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Increased Abundance Coincides with Range Expansions and Phenology Shifts: A Long-Term Case Study of Two Noctuid Moths in Sweden

Per-Eric Betzholtz *, Anders Forsman and Markus Franzén

Department of Biology and Environmental Science, Linnaeus University, SE-39182 Kalmar, Sweden; anders.forsman@lnu.se (A.F.); markus.franzen@lnu.se (M.F.)
* Correspondence: per-eric.betzholtz@lnu.se

Abstract: Environmental and climatic changes are inducing population declines in numerous species. However, certain species demonstrate remarkable resilience, exhibiting both population growth and range expansion. This longitudinal study in Sweden carried out over two decades (2004–2023) examines the noctuid moths *Mythimna albipuncta* and *Hoplodrina ambigua.* Abundance and phenology data were gathered from three light traps in southeastern Sweden and integrated with distribution and phenology data from the Global Biodiversity Information Facility. In *M. albipuncta*, the distribution area expanded from 7 to 76 occupied grids (60 km^2) and the abundance increased from 7 to 6136 individuals, while in *H. ambigua*, the distribution area expanded from 1 to 87 occupied grids and the abundance increased from 0 to 6937 individuals, during the course of the study. Furthermore, a positive yearly association was observed between the number of occupied grids and light trap abundance for each species. We also found significant extensions in the adult flight periods of more than 100 days in both species. Light traps emerged as an effective monitoring tool, with light trap abundance as a reliable proxy for distribution changes. Our findings demonstrate that the studied species cope very well with environmental and climatic changes. Given their role as dominant links between primary producers and higher trophic levels, abundance and distribution shifts of these ecological engineers have the potential to cascade up and down in the ecosystem.

Keywords: citizen science; exponential growth; geographic range; Lepidoptera; light trap; population dynamics; Sweden

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1. Introduction

The rapid global decline in insect populations is a topic that has induced substantial academic and public attention, given its profound implications for biodiversity and ecosystem functionality [1–5]. However, this decline is not omnipresent; the patterns of temporal shifts in insect abundance show both taxonomic and geographical variation [6–8]. For instance, certain Lepidopteran species are undergoing range expansions at higher latitudes, e.g., in northern Europe, a phenomenon that at least partly seems to be driven by climate change [9–12]. While there is evidence of remarkable changes in species abundance and range distributions, the exact extent and rate of these shifts remain insufficiently understood [13].

Empirical data indicate that phenological seasons are progressively lengthening [14]. Range-expanding species often exhibit phenological flexibility, including the ability to produce multiple generations and prolong their flight activity periods [15,16]. These traits not only underscore their adaptability but may also signify a wider ecological resilience. Such alterations in phenology could be a response to different environmental variables, including temperature and photoperiod [17]. This adaptability may be particularly relevant in the context of climate change, as species showing this capacity could be better equipped to handle fluctuating environmental conditions and expand their ranges [2,18].

Citizen science databases have been increasingly recognised for their utility in monitoring biodiversity trends [19]. These databases offer large-scale, temporally rich datasets that are crucial for documenting and understanding changes in species abundance and range. Further, targeted monitoring programmes using light traps provide precise, location-specific data on species activity and are often implemented in academic and government research [20,21]. Combining citizen science data with light trap monitoring thus offers a robust framework for analysing species phenology, abundance, and distribution and potentially allows local abundance to serve as a proxy for geographical range shifts [11].

Moths are important players in terrestrial ecosystems, acting as intermediaries between primary producers and higher trophic levels. Their rapid response to environmental alterations and diverse feeding ecology make them well suited for studying spatiotemporal dynamics [22]. Here, we scrutinise two recently established and rapidly expanding moth species in Sweden: *Mythimna albipuncta* and *Hoplodrina ambigua*. We utilise a robust methodological framework that includes longitudinal light trap data over 20 years (2004–2023) from three disparate sites in southeast Sweden and geospatial data from the Global Biodiversity Information Facility (hereafter called GBIF), including the distribution area and length of the adult flight period. By combining these sources of information, this work offers a comprehensive examination of the spatiotemporal changes in the range, abundance, and flight period of the two species under study. Specifically, this study aims to (a) quantify and describe changes in range and abundance during the course of the study, (b) explore if the abundance shifts recorded in the light traps correlate with concurrent range expansions of the studied species, and (c) assess temporal trends in adult flight periods over the 20-year study period.

2. Material and Methods

2.1. Study Design

This study spans over 20 years, from 2004 to 2023. It is based on abundance data from three light traps situated in southeast Sweden, which we integrated with citizen science data on range expansions and changes in phenology in Sweden.

2.2. Study Species

This study focuses on two range-expanding moths from the family Noctuidae. The White-point, *M. albipuncta* (Denis and Schiffermüller, 1775) (Figure 1a), is relatively common in large parts of Europe, and the species has recently expanded its distribution range into Sweden. Before 2005, there were only scattered records in the most southern and southeastern regions of Sweden. The species mainly inhabits open country, where the larvae predominantly feed on various grasses. The Vine's rustic, *H. ambigua* (Denis and Schiffermüller, 1775) (Figure 1a), has a distribution range from North Africa across large parts of Europe. Before the year 2000, there were only scattered records from the most southern regions of Sweden. This species inhabits a wide range of habitats, from open country to woodland clearings and edges. The larvae are polyphagous, feeding on a diverse range of plants.

2.3. Citizen Science Data on Spatial Distribution and Variation in Flight Period

Data on distribution area and timing of the adult flight periods of the two study species, *M. albipuncta* and *H. ambigua*, were downloaded from GBIF on 15 October 2023. The GBIF search was limited to Sweden and captured all records of the two focal species ranging from latitude 55° N to 62° N and from longitude 12° E to 14° E. For each species, annual range expansion was quantified by counting the number of occupied grids. A spatial grid was constructed by rounding the latitude coordinates to one decimal place and the longitude coordinates to two decimal places. This approximates a grid resolution of 10 km in the south–north direction and 6 km in the east–west direction (grid size 60 km^2). The duration of the adult flight period for each species was calculated annually. This was achieved by determining the number of days between the first and last observations of each species and year.

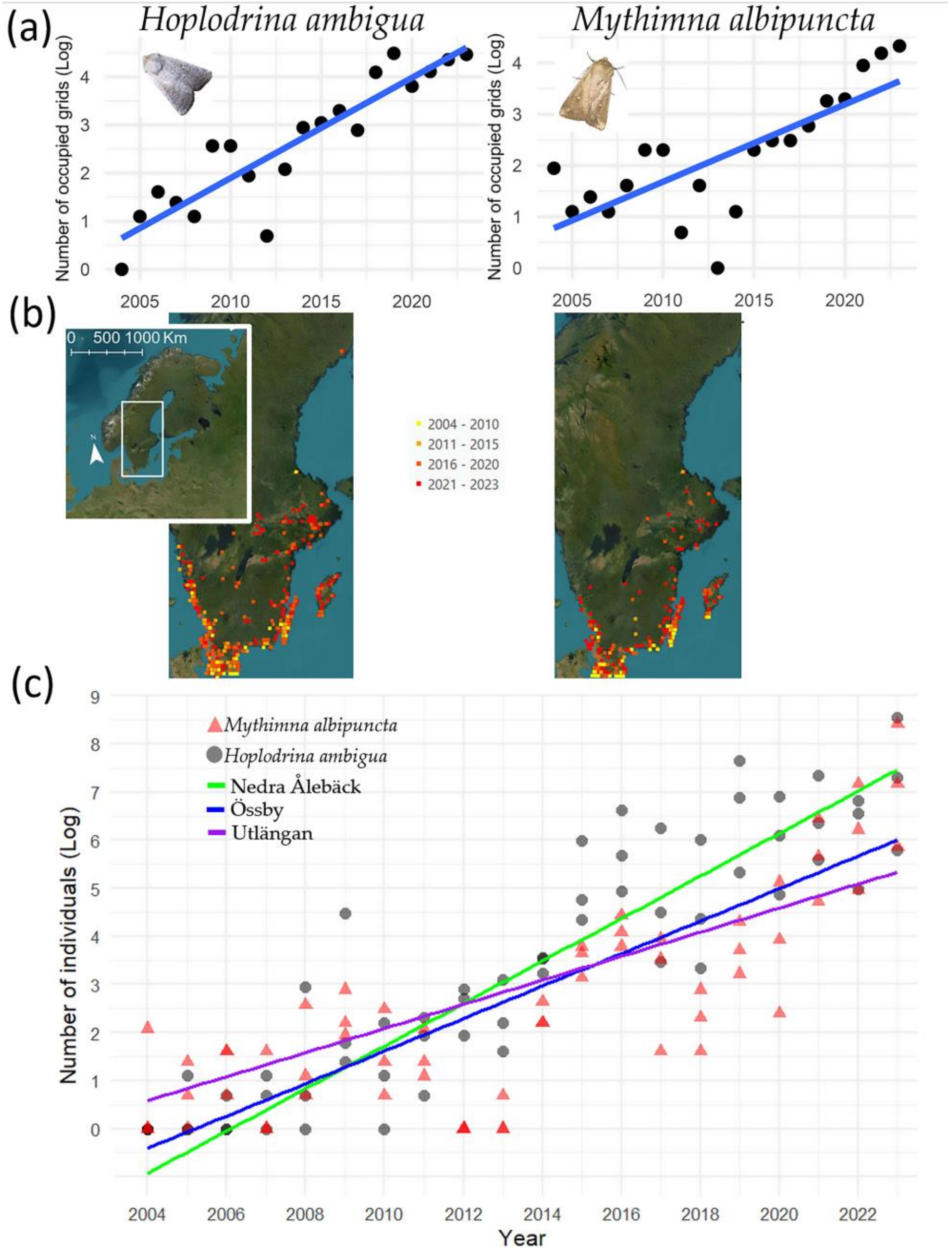


Figure 1. Spatiotemporal abundance and distribution trends, from 2004 to 2023, of *H. ambigua* and *M. albipuncta* in Sweden. Panel (**a**) shows the number of occupied grids (*H. ambigua* to the left and *M. albipuncta* to the right), panel (**b**) shows distribution changes during the course of the study. Each grid corresponds to a size of 10 × 6 km (60 km^2), and the colour represents the first year the species was recorded in a grid. Panel (**c**) shows recorded abundance across the three light trap sites for each study species. Nedra Ålebäck. Figure is based on raw data from the light traps. Photographs: Markus Franzén.

2.4. Light Trap Data on Abundance

We counted all individuals of the two focal species recorded from three light trap sites located in southeastern Sweden: Nedra Ålebäck and Össby in the province of Öland and Utlängan in the province of Blekinge [9]. The light traps were equipped with 125W Philips mercury vapour lamps and were in operation on a nightly basis from May to October over the 20-year study period. Traps were emptied every second to third week, and the two focal species were counted and identified to species level by one of the authors (P.E.B.).

Utlängan (56.022731 N/15.797629 E) is an island of 215 ha, positioned 7 km southeast of the mainland in the region Blekinge. The island is characterised by woods and meadows. The light trap is situated 3 m above sea level and 210 m from the Baltic Sea coastline. Össby (56.270783 N/16.490312 E) and Nedra Ålebäck (56.605853 N/16.686114 E) are small villages on the island of Öland, surrounded predominantly by meadows and farmlands. Össby is situated at 6 m elevation, 370 m from the Baltic Sea, while Nedra Ålebäck is situated at 2 m elevation and 820 m from the sea. The distance between the most northern trap, Nedra Ålebäck, and the southernmost trap, Utlängan, is 92.0 km. The general climate in the area where the light traps are situated experiences cold winters and warm, dry summers, with a daily mean temperature ranging from −1 to 2 °C in mid-winter and 16 to 17 °C in summer.

2.5. Statistical Analysis

Data analysis was executed using R statistical software, version 4.3.0 [23].

2.6. Occupied Grid Modelling

A generalised linear model (GLM) with Poisson distribution suitable for count data was constructed to quantify the annual number of occupied grids in relation to species and year. The dependent variable was the count of occupied grids per year, whereas the independent variables comprised species, year, and number of records. We also tested for the interaction between species and year. The number of records was the number of the yearly records of each species from GBIF data. Incorporating the number of records was critical for statistically accounting for potential artefacts due to variability in record counts. The statistical significance of fixed and random effects was assessed through Type II Wald Chi-square tests facilitated by the ANOVA function from the car package [24]. Furthermore, the summary function was invoked for an in-depth examination of parameter estimates, thereby elucidating the impact of each variable in the model.

2.7. Species Abundance Modelling

To model abundance variation, a generalised linear mixed model (GLMM) with Poisson distribution was constructed using the glmmTMB package, version [25]. The response variable was the abundance, defined as the count of individuals for each species per trap and year. Fixed effects integrated into the model encompassed year and species. We also tested for the interaction between species and year. The year variable was scaled to mean zero and unit variance to mitigate convergence issues. The random intercept term included trapping site corresponding to three distinct light trap locations in Sweden (Nedra Ålebäck, Össby, and Utlängan).

2.8. GLMM for Occupied Grids and Light Trap Abundance

A GLMM was constructed via glmmTMB to explore the association between the log-transformed number of annually occupied grids, species identity, and log-transformed (+1) individual abundance from traps. Random effects accounting for site variations were included to adjust for nonindependence among observations within each site.

2.9. Phenology

We employed a GLMM with a negative binomial distribution (family = nbinom2) implemented via the glmmTMB package to analyse variation in the duration of the adult flight length period in the traps. As the count data exhibited overdispersion, a negative binomial distribution was justified. The dependent variable was the number of active days measured from the first day of observation until the last day of observation, based on the day the traps were checked. The fixed effects included scaled year, and species year had to be scaled due to convergence problems. The site was incorporated as a random intercept term to control for the clustering of data points within the same trapping site. Similarly, for the GBIF data, we employed a GLM with a negative binomial distribution to analyse the flight length period in Sweden.

3. Results

3.1. Spatial Distribution Shifts

The number of occupied grids in Sweden of *M. albipuncta* and *H. ambigua* increased from 1 and 7 in 2004 to 87 and 76 in 2023, respectively. The number of occupied grids increased with the year ($\chi^2 = 98.53$, df = 1, $p < 0.001$), was different between the two species ($\chi^2 = 11.36$, df = 1, $p < 0.001$), and increased with the increasing number of records ($\chi^2 = 20.24$, df = 1, $p < 0.001$) (Figure 1, Table 1). *H. ambigua* significantly occupied more grids than *M. albipuncta* (Figure 1, Table 1).

Table 1. Regression summary for species, year, and number of records in relation to the number of occupied grids in Sweden.

Variable	Estimate	Std. Error	*t*-Value	*p*-Value
(Intercept)	1.26668	0.16889	7.500	<0.0001
Year	0.13986	0.01409	9.926	<0.0001
Species (*M. albipuncta*)	−0.27418	0.08134	−3.371	<0.0001
Number of records	0.23756	0.05280	4.499	<0.0001

3.2. Abundance Shifts

The abundance of *M. albipuncta* and *H. ambigua* recorded in the three light traps increased from 7 and 0 in 2004 to 6136 and 6937 in 2023, respectively. The increase in abundance was consistent among the light traps and revealed a statistically significant interaction effect between year and species ($\chi^2 = 2348.9$, df = 1, $p < 0.001$), indicative of an exponential increase in abundance for both species (Figure S1, Table S1). Further, *H. ambigua* had a significantly lower increase than *M. albipuncta* (Figure 1, Table 2).

Table 2. Generalised linear mixed model (GLMM) summary for abundance in the three light traps in relation to year and species, and the interaction term year * species. The model incorporates a random intercept term to account for site-specific variations in trapping locations.

Variable	Estimate	Std. Error	Z-Value	*p*-Value
Intercept	4.00921	0.45907	8.73	<0.0001
Year (scaled)	1.95315	0.01457	134.03	<0.0001
Species (*M. albipuncta*)	−3.61106	0.06546	−55.17	<0.0001
Year * Species	2.15215	0.04441	48.47	<0.0001

The number of occupied grids and the abundance recorded in the light traps exhibited a statistically significant positive association ($\chi^2 = 251.03$, df = 1, $p < 0.0001$) (Figure 2). Notably, this response appeared to be conserved across the two species under study, as evidenced by the nonsignificant difference in their effect sizes ($\chi^2 = 1.39$, df = 1, $p = 0.237$).

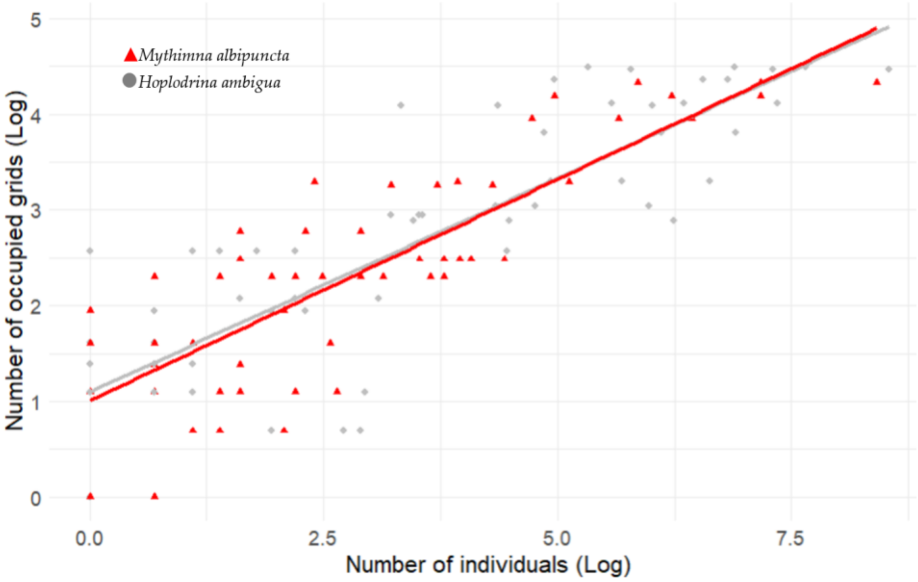
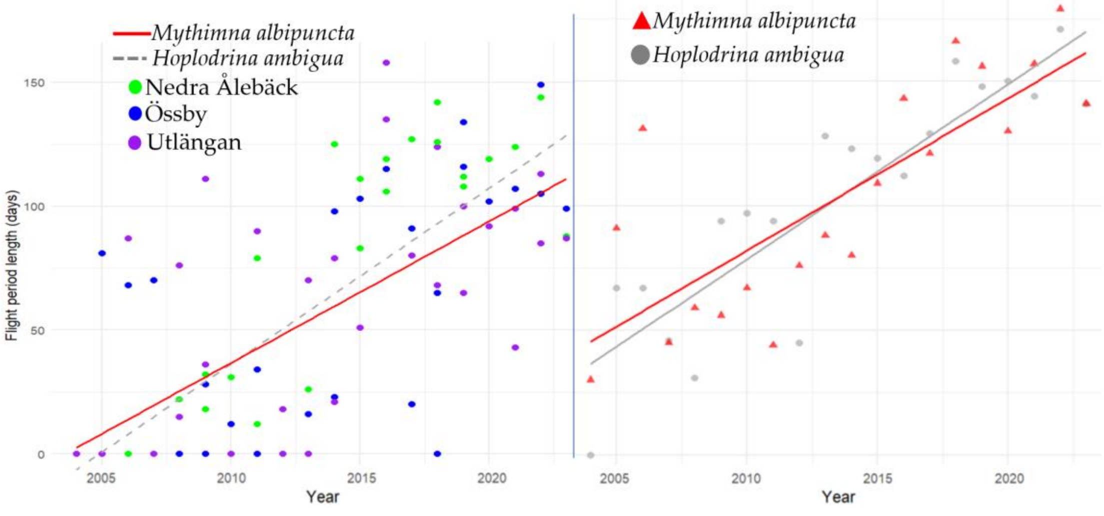


Figure 2. The number of occupied grids increased with increasing abundance of *M. albipuncta* and *H. ambigua* in the three light traps. Figure is based on raw data from the three light traps.

3.3. Phenology Shifts

Regarding phenology shifts, data from the three light traps indicated a statistically significant increase of more than 100 days in the duration of the adult flight period during the course of the study (χ^2 = 26.57, df = 1, p < 0.0001), with no difference between the two species (χ^2 = 0.25, df = 1, p = 0.6194) (Figure 3a). The nationwide GBIF data also indicated a significant extension of the adult flight period (χ^2 = 42.95, df = 1, p < 0.0001), with no difference between the two species (χ^2 = 0.09, df = 1, p = 0.759) (Figure 3b).



(**a**) (**b**)

Figure 3. Temporal trends in the length of the adult flight period (days) for *M. albipuncta* and *H. ambigua*. Panel (**a**) shows data from the three light trap sites, while panel (**b**) shows GBIF data from Sweden. Figures are based on raw data.

4. Discussion

In this longitudinal study spanning 20 years (2004 to 2023), we used a multiscale approach and integrated abundance data on the moths *M. albipuncta* and *H. ambigua* from three light traps sites situated in southeast Sweden with citizen science data on range expansions and changes in phenology in Sweden. We found an unprecedented increase in the distribution area and abundance in both species and a behavioural shift towards longer adult flight periods, showing that these species have successfully coped with the challenges following from ongoing environmental and climatic changes. Further, the results demonstrated a strong positive association between abundance, as recorded in the light traps, and distribution range, as extracted from citizen science data, indicating that abundance data from light traps might offer a reliable proxy for assessing range expansions.

From a wider perspective and contrary to the general trend of biodiversity loss and species decline [1,3,5], *M. albipuncta* and *H. ambigua* showed a remarkable resilience and expansion in Sweden. In fact, the rapid increase in abundance exhibited an exponential pattern from 2015 (Figure S1). Such trajectories of abundance in wildlife populations are atypical and generally signify substantial shifts in underlying ecological conditions [26]. These patterns are rarely observed in the broader community of flora and fauna [27], with one possible reason being the scarcity of longitudinal studies offering comprehensive possibilities to examine the spatiotemporal population dynamics of species [28]. Importantly, the two studied species have become two of the most dominating species recorded in the light traps during the study period, along with long-established species such as *Xestia c-nigrum* (Linnaeus, 1758), *Xestia xanthographa* (Denis and Schiffermüller, 1775), *Luperina testacea* (Denis and Schiffermüller, 1775), and *Noctua pronuba* (Linnaeus, 1758). As a reference, we counted the number of individuals in *X. c-nigrum*, and at the trap-site Nedra Ålebäck, both studied species were indeed more abundant in 2023 than *X. c-nigrum* (3798 *X. c-nigrum*; 4491 *M. albipuncta* and 5137 *H. ambigua* individuals, respectively).

In evaluating the exponential growth in populations of *H. ambigua* and *M. albipuncta*, it is imperative to consider the underlying drivers that could precipitate such trends. The recent literature suggests that climatic and environmental conditions have not undergone exponential changes in the past few decades [29,30]. Specifically, Peters et al. [31] reported that temperature patterns have shown only incremental alterations, with no evidence of rapid shifts that correspond to the growth trajectories observed in the moth populations. Lande et al. [32] also underscore the relative stability of environmental factors, concluding that these have not exhibited the exponential variations that might account for the observed population dynamics. Instead, the proliferation of habitats conducive to the survival and reproduction of these two moth species, coupled with an increase in resource availability, may have facilitated their rapid expansion [33]. The absence of natural enemies in newly colonized areas may also lead to population explosions [34]. Furthermore, the emergence of novel areas that have become climatically suitable in recent years may offer unoccupied niches that these species have been able to successfully exploit [35,36]. In summary, we propose that the exponential growth patterns of *H. ambigua* and *M. albipuncta* are more likely attributable to changes in habitat and resource availability, the absence of natural enemies, and the opportunity to colonise novel areas that have become climatically favourable, rather than the direct consequences of exponential changes in climate or broad environmental conditions.

Both *M. albipuncta* and *H. ambigua* significantly expanded their distribution ranges during the course of the study and were recorded in 360 and 564 grids (60 km^2), respectively (cf. Figure 1b), which implies a considerable ecological footprint. Their success is probably influenced by multiple interacting factors. Climate change is likely to be a significant driver, with higher temperatures enabling latitudinal range expansions [2,10,11,37,38]. Changes in land use, including agricultural expansion and urbanisation, could also offer new niches for these range-expanding moths to successfully exploit [15,39]. In addition, their generalist habitat and feeding strategy and potential for rapid life-cycle adaptations, such as multiple generations per year [10,18,40,41], might contribute to their success.

The rapid increase in *M. albipuncta* and *M. ambigua* in terms of abundance and spatial distribution aligns well with theories of species invasiveness and ecological fitting [42]. Previous research has shown that novel or invading species can experience ecological release in new habitats due to fewer natural enemies, such as predators and parasitoids, and lower competitive pressures [43]. Further, larvae of generalist Lepidopteran species are known to infest various crops and grasses, having the capacity of switching and utilising novel food plants within their new ranges, potentially leading to economic losses [44]. The new state of super-abundancy of the studied species might, therefore, have ecological consequences if their larval feeding on native plants should lead to shifts in plant community composition [45]. If these moths were to outcompete native herbivores for food resources, they could indirectly affect the populations of species dependent on those native herbivores, thereby disrupting established food webs [46].

The significant prolongation of the adult flight period of more than 100 days in the focal species also comes with potential wide-ranging ecological implications. An extended flight period could lead to (or result from) multiple generations within a year, accelerating population growth [21,47,48]. An extended flight period may also expand the window of ecological interactions, such as predation and herbivory, thus affecting the local food webs and potentially disrupting established ecological equilibria [49]. For example, these moths could benefit nocturnal predators, such as bats and birds [50,51], and serve as a stable and abundant food source, thereby also potentially influencing the population dynamics of their predators [52]. Hence, their success may also influence the food webs in their habitats, being a dominant actor between primary producers and higher trophic levels [53]. The extended phenology found in this study aligns with patterns reported in many other types of organisms, from plants to birds [54–56].

We found a significant association between the abundance recorded in the light traps and the number of occupied grids recorded from GBIF data. This is in line with foundational ecological theories that posit a positive relationship between population size and range expansions into new distribution areas [57,58]. It is also in agreement with the previous finding of an association across moth species between local abundance and range expansions, reported in [11]. The strong correlation between abundance data from the light traps and species range size thus indicates that trap data can be used as a reliable proxy for assessing range expansions in moths. This offers a more resource-efficient methodology for future ecological studies, corroborating similar findings in other taxa [59,60]. A strong relationship between light trap abundance and range size can also streamline monitoring efforts, making it easier to identify at-risk or invasive species early in their range expansions [61]. This, in turn, offers a valuable tool for conservationists and policy-makers for proactive ecosystem management [62], forecasting possible resource competition or ecosystem disruption.

In this study, we integrated GBIF data with data from light traps, enabling us to work at multiple ecological scales. While local trap data provide high-resolution information on specific sites, the citizen science data offer a broader geographical and temporal context. Thus, the combination of approaches enhances the ability to capture and understand biodiversity patterns, allowing for more comprehensive ecological interpretations [63]. Citizen science data complement traditional scientific research in that they offer cost-effective means of data collection over large spatial and temporal scales [64]. Moreover, citizen science engages the public in scientific discourse, enhancing societal awareness of biodiversity and conservation issues [65]. The association between trap and citizen science data also adds a layer of empirical robustness to this study, making our findings less susceptible to local biases and stochastic events. Recent years have seen a significant rise in citizen science contributions, particularly facilitated by the widespread adoption of smartphones and mobile data input platforms [66]. This technological ease has likely contributed to the increased frequency of data submissions to databases like the Global Biodiversity Information Facility (GBIF) and connected databases. Consequently, it becomes essential to discern whether the apparent surge in moth sightings reflects an actual increase in populations or merely an augmented reporting frequency. It should be emphasised here that we accounted for this potential bias in the present study by including the yearly number of records as an explanatory factor in our statistical models, and the results regarding the effects of year and species remained significant.

5. Conclusions

In summary, the success story of *M. albipuncta* and *H. ambigua* in Sweden over the past two decades illustrates their adaptability to shifting environmental conditions. It remains to be investigated whether the roles of these two species as ecological engineers are sufficiently important to significantly impact the structure and functioning of their ecosystems. However, this study offers valuable insights into the mechanisms of species expansion, providing an empirical foundation for future research and management strategies aimed at biodiversity monitoring and conservation.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15121177/s1, Figure S1: Distribution area and abundance of *Mythimna albipuncta* and *Hoplodrina ambigua* during the course of the study (2004–2023); Table S1: The recorded abundance of *Mythimna albipuncta* and *Hoplodrina ambigua* per trap and year.

Author Contributions: Conceptualization, P.-E.B.; data curation, P.-E.B. and M.F.; investigation, P.-E.B.; methodology, P.-E.B., A.F. and M.F.; software, M.F.; writing—original draft, P.-E.B. and M.F.; writing—review and editing, P.-E.B., A.F., and M.F. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available in the manuscript and Supplementary Materials.

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Conflicts of Interest: The authors declare no conflict of interest.

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