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# Bucking the trend: the diversity of Anthropocene 'winners' among British moths

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**Abstract**

An appreciation of how some species are becoming more common despite unprecedented anthropogenic pressures could offer key insights for mitigating the global biodiversity crisis. Research to date has largely focused on declining species, while species that are becoming more common have received relatively little attention. Macro-moths in Great Britain are well-studied and species-rich, making them an ideal group for addressing this knowledge gap. Here, we examine changes in 51 successful species between 1968 and 2016 using 4.5 million occurrence records and a systematic monitoring dataset. We employ 3D graphical analysis to visualise long-term multidimensional trends in prevalence (abundance and range) and use vector autoregression models to test whether past values of local abundance are useful for predicting changes in the extent of occurrence. The responses of Anthropocene winners are heterogeneous, suggesting multiple drivers are responsible. Changes in range and local abundance frequently occur intermittently through time, demonstrating the value of long-term, continuous monitoring. There is significant diversity among the winners themselves, which include widespread generalists, habitat specialists, and recent colonists. We offer brief discussion of possible causal factors and the wider ecosystem implications of these trends.

**Highlights**

- Trends in abundance and occurrence are described for 51 British macro-moths that have become more common, using data from two long-term recording schemes
- We expected to find evidence of range expansion in years following high abundance, but this was supported for only six species
- Nine species showed instantaneous correlation between local abundance and range extent, likely driven by increased detectability in range margins
- Among British moths, successful species ('winners') are ecologically diverse and include habitat specialists
- Changes in abundance and range size seldom occur smoothly, frequently being non-linear and sometimes non-monotonic
- Long-term monitoring of multiple facets of rarity (e.g. abundance, range) is necessary to comprehensively assess changes in prevalence.

**Keywords**

Abundance, biodiversity change, climate change, commonness, insects, Lepidoptera, macro-moths, occupancy, range expansion, successful species

## Introduction

A new geological epoch, the 'Anthropocene', has been proposed in recognition of the vast and varied influences modern humans exert on the planet (Steffen et al. 2007). These anthropogenic changes have profound consequences for biodiversity. It has been estimated that species are being lost at more than one hundred times the natural background rate (Ceballos et al. 2015, De Vos et al. 2015), prompting concerns we are entering the sixth mass extinction event (Barnosky et al. 2011). Global vertebrate populations are estimated to have fallen by 60% over the last five decades (WWF 2018) and there is evidence of population declines across many insect groups (Sánchez-Bayo and Wyckhuys 2019, but see Thomas et al. 2019).

However, biodiversity trends are not universally negative (McGill et al. 2015). Monitoring programmes

tend to reveal mixed fortunes, with some species declining ('losers'), others showing little change, and some species increasing ('winners') (Dornelas et al. 2019). Conservation scientists have understandably focused on declining species, yet, there are reasons why winners deserve consideration. Understanding how some species manage to flourish under conditions that prove detrimental to many others may offer clues for mitigating the drivers and impacts of biodiversity loss. Furthermore, increases and declines of species are happening simultaneously and are unlikely to be completely detached from each other; a better appreciation of increasing species may shed new light on processes such as biotic homogenisation (Godet et al. 2015). Finally, Anthropocene winners are likely to become increasingly important. If current rates of loss continue, the winners may become central to maintaining ecosystem functioning.

In order to consider changes in the commonness/rarity of species, it is useful to disaggregate the components across multiple axes. To this end, Rabinowitz (1981) recognised three distinct gradients in size of range, local abundance, and in habitat breadth, each of which she subdivided into low and high values to generate a framework of seven kinds of rarity alongside an eighth category of commonness (Fig. 1). Over ecological time, it is expected that species that are declining or increasing typically move through this 'prevalence space' predominantly by changing range and/or local abundance. In species status assessments, such as the IUCN Red List procedure, changes in rarity, especially simultaneous changes in geographical range and population densities, are employed to classify species into risk categories (Mace et al. 2008). However, with the notable exception of work on population dynamics in invasive species and on range expansion using bioclimatic envelope models, there has been relatively little attention given to how and why species become more common (Gaston 2011, McGeoch and Latombe 2016).

Moths are evolutionarily and ecologically diverse, making them an ideal group for addressing this knowledge gap. In Great Britain (GB), the dynamic nature of the macro-moth fauna has been well documented during the past half-century by two long-term datasets. The Rothamsted Insect Survey, a standardised network of light-traps, provides detailed information on abundance change for the most frequently caught species (Conrad et al. 2004). These data have revealed that two-thirds of GB's commonest macro-moths have declined since 1968, while 84 of the 334 species examined showed statistically significant positive trends in abundance (Conrad et al. 2006a, Fox et al. 2013). Trends in frequency of occurrence have been produced for 673 species (approximately 80% of GB macro-moths), using the National Moth Recording Scheme, a citizen science project that contains millions of biological records and can offer high-resolution insights into range change (Fox et al. 2011). Between 1970 and 2010, significant declines were detected in the frequency of occurrence (at the 10km x 10km grid square scale) for 260 species, whereas 160 others showed significant positive trends (Fox et al. 2014).

The two long-term datasets covering GB macro-moths allow changes in different components of commonness to be examined. Together they present a unique opportunity to describe and ultimately understand how biological success manifests in a species-rich insect taxon. Here, we examine simultaneous changes in the local abundance and range of 51 macro-moths that have become more common since the late 1960s. In considering the two most plastic properties of rarity, range size and local population size, we ask whether these winners demonstrate shared pathways of success as they move through the multidimensional space of rarity/commonness? Our analyses are intended to

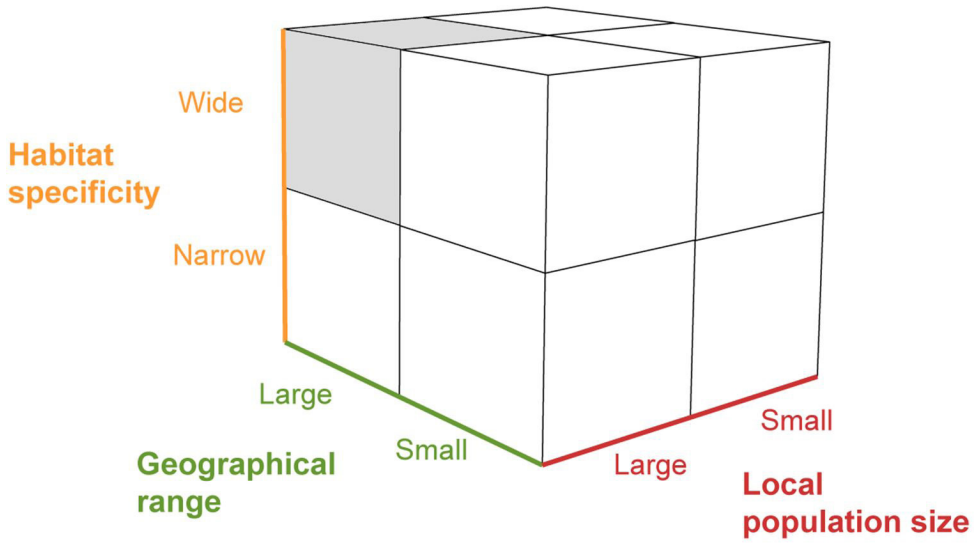


**Figure 1.** Rabinowitz's (1981) rarity typology rendered as a cube. It identifies seven forms of rarity, along with an eighth state showing no traits of rarity (shaded cube), when species are dichotomously classified along three axes.

  

showcase the information return and insights that can be generated from simple graphical analysis inspired by the models of rarity developed initially by Rabinowitz (1981) and to demonstrate the heterogeneity in the response of these successful moth species. We offer a brief assessment of the plausible drivers relating to the third conceptual axis of Rabinowitz's rarity cube, i.e., aspects of the ecological traits of the species concerned.

In order to understand how success manifests in a species-rich insect taxon, we use vector autoregression models to test whether past values of local abundance are useful for predicting subsequent values of range size. Range and local abundance are not expected to be independent (for reviews see Brown 1984, Venier and Fahrig 1998, Gaston et al. 2000). We hypothesise that local mean abundance at time *t* will contain useful information for predicting range size at *t+n*, as elevated local population sizes are expected to result in increased dispersal and thus facilitate the colonisation of novel range (Warren et al. 2001, Mair et al. 2014).

## Methods

### *Long-term datasets*

Two separate datasets covering GB's moths were used to explore changes in commonness. The Rothamsted Insect Survey (RIS) run by Rothamsted Research is one of the longest-running and spatially extensive monitoring programmes for insects anywhere in the world (Harrington and Woiwod 2007). Since the late 1960s, a GB-wide network of standardised light-traps has been operated nightly and all macro-moths caught are identified and counted. The Rothamsted trap is designed to collect small but consistent samples, generating readily comparable data on species abundance (Williams 1948, Conrad et al. 2004). The National Moth Recording Scheme (NMRS) run by Butterfly Conservation has collated 25 million observational records of macro-moths made by citizen scientists (Fox et al. 2011). These opportunistic records date back to the eighteenth century but recording intensity has increased substantially over the past few decades. The period 1968 to 2016 was selected for this study as it offered good coverage across both datasets.

### *Selecting winners*

Successful species were identified using published GB trends for abundance (1968-2007; Fox et al. 2013) and frequency of occurrence (1970-2010; Fox et al. 2014), which had been calculated using RIS and NMRS data respectively. Of the 330 macro-moths that had published trends for both abundance and occupancy, 48 species showed statistically significant increases in both measures. Taxonomic confusion is likely to have led to inconsistent recording of *Ectropis bistortata* (Waring and Townsend, 2017) so this taxon was excluded, leaving 47 species. RIS abundance trends have only been produced for the most frequently caught moths (>500 total individuals captured over the sampling period (Conrad et al. 2004)), which constrains analysis to species in a similar state of commonness. To diversify the winners considered here, species without published abundance trends but with the largest (top 5%) occupancy increases in Fox et al. (2014) were also considered. From these, an additional four species had been caught in sufficient numbers in the RIS, subsequent to the published trends, to enable us to explore abundance changes (exceeding the threshold of 500 individuals captures across the RIS network). The 51 focal species are listed in Appendix S1.

### *Assessing changes in commonness*

Extent of occurrence (EOO) was selected as the range metric as it is relatively insensitive to sampling bias (Fattorini et al. 2013). The R package ConR (Dauby et al. 2017) was used to calculate the area of a convex hull around all points (ocean area excluded). For each species, EOO was calculated for every year using NMRS and RIS data separately; this provided two independent estimates of EOO for each year. Sampling has not been consistent throughout time for either dataset. Funding cuts have reduced the number of RIS traps, whilst the growing popularity of moth recording has led to increased NMRS coverage in recent decades. As the overall sampling extent in the NMRS has increased by roughly the same amount as it has decreased in RIS (Figure S1), the mean of the NMRS and RIS estimates for EOO for each species in a given year was taken.

Local mean abundance (LMA) was calculated as the mean of the total annual count at RIS sites that had caught the species in a given year. The RIS sampling methodology has remained unchanged throughout its history, meaning the scheme offers readily comparable abundance data (Conrad et al. 2004). The traps are emptied daily and are operated throughout the year; however, for some sites, there are gaps in the data. Gaps are liable to affect the annual count, so years were excluded in which the operation of a RIS trap was incomplete (as defined by Conrad et al. (2004)).

To reveal how local abundance and range extent has changed for each winner species, three-dimensional species trajectories were plotted using the package plot3D (Soetaert 2013), with the axes of time (year), LMA, and EOO. Locally weighted regression was employed to smooth LMA and EOO values, using the 'loess' function from the core stats package with smoothing factor, $\alpha = 0.33$ (R Core Team, 2018). To facilitate comparisons between species, the axes on all 3D plots were fixed: x = 0 − 220,000km$^2$; y = 1968 − 2016; z = 0 − 105.

### *Interaction between local abundance and range size*

Vector autoregression (VAR) models were constructed for each species using the R package vars (Pfaff 2008) to investigate the relationship between LMA and EOO through time. In VAR models, the values of one variable are trained with time-lagged values of both itself and historical values of other variables.

For each species, annual values of LMA and EOO were combined to form a 48-year bivariate time series. The optimal lag order (the maximum number of lagged observations to be included in the VAR) was determined

  

using the 'VARselect' function, and the value with the lowest Akaike information criterion (AIC) was selected. All models initially included trend (over time, in years) and intercept regressors; however, the intercept was dropped in the final model of five species as it was non-significant ($p>0.05$), i.e., the range size or local abundance in 1968 was near zero.

All models were tested for serially correlated residuals using an asymptotic portmanteau test. In cases where the null hypothesis of no autocorrelation was rejected (n=3), the lag order was changed (progressively, by the lowest AIC value) and the model retested until the residuals were not serially autocorrelated. The 'roots' function was used to confirm all eigenvalues were <1, indicating the model is stable.

The 'causality' function was applied to each VAR model to test for instantaneous correlations and Granger causality. Wald tests were employed to examine whether instantaneous cross-correlation exists between the two variables. F-type Granger tests were used to determine whether LMA contains unique information for predicting future values of EOO. Where Granger-causality was established, impulse-response analysis was used to determine the direction of this effect. Cumulative impulse-response functions were produced with the vars package, using 1,000 bootstrap replicates, and the direction of the response was noted.

### *Life histories of the winners*

British moths that feed on lichens or coniferous plants tend to show positive abundance trends on average (Conrad et al. 2004). To determine if these larval associations are prevalent among the 51 winners considered here, species were grouped as 'lichen-feeders' or 'conifer-feeders', where applicable, using information from Waring and Townsend (2017). It was noted whether the species is thought to have colonised Britain in recorded history, otherwise, the species was assumed to be a long-term resident.

To assess ecological specialism/generalism, Waring and Townsend (2017) was used to broadly categorise species as either generalist (no overt habitat preference indicated) or specialist (species has a marked preference for one habitat type).

## Results

### *Examples of successful species*

Two of the 51 species considered here colonised southern England during the 20th century. *Eupithecia phoeniceata* (Cypress Pug; Geometridae) and *Lithophane leautieri* (Blair's Shoulder-knot; Noctuidae) became established in the 1950s, but have since shown divergent trajectories, particularly in terms of range change (Fig. 2). *Eupithecia phoeniceata* has remained largely confined to southern England, whilst *L. leautieri* has spread widely throughout England and Wales, recently reaching Scotland. Both species have shown only slight increases in local abundance.

The majority of the successful moths are not recent colonists. *Deltote pygarga* (Marbled White Spot; Noctuidae) and *Apamea scolopacina* (Slender Brindle; Noctuidae) are habitat specialists. The former is largely restricted to damp habitats on acidic soils, and the latter is strongly associated with woodland. *Deltote pygarga* has predominately 'filled-in' the area around its historic range, with some northward

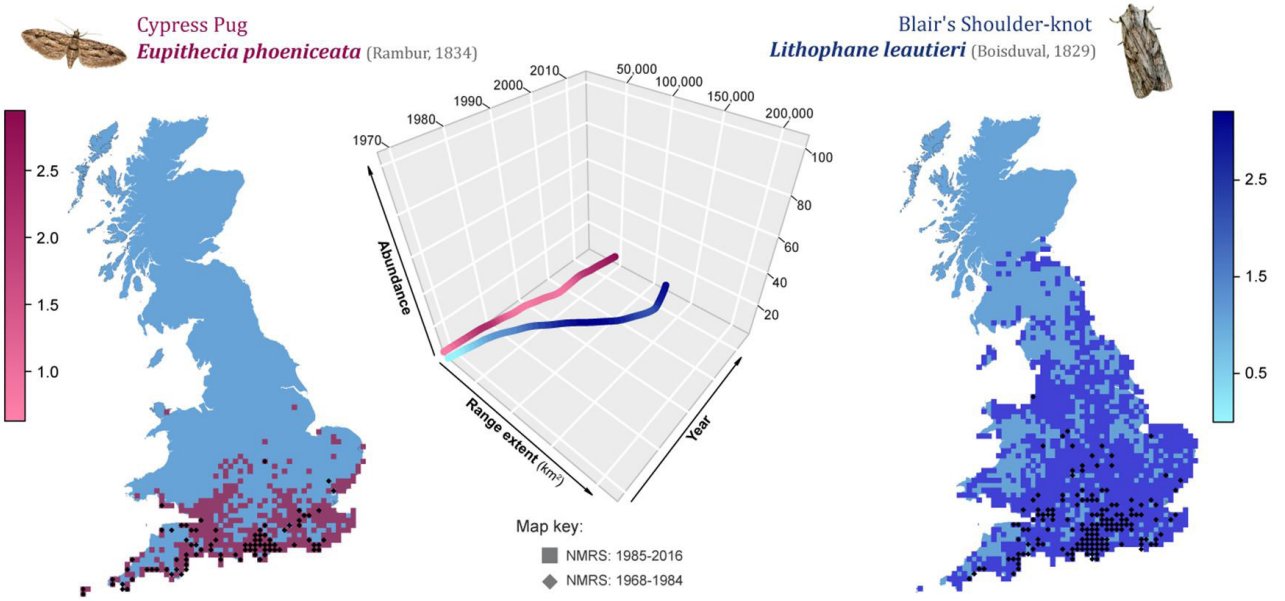


**Figure 2.** Changes in the commonness of two macro-moths that colonised GB in the 1950s. Maps show NMRS 10km$^2$ occurrence of each species, with the historic distribution (<1985) shown with black diamonds. Darker colours in the 3D trajectories illustrate periods of higher local mean abundance, as shown on the vertical scale bars. The abundance axis on the 3D trajectories represents annual local mean abundance, derived from RIS data; the range axis is the extent of occupancy (the mean of the RIS and NMRS estimates).

  

movement. *Apamea scolopacina* has shown pronounced northward expansion, extending its northern range margin several hundred kilometres into Scotland. Both species have undergone large increases in local abundance, particularly in recent years (Fig. 3).

Many of the species already occupied a large portion of GB at the beginning of the study period, meaning they have little opportunity for range expansion. These moths largely showed change along the abundance axis. Annual counts of *Colostygia pectinataria* (Green Carpet; Geometridae) have steadily grown since the 1960s. In contrast, population changes in *Omphaloscelis lunosa* (Lunar Underwing; Noctuidae) have been more irregular, displaying boom and bust cycles (Fig 4).

## *Diverse pathways of success*

The species trajectories differ greatly in magnitude, direction, and form (Fig. 5). Twenty-one species increased their range extent by more than 100% during

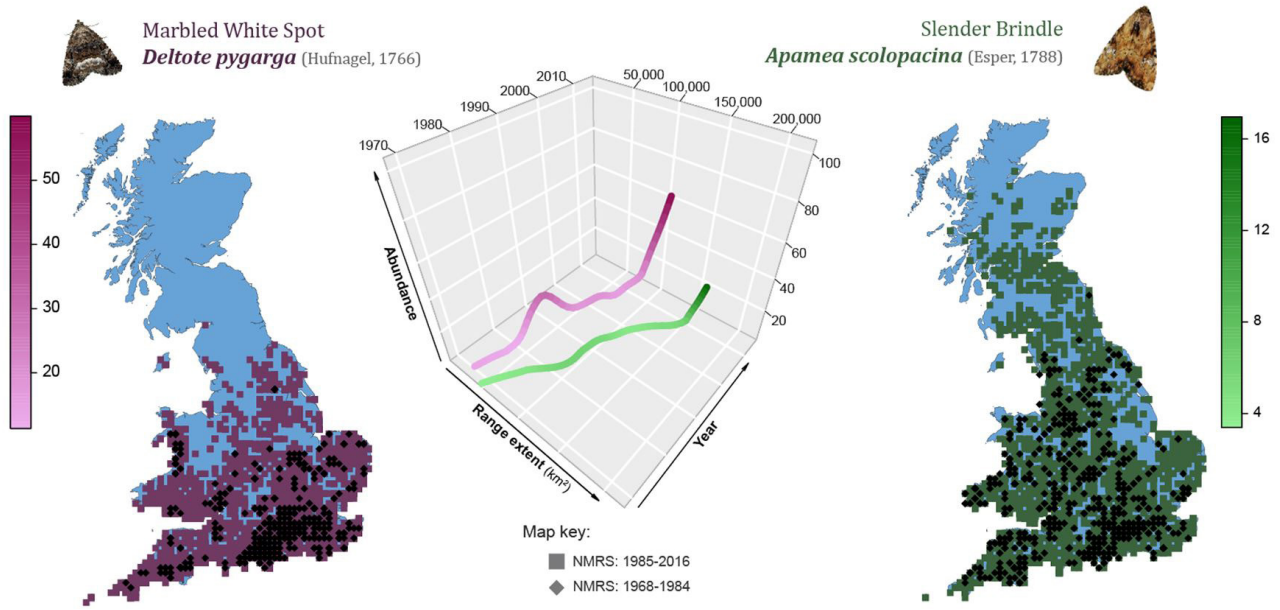


**Figure 3.** Changes in the commonness of two successful macro-moths that have specialist habitat associations. Maps show NMRS 10km$^2$ occurrence of each species, with the historic distribution (<1985) shown with black diamonds. Darker colours in the 3D trajectories illustrate periods of higher local mean abundance, as shown on the vertical scale bars.

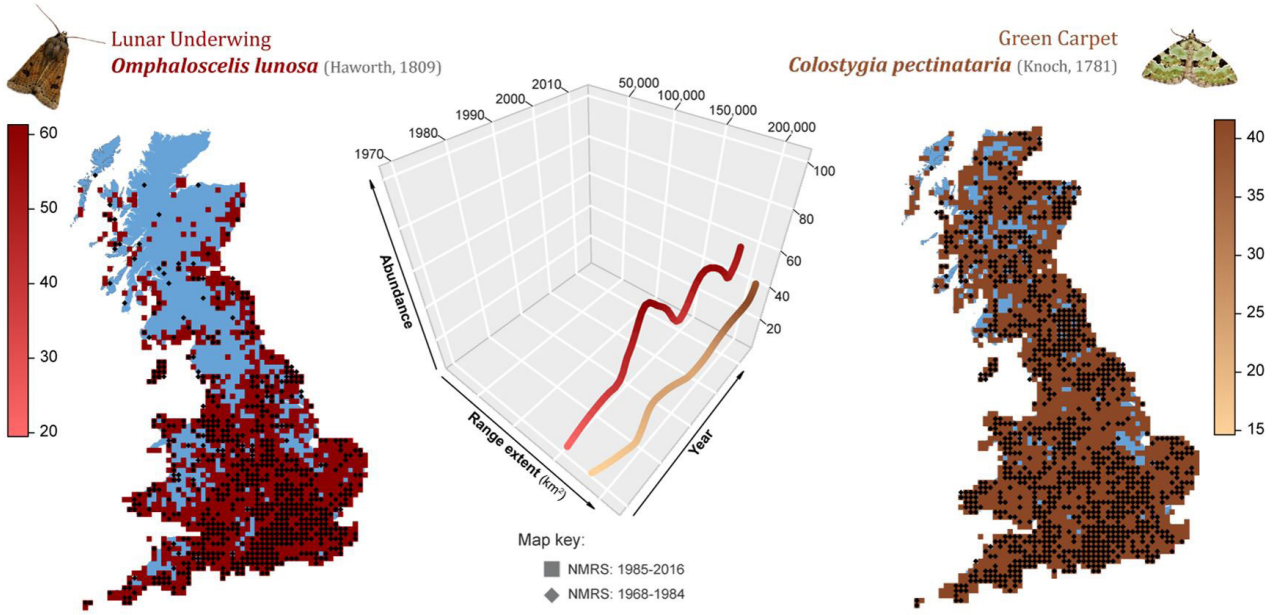


**Figure 4.** Long-term changes in the commonness of two widespread macro-moths. Maps show NMRS 10km$^2$ occurrence of each species, with the historic distribution (<1985) shown with black diamonds. Darker colours in the 3D trajectories illustrate periods of higher local mean abundance, as shown on the vertical scale bars.

  

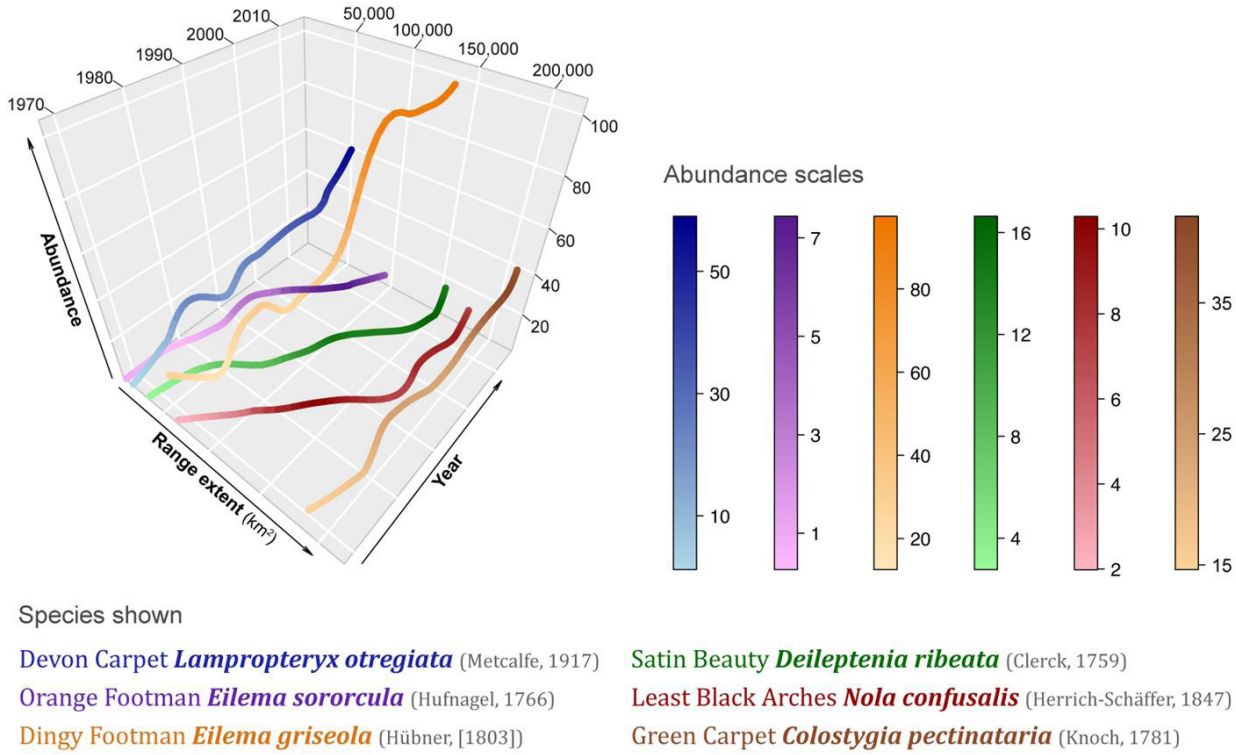


**Figure 5.** A selection of six species paths to illustrate the diversity of trends in the local abundance and extent of occurrence for successful GB moths over the last 48 years.

the 48-year period. This was typically accompanied by increases in local abundance (for instance, *Eilema griseola*, *Deileptenia ribeata*, and *Nola confusalis*, shown in Fig 5). Other species underwent significant increases in local abundance with only modest changes in range size (e.g. *Colostygia pectinataria*).

### *Relationships between LMA and EOO in successful moths*

Annual LMA contained useful information for predicting future values of EOO in seven out of the 51 species (i.e., LMA 'Granger-causes' EOO). Impulse-response analysis indicated the direction of this effect was positive in six of these cases (i.e., an increase in local abundance tends to be followed range expansion) and negative in the remaining one. The median lag order for the significant results was three years (range: 1–5) (Appendix S3 contains the lag order and variables included for each VAR, along with the test statistic, degrees of freedom, and p-values). Instantaneous correlation was found in yearly values of LMA and EOO for nine species.

### *Life histories of the winners*

Six of the species use coniferous plants as a larval resource and six are lichenophagous. Two species colonised GB during the 20th century, while a third became established in the 19th century.

The majority (42/51) of the winners are broadly habitat generalists. Seven species have a strong habitat preference for broadleaved woodland, one is found predominantly in coniferous woodlands, and one favours damp habitats on acidic soils (for traits of all species see Appendix S1).

## Discussion

We used existing GB trends for macro-moths to select 51 winners and examine concurrent changes in their local abundance and range extent over the last five decades. The 3D plots reveal that changes in local abundance and range rarely proceed smoothly through time and are frequently non-linear and sometimes non-monotonic (Appendix S2). Species can undergo large increases over a few years before remaining relatively stable for long periods, or even enter a period of decline. This emphasises the need for continual monitoring of species and cautions against assessing success simplistically, using single components of rarity/commonness over short periods.

In addition to the diversity of responses shown, the species themselves are heterogeneous in terms of their natural history. This is consistent with a recent trait-trend analysis that largely failed to predict winners among GB macro-moths using a wide range of life history traits (Coulthard et al. 2019). The winners considered in this study include ubiquitous ecological

  

generalists, formerly restricted habitat specialists, and newly established colonists.

### *Why are these species becoming more common?*

Life history traits, including those relating to habitat specificity, the third axis of Rabinowitz's typology, are commonly used to try to explain inter-specific variation in population trends. For British moths, there is little evidence at present to support the common assumption that losers are specialists and winners are generalists (Conrad et al. 2004, Fox et al. 2014, Coulthard et al. 2019).

Ten of the winners examined here are specialists: one is restricted to areas with acidic soils and nine have a strong association with woodland. However, the majority of the winners examined here are broadly habitat generalists, in that they feed on multiple larval hostplants and across multiple habitat types (Waring and Townsend 2017). This may be partly because species that occur across a wide range of habitats are more likely to be caught in sufficient numbers across the RIS network to permit robust examination of abundance trends, and hence to be included in the present analysis. The requirement for mains electricity and daily visits by a volunteer may bias the scheme's sampling towards more human-influenced areas, and thus more generalist species. Most RIS traps are near private dwellings, universities, field centres, and farms (Taylor 1974). Of the macro-moths with both RIS and NMRS trends, 78% (259/330) show no overt habitat preference. This level of generalism is broadly comparable with the subset of winners examined here (42/51; 82%).

While trait-trend analyses for British moths have typically had little success in identifying traits associated with winners, the broad class of larval hostplant is thought to be significant for explaining the success of certain British moths, namely those with lichenophagous and coniferophagous larvae. These groups tend to display more positive abundance trends (Conrad et al. 2004) and are thought to be responding to increased hostplant availability, due to improvements in air quality (Pescott et al. 2015) and the expansion of coniferous forestry plantations respectively. Some conifer feeders have also benefited from the widespread cultivation of ornamental conifers in gardens (Agassiz 2004). However, these associations only have the potential to contribute to the success of ten of the 51 species considered here, as the majority do not feed on lichens or conifers (Fig. 6).

In Table 1 we offer hypotheses to explain the diversity of trends in British macro-moths that have become more prevalent over the last five decades. Climate change is likely to be involved in the trends of many of the 51 species considered here. Northward shifts in the range margin of British macro-moths are consistent with warming temperatures (Mason et al. 2015), and moths with more southerly European distributions tend to display the strongest population increases in GB (Morecroft et al. 2009). It remains unclear why only some species appear to be responding positively to climatic warming (MacLean and Beissinger 2017).

The range expansion of two well-studied species of British butterfly, *Aricia agestis* (Brown Argus) and *Polygonia c-album* (Comma), has been linked to warming temperatures, which have mediated shifts to more widespread larval foodplants in both cases (Braschler and Hill, 2007, Pateman et al. 2012). Trophic rewiring facilitated by climate change has been reported for a range of taxa globally (Bartley et al. 2019). It remains to be seen if this is a frequent cause of increases in range and/or abundance among British Lepidoptera. It is likely that multiple and sometimes conflicting drivers are at work in driving changes in the rarity/commonness of Lepidoptera in Britain (Table 1; Warren et al. 2001, Fox et al. 2014, Mair et al. 2014).

It is worth emphasising that climate change is also predicted to have negative impacts on some British Lepidoptera. Moreover, there is evidence climate change is implicated in the population declines of some British moths (Conrad et al. 2002, Fox et al. 2014, Martay et al. 2017).

### *Interactions between LMA and EOO over time*

In line with our prediction, we found that LMA 'Granger-causes' EOO in some successful GB moths. That is to say, the predictive power for EOO was improved when lagged values of LMA were included

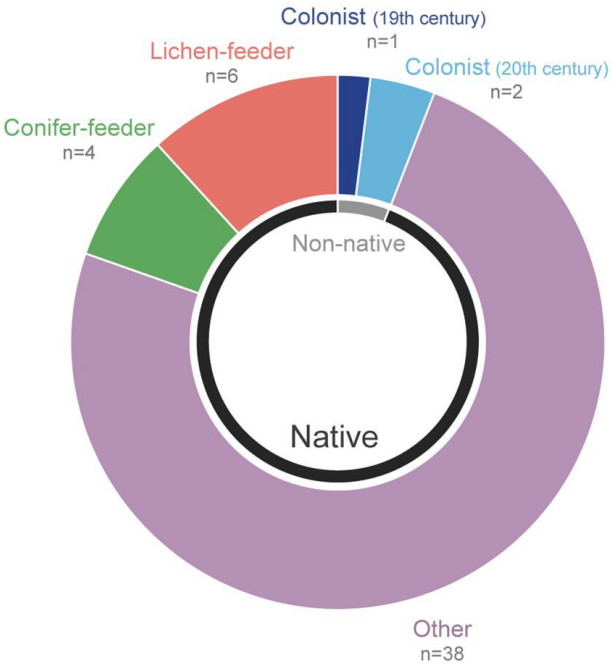


**Figure 6.** Hostplant associations of the 51 species of successful British moths examined in this study. Only ten are associated with lichens or conifers; both these resources are now more widely available in the GB countryside, which may have contributed to the positive trends shown by these moths. Three of the 51 species are recent colonists which explains their positive trends. Two species are both a recent colonist and a conifer feeder, which were classified as a colonist for the purpose of this figure. The groupings are given in Appendix S1.

  

**Table 1:** Contributory hypotheses that may help explain the diversity of positive trends observed in British moths.

| Proposed cause | Description | Supporting evidence and counterevidence |
|---|---|---|
| 'Background' biodiversity change | Observed trends may not represent recent responses to anthropogenic factors but rather a continuation of trajectories that began thousands of years ago and are dictated predominately by evolutionary history. | • The fossil record shows ecological communities are rarely static (Jablonski & Sepkoski 1996, Liow & Stenseth 2007). |
| Conservation and policy action | There is significant expenditure on conservation in GB, including direct habitat management for threatened species and agri-environment schemes for more widespread species. | • There are numerous examples of British moths responding positively to conservation interventions (Ellis et al. 2012); however, bespoke management is typically reserved for only the most threatened species.<br>• European agri-environment schemes are usually considered to have delivered little for biodiversity (Pe'er et al. 2014, Batáry et al. 2015); although there is evidence, they have the potential to benefit moth populations (Fuentes-Montemayor et al. 2011, Alison et al. 2017).<br>• Improvements in air quality since industrial times have increased the abundance of certain lichens, and consequently, some lichenophagous moths (Pescott et al. 2015). |
| Habitat change and novel ecosystems | Modern agricultural practices are thought to be a major driver of British moth declines (Fox 2013), but these shifts may also represent an opportunity for some species. For instance, the widespread application of fertiliser may be beneficial to moths that feed on nitrophilous plants. Humans have also created novel habitats, such as forestry plantations and urban areas, which can be successfully exploited by some species. | • Moths favouring plants associated with high levels of nitrogen tend to show more positive trends (Betzholtz et al. 2013, Fox et al. 2014); however, nitrogen enrichment has been shown to increase larval mortality in some common lepidopterans (Kurze et al. 2018).<br>• The expansion of commercial forestry plantations is thought to have offered a significant opportunity to conifer-feeding moths (Conrad et al. 2004). |
| Climate change | Climate change may be providing increasingly favourable conditions for some species, enabling range expansion and facilitating larger population sizes. | • An assessment of 422 British moths showed climate change represented an opportunity for more species than it posed a risk to, in terms of potential range change (Pearce-Higgins et al. 2017).<br>• Recent range expansions in British moths are consistent with expectations from warming temperatures (Mason et al. 2015).<br>• Moths with southerly European distributions appear to show larger population increases in Britain (Morecroft et al. 2009, Fox et al. 2014).<br>• Climate change is enabling some moths to produce additional generations each year (Altermatt 2010); although the implications of this on fitness are not well understood. |

  

**Table 1:** Continued...

| Proposed cause | Description | Supporting evidence and counterevidence |
|---|---|---|
| Colonisation of novel genotypes | Warming temperatures in southern Europe are thought to be driving increases in both the abundance and diversity of migrant moths into GB (Sparks et al. 2007, Fox et al. 2013). These influxes are likely to contain cryptic diversity of resident species. Continental strains could be better adapted to contemporary conditions or give rise to hybrid vigour. | • The number of new moths arriving in Britain each year is rising (Fox et al. 2013). Novel intra-specific diversity is also expected to be reaching the UK.<br>• There is consistent variation in the colour forms of *Sphinx pinastri* (Pine Hawk-moth) across its range. Forms originating from central Europe colonised England's South Coast during the 20$^{th}$ century and rapidly displaced resident strains, as well as expanding into novel range (Pratt 2002). |
| Evolutionary adaptation | Anthropogenic pressures represent extreme selective forces. The short generation time of insects means some species may be able to develop effective adaptations. | • Evolutionary changes related to dispersal ability are commonly observed in range-expanding insects (Hill et al. 2011); however, the proximal cause of these range shifts is typically climate change.<br>• Genetic changes in the butterfly *Aricia agestis* have facilitated a switch to a more widespread larval hostplant (Buckley et al. 2012, Bridle et al. 2014). |
| Network disruption | The positive trends in some winners could be causally linked to negative trends in losers; for instance, a species may become more abundant after the loss of a competitor or natural enemy. | • Enemy release from parasitoids has been demonstrated to accelerate range expansion in *A. agestis* (Menéndez et al. 2008). |

in the VAR (compared to predictions made using past values of EOO alone). This effect was positive in six out of seven cases, which suggests that favourable years with high local abundance tend to be followed by range expansion in subsequent years. This is consistent with studies looking at British butterflies (Warren et al. 2001, Mair et al. 2014), and may offer potential to predict future range expansion based on years with high local abundance. One mechanism that may explain this effect is metapopulation theory (Hanski 1998) which states larger populations have more emigration and thus, increased colonisation of new patches (Gaston et al. 1997).

However, this expected effect was only detected for six of the 51 winners, suggesting that increased local population size may not be a universal signature for future range expansion. A recent study by Dennis et al. (2019) found macro-moth trends for abundance and occupancy in Scotland were not closely correlated, with some species having positive occupancy trends but negative abundance trends over the same period.

The association between local abundance and range size may have been obscured in this study due to the coarse range metric used. Just as rates of decline can be greatly underestimated if measured at coarse spatial resolution (Thomas and Abery 1995), so local range expansion may be undetected and, therefore, appear decoupled from population-level change. Finer scale range metrics (e.g., area of occupancy) are expected to be more closely associated with abundance (Gaston and Fuller 2009). Furthermore, recording coverage in both the NMRS and RIS dataset are geographically incomplete, so the current range of species may not be fully captured. Scarce but expanding moth species can have low probabilities of detection, even in parts of Britain with high human population density (Pocock et al. 2017), and even common moths may be under-recorded in sparsely populated areas. Aside from these detection issues, there are also ecological factors that may weaken the relationship between abundance and occupancy change. Habitat specialists tend to occupy only a small proportion of the local landscape (Cowley et al. 1999) and there may be no suitable habitat available for colonisation within the dispersal range of the species (Warren et al. 2001). Habitat fragmentation may also reduce colonisation rates relative to population growth (Wilson et al. 2009, Hill et al. 2001).

Instantaneous correlation between LMA and EOO was observed in nine species. This most likely reflects enhanced detectability at the range margins during favourable years when the species experience larger population sizes.

  

### *Caveats and limitations*

The variety of Anthropocene winners among GB macro-moths detailed here is not comprehensive. The Rothamsted light-trap (Williams 1948) is designed to catch relatively small samples sizes, which restricts meaningful analysis to the most frequently caught species. Since the 1900s, over 40 macro-moths have become newly established in Britain (Parsons 2003, 2010); however, only two of these had accumulated sufficient RIS captures to be included here. Formerly scarce residents that have increased but remain relatively uncommon may be overlooked for the same reason. Also, moths that are not caught in RIS traps (e.g., because they are diurnal or only weakly attracted to light) could not be included in this study.

Abundance change was calculated using combined annual totals across all sites. Ideally, abundance trends should be calculated individually for each site (Buckland et al. 2017) as this reduces confounding variables and prevents potential bias arising from site turnover. However, site turnover has been shown to not represent a major source of bias in the RIS dataset (Conrad et al. 2004). The range metric used in our analysis, EOO, is relatively insensitive to sampling bias (Fattorini et al. 2013). Uneven sampling has occurred throughout time in both the RIS and NMRS datasets. While this was not formally addressed, the mean EOO estimate was taken on the grounds that the extent of sampling in the NMRS has increased by approximately as much as it has fallen in the RIS (Figure S1).

A number of the moths considered here already occurred across a large portion of GB at the beginning of the data series (e.g., Fig 4). These species had relatively little opportunity for range expansion at the coarse scale assessed by EOO, and thus their responses along the range axis were constrained. The trajectories of these species may have taken a different form had there been more land area for these species to expand into, or if a finer-scale range metric was examined. Additionally, GB represents only a small part of the global range of most of its moths. For most other countries in Europe (particularly southern Europe), there is insufficient data to assess changes in the prevalence of moths. Species may be faring badly in other parts of their global range; thus, the success of the winners documented here might be relatively localised.

### *Winners take all?*

The process of natural selection means that life on Earth is ultimately shaped by successful species. In GB, more species of common macro-moth are declining than are increasing, and the total number of individuals caught in RIS light-traps fell by 28% between 1968 and 2007 (Fox et al. 2013). Such declines are expected to correspond to a fall in ecosystem functions carried out by moths, including pollination (Macgregor et al. 2015), and the provision of food for other taxa (e.g. Denerley et al. 2019).

An extensive body of literature on biodiversity–ecosystem function relationships suggests that a large number of species are required for healthy functioning ecosystems (Balvanera et al. 2006; Tilman et al. 2014; but see, Kleijn et al. 2015), particularly in the longer term (Oliver et al. 2015). Thus, the increasing dominance of a minority of winners may only temporarily help to mitigate the consequences of the declines in other species.

Anthropocene winners are sometimes regarded as 'pests', 'weeds', or otherwise causing damage. Of the 51 species considered in this study, one winner can be a pest of commercial forestry. *Panolis flammea* (Pine Beauty) is indigenous but can inflict significant damage in monocultures of the exotic conifer *Pinus contorta* (Lodgepole Pine) (Hicks et al. 2008). We are not aware of other evidence that this group of winners cause economic or ecological harm; however, the possibility of undocumented negative effects cannot be excluded.

As the 3D trajectories show, trends in commonness of these insects over the last five decades have not been consistent (Figures 2-5; Appendix S2). Some species show clear breakpoints, where the rate of change increases or decreases significantly. There are also some examples of apparent trend reversal, which may imply success is a transient state; it may be that some of these species will only be winners for a relatively short period of ecological time.

### *Future directions*

Trait-based approaches have had limited success in explaining the diversity of species responses to anthropogenic change (Bartomeus et al. 2018, Estrada et al. 2018). This may be partly due to the quality of trait data available. The identification of 'successful traits' may also be hindered by their plasticity. Habitat preference is not necessarily static (Oliver et al. 2009, Barnagaud et al. 2011) and significant changes may have occurred in winners, perhaps mediated through cryptic processes such as genetic change (Table 1). Unlike the other axes in Rabinowitz's (1981) framework, temporal variation in habitat specificity is not readily quantified. However, statistical modelling approaches can be used to quantify habitat preference, using existing opportunistic occurrence records and land use data (e.g., Redhead et al. 2016, Chetcuti et al. 2019), which may offer the potential to identify shifts in habitat use. In addition, more sophisticated spatial analyses are needed to improve understanding of the spatial dependency of changes in abundance and range (e.g., Conrad et al., 2006b).

More broadly, work is needed to better understand the effects of increasing species on ecosystems as a whole. Disruptive effects are likely to be inevitable, but so too are positive effects. There is a need to critically and pragmatically examine the delivery of ecosystem services in the Anthropocene, including assessing the ability of winners to mitigate the consequences of wider biodiversity declines.

## Conclusions

Biodiversity trends are not universally negative. Declines only tell part of the story of contemporary biodiversity change. Some species are not only persisting

  

in the face of unprecedented anthropogenic pressure but appear to be thriving. Whilst it is important these positive trends are framed within the wider context, such species should not be ignored.

Here, we have demonstrated significant variation in the responses of 'Anthropocene winners' among 51 British moth species, using a multidimensional framework of rarity. The 3D plots demonstrate how increases in local abundance and range are typically intermittent and non-linear, calling attention to the importance of long-term monitoring of increasing species. We highlight the value of simple graphical analyses in visual assessments of species trends and as an effective communication tool for wider audiences, such as the citizen scientists that contribute to recording schemes.

The heterogeneity of the responses shown by winners suggests that multiple drivers may be involved (Table 1). These drivers are poorly understood, although changing climatic conditions are likely to have contributed to the positive trends in many of these moths. Moreover, it is not clear why these species, and not others, have responded positively. The search for ecological traits associated with winners is an obvious topic for future investigation, but the influence of hidden processes, such as evolutionary adaptation, should also be considered.

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**Author contributions:** DHB conceived the study and conducted the analysis, which builds upon work carried out when a student on the MSc Biodiversity, Conservation and Management course, University of Oxford. All authors contributed to writing the manuscript.

## Supplementary Materials

The following materials are available as part of the online article from https://escholarship.org/uc/fb

**Figure S1.** Temporal variation in the extent of area sampled by the NMRS and RIS (1968-2016).

**Appendix S1.** Information on the 51 winner species.

**Appendix S2.** Individual 3D trajectories for all 51 winner species.

**Appendix S3.** Vector autoregression model details and results.

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