JNCC Report 775

Air Pollution Recovery Indicators (APRI)

Development of a Butterfly/Moth Indicator

Project Report

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January 2025

ISSN 0963 8091

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This report was produced for JNCC under an external contract, by Risser, H.A. (UKCEH), Jarvis, S.G. (UKCEH), Rowe, E. (UKCEH), and Stevens, C. (Lancaster University) for contract F21-0708-1581 (112).

This document should be cited as:
Risser, H.A.[1], Jarvis, S.G.[1], Rowe, E.[1] & Stevens, C.[2] (2025). Air Pollution Recovery Indicators (APRI): Development of a Butterfly/Moth Indicator. *JNCC Report 775 (Project Report)*. JNCC, Peterborough, ISSN 0963-8091.
https://hub.jncc.gov.uk/assets/f1bef108-faaf-4759-9133-55a1336fc781.

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Acknowledgements:
Major thanks to several UKCEH colleagues, including Colin Harrower for providing us with the RIS GAI data, Sam Tomlinson and Cristina Martin Hernandez for their help with accessing and understanding the atmospheric pollutant datasets, Thomas Mondain-Monval for providing JASMIN support, and Aneurin O'Neil for mapping support. We would also like to thank all volunteers and staff who have contributed records to the UK Butterfly Monitoring Scheme and Rothamsted Insect Survey.

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Summary

This project was undertaken to better understand the potential effects of atmospheric nitrogen (N) pollution upon butterflies and moths (Lepidoptera) in the UK. We used data from long-term monitoring schemes to understand the potential effects of N upon individual Lepidoptera species, summary metrics such as community richness, and within trait groupings. We used a spatiotemporal Generalised Additive Modelling (GAM) approach to test the response of each variable to N, whilst also accounting for other important drivers of change in Lepidoptera (e.g. climate).

We found strong evidence that total butterfly richness was negatively correlated with historic N pollution, but no evidence that total butterfly abundance was impacted by historic N. Both total moth abundance and richness were negatively correlated with the percentage change in N at the site over time, but positively correlated with historic N. The strength and direction of responses of Lepidopteran trait groupings and individual species to N were varied and complex. The abundance of many butterfly and moth species was negatively correlated with historic N. Conversely, the abundance of certain other species was positively correlated with historic N. This demonstrates that individual species may respond very differently to N, with some being favoured whilst others lose out. These results act as a baseline for our understanding of the potential effects of N on invertebrate fauna in the UK.

Using this knowledge of the effects of N on Lepidoptera, we then scoped ideas for the development of an air pollution recovery indicator for Lepidoptera species in the UK. We also suggested potential follow-on work needed to achieve this recovery indicator for Lepidoptera.

Contents

1. Introduction

Atmospheric nitrogen (N) pollution is a leading cause of biodiversity loss in the UK and other countries. Several recent studies have highlighted the potential link between N pollution and changes in the abundance, richness, and distribution of butterflies (e.g. Betzholtz *et al.* 2013; Klop *et al.* 2015; Öckinger *et al.* 2006; Roth *et al.* 2021; Wallisdevries & Swaay 2013). In the UK, there is a lack of published evidence that nitrogen pollution affects butterflies. In addition, the potential impacts of N on moths have been generally understudied. A recently published master's thesis by Risser (2023) began to disentangle the complex relationships between N and butterflies in the UK and provides a comprehensive overview of the relevant literature on this topic.

As some areas of the UK continue to receive declining pressure from atmospheric nitrogen deposition, it is important from a policy perspective to measure whether seminatural habitats and the species inhabiting them are undergoing any associated recovery. Initial scoping of these potential recovery indicators is described in Perring *et al.* (2024). This report highlighted the importance of including an indicator of recovery for butterflies and/or moths, partly because they are of great public appeal.

In this report, we conducted a study using data from long-term monitoring schemes to understand the potential effects of N upon individual Lepidoptera species, summary metrics such as community richness, and within trait groupings. These results act as a baseline for our understanding of the potential effects of N on invertebrate fauna in the UK. Using this knowledge of the effects of N on Lepidoptera, we then scoped ideas for the development of an air pollution recovery indicator for butterfly species in the UK. We also suggested potential follow-on work needed to achieve this recovery indicator for Lepidoptera.

2. Data collation: Datasets

In this section, we briefly describe the datasets available on Lepidoptera abundance and occurrence in the UK, outlining the strengths and weaknesses of each and discussing which are most suitable for use in the analysis. Similarly, we describe the various driver datasets available, including those on pollutant deposition, climate, and land-use. We chose to use a single butterfly and a single moth dataset in this analysis rather than integrating data from multiple datasets due to the methodological complexity that would involve.

2.1. Lepidoptera abundance/occurrence

2.1.1. Standardised monitoring schemes: UK Butterfly Monitoring Scheme and Wider Countryside Butterfly Survey

The United Kingdom Butterfly Monitoring Scheme (UKBMS) began recording data in 1976 and now records information on 71 species at over 2,000 sites per year using a combination of fixed transects, the Wider Countryside Butterfly Survey (WCBS), timed counts, and egg and larval nest monitoring. Long-term temporal trends were created for 56 of the 59 UK butterflies in 2015 (Fox *et al.* 2015). Chequered Skipper *Carterocephalus palaemon*, Cryptic Wood White *Leptidea juvernica* and Mountain Ringlet *Erebia epiphron* were excluded due to insufficient data being available for those species. Samples are not evenly distributed across the UK because transect locations are usually chosen by the recorder. In addition, transect-based surveys may vary in length. Data are collected by competent volunteers and verified by automated checks, UKBMS Branch Coordinators, and staff at Butterfly Conservation and UKCEH. UKBMS data are used to produce the UK Biodiversity Indicator C6 for butterflies.

Using these data, a Generalised Abundance Index (GAI) is calculated which considers all butterflies recorded across the whole season to create an overall index of maximum species abundance at a site in a particular year, whilst accounting for seasonal variation and missing data (Dennis *et al.* 2016). The GAI site indices are produced using Generalised Additive Models (GAMs) individually fitted to data for each species/site/year combination and so are only available for sites/species/years with sufficient counts. They are reliant on data for the site and year and do not consider species dynamics at other sites. Site index data are openly available (Botham *et al.* 2023).

In this study, we chose to use butterfly data from the UKBMS. Despite the slight spatial biases detailed above, the dataset provides unmatched spatial and temporal coverage.

2.1.2. Standardised monitoring schemes: Rothamsted Insect Survey

The Rothamsted Insect Survey (RIS) Light-trap Network, set up in the 1960s, collects data on (primarily) macro-moths at around 80 traps in the UK and Ireland (Stewart *et al.* 2007). The scheme uses high-powered night traps to sample nocturnal moths. RIS data contribute to the creation of UK moth trends, including the state of moths' report (Fox *et al.* 2021).

This dataset provides the longest time series of standardised moth trap data from across the UK and is therefore very useful for detecting temporal trends. Spatial coverage of RIS traps is not random, therefore the data are likely to be somewhat spatially biased across the UK. Additionally, the traps require mains power and so are unlikely to be placed in extremely remote locations. Despite these caveats, the RIS dataset provides the best long-term standardised survey of moths with decent spatial coverage of the UK.

2.1.3. Other monitoring schemes

2.1.3.1. Garden Moth Scheme

The Garden Moth Scheme (GMS) is a citizen science programme designed to collect standardised data from garden moth traps by encouraging participants to record data weekly over the March-November survey season. Data from the scheme has been used in several studies (e.g. Bates *et al.* 2014; Wilson *et al.* 2018). GMS data collection from across the UK only began in 2007, and therefore does not provide us with a sufficiently long time-series for use in this analysis.

2.1.3.2. Big Butterfly Count

The Big Butterfly Count (BBC), run by Butterfly Conservation, is a citizen science survey launched in 2010. The method requires volunteers to count butterflies for 15 minutes during specific weeks in the summer. Recorders only count selected species of butterflies and a few macro-moths from a pre-defined species list, meaning that not all species are surveyed. BBC data can be used complement, but not replace, more standardised monitoring schemes like the UKBMS (Dennis *et al.* 2017).

2.1.3.3. Garden Butterfly Survey

The Garden Butterfly Survey (GBS) is a citizen science scheme run by the charity Butterfly Conservation in the UK. The GBS collects records in private gardens, community gardens, and allotments. Species data from the scheme are verified by county recorders. The scheme also collects information about surveyors' gardens to allow researchers to explore, for example, the impact of wildlife friendly garden practices on butterflies. Volunteer recorders are not required to follow a set method which can be challenging for replication and makes it important to have larger numbers of samples to accommodate the expected variation when trying to detect change.

2.1.3.4. National Moth Recording Scheme

The National Moth Recording Scheme (NMRS), launched in 2007 but including data from much earlier, is a database of moth records from the UK. The database holds over 34 million records, all of which are verified by county moth recorders.

The NMRS data provide the greatest spatial coverage of any moth recording scheme and contribute to the creation of UK-wide occupancy trends (Randle *et al.* 2019). The scheme covers all moth species (macro or micro) found in the UK, including those that are diurnal as well as nocturnal. Data also contribute to the creation of UK moth trends, including the state of moths' report (Fox *et al.* 2021). NMRS data are mainly collected by opportunistic recorders rather than using a standardised method, so any analyses using the data must account for differences such as in recording effort or the type of trap used.

2.1.4. Opportunistic data

Much of the opportunistic moth data collected by recorders is collated and verified by the NMRS as detailed above. County butterfly recorders collate data in a similar manner, ensuring that records are verified. They often collate data from various sources, including those submitted directly to them and through platforms such as iRecord. Various other data sources exist, such as iNaturalist and social media posts, but it is often difficult to verify the identification and location accuracy of these records.

2.2. Lepidoptera traits

Trait data for macro-Lepidoptera (butterflies and macro-moths) were taken from the Cook *et al.* (2024) dataset. This database contains information from a variety of published sources and reports information on each species' life cycle, host plants, habitat, and trends over time in abundance and distribution. Similar trait information is available for selected micro-moth species should micro-moths be considered in any future analysis (Howell *et al.* 2023). An analysis of all micro-moth species would necessitate the creation of a more comprehensive traits database covering a wider array of species because such a database does not currently exist. It is worth noting that trait databases are a collation of relevant evidence from literature, so traits data may not be comprehensive for species whose traits are poorly understood. This is most likely to be the case for rare or elusive species. In this study, we use the trait database created by Cook *et al.* (2024) because it includes the best available trait data for UK butterfly and macro-moth species.

2.3. Pollutant deposition

In this analysis, we used a single static measure of historic total nitrogen deposition as in Henrys *et al.* (2011). We calculated a measure of historic total nitrogen deposition as the estimated value in 1996 from the Concentration Based Estimated Deposition (CBED) model for deposition to moorland (Levy *et al.* 2020). Data from 1996 were chosen because this represents the approximate mid-point of the two main Lepidoptera datasets used. Note that each year of data in the CBED dataset is the average of the current, previous, and next year, meaning that the 1996 data points are the average of the values in 1995–1997. We also used a measure of change over time in nitrogen deposition at a site, calculated as the percentage change between deposition in 1986 and 2012 from the CBED model for deposition to moorland (Levy *et al.* 2020). Both metrics were calculated at 5 x 5 km resolution. The scale of this data means that we are likely to miss finer-scale variation in pollutant deposition values, however, we judged it to be the most suitable dataset to use in this analysis.

In the scoping work for this project, we identified a stage in the modelling of UK-wide nitrogen datasets whereby historic emissions are calculated using a more recent ammonia emissions field. Thus, older estimates of nitrogen deposition may not be as spatially granular. Therefore, we have been cautious when interpreting the model results with respect to spatial change in nitrogen deposition over time.

There are several other datasets on UK pollutant emissions available which were not used in this project, including datasets created using the Fine Resolution Multi-pollutant Exchange (FRAME) model (Tomlinson *et al.* 2020) and the EMEP4UK model (Scheffler and Vieno, 2022; Scheffler *et al.* 2024). Following discussion with atmospheric nitrogen pollution experts at UKCEH and given that the 2024 EMEP4UK outputs were not available at the time of performing the analyses, we chose to use the CBED dataset for deposition to moorland.

2.4. Climate

The impact of weather variables on butterflies is complex and species dependent (Roy *et al.* 2001). We represented summer temperature from the current and previous years using the average June temperature from each year, and summer rainfall as the June rainfall from each year. Whilst these may not be ideal for all species, particularly those for which climate associations are still untested (including many of the moths), they were used in this analysis to provide a generalised approach. Annual data were obtained from the Met Office HadUK-Grid at 1 km resolution (Met Office *et al.* 2023).

2.5. Land Use

The UKCEH Land Cover Map (LCM) provides information on land cover in the UK at 1 km resolution in 21 target habitat classes. To calculate land use intensity (LUI), we calculated the sum of arable land and improved grassland in each 1 km square in both 1990 (Rowland *et al.* 2020a, 2020b) and 2015 (Rowland *et al.* 2017a, 2017b) to give us a representation of land use intensity which is equal to the proportion of intensive habitats within the square. For example, if 5% of a square was classified as arable land and 12% as improved grassland, the square would have an LUI value of 17 out of 100. This gives an idea of intensity within the square that each UKBMS transect is placed at these two time points. We found that LUI across the UK in 1990 and 2015 were strongly positively correlated, with a Pearson's correlation coefficient of 0.97. We therefore chose to use the LUI value for 1990 only in all further analysis. Due to the limited coverage of the LCM, we could not calculate the LUI for the Republic of Ireland, Isle of Man, and Channel Islands.

2.6. Data limitations

Whilst we did show that the UKBMS and RIS sites cover a broad range of N deposition values (Figures 4 and 5, Section 3.2.1) enabling us to model the effects of both extremely low and high deposition, there is uncertainty in the deposition values and potential issues affecting our ability to detect spatial change in deposition. These potential issues are discussed in section 2.3 of this report.

It is worth noting that all driver datasets used in this analysis give modelled estimates of the variable of interest, meaning that there may be some uncertainty in the final values. Additionally, the spatial scale of the driver datasets will impact the accuracy of the value assigned to the specific UKBMS transect or RIS trap. Climate and LUI variables were calculated at 1 x 1 km scale, whereas pollutant deposition variables were calculated at 5 x 5 km scale. This means that finer scale variation in the driver variables, particularly those representing pollutant deposition, is likely to be lost as values are averaged across the grid square.

There are various caveats to the Lepidopteran datasets used within this analysis that are important to note. Both the UKBMS and RIS have a non-random location structure, and therefore do not provide an unbiased coverage of the UK. RIS trap placement is somewhat dictated by proximity to power sources. UKBMS transects have some tendency to be in higher quality areas in close proximity to towns or cities, due to the nature of the transects being set up in areas where volunteers can feasibly get to and actively want to record at on a weekly basis. The inclusion of data from the WCBS helps to overcome this but likely does not solve all issues of bias.

This analysis provides robust correlative evidence of the impacts of N on resident UK butterfly species. Evidence of the impacts of N on UK resident moths is poorer due to the relatively limited spatial and taxonomic coverage of the moth dataset used. As with all moth data recorded using light traps, it is also worth noting that high-powered traps like those used by the RIS likely attract moths from a relatively large distance due to their flight response towards to the high-powered light, meaning that moths may be drawn in from outside of the habitat immediately surrounding the trap. The attraction range may also vary by moth size, sex, group, and the level of artificial light pollution in the surrounding area (Van de Schoot *et al.* 2024), which we have not accounted for. In addition, there is some potential loss of spatial independence in the RIS GAI data due to reliance on yearly flight curves from UK-wide sites to fill in missing data at individual sites. We attempted to mitigate this by filtering out rows of data where most of a species' flight curve was not sampled in a particular site and year, but some interdependence may remain.

3. Data collation: Methodology

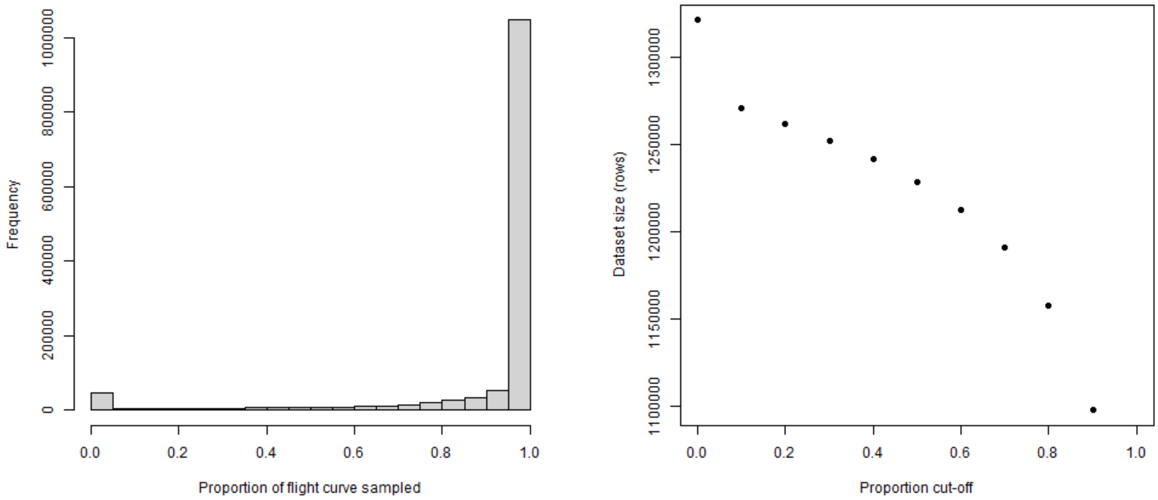
In this section, we used data from long-term monitoring schemes to model the potential effects of nitrogen upon individual Lepidoptera species, summary metrics such as community richness, and within trait groupings.

3.1. Methods

3.1.1. Data transformation

In the UKBMS site indices dataset, values of '-2' are given where the species was present but insufficient data were available to calculate the GAI. These values were treated differently in the abundance and richness models detailed below in sections 3.1.3, 3.1.4, and 3.1.5, with -2 values being transformed to: NA for abundance models, and 1 for richness models. This allows us to include the species presence in the richness estimates even though there is insufficient information to estimate abundance accurately. Site indices are only given for species observed at that site within the survey season. Thus, zero values were assigned for the site index of Lepidoptera species not recorded in the site and survey year. In addition, the data were filtered on a species-by-species basis to only include sites where the species had been observed at least once within the time series. At sites where the individual species has been observed in at least one year, we removed rows showing zero or NA counts from before that year. For example, imagine a situation at site X which has undergone UKBMS surveying from 1992–2022 where the species *Aglais io* had its first positive count in 2005. Only data from 2005 onwards at that site would therefore be included in the single species analysis. This is because we are interested in testing the potential effect of N on each individual species' abundance, not their occurrence.

In the RIS GAI dataset, the proportion of the annual flight curve/flight period for that species that was surveyed at that site (using weekly data) is noted. The flight curve of a species represents the dates during which the adults are actively flying. The distribution of a species' flight curve may be unimodal, bimodal, or multimodal depending on the number of generations it has in a given year. Due to the intensive sampling method used by the RIS, most proportions of annual flight curve/flight period are higher than 0.9 (Figure 1a). Where the proportion of the flight curve sampled is very low, the resulting calculation of the site index may be misleading. Thus, it is sensible to filter the dataset to only include samples with a large proportion of the flight curve sampled. We chose to only use data points where at least 90% of the flight curve of that species in that site and year had been sampled because this gave the most trustworthy GAI estimates without causing a large reduction in the amount of data available for analysis (Figure 1b). The zero and NA count data were treated similarly to the UKBMS GAI dataset. Due to the different method used to create the RIS GAI, values of '-2' are not present in the original dataset.



(a) **(b)**

Figure 1a & 1b: Histogram of the frequency of values present in the RIS GAI dataset for the variable representing the proportion of the annual flight curve for that species that was surveyed at that site (1a). Size of RIS GAI dataset (number of rows) when filtered to different cut-off proportions of the annual flight curve surveyed, where a cut-off of 0.0 includes the whole dataset and a cut-off of 0.2 includes rows where >20% of the flight curve for that species was sampled (1b).

Within the RIS dataset, data were collected on three micro-moth species: *Nomophila noctuella*, *Plutella xylostella*, and *Udea ferrugalis*. These were not considered in our analysis due to insufficient trait data being available in the Cook *et al.* (2024) database. The RIS do not distinguish the macro-moths *Mesapamea secalis* and *M. didyma* to species level, rather recording them as their aggregate *M. secalis/didyma*. This is common practice because these two species cannot be accurately identified without microscopic examination of their genitalia. In Cook *et al.* (2024), traits are resolved to species level for this genus. Where the traits we are interested in for this study (Table 1, Section 3.1.5) were similar for these two species, such as their voltinism, overwintering stage, hostplant category, flight season, and habitat, we aggregated trait values. Their aggregated hostplant specificity was assigned an NA value because it differs, with *M. didyma* being oligophagous whereas *M. secalis* is polyphagous.

The spatial coverage of the final UKBMS and RIS datasets used in this analysis are detailed in Section 3.2.1 (Figures 3a and 3b). For each UKBMS transect and RIS trap to have co-located land cover driver data for each year, we had to filter out certain locations, including the Republic of Ireland, Isle of Man, and Channel Islands.

3.1.2. Introduction to modelling

The aim of this modelling is to establish a baseline of evidence of N impacts on butterflies and moths. We analysed the data at three levels to see if/where important relationships are present. We used a Generalised additive model (GAM) approach to identify potential relationships, including those that are non-linear. The GAM approach will allow us to explore relationships between N and Lepidoptera without constraining the relationships to be linear so we can identify (e.g. saturating relationships, or hump-backed relationships where N is beneficial in small amounts). This flexible approach at this stage of indicator exploration ensures the greatest likelihood to identify any potential relationships.

One potential disadvantage of GAMs is that they can overfit the data, indicating changes in relationships that are not generalisable beyond the specific input data used. This can be a particular problem where the datasets are large, as is the case for some of the models in this report. To avoid this, we limited the potential flexibility of the models by setting the number of basis functions to 4 (where more basis functions allows more wiggly relationships and hence higher potential for overfitting). This choice of basis functions still allows the model to capture a range of non-linear relationships but means the potential for overfitting should be low.

We chose to fit a consistent set of predictors in each GAM model, described below, which were chosen to represent the most important drivers across all Lepidopteran species. To ensure models could be fit to responses where we had less data (e.g. individual species models) we selected a limited set of predictors which could be applied to as many models as possible. This means we may not be able to capture the complexity of ecological relationships for each species, but we are able to model many species.

All models were fit using the bam function from the mgcv R package (Wood, 2017) with a negative binomial distribution. Model predictions were produced using the ggeffects (Lüdecke 2018) package and plotted using the ggplot2 (Wickham 2009) package. Due to the complexity of the models and the associated computing power required, models were run on the JASMIN data analysis platform.

3.1.3. Single species modelling

To identify the impact of nitrogen on each butterfly and moth species, we fit a separate GAM to each species for which we had sufficient data. Models were fit as follows:

$$\begin{aligned} \textit{Abundance of individual species} \sim\ & \textit{Year} + \textit{Historic N deposition} \\ & + \textit{Change in N deposition over time} + \textit{Historic S deposition} \\ & + \textit{June temperature} + \textit{Previous June temperature} + \textit{Land Use Intensity} \\ & + \textit{June rainfall} + \textit{Location} + \textit{Site number} \end{aligned}$$

3.1.4. Combined species metrics modelling

To identify the potential impact of nitrogen on the higher-level metrics of richness and total abundance of the whole community, we fitted a separate GAM to each metric for butterflies and moths separately. Models were fit as follows:

$$\begin{aligned} \textit{Richness} \sim\ & \textit{Year} + \textit{Historic N deposition} + \textit{Change in N deposition over time} \\ & + \textit{Historic S deposition} + \textit{June temperature} + \textit{Previous June temperature} \\ & + \textit{Land Use Intensity} + \textit{June rainfall} + \textit{Location} + \textit{Site number} \end{aligned}$$

$$\begin{aligned} \textit{Total abundance} \sim\ & \textit{Year} + \textit{Historic N deposition} + \textit{Change in N deposition over time} \\ & + \textit{Historic S deposition} + \textit{June temperature} + \textit{Previous June temperature} \\ & + \textit{Land Use Intensity} + \textit{June rainfall} + \textit{Location} + \textit{Site number} \end{aligned}$$

3.1.5. Trait modelling

There are a few ways modelling the impacts of N on Lepidoptera could have been approached considering the traits we expect to impact this relationship. The simplest method is to provide a qualitative summary of the number of species in each trait group responding positively or negatively to N identified in the single species modelling above, as done in Risser (2023).

We quantitatively tested the effect of N on multiple groups of the Lepidoptera subset by traits, as in Staley *et al.* (2022). We calculated metrics such as the abundance of univoltine butterflies and fit the same GAM structure as shown for combined species metrics. This allowed us to understand the potential differences in response of the combined species metrics when considering data from specific trait groupings rather than all species. This is a commonly applied approach and lets us confidently review the impacts quantitatively.

The traits we tested based on evidence suggesting that they are likely to be impacted by N are described in Table 1.

Table 1: Traits tested in the trait modelling analyses.

Trait grouping	Traits
Habitat	Heathland, moorland, calcareous grassland, acid grassland, bogs mosses and mires
Overwintering stage	Egg, larva, pupa, adult
Voltinism	Univoltine, multivoltine
Flight season	Early Lepidoptera or Late Lepidoptera
Hostplant specificity	Monophagous, Oligophagous, Polyphagous
Broad hostplant category	Grasses, forbs, lichens

It was not possible to test all trait groupings as there may be insufficient data for some groups. Where this occurred, we note this in the results. Note that none of the resident UK butterfly species feed on lichen, thus we were only able to test the effect of N on moth species with lichen as a larval food. We attempted to test the effect of N on Lepidoptera species associated with mosses, however, none of the resident UK butterfly species feed on mosses and insufficient data were available for moss-feeding moths. Some moths feed on mosses as larva, however, only one such species was recorded in the survey, the Gold Swift *Phymatopus hecta* which has been observed feeding on *Mnium hornum* (Henwood *et al.* 2020). This did not provide us with enough data to run the model.

3.2. Results

3.2.1. Data exploration

Deposition of total N (measured in kg N ha-1) varies both spatially and temporally (Figures 2a, 2b & 2c). In general, deposition values have lowered over time. In 1986 and 1996, deposition is generally highest in western GB. Deposition in Northern Ireland appears to have increased over time. Deposition values in 1986 and 1996 are very highly collinear with a correlation value of 0.88 (Figure 2d). Values in 1986 and 2012 are not strongly correlated with a correlation value of 0.44.

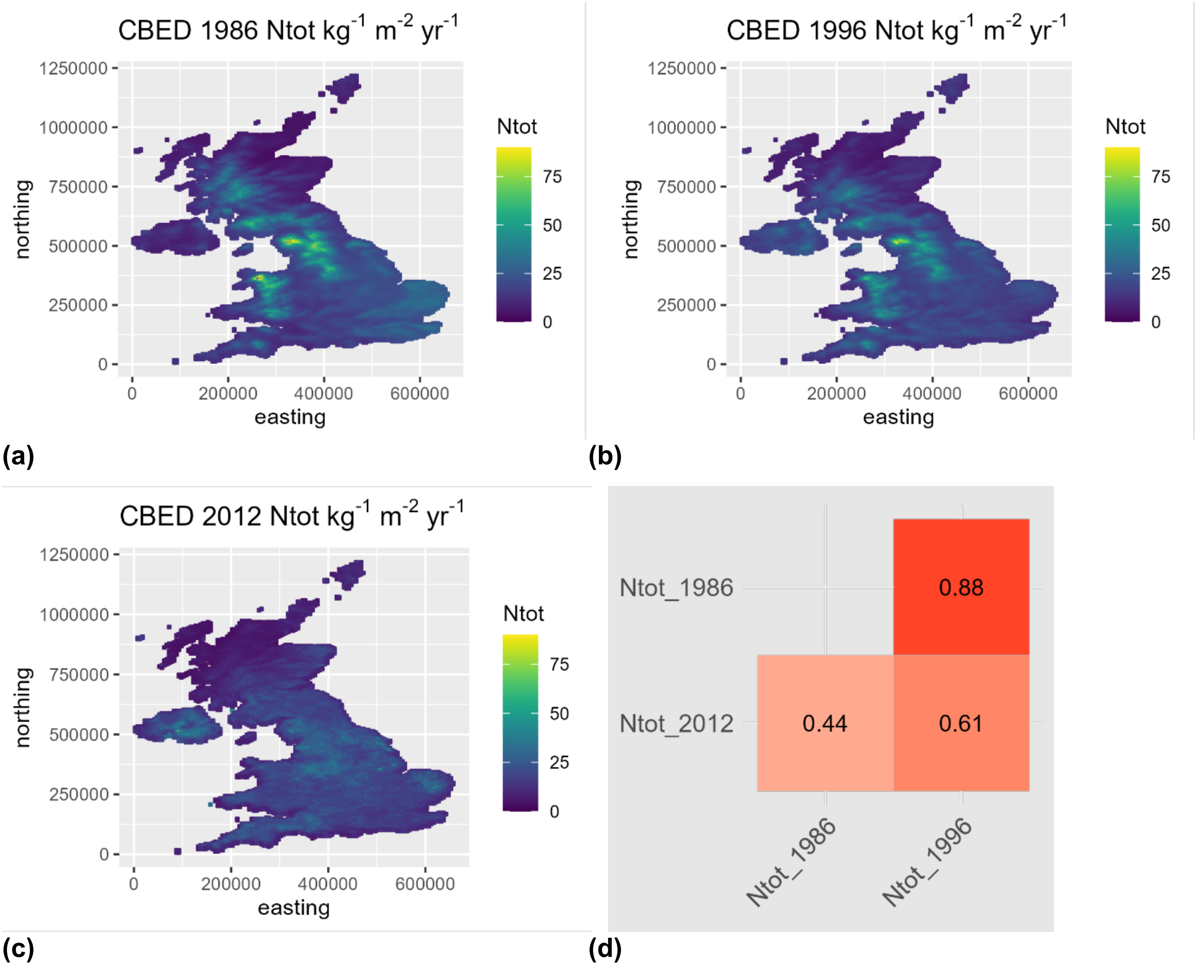
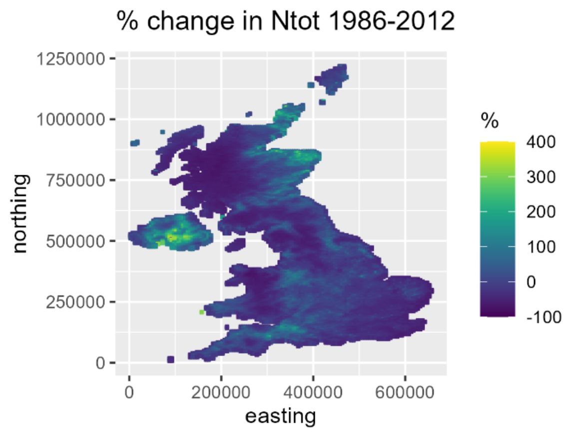
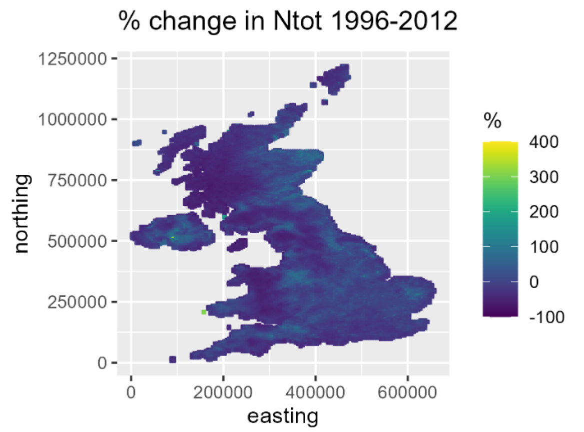


Figure 2a, 2b, 2c & 2d: Deposition of total N (kg N ha^{-1}) to UK in 1986 (a), 1996 (b), and 2012 (c) from the CBED model of deposition to moorland. 2d shows the correlation between these three variables.

Percentage change in deposition of total N (measured in kg N ha^{-1}) between the two time points tested varies both spatially and temporally. Percentage change is greatest over the UK between 1986 and 2012 (Figure 3a). Despite clear visual differences in the spatial signal of the two time periods shown, the overall values are strongly colinear with a correlation value of 0.77.



(a)



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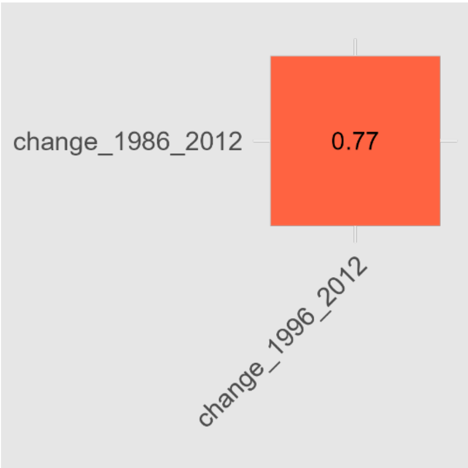
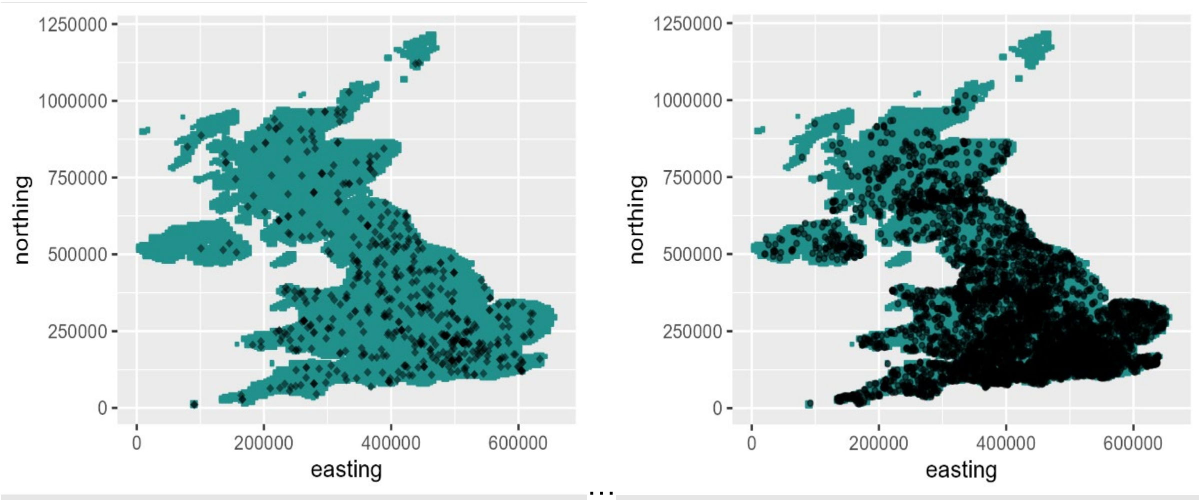


(c)

Figure 3a, 3b & 3c: Percentage change in deposition of total N (kg N ha^{-1}) to UK between 1986–2012 (a) and 1996–2012 (b) from the CBED model of deposition to moorland. 3c shows the correlation between these two variables. NB: panel (a) excludes a single % change value of > 400 (‘868.17’) in Northern Ireland.

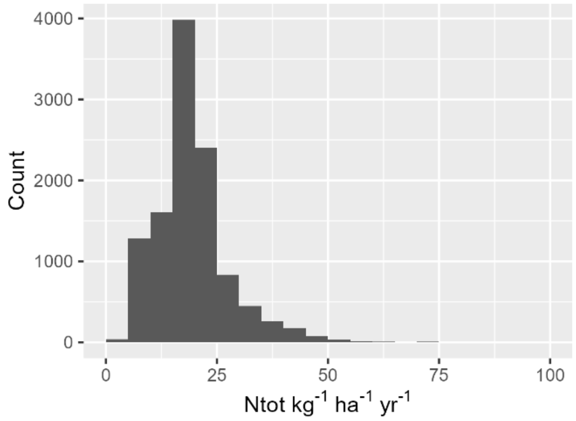
The spatial coverage of the two Lepidopteran datasets used in this analysis differ (Figures 4a and 4b). The RIS dataset provides relatively even coverage of the UK, with slightly sparser data in the far north of Scotland and western Northern Ireland, and more dense coverage in south-eastern England. The UKBMS has slightly more uneven coverage, especially in northern Scotland and rural upland areas generally. Both datasets have limited coverage of Scottish Islands and the Isle of Man. The datasets also differ in the total number of sample locations, with the UKBMS having approximately 25 times more sampling sites than the RIS.



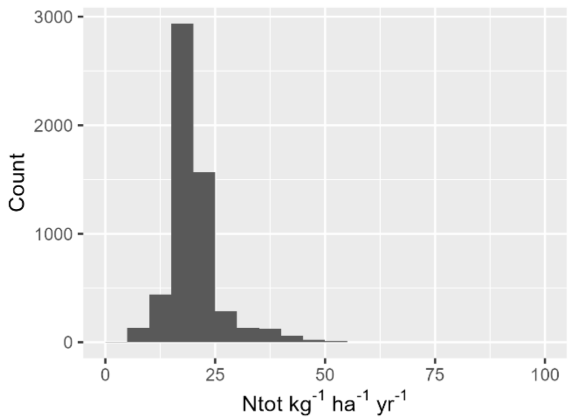
(a) **(b)**

Figure 4a & 4b: Locations of RIS (a) and UKBMS (b) monitoring sites. RIS sites were monitored between 1968–2021, whereas UKBMS sites were monitored between 1973–2022. Note that not all sites are monitored in every year, some sites only have data for a very limited number of years, and some sites will have stopped being monitored fairly early on in the time series.

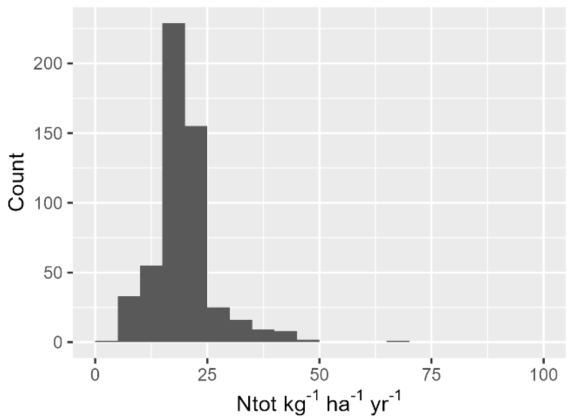
The gradient of total N deposition in 1996 (Figure 5a) is well covered by both the UKBMS (Figure 5b) and the RIS (Figure 5c), with neither survey scheme oversampling extremely high N deposition values. There is perhaps some under sampling by the UKBMS at the lower end of the N deposition range, which can be seen by visually comparing Figures 5a and 5b.



(a)



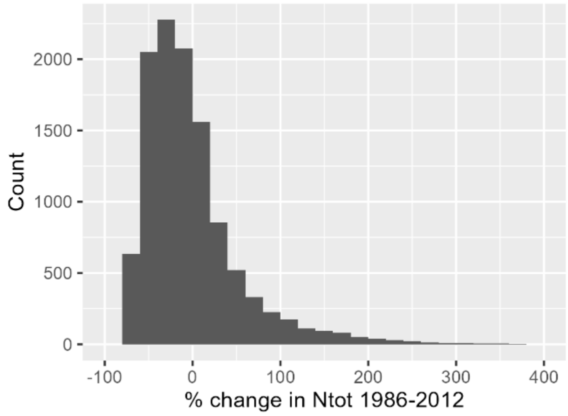
(b)



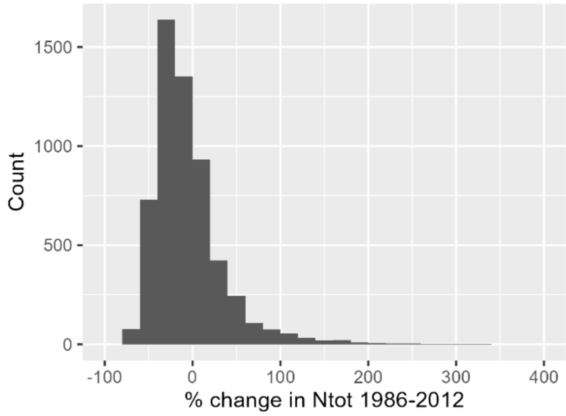
(c)

Figure 5a, 5b & 5c: Distribution of total N deposition values in 1996 across all 5 km squares in the UK (a), UKBMS site locations (b), and RIS site locations (c). Values are taken from the CBED model of deposition to moorland.

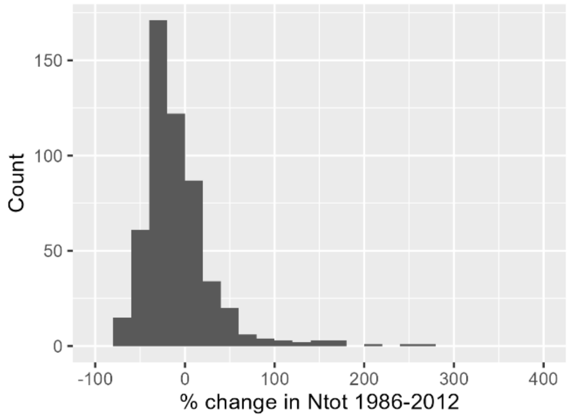
The gradient of percentage change in total N deposition values between 1986–2012 (Figure 6a) is well covered by both the UKBMS (Figure 6b) and the RIS (Figure 6c).



(a)



(b)



(c)

Figure 6a, 6b & 6c: Distribution of percentage change in total N deposition values between 1986–2012 across all 5 km squares in the UK (a), UKBMS site locations (b), and RIS site locations (c). Values are taken from the CBED model of deposition to moorland. NB: panel (a) excludes a single % change value of > 400 ('868.17') in Northern Ireland because it heavily skews the plot.

The area of the UK categorised as experiencing an increase, decrease, or no change in deposition varies depending on the threshold used to characterise the categories (Figures 7a, 7b, 7c & 7d). There are clear spatial clusters of the categories. Areas that have experienced a decrease in deposition tend to be in western and south-eastern Great Britain (GB), although this decrease in south-eastern GB is much less apparent at higher threshold values. In GB, increases in deposition are concentrated in the east coast of Scotland, western England, and south-western England. At all thresholds, Northern Ireland has primarily experienced an increase in deposition.

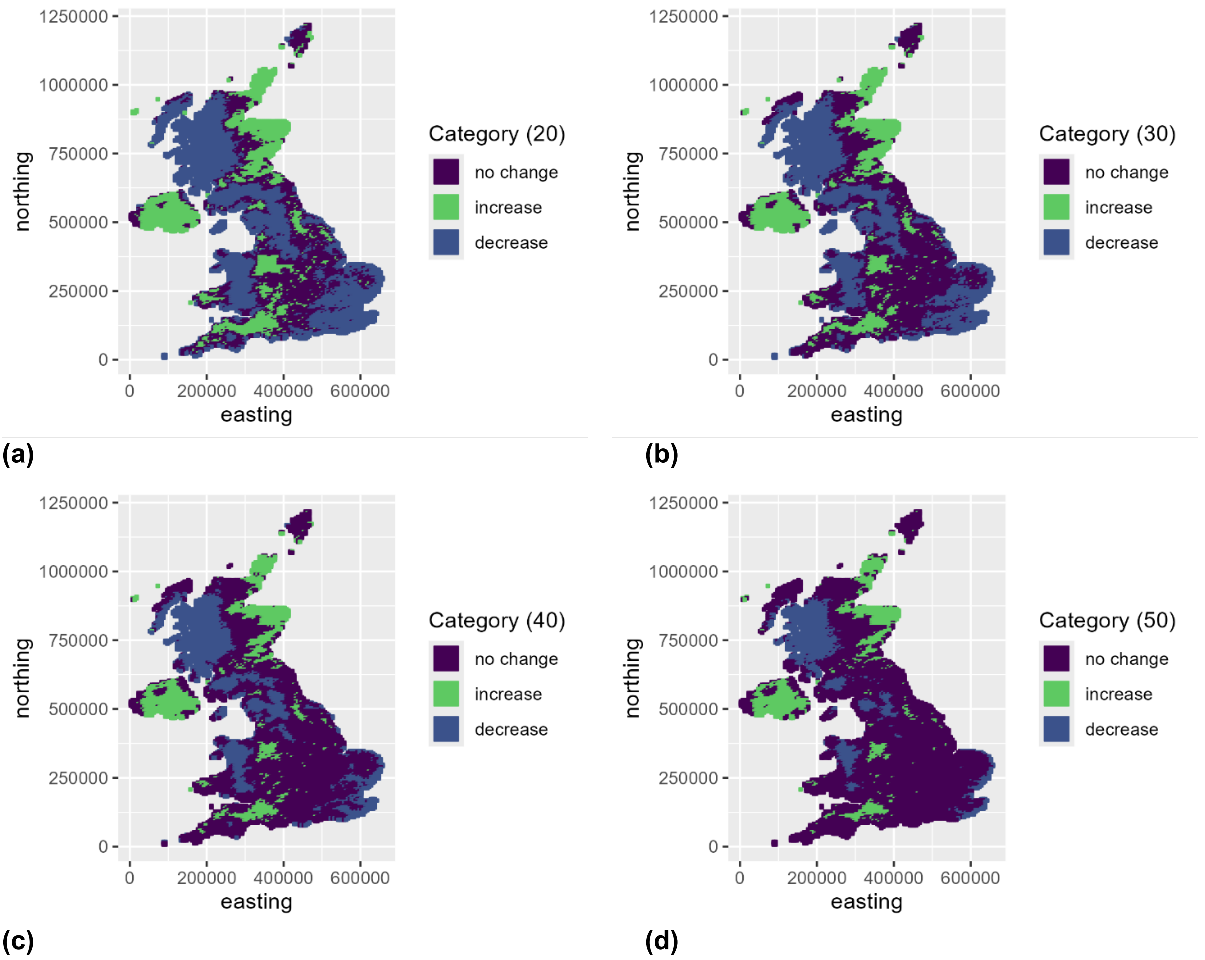


Figure 7a, 7b, 7c & 7d: Categorical groups of the percentage change in nitrogen in each 5 km grid square across the UK between 1986–2012 to represent decline, no change, and increase. In panel a, decline denotes values of ≤ -20%, increase of ≥ 20%, and no change of -20 < x < 20. In panel b, decline denotes values of ≤ -30%, increase of ≥ 30%, and no change of -30 < x < 30. In panel c, decline denotes values of ≤ -40%, increase of ≥ 40%, and no change of -40 < x < 40. In panel d, decline denotes values of ≤ -50%, increase of ≥ 50%, and no change of -50 < x < 50.

At all thresholds, there are more 5 km squares that experienced a decrease or no change in deposition than an increase (Figures 8a, 8b, 8c & 8d). Increasing the threshold from 20% to 50% has a far greater impact on the number of 5 km squares classed as decreasing than those classed as increasing.

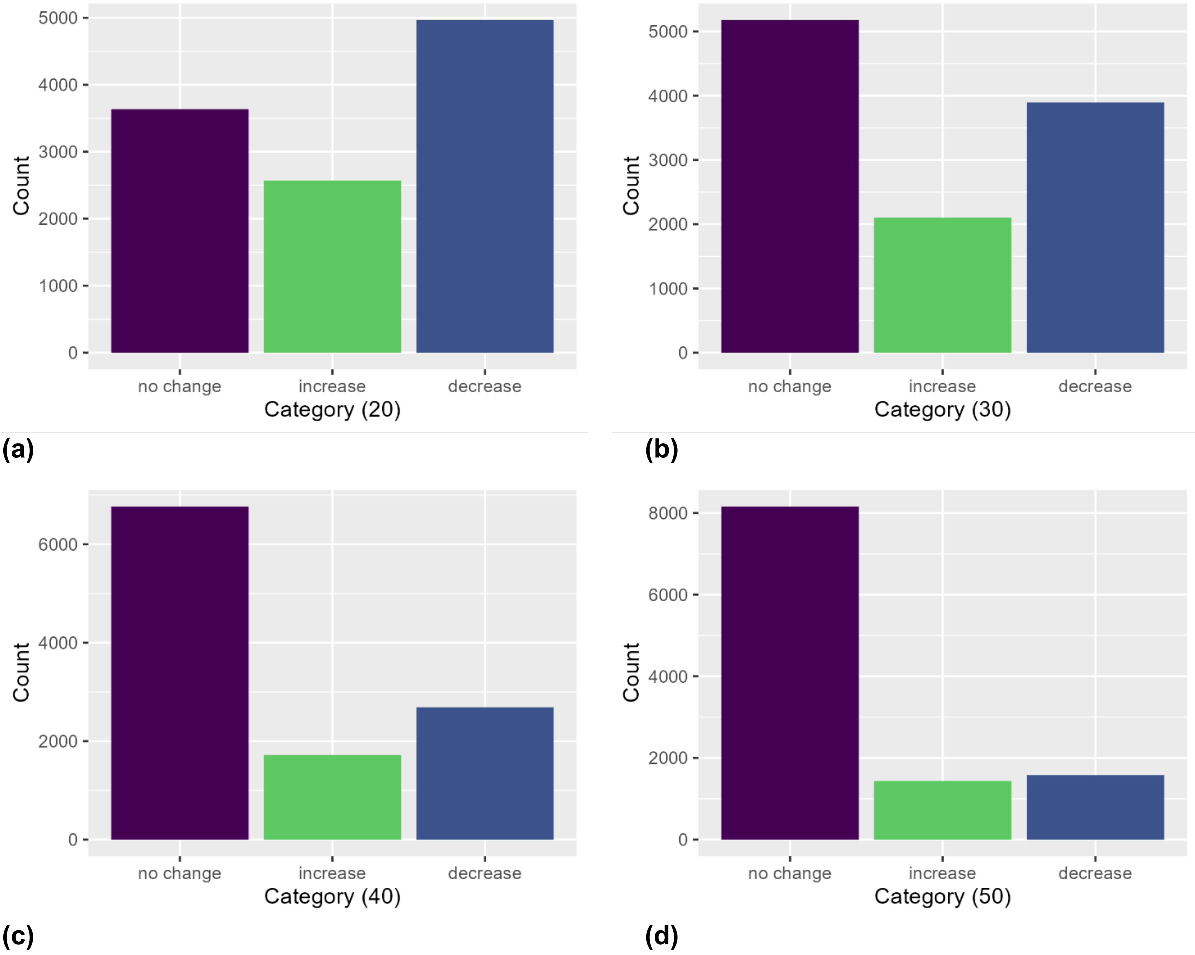


Figure 8a, 8b, 8c & 8d: Counts of the number of 5 km squares in each category of percentage change in nitrogen in each 5 km grid square between 1986–2012. In panel a, decline denotes values of ≤ -20%, increase of ≥ 20%, and no change of -20 < x < 20. In panel b, decline denotes values of ≤ -30%, increase of ≥ 3 0%, and no change of -30 < x < 30. In panel c, decline denotes values of ≤ -40%, increase of ≥ 40%, and no change of -40 < x < 40. In panel d, decline denotes values of ≤-50%, increase of ≥ 50%, and no change of -50 < x < 50.

3.2.2. Single species modelling

Models were fit for 56 butterfly species (Table 2). Of these, results for 8 species were inconclusive due to insufficient input data, usually because the species is rare or very range restricted. We noted where species are primarily migratory as the factors influencing their population trends are likely to be poorly explained by our models, given that much of their life cycle takes place in another country.

Responses to historic N were mixed, with the abundance of 10 species showing a negative correlation with the variable, two species showing a hump-backed relationship, two species showing a significant trend with no clear relationship, and 14 species showing a positive correlation. The abundance index of 20 butterfly species had no significant association with historic N.

Modelled responses to the percentage change in N deposition at a site over time were also mixed, with the abundance of four species showing a negative correlation with the variable, four species showing a hump-backed relationship, three species showing a significant trend with no clear relationship, and 6 species showing a positive correlation. The abundance index of 31 butterfly species had no significant association with historic N.

The abundance of only two species, Wall *Lasiommata megera* and Gatekeeper *Pyronia tithonus*, showed a negative correlation with both historic N and percentage change in N over time (Figures 9 and 10). The abundance index of the Marbled White *Melanargia galathea* and Speckled Wood *Pararge aegeria* both showed a hump-backed response to historic N (Figures 11 and 12).

Table 2: Table of results showing the direction (↑ = positive trend; ↓ = negative trend) and significance of relationships between abundance of individual butterfly species and deposition driver variables (∩ = humpbacked relationship; ~ = no significant trend) (*** = P < 0.001; ** = 0.001 < P < 0.01; * = 0.01 < P < 0.005; n.s. = non-significant; NA (not applicable) values are given where the model did not converge or was not run).

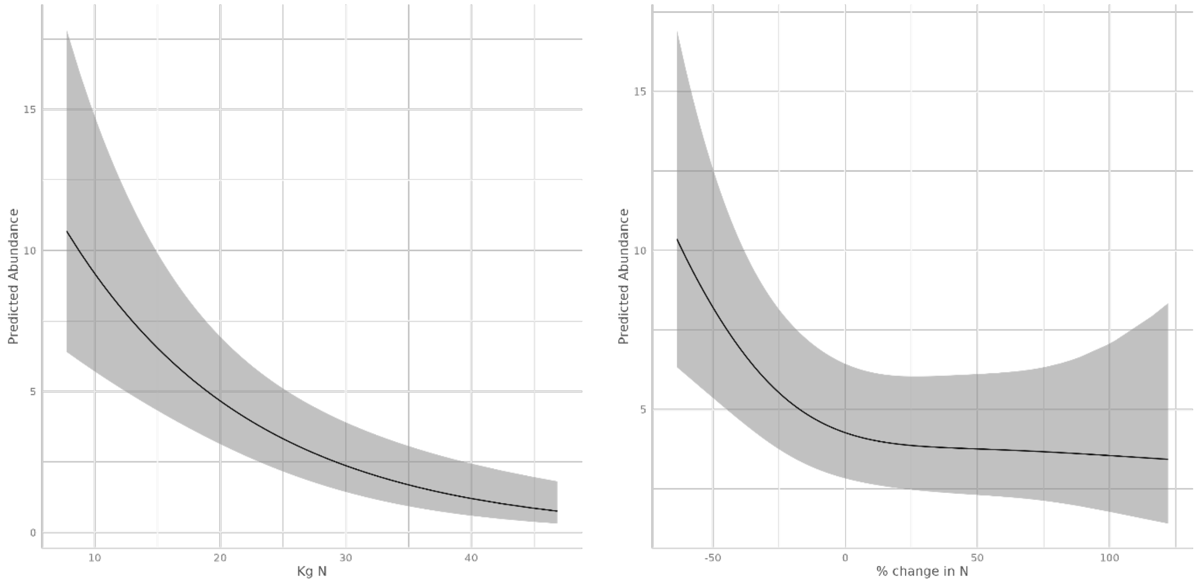
Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
Aglais io	Peacock	n.s.	∩ ***	↓ ***	-
Aglais urticae	Small Tortoiseshell	n.s.	↑ ***	↑ **	-
Anthocharis cardamines	Orange-tip	↑ **	↑ ***	n.s.	-
Apatura iris	Purple Emperor	NA	NA	NA	Insufficient data (n = 401)
Aphantopus hyperantus	Ringlet	↑ ***	∩ *	↓ ***	-
Argynnis paphia	Silver-washed Fritillary	↑ ***	n.s.	↓ ***	-
Aricia agestis	Brown Argus	↑ ***	~ **	↓ ***	-
Aricia artaxerxes	Northern Brown Argus	n.s.	n.s.	n.s.	-
Boloria euphrosyne	Pearl-bordered Fritillary	n.s.	n.s.	n.s.	-
Boloria selene	Small Pearl-bordered Fritillary	↑ **	n.s.	↓ *	-
Callophrys rubi	Green Hairstreak	n.s.	n.s.	n.s.	-

Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
Celastrina argiolus	Holly Blue	↓ ***	↑ *	↑ ***	-
Coenonympha pamphilus	Small Heath	↑ ***	n.s.	↓ ***	-
Coenonympha tullia	Large Heath	NA	NA	NA	Insufficient data (n = 188)
Colias croceus	Clouded Yellow	↓ *	n.s.	n.s.	Primarily migratory
Cupido minimus	Small Blue	n.s.	n.s.	n.s.	-
Erebia aethiops	Scotch Argus	NA	NA	NA	Insufficient data (n = 285)
Erebia epiphron	Mountain Ringlet	NA	NA	NA	Insufficient data
Erynnis tages	Dingy Skipper	n.s.	n.s.	n.s.	-
Euphydryas aurinia	Marsh Fritillary	n.s.	n.s.	n.s.	-
Fabriciana adippe	High Brown Fritillary	n.s.	↓ *	n.s.	-
Favonius quercus	Purple Hairstreak	n.s.	n.s.	n.s.	-
Gonepteryx rhamni	Brimstone	↑ **	n.s.	↓ ***	-
Hamearis lucina	Duke of Burgundy	n.s.	n.s.	n.s.	-
Hesperia comma	Silver-spotted Skipper	n.s.	n.s.	n.s.	-

Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
Hipparchia semele	Grayling	n.s.	↓ *	n.s.	-
Lasiommata megera	Wall	↓ ***	↓ ***	↑ *	-
Leptidea juvernica	Cryptic Wood White	NA	NA	NA	Insufficient data (n = 64)
Leptidea sinapis	Wood White	n.s.	n.s.	n.s.	-
Limentis camilla	White Admiral	n.s.	n.s.	↓ *	-
Lycaena phlaeas	Small Copper	↑ *	n.s.	n.s.	-
Maniola jurtina	Meadow Brown	↓ *	n.s.	↓ ***	-
Melanargia galathea	Marbled White	∩***	n.s.	↓ *	-
Melitaea athalia	Heath Fritillary	NA	NA	NA	Insufficient data (n = 267)
Melitaea cinxia	Glanville Fritillary	NA	NA	NA	Insufficient data (n = 62)
Ochlodes sylvanus	Large Skipper	↑ **	n.s.	↓/U ***	-
Papilio machaon	Swallowtail	NA	NA	NA	Insufficient data (n = 101)
Pararge aegeria	Speckled Wood	∩***	n.s.	↑ **	-
Pieris brassicae	Large White	↓ ***	∩ ***	↑ **	-

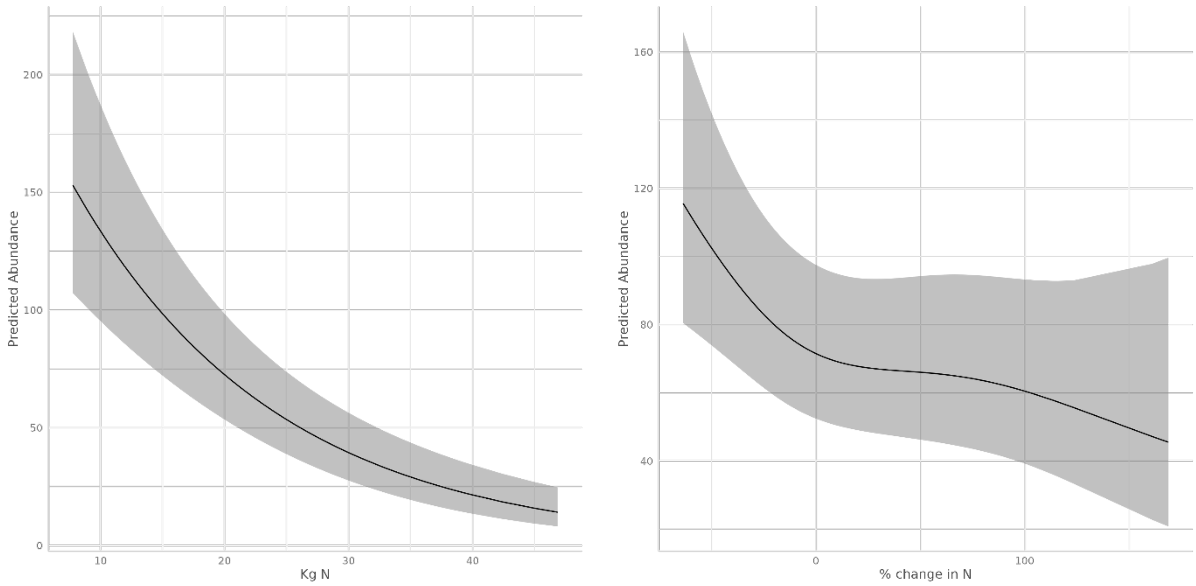
Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
Pieris napi	Green-veined White	↑ **	↑ ***	n.s.	-
Pieries rapae	Small White	↓ ***	∩ ***	↑ ***	-
Plebejus argus	Silver-studded Blue	n.s.	n.s.	n.s.	-
Polygonia c-album	Comma	↓ ***	↑ **	n.s.	-
Polyommatus bellargus	Adonis Blue	~*	~ **	∩/~**	-
Polyommatus coridon	Chalk Hill Blue	n.s.	n.s.	n.s.	-
Polyommatus icarus	Common Blue	↑ ***	n.s.	↓ ***	-
Pyrgus malvae	Grizzled Skipper	n.s.	~ *	n.s.	-
Pyronia tithonus	Gatekeeper	↓ ***	↓ **	n.s.	-
Satyrium pruni	Black Hairstreak	~*	n.s.	n.s.	-
Satyrium w-album	White-letter Hairstreak	n.s.	n.s.	n.s.	-
Speyeria aglaja	Dark Green Fritillary	↑ **	n.s.	↓ **	-
Thecla betulae	Brown Hairstreak	↑ *	n.s.	n.s.	-
Thymelicus lineola	Essex Skipper	↓ **	n.s.	n.s.	-

Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
Thymelicus sylvestris	Small Skipper	n.s.	⬆ *	n.s.	-
Vanessa atalanta	Red Admiral	⬆ *	n.s.	⬇/U ***	Primarily migratory. Recent (post-2000s) evidence of overwintering in southern England.
Vanessa cardui	Painted Lady	⬇ ***	n.s.	⬆ ***	Primarily migratory. Larvae unable to overwinter in UK.



(a) **(b)**

Figure 9a & 9b: Predicted abundance index of *Lasiommata megera* (Wall) at an average site against (a) increasing total N deposition (kg N ha^{-1} in 1996) and (b) percentage change in N deposition 1986–2012.



(a) **(b)**

Figure 10a & 10b: Predicted abundance index of *Pyronia tithonus* (Gatekeeper) at an average site against (a) increasing total N deposition (kg N ha^{-1} in 1996) and (b) percentage change in N deposition 1986–2012.

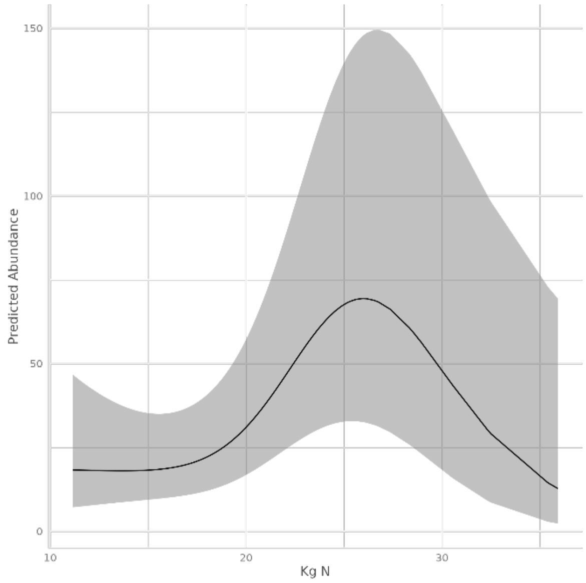


Figure 11: Predicted abundance index of *Melanargia galathea* (Marbled White) at an average site against increasing total N deposition (kg N ha^{-1} in 1996).

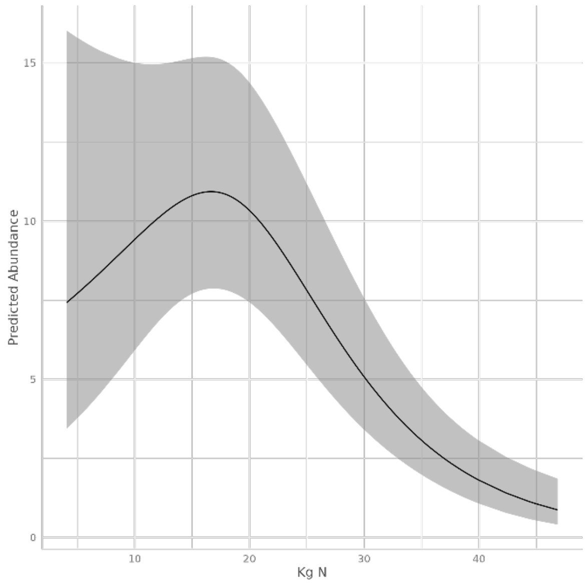


Figure 12: Predicted abundance index of *Pararge aegeria* (Speckled Wood) at an average site against (a) increasing total N deposition (kg N ha^{-1} in 1996).

Models were fit for 473 moth species (Table 3). Of these, results for six species were inconclusive due to insufficient input data. We were unable to note where species are primarily migratory due to time constraints.

As observed for the butterflies, responses of moths to historic N were mixed. The abundance index of 31 species showed a negative correlation with historic N, eight species showed a hump-backed relationship, 11 species showed a significant trend with no clear relationship, and 64 species showed a positive correlation. The abundance index of 353 moth species had no significant association with historic N.

Modelled responses of moths to the percentage change in N deposition at a site over time were also mixed. The abundance index of 85 species showed a negative correlation with historic N, seven species showed a hump-backed relationship, four species showed a significant trend with no clear relationship, and 10 species showed a positive correlation. The abundance index of 361 moth species had no significant association with historic N.

Overall, we found that, as expected, individual Lepidopteran species showed a wide range of relationships to N and S deposition, with some being strongly positively correlated to high deposition and some strongly negatively correlated. For individual butterfly species, in most, but not all, cases, the responses to the variables reflecting historic N and the change in N at a site over time were not conflicting.

Table 3: Full table of results showing the direction (🠕 = positive trend; 🠗 = negative trend) and significance of relationships between abundance of individual moth species and all driver variables (∩ = humpbacked relationship; ~ = no significant trend) (*** = P < 0.001; ** = 0.001 < P < 0.01; * = 0.01 < P < 0.005; n.s. = non-significant; NA (not applicable) values are given where the model did not converge or was not run).

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
80	*Laothoe populi*	Poplar Hawk-moth	🠕**	n.s.	🠗**	n = 2,757
95	*Deilephila porcellus*	Small Elephant Hawk-moth	NA	NA	NA	Insufficient data (n = 90)
96	*Deilephila elpenor*	Elephant Hawk-moth	n.s.	n.s.	n.s.	n = 207
102	*Furcula furcula*	Sallow Kitten	n.s.	n.s.	n.s.	n = 164
104	*Stauropus fagi*	Lobster Moth	n.s.	n.s.	n.s.	n = 269
106	*Drymonia dodonaea*	Marbled Brown	🠗**	n.s.	🠕**	n = 605
107	*Drymonia ruficornis*	Lunar Marbled Brown	n.s.	n.s.	n.s.	n = 541
108	*Pheosia tremula*	Swallow Prominent	n.s.	n.s.	n.s.	n = 588
109	*Pheosia gnoma*	Lesser Swallow Prominent	n.s.	n.s.	n.s.	n = 1,579
110	*Notodonta ziczac*	Pebble Prominent	n.s.	n.s.	n.s.	n = 1,053
111	*Notodonta dromedarius*	Iron Prominent	n.s.	n.s.	n.s.	n = 703
114	*Peridea anceps*	Great Prominent	n.s.	n.s.	n.s.	n = 566

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
117	*Ptilodon capucina*	Coxcomb Prominent	↑*	n.s.	n.s.	n = 2,472
118	*Odontosia carmelita*	Scarce Prominent	n.s.	n.s.	n.s.	n = 283
120	*Pterostoma palpina*	Pale Prominent	↑**	n.s.	↓**	n = 2,028
121	*Phalera bucephala*	Buff-tip	↑**	n.s.	n.s.	n = 1,639
122	*Clostera curtula*	Chocolate-tip	n.s.	n.s.	n.s.	n = 400
125	*Habrosyne pyritoides*	Buff Arches	n.s.	n.s.	n.s.	n = 1,739
126	*Thyatira batis*	Peach Blossom	n.s.	n.s.	n.s.	n = 1,563
127	*Tethea ocularis*	Figure of Eighty	n.s.	n.s.	n.s.	n = 303
129	*Ochropacha duplaris*	Common Lutestring	n.s.	n.s.	n.s.	n = 1,018
130	*Tetheella fluctuosa*	Satin Lutestring	n.s.	↓***	n.s.	n = 169
131	*Cymatophorina diluta*	Oak Lutestring	n.s.	n.s.	n.s.	n = 289
132	*Achlya flavicornis*	Yellow Horned	n.s.	n.s.	n.s.	n = 986
133	*Polyploca ridens*	Frosted Green	n.s.	n.s.	n.s.	n = 324

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
135	*Orgyia antiqua*	The Vapourer	n.s.	n.s.	n.s.	n = 243
137	*Calliteara pudibunda*	Pale Tussock	n.s.	n.s.	**	n = 1,404
138	*Euproctis chrysorrhoea*	Brown-tail	↓**	n.s.	↑*	n = 239
139	*Euproctis similis*	Yellow-tail	n.s.	n.s.	↓***	n = 2,132
142	*Leucoma salicis*	White Satin Moth	n.s.	n.s.	n.s.	n = 140
144	*Lymantria monacha*	Black Arches	↓**	n.s.	↑***	n = 721
145	*Malacosoma neustria*	The Lackey	↓*	n.s.	n.s.	n = 868
147	*Trichiura crataegi*	Pale Eggar	n.s.	↑*	n.s.	n = 809
148	*Poecilocampa populi*	December Moth	↑*	n.s.	n.s.	n = 1,593
150	*Lasiocampa quercus*	Oak Eggar	↑*	n.s.	n.s.	n = 346
152	*Macrothylacia rubi*	Fox Moth	n.s.	n.s.	n.s.	n = 524
154	*Euthrix potatoria*	The Drinker	n.s.	↓*	n.s.	n = 2,226
159	*Saturnia pavonia*	Emperor Moth	n.s.	n.s.	n.s.	n = 159

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
161	*Watsonalla binaria*	Oak Hook-tip	n.s.	n.s.	n.s.	n = 913
162	*Watsonalla cultraria*	Barred Hook-tip	n.s.	n.s.	n.s.	n = 121
163	*Drepana falcataria*	Pebble Hook-tip	↑*	n.s.	n.s.	n = 1,172
164	*Falcaria lacertinaria*	Scalloped Hook-tip	n.s.	n.s.	n.s.	n = 891
165	*Cilix glaucata*	Chinese Character	n.s.	n.s.	n.s.	n = 2,354
166	*Nola cucullatella*	Short-cloaked Moth	n.s.	n.s.	n.s.	n = 1,587
168	*Meganola albula*	Kent Black Arches	n.s.	n.s.	n.s.	n = 187
169	*Nola confusalis*	Least Black Arches	n.s.	n.s.	n.s.	n = 1,208
172	*Nudaria mundana*	Muslin Footman	n.s.	n.s.	n.s.	n = 851
173	*Thumatha senex*	Round-winged Muslin	n.s.	n.s.	n.s.	n = 467
174	*Miltochrista miniata*	Rosy Footman	n.s.	n.s.	↑*	n = 678
176	*Cybosia mesomella*	Four-dotted Footman	n.s.	n.s.	n.s.	n = 844
178	*Eilema depressa*	Buff Footman	↑**	↓*	↓**	n = 669
179	*Eilema griseola*	Dingy Footman	n.s.	↓**	↓***	n = 1,365

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
180	*Eilema lurideola*	Common Footman	↑*	↓**	↓***	n = 2,894
181	*Eilema complana*	Scarce Footman	~*	n.s.	n.s.	n = 855
185	*Eilema sororcula*	Orange Footman	n.s.	n.s.	n.s.	n = 274
191	*Tyria jacobaeae*	The Cinnabar	n.s.	n.s.	n.s.	n = 1,739
192	*Spilosoma lubricipeda*	White Ermine	↑**	↓***	↓***	n = 3,836
194	*Spilosoma lutea*	Buff Ermine	∩***	↓*	↓***	n = 3,096
195	*Diaphora mendica*	Muslin Moth	n.s.	n.s.	↓**	n = 2,029
196	*Diacrisia sannio*	Clouded Buff	n.s.	n.s.	n.s.	n = 278
197	*Phragmatobia fuliginosa*	Ruby Tiger	n.s.	↓*	↓**	n = 1,620
200	*Arctia caja*	Garden Tiger	n.s.	n.s.	n.s.	n = 1,852
266	*Hepialus humuli*	Ghost Moth	n.s.	n.s.	n.s.	n = 1,557
267	*Triodia sylvina*	Orange Swift	n.s.	n.s.	n.s.	n = 2,189
268	*Korscheltellus fusconebulosa*	Map-winged Swift	n.s.	n.s.	n.s.	n = 1,388

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
269	*Korscheltellus lupulina*	Common Swift	↓**	n.s.	n.s.	n = 2,525
270	*Phymatopus hecta*	Gold Swift	n.s.	n.s.	n.s.	n = 260
273	*Euxoa nigricans*	Garden Dart	n.s.	n.s.	n.s.	n = 462
274	*Euxoa tritici*	White-line Dart	n.s.	↓*	↓*	n = 251
277	*Agrotis segetum*	Turnip Moth	n.s.	↓*	n.s.	n = 1,229
278	*Agrotis vestigialis*	Archer's Dart	n.s.	n.s.	n.s.	n = 182
280	*Agrotis clavis*	Heart & Club	↑*	n.s.	↓**	n = 672
282	*Agrotis puta*	Shuttle-shaped Dart	n.s.	n.s.	↓*	n = 1,695
285	*Agrotis exclamationis*	Heart & Dart	n.s.	n.s.	↓*	n = 3,604
286	*Agrotis ipsilon*	Dark Sword-grass	n.s.	n.s.	n.s.	n = 457
289	*Lycophotia porphyrea*	True Lover's Knot	n.s.	↓*	n.s.	n = 1,609
292	*Peridroma saucia*	Pearly Underwing	n.s.	n.s.	n.s.	n = 119
297	*Graphiphora augur*	Double Dart	n.s.	n.s.	n.s.	n = 962

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
298	*Diarsia brunnea*	Purple Clay	⬆/∩**	n.s.	n.s.	n = 2,030
299	*Diarsia mendica*	Ingrailed Clay	n.s.	⬇*	n.s.	n = 3,325
301	*Diarsia dahlii*	Barred Chestnut	n.s.	n.s.	n.s.	n = 660
302	*Diarsia rubi*	Small Square-spot	n.s.	n.s.	n.s.	n = 3,604
304	*Ochropleura plecta*	Flame Shoulder	⬆***	⬇***	⬇**	n = 3,759
305	*Xestia agathina*	Heath Rustic	n.s.	⬇*	n.s.	n = 268
309	*Eugnorisma glareosa*	Autumnal Rustic	n.s.	n.s.	n.s.	n = 1,040
310	*Xestia castanea*	Neglected Rustic	n.s.	n.s.	n.s.	n = 288
311	*Xestia baja*	Dotted Clay	n.s.	n.s.	n.s.	n = 1,738
312	*Eugnorisma depuncta*	Plain Clay	n.s.	⬇**	⬇.	n = 138
313	*Xestia c-nigrum*	Setaceous Hebrew Character	n.s.	n.s.	⬇*	n = 2,773
314	*Xestia ditrapezium*	Triple-spotted Clay	n.s.	n.s.	n.s.	n = 526
315	*Xestia triangulum*	Double Square-spot	n.s.	n.s.	⬇*	n = 2,741

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
317	*Xestia sexstrigata*	Six-striped Rustic	n.s.	n.s.	n.s.	n = 2,531
318	*Xestia xanthographa*	Square-spot Rustic	↓*	n.s.	n.s.	n = 3,894
319	*Axylia putris*	The Flame	n.s.	n.s.	↓*	n = 2,392
320	*Anaplectoides prasina*	Green Arches	↑*	n.s.	n.s.	n = 772
321	*Eurois occulta*	Great Brocade	n.s.	n.s.	n.s.	n = 104
323	*Cerastis rubricosa*	Red Chestnut	n.s.	↓**	n.s.	n = 2,073
324	*Naenia typica*	The Gothic	n.s.	n.s.	n.s.	n = 557
327	*Noctua comes*	Lesser Yellow Underwing	↓***	n.s.	↑**	n = 3,027
329	*Noctua janthe*	Lesser Broad-bordered Yellow Underwing	n.s.	n.s.	n.s.	n = 3,315
330	*Noctua interjecta*	Least Yellow Underwing	n.s.	n.s.	n.s.	n = 298
331	*Noctua pronuba*	Large Yellow Underwing	n.s.	n.s.	n.s.	n = 4,069
332	*Noctua fimbriata*	Broad-bordered Yellow Underwing	n.s.	n.s.	n.s.	n = 622
345	*Mamestra brassicae*	Cabbage Moth	n.s.	∩*	n.s.	n = 1,600

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346	*Melanchra persicariae*	Dot Moth	n.s.	n.s.	n.s.	n = 983
349	*Polia nebulosa*	Grey Arches	n.s.	n.s.	↑*	n = 510
351	*Lacanobia oleracea*	Bright-line Brown-eye	↓***	n.s.	↑***	n = 2,873
353	*Ceramica pisi*	Broom Moth	n.s.	↓**	n.s.	n = 1,595
354	*Hada plebeja*	The Shears	n.s.	n.s.	n.s.	n = 1,300
355	*Anarta trifolii*	Nutmeg	n.s.	n.s.	~*	n = 561
358	*Lacanobia suasa*	Dog's Tooth	n.s.	n.s.	n.s.	n = 117
359	*Lacanobia thalassina*	Pale-shouldered Brocade	n.s.	↓**	n.s.	n = 1,684
361	*Papestra biren*	Glaucous Shears	n.s.	n.s.	n.s.	n = 317
363	*Hecatera bicolorata*	Broad-barred White	n.s.	n.s.	n.s.	n = 490
366	*Hadena confusa*	Marbled Coronet	n.s.	n.s.	n.s.	n = 129
368	*Hadena bicruris*	The Lychnis	n.s.	n.s.	n.s.	n = 821
370	*Sideridis rivularis*	Campion	n.s.	↓*	n.s.	n = 564

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371	*Hadena perplexa*	Tawny Shears	~**	n.s.	n.s.	n = 178
376	*Tholera decimalis*	Feathered Gothic	n.s.	n.s.	n.s.	n = 1,389
377	*Tholera cespitis*	Hedge Rustic	n.s.	n.s.	n.s.	n = 599
378	*Cerapteryx graminis*	Antler Moth	↑***	↓**	n.s.	n = 2,155
382	*Orthosia gothica*	Hebrew Character	↑***	↓**	↓***	n = 3,216
383	*Orthosia miniosa*	Blossom Underwing	~*	n.s.	n.s.	n = 127
384	*Orthosia cruda*	Small Quaker	↑**	n.s.	↓*	n = 2,094
385	*Orthosia cerasi*	Common Quaker	↑**	↓*	↓*	n = 2,823
386	*Orthosia populeti*	Lead-coloured Drab	n.s.	n.s.	n.s.	n = 299
387	*Orthosia incerta*	Clouded Drab	↑**	↓*	↓*	n = 2,554
388	*Anorthoa munda*	Twin-spotted Quaker	↑*	n.s.	↓*	n = 1,515
390	*Orthosia gracilis*	Powdered Quaker	n.s.	↓**	n.s.	n = 1,157
391	*Panolis flammea*	Pine Beauty	n.s.	n.s.	n.s.	n = 655
393	*Mythimna pallens*	Common Wainscot	n.s.	n.s.	n.s.	n = 2,744

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395	*Mythimna impura*	Smoky Wainscot	n.s.	n.s.	n.s.	n = 3,935
397	*Mythimna pudorina*	Striped Wainscot	n.s.	n.s.	n.s.	n = 130
400	*Leucania comma*	Shoulder-striped Wainscot	n.s.	n.s.	n.s.	n = 1,157
406	*Mythimna albipuncta*	White-point	n.s.	n.s.	n.s.	n = 201
407	*Mythimna ferrag*	The Clay	n.s.	↓*	n.s.	n = 2,838
408	*Mythimna conigera*	Brown-line Bright-eye	n.s.	n.s.	n.s.	n = 1,221
410	*Stilbia anomala*	The Anomalous	n.s.	↓*	n.s.	n = 541
411	*Rhizedra lutosa*	Large Wainscot	n.s.	↓**	n.s.	n = 323
413	*Denticucullus pygmina*	Small Wainscot	↑*	↓***	n.s.	n = 1,996
415	*Photedes fluxa*	Mere Wainscot	~*	↓*	∩**	n = 153
419	*Arenostola phragmitidis*	Fen Wainscot	↑*	↓*	∩**	n = 129
425	*Archanara dissoluta*	Brown-veined Wainscot	NA	NA	NA	Insufficient data (n = 98)
427	*Coenobia rufa*	Small Rufous	n.s.	n.s.	n.s.	n = 320

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429	*Charanyca trigrammica*	Treble Lines	n.s.	n.s.	↓*	n = 1,192
430	*Caradrina morpheus*	Mottled Rustic	↓*	n.s.	n.s.	n = 2,609
431	*Hoplodrina octogenaria*	Uncertain	n.s.	n.s.	↓*	n = 2,678
432	*Hoplodrina blanda*	The Rustic	n.s.	n.s.	n.s.	n = 2,054
433	*Hoplodrina ambigua*	Vine's Rustic	↓***	n.s.	n.s.	n = 839
435	*Caradrina clavipalpis*	Pale Mottled Willow	n.s.	n.s.	↑***	n = 672
438	*Dypterygia scabriuscula*	Bird's Wing	n.s.	n.s.	n.s.	n = 134
441	*Apamea lithoxylaea*	Light Arches	↓*	n.s.	n.s.	n = 1,813
444	*Apamea monoglypha*	Dark Arches	↑/U*	↓***	n.s.	n = 4,188
446	*Apamea epomidion*	Clouded Brindle	n.s.	n.s.	n.s.	n = 174
447	*Apamea crenata*	Clouded-bordered Brindle	n.s.	n.s.	n.s.	n = 1,649
448	*Apamea sordens*	Rustic Shoulder-knot	n.s.	n.s.	n.s.	n = 1,619

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449	*Apamea unanimis*	Small Clouded Brindle	n.s.	n.s.	n.s.	n = 244
452	*Apamea anceps*	Large Nutmeg	n.s.	n.s.	n.s.	n = 434
454	*Apamea remissa*	Dusky Brocade	n.s.	n.s.	n.s.	n = 1,213
455	*Apamea scolopacina*	Slender Brindle	n.s.	n.s.	n.s.	n = 787
457	*Lateroligia ophiogramma*	Double Lobed	n.s.	n.s.	n.s.	n = 240
458	*Apterogenum ypsillon*	Dingy Shears	n.s.	↑*	n.s.	n = 183
461	*Eremobia ochroleuca*	Dusky Sallow	n.s.	n.s.	n.s.	n = 777
462	*Oligia strigilis*	Marbled Minor	n.s.	↓**	n.s.	n = 2,184
463	*Oligia latruncula*	Tawny Marbled Minor	n.s.	n.s.	n.s.	n = 1,898
464	*Oligia versicolor*	Rufous Minor	n.s.	n.s.	n.s.	n = 1,033
465	*Oligia fasciuncula*	Middle-barred Minor	n.s.	n.s.	n.s.	n = 3,387
466	*Litoligia literosa*	Rosy Minor	n.s.	n.s.	n.s.	n = 860
467	*Mesoligia furuncula*	Cloaked Minor	↓*	n.s.	↑**	n = 1,908

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469	*Luperina testacea*	Flounced Rustic	↓***	n.s.	n.s.	n = 3,469
472	*Euplexia lucipara*	Small Angle Shades	~*	↓*	n.s.	n = 1,711
473	*Phlogophora meticulosa*	Angle Shades	n.s.	n.s.	n.s.	n = 2,878
475	*Hyppa rectilinea*	The Saxon	~*	n.s.	∩/↓*	n = 157
476	*Thalpophila matura*	Straw Underwing	n.s.	n.s.	n.s.	n = 1,587
478	*Photedes minima*	Small Dotted Buff	↑***	n.s.	n.s.	n = 2,794
481	*Celaena haworthii*	Haworth's Minor	n.s.	n.s.	n.s.	n = 400
482	*Helotropha leucostigma*	Crescent	↓**	n.s.	↑**	n = 311
484	*Amphipoea oculea*	Ear Moth	n.s.	↓**	n.s.	n = 659
486	*Amphipoea lucens*	Large Ear	n.s.	n.s.	n.s.	n = 479
487	*Amphipoea crinanensis*	Crinan Ear	n.s.	n.s.	n.s.	n = 303
488	*Hydraecia micacea*	Rosy Rustic	n.s.	n.s.	n.s.	n = 3,462
490	*Gortyna flavago*	Frosted Orange	↑*	n.s.	n.s.	n = 1,773

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493	*Cosmia pyralina*	Lunar-spotted Pinion	n.s.	∩**	n.s.	n = 425
494	*Cosmia affinis*	Lesser-spotted Pinion	n.s.	∩**	n.s.	n = 184
496	*Cosmia trapezina*	The Dun-bar	n.s.	n.s.	n.s.	n = 2,574
500	*Ipimorpha subtusa*	The Olive	n.s.	∩*	n.s.	n = 324
502	*Amphipyra pyramidea*	Copper Underwing	n.s.	n.s.	n.s.	n = 461
503	*Amphipyra tragopoginis*	Mouse Moth	n.s.	↑*	n.s.	n = 1,958
504	*Rusina ferruginea*	Brown Rustic	n.s.	↓***	n.s.	n = 3,012
505	*Mormo maura*	Old Lady	n.s.	n.s.	n.s.	n = 104
506	*Bryophila domestica*	Marbled Beauty	n.s.	∩*	n.s.	n = 1,474
512	*Acronicta leporina*	The Miller	NA	NA	NA	Insufficient data (n = 81)
514	*Subacronicta megacephala*	Poplar Grey	n.s.	↑*	n.s.	n = 236
517	*Acronicta tridens*	Dark Dagger	n.s.	n.s.	n.s.	n = 113
518	*Acronicta psi*	Grey Dagger	n.s.	n.s.	n.s.	n = 601

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523	*Acronicta rumicis*	Knot Grass	n.s.	n.s.	n.s.	n = 844
524	*Craniophora ligustri*	The Coronet	n.s.	n.s.	n.s.	n = 301
527	*Cucullia umbratica*	The Shark	n.s.	n.s.	n.s.	n = 174
539	*Lithophane socia*	Pale Pinion	n.s.	n.s.	n.s.	n = 241
540	*Lithophane leautieri*	Blair's Shoulder-Knot	n.s.	n.s.	n.s.	n = 491
543	*Lithophane ornitopus*	Grey Shoulder-knot	n.s.	n.s.	n.s.	n = 441
545	*Xylena vetusta*	Red Sword-grass	↓*	n.s.	n.s.	n = 370
546	*Xylocampa areola*	Early Grey	↑*	n.s.	n.s.	n = 1,352
550	*Asteroscopus sphinx*	The Sprawler	n.s.	n.s.	n.s.	n = 983
552	*Brachylomia viminalis*	Minor Shoulder-knot	↓**	↓*	↑*	n = 1,017
553	*Aporophyla lutulenta*	Deep-brown Dart	n.s.	n.s.	n.s.	n = 634
554	*Aporophyla lueneburgensis*	Northern Deep-brown Dart	n.s.	n.s.	n.s.	n = 108
555	*Aporophyla nigra*	Black Rustic	n.s.	n.s.	n.s.	n = 1,155

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557	*Allophyes oxyacanthae*	Green-brindled Crescent	n.s.	n.s.	⬇**	n = 2,782
559	*Griposia aprilina*	Merveille du Jour	n.s.	n.s.	n.s.	n = 628
562	*Mniotype adusta*	Dark Brocade	⬆**	n.s.	n.s.	n = 510
563	*Polymixis lichenea*	Feathered Ranunculus	⬇*	n.s.	n.s.	n = 381
564	*Parastichtis suspecta*	The Suspected	NA	NA	NA	Insufficient data (n = 94)
565	*Dryobotodes eremita*	Brindled Green	n.s.	n.s.	n.s.	n = 954
567	*Dasypolia templi*	Brindled Ochre	n.s.	n.s.	n.s.	n = 264
568	*Polymixis flavicincta*	Large Ranunculus	n.s.	n.s.	n.s.	n = 175
569	*Antitype chi*	Grey Chi	n.s.	n.s.	n.s.	n = 493
571	*Eupsilia transversa*	The Satellite	n.s.	n.s.	n.s.	n = 1,286
573	*Conistra rubiginea*	Dotted Chestnut	n.s.	n.s.	n.s.	n = 194
574	*Omphaloscelis lunosa*	Lunar Underwing	n.s.	n.s.	⬇***	n = 2,906
575	*Agrochola lota*	Red-line Quaker	n.s.	n.s.	n.s.	n = 2,132

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576	*Agrochola macilenta*	Yellow-line Quaker	↑*	↓*	n.s.	n = 2,465
577	*Agrochola circellaris*	The Brick	↑*	n.s.	n.s.	n = 1,610
578	*Agrochola lychnidis*	Beaded Chestnut	n.s.	n.s.	↓**	n = 1,985
579	*Agrochola helvola*	Flounced Chestnut	n.s.	n.s.	n.s.	n = 515
580	*Agrochola litura*	Brown-spot Pinion	n.s.	n.s.	n.s.	n = 1,897
581	*Atethmia centrago*	Centre-barred Sallow	n.s.	↓*	n.s.	n = 1,253
582	*Tiliacea citrago*	Orange Sallow	n.s.	n.s.	n.s.	n = 326
583	*Tiliacea aurago*	Barred Sallow	n.s.	n.s.	n.s.	n = 895
584	*Xanthia togata*	Pink-barred Sallow	↑**	n.s.	↓*	n = 1,914
585	*Cirrhia icteritia*	Sallow	↑*	n.s.	↓*	n = 2,025
586	*Cirrhia gilvago*	Dusky-lemon Sallow	n.s.	n.s.	n.s.	n = 235
590	*Conistra vaccinii*	The Chestnut	n.s.	n.s.	n.s.	n = 1,239
591	*Conistra ligula*	Dark Chestnut	n.s.	n.s.	n.s.	n = 556
592	*Pseudoips prasinana*	Green Silver-lines	n.s.	n.s.	n.s.	n = 563

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595	*Nycteola revayana*	Oak Nycteoline	n.s.	n.s.	n.s.	n = 352
603	*Deltote pygarga*	Marbled White Spot	n.s.	n.s.	n.s.	n = 581
606	*Deltote uncula*	Silver Hook	n.s.	n.s.	n.s.	n = 118
610	*Catocala nupta*	Red Underwing	n.s.	n.s.	n.s.	n = 192
617	*Colocasia coryli*	Nut-tree Tussock	n.s.	n.s.	n.s.	n = 1,699
619	*Diloba caeruleocephala*	Figure of Eight	n.s.	n.s.	n.s.	n = 828
621	*Polychrysia moneta*	Golden Plusia	NA	NA	NA	Insufficient data (n = 90)
623	*Diachrysia chrysitis*	Burnished Brass	↑*	n.s.	↓*	n = 2,784
626	*Autographa bractea*	Gold Spangle	n.s.	↓*	n.s.	n = 665
627	*Plusia festucae*	Gold Spot	n.s.	n.s.	n.s.	n = 580
630	*Autographa jota*	Plain Golden Y	n.s.	n.s.	n.s.	n = 1,077
631	*Autographa pulchrina*	Beautiful Golden Y	n.s.	↓**	n.s.	n = 1,907
635	*Autographa gamma*	Silver Y	↓*	n.s.	n.s.	n = 3,652

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636	*Syngrapha interrogationis*	Scarce Silver Y	↓**	↓***	↑.	n = 218
638	*Abrostola triplasia*	Dark Spectacle	n.s.	n.s.	n.s.	n = 293
639	*Abrostola tripartita*	The Spectacle	↑*	n.s.	n.s.	n = 2,375
644	*Lygephila pastinum*	The Blackneck	n.s.	n.s.	n.s.	n = 188
648	*Rivula sericealis*	Straw Dot	n.s.	↓*	n.s.	n = 2,350
650	*Parascotia fuliginaria*	Waved Black	n.s.	n.s.	n.s.	n = 426
651	*Scoliopteryx libatrix*	The Herald	n.s.	n.s.	n.s.	n = 287
652	*Hypena crassalis*	Beautiful Snout	n.s.	n.s.	n.s.	n = 235
653	*Hypena proboscidalis*	The Snout	↑*	n.s.	↓*	n = 3,880
658	*Schrankia costaestrigalis*	Pinion-streaked Snout	~/U*	↓*	n.s.	n = 338
659	*Hypenodes humidalis*	Marsh Oblique-barred	n.s.	~***	↑***	n = 110
661	*Herminia tarsipennalis*	The Fan-foot	↑**	n.s.	↓**	n = 2,224

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662	*Herminia grisealis*	Small Fan-foot	↑**	n.s.	↓*	n = 2,043
666	*Laspeyria flexula*	Beautiful Hook-tip	↑**	∩*	n.s.	n = 872
669	*Alsophila aescularia*	March Moth	n.s.	n.s.	n.s.	n = 1,500
671	*Pseudoterpna pruinata*	Grass Emerald	~**	n.s.	n.s.	n = 444
672	*Geometra papilionaria*	Large Emerald	n.s.	n.s.	n.s.	n = 1,257
673	*Comibaena bajularia*	Blotched Emerald	n.s.	n.s.	n.s.	n = 364
674	*Hemithea aestivaria*	Common Emerald	↑**	n.s.	n.s.	n = 2,173
679	*Hemistola chrysoprasaria*	Small Emerald	n.s.	n.s.	n.s.	n = 501
680	*Jodis lactearia*	Little Emerald	↑***	n.s.	n.s.	n = 741
681	*Timandra comae*	Blood-vein	↑*	n.s.	↓***	n = 2,272
682	*Cyclophora albipunctata*	Birch Mocha	n.s.	n.s.	n.s.	n = 342
687	*Cyclophora punctaria*	Maiden's Blush	n.s.	n.s.	n.s.	n = 555

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688	*Cyclophora linearia*	Clay Triple-lines	n.s.	~*	n.s.	n = 364
689	*Scopula ternata*	Smoky Wave	n.s.	n.s.	n.s.	n = 313
692	*Scopula marginepunctata*	Mullein Wave	⬇*	n.s.	n.s.	n = 241
694	*Scopula imitaria*	Small Blood-vein	n.s.	⬆*	⬇*	n = 1,773
698	*Scopula immutata*	Lesser Cream Wave	n.s.	n.s.	n.s.	n = 338
699	*Scopula floslactata*	Cream Wave	~/U***	n.s.	⬆*	n = 718
701	*Idaea rusticata*	Least Carpet	⬇**	n.s.	∩/⬆*	n = 515
702	*Idaea fuscovenosa*	Dwarf Cream Wave	⬇*	n.s.	n.s.	n = 1,192
707	*Idaea dimidiata*	Single-dotted Wave	n.s.	n.s.	n.s.	n = 3,030
710	*Idaea seriata*	Small Dusty Wave	n.s.	n.s.	n.s.	n = 1,871
711	*Idaea subsericeata*	Satin Wave	⬆*	n.s.	⬇.	n = 648
716	*Idaea straminata*	Plain Wave	n.s.	n.s.	n.s.	n = 277
717	*Idaea aversata*	Riband Wave	⬆*	n.s.	⬇***	n = 3,937
718	*Idaea trigeminata*	Treble Brown Spot	n.s.	n.s.	n.s.	n = 939

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
719	*Idaea biselata*	Small Fan-footed Wave	n.s.	n.s.	↓*	n = 3,295
720	*Idaea emarginata*	Small Scallop	n.s.	n.s.	n.s.	n = 1,218
721	*Rhodometra sacraria*	The Vestal	n.s.	n.s.	n.s.	n = 347
723	*Xanthorhoe quadrifasiata*	Large Twin-spot Carpet	n.s.	n.s.	n.s.	n = 667
724	*Xanthorhoe decoloraria*	Red Carpet	↑**	n.s.	n.s.	n = 537
725	*Xanthorhoe ferrugata*	Dark-barred Twin-spot Carpet	n.s.	n.s.	↓**	n = 2,351
726	*Xanthorhoe spadicearia*	Red Twin-spot Carpet	n.s.	↓*	↓*	n = 2,461
728	*Xanthorhoe designata*	Flame Carpet	↑/∩***	↓*	n.s.	n = 2,341
729	*Xanthorhoe montanata*	Silver-ground Carpet	↑***	↓**	↓**	n = 3,931
730	*Xanthorhoe fluctuata*	Garden Carpet	↓*	∩*	n.s.	n = 3,824
731	*Nycterosea obstipata*	Gem	n.s.	n.s.	n.s.	n = 169

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
732	*Colostygia olivata*	Beech-green Carpet	n.s.	↓*	n.s.	n = 204
733	*Colostygia pectinataria*	Green Carpet	↑*	↓*	↓*	n = 3,069
734	*Coenotephria salicata*	Striped Twin-spot Carpet	n.s.	n.s.	↑**	n = 476
735	*Colostygia multistrigaria*	Mottled Grey	n.s.	↓***	n.s.	n = 1,154
736	*Mesotype didymata*	Twin-spot Carpet	n.s.	↓*	n.s.	n = 1,779
738	*Earophila badiata*	Shoulder-stripe	n.s.	n.s.	n.s.	n = 1,958
739	*Anticlea derivata*	The Streamer	n.s.	↓*	n.s.	n = 2,246
740	*Mesoleuca albicillata*	Beautiful Carpet	n.s.	n.s.	n.s.	n = 521
741	*Entephria caesiata*	Grey Mountain Carpet	n.s.	↓**	n.s.	n = 372
744	*Perizoma blandiata*	Pretty Pinion	n.s.	n.s.	n.s.	n = 128
746	*Perizoma affinitata*	The Rivulet	↑*	n.s.	↓**	n = 1,454
747	*Perizoma alchemillata*	Small Rivulet	↑***	n.s.	↓**	n = 3,217

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
748	*Perizoma flavofasciata*	Sandy Carpet	n.s.	n.s.	n.s.	n = 1,917
749	*Perizoma albulata*	Grass Rivulet	n.s.	n.s.	n.s.	n = 547
750	*Perizoma bifaciata*	Barred Rivulet	n.s.	n.s.	n.s.	n = 284
752	*Euphyia unangulata*	Sharp-angled Carpet	n.s.	n.s.	n.s.	n = 519
754	*Euphyia biangulata*	Cloaked Carpet	n.s.	↓*	~**	n = 245
756	*Catarhoe rubidata*	Ruddy Carpet	n.s.	n.s.	n.s.	n = 163
758	*Camptogramma bilineata*	Yellow Shell	n.s.	n.s.	n.s.	n = 2,067
759	*Melanthia procellata*	Pretty Chalk Carpet	n.s.	n.s.	n.s.	n = 449
761	*Cosmorhoe ocellata*	Purple Bar	n.s.	↓***	↑/~*	n = 2,375
762	*Lampropteryx suffumata*	Water Carpet	n.s.	n.s.	n.s.	n = 1,920
763	*Lampropteryx otregiata*	Devon Carpet	n.s.	n.s.	n.s.	n = 306
764	*Electrophaes corylata*	Broken-barred Carpet	n.s.	n.s.	n.s.	n = 1,231

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
765	*Ecliptopera silaceata*	Small Phoenix	n.s.	n.s.	n.s.	n = 2,508
767	*Eulithis prunata*	The Phoenix	n.s.	n.s.	n.s.	n = 1,104
768	*Eulithis testata*	The Chevron	n.s.	U**	n.s.	n = 1,622
769	*Eulithis populata*	Northern Spinach	↑***	↓**	n.s.	n = 1,383
770	*Eulithis mellinata*	The Spinach	n.s.	n.s.	n.s.	n = 405
771	*Gandaritis pyraliata*	Barred Straw	n.s.	↓*	n.s.	n = 3,572
772	*Cidaria fulvata*	Barred Yellow	n.s.	↓*	n.s.	n = 2,645
773	*Plemyria rubiginata*	Blue-bordered Carpet	n.s.	n.s.	n.s.	n = 706
774	*Chloroclysta siterata*	Red-green Carpet	↑*	↓***	↓***	n = 1,651
775	*Chloroclysta miata*	Autumn Green Carpet	n.s.	↓*	n.s.	n = 1,055
776	*Dysstroma truncata*	Common Marbled Carpet	n.s.	n.s.	n.s.	n = 3,698
778	*Dysstroma citrata*	Dark Marbled Carpet	n.s.	↓**	n.s.	n = 1,733
779	*Thera obeliscata*	Grey Pine Carpet	n.s.	↓***	n.s.	n = 2,061
780	*Thera britannica*	Spruce Carpet	n.s.	↓**	↓*	n = 944

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
782	*Pennithera firmata*	Pine Carpet	n.s.	n.s.	n.s.	n = 792
783	*Thera juniperata*	Juniper Carpet	n.s.	n.s.	n.s.	n = 361
784	*Hydriomena furcata*	July Highflyer	↑***	↓*	↓**	n = 3,513
785	*Hydriomena impluviata*	May Highflyer	↑*	n.s.	↓.	n = 787
786	*Hydriomena ruberata*	Ruddy Highflyer	n.s.	n.s.	n.s.	n = 157
787	*Philereme vetulata*	Brown Scallop	n.s.	n.s.	n.s.	n = 140
788	*Philereme transversata*	Dark Umber	n.s.	n.s.	n.s.	n = 559
789	*Triphosa dubitata*	The Tissue	n.s.	n.s.	n.s.	n = 168
790	*Hydria cervinalis*	Scarce Tissue	n.s.	n.s.	n.s.	n = 144
791	*Hydria undulata*	Scallop Shell	n.s.	n.s.	n.s.	n = 575
794	*Epirrhoe rivata*	Wood Carpet	∩*	n.s.	n.s.	n = 394
795	*Epirrhoe alternata*	Common Carpet	↑/∩*	n.s.	↓**	n = 3,640
797	*Epirrhoe galiata*	Galium Carpet	n.s.	n.s.	n.s.	n = 231

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
800	*Chesias legatella*	The Streak	n.s.	n.s.	n.s.	n = 1,108
801	*Chesias rufata*	Broom-tip	n.s.	n.s.	↑**	n = 171
803	*Aplocera plagiata*	Treble-bar	n.s.	n.s.	n.s.	n = 766
804	*Aplocera efformata*	Lesser Treble-bar	n.s.	n.s.	n.s.	n = 250
807	*Horisme vitalbata*	Small Waved Umbe	n.s.	n.s.	n.s.	n = 493
809	*Horisme tersata*	The Fern	n.s.	n.s.	n.s.	n = 474
810	*Lobophora halterata*	The Seraphim	n.s.	n.s.	n.s.	n = 157
811	*Pterapherapteryx sexalata*	Small Seraphim	n.s.	n.s.	n.s.	n = 359
812	*Acasis viretata*	Yellow-barred Brindle	n.s.	n.s.	n.s.	n = 1,245
814	*Trichopteryx carpinata*	Early Tooth-striped	n.s.	n.s.	n.s.	n = 1,045
815	*Orthonama vittata*	Oblique Carpet	n.s.	n.s.	n.s.	n = 504
816	*Scotopteryx mucronata*	Lead Belle	n.s.	n.s.	n.s.	n = 292
817	*Scotopteryx luridata*	July Belle	↑**	n.s.	n.s.	n = 415

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
818	*Scotopteryx chenopodiata*	Shaded Broad-bar	n.s.	n.s.	↓*	n = 2,369
822	*Larentia clavaria*	The Mallow	n.s.	n.s.	n.s.	n = 660
823	*Pelurga comitata*	Dark Spinach	↑*	n.s.	↓*	n = 408
824	*Epirrita autumnata*	Autumnal Moth	~*	n.s.	n.s.	n = 1,196
825	*Epirrita filigrammaria*	Small Autumnal Moth	n.s.	n.s.	n.s.	n = 628
826	*Epirrita dilutata*	November Moth	↑*	n.s.	n.s.	n = 2,637
827	*Epirrita christyi*	Pale November Moth	n.s.	n.s.	n.s.	n = 1,199
828	*Operophtera brumata*	Winter Moth	n.s.	↑**	↑*	n = 629
829	*Operophtera fagata*	Northern Winter Moth	n.s.	n.s.	n.s.	n = 933
830	*Asthena albulata*	Small White Wave	n.s.	n.s.	n.s.	n = 353
832	*Hydrelia flammeolaria*	Small Yellow Wave	n.s.	n.s.	n.s.	n = 372
834	*Euchoeca nebulata*	Dingy Shell	n.s.	n.s.	n.s.	n = 291
835	*Venusia cambrica*	Welsh Wave	n.s.	↓*	n.s.	n = 491

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
839	*Eupithecia subumbrata*	Shaded Pug	NA	NA	NA	Insufficient data (n = 79)
840	*Eupithecia simpliciata*	Plain Pug	n.s.	n.s.	n.s.	n = 138
843	*Eupithecia tenuiata*	Slender Pug	n.s.	n.s.	n.s.	n = 468
844	*Eupithecia inturbata*	Maple Pug	n.s.	n.s.	n.s.	n = 320
845	*Eupithecia haworthiata*	Haworth's Pug	n.s.	n.s.	n.s.	n = 341
847	*Eupithecia linariata*	Toadflax Pug	n.s.	n.s.	n.s.	n = 439
848	*Eupithecia pulchellata*	Foxglove Pug	n.s.	↓***	n.s.	n = 1,476
850	*Eupithecia exiguata*	Mottled Pug	n.s.	↓*	n.s.	n = 1,281
854	*Eupithecia venosata*	Netted Pug	n.s.	n.s.	n.s.	n = 196
855	*Eupithecia centaureata*	Lime-speck Pug	n.s.	n.s.	n.s.	n = 1,391
857	*Eupithecia intricata*	Freyer's Pug	↓*	↑***	↑*	n = 737
858	*Eupithecia satyrata*	Satyr Pug	↓*	n.s.	n.s.	n = 363

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
859	*Eupithecia tripunctaria*	White-spotted Pug	n.s.	n.s.	n.s.	n = 863
860	*Eupithecia absinthiata*	Wormwood Pug	n.s.	↓**	n.s.	n = 1,282
863	*Eupithecia assimilata*	Currant Pug	n.s.	n.s.	n.s.	n = 950
864	*Eupithecia vulgata*	Common Pug	n.s.	n.s.	n.s.	n = 2,228
866	*Eupithecia subfuscata*	Grey Pug	n.s.	↓*	n.s.	n = 1,478
867	*Eupithecia icterata*	Tawny Speckled Pug	n.s.	↓*	n.s.	n = 1,649
868	*Eupithecia succenturiata*	Bordered Pug	n.s.	n.s.	n.s.	n = 812
869	*Eupithecia indigata*	Ochreous Pug	n.s.	n.s.	n.s.	n = 201
872	*Eupithecia nanata*	Narrow-winged Pug	n.s.	U**	n.s.	n = 1,207
873	*Eupithecia innotata*	Angle-barred Pug	n.s.	n.s.	n.s.	n = 231
876	*Eupithecia virgaureata*	Golden-rod Pug	n.s.	n.s.	n.s.	n = 489

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
877	*Eupithecia abbreviata*	Brindled Pug	n.s.	↓*	n.s.	n = 1,183
878	*Eupithecia dodoneata*	Oak-tree Pug	n.s.	n.s.	n.s.	n = 647
879	*Eupithecia phoeniceata*	Cypress Pug	↓*	↑**	↑*	n = 135
880	*Eupithecia pusillata*	Juniper Pug	n.s.	n.s.	n.s.	n = 727
882	*Eupithecia lariciata*	Larch Pug	n.s.	n.s.	n.s.	n = 392
883	*Eupithecia tantillaria*	Dwarf Pug	n.s.	n.s.	n.s.	n = 291
884	*Chloroclystis v-ata*	The V-Pug	n.s.	↓**	n.s.	n = 1,013
886	*Pasiphila rectangulata*	Green Pug	n.s.	n.s.	n.s.	n = 2,129
887	*Gymnoscelis rufifasciata*	Double-striped Pug	n.s.	↓***	n.s.	n = 1,621
888	*Abraxas sylvata*	Clouded Magpie	↓*	n.s.	n.s.	n = 126
889	*Abraxas grossulariata*	The Magpie	n.s.	n.s.	n.s.	n = 2,447

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
891	*Lomaspilis marginata*	Clouded Border	↑***	n.s.	↓**	n = 3,176
892	*Ligdia adustata*	Scorched Carpet	n.s.	n.s.	n.s.	n = 1,033
894	*Lomographa bimaculata*	White-pinion Spotted	n.s.	n.s.	n.s.	n = 671
895	*Lomographa temerata*	Clouded Silver	n.s.	n.s.	n.s.	n = 1,867
896	*Cabera pusaria*	Common White Wave	↑***	↓*	↓**	n = 3,073
897	*Cabera exanthemata*	Common Wave	↑*	n.s.	n.s.	n = 2,997
898	*Hylaea fasciaria*	Barred Red	n.s.	↓*	n.s.	n = 1,602
899	*Campaea margaritaria*	Light Emerald	∩*	↓*	↓*	n = 3,318
901	*Macaria notata*	Peacock Moth	n.s.	n.s.	n.s.	n = 404
902	*Macaria alternata*	Sharp-angled Peacock	~**	n.s.	∩**	n = 455
903	*Macaria liturata*	Tawny-barred Angle	n.s.	↓**	↓**	n = 1,133
904	*Theria primaria*	Early Moth	n.s.	n.s.	n.s.	n = 374

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
905	*Agriopis leucophaearia*	Spring Usher	↓*	n.s.	↑**	n = 422
906	*Agriopis aurantiaria*	Scarce Umber	n.s.	n.s.	n.s.	n = 1,473
907	*Agriopis marginaria*	Dotted Border	n.s.	n.s.	n.s.	n = 1,496
908	*Erannis defoliaria*	Mottled Umber	n.s.	n.s.	n.s.	n = 839
909	*Plagodis pulveraria*	Barred Umber	n.s.	n.s.	↑*	n = 700
910	*Ennomos autumnaria*	Large Thorn	n.s.	↓**	n.s.	n = 107
911	*Ennomos quercinaria*	August Thorn	n.s.	n.s.	n.s.	n = 786
912	*Ennomos alniaria*	Canary-shouldered Thorn	n.s.	n.s.	n.s.	n = 2,448
913	*Ennomos fuscantaria*	Dusky Thorn	n.s.	↓*	n.s.	n = 1,098
914	*Ennomos erosaria*	September Thorn	n.s.	n.s.	n.s.	n = 799
915	*Selenia dentaria*	Early Thorn	∩***	n.s.	↓**	n = 3,546
916	*Selenia lunularia*	Lunar Thorn	n.s.	n.s.	n.s.	n = 961

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
917	*Selenia tetralunaria*	Purple Thorn	n.s.	n.s.	n.s.	n = 1,359
918	*Apeira syringaria*	Lilac Beauty	n.s.	n.s.	n.s.	n = 1,258
919	*Odontopera bidentata*	Scalloped Hazel	∩***	↑*	n.s.	n = 2,851
920	*Colotois pennaria*	Feathered Thorn	n.s.	n.s.	n.s.	n = 2,635
921	*Crocallis elinguaria*	Scalloped Oak	∩/↓*	n.s.	n.s.	n = 3,470
922	*Plagodis dolabraria*	Scorched Wing	n.s.	n.s.	n.s.	n = 1,253
923	*Opisthograptis luteolata*	Brimstone Moth	∩/↑**	n.s.	↓***	n = 3,993
924	*Epione repandaria*	Bordered Beauty	n.s.	n.s.	n.s.	n = 1,365
928	*Ourapteryx sambucaria*	Swallow-tailed Moth	↑*	n.s.	n.s.	n = 2,033
930	*Apocheima hispidaria*	Small Brindled Beauty	n.s.	n.s.	n.s.	n = 315
933	*Lycia hirtaria*	Brindled Beauty	n.s.	n.s.	n.s.	n = 1,352
934	*Biston strataria*	Oak Beauty	n.s.	n.s.	n.s.	n = 1,009

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
935	*Biston betularia*	Peppered Moth	n.s.	n.s.	n.s.	n = 1,419
936	*Menophra abruptaria*	Waved Umber	⬆/~*	n.s.	n.s.	n = 967
938	*Peribatodes rhomboidaria*	Willow Beauty	n.s.	n.s.	n.s.	n = 2,696
939	*Cleorodes lichenaria*	Brussels Lace	n.s.	n.s.	n.s.	n = 442
940	*Deileptenia ribeata*	Satin Beauty	n.s.	n.s.	n.s.	n = 493
941	*Alcis repandata*	Mottled Beauty	n.s.	⬇**	n.s.	n = 3,132
943	*Alcis jubata*	Dotted Carpet	n.s.	n.s.	n.s.	n = 432
944	*Hypomecis roboraria*	Great Oak Beauty	n.s.	n.s.	n.s.	n = 160
945	*Hypomecis punctinalis*	Pale Oak Beauty	n.s.	n.s.	n.s.	n = 483
946	*Ectropis bistortata*	The Engrailed	n.s.	⬇*	n.s.	n = 2,537
948	*Paradarisa consonaria*	Square Spot	n.s.	n.s.	n.s.	n = 175
949	*Parectropis similaria*	Brindled White-spot	⬇**	n.s.	⬆**	n = 303
950	*Aethalura punctulata*	Grey Birch	⬆*	n.s.	n.s.	n = 471

Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
952	*Pachycnemia hippocastanaria*	Horse Chestnut	n.s.	n.s.	n.s.	n = 194
959	*Bupalus piniaria*	Bordered White	n.s.	↓*	n.s.	n = 451
961	*Macaria wauaria*	The V-Moth	n.s.	n.s.	n.s.	n = 514
963	*Petrophora chlorosata*	Brown Silver-line	↑**	↓***	↓*	n = 2,097
964	*Chiasmia clathrata*	Latticed Heath	↑**	n.s.	↓**	n = 1,420
965	*Dyscia fagaria*	Grey Scalloped Bar	n.s.	↓*	↓/~*	n = 181
968	*Aspitates ochrearia*	Yellow Belle	n.s.	n.s.	n.s.	n = 183
969	*Perconia strigillaria*	Grass Wave	n.s.	n.s.	n.s.	n = 144
1001	*Nomophila noctuella*	Rush Veneer	n.s.	↓**	n.s.	n = 639
1015	*Udea ferrugalis*	Rusty Dot Pearl	n.s.	↓*	n.s.	n = 1,002
2178	*Plutella xylostella*	Diamond-back Moth	↓**	n.s.	n.s.	n = 2,357
2452	*Phigalia pilosaria*	Pale Brindled Beauty	n.s.	n.s.	n.s.	n = 631
2510	*Plusia putnami*	Lempke's Gold Spot	∩**	n.s.	↑***	n = 185

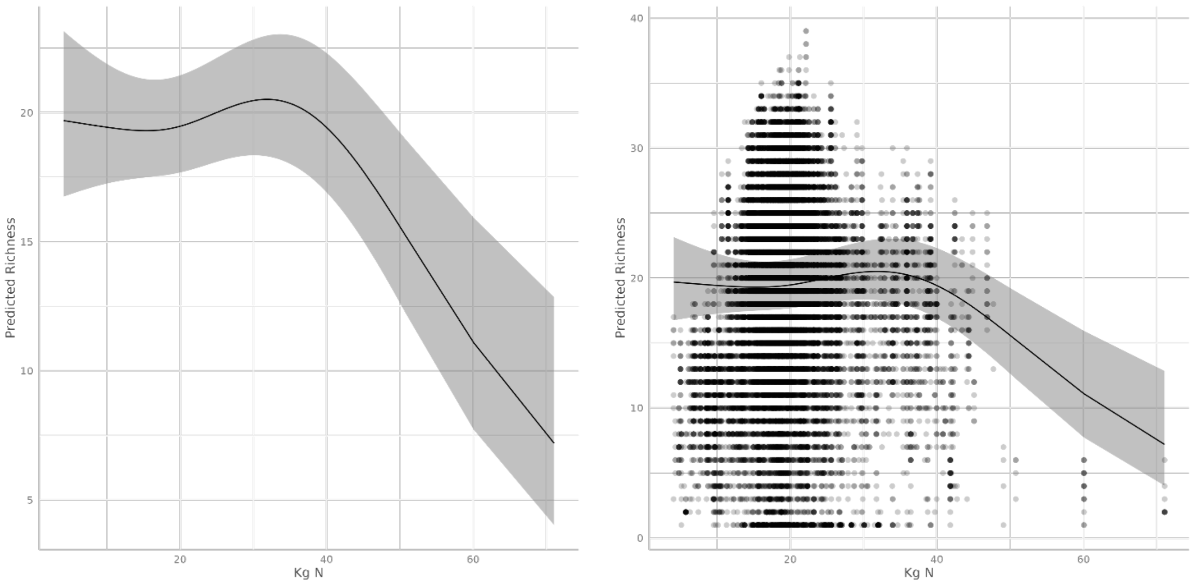
Species number	Latin name	Common name	Historic N	Change in N 1986–2012	Historic S	Data issue
2513	*Amphipoea fucosa*	Saltern Ear	↓**	n.s.	↑*	n = 160
3392	*Mesapamea secalis/didyma*	Common Rustic/Lesser Common Rustic	n.s.	↑*	n.s.	n = 4,081
3394	*Amphipyra berbera*	Svensson's Copper Underwing	n.s.	n.s.	n.s.	n = 421

3.2.3. Combined species metric modelling

We also tested the response of the total abundance of richness of butterflies and moths to nitrogen and other driver variables. These models test whether the Lepidopteran community responds to historic N deposition, percentage change in N between 1986–2012, and historic S deposition, as well as the other driver variables detailed in section 3.1. Neither historic N nor change in N over time at a site were significant drivers of total butterfly abundance (Table 4). We found strong evidence that butterfly richness was negatively correlated with historic N (Figures 13a and 13b). We observed similar responses of moth richness and total abundance to the nitrogen driver variables, with responses positively correlated with historic N (Figures 14a, 14b, 16a and 16b) but negatively correlated with percentage change in N between 1986–2012 N (Figures 15a, 15b, 17a and 17b). We also found very strong evidence that all four combined species metric responses tested were negatively correlated with historic S deposition (Table 4).

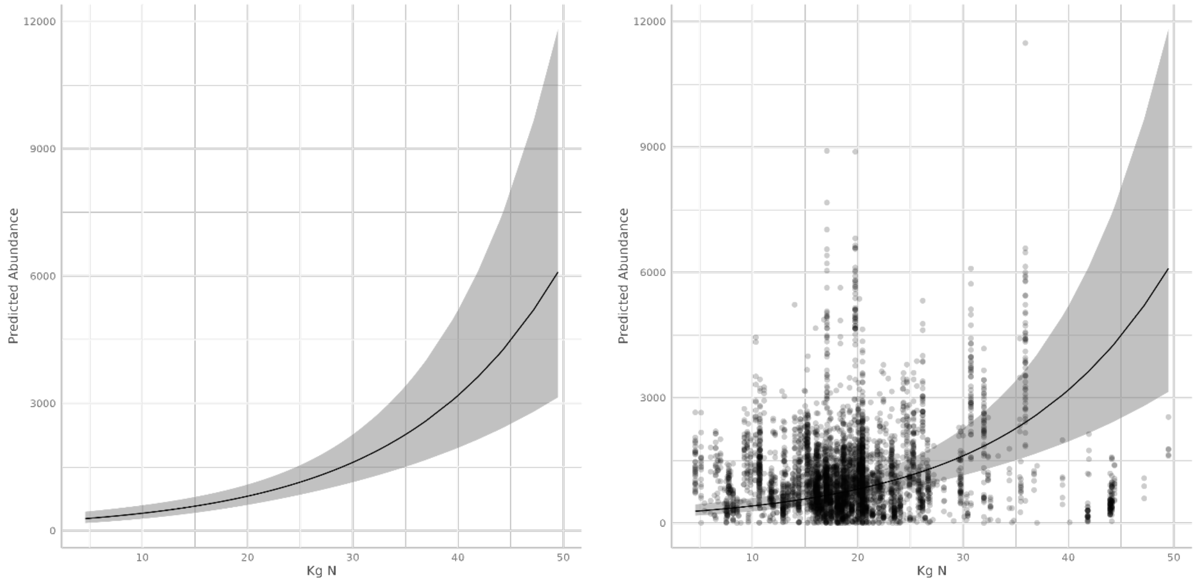
Table 4: Table of results showing the direction (↑ = positive trend; ↓ = negative trend) and significance of relationships between richness and abundance of Lepidoptera and nitrogen driver variables (*** = P < 0.001; ** = 0.001 < P < 0.01; * = 0.01 < P < 0.005; n.s. = non-significant).

Trait	Response	Historic N	Change in N 1986–2012	Historic S
Butterflies	Abundance	n.s.	n.s.	↓ ***
	Richness	↓ **	n.s.	↓ ***
Moths	Abundance	↑ ***	↓ ***	↓ ***
	Richness	↑ ***	↓ **	↓ ***



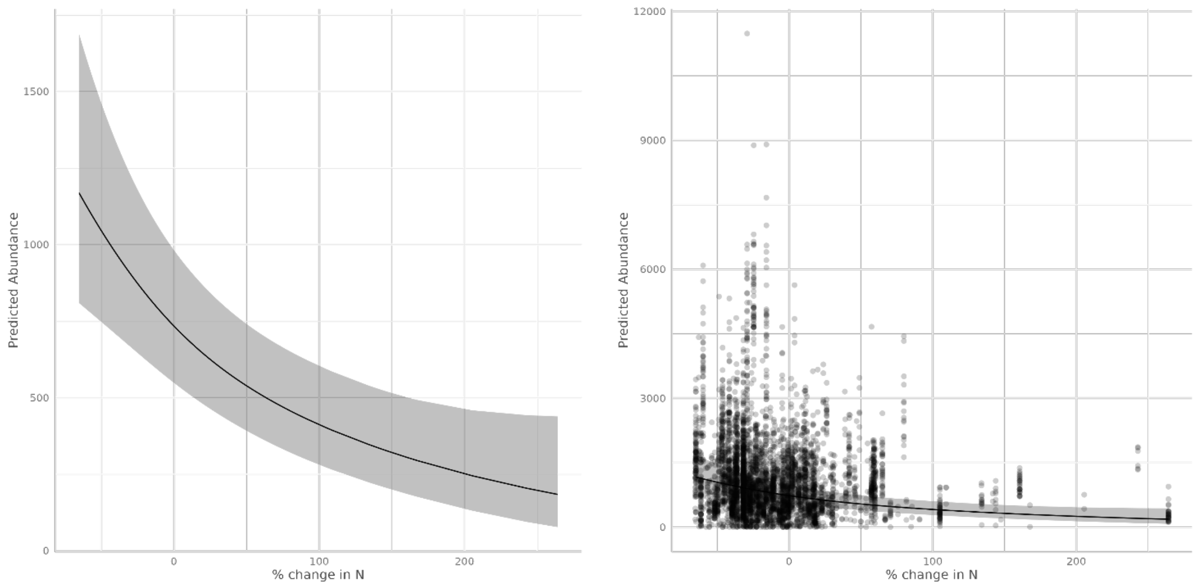
(a) **(b)**

Figure 13a & 13b: Predicted butterfly richness at an average site against increasing total N deposition (kg N ha^{-1} in 1996) without (a) and with (b) raw data.



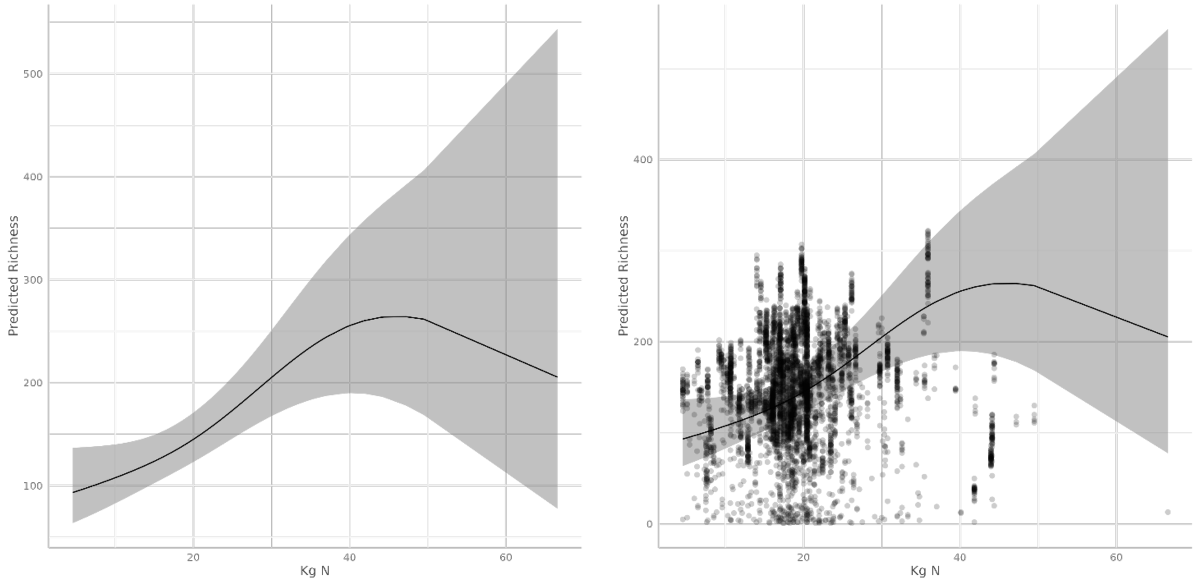
(a) **(b)**

Figure 14a & 14b: Predicted moth abundance at an average site against increasing total N deposition (kg N ha^{-1} in 1996) without (a) and with (b) raw data.



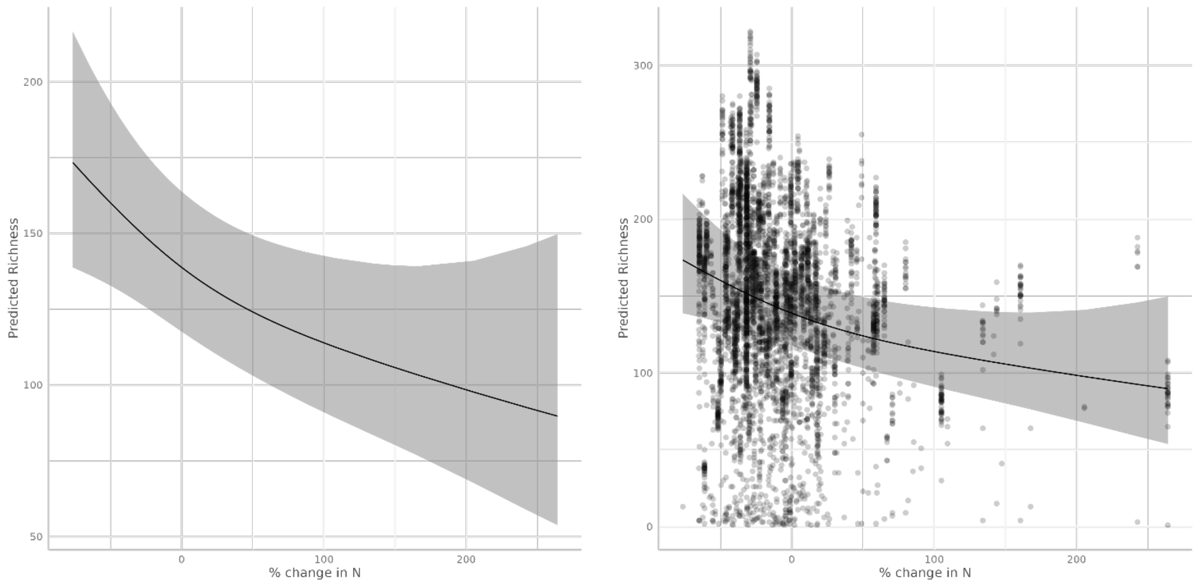
(a) **(b)**

Figure 15a & 15b: Predicted moth abundance at an average site against percentage change in N deposition 1986–2012 without (a) and with (b) raw data.



(a) **(b)**

Figure 16a & 16b: Predicted moth richness at an average site against increasing total N deposition (kg N ha^{-1} in 1996) without (a) and with (b) raw data.



(a) **(b)**

Figure 17a & 17b: Predicted moth richness at an average site against percentage change in N deposition 1986–2012 without (a) and with (b) raw data.

3.2.4. Trait modelling

Models were fit for 19 individual butterfly trait groupings to understand whether traits could be used as good predictors of responses to deposition variables (Table 5). Responses to both historic N and percentage change in N at a site over time were mixed and to some extent varied by trait. However, trait grouping responses to N were often conflicting when comparing the species richness to the total abundance. For example, we found very strong evidence that the abundance of late butterflies was positively correlated with historic N, but also found strong evidence that the species richness of late butterflies was negatively correlated with historic N. Most of the significant responses to historic S deposition were negative, as observed in the combined species analysis.

Overall, the total abundance of two trait groups were negatively correlated with historic N, the abundance of two were hump-backed, five were positive, one showed a significant relationship with N but in no clear direction, and six showed no significant relationship with historic N. Modelled abundance responses of butterfly trait groups to the percentage change in N deposition at a site over time were also mixed. The abundance index of five groups showed a negative correlation with historic N, two groups showed a hump-backed relationship, and two groups showed a positive correlation. The total abundance index of seven trait groups had no significant association with historic N.

Table 5: Table of results showing the direction (↑ = positive trend; ↓ = negative trend) and significance of relationships between richness and abundance of butterflies (filtered by traits) and deposition driver variables (∩ = humpbacked relationship; ~ = no significant trend) (*** = P < 0.001; ** = 0.001 < P < 0.01; * = 0.01 < P < 0.005; n.s. = non-significant).

Trait grouping	Trait	Response	Historic N	Change in N 1986–2012	Historic S
Flight season	Early	Abundance	n.s.	↑ ***	n.s.
		Richness	↓ **	n.s.	↓ ***
	Late	Abundance	↑ ***	n.s.	↓ ***
		Richness	↓ **	n.s.	↓ ***
Habitat	Acid grassland	Abundance	n.s.	↓ **	↓ ***
		Richness	↓ ***	↓ ***	↓ ***
	Bog	Abundance	↑ **	↓ *	↓ **
		Richness	↓**	n.s.	↓ ***
	Calcareous grassland	Abundance	n.s.	↓ *	↓ ***
		Richness	↓ **	n.s.	↓ ***
	Heathland	Abundance	~ *	↓ **	↓ ***
		Richness	↓ **	↓ ***	↓ ***
	Moorland	Abundance	↑ ***	↓ **	↓ ***
		Richness	∩ ***	↓ ***	↓ ***

Trait grouping	Trait	Response	Historic N	Change in N 1986–2012	Historic S
Host plant category	Forbs	Abundance	n.s.	∩ *	↓ **
		Richness	∩ ***	n.s.	↓ ***
	Grasses	Abundance	n.s.	n.s.	↓ ***
		Richness	↓ ***	↓**	↓ ***
Larval host specificity	Monophagous	Abundance	↑ **	n.s.	↓ ***
		Richness	↑/∩ ***	n.s.	↓ ***
	Oligophagous	Abundance	∩ **	n.s.	↓ ***
		Richness	∩ **	n.s.	↓ ***
	Polyphagous	Abundance	↓ ***	n.s.	↑ **
		Richness	↓ *	↑ ***	n.s.
Voltinism	Univoltine	Abundance	∩ *	n.s.	↓***
		Richness	∩ ***	n.s.	↓ ***
	Multivoltine	Abundance	n.s.	∩ *	n.s.
		Richness	↓ ***	∩ **	∪ *
Overwintering stage	Egg	Abundance	n.s.	↓ ***	↓ **
		Richness	↓**	n.s.	↓ ***
	Larva	Abundance	↑ *	n.s.	↓ ***
		Richness	∩ ***	↓ ***	↓ ***
	Pupa	Abundance	↓ **	∩/↑ ***	↑ **
		Richness	∩ ***	↑ ***	↑/∪ ***
	Adult	Abundance	↑ *	∩/↑ ***	↓ ***
		Richness	∩ ***	↑ ***	↓ ***

The richness response of 11 trait groups was negatively correlated with historic between 1986–2012, seven hump-backed, and one positive. None of the richness responses of the trait groupings tested showed no significant relationship with historic N. Modelled richness responses of butterfly trait groups to the percentage change in N deposition at a site over time were also mixed. The richness response of five groups showed a negative correlation with change in N, one group showed a hump-backed relationship, and three groups showed a positive correlation. The richness response of nine trait groups had no significant association with percentage change in N.

For moths the trait analysis demonstrated that filtering by traits group does not change the overall direction of the trend with any of the atmospheric pollution variables (Table 6). For all trait groupings, the response to historic N was still positive, the response to change in N negative, and the response to historic S negative. There were some changes in the significance levels for some trends within trait groupings, but none that changed the overall direction of the trend.

Table 6: Table of results showing the direction (↑ = positive trend; ↓ = negative trend) and significance of relationships between richness and abundance of moths (filtered by traits) and deposition driver variables (*** = P < 0.001; ** = 0.001 < P < 0.01; * = 0.01 < P < 0.05; n.s. = non-significant).

Trait grouping	Trait	Response	Historic N	Change in N 1986–2012	Historic S
Flight season	Early	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***
	Late	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ **	↓ ***
Habitat	Acid grassland	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***
	Bog	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***
	Calcareous grassland	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ **	↓ ***
	Heathland	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***

Trait grouping	Trait	Response	Historic N	Change in N 1986–2012	Historic S
Habitat	Moorland	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***
Host plant category	Forbs	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ **	↓ ***
	Grasses	Abundance	↑ **	↓ ***	↓ ***
		Richness	n.s.	↓ **	↓ ***
	Lichens	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***
Larval host specificity	Monophagous	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***
	Oligophagous	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***
	Polyphagous	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ **	↓ ***
Voltinism	Univoltine	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ **	↓ ***
	Multivoltine	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ **	↓ ***
Overwintering stage	Egg	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***
	Larva	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***

Trait grouping	Trait	Response	Historic N	Change in N 1986–2012	Historic S
Overwintering stage	Pupa	Abundance	↑ ***	↓ ***	↓ ***
		Richness	↑ ***	↓ ***	↓ ***
	Adult	Abundance	↑ ***	↓ ***	↓ **
		Richness	↑ ***	↓ ***	↓ ***

Overall, the responses of Lepidopteran trait groupings to N are somewhat unclear. Several of the responses of butterfly richness within trait groupings to historic N were hump-backed rather than negative, as we found in the combined species analysis. Additionally, several of the responses of butterfly richness within trait groupings to change in N over time were significantly negative, whereas this relationship was non-significant in the combined species analysis. The total abundance responses of different trait groupings to both N variables were unclear and sometimes conflicting.

4. Discussion

4.1. Single species

The strength and direction of responses of individual butterfly species to the different drivers were varied and complex, as seen in Table 2. Of the species tested, the relationship between historic N and the butterfly abundance index was negative for 10 and hump-backed for two. The modelled relationship between percentage change in N at a site between 1986–2012 and the butterfly abundance index was negative for four, and hump-backed for four. These results suggest that atmospheric nitrogen pollution may have a negative effect on certain butterflies in the UK. They also suggest potential evidence that certain species respond positively to N up to a point above which the response become negative. This fits in with the theory of critical loads and levels of N whereby significant harmful effects of N are not expected to cause damage to sensitive habitats or species until they reach a certain threshold. The results from this single species butterfly analysis largely reflect the trends found by Risser (2023).

Two species, *Lasiommata megera* (Wall) and *Pyronia Tithonus* (Gatekeeper) demonstrated negative relationships with both historic N and percentage change in N (Figures 8a, 8b, 9a and 9b). Both species are found in the family Nymphalidae within the subfamily Satyrinae, more commonly known as the satyrids or browns. They share some trait similarities, with both being oligophagous, feeding on grasses as larva, and overwintering primarily as larva. There are however many differences between them, including in their flight periods and voltinism. *L. megera* is listed as Near Threatened in GB and is a Section 41 species under the NERC Act in England, whereas *P. tithonus* has much lower conservation status, being listed as Least Concern in GB but Near Threatened in Ireland. There is strong evidence that declines in *L. megera* in the Netherlands are correlated with levels of N deposition (Klop *et al.* 2015) as well as climate change (Van Dyck *et al.* 2015). It is thought that the main pathway by which N affects *L. megera* is through microclimatic cooling during larval development of the early-spring emerging generation of adults. It seems somewhat unlikely that this is the same mechanism by which N affects *P. tithonus* because its single generation of adults emerges in the warmer summer months and therefore larval development occurs later, and thus in generally warmer conditions, than in *L. megera*. Further work is needed to understand the potential causes of this negative effect of N on *P. tithonus* that we found in this study.

A GAM approach was used in this analysis to allow for non-linear responses to drivers, given the expectation that some species may respond to N in a hump-backed way. We observed some evidence of this hump-backed response to historic N in two species, *Melanargia galathea* (Marbled White) and *Pararge aegeria* (Speckled Wood) (Figures 10 and 11, Section 3.2.2), although the confidence intervals on the predictions were wide.

The relationship between historic S and the butterfly abundance index was also mixed. Both temperature variables were consistently statistically significant drivers of change in the abundance index of individual species. This consistently statistically significant effect of temperature on abundance supports the findings of many other studies (e.g. Fourcade *et al.* 2017; Isaac *et al.* 2011; Roy *et al.* 2001). We found that the direction of the temperature effects varies between species.

Management intervention and intensity are important drivers of many butterfly species, particularly habitat specialists. Management was not included as a term in the models due to insufficient data being available. Further research into the potential effects of N on specific species, particularly those with limited ranges and high intensity targeted management interventions such as *Boloria euphrosyne* (Pearl-bordered Fritillary), should consider including the type and duration of management in their analyses.

As observed for the butterflies, responses of individual moth species to atmospheric N pollution varied. The abundance index of 30 moth species showed a negative correlation with historic N, whilst five species showed a hump-backed relationship. The abundance index of 80 moth species showed a negative correlation with historic N, whilst seven species showed a hump-backed relationship. The GAI of only two moth species, *Brachylomia viminalis* (Minor Shoulder-knot) and *Syngrapha interrogationis* (Scarce Silver Y) exhibited a negative correlation with both metrics of N pollution tested. *S. interrogationis* was recently highlighted as one of the UK's larger moths with the highest rate of decline in distribution over an average 10-year period (Fox *et al.* 2021). *B viminalis* has also experienced significant declines in both abundance and distribution over the past half century (Cook *et al.* 2024). Both moth species are characteristic of nutrient-poor habitats and therefore are expected to be sensitive to N addition.

4.2. Combined species metrics

We found strong effects of atmospheric nitrogen pollution on butterfly richness, moth richness, and moth abundance. No significant trends were seen with total butterfly abundance. We found that historic N was negatively correlated with butterfly richness, whereas it was positively correlated with both moth abundance and moth richness.

Despite the positive correlation between moth metrics and historic N, we observed a significant negative relationship between both moth metrics and the percentage change in N at the site over time. This suggests that moth richness is highest at sites with higher "historic" N loading, while moth richness is also highest at sites that have shown a decline in N pressure, and lowest at sites that have experienced an increase in N pressure. This is an unexpected result and requires further investigation to understand the causes of these opposing trends. We expect that this slightly counterintuitive result could be explained should the modelling methods be tailored to better reflect variables that are likely to impact moths, such as light pollution.

The overall abundance and richness of both butterflies and moths were significantly negatively correlated with sulphur deposition. Little research has been done on the direct effects of S on Lepidoptera and therefore more research is needed to begin to explore the full causal reasoning behind this. A recent study of Lepidoptera communities along a gradient of sulphur dioxide and metal-containing particulate matter exposure in Russia found that the abundance of many species increased with distance from the source (Kozlov *et al.* 2022). This effect of pollution on Lepidoptera varied by trait groupings such as hostplant specificity, feeding mechanism, and overwintering stage. They also found that reductions in emissions over time led to an increase in the diversity, but not the overall abundance, of Lepidoptera species present in the most heavily polluted areas. However, more work needs to be done to disentangle the potentially differing effects of sulphur dioxide and metal dust, as well as to move towards a more mechanistic understanding of how S pollution might be affecting Lepidoptera. A recent study demonstrated that plant community composition is gradually showing a recovery from sulphur deposition in seminatural habitats across GB (Seaton *et al.* 2023). Whilst associated recovery from S in Lepidoptera may take longer, it seems possible that this long-term decline in S deposition will have already had or will start to influence Lepidoptera given their reliance on vegetation for food sources, shelter, and other key parts of their life cycles.

4.3. Traits

We found that traits do not explain moth responses to atmospheric N pollution. For moths, almost all the trait groupings we tested did not differ in their responses to N and S when compared to the combined species model. However, we did observe differing responses in the single species moth analysis. This suggests that the responses of moths to atmospheric pollution are incredibly complex, and the complexity of responses is not captured by such broad trait groupings. It is possible that we might see trait responses if we filtered to much more specific groupings. The only real differing trend observed within the moth trait grouping analysis was for the richness of moths with grasses as their larval hosts, where there was no significant effect of historic N on the abundance index. This differs from the positive effect of historic N seen in the combined species analysis.

Previous studies have shown that trait analyses can have inconclusive and sometimes contradictory results. For example, a recent study of British moth abundance and distribution trends found that, despite there being strong associations for several traits, outcomes differed between the abundance and distribution trends with no trait being significant for both (Tordoff *et al.* 2022). Our results contribute to this evidence base suggesting that drivers of change in moth populations are incredibly complex and are not easily explained by broad trait groupings. We also have an incomplete knowledge of moth traits, particularly for rarer or more elusive species.

The RIS Light Trap Network may not provide data on certain moths due to the methodological nature of the trap placement. Their traps run on mains energy, and therefore need to be placed within reasonable distance of a power source. This means that we have less data from truly remote locations. This is a potentially key issue and a potential reason why we saw no interesting moth responses to N when filtered by trait grouping. Studies on the effects of N on plants highlight the negative impact on plants of nutrient-poor habitats such as heaths and bogs, which may be under-sampled due to this moth trapping methodology. Additionally, the moth traps may have been affected by artificial light pollution from surrounding urban developments, which was not accounted for in our analysis.

Several of the responses of butterfly richness within trait groupings to historic N were hump-backed rather than negative, as we found in the combined species analysis. This was the case for moorland butterflies, univoltine butterflies, oligophagous butterflies, butterflies whose larva feed on forbs, and butterflies who overwinter as larva, pupa, or adults. This is interesting and could suggest potential evidence of a critical load for butterflies in some cases. Additionally, several of the responses of butterfly richness within trait groupings to the variable representing change in N over time were significantly negative, whereas this relationship was non-significant in the combined species analysis. Both findings warrant further investigation. The total abundance responses of different trait groupings to both N variables were unclear and often conflicted with the richness trends. This might indicate that the positive abundance trends are being driven by a few common species which are nitrophilic.

4.4. Further work and indicator development

4.4.1. Introduction

Based on the results from this modelling study, we suggest that an indicator of recovery from nitrogen pollution be based on a group of selected butterfly and moth species, rather than total richness or abundance of all species or of species within specific trait groupings. This indicator should be informed by this study, further analysis of Lepidoptera data with co-located atmospheric and vegetation data, as well as expert input from taxonomic specialists.

Now that we established the evidence base of potential N impacts on Lepidoptera in the UK, we could undertake further analysis of ecological metrics on different sets of sites, representing areas that have recovered from air pollution, areas where deposition has remained static, and areas where deposition has increased (as briefly highlighted in Figures 6 and 7, Section 3.2.1). Within this analysis, the direction of change in the different forms of N, oxidized nitrogen (NOx) and reduced nitrogen (NHx), could also be considered. Due to uncertainties in our ability to accurately detect spatial change in N pollution due to modelling constraints mentioned above, we could use sites with co-located atmospheric nitrogen monitoring stations to enable us to sense-check the modelled data. We propose that a viable route forward would be to undertake further analysis work on Lepidoptera data from Environmental Change Network sites, which is co-located with atmospheric and vegetation monitoring data. In these case study areas, we could model Lepidoptera abundance and richness in relation to N and other drivers at the individual site level and assess whether any evidence of recovery from N can be detected at this fine scale. In addition, we feel that further targeted analysis of the impacts of N on uncommon bog specialist butterfly species not covered in this report due to insufficient data availability would be beneficial.

From here, we would identify a list of candidate species for inclusion in an indicator. This list could be taken to a group of taxonomic experts for guided discussion which species to use in the indicator. From this work we can identify two potential candidate indicator butterfly species: the Wall *Lasiommata megera* and Gatekeeper *Pyronia tithonus*. Further analysis as discussed in Section 4.4.3 would enable us to understand whether other nutrient-poor habitat specialist species not covered in this analysis could be included as candidate species. This indicator of recovery from nitrogen pollution could be similar to UK Biodiversity Indicator 'Insects of the wider countryside (butterflies)' and detail the percentage of species undergoing change in the short- and long-term. Alternatively, it could take the form of a Community Nitrogen Index indicator as proposed by WallisDeVries and van Swaay (2017). Further scoping work is needed to identify the best route forward given the data we have available.

4.4.2. Nitrogen datasets

Further work is needed to understand the extent to which potential issues with the nitrogen driver datasets impact our ability to accurately detect spatial trends in pollutant impacts in the UK over time.

4.4.3. Additional analyses

Due to the tight time constraints on this project, follow-on work could involve more in-depth consideration of the results with regards to the potential ecological reasons behind the observed modelled responses, particularly for the moths. In addition, we would suggest further involvement from taxonomic experts in interpreting the moth results with relation to potential conservation implications. Future analytical work may also wish to incorporate a broader range of moth datasets, such as from the National Moth Recording Scheme, to increase spatial and taxonomic coverage of the moth analysis. Further analysis could also account for potential additional drivers of change in moths, such as the degree of artificial light at night (ALAN).

As mentioned in Section 4.4.1, further targeted analysis of the effects of N on individual bog specialist species that were not covered in this report should be considered. We were unable to run the complex single species models for the Large Heath *Coenonympha tullia* and Scotch Argus *Erebia aethiops*, both of which are specialists of nutrient-poor habitats and could potentially be important indicators of recovery from N. Further analysis of UKBMS data using less spatially complex models is highly recommended to understand this potential link.

The models used in the single species, combined species, and traits analyses did not consider the potential impact of habitat type. We expect that N enrichment will impact the metrics differently depending on which habitat the site is in. Further work could therefore test the potential effect of N on richness and total abundance whilst directly accounting for the habitat sampled, for example by including the dominant land cover in the surrounding area as a term in the models.

We tested the response of individual trait groupings to N pollution. Given the complexity of our findings, especially for the butterflies, it seems possible that there may be interactive effects of traits on Lepidopteran abundance and richness. Further work could take a much more complex approach to this trait modelling whereby multiple traits and their interactions can be included in the same model. This would allow us to understand whether it is a combination of traits, rather than the individual traits on their own that drive responses to N. This could perhaps be achieved using a joint species distribution modelling (jSDM) approach.

4.4.4. Developing a causal understanding of N impacts on Lepidoptera

Inherently, the results of this analysis only give us an understanding of the potential correlative links between N and Lepidoptera. Further work is needed to understand the causal mechanisms behind these responses. Co-located atmospheric pollutant, Lepidoptera, and plant monitoring data would allow us to have more confidence in our understanding of the causal effects of N on Lepidoptera and their hostplants and surrounding habitats. Such co-located data are currently limited to the few terrestrial Environmental Change Network (ECN) sites. Greater connectivity between monitoring networks would be hugely beneficial to further research into this type of question. Recent innovations in automatic monitoring of biodiversity provide a potential low-cost solution. For example, placement of UKCEH AMI-traps at vegetation and atmospheric monitoring sites would offer a low-cost, low-effort solution to increase the amount of co-located data. Placing AMI-traps at ECN sites where RIS traps are already located would allow us to test the effectiveness in terms of detection and quantification of species richness of AMI traps compared to the high-effort, high-cost RIS light traps.

There is also a need for controlled laboratory and field-based studies, for example to test whether the nutritional composition of N-enriched plants impacts survival and fecundity in UK Lepidoptera. Field-based gradient studies could also be used to detect potential impacts of point sources of ammonia on Lepidoptera by placing low-powered moth traps along a gradient of exposure, similar to how researchers would undergo a study over an elevation gradient.

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Glossary

Table 7. Glossary of terms.

Term	Definition
ALAN	Artificial light at night
AMI system	Automated Monitoring of Insects
BBC	Big Butterfly Count
CBED	Concentration Based Estimated Deposition
ECN	Environmental Change Network
EMEP	European Monitoring and Evaluation Program
FRAME	Fine Resolution Multi-pollutant Exchange
GAI	Generalised Abundance Index
GAM	Generalised Additive model is a model in which the linear response variable depends on unknown smooth functions of some predictor variables, and interest focuses on inference about these smooth functions.
GBS	Garden Butterfly Survey
GMS	Garden Moth Scheme
JASMIN	The UK's data analysis facility for environmental Science
JSDM	Joint Species Distribution Modelling
LCM	Land Cover Map
Lepidoptera	An order of insects that includes butterflies and moths.
LUI	Land Use Intensity
mgcv	Mixed GAM Computation Vehicle
N	Nitrogen
NA	Not Applicable.
Nitrogen Deposition	The input of reactive nitrogen from the atmosphere to the biosphere, both as a gas (dry deposition) and precipitation (wet deposition).
NMRS	National Moth Recording Scheme
RIS	Rothamsted Insect Survey
UKBMS	United Kingdom Butterfly Monitoring Scheme
UKCEH	United Kingdom Centre for Ecology and Hydrology
WCBS	Wider Countryside Butterfly Survey