation between the year of records (as a proxy for time) and occurrence latitude for each species separately to identify underlying trends and over the 53-year time span. All statistical tests, median calculations, as well as the visualization of LOESS regressions were performed using Jamovi 2.4.14.

3. RESULTS

TABLE 1: Species list and overview of recorded occurrences in five decade intervals: |1970-1983| 1984-1993|1994-2003|2004-2013|2014-2023| including the total summary of occurrence data per decade interval

Species list	**Occurrences 1970 – 1983**	**Occurrences 1984 – 1993**	**Occurrences 1994 – 2003**	**Occurrences 2004 – 2013**	**Occurrences 2014 – 2023**
Aedia leucomelas	21	8	23	40	173
Athetis hospes	65	285	271	665	2687
Auchmis detersa	559	389	346	479	515
Autographa aemula	428	148	180	207	96
Calliergis ramosa	435	324	179	302	412
Callopistria latreillei	176	189	99	315	470
Caradrina gilva	334	292	175	251	274
Caradrina kadenii	82	206	176	2152	6858
Chersotis margaritacea	541	484	225	363	253
Chersotis multangula	709	453	281	323	327
Cucullia verbasci	1231	1128	3271	8462	13446
Egira conspicillaris	847	886	894	1934	2730
Episema glaucina	145	245	69	153	296
Eucarta amethystina	70	52	168	102	326
Euxoa aquilina	372	232	111	94	88
Euxoa decora	997	542	395	720	349
Hadena magnolii	225	158	120	252	224
Hoplodrina superstes	231	235	230	162	171
Mythimna sicula	633	664	797	1274	3008
Ochropleura musiva	475	172	130	134	96
Phlogophora scita	382	220	161	120	98
Polymixis xanthomista	717	435	611	1194	622
Polyphaenis sericata	159	219	317	708	3537
Trigonophora flammea	331	465	330	1034	1761
Total Occurrences	**10165**	**8431**	**9559**	**21440**	**38817**

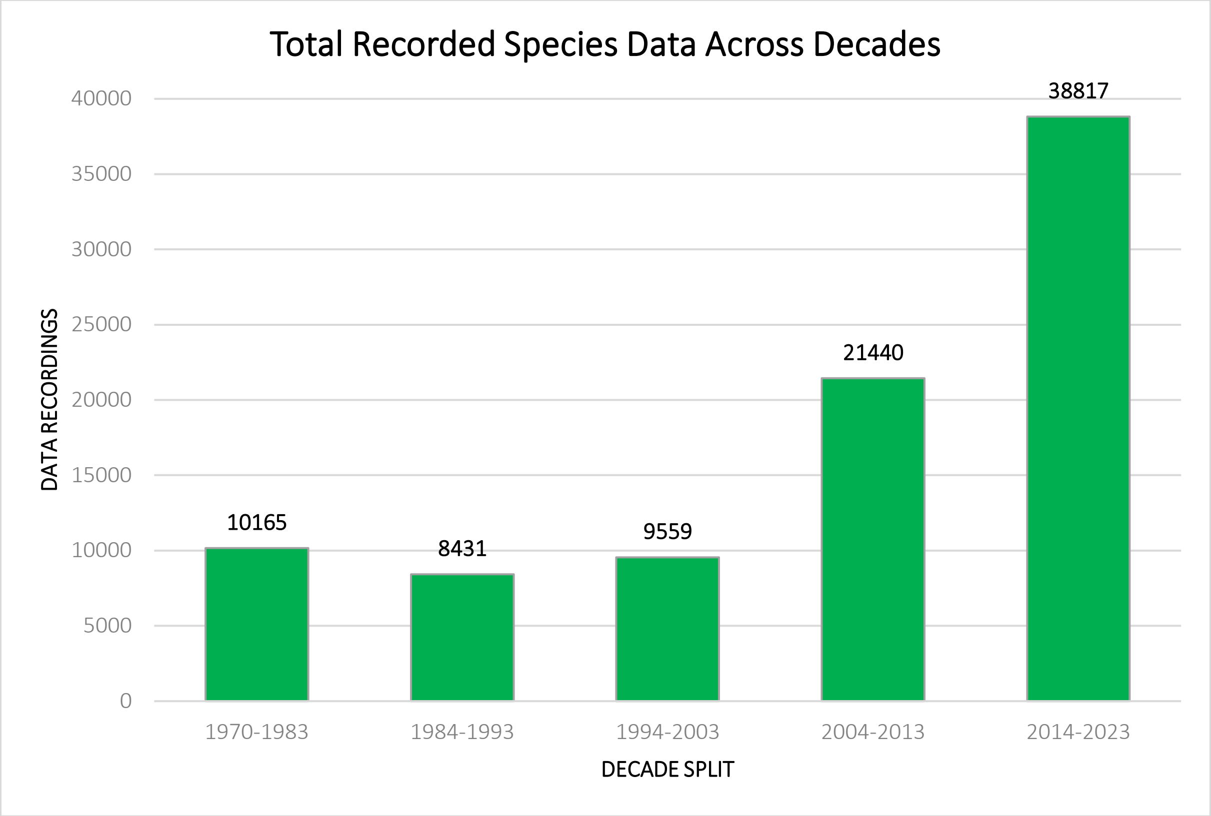

Figure 2: Bar chart visualizing the total number of available species data in the dataset (y = data recordings) for all moth species across decade intervals (x = decade split): |1970-1983| 1984-1993|1994-2003|2004-2013|2014-2023|

Fig. 2 depicts the quantity of available moth species data in my dataset compiled from GBIF for each decade, spanning from 1970 to 2023. The graph shows a noticeable upward trend from 2004 onwards. Initially, available data recordings were relatively modest, with around 10,000 per decade. Substantial increases in available data are evident in the last two decades. This trend may reflect enhanced monitoring efforts as well as creased internet connectivity and database accessibility amongst citizen science entomologists.

3.1 STATISTICAL TEST RESULTS

TABLE 2: Species list including statistical test results: one-way Anovas (non-parametric) and Fligner-Kileen tests (non-parametric) – tested dependent variable: latitude coordinate, grouping variable: decade split = |1970-1983|1984-1993|1994-2003|2004-2013|2014-2023|with ($p \leq 0.05$) and *df*=4.

Species list	**Kruskal Wallis χ^2**	**Kruskal Wallis p**	**Fligner-Kileen χ^2**	**Fligner-Killeen p**
Aedia leucomelas (Linnaeus, 1758)	15.9	**0.003**	17.026	**0.001**
Athetis hospes (Freyer, 1831)	812	**<.001**	346.88	**<.001**
Auchmis detersa (Hufnagel, 1766)	40.8	**<.001**	317.3	**<.001**
Autographa aemula (Denis & Schiffermüller, 1775)	158	**<.001**	7.3727	**0.117**
Calliergis ramosa (Esper, 1786)	43.6	**<.001**	126.14	**<.001**
Callopistria latreillei (Duponchel, 1827)	489	**<.001**	292.41	**<.001**
Caradrina gilva (Donzel, 1837)	267	**<.001**	147.84	**<.001**
Caradrina kadenii (Freyer, 1836)	3137	**<.001**	134.83	**<.001**
Chersotis margaritacea (Villers, 1789)	182	**<.001**	219.23	**<.001**
Chersotis multangula (Hübner, 1803)	220	**<.001**	366.49	**<.001**
Cucullia verbasci (Linnaeus, 1758)	321	**<.001**	433.71	**<.001**
Egira conspicillaris (Linnaeus, 1758)	142	**<.001**	607.56	**<.001**
Episema glaucina (Esper, 1789)	156	**<.001**	243.23	**<.001**
Eucarta amethystina (Hübner, 1803)	90.9	**<.001**	69.837	**<.001**
Euxoa aquilina (Denis & Schiffermüller, 1775)	171	**<.001**	86.619	**<.001**
Euxoa decora (Denis & Schiffermüller, 1775)	37.7	**<.001**	213.87	**<.001**
Hadena magnolii (Boisduval, 1829)	212	**<.001**	93.104	**<.001**
Hoplodrina superstes (Ochsenheimer, 1816)	59.3	**<.001**	173	**<.001**
Mythimna sicula (Treitschke, 1835)	1856	**<.001**	742.57	**<.001**
Ochropleura musiva (Hübner, 1803)	170	**<.001**	109.32	**<.001**
Phlogophora scita (Hübner, 1790)	29.2	**<.001**	47.467	**<.001**
Polymixis xanthomista (Hübner, 1819)	18.4	**0.001**	98.626	**<.001**
Polyphaenis sericata (Esper, 1787)	68.9	**<.001**	567.71	**<.001**
Trigonophora flammea (Esper, 1785)	521	**<.001**	970.95	**<.001**

Across the 24 examined Noctuidae species, both Kruskal-Wallis and Fligner-Killeen tests generally showed significant results, indicating notable shifts in the distributions across the different decades in Europe. The significant results in both tests, indicate that both the central tendencies (median latitude) and the spread of their distributions (variances) have changed over time. For *Autographa aemula*, the non-significant Fligner-Killeen result (p = 0.117) suggests that while the median latitude may have shifted (Kruskal-Wallis test p <0.001), the latitudinal spread of its distribution has not significantly changed over the decades. Statistically significant results in the Fligner-Killeen test indicate that there are differences in the variances of the latitude distributions of the species, implying that the distribution patterns of these moth species have undergone considerable changes in terms of how widely they are spread across latitudes over the decades.

3.2 SPECIES SHOWING A NORTHWARD EXPANSION

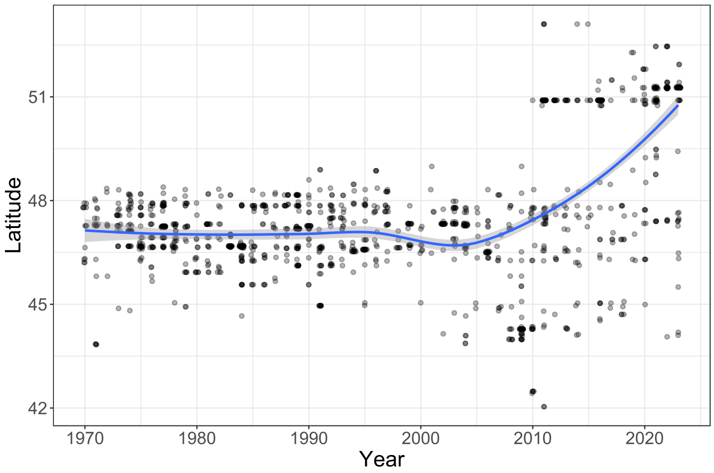

Figure 3: LOESS-regression showing *Caradrina gilva* (Donzel, 1837) latitudinal shift from 1970-2023

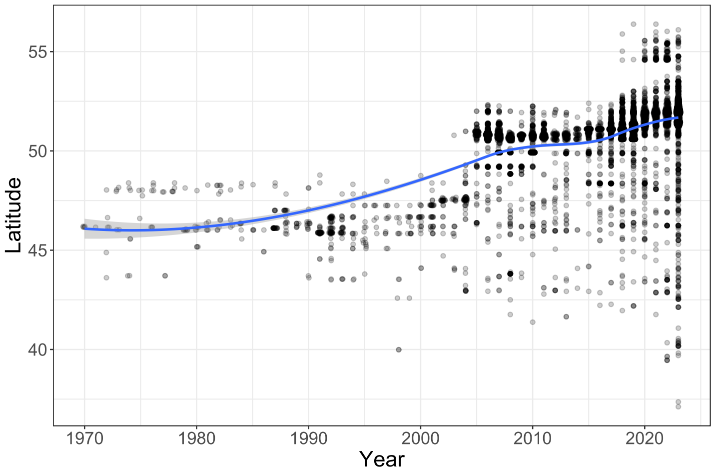

Figure 4: LOESS-regression showing *Caradrina kadenii* (Freyer, 1836) latitudinal shift from 1970-2023

Two out of the 24 tested moth species (viz. *Caradrina kadenii* and *Caradrina gilva*) revealed a substantial northward expansion of their European ranges (Fig. 3 and 4). LOESS-regressions reveal not only a pronounced overall expansion of distribution ranges but also a distinct northward shift in these two species, particularly since the 2000s. The observed changes are further elucidated in the Fig. 5 and 6.

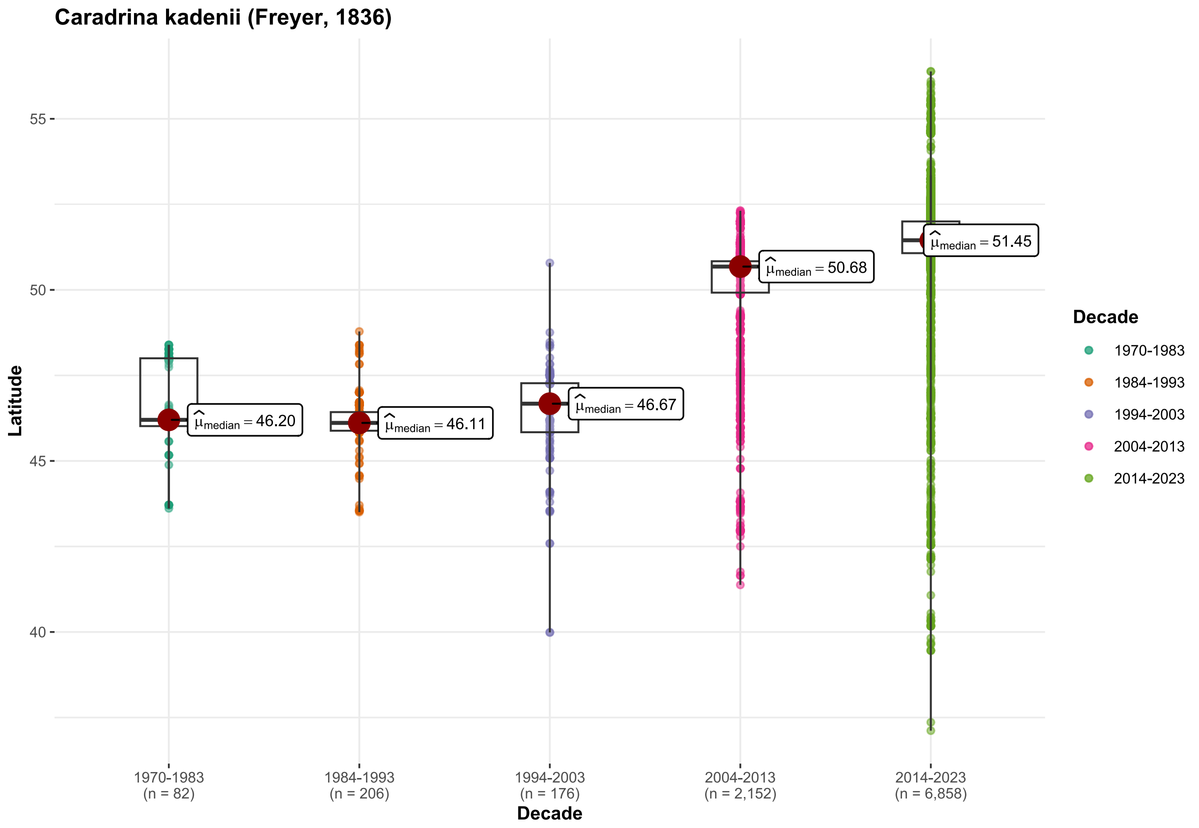

Figure 5: Boxplot of *Caradrina kadenii* (Freyer, 1836) records grouped into decades: |1970-1983|1984-1993|1994-2003|2004-2013|2014-2023|

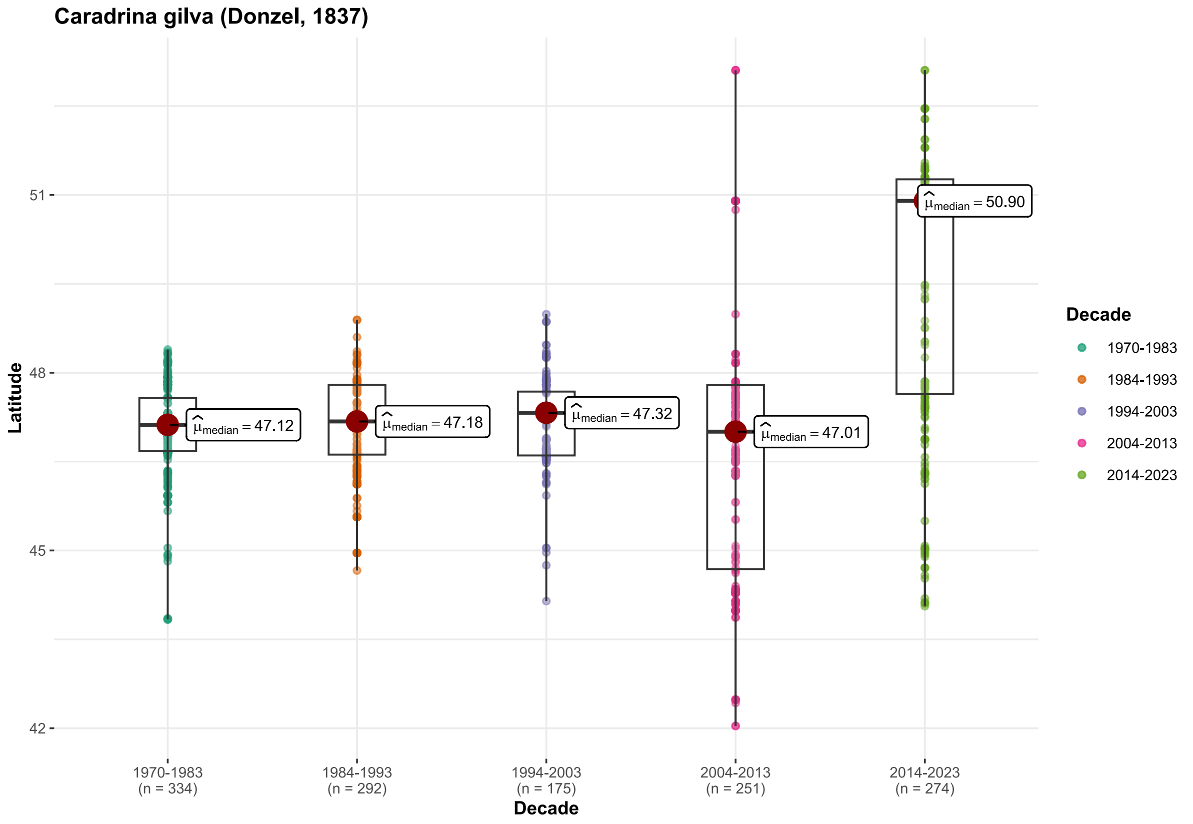

Figure 6: Boxplot of *Caradrina gilva* (Donzel, 1837) records grouped into decades: |1970-1983|1984-1993|1994-2003|2004-2013|2014-2023|

3.3 SPECIES SHOWING A SOUTHWARD EXPANSION

While only two out of 24 Noctuidae species revealed substantial northward expansions of their Central European ranges, in **9** species rather the reverse pattern became apparent from the analysis of distribution records hosted in GBIF. The most prominent southward shift is seen in *Athetis hospes*, *Hadena magnolii*, *Trigonophora flammea* and *Callopistria latreillei* (Figs. 7, 8, 9, 10).

Additionally, less pronounced southward shift tendencies were observed for *Mythimna sicula* (Fig. 11), *Egira conspicillaris* (Fig. 12), *Episema glaucina*, *Chersotis margaritacea* and *Polymixis xanthomista*.[1]

The LOESS regression for *Athetis hospes* shows an initially stable position in latitude until around the year 2005, followed by a strong decline in latitude afterwards suggesting that this species did not exhibit much change in its latitudinal distribution up to 2005. However, post-2000, there is a marked southward shift, indicating that this species has moved to lower latitudes in recent years.

Callopistria latreillei and *Hadena magnolii* show similar patterns indicating a gradual decrease in latitude since around 1995.

Trigonophora flammea initially showed a relatively stable distribution range, however starting around 2010, this

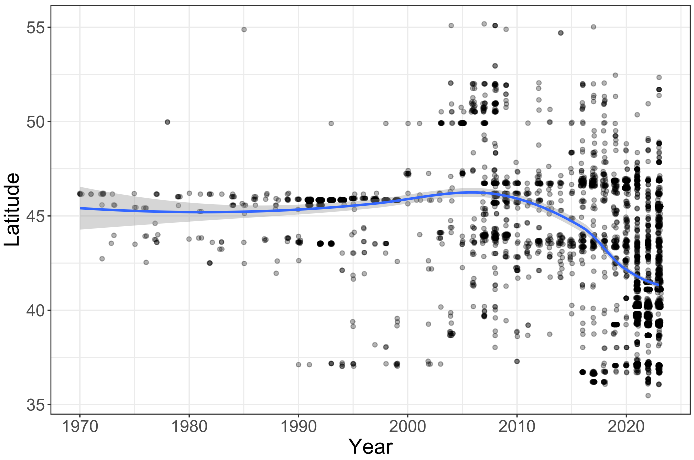

Figure 7: LOESS-regression showing *Athetis hospes* (Freyer, 1831) latitudinal shift from 1970-2023

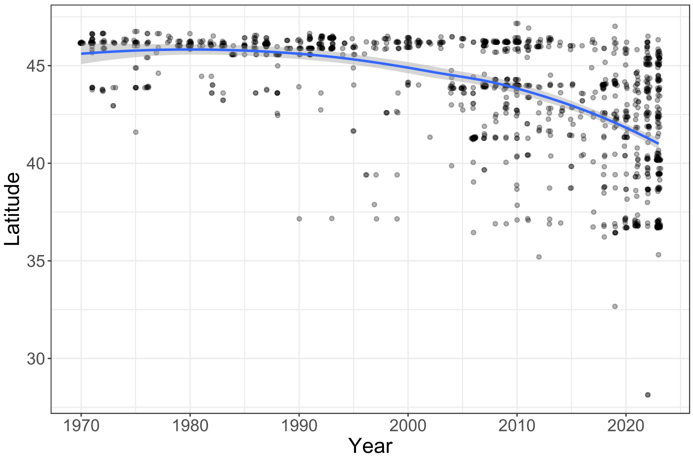

Figure 8: LOESS-regression showing *Callopistria latreillei* (Duponchel, 1827) latitudinal shift from 1970-2023

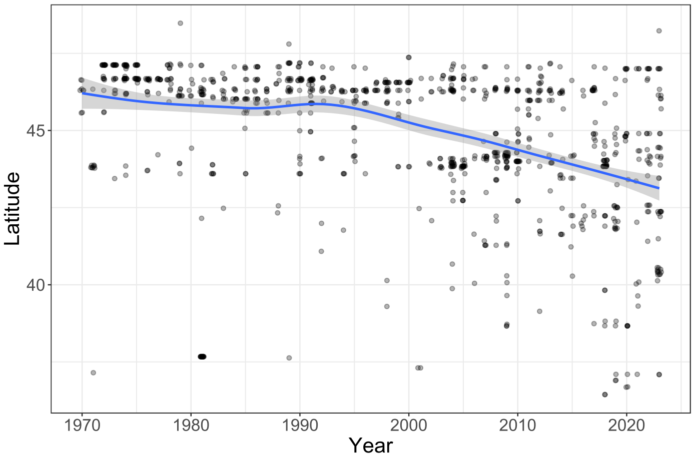

Figure 9: LOESS-regression showing *Hadena magnolii* (Boisduval, 1829) latitudinal shift from 1970-2023

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[1] *see Appendix: Figures 27, 28 and 35*

species has undergone a pronounced and steep southward shift. This latitudinal shift is accompanied by numerous expansions attempts towards the north and south, as indicated by the increased incidence of outliers particularly evident in the last two decades.

Similar patterns and putative expansion attempts can also be observed in *Athetis hospes*, *Mythimna sicula* and *Egira conspicillaris*.

Notably, *Mythimna sicula* exhibits an intriguing temporal pattern in its European distribution, initially showing indications of an overall northward expansion during the 1990s, followed by a gradual shift southward and lastly extending its distribution prominently in both directions but concentrating further south since the 2010s.

Egira conspicillaris demonstrates a slight southward adjustment. The prominent outliers in both directions suggest potential attempts by the species to expand its distribution range.

The observed changes are further elucidated and depicted in the box-and-whisker plot below, illustrating the notable shift in medians, particularly evident in the last 10 to 20 years (Figs. 13-18).

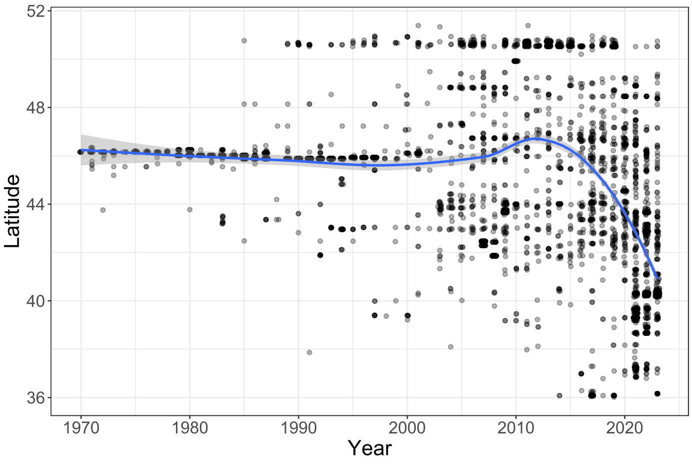


Figure 10: LOESS-regression showing *Trigonophora flammea* (Esper, 1785) latitudinal shift from 1970-2023

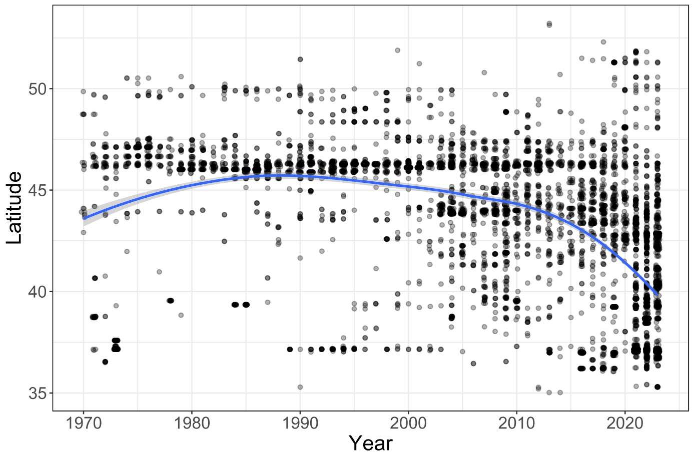


Figure 11: LOESS-regression showing *Mythimna sicula* (Treitschke, 1835) latitudinal shift from 1970-2023

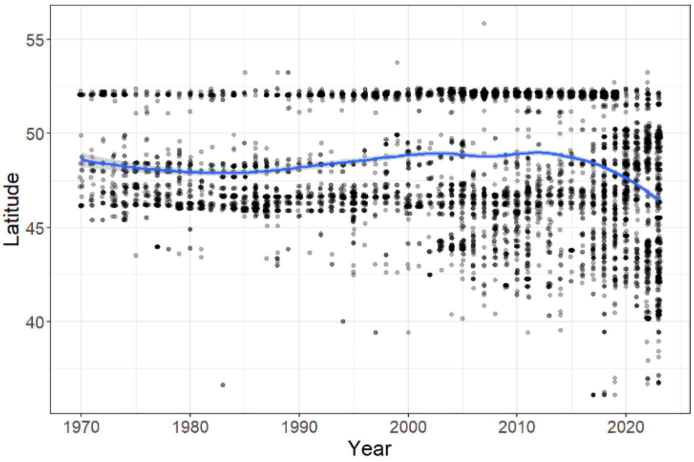


Figure 12: LOESS-regression showing *Egira conspicillaris* (Linnaeus, 1758) latitudinal shift from 1970-2023

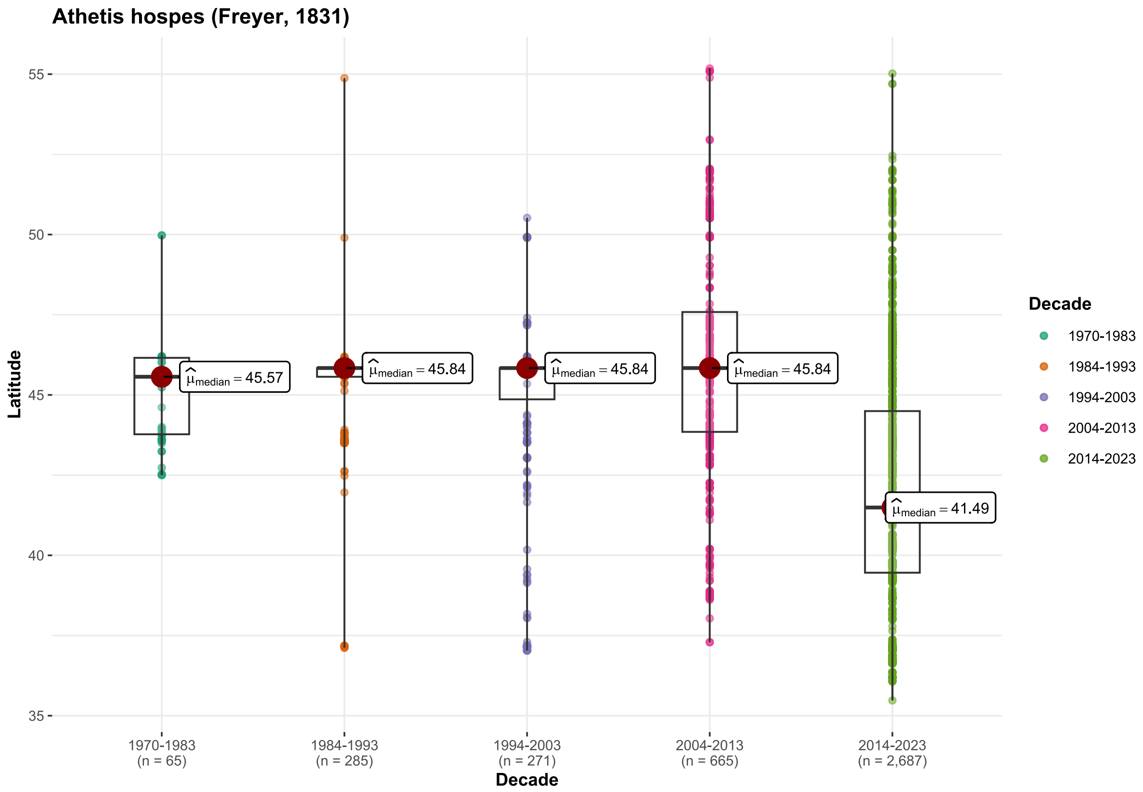


Figure 13: Boxplot of *Athetis hospes* (Freyer, 1831) occurrences grouped into decades: |1970-1983| 1984-1993|1994-2003|2004-2013|2014-2023|

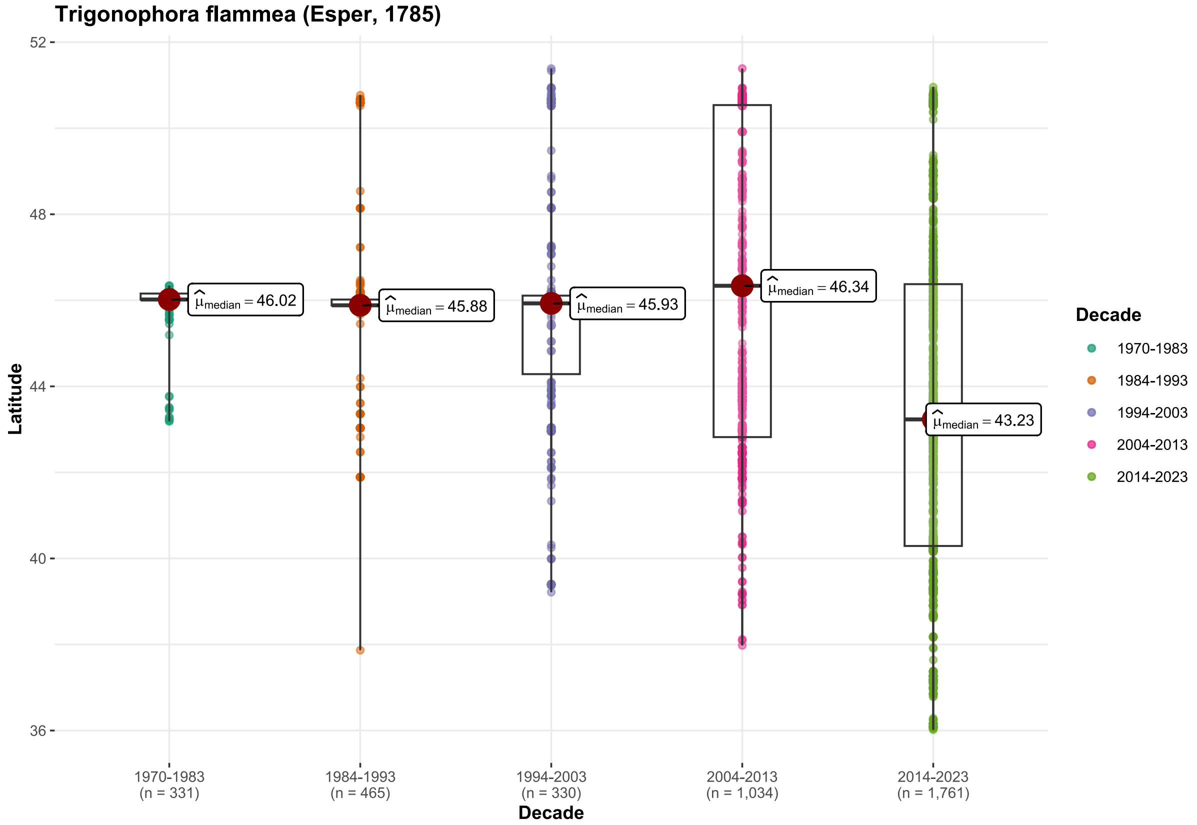


Figure 14: Boxplot of *Trigonophora flammea* (Esper, 1785) records grouped into decades: |1970-1983|1984-1993|1994-2003|2004-2013|2014-2023|

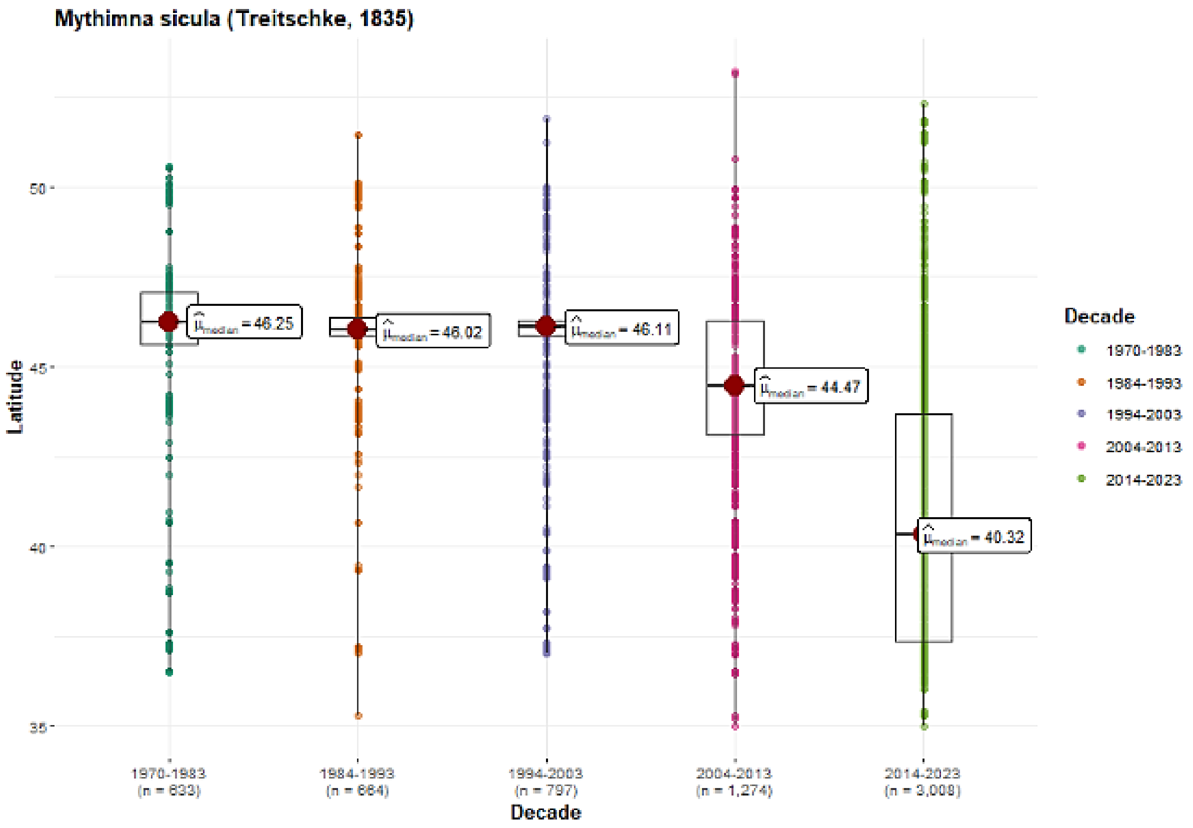


Figure 15: Boxplot of *Mythimna sicula* (Treitschke, 1835) records grouped into decades: |1970-1983| 1984-1993|1994-2003|2004-2013|2014-2023|

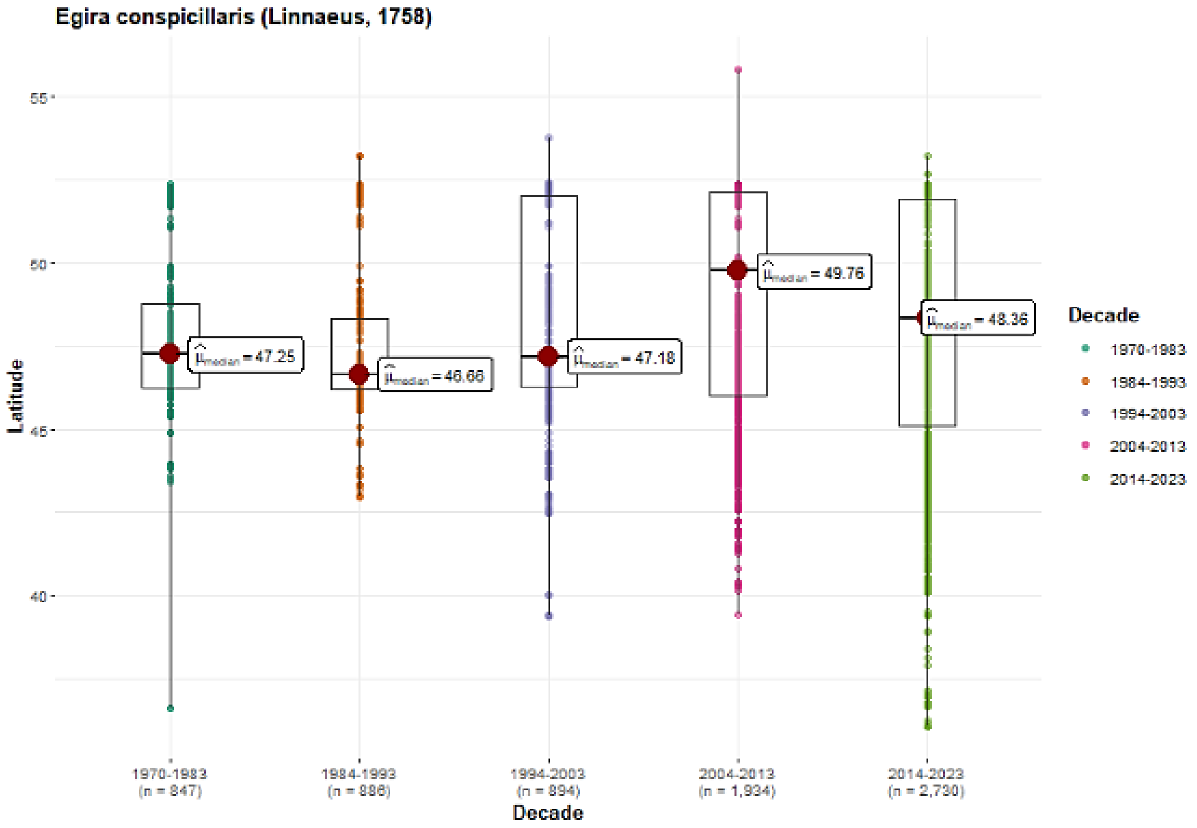
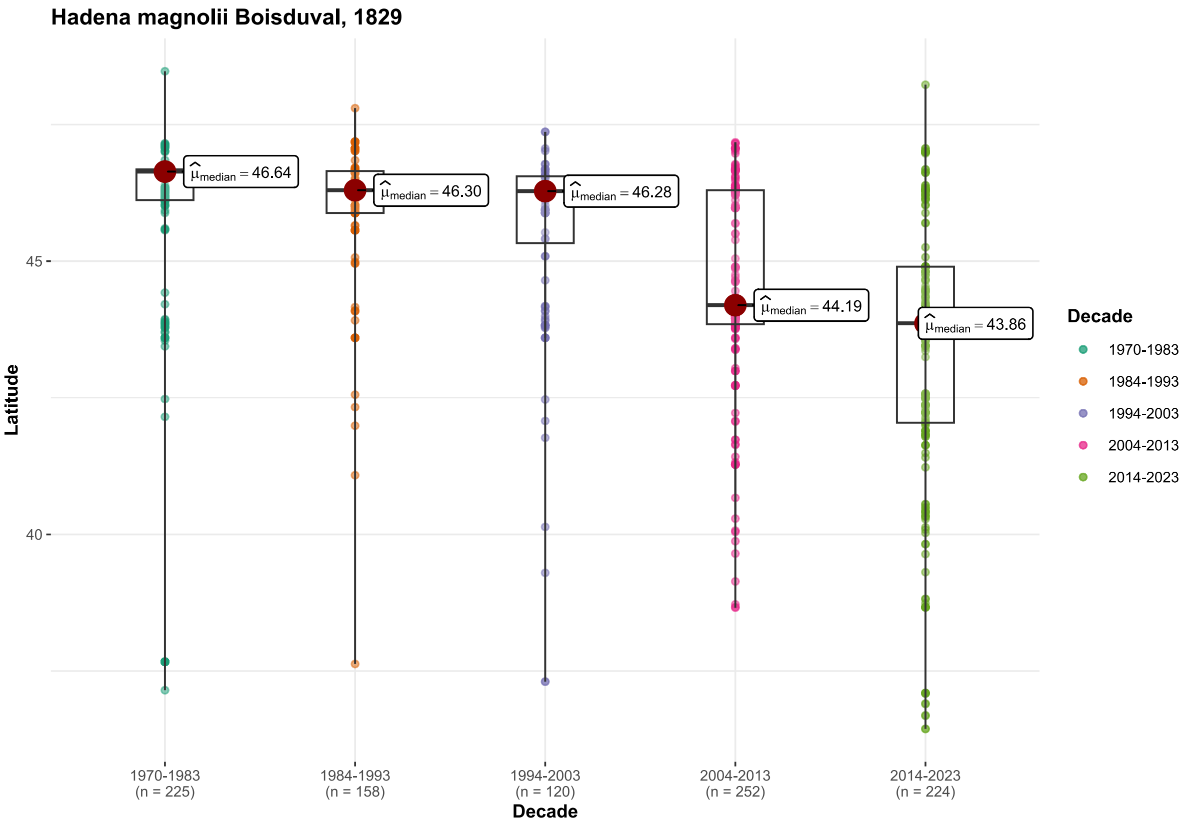
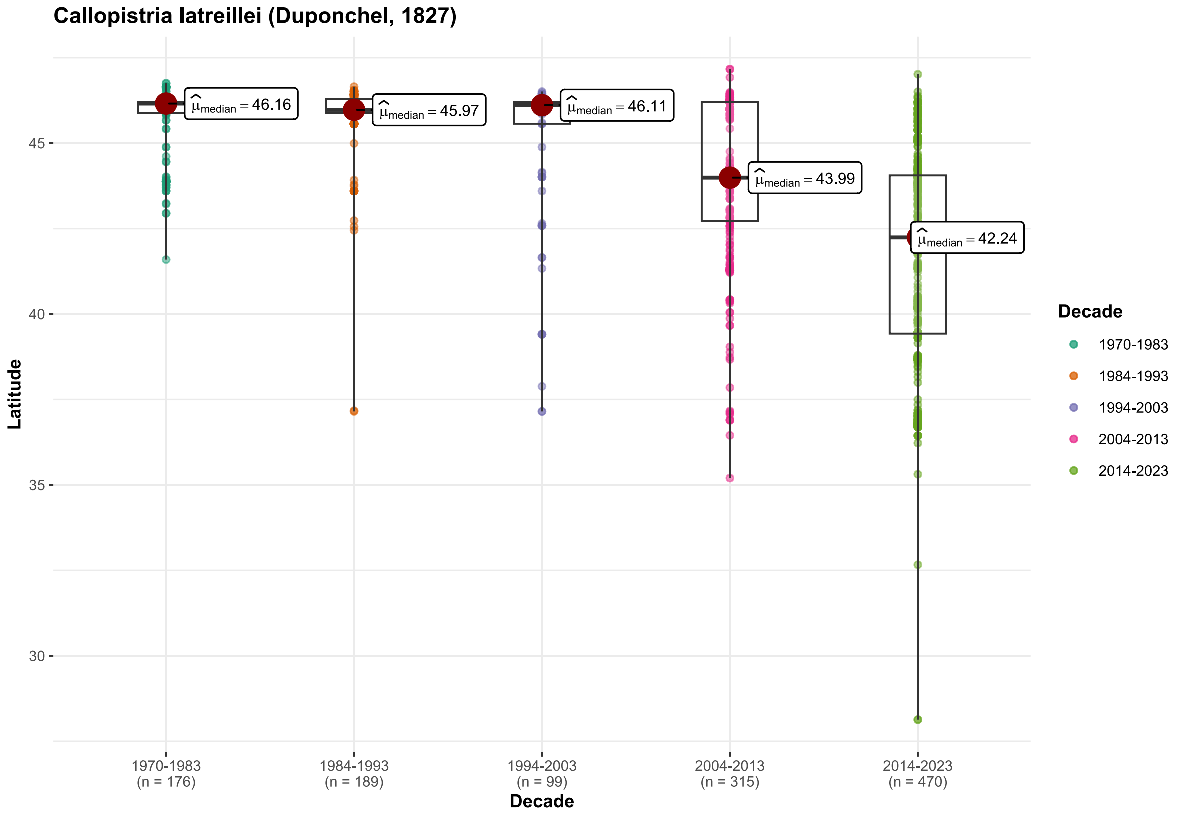


Figure 16: Boxplot of *Egira conspicillaris* (Linnaeus, 1758) occurrences grouped into decades: |1970-1983|1984-1993|1994-2003|2004-2013|2014-2023|



Hadena magnolii Boisduval, 1829

Figure 17: Boxplot of *Hadena magnolii* (Boisduval, 1829) records grouped into decades: |1970-1983|1984-1993|1994-2003|2004-2013|2014-2023|



Callopistria latreillei (Duponchel, 1827)

Figure 18: Boxplot of *Callopistria latreillei* (Duponchel, 1827) occurrences grouped into decades: |1970-1983|1984-1993|1994-2003|2004-2013|2014-2023|

3.4 SPECIES WITH EVIDENT EXPANSION BUT WITHOUT A CLEAR DIRECTIONAL EXPANSION

Looking at the LOESS regressions, the **3** species *Aedia leucomelas*, *Polyphaenis sericata* and *Cucullia verbasci*, seem to exhibit a discernible dispersal trend (Figs. 19, 20, 21). The data could also align with the interpretation that there have simply been more reports in recent decades, particularly from Mediterranean countries, due to increased participation from entomologists or institutions in data reporting.

Regarding *Aedia leucomelas*, putative expansion attempts appear to become more frequent starting around 2015, but there is no strong directional shift in latitude. Although it seems premature to assert a genuine expansion of the distribution range at this stage the presence of more data points suggests possibly a slightly wider distribution and increased reporting and documentation.

Putative expansion attempts seem more strongly evident in *Polyphaenis sericata* and *Cucullia verbasci*, particularly from the 2000s onward. However, there is no clear directional shift towards the north or south, but rather a general dispersal in both directions.

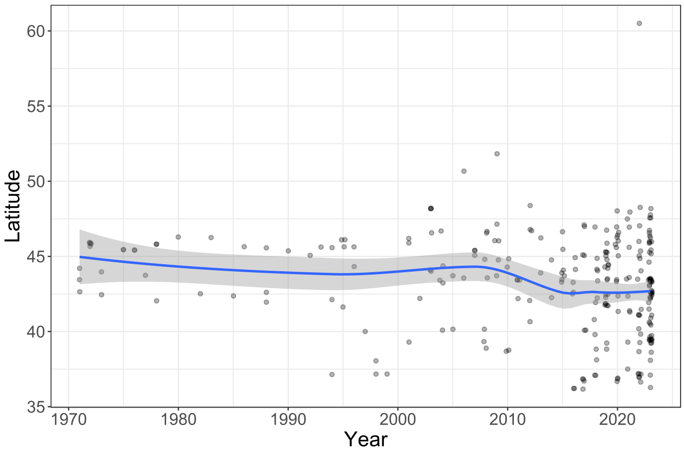


Figure 19: LOESS-regression showing *Aedia leucomelas* (Linnaeus, 1758) latitudinal shift from 1970-2023

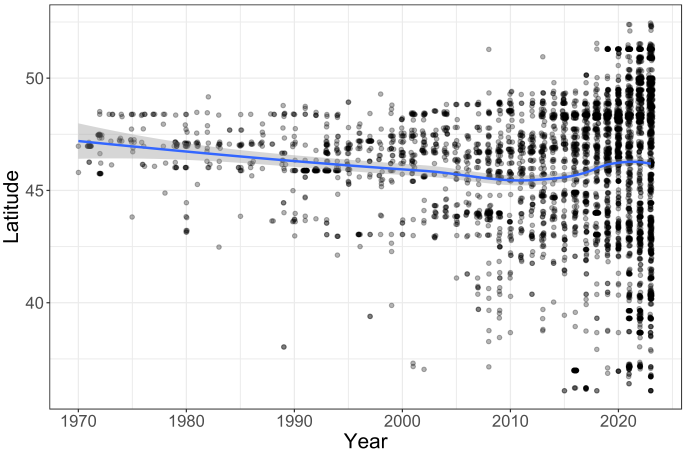


Figure 20: LOESS-regression showing *Polyphaenis sericata* (Esper, 1787) latitudinal shift from 1970-2023

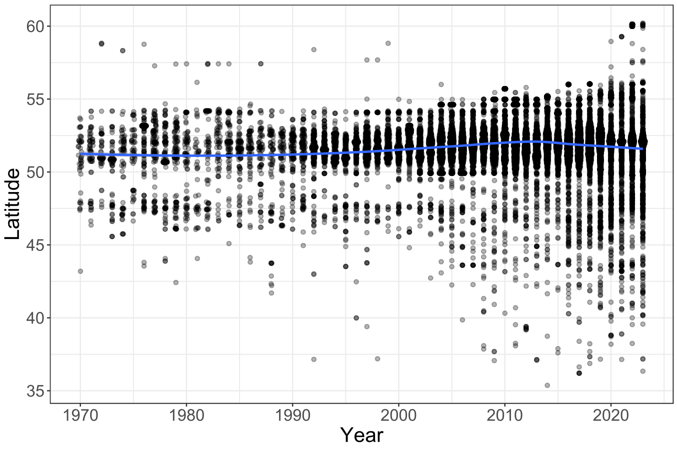


Figure 21: LOESS-regression showing *Cucullia verbasci* (Linnaeus, 1758) latitudinal shift from 1970-2023

3.5 SPECIES WITHOUT A CLEAR TREND

Among the depicted Noctuidae (Figs. 22, 23, 24), the **3** species *Euxoa decora*, *Calliergis ramosa* and *Autographa aemula* show no consistent trend over the observed 53-year timespan. Likewise, there appears to have been limited to no evident attempts at northward or southward expansion. Overall, the distribution of these three species in Europe seems to have remained largely unchanged over the years.

Similar observations were made for the remaining **7** species: *Hoplodrina superstes*, *Auchmis detersa*, *Eucarta amethystina*, *Ochropleura musiva*, *Chersotis multangula*, *Euxoa aquilina*, and *Phlogophora scita*.[2]

My analyses suggest a stable distribution pattern without observable shifts in latitude nor a notable increase in outlier occurrences, which could be interpreted as dispersing stray individuals outside the core ranges.

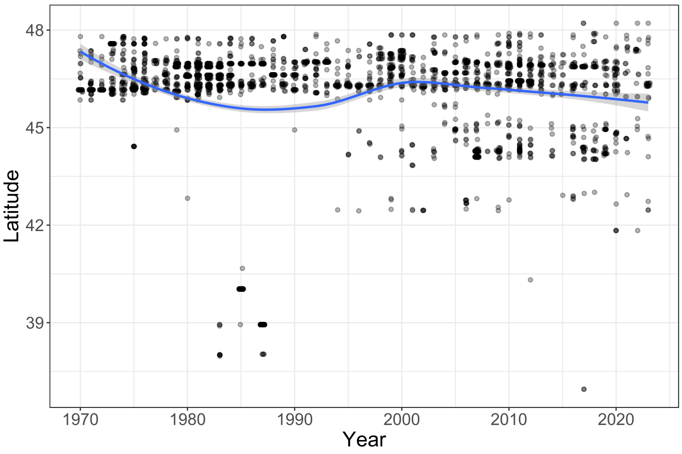


Figure 22: LOESS-regression showing *Euxoa decora* (Denis & Schiffermüller, 1775) latitudinal shift from 1970-2023

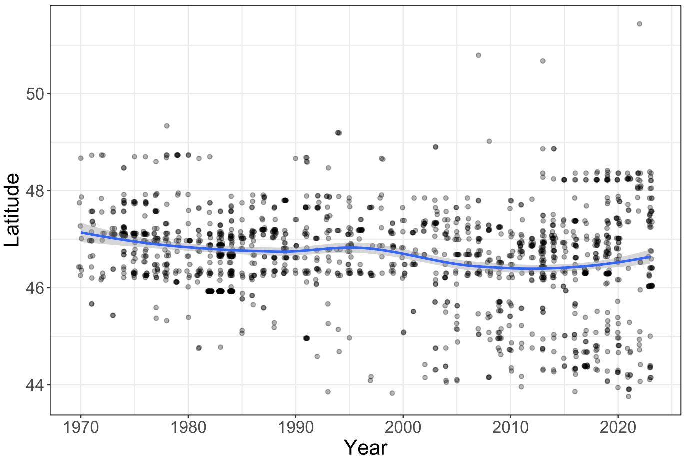


Figure 23: LOESS-regression showing *Calliergis ramosa* (Möschler, 1880) latitudinal shift from 1970-2023

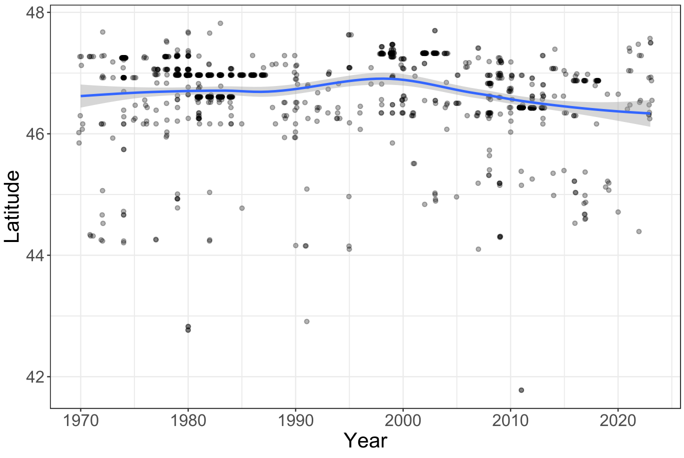


Figure 24: LOESS-regression showing *Autographa aemula* (Grote, 1864) latitudinal shift from 1970-2023

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[2] *see Appendix: Figures 25, 26, 29, 30, 31, 32, 33 and 34*

4. DISCUSSION

This study aimed to elucidate how a diverse array of 24 Noctuidae species in Central Europe have responded to recent rapid climatic changes by examining shifts in their geographic distribution over 53 years, in line with the well-documented trend of species adapting to climate change through latitude and altitude shifts (Schai-Braun *et al.*, 2021). Furthermore, this study tried to analyse whether the moths experiencing such distribution shifts share similar traits or ecological strategies that might be beneficial (or constraining) in the face of recent climate change.

Across all 24 examined Noctuidae species, the statistical tests revealed significant results indicating notable re-arrangements in species distributions in both latitude and spread over the past five decades. Only *Autographa aemula* showed a statistically significant results, implying potential changes in median latitude without significant variance in its distribution records, which could be contributed to faunal discoveries in under-researched regions, rather than a real expansion change (Huemer *et al.*, 2011). Notably, only 14 of the 24 species exhibited visible latitudinal alterations and distribution changes also according to the LOESS regressions, with most shifts becoming apparent between the 1990s and 2010s. Of these 14 species, 2 showed a distinct northward shift, 9 exhibited a dominant southward shift, and 3 displayed evident expansion without a clear directional trend in latitude.

4.1 BACKGROUND ANALYSIS OF NORTHWARD EXPANSION IN *CARADRINA KADENII* AND *CARADRINA GILVA*

Contrary to my initial expectation, only two species, *Caradrina kadenii* and *Caradrina gilva,* exhibited a strong northward shift. My initial hypothesis was that climate change would likely facilitate similar northward expansions in more species, as already shown and documented in multiple species of butterflies and moths responding to pronounced climate warming and the resulting expansion of suitable habitats in northern latitudes (Chen *et al.*, 2011; Sunde *et al.*, 2023; Hällfors *et al.*, 2024).

The results on *Caradrina kadenii* and *Caradrina gilva* are fully in line with other scientific documentations regarding their northward range expansions, which, based on the LOESS-regressions above (Figs. 3 and 4), began roughly in the 21st century (Ebert and Steiner, 1997, 1998; Ebert and Bastian, 2005; Sage, 2005; van Vuume, 2007; Tabbert, 2022). *Caradrina kadenii*'s newest documentation includes reaching Mecklenburg-Vorpommern by 2022, as well as Neubrandenburg and Negast near Stralsund in 2021, all in northeastern Germany: Tabbert, 2022). In 2006 the species was first recorded in the Netherlands, likely due to immigration (van Vuume, 2007). Even despite adverse weather conditions in 2005, *Caradrina kadenii* managed to expand continuously, favouring climatically suitable valleys along major rivers such as the Rhine, Danube, and Inn in southern Germany, historically important migration corridors for many species (Sage, 2005). *Caradrina kadenii*'s larvae are polyphagous, feeding on low growing herbaceous plants, including various dock species and dandelions (Ebert and Steiner, 1997, 1998). It typically inhabits warm, rocky areas, including open grasslands, meadows, and can tolerate occasionally disturbed and even urban habitats. *Caradrina gilva*, long considered a species confined to the Mediterranean region and the Southern Alps, began showing a notable range expansion in the 1980s, with a significant increase in reports from northwestern Europe. Interestingly, these documented sightings suggest that *C. gilva*'s northward expansion started even earlier than what I could find in the LOESS regression (Fig. 3) (Ebert and Steiner, 1997, 1998; Prins, Steeman and Sierens, 2015). This species primarily inhabits natural habitats in the Alpine region and southern Europe, favouring rocky and scree slopes. In Central Europe, it is more often registered in urban areas, suggesting an adaptation to anthropogenic niches resembling its natural habitats. Larvae develop in ruderal habitats such as roadsides, railway embankments, urban gravel paths, harbour embankments, building edges in construction areas, and gardens, as well as semi-dry and calcareous grasslands. These open, rocky areas with sparse vegetation and high light exposure enhance warmth retention, making them suitable habitats for this species (Ebert and Steiner, 1997, 1998). Both species demonstrate larval polyphagy, flexibility and adaptability to diverse habitats, including urban and humanly altered environments. These traits likely contribute to their successful northward range expansions amidst climate change and changing land use patterns.

Rödder's study demonstrated that warm-adapted butterfly species generally have been more successful in expanding their ranges and colonizing new areas in the northern Alps, especially where semi-natural habitats are dispersed. Such dispersed habitats offer significant advantages, including increased connectivity that forms a network of "stepping-stone" environments. This network facilitates the movement of warm-adapted species across broader areas and enables them to track shifting climate zones more effectively, migrating into regions that become suitable as temperatures rise (Rödder *et al.*, 2021).

4.2 BACKGROUND ANALYSIS OF SOUTHWARD EXPANSION SPECIES

Nine of the 24 analysed moth species showed a southward expansion of published records, with the most pronounced latitudinal patterns observed in *Athetis hospes, Hadena magnolii, Trigonophora flammea,* and *Callopistria latreillei*. This shift might not necessarily indicate a successful expansion; rather, it could suggest that these species are losing areas at their northern range limits, potentially due to habitat loss or land-use changes. These species, which are habitat specialists, might be retreating southward into Mediterranean and sub-Mediterranean areas as their northern populations increasingly come under pressure. This trend could also be influenced by an increase in reports from southern regions in recent decades due to more active entomological research there.

Many species within in this group, including *Athetis hospes, Hadena magnolii, Trigonophora flammea*, and *Callopistria latreillei*, demonstrate a marked preference for xerothermic environments while still displaying some level of adaptability when it comes to habitat usage, thriving in both natural and anthropogenic environments. Furthermore, many of these moths display polyphagous feeding behaviours as larvae and employ a variety of dormancy and reproductive strategies. These include producing multiple generations annually and having distinct life cycle timings. (Forster and Wohlfahrt, 1980; Ebert and Steiner, 1997, 1998; Wagner, 2005)

Athetis hospes warrants detailed discussion due to its rather conflicting results, which could be attributed to various factors. As a primarily Mediterranean species, *A. hospes* exemplifies adaptability to the warm climates typical of the Mediterranean hard-leaf zone (Wüst, 1994; Rennwald, 1995; Prins, 2008). Similar to *Caradrina kadenii* and *Caradrina gilva,* the polyphagous nature of *Athetis hospes* likely contributes to its range expansion, and its preference for warmth may offer advantages in the context of climate change (Horstmann, 2011).

Contrary to what the LOESS-regression (Fig. 7.) numerous recent records indicate a northward dispersion of *A. hospes*, possibly aided by human activities, although its presence in Central Europe remains sporadic and often results from accidental transportation. (Wüst, 1994; Rennwald, 1995; Prins, 2008; De Vos *et al.*, 2010; Szeőke and Avar, 2019). The LOESS-regression, while suggesting dispersion trends both north and south, leans more strongly toward a southward expansion trend. This may be linked to an increased frequency of *A. hospes* reporting's in the Mediterranean region, where the species may be increasingly perceived as a pest in numerous crops, such as cotton, maize, soybean, tomato, and beans. The implementation of potential management strategies for controlling Athetis hospes populations could further account for the increased monitoring and reporting of this species (Horstmann, 2011; CABI, 2022).

The relatively low number of individuals in northern populations (Wüst, 1994; Rennwald, 1995; Prins, 2008; De Vos *et al.*, 2010; Szeőke and Avar, 2019) may have been obscured by more extensive reporting from the south, potentially explaining why the LOESS-regression alone did not detect a northward expansion of *Athetis hospes,* unlike *Caradrina kadenii* and *Caradrina gilva.*

Hadena magnolii is a ponto-Mediterranean faunal element typically found in specific habitats characterized by rocky, steep, west-facing slopes that retain warmth until late in the evening. This thermal retention has been thought to favour the moths' nocturnal feeding flights (Ebert and Steiner, 1997, 1998). However, recent observations and analyses suggest a more complex picture of this species' response to climate change.

Contrary to my initial assumption that milder nights due to climate change might benefit *H. magnolii,* (Cox *et al.*, 2020) the LOESS-regression indicates that the species may rather be retreating southward in Central Europe. This trend might indicate that the specialized habitats of *H. magnolii*, being rocky xerothermic sites, are under pressure from various factors, such as land-use changes, potential eutrophication due to nitrogen deposition, and increased vegetation growth, like bushes encroaching on open areas (Sala *et al.*, 2000). Land-use change is the primary driver affecting biodiversity globally, especially in Mediterranean ecosystems, which often include rocky xerothermic sites. These sites are sensitive to land-use changes due to the high degree of specialization of their flora and fauna.

Human activities, such as agriculture and urban development, threaten these habitats by altering the land significantly. Furthermore, climate change, particularly warming and changes in precipitation, can drastically affect biodiversity in rocky xerothermic habitats. These ecosystems are adapted to specific climatic conditions, and any shifts can impact species survival and distribution. While increased nitrogen deposition and atmospheric CO2 levels are less directly impactful compared to land-use and climate change, they can still influence plant growth and soil chemistry in xerothermic sites. This can potentially alter species composition and ecosystem dynamics, further threatening biodiversity (Sala *et al.*, 2000).

Potential adaptability of moths to climate change is closely linked to their relationships with host plants, which are critical for their survival and reproduction (Hill *et al.*, 2021). In this case *H. magnolii*'s relationship with its host plants further complicates its response to environmental changes as the species primarily feeds on *Caryophyllaceae* flowers, such as *Silene nutans,* and occasionally on other *Silene* species, *Dianthus,* and *Saponaria* (Wagner and Beshkov, 2018). *Silene nutans,* mainly pollinated by nocturnal moths, occurs in xeric habitats like rock outcrops in dry, thermophilus grasslands, open woodlands and edges—habitats previously stated to be increasingly threatened by land-use and climatic changes (Sala *et al.*, 2000; Cornet, Noret and Van Rossum, 2022).

The southern retreat of *H. magnolii* could therefore also be linked to its host plant. Although *S. nutans* is widely distributed across Western Europe, extending to the Caucasus, southern Scandinavia, and Siberia, it is rare at its western border in regions like Great Britain, Northwest France, Belgium, and the Netherlands, showing patchy, vulnerable distribution with scattered populations (Van Rossum *et al.*, 1999). This scarcity could contribute to the moth's southern retreat, where host plant populations might currently be more abundant and better connected.

It is important to note that the southwestern areas to which *H. magnolii* is retreating are also threatened by climate change and face challenges similar to those in more northern habitats. Water is already a major limiting factor for Mediterranean vegetation, and increased drought could significantly impact population dynamics, especially for populations near their range limits. Aridification due to reduced precipitation in the Mediterranean region has been shown to negatively affect seedling recruitment and vital rates, such as fecundity and adult plant mortality, in *Silene nutans*. These negative effects are observed regardless of whether populations are at their warmer or colder distributional limits, further highlighting the need for targeted conservation strategies (Garnier *et al.*, 2021).

Callopistria latreillei predominantly inhabits the Mediterranean region and is documented in Central Europe only in Hungary, Slovenia, and once southern Austria, specifically in Carinthia (Huemer, 2013). This species occupies xerothermic, rocky habitats with fern-covered walls. The larval host plant is primarily *Asplenium ceterach*, which is abundant in the Mediterranean but scarce north of the Alps (Woodward and British Museum (Natural History), 1922; Kozár and Dávid, 1986; Wagner, 2005; Lubienski, 2017; Šumpich and Liška, 2018). Reports of the moth's northward movement are limited, with some specimens found in Czechia and South Tyrol (Huemer, 2013, 2020; Šumpich and Liška, 2018). This is noteworthy because, although *Asplenium ceterach* could support moth populations further north, the moth does not currently show significant expansion in that direction. In Germany, for instance, *A. ceterach* exhibits a distinct southwest-northeast gradient, with concentrations in the states of Rhineland-Palatinate, Hesse, and Baden-Württemberg, particularly in the Middle Rhine Valley and the river valleys of the Mosel, Lahn, Nahe, Main (Lubienski, 2017). Despite these potential habitats, the moth has not yet been observed in these regions.

The species more notable southward expansion attempts, as well as its southward latitudinal shift, can be observed in the LOESS-regression (Fig. 8). Both host plant and moth have demonstrated their physiological ability to cope with hotter and drier climates, which could contribute to their observed southward expansion. In southern regions, adult moths fly continuously across generations, with possible dormancy phases during dry summer periods (Wagner, 2005). Dormancy (e.g. diapause and quiescence) is an inactive state characterized by metabolic depression and halted development, enabling insects to survive harsh environmental conditions such as extreme temperatures, moisture scarcity, and reduced food quality or availability (Lee, 2009; Wadsworth *et al.*, 2013). Their ability to withstand harsh climatic conditions, such as drought and extreme temperatures, may provide them with a survival advantage during the increasingly frequent heatwaves and dry periods in the Mediterranean region, where they appear to be expanding. This adaptability could enhance their resilience to recent climate change, especially given their established preference for warm environments.

Mythimna sicula, Egira conspicillaris, Episema glaucina, Chersotis margaritacea, and *Polymixis xanthomista* have shown less pronounced southward shifts in the LOESS-regression compared to the more robust latitudinal shifts and, in some cases, range expansions observed in species like *A.hospes.* Nonetheless, they share important traits with these species that are more pronounced in their southward expansion:

Most moth species in this group demonstrate a strong association with xerothermic habitats, favouring dry, rocky slopes, walls, embankments, and other sun-exposed areas. They occasionally utilize calcareous, semi-dry, dry grasslands and rarely urbanised habitats. Furthermore, the widespread prevalence of oligo- and polyphagy among those moth species is also notable (Forster and Wohlfahrt, 1980; Ebert and Steiner, 1997, 1998). Although traits such as warm adaptation have been shown to be favoured by recent climate change (Betzholtz, Forsman and Franzén, 2023; Hällfors *et al.*, 2024) most moths in this group seem to have not significantly benefited from climate warming. Their expansion is potentially constrained by the scarcity of suitable habitats in managed landscapes, where land use changes impose significant limitations. Moreover, many of their current habitats are expected to become increasingly threatened by climate and land use change in the future (Sala *et al.*, 2000).

4.3 BACKGROUND ANALYSIS ON SPECIES WITH EVIDENT EXPANSION BUT WITHOUT A CLEAR DIRECTIONAL SHIFT

The species *Aedia leucomelas*, *Cucullia verbasci*, and *Polyphaenis sericata* have demonstrated notable expansions in their distribution as evidenced by my statistical. Although an expansion is visible, there is no clear northward or southward shift in their latitudinal distribution. Despite the lack of a directional latitudinal shift, the significant increase in sightings outside their typical range suggests an adaptive response to environmental changes, likely driven by climate change and shifts in habitat availability.

Like other species that have exhibited latitudinal shifts or range expansions in this study, these three moth species share their thermophilic nature, which likely facilitated their expansion in response to rising global temperatures (Rödder *et al.*, 2021).

Aedia leucomelas (Linnaeus, 1758), was initially included in the dataset despite having only 265 data points, due to its particularly notable occurrences over the past 25 years This thermophilic species, typically found in Mediterranean to subtropical regions, has been recorded increasingly north of the Alps and Hungary. Since 2006, migratory specimens of *A. leucomelas* have been recorded in southern England, with individual sightings in the Netherlands in 1987 and 2014. In 2023, Mégane Thery and Thomas Huet documented an individual near the Seine at Sotteville-sous-le-Val, marking the first observation for the Seine-Maritime département and one of the few records so far north in France. Steeman and Sierens reported the species for the first time in Belgium in 2022 (Szabóky, Uherkovich and Ábrahám, 2001; Knill-Jones, 2007; *De Vlinderstichting*, 2014; *Aedia leucomelas (Linnaeus, 1758)*, 2024; Bury, 2015; Steeman and Sierens, 2022).

This remarkable distribution and dispersal pattern, likely linked to its highly adaptable, successful and invasive host plant, bindweed (Convolvulaceae) (Steeman and Sierens, 2022).

Convolvulaceae, have successfully colonized temperate regions across all continents over the past 18 million years, exhibiting eight major disjunctions that explain its broad distribution. These generalist plants can thrive in diverse environments, tolerating soil pH ranging from 4 to 9 and moisture levels from riparian to dry habitats. Their extensive root systems confer significant drought resilience. Furthermore, field bindweed (*Convolvulus arvensis*) has exhibited strong invasive tendencies, particularly in disturbed ecosystems, demonstrating potentially advantageous traits that may confer a competitive edge in the context of recent climate change (Mitchell *et al.*, 2016; Steeman and Sierens, 2022).

Although the performed LOESS-regression (Fig. 19) failed to show a strong directional shift in latitude, both the performed Fligner-Killeen and Kruskal-Wallis tests yielded significant results, still suggesting a statistically significant re-arrangement of *A. leucomelas* distribution. his trend, particularly evident since the 2000s, is supported by numerous entomological studies (Szabóky, Uherkovich and Ábrahám, 2001; Knill-Jones, 2007; *De Vlinderstichting*, 2014; Bury, 2015; Steeman and Sierens, 2022), suggesting the possible onset of a northward expansion. While it is premature to confirm new population establishments, the adaptation of *A. leucomelas* to warm climates, along with the widespread availability of its highly invasive host plants, may facilitate its dispersal further and increase the likelihood of establishing new populations (*De Vlinderstichting*, 2014; *Aedia leucomelas (Linnaeus, 1758)*, 2024; Mitchell *et al.*, 2016; Steeman and Sierens, 2022).

Polyphaenis sericata thrives in thickets with abundant *privet (Ligustrum vulgare),* open woodlands, forest edges, overgrown dry grasslands and even urban areas. Observations from urban environments indicate that *P. sericata* has increasingly colonized anthropogenic habitats over the past few decades, likely due to the introduction and cultivation of its host plant, *Ligustrum vulgare*, in these settings (Ebert and Steiner, 1997, 1998). The anthropogenic cultivation of its host plants might increase connectivity, forming a network of "stepping-stone" environments that could potentially benefit the range expansion of *Polyphaenis sericata* (Rödder *et al.*, 2021).

Ligustrum vulgare thrive within urban environments, demonstrating their resilience and adaptability to a broad spectrum of habitats. *Ligustrum vulgare,* a versatile generalist prefers direct sunlight but is also shade-tolerant, allowing it to invade forest edges, shady areas, and degraded environments. It tolerates most soil types and thrives in humid areas. This plant flowers abundantly, producing over 10,000 fruits per shrub, each containing 1-4 seeds. These fruits are dispersed by birds and other wildlife, facilitating its spread into vegetated areas and further enhancing its invasive potential. Furthermore, a positive correlation has been observed between invasions and mean extreme maximum temperatures, with no invasions detected in areas where the mean extreme maximum temperature is below 35°C (95°F). This suggests that climate change, manifesting as increased maximum temperatures, could further facilitate the spread of this species (Ebert and Steiner, 1997, 1998; Wang and Grant, 2012; Ziller, 2022).

Since the 1980s, moths have been regularly observed, the Albvorland foothills, and the Kraichgau region, within and around towns and villages (Ebert and Steiner, 1997, 1998). Additionally, studies increasingly show that, after decades of decline or absence in parts of Germany and Belgium, these moths have begun to reestablish themselves, effectively reclaiming lost historical territory (Prins, 2016; Füldner, 2020; Zub, Nässig and Weyh, 2024). Together, these studies, along with the statistical results and LOESS-regression (Fig. 20), indicate an intensification and significant dispersal of the species both northward and southward, especially since the 2010s.

Cucullia verbasci is primarily found in warm, xerothermic, and open landscapes, exhibiting the widest habitat range among the brown noctuid moths. This species inhabits both small and large associations of native and various species of *Verbascum* (mullein) plants, occasionally thriving on solitary plants, butterfly bush (*Buddleja davidii*) and figwort (*Scrophularia spp.*). *Cucullia verbasci* thrives in a variety of environments including edge communities, rocky and gravelly areas, stone walls and dry-stone terraces in vineyards, the periphery of dry grasslands, quarry sites, ruderal areas, debris heaps, dry roadsides, embankments, railway tracks, sandy and gravelly plains, and sometimes the edges of open forests or wide forest paths. It has even managed to inhabit more urbanized areas with *Verbascum* occurrences, such as gardens and parks, provided these areas offer a certain level of warmth and dryness (Ebert and Steiner, 1997, 1998).

Cucullia verbasci's preference for warm, dry, open landscapes, its adaptability to diverse and even urban habitats, and its reliance on the ubiquitous and common host plant *Verbascum* all contribute to its recent successful dispersal and range expansion. Its resilience during intensifying heatwaves and dry periods could further enhance its success even in the face of climate change (Ebert and Steiner, 1997, 1998).

In conclusion, the observed expansions of *Aedia leucomelas*, *Cucullia verbasci*, and *Polyphaenis sericata*, despite lacking a clear directional shift, highlight their adaptability to warm climates and their advantage from the widespread availability and even anthropogenic cultivation of their host plants maybe serving as "stepping-stone" habitats. Their ability to thrive in diverse environments, including anthropogenic and semi-natural habitats could have facilitated the successful in expanding their ranges and colonizing new areas potentially further help their expansion (Rödder *et al.*, 2021). Climate change, with its rising maximum temperatures, may continue to facilitate the spread of these species and their associated host plants, potentially allowing them to establish stable populations in new areas in the future (Steeman and Sierens, 2022).

4.4 BACKGROUND ANALYSIS ON SPECIES WITHOUT A CLEAR TREND

Lastly, 10 out of the 24 Noctuidae species studied showed no observable trend in their distributions. These species included *Euxoa aquilina, Euxoa decora, Calliergis ramosa, Autographa aemula, Hoplodrina superstes, Auchmis detersa, Eucarta amethystina, Dichagyris musiva, Chersotis multangula,* and *Phlogophora scita.*

Many of these moth species exhibit common traits and share similar habitat preferences, displaying high specialization and adaptation to specific environments like rocky slopes, dry grasslands, and montane areas. Preferred habitats typically have average annual temperatures between 6 and 9°C, indicating their adaptation to cooler conditions. Climate change is causing rising temperatures that alter habitat conditions, particularly in mountainous regions (Knight, 2022). This is particularly concerning, for biodiversity in these areas, as many species occupy specific climatic niches and exhibit high ecological specialization, making them highly sensitive to environmental change (Rödder *et al.*, 2021).

Euxoa decora for example is a mountainous species that typically inhabits rocky and stony environments. It is often found in vegetation-poor, sun-exposed steep slopes and scree, even above the treeline. Specific habitat preferences like those can greatly restrict its ability to adapt or migrate to other environments, thereby limiting its potential for successful dispersal and range expansion, increasing their risk of endangerment or even extinction in the long run (Forster and Wohlfahrt, 1980; Ebert and Steiner, 1997, 1998; Rödder *et al.*, 2021; Wagner, no date c). Our species pool illustrates this trend: 8 out of 10 species for which no visible trend was detected have declined, with *Dichagyris musiva* even having gone extinct in Germany (last recorded in 1950) (*Eulenfalter, Trägspinner, Graueulchen (Lepidoptera: Noctuoidea)*, no date).

Overall, many of these species seemingly prefer mountainous regions, where they occupy specific altitudinal ranges. This implies that these species have limited potential to adapt their horizontal distribution to climate change, thereby appearing to have a stable trend in our analyses. However, these species may experience shifts in vertical or altitudinal distribution. As temperatures rise, suitable habitats may shift upward, potentially leading to habitat loss if they cannot migrate to higher altitudes (Rödder *et al.*, 2021). This phenomenon is not well-captured by historical GBIF data, due to the lack of reliable altitude information.

For instance, *Calliergis ramosa* is typically found in the Alps up to about 1800 meters, indicating its preference for specific elevation ranges. Similarly, *Autographa aemula* and *Dichagyris musiva* occupy montane to subalpine habitats usually at elevations of 1000 to 2000 meters. *Phlogophora scita* also resides in mountainous areas (Ebert and Steiner, 1997, 1998; Wagner, 2024, no date d, no date a, no date b). The specialized altitude and temperature preferences of these species make them particularly vulnerable to climate change. As their preferred habitats shift upward, they may face significant challenges in finding new suitable environments, particularly when compounded by additional threats such as habitat loss and fragmentation (Rödder *et al.*, 2021).

Urbanization and agricultural intensification have resulted in habitat loss and fragmentation, which significantly affect population gene flow, adaptability, and species distributions. These changes may especially hinder successful dispersal for cold-adapted butterfly and moth species (Rödder *et al.*, 2021). Cold-adapted and specialist species in general have been shown to face increased extinction risks in fragmented environments as their survival depends on finding suitable patches (Fourcade *et al.*, 2021; Rödder *et al.*, 2021).

Several moth species in this group exhibit a degree of monophagy, relying on specific host plants for their larvae. This dependence can also further restrict their distribution especially if these plants are affected by climate change. For instance, *Chersotis multangula* exclusively feeds on *Galium* species, while *Calliergis ramosa* primarily feeds on *Lonicera xylosteum* and other *Lonicera* species. *Lonicera xylosteum* is already experiencing visible changes in its growing season due to climate change. There are indications that the timing of autumn leaf senescence is being affected, influencing the plant's performance and its role in biogeochemical cycles. These changes can directly impact specialized herbivores. The nutritional quality of the plant (such as carbon, nitrogen, and defensive metabolites) directly affect potential and achieved herbivore fecundity upon which a caterpillar feeds directly affects the caterpillar's developmental time, survival, adult mass, and fecundity (Awmack and Leather, 2002).

Additional indirect effects of climate change include changes in competitive dynamics among plant species, which may benefit invasive species at the expense of native ones, reshaping species composition and even the broader ecological community in ecosystems that host Lonicera species (Vardanyan *et al.*, 2024). Even species with some dietary variety, like *Autographa aemula*, are particularly associated with specific herbaceous plants found only in montane habitats (Ebert and Steiner, 1997, 1998; Wagner, no date b).

In summary, factors such as habitat specialization, larval monophagy, dependence on specific host plants, and restricted altitudinal ranges—combined with population and habitat fragmentation, habitat loss, and increased vulnerability to climate change—may limit these moth species' ability to expand their horizontal distribution in response to climatic changes from 1970 to 2023. However, it is important to note that shifts in vertical or altitudinal distribution might occur that are not visible in our statistical analysis due to the limitations in historical GBIF data, which lacks reliable altitude information.

4.5 OTHER POTENTIAL CONTRIBUTING VARIABLES

While many studies support the results discussed, it is essential to consider potential biases and other influencing factors. The statistical analysis might be biased due to increased reporting activity of citizen scientists since the 2000s, particularly from the Mediterranean region, as more entomologists and institutions have participated in monitoring efforts, data collection, and reporting. Additionally, the limited data available before the 1990s introduces another bias, as the rise of internet use and online databases has provided more data for the more recent years of the study period.

Generally, the number of available data points from countries such as the Balkan states, Spain, Portugal, and Italy is significantly lower throughout the 53-year study period compared to countries like England, Germany, Switzerland, and Austria. This discrepancy may lead to the observed dispersal and latitudinal trends being either exaggerated or underestimated.

Moreover, there is a potential identification bias concerning various Noctuidae species, as the data were collected online and cannot be fully verified for quality. Although I have made strong efforts to exclude the most difficult-to-identify species from the study and eliminate obvious misidentifications, some identification errors in the GBIF data cannot be entirely ruled out. Assessments of species identifications in GBIF revealed notable taxonomic inconsistencies highlighting the need for continuous taxonomic updates and caution when using biodiversity big data to avoid misleading conclusions (Freitas *et al.*, 2020). Moreover, an investigation into the completeness and geographical biases of insect data within the Global Biodiversity Information Facility (GBIF) has shown that GBIF, despite being the largest primary biodiversity database, does not fully represent the global distribution of insects. Although our study covered a smaller range compared to the global scale, potential biases in the data still need to be considered (Garcia-Rosello *et al.*, 2023).

4.6 FUTURE RESEARCH QUESTIONS AND TOPICS

This study highlights several key areas for further research into how moth species are responding to climate change. First, there is a need for expanded data coverage, particularly in Mediterranean countries and regions like Romania, where data limitations prevented their inclusion in this study. Additionally, some moth species remain inadequately documented in terms of their life history, ecology, and larval host plants. Comprehensive data on these aspects is essential for developing a clearer understanding of population dynamics and potential range shifts, especially given the critical role insects play in ecological functions. This underscores the urgency of obtaining more representative data to improve predictive capabilities, particularly in light of the alarming decline in insect diversity and abundance (Garcia-Rosello *et al.*, 2023).

Expanding research to include a broader range of moth species and regions beyond Europe would greatly enhance our understanding. A global perspective would offer a more comprehensive view of distribution patterns and the factors driving change, providing insights applicable across diverse environments. Additionally, examining potential shifts in altitudinal ranges, particularly in species with a strong affinity for mountainous habitats, could reveal important trends. Many species in this study are found at specific elevations, and understanding how these altitudinal preferences might be changing could offer valuable information about their response to shifting climates.

Investigating potential adaptations and changes in biotic interactions, such as identifying new or alternative host plants in newly colonized areas or as a consequence of climate change, is another promising area of research. This approach could provide valuable insights into how species may respond to rapid environmental changes (Bovay *et al.*, 2024; Zhang *et al.*, 2024).

Additionally, assessing the ability and the limits of moths and other Lepidoptera species to cope with climate change is vital. Understanding the impacts of extreme climate events, such as droughts and heatwaves, on even heat-tolerant species and their habitats will help identify emerging risks that could become increasingly prevalent in the future. This information is essential for developing targeted and effective conservation strategies.

By addressing these research gaps and exploring further ecological topics, we can deepen our understanding of how various species respond to climate change, including distribution shifts and threats to vulnerable species. This knowledge could inform effective conservation measures to protect vital components of terrestrial ecosystems and habitats.

5. CONCLUSION

This study provides compelling evidence that a diverse array of 24 Noctuidae moth species native to Europe have undergone significant distribution re-arrangements in response to recent rapid climate change over the past 53 years (1970-2023). The results reveal that 14 out of the 24 species examined have exhibited notable latitudinal changes in their distributions, with most shifts becoming apparent between the 1990s and 2010s. Specifically, two species showed a distinct northward shift, nine displayed a predominant southward shift, and three expanded their ranges without a clear latitudinal trend.

The study also found that the moth species which successfully expanded or shifted their ranges often share several common traits, including larval polyphagy, warm-adaptation, generalist habitat requirements, and the ability to utilize widespread human-introduced or climate-resilient host plants. These adaptations likely provide them with advantages, enabling them to more effectively track shifting climate zones and colonize new areas as conditions change.

In contrast, the 10 species that did not show a visible trend also exhibit shared traits. In summary, the interplay of habitat specialization, monophagy, dependence on specific host plants, restricted altitudinal ranges, along with population and habitat fragmentation, habitat loss, and heightened vulnerability to climate change, may be key factors limiting these moth species' ability to expand their distribution in response to changing climatic conditions from 1970 to 2023.

This study also revealed that theoretically advantageous traits does not necessarily guarantee success or range expansion in response to climate change as some studied moth species seemed constrained by the scarcity of suitable habitats in managed landscapes, where land use changes impose significant limitations.

These findings underscore the importance of understanding species responses to rapidly changing environmental and habitat conditions especially in the context of ongoing climate change, as they may inform conservation strategies aimed at protecting crucial components of terrestrial ecosystems and highlight the need for targeted measures to protect cold-adapted species, which are at higher risk of habitat loss, population decline and even extinction.

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8. APPENDIX

Table 3: All excluded Noctuidae species due to insufficient data in GBIF, as of November 11th, 2023

SPECIES	**DP COUNT**	**SPECIES**	**DP COUNT**	**SPECIES**	**DP COUNT**
Acosmetia caliginosa *(Hübner, 1813)*	510	Dichonia aeruginea *(Hübner, 1803)*	81	Polymixis serpentina *(Treitschke, 1825)*	45
Actebia fugax *(Treitschke, 1825)*	24	Dichonia convergens *(Denis & Schiffermüller), 1775*	531	Pseudluperina pozzii *(Curó, 1883)*	10
Actebia multifida *(Lederer,1870)*	18	Dryobotodes carbonis *(Wagner, 1931)*	72	Pyrrhia purpura *(Hübner)*	4
Actinotia radiosa *(Esper, 1804)*	222	Dryobotodes monochroma *(Esper, 1790)*	421	Rhyacia lucipeta *(Denis & Schiffermüller), 1775*	385
Aegle kaekeritziana *(Hübner, 1799)*	74	Enargia abluta *(Hübner)*	61	Rileyiana fovea *(Treitschke, 1825)*	27
Agrochola humilis *(Denis & Schiffermüller), 1775*	153	Epipsilia latens *(Hübner)*	447	Schinia cardui *(Hübner, 1790)*	133
Agrochola laevis *(Hübner, 1803)*	582	Episema tersa *(Denis & Schiffermüller), 1775*	36	Schinia cognata *(Freyer)*	44
Agrochola ruticilla *(Esper, 1791)*	671	Euchalcia consona *(Fabricius, 1787)*	41	Scotochrosta pulla *(Denis & Schiffermüller), 1775*	149
Amphipyra cinnamomea *(Goeze, 1781)*	92	Euxoa birivia *(Denis & Schiffermüller), 1775*	254	Shargacucullia blattariae *(Esper, 1790)*	10
Amphipyra tetra *(Fabricius, 1787)*	120	Euxoa culminicola *(Staudinger, 1870)*	375	Shargacucullia gozmanyi *(G.Ronkay & L.Ronkay, 1994)*	27
Anarta dianthi *(Tauscher, 1809)*	21	Euxoa distinguenda *(Lederer,1875)*	413	Shargacucullia prenanthis *(Boisduval, 1840)*	397
Apamea platinea *(Treitschke, 1825)*	661	Euxoa hastifera *(Donzel, 1848)*	65	Shargacucullia thapsiphaga *(Treitschke, 1825)*	40
Apaustis rupicola *(Denis & Schiffermüller), 1775*	29	Hadena christophi *(Möschler, 1862)*	0	Sideridis kitti *(Schawerda, 1914)*	473
Atethmia ambusta *(Denis & Schiffermüller), 1775*	80	Hadena luteocincta *(Rambur, 1834)*	131	Sideridis lampra *(Schawerda, 1913)*	695
Athetis furvula *(Hübner)*	180	Hadena tephroleuca *(Boisduval, 1833)*	587	Simyra nervosa *(Denis & Schiffermüller), 1775*	110
Bryophila felina *(Eversmann, 1852)*	8	Hecatera cappa *(Hübner)*	103	Standfussiana dalmata *(Staudinger, 1901)*	20
Calophasia opalina *(Esper)*	130	Heliothis ononis *(Denis & Schiffermüller), 1775*	113	Tiliacea sulphurago *(Denis & Schiffermüller), 1775*	282
Calophasia platyptera *(Esper)*	366	Jodia croceago *(Denis & Schiffermüller), 1775*	593	Valeria jaspidea *(Villers, 1789)*	695
Caradrina aspersa *(Rambur, 1834)*	637	Lacanobia aliena (= "amurensis") *(Hübner)*	646	Valeria oleagina *(Denis & Schiffermüller), 1775*	337
Caradrina ingrata *(Staudinger, 1897)*	62	Lamprosticta culta *(Denis & Schiffermüller), 1775*	417	Vialophotia molothina *(Esper, 1789)*	313
Caradrina terrea *(Freyer, 1840)*	112	Meganephria bimaculosa *(Linnaeus, 1767)*	218	Xestia ochreago *(Hübner, 1790)*	621

Chersotis alpestris *(Boisduval)*	467	Mesogona acetosellae *(Denis & Schiffermüller), 1775*	697	Xestia viridescens *(Turati, 1919)*	37
Chersotis fimbriola *(Esper)*	680	Mesotrosta signalis *(Treitschke, 1829)*	0		
Chersotis rectangula *(Denis & Schiffermüller), 1775*	224	Mniotype solieri *(Boisduval, 1829)*	668		
Cleoceris scoriacea *(Esper, 1789)*	362	Mythimna andereggii *(Boisduval, 1840) NICHT WERTBAR*	3319		
Conisania leineri *(Freyer, 1836)*	548	Oligia dubia *(Heydemann, 1942)*	128		
Conisania poelli *(Stertz, 1915)*	133	Omia cymbalariae *(Hübner, 1809)*	221		
Conistra veronicae *(Hübner, 1813)*	203	Omphalophana antirrhinii *(Hübner, 1803)*	317		
Cryphia fraudatricula *(Hübner)*	412	Orbona fragariae *(Vieweg, 1790)*	133		
Cryphia receptricula *(Hübner, 1803)*	66	Oria musculosa *(Hübner, 1808)*	282		
Cucullia balsamitae *(Boisduval, 1840)*	26	Oxicesta geographica *(Fabricius, 1787)*	104		
Cucullia campanulae *(Freyer)*	600	Panchrysia deaurata *(Esper, 1787)*	189		
Cucullia dracunculi (*Hübner)*	43	Panchrysia vargenteum *(Esper, 1798)*	699		
Cucullia scopariae *(Dorfmeister, 1853)*	4	Perigrapha i-cinctum *(Denis & Schiffermüller), 1775*	180		
Cucullia xeranthemi *(Boisduval, 1840)*	181	Periphanes delphinii *(Linnaeus, 1758)*	177		
Diachrysia nadeja *(Oberthür, 1880)*	256	Photedes morrisii *(Dale, 1837)*	698		
Dichagyris candelisequa *(Denis & Schiffermüller), 1775*	505	Phyllophila obliterata *(Rambur, 1833)*	247		
Dichagyris forcipula *(Denis & Schiffermüller), 1775*	215	Polia serratilinea *(Treitschke, 1825)*	21		
Dichagyris nigrescens *(Höfner, 1888)*	229	Polymixis rufocincta *(Geyer, 1828)*	523		

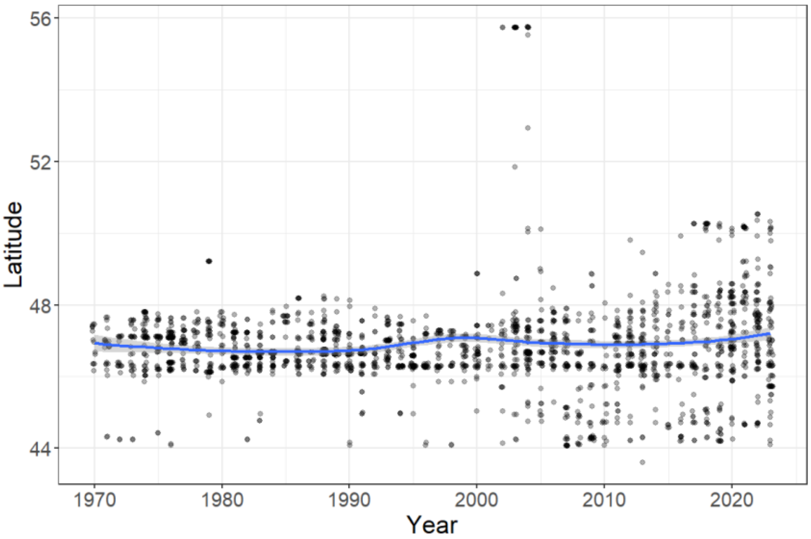

FIGURE 25: LOESS-regression showing *Auchmis detersa* (Hufnagel, 1766) latitudinal shift from 1970-2023

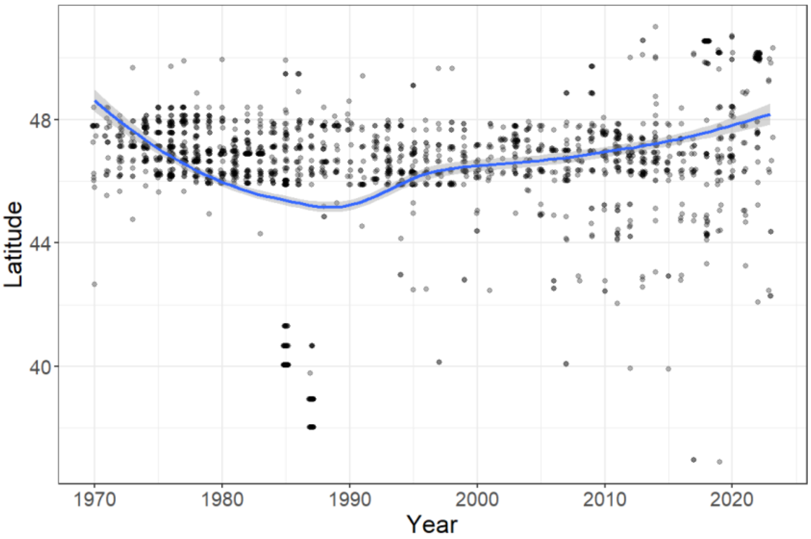

FIGURE 26: LOESS-regression showing *Chersotis multangula* (Hübner, 1803) latitudinal shift from 1970-2023

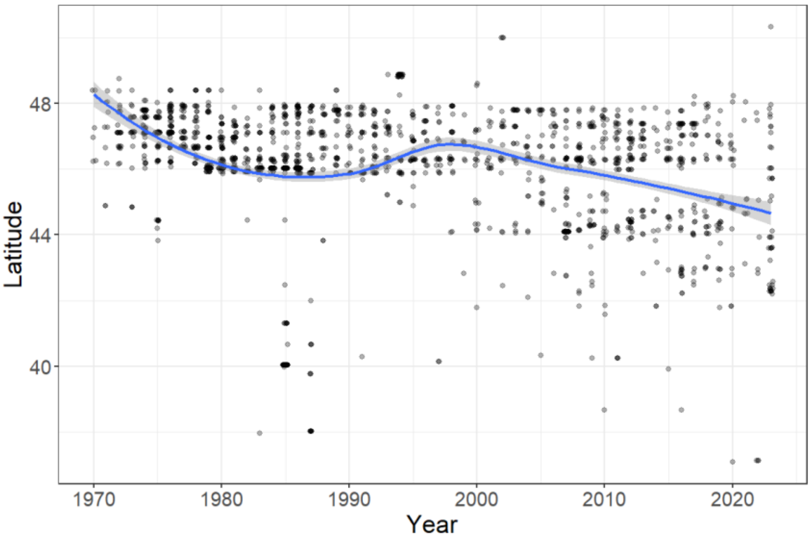

FIGURE 27: LOESS-regression showing *Chersotis margaritacea* (Villers, 1789) latitudinal shift from 1970-2023

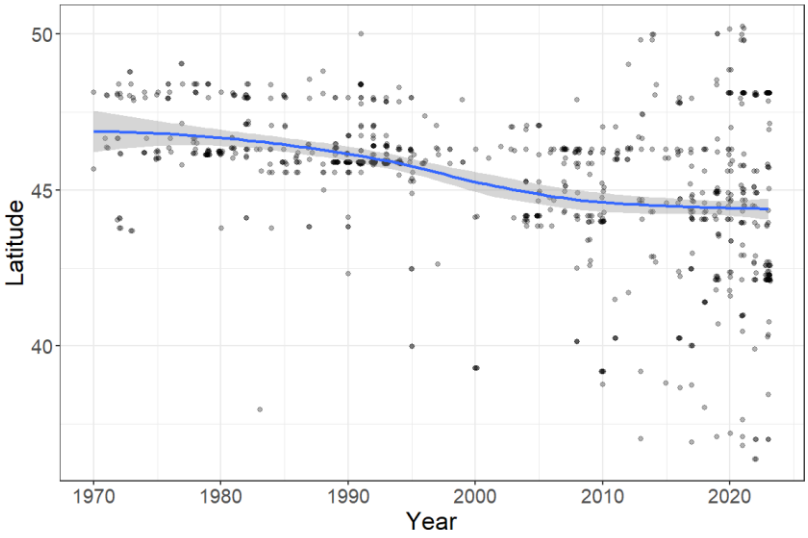

FIGURE 28: LOESS-regression showing *Episema glaucina* (Esper, 1789) latitudinal shift from 1970-2023

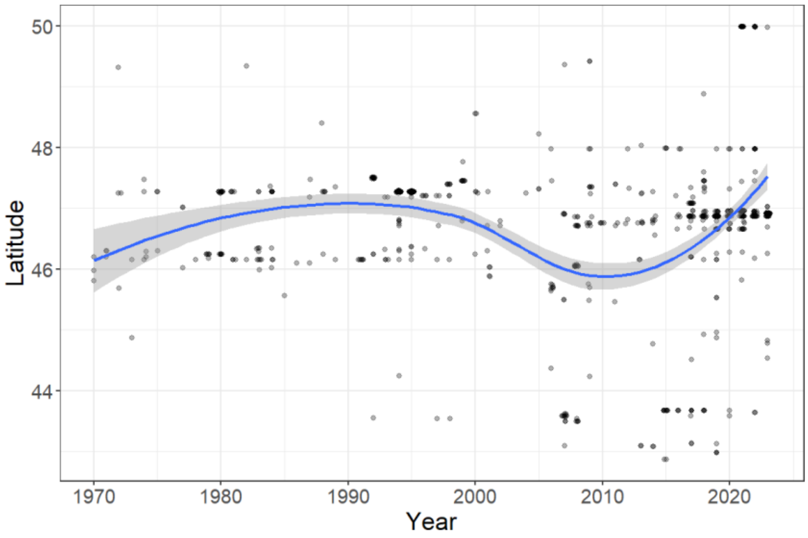

FIGURE 29: LOESS-regression showing *Eucarta amethystina* (Hübner, 1803) latitudinal shift from 1970-2023

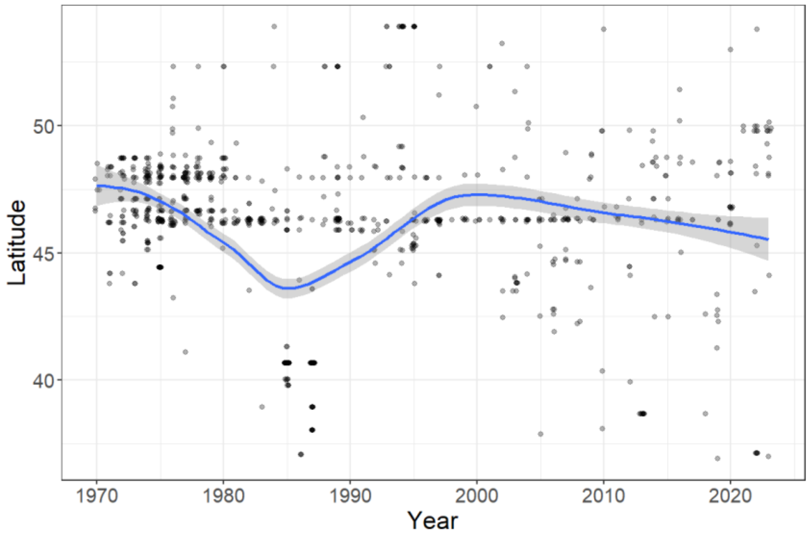

FIGURE 30: LOESS-regression showing *Euxoa aquilina* (Denis & Schiffermüller 1775) latitudinal shift from 1970-2023

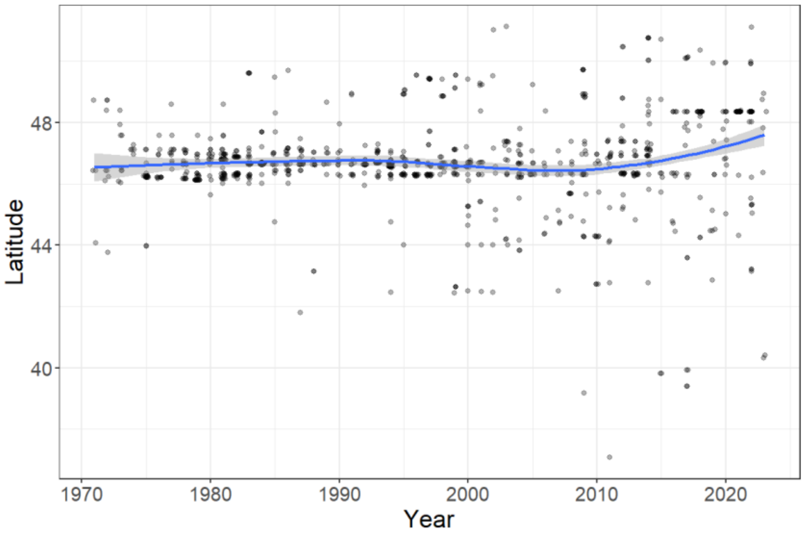

FIGURE 31: LOESS-regression showing *Hoplodrina superstes* (Ochsenheimer, 1816) latitudinal shift from 1970-2023

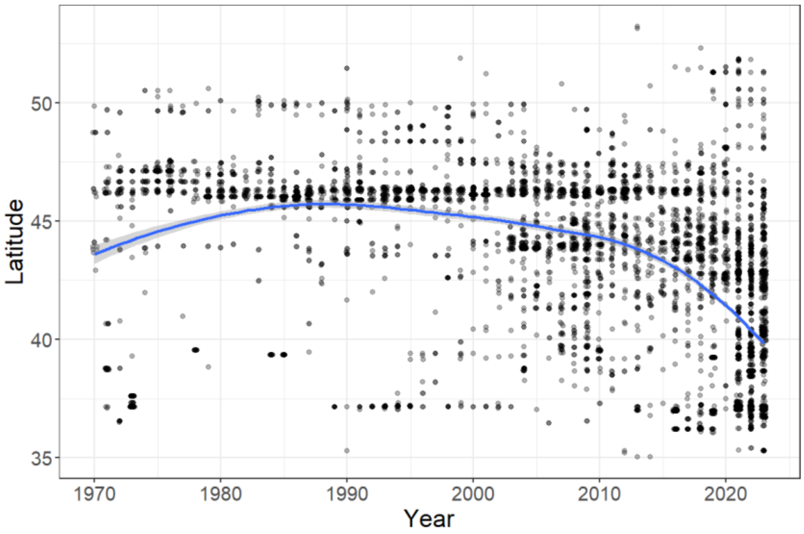

FIGURE 32: LOESS-regression showing *Mythimna sicula* (Treitschke, 1835) latitudinal shift from 1970-2023

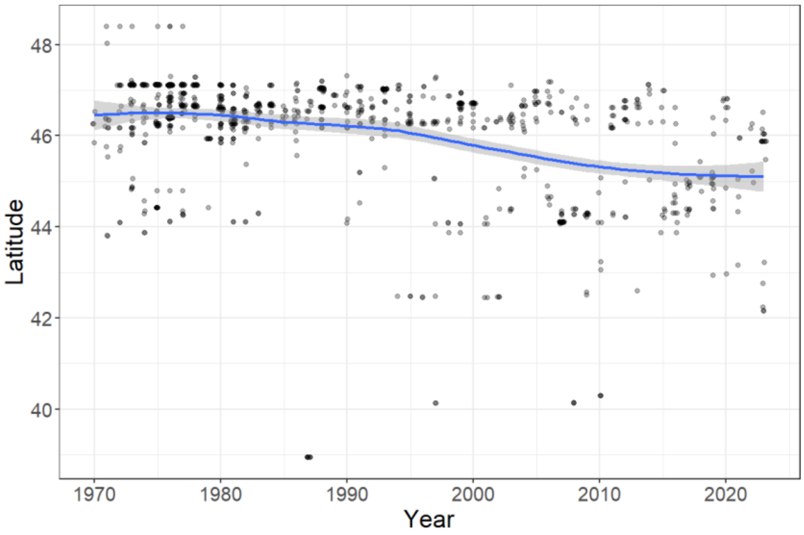

FIGURE 33: LOESS-regression showing *Ochropleura musiva* (Hübner, 1803) latitudinal shift from 1970-2023

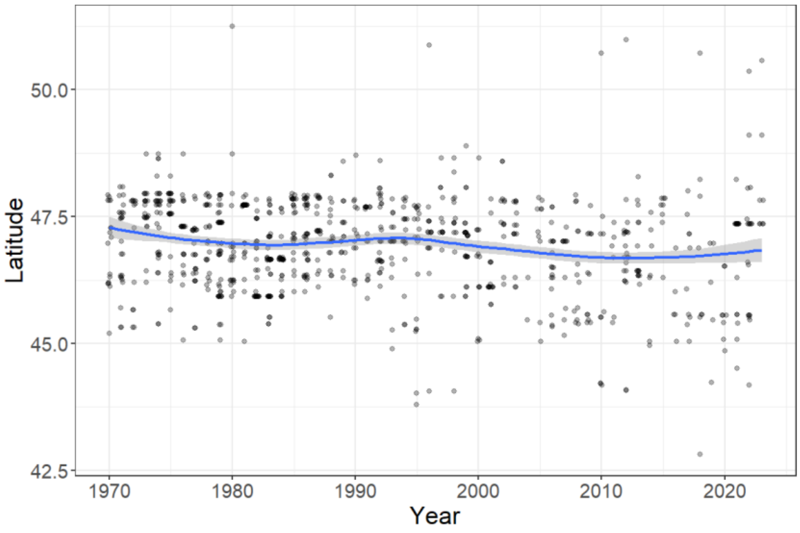

FIGURE 34: LOESS-regression showing *Phlogophora scita* (Hübner, 1790) latitudinal shift from 1970-2023

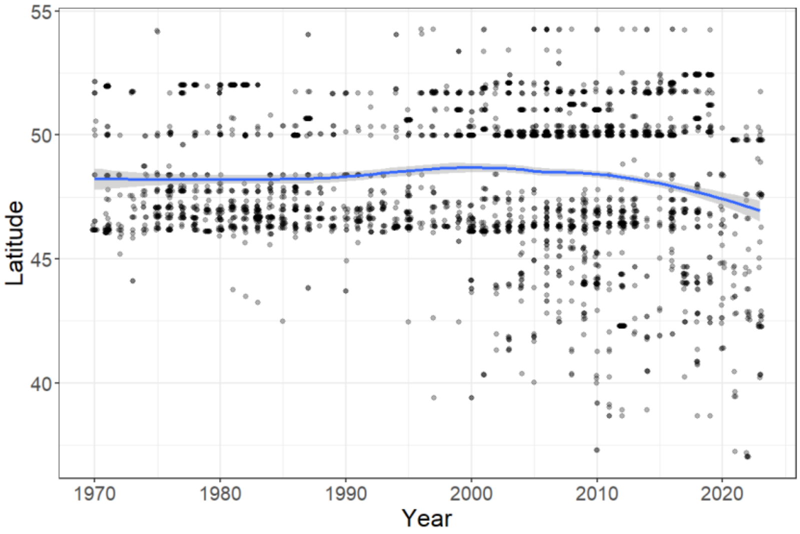

FIGURE 35: LOESS-regression showing *Polymixis xanthomista* (Hübner, 1819) latitudinal shift from 1970-2023