DATA PATTERNS IN LONG-TERM LIGHT-TRAPPING PROGRAMMES FOR LARGER MOTHS (LEPIDOPTERA) IN THE ROTHAMSTED INSECT SURVEY, AND THEIR IMPLICATIONS FOR UNDERSTANDING SITE FAUNAS

A. G. BLUNT and D. J. POYNTON

This study analyses patterns in annual data for 537 species of larger moths (Lepidoptera) at 18 selected sites across Britain sampled by standardized light-trapping for 17-53 near-continuous years within the Rothamsted Insect Survey (RIS). Significant positive correlations were found between sampling intensity and site species richness, and between frequency and abundance of species entering traps. A significant negative correlation was found between species diversity and latitude: diversity decreased progressively with increasing latitude.

Here we create five distinct and standardized 'bands' which group moth species by their level of frequency and abundance. The proportionate distribution of faunas in bands was found to be site-specific, whereas patterns in recruitment of new species to sites and in percentage similarity between total site faunas were similar across all sites. Species with highest frequency-abundance were largely recruited to faunas in early years of trap operation, while those with lowest accounted for most recruitment of new species in later years. Percentage similarities between total site faunas are used to identify five potential regional assemblages, four along broadly latitudinal lines and one longitudinal, which may offer clues to regional species pools within the British fauna.

We propose that our research identifies inherent properties of light-trapping in sampling both a local and a dispersive fauna, and that the latter forms at least 12% to 25% of species captured by Rothamsted traps operating over longer periods. Our findings may be used to inform the design and interpretation of other investigations using light-traps, and the frequency-abundance relationship explored in this paper may aid a more informative approach to mapping moth distributions.

INTRODUCTION

The use of light-traps to capture moths (Lepidoptera) for study received a major boost from two developments in the late 1940s. The commercially-produced Robinson trap using a mercury vapour light bulb (Robinson & Robinson, 1950) gained rapid popularity among entomologists as a result of the unexpectedly large and diverse catches taken by it. This success led to the design of other traps employing a variety of lamp types, with research into their relative effectiveness and other factors influencing moth catches (Fayle, Sharp & Majerus, 2007; Fry & Waring, 2020). Light-traps are now used by many amateur entomologists in Britain and produce the largest body of distributional data for moths of macrolepidoptera families (the 'larger moths' or 'macro-moths') (Randle *et al*., 2019). They are typically operated as an opportunistic catch-release method that incurs several biases such as potential multiple counting of re-trapped specimens, thereby limiting their suitability for scientific applications; they have, however, been used successfully for standardized mark-release-recapture studies of moth dispersal (Nieminen, 1996; Merckx *et al*., 2009; Truxa & Fiedler, 2012).

The second key development was the Rothamsted Insect Survey (RIS) light-trap (Williams, 1948). A static trap of standard design using a relatively weak tungsten-filament bulb for catching and killing moths on a scale that does not affect local populations, it is operated nightly under Rothamsted protocols for sampling, identification and data recording. Traps are located widely across Britain and elsewhere, their samples are identified by a network of experienced lepidopterists, and data are forwarded to Rothamsted for collation and analysis. Standardization of equipment and operation gives good quality statistical data that have been used in a wide variety of scientific studies, into temporal and spatial population dynamics, diversity at site and regional levels, responses to climate change and land use, moth distributions and phenology, and more (Woiwod & Harrington, 1994). Moths are now seen as an important component in many studies that seek to track biodiversity and climate change (NatureScot, 2021).

Recent empirical research using data obtained by a variety of moth traps and light types has focused mostly on site species richness (Brose, Martinez & Williams, 2003; Summerville & Crist, 2005), moth community composition (Summerville *et al*., 2003; Matos da Costa & Sielezniew, 2023), and moth dispersal ability in relation to morphology, life history traits and landscape features (Hilt & Fiedler, 2005; Baguette & Van Dyck, 2007; Truxa & Fiedler, 2012; Slade *et al*., 2013; Merckx & Slade, 2014). Studies have typically involved short-term sampling over one or two years. This research field is still in development and has yet to produce a synthesis of key factors influencing moth diversity at site level.

A stimulus for research into data patterns in long-term trapping programmes came from Blunt, Trueman & Burkmar's (2021) analysis of a 25-year data set for Shropshire microlepidoptera by the computer program TWINSPAN (Hill, 1979; Hill & Šmilauer, 2005). Its output separated light-trapped samples into groups on the basis of their species numbers: those with more species obtained from greater trapping intensity were placed on the opposite side of the primary division to samples with fewer species obtained from lower trapping intensity. While a relationship between sampling intensity and species numbers is to be expected (Azovsky, 2011), in this case it clearly overrode all other factors including trap and lamp types, altitude, habitat and distance between sites, and implied that the species composition of samples obtained under very different conditions progressively converged with more trapping. The authors suggested that this pattern may mean that light-traps operating with greater frequency increasingly catch moths that are transient through an area; if so, there may be implications for understanding and mapping moth distributions. The present study investigates these issues across a geographically wide sample of sites.

AIMS

The following aims were established:

1. Consider available data sources and select the most suitable for studying data patterns in long-term light-trapping;
2. Establish criteria for selecting sites and moth species for this study, and make a selection of both;
3. Carry out an initial data analysis by comparing patterns in the data for selected sites;
4. Discuss implications of the findings and how they may inform a better understanding of light-trapping data.

METHODS

The nature and range of information needed for this study were considered. As far more lepidopterists trap and identify moths of macrolepidoptera families than microlepidoptera, it was judged that data on the former would be available in greater quantity and would present fewer identification problems. The consistency of samples taken by the Rothamsted trap (Taylor & French, 1974), the wide geographical spread of those traps in Britain, and the statistical integrity of their data, made those data especially suitable for this study. The Rothamsted Insect Survey (RIS) was approached and agreed to provide data files for selected sites.

Selection of sites

To facilitate investigation of long-term trapping at sites that represent a variety of conditions the following selection criteria were established:

- Sites should have continuous or near-continuous annual data for 20 or more years (following Woiwod & Harrington, 1984) to the decade 2010-2019;
- Sites should, as far as possible, represent a wide geographical, altitudinal and habitat range.

Thirty-seven Rothamsted sites across Britain potentially met the first criterion. Of these, 18 were selected as best meeting the second criterion, while limiting the extensive data processing for this study to manageable levels (Table 1). Available site data did not allow complete habitat, geographical and altitudinal ranges across Britain to be represented. Data for all years of trap operation at the sites were made available by the RIS (Fig. 1). Nine sites had 1-4 incomplete data years as defined by RIS protocols; these years were excluded from the study: Braemar thus fell short of 20 complete years but was retained in the selection as having extensive recent data at high altitude in Scotland. Further exclusions of earlier periods of trap operation were made for two sites, Rowardennan and Malham Tarn, because of a greater number (6) of incomplete early years (Rowardennan) and an 11-year break in trapping (Malham Tarn).

Table 1. Characteristics of the 18 sites selected for this study. Abbreviations: Roth no., Rothamsted site number; Code, the site code used in this study; VC, Watsonian vice-county number; Full years, the number of complete or near-complete years of data; Mean *α*, the geometric mean of annual log-series *α* scores from 1980 to 2016; Habitat score and Stability score, see text below.

Roth no.	Site	Code	VC	Data years	Full years	Total species	Altitude (m)	Mean *α*	Habitat score	Stability score
45	Malham Tarn	MT	64	1991-2018	26	215	400	22.32	6	17.5
46	Alice Holt	AH	12	1967-2019	53	409	129	56.02	7	30
97	Rowardennan	RO	86	1995-2016	21	251	15	26.62	7	19
111	Llysdinam	LL	42	1975-2014	40	342	200	40.63	7	35.5
212	Hereford	HE	36	1974-2018	44	294	90	26.28	1	34.5
293	Auchincruive II	AU	75	1975-2019	44	256	50	24.91	5	45
331	Tregaron	TR	46	1976-2019	44	368	198	43.13	4	11
336	Cockayne Hatley	CH	30	1976-2019	44	354	76	36.85	4	31
382	Preston Montford II	PM	40	1978-2019	42	332	61	39.54	5	37.5
416	Forest-in-Teesdale	FT	65	1981-2019	39	154	381	15.12	3	6.5
451	Perry Wood	PW	15	1985-2019	35	371	80	41.68	2	23
467	Castle Eden Dene 1	CE	66	1987-2012	22	248	91	30.11	2	50
543	North Wyke	NW	4	1993-2018	26	285	165	30.81	5	43
544	Sourhope	SO	80	1993-2014	21	204	230	25.29	6	8.5
553	Pennerley	PE	40	1996-2019	23	297	363	40.31	4	53
560	Loddington	LO	55	1995-2019	23	287	140	34.43	1	11
567	Glensaugh II	GL	91	1996-2018	23	217	180	30.55	3	29
573	Braemar	BR	92	1999-2019	17	227	352	25.26	5	28

In Table 1 Watsonian vice-county (VC) numbers were chosen to represent site locations. Vice-county boundaries are consistent and not subject to political change; their numbers follow a latitudinal progression from south to north, with a longitudinal dimension also involved. As VC numbers are easier to conceptualize than site co-ordinates, we tested whether they could be used in this study as a proxy measure for latitude. Spearman correlation coefficient (r_s) tests were therefore carried out on the relationships between VC numbers and site latitude and longitude co-ordinates for the 18 selected sites. They showed a highly significant positive correlation between VC numbers and latitude ($r_s = 0.970$, $p = < 0.01$, $n = 18$) but no significance with longitude ($r_s = 0.450$, $p = > 0.05$, $n = 18$). VC numbers are therefore adopted in this study as a proxy measure for latitude.

In the table, Total species refers to a site's total number of selected species after exclusion of critical species: see the following section.

Available habitat data were restricted to simple broad habitat descriptors. For use in analyses these were transformed to a numerical scale representing a notional stability gradient from most stable (woodland) to least stable (farmland) habitats, in which 7 = woodland, 6 = moorland, 5 = parkland, 4 = mixed habitats, 3 = scrubland, 2 = urban, 1 = farmland. These constitute the habitat scores shown in Table 1.

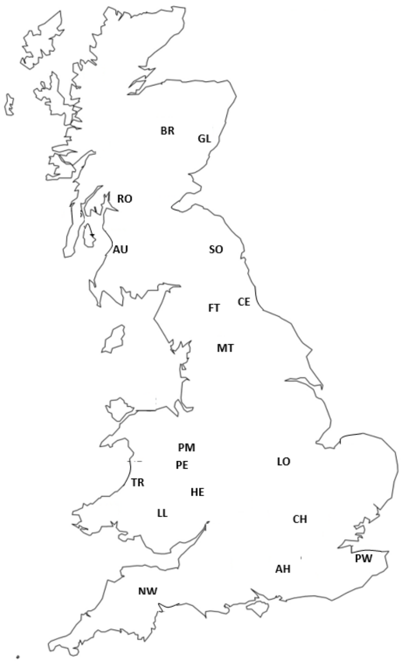


FIGURE 1. Location of sites selected for this study. Site codes are those shown in Table 1.

Selection of moth species

Data files comprised annual totals for all Lepidoptera species recorded at each site. Files were initially reduced by excluding all butterflies, microlepidoptera, unidentified moths and those identified only to genus level. Data for critical species (i.e., those posing most identification problems) were then examined. While samples for all sites had been identified by experienced lepidopterists, at some sites the personnel identifying samples had changed over the years; some variation in recording practices for critical species was observed, e.g., in the proportions of specimens confirmed by dissection or recorded only to genus; and pugs of *Eupithecia* spp. were considered to have been inconsistently identified in Rothamsted samples before 1986 (Randle *et al*., 2019). For better comparability of data across sites it was decided to exclude certain critical species from the study:

- Those for which dissection is required to establish identity, as defined by RIS protocols:
  - (Noctuidae) *Acronicta tridens* ([Denis & Schiffermüller], 1775) & *A. psi* (Linnaeus, 1758); *Mesapamea secalis* (Linnaeus, 1758) & *M. didyma* (Esper, 1788); *Oligia strigilis* (Linnaeus, 1758), *O. latruncula* ([Denis & Schiffermüller], 1775) & *O. versicolor* (Borkhausen, 1792); all species of *Amphipoea* Billberg, 1820;
  - (Geometridae) all species of *Epirrita* Hübner, 1822.
- Those considered by the authors to present most difficulties of identification on superficial characters, especially with worn individuals that form a regular proportion of specimens in Rothamsted samples:
  - (Noctuidae) all species of *Hoplodrina* Boursin, 1937;
  - (Geometridae) *Xanthorhoe spadicearia* ([Denis & Schiffermüller], 1775) and *X. ferrugata* (Clerck, 1759); and all pug species of the genera *Eupithecia* Curtis, 1825, *Pasiphila* Meyrick, 1883, plus *Chloroclystis v-ata* (Haworth, 1809) and *Gymnoscelis rufifasciata* (Haworth, 1809).

After application of these exclusions the data selected for this study comprised 5,111 site species records involving 1,748,683 individuals and 537 species in 11 families: Hepialidae, Limacodidae, Drepanidae, Lasiocampidae, Saturnidae, Sphingidae, Geometridae, Notodontidae, Erebidae, Noctuidae, Nolidae. The taxonomic scheme and nomenclature of Lepidoptera in this study follow Agassiz, Beavan & Heckford (2013).

Data for each site were held in a Microsoft® Excel® spreadsheet containing the following information for each species at that site:

- The number of years from its first to its last appearances in annual totals (its ‘potential years’ of occurrence);
- Its frequency, calculated as the percentage of potential years represented by the actual number of years in which it was trapped;
- The range of its annual totals of specimens trapped;
- Calculation of the median and mean values of its annual totals of specimens; these calculations incorporated a zero value for each potential year in which the species was not trapped.

Selection of abundance and diversity measures

Inspection of annual totals for all species at all sites revealed consistently skewed distributions: species typically had many smaller annual totals and relatively few larger totals. Comparison of median and mean abundance values further confirmed that annual totals for species did not conform to a normal (Gaussian) distribution. The median value of each species’ annual totals at each site was therefore selected for this study as the most appropriate measure of its average abundance at that site.

Two diversity measures were available for analysing site data, as shown in Table 1: species richness, i.e., the total number of selected species in site faunas, and α of the log series, which expresses a measure of both the number of species and evenness in distribution of individuals among species (Fisher, Corbet & Williams, 1943). Log-series α has been used in a wide range of ecological applications as a robust statistic with good discriminating ability and sample-size independence (Kempton & Wedderburn, 1978; Southwood, 1978; Taylor, 1978; Magurran, 1988; Hayek & Buzas, 1997). Annual measures of log-series α were calculated by the RIS for each site operating in the period 1980-2016; from these a geometric mean *α* score was obtained for each site in this study as shown in Table 1. The table also gives a stability score for each site, derived from the relationship between its geometric mean log-series *α* value and the interquartile range of its annual α values. Stability scores in Table 1 represent a notional gradient from most stable (lowest) to least stable (highest). Scores were compared visually with graphs plotting annual α measures for each site and showed a good match with the smoothness or otherwise of graph lines, except for site FT, whose graph implied rather less stability than its score did.

The terms α and log-series α in this paper refer to the geometric mean log-series α values shown in Table 1.

Methods of data exploration

An initial analysis was made on the relationship between sites' faunal diversity and the site characteristics shown in Table 1, and between the frequency and abundance of species at sites. This latter relationship was then used to create five groups (bands) of species at each site. Band boundaries were provisionally established for each site by data inspection, then standardized across all sites through χ^2 tests of association. Full details are given below. Bands were then used to explore structures of site faunas, patterns of species accumulation, and scale of similarity in the species composition of sites.

RESULTS

Relationship between sites' faunal diversity and site characteristics

An initial analysis was made of the strength of relationships between the diversity of site faunas and site characteristics represented by data in Table 1. Species richness and log-series α values were tested separately by the Spearman correlation coefficient (r_s) against each site characteristic.

In tests using species richness, no significant relationship was found between number of species at a site and altitude, habitat score or stability score. A significant positive correlation was found between number of species and number of full years of trapping ($r_s = 0.626$, $p < 0.01$, $n = 18$) and a significant negative one between number of species and latitude as represented by VC numbers ($r_s = -0.743$, $p < 0.01$, $n = 18$). Thus, species richness of site faunas increased significantly in relation to greater trapping intensity, and declined significantly at progressively higher latitudes. Figure 2 plots the relationship between VC numbers and species richness after 17 complete years' trapping at each site (the total number of complete years at BR) (Figure 2A), and at the end of each site's full trapping programme (Figure 2B). Sites in southern England are shown in black, Midlands and Welsh sites in blue, northern English sites in orange-brown and Scottish sites in green. Trend lines and coefficients of determination (R^2) are fitted by Microsoft® Excel® software.

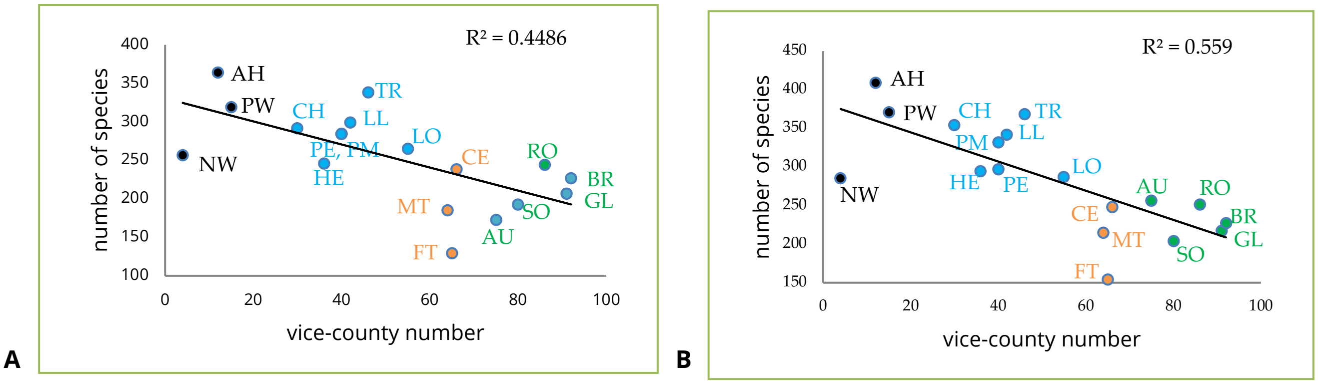


FIGURE 2. Scattergrams showing the relationship between species numbers and vice-county locations of sites. Figure 2A presents the relationship after 17 complete years of trapping at each site; Figure 2B shows the relationship at the end of sites' full trapping programmes. Sites are coloured as follows: **black** for southern England, **blue** for the English Midlands and Wales, **orange-brown** for northern England, **green** for Scotland.

The relationship between site species richness and latitude as expressed by VC numbers after 17 complete years of trapping was significant ($r_s = -0.699$, $p < 0.01$, $n = 18$) and became stronger towards the end of the trapping programmes, as shown by the r_s value given above (-0.743) and the higher R^2 value in Figure 2B. The position in both scattergrams of North Wyke (NW), Forest-in-Teesdale (FT) and, to a lesser extent, Malham

Tarn (MT) shows that these sites trapped distinctly fewer species than might be expected from their latitudes; the reverse is the case for Alice Holt (AH) and Tregaron (TR). No consistent pattern emerged for the four sites at highest altitude: MT and FT trapped low species numbers relative to their latitudes; Braemar (BR) and Pennerley (PE) trapped close to expected numbers.

Log-series *α* values were then tested against site characteristics. A significant positive correlation was found between α and total species (r_s = 0.889, p < 0.001, n = 18) and a significant negative one between α and VC locations (r_s = -0.623, p < 0.02, n = 18). No significant correlation was found between α and number of full years of trapping, altitude, habitat scores or stability scores. Since *α* values incorporate measures of species richness, a significant correlation between these variables is unsurprising. Tests using the two diversity measures imply that, of the site characteristics tested, latitude is the strongest influence on the diversity of site faunas. This result should be interpreted in light of a trend for more northerly sites to have been sampled over fewer years than more southerly ones: the relationship between number of full years' trapping and vice-county numbers is significantly negative (r_s = -0.620, p < 0.02, n = 18); but the relationship retrieved by species richness measures when trapping duration was standardized across all sites (Fig. 2A), and by the sample-size independent α values, endorses latitude as a key influence on site species richness of larger moths in Britain.

Relationship between frequency and abundance of species

To compare the strength of the relationship between frequency and abundance of species trapped over the longer term at each site, measures of frequency and abundance of each species at a site, calculated as described above, were plotted against each other in scattergrams. As both variables included very large and very small values they were $\log_{10}$ transformed. To improve representation of underlying trends in the data, species that occurred at sites in only one year (occasionally only two or rarely three consecutive years) were excluded from the comparison, as their frequency-abundance relationship was atypical (frequency 100%, abundance ~1).

Scattergrams for all sites showed a very similar curvilinear pattern: a long tail of low values rising to a more clustered peak of high values (Figure 3). Two sites, Pennerley (PE) (Figure 3A) and Braemar (BR) (Figure 3B) were selected as being a good representation of the relationship found across sites. The scattergram for BR (Figure 3B) shows a distribution that is least similar to those for other sites, but the same basic pattern of the frequency-abundance relationship is readily apparent.

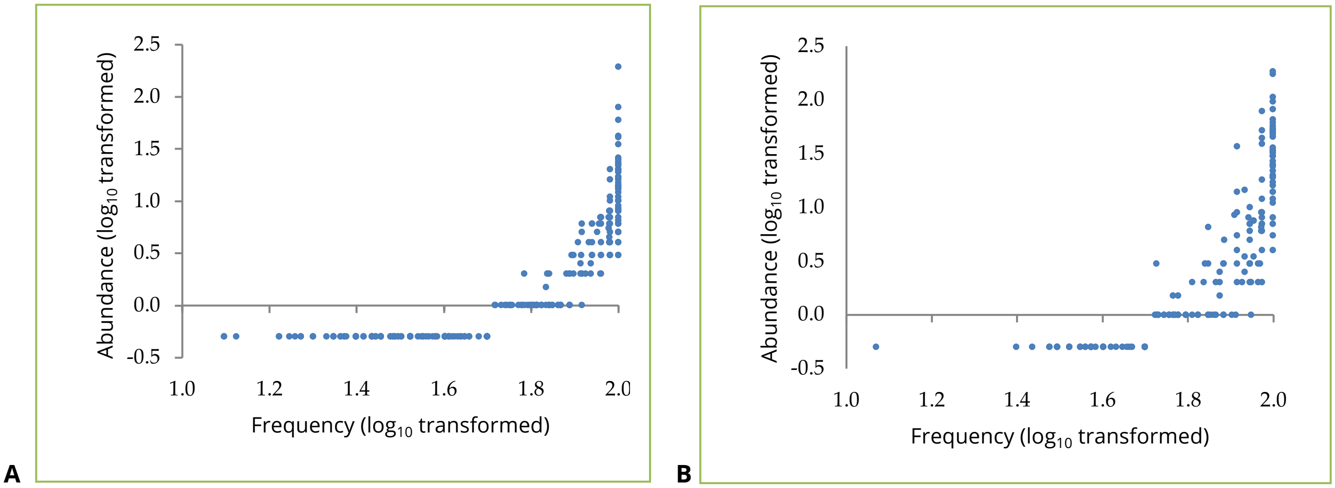


FIGURE 3. Scattergrams showing the relationship between species' frequency and abundance in samples. Figure 3A shows the relationship for Pennerley (PE); Figure 3B shows that for Braemar (BR).

These scattergrams show that the 18 Rothamsted traps, selected to represent a wide geographical, altitudinal and broad habitat range, sampled their site faunas in the same way. They reveal a direct relationship between the frequency with which a species appeared in a trap and its abundance in trap samples. The strength of this relationship was tested for each site by the Spearman correlation coefficient (r_s) on a random sample of 30 species selected by random number tables. There was a very strong positive correlation between frequency and abundance for every site: r_s values ranged from 0.839 (for BR) to 0.974 (for PM), with a probability $p < 0.01$. The tests confirm the strength of the relationship and show that either measure – frequency or abundance – may be used to characterize site faunas.

This finding was important in allowing site faunas to be divided into groups of species that could be explored separately as well as accumulatively, as described below. Its further implications for mapping species' distributions are addressed in the Discussion.

Inspection of scattergrams for all sites suggested that data points fell into broad groups, separable to a reasonable extent on frequency-abundance measures. To establish group boundaries, transformed and untransformed frequency and abundance data for each site were examined. Data were sorted first by frequency and then by abundance; site-specific species groupings were provisionally established, first on frequency and then on abundance values, that broadly reflected data point distributions in the scattergram for each site; and these groupings were compared across all sites to suggest standardized measures for group divisions. As χ^2 tests of association gave no significant difference between site-specific and standardized measures, the latter were adopted for this study as giving best comparability between sites. This exercise further showed that frequency produced more coherent groups than did abundance; it is therefore used here as the defining measure separating site faunas into groups (bands) of species.

Measures for the five standardized bands established in this manner are shown in Table 2 as untransformed data. Band divisions for the typical site PE are broadly indicated in Figure 3A at the following co-ordinates: Bands 1-2 (1.98, 0.74); Bands 2-3 (1.88, 0.3); Bands 3-4 (1.72, 0). Band 4 is represented by data at co-ordinates ≤ 1.70, -0.3; Band 5 is not plotted in Figure 3 because of its atypical frequency-abundance relationship.

Table 2. Distribution of species in five bands representing standardized frequency and abundance value ranges (untransformed data). Abundance range is the range of median abundance values for all species in each frequency range at each site.

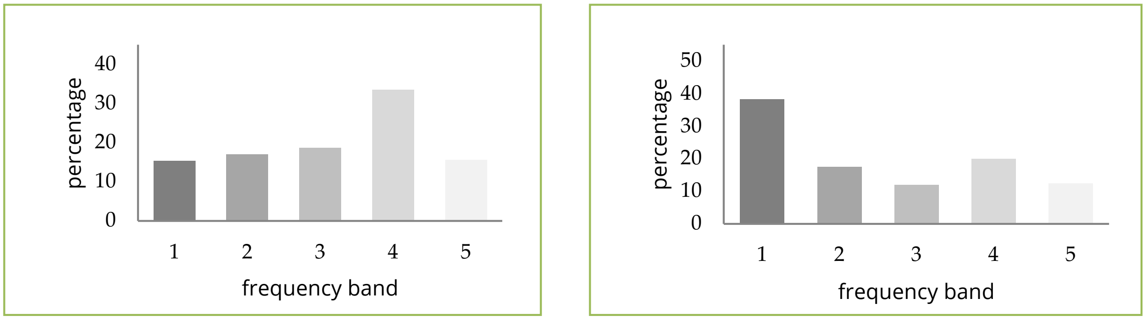
Band	Frequency range	Abundance range
1	95% – 100%	9 – 31.25
2	75% – 94%	2 – 4.5
3	51% – 74%	1
4	≤ 50%	0 – 0.5
Band 5 criteria: occurring in only one year, or two or three consecutive years, with any abundance		

While offering a broadly consistent distribution of site faunas, standardization of frequency measures occasionally led to placement of some species at a site into a higher or lower band than their abundance values indicated. The scale of this was relatively small (11% of the fauna of site PE) and mostly reflected the less easily definable boundary between Bands 1 and 2 than between other bands. Median abundance values derived from all species in a band at a site, however, fell into clearly separated frequency-abundance ranges for Bands 1-4 across all sites (Table 2). Band 5, consisting of species that were rare in samples, is defined purely on frequency as shown in Table 2.

In the following analyses the species composition of each band is always site-specific. The term 'Band *X* species' does not indicate a discrete group of species forming that band across all sites. Bands may be referred to for brevity as 'frequency bands', but their additional representation of abundance is always implied. Table 2 further implies that bands show the relative strength of association of groups of species with sites, on a decreasing scale from Band 1 to Band 5.

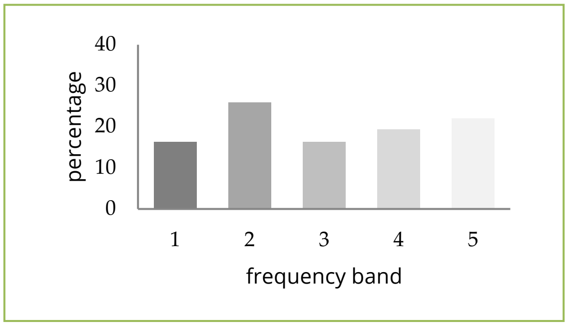
Structures of site faunas by frequency bands

The proportional distribution of site faunas across the five frequency bands was calculated for each site. Three main patterns emerged: Band 4 formed the largest component of the fauna of 14 sites; Band 1 formed the largest component at three sites, and Band 2 did so at one site. Examples of the three main patterns, as represented by the faunas of Perry Wood (PW), Rowardennan (RO) and Braemar (BR), are shown in Figures 4A, 4B and 4C respectively.



A - Perry Wood

B - Rowardennan



C - Braemar

FIGURE 4. Patterns of distribution of frequency bands across sites: Figure 4A, Perry Wood; Figure 4B, Rowardennan; Figure 4C, Braemar.

Within these main distribution patterns site faunas were well differentiated, particularly in respect of the proportions of species in Bands 1 and 4. Table 3 shows the range of percentage values represented by each band across all 18 sites.

Table 3. Proportional distribution of site faunas across five bands at the 18 selected sites, showing the smallest and largest proportions of site faunas in each band, their percentage point difference, and the median and interquartile range values for each band. Sites representing extreme values in each band are indicated.

Band	Lowest % value	Site	Highest % value	Site	% point difference	Median % value	Interquartile range (% points)
1	4.3	AU	41.3	TR	37.0	16.1	11.4
2	10.5	NW	26.0	BR	15.5	15.3	4.3
3	9.1	FT	23.4	AU	14.3	15.5	3.9
4	19.4	BR	47.3	HE	27.9	33.1	11.7
5	6.5	TR	24.7	MT	18.2	17.1	7.7

A χ^2 test of association showed significant difference in the proportional distribution of site faunas across the five bands ($\chi^2 = 487.64$ with 68df, $p < 0.001$). The largest contributions to the difference were:

- Low proportions of Band 1 at AU, HE, NW; of Band 4 at BR, RO; of Band 5 at AH, TR;
- High proportions of Band 1 at RO, TR; of Band 2 at BR; of Band 3 at AU; of Band 4 at HE, NW; of Band 5 at MT.

After exclusion of the six sites contributing the largest differences (AU, BR, HE, NW, RO, TR), a further χ^2 test of association was carried out on the remaining 12 sites. This also showed significant difference ($\chi^2 = 142.47$ with 44df, $p < 0.001$), with the largest contributions to the difference being:

- High proportions of Band 1 at LL, PE, SO;
- Low proportion of Band 4 at SO;
- Low proportion of Band 5 at AH and high proportion at MT.

Percentage values of frequency bands for all sites were then compared with six site characteristics: number of full years of trapping, total species, vice-county location, altitude, habitat score and stability score. Spearman tests highlighted mostly very weak correlations between the variables, but three significant correlations were retrieved: positive ones between the percentage of Band 3 species and stability scores ($r_s = 0.481$, $p < 0.05$, $n = 18$) and between the percentage of Band 4 species and number of full years of trapping ($r_s = 0.658$, $p < 0.01$, $n = 18$); and a negative one between the percentage of Band 5 species and total species numbers ($r_s = -0.767$, $p < 0.01$, $n = 18$). In effect, the proportion of Band 4 species in site faunas increased significantly in relation to sampling intensity, while the proportion of Band 5 species decreased significantly in relation to increasing site species richness. There are negligible relationships between the proportions of Bands 1, 2 and 3 in site faunas and the site characteristics investigated in this study, except that the proportion of Band 3 species was significantly related to site stability scores: this finding invites no clear interpretation.

Patterns of species accumulation by sites

The rate of accumulation of new species in the five frequency bands was investigated for each site, and revealed a similar pattern for all sites. The species complements of Bands 1 to 3 were largely established in the early years of trap operation, at a progressive rate from Band 1 (most species recorded by year 3) to Band 3 (most species recorded by year 7), with very low recruitment rates of new species to these bands thereafter. By contrast, new Band 5 species were regularly recruited in small numbers throughout the duration of trapping programmes, with no marked early recruitment peak. Band 4 species showed an intermediate pattern: an early recruitment peak leading to a progressive fall in recruitment of new species until about year 12; after this, further recruitment of small numbers of new Band 4 species followed the pattern for Band 5.

Figure 5 shows typical examples of species accumulation patterns: Figure 5A shows the pattern across all five bands for North Wyke (NW); Figure 5B shows the pattern for Bands 4 and 5 at Forest-in-Teesdale (FT); and Figure 5C shows the Band 5 pattern across 26 years of trap operation (1992-2017) at four sites (AH, HE, FT, AU). These years were selected to allow comparison with the annual recruitment of new species to the British larger moth fauna in the same period (Figure 5D). Data for Britain for 1992-2013 were calculated from Agassiz, Beavan & Heckford (2013), and for 2014-2017 from Clancy (2018; 2019; 2020; 2021); they include only those species considered by the sources to be natural immigrants or vagrants.

Rates of accumulation of species in bands during early years of trap operation were investigated. The percentage of each site's total fauna represented by samples obtained after one and three years of trapping were calculated. Table 4 shows the percentage value range and median values for each band across all 18 sites after one and three years of trapping.

Table 4. Range of percentages of total site faunas in each band, and their median percentage values across all sites, obtained after one and three years of trapping at each site.

Band	**After 1 year's trapping**		**After 3 years' trapping**	
	% range	**median % value**	**% range**	**median % value**
1	72-100	94.8	93-100	98
2	49-89	73.9	69-100	90
3	30-70	48.9	45-89	71.4
4	14-39	26.5	31-66	50.8
5	0-20	6.6	2-33	14.7

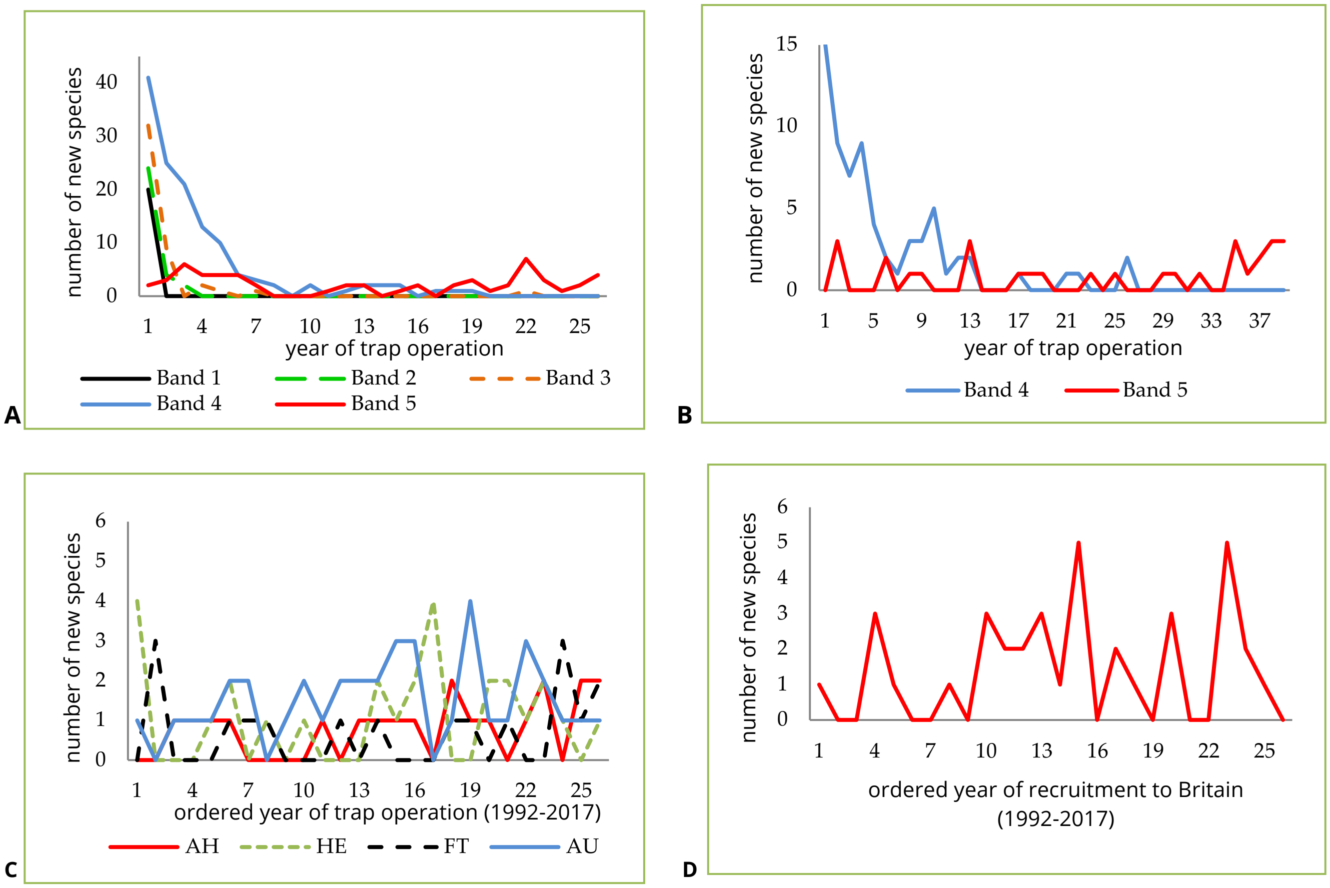


FIGURE 5. Examples of species accumulation patterns: Figure 5A, for all bands (site NW); Figure 5B, for Bands 4 and 5 (site FT); Figure 5C, for Band 5 at sites AH, HE, FT, AU in the years 1992-2017; Figure 5D, the annual recruitment of new larger moth species to the British fauna in the years 1992-2017.

Figure 5 and Table 4 together show a consistent pattern for all sites in the rate of accumulation of species in the five bands. This rate is determined by frequency and abundance measures: the more frequent and abundant a species is in annual samples, the more likely it is to occur early in the trapping period, and at a fairly predictable rate. Site faunas recruited few new Bands 1-3 species in later years of trapping, and species accumulation in later years was mostly confined to Bands 4 and 5 species. The pattern of recruitment of new species to the British fauna (Figure 5D) is broadly similar to that of new Band 5 species at sites (Figure 5C), which may suggest a similar process in recruitment of largely transient species at these very different spatial scales.

The correlation between six site characteristics and number of species in bands was tested across all sites for Band 1 and then at each incremental addition of the next frequency band, up to full site faunas (Bands 1-5). No significance was found when testing species numbers in bands against altitude, α values, habitat scores or stability scores. Significant correlations were found for Bands 1-4 and 1-5 in relation to number of full years of trapping and latitude as represented by vice-county numbers. Table 5 shows the data.

Table 5. Spearman coefficient calculations (r_s) of the relationship across all 18 sites between numbers of species incrementally accumulated in frequency bands, and two site characteristics: number of full trapping years, and latitude as represented by vice-county numbers. Significant correlations are shown in bold type.

n = 18	**full trapping years**		**latitude**	
	r_s	**p**	r_s	**p**
Band 1	-0.029	> 0.1	-0.090	> 0.1
Bands 1-2	0.184	> 0.1	-0.265	> 0.1
Bands 1-3	0.273	> 0.1	-0.309	> 0.1
Bands 1-4	**0.609**	**< 0.02**	**-0.720**	**< 0.01**
Bands 1-5	**0.626**	**< 0.01**	**-0.743**	**< 0.01**

Table 5 shows a very weak relationship between variables in respect of the number of Band 1 species across the 18 sites. The strength of correlation increased with the incremental addition of further bands, but remained relatively weak up to and including the addition of Band 3 to calculations. It then increased dramatically and with significance when Band 4 was added, followed by a further but smaller increase with the addition of Band 5. The table thus implies that the number of species in site faunas became progressively more similar in relation to increased duration of trapping but progressively less similar along a latitudinal gradient from south to north, both trends reaching significance at the addition of Bands 4 and 5 species to site faunas. Data in Table 2 further suggest that these trends were driven by the progressive accumulation of species with decreasing strength of association to sites.

Similarity in the species compositions of site faunas

In order to investigate the degree of similarity between the species compositions of site faunas the Sørensen Similarity Index (SI) coefficient was calculated for 918 pairwise comparisons of each site with each other site. SI was initially calculated for Band 1 alone, then again after each incremental addition of the next frequency band of species, from Bands 1-2 to Bands 1-5. SI was also calculated for Band 4 alone. Table 6 gives measures of similarity of site faunas, expressed as percentages, derived from these calculations.

Table 6. Percentage similarity of species compositions of site faunas, based on Sørensen Similarity Index (SI) coefficient calculations for every site in comparison with every other site: for Band 1 alone, Band 4 alone, and four incremental band ranges (Bands 1-2 to Bands 1-5). The SI range shows the lowest to highest percentage similarity values obtained in pairwise comparisons for each band range.

Measure (%)	**Band 1**	**Bands 1-2**	**Bands 1-3**	**Bands 1-4**	**Bands 1-5**	**Band 4**
SI range	9-68	22-80	26-81	43-86	48-87	7-55
mean	39.4	51	56.9	68	71.4	25.1
median	40	50	57	70	73.5	24
interquartile range (Q3-Q1)	20	17.5	15.5	13	12	15

All pairwise comparisons showed a progressive increase in percentage similarity of site faunas through their shared species, from relatively low similarity for Band 1 species alone to most similarity for Bands 1-5, i.e., total site faunas. This gradient was observed for every site in comparison with every other site. The pattern implies that the species composition of site faunas was more dissimilar in respect of those species with strongest association to sites and increased in similarity as species with progressively lower levels of association to sites were added to calculations.

SI values calculated for full site faunas allow identification of groups of sites with highest percentages of shared species. Five groups are proposed from inspection of the data; these are shown in Table 7 and mapped in Figure 6. All pairs of sites in a group have SI values that fall within the range shown for that group.

Table 7. Proposed groups of sites based on percentage similarity of number of shared species as given by Sørensen Similarity Index (SI) pairwise comparisons for total site faunas.

Group	Sites	SI value range (%)
Scottish	BR, GL, RO	74-80
Northern	AU, CE, GL, MT, SO	74-80
Midlands	CH, HE, LO, PM	81-85
Southern	AH, CH, LL, PM, PW	81-85
Western	LL, NW, PE, PM, TR	80-87

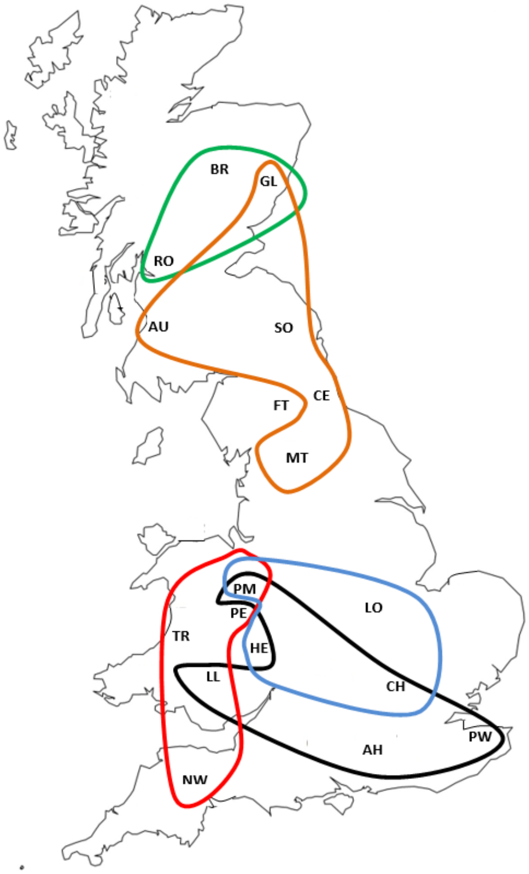


FIGURE 6 (right). Map showing proposed groups of sites as suggested by their shared Sørensen Similarity Index (SI) coefficient values.

In Table 7 four sites (CH, GL, LL, PM) are placed in more than one group; their percentage of shared species with each site in each group to which they are assigned falls within the SI value range for that group. Four pairs of sites that cross group boundaries also have high SI values for their shared species composition: they are AU-LL (77%), CE-LO (77%), FT-SO (75%), HE-NW (81%).

Inspection of Table 7 and Figure 6 points to groups falling into reasonably coherent geographical regions, of which four represent a broadly latitudinal gradient and the fifth a longitudinal one. There is some overlap between groups, especially the Midlands and Southern groups; both include Preston Montford (PM), which lies at 61m altitude in the warm corridor of the Severn valley in Shropshire, but exclude Pennerley (PE), only 16km away on the Stiperstones ridge at 363m (Blunt, 2014). The topography of the English-Welsh border produces complex climates in which land eastward of high ground forms a distinct rain-shadow area with climatic conditions relating more closely to central Britain (Mitchell, 1995). Similarly in eastern Scotland climates in the lee of the Grampian massif may in some respects approach those of north-east England (*cf*. Met Office, 2025). Table 7 and Figure 6 may therefore suggest a measure of climatic influence impacting at both a latitudinal level and in the level of SI percentage similarity attained by Southern and Midlands groups compared with Northern and Scottish ones. The Western group of Welsh, Shropshire and Devonshire sites may represent a group responding to an Atlantic climate. The groups as defined here may offer clues to the distribution of regional species pools within the British larger moth fauna.

DISCUSSION

This analysis of long-term trapping data for larger moths at 18 sites across Britain has found a number of consistent patterns and relationships. Two significant correlations emerged between site faunas and site characteristics investigated in this study. The first was a positive correlation between sampling intensity, measured by duration of trapping programmes, and moth species richness. The second was between faunal diversity and latitude as represented by Watsonian vice-county numbers: diversity decreased significantly along a latitudinal gradient from south to north. This gradient is considered the main though not sole influence on regional species richness of British Lepidoptera by Fox *et al*. (2013; 2021). Fig. 6 implies that the gradient is not simply linear but driven by climatic variation in which pockets of climate typical of more southerly latitudes occur locally further north, so supporting the propositions of Turner, Gatehouse & Corey (1986) and Woiwod & Harrington (1994). Our interpretation of sites in Wales and western England as representing a fauna responding to an Atlantic climate may be understood in relation to rates of actual evapotranspiration in warm, moist climates that were found by Hawkins & Porter (2003) to be a main factor in species richness patterns of European butterflies.

Another key finding of our study was the strongly significant positive relationship between frequency and abundance of larger moth species entering Rothamsted Insect Survey traps. This relationship allowed assemblage of faunas into five novel site-specific species groups (bands) based on standardized frequency and abundance measures. These bands are used to investigate and compare sites' faunal structures; patterns of accumulation of new species; and similarity in species composition of site faunas. Main findings are that site faunas were most differentiated in their proportionate distribution of species into bands; they were most similar in patterns of accumulation of new species in different bands, and in the species composition of total site faunas. The species composition of site faunas became progressively similar as bands that recruited species over longer time periods were added to calculations, reaching greatest similarity when Bands 4 and 5 were added to calculations.

We propose that these findings represent a gradient measuring the strength of association of bands with sites, from strongest for Band 1 to weakest for Band 5, under the influence both of local factors (habitat, climate, management) and moth dispersal capacity.

Moths are caught after entering a zone within which a light source may affect flight behaviour and cause them to enter traps (Fabian *et al*., 2024). Species which fly most often and in greatest numbers into that zone are likely to be those breeding locally; they are represented here by Band 1. Patterns of species accumulation in Figure 5 and Table 5 suggest that the species compositions of Bands 2 and 3 were also determined by mostly local factors. Any significance of specific local factors could not be demonstrated from data available for this study, and detailed analysis would need more precise information on local environments and management than currently available for the sites.

It was with the addition of Bands 4 and 5 to calculations that the picture noticeably changed. Species that occur rarely in samples, represented here by Band 5 species and some of Band 4, are a consistent feature of light-trapping. They are reported from trapping at different geographical, climatic, temporal and spatial scales, in different habitats and using various trap and lamp types: in Britain (Riley, 1990), central Europe (Truxa & Fiedler, 2012; Jonason, Franzén & Ranius, 2014; Matos da Costa & Sielezniew, 2023), North America (Summerville *et al*., 2003; Summerville & Crist, 2005), Papua New Guinea (Hebert, 1980), peninsular Malaysia (Barlow & Woiwod, 1989) and the Ecuadorian Andes (Hilt & Fiedler, 2005). Where authors speculate on reasons for this pattern, they see it as representing a stream of casual visitors from outside the trapping area, with the caveat that our knowledge of moth mobility is as yet too limited to reach firm conclusions.

We found that the addition of Band 4 to calculations produced the greatest change in data trends. Band 4 species are those trapped at a site in ≤ 50% of potential years and generally in low single figures. Band 4 constituted the highest proportion of the fauna of most sites; the highest proportionate band average (Table 3); and, when incrementally added to Bands 1-3, produced a large increase to significance in relationships between site species richness and both trapping duration and latitude (Table 5). In later years of trap operation the recruitment of new Band 4 species to site faunas followed a similar pattern to that of new Band 5 species, and of new species to the British fauna (Figure 5). Criteria used to define Band 4 probably account for the significant decrease of Band 5 species in site faunas in relation to site species richness: more sampling, which increased species richness, gave more chance for a Band 5 species to recur in later years, thus moving it into Band 4 by the methodology.

Table 5 shows that progressive addition of bands of species led to progressive convergence of site faunas at species level, while simultaneously producing progressive differentiation between sites along latitudinal lines. Both trends reached significance with the addition of Bands 4 and 5 to site faunas. We interpret these trends as showing that, over longer time periods, traps increasingly sampled species drawn from regional rather than just local species pools. Our findings are consistent with those of Summerville *et al*. (2003) from light-trapping data at site, forest and ecoregional scales in North America: they proposed that local factors determined species dominance, whereas community composition was most significantly influenced by ecoregional differences, while turnover in species richness occurred equally across all spatial scales because numerically rare species were continually encountered.

Though imperfectly known, the dispersal capacity of moths is a critical element for understanding such trends (Nieminen, Rita & Uuvana, 1999; Betzholtz and Franzén, 2011). Two important parameters are the distances moths can travel from a population source, and encounter rates in relation to distance. Empirical research using mark-release-recapture (MRR) offers limited data on the former because of the relatively short times and distances and relatively small numbers of moths involved in such research; but MRR programmes have consistently shown a progressive decrease in recapture rates with increasing distance from source (Hilt & Fiedler, 2005; Truxa & Fiedler, 2012; Matos da Costa & Sielezniew 2023 and references therein). This relationship has been confirmed for a wide range of animal taxa (Taylor, Woiwod & Perry, 1978).

While the capacity of some moths to fly long distances on migration is well known, the dispersal ability of others has only recently begun to be addressed. Using moths tethered to flight mills, Jones (2014) found that maximum distances flown in a night by 24 of 32 species of British Noctuidae exceeded 1km, five of them surpassing 5km; though these results do not necessarily imply flight behaviour in the wild, or straight-line movements. Perhaps the best current evidence for moth mobility is offered by data on species that make sea crossings. From Clancy (2018; 2019; 2020; 2021) we may adduce that individuals of 70 or more species of larger moths potentially arrive in Britain each year from the continent, a minimum sea crossing of 35km. Longer crossings are achieved by moths arriving in Shetland, which must make a journey of at least 45km from the nearest Orkney island, 130km from the Scottish mainland or 320km from continental Europe. Pennington & Harvey (2022) class 101 of the 166 larger moth species recorded in Shetland (excluding adventives and those of uncertain status) as immigrants or vagrants. These sources together indicate that, of the 537 species selected for our study, at least 121 have the capacity for long-distance flight.

In reviewing empirical studies of dispersal in various animal taxa including Lepidoptera, Baguette & Van Dyck (2007) argued that dispersal is not a species-specific fixed trait but an individual trait that varies both within and among populations. Several other studies support this (e.g. Bowler & Benton, 2005; Stevens, Pavoine & Baguette, 2010; Menz *et al*., 2019). They offer a better explanation of patterns of low frequency and abundance in our study than would an alternative explanation based on species-specific differences in mobility or in strength of response to light sources. If these latter factors were significant, we should expect greater similarity between sites in the species composition of Band 4 in particular than this study found (Table 6). We may note that, of the 37 species placed in Bands 4 and 5 in > 60% of their site occurrences, only four did not occupy a higher frequency band at one or more other sites.

We believe that the data patterns found in this study confirm the suspicions of Blunt, Trueman & Burkmar (2021) that the species composition of site faunas progressively converges with more trapping, and that a key element in this pattern is the trapping of moths that are essentially transient from more distant sources. We also propose that these patterns are inherent properties of light-trapping that hold good for all types of trap and light: this proposal is based on the consistency of some patterns across studies using different trap and light types, but it remains to be confirmed.

If we are right, these data patterns may usefully inform the design and interpretation of light-trapping research and moth distribution maps. In comparisons of faunas caught by different traps and light sources, results are best interpreted in relation to sampling effort, as differences observed in the shorter term may become progressively less so with increased sampling. Shorter trapping programmes – three years using Rothamsted Insect Survey traps – may catch a high proportion of local resident species, with a relatively low (but not negligible) proportion of species that have a weak association with sites (Table 4). In the debate whether species that occur rarely in samples should be included in estimations of site species richness (Matos da Costa & Sielezniew, 2023 and references), our findings suggest that, in the fragmented and highly managed landscapes of Britain, such species offer little to our understanding of site faunas, and their inclusion in richness estimation may bias results. We conservatively estimate that between 12% and 25% of site faunas in this study represent species with very low probability of breeding locally to a site.

Our study findings also offer a means of improving the information conveyed by distribution maps for moths. These use dots as symbols to show points of occurrence. They conventionally follow the model pioneered by Perring & Walters (1962) for the British flora, i.e., dots are of one size and all valid records of a species are mapped. An alternative approach developed for bird distributions by Sharrock (1976) weights symbols according to strength of breeding evidence and excludes records of transients. This allows readers to distinguish relative population densities of mapped species, without the distorting effect of transients. Every plant record is a *de facto* breeding record, but that is not so for mobile taxa; and conventional mapping of Lepidoptera may school readers into viewing maps simply as showing breeding populations. Butterfly atlases for Britain now weight symbols by number of specimens recorded (Asher *et al*., 2001; Butterfly Conservation, 2023). The consistent frequency-abundance relationship found in our study should allow similar mapping of larger moth distributions by either measure to show relative population sizes and breeding densities and exclude likely transience. Given the huge body of data now available for larger moths – 25.6 million records were incorporated into the most recent atlas for Britain (Randle *et al*., 2019) – this approach is both feasible and desirable.

CONCLUSIONS

Programmes that collect statistically robust data at many geographically widespread sites over many years are rare, as the effort needed to sustain them is formidable. The Rothamsted Insect Survey is thus exceptional. Using RIS data we have explored patterns that emerge from standardized trapping of larger moths in the longer term. We have found consistent patterns that imply the existence of inherent properties of light-trapping and help elucidate factors that underlie results. Light-traps sample both resident faunas and casual visitors, and our findings suggest that proportions of the latter are far from negligible. Moths are a highly mobile group of species, many of which show a capacity to disperse over long distances, and the scale of their dispersal as represented by trap samples may be underappreciated.

Our study offers insights that may inform the design and interpretation of other investigations using light-traps, and aid a more informative approach to mapping moth distributions. This study is an initial analysis of data, and further exploration of patterns that emerge from long-term trapping at other sites, with other types of equipment, over a wider range of species, and with more rigorous statistical tests remains to be carried out: we hypothesize that it will broadly confirm the findings of this study. Detailed environmental and management information for areas surrounding traps may offer more insights into the species composition of local faunas, but that information was not directly available for our study. Our research has, however, gathered a large body of data on individual moth species and families, which may throw some light on such matters.

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