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Ecological traits predict population changes in moths

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ABSTRACT

Understanding the ecological traits which predispose species to local or global extinction allows for more effective pre-emptive conservation management interventions. Insect population declines are a major facet of the global biodiversity crisis, yet even in Europe they remain poorly understood. Here we identify traits linked to population trends in 'common and widespread' UK moths. Population trend data from the Rothamsted Research Insect Survey spanning 40 years was subject to classification and regression models to identify common traits among species experiencing a significant change in occurrence. Our final model had an accuracy of 76% and managed to predict declining species on 90% of occasions, but was less successful with increasing species. By far the most powerful predictor associated for declines was moth wingspan with large species declining more frequently. Preference for woody or herbaceous larval food sources, nocturnal photoperiod activity, and richness of habitats occupied also proved to be significantly associated with decline. Our results suggest that ecological traits can be reliably used to predict declines in moths, and that this model could be used for Data Deficient species, of which there are many.

1. Introduction

Monitoring suggests significant global losses in biodiversity, leading to the consensus that we are experiencing a crisis comparable to that of a mass extinction event (Biesmeijer et al., 2006; Butchart et al., 2010; Pimm et al., 2014; Pimm and Raven, 2000; Potts et al., 2010; Worm et al., 2006). Biodiversity assessment and monitoring are recognised as important tools to inform conservation management (Noss, 1990). Such monitoring is critical to assess the status of a range of taxa, to predict population trends and thus inform effective management strategies (IUCN, 2012; McGeoch et al., 2010). There are, however, significant challenges in attempting to measure total biodiversity, including time, financial constraints and expertise (Myers et al., 2000; Pimm et al., 2014). One solution is to monitor taxa which are correlated with habitat health and overall ecosystem function (Carignan and Villard, 2002; Niemi and Mcdonald, 2004), to evaluate expected stability or change in order to proactively manage it (Caro and O'Doherty, 1999; Lindenmayer and Likens, 2011). Taxa championed as particularly valuable biological indicators include bats (Jones et al., 2009), amphibians (Heyer et al., 2014), birds (Blair, 1999), and, particularly, terrestrial invertebrates due to their high relative abundance and diversity (Hilty and Merenlender, 2000; McGeoch, 1998). Arthropods are generally cost effective, informative bioindicators of ecosystem health (Hilty and Merenlender, 2000), which have direct value as providers of ecosystem services (Lavelle et al., 2006; Losey and Vaughan, 2006), specifically the pollination of around 87% of flowering plant species globally (Ollerton et al., 2011). Despite their importance, alarming data from a 2017 study suggested that the biomass of flying insects had declined by over 75% in protected areas across Germany in 27 years (Hallmann et al., 2017).

While many arthropod taxa are of specific conservation concern (e.g., bumblebees, butterflies and dragonflies; Clausnitzer et al., 2009; Goulson et al., 2008; Smart et al., 2000), the Lepidoptera are particularly interesting due to their service as pollinators and sensitivity to changes in ecosystem health and function (Merckx et al., 2013; Ricketts et al., 2002; Thomas, 2005). There is evidence that Lepidoptera, particularly moths, are experiencing long-term declines (Forsman et al., 2016; Fox, 2013; Franzén and Johannesson, 2007; Groenendijk and Ellis, 2011; Valtonen et al., 2017). For example, Fox et al. (2013) provide evidence that moth abundance declined by 28% across the UK. Similar long-term data analysis from Hungary has shown significant declines in both species richness and beta diversity (Valtonen et al., 2017). In Sweden, analysis suggests that species are shifting in terms of their latitudinal range (Forsman et al., 2016), and many species have gone extinct since the 1950s (Franzén and Johannesson, 2007). Possibly the worst picture in terms of losses comes from the Netherlands where

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Table 1
Review of literature surrounding ecological traits and distribution changes, population trends, and extinction risk in Lepidoptera.

Authors, Date	Location	Taxa	Key findings
Ekroos et al., 2010	Finland	Butterflies	Increasing abundance in generalists and higher dispersal species linked with increased agricultural intensity.
Forsman et al., 2016	Sweden	Macro-moths	Species with increased variation in colour patterns associated with larger range, particularly northwards. Species overwintering as a pupa had slower northern range expansion than others.
Franzén and Johannesson, 2007	Sweden	Macro-lepidoptera	Diurnal species had declined more than nocturnal species. Larval specificity, shorter flight periods and open habitat species associated with extinction risk. Species feeding on herbs or grasses were also more likely to have gone extinct. Wetland and dry grassland species more likely to be extinct.
Hunter et al., 2014	Finnish Lapland	Macro-moths	Majority of species found to be stable or increasing in terms of their abundance, but abundance not found to be positively associated with climate change. Life-history traits were also not linked to population changes. Non-vascular plant feeders were negatively associated with climate change.
Mattila et al., 2009	Finland	Noctuid moths	Larval specificity linked to extinction risk. Host plant type was also important, with herbaceous feeders declining most significantly. Different guilds had differing success in terms of other traits i.e. tree feeders had more success when overwintering as an egg.
Mattila et al., 2008	Finland	Geometrid moths	Larval specificity, overwintering form and flight period predicted both distribution change and extinction risk. Body size linked to larval specificity in predictions. For larval specialists, host plant distributions predicted extinction risk.
Mattila et al., 2006	Finland	Noctuid moths	No one trait predicted extinction; however extinction risk could be predicted by combinations of traits.
Merckx et al., 2018	Belgium	Macro-moths	Larger and therefore more mobile moth species and individuals were selected for at the community level with increasing urbanisation.
Potocký et al., 2018	Central Europe	Macro-moths	Habitat preferences and voltinism were found to be the best predictors of population status, with woodland species more likely to be more common than others, and larger, multi-voltine species more likely to be common.
Pöyry, J. et al., 2016	Europe	Lepidoptera	Increased nitrogen linked to larger body sizes and the number of generations per year, suggesting that nitrogen deposition will have a positive impact on species dispersal and reproductive success.
Slade et al., 2013	UK	Macro-moths	Forest moths generally had lower dispersal abilities, with large, mobile forest species at higher risk of extinction from forest habitat fragmentation. Phylogeny was independent of ecological traits.
Valtonen et al., 2017	Central Europe	Macro-moths	Rapid species losses across central Europe, with increasing homogenisation of communities. Species with limited ranges, specialist diets or from dry grasslands were associated with extinction risk.
van Langevelde et al., 2011	Netherlands	Macro-moths	Nocturnal moths more likely to be declining, likely due to increased artificial lighting use at night, and its effects on species attracted to light.
Végvári et al., 2015	Europe	Noctuid moths	Changes in emergence linked to larval food preferences and hibernation strategies, with species feeding on woody plants, and overwintering as adults more likely to have shifted their emergence dates significantly.
Öckinger et al., 2010	Global	Lepidoptera	Reduced mobility, feeding specialism and low reproductive rates all contributed to the effects of habitat loss on species richness.

data shows that 70% of species recorded have declined in abundance, and around one third of species has declined so severely that they can be considered threatened (Groenendijk and Ellis, 2011). While it is suggested that possible drivers include climate change, habitat loss, agricultural intensification and pollution (Altermatt, 2010; Fox, 2013; Pöyry et al., 2017), studies into the ecological determinants which drive population trends are conflicting. A meta-analysis of Lepidoptera research did reveal that a range of ecological traits are linked to the effect which habitat loss plays on species richness (Öckinger et al., 2010).

One approach to understanding biodiversity declines and changes in distributions is to identify ecological and morphological traits associated with trends in monitoring data. This approach has been used in both moths and butterflies, with mixed success (Table 1). A search of the literature found that the most common traits linked with population or distribution change, and extinction risk were larval specificity (species which feed only on very few plant species), size, photoperiod activity (nocturnal, diurnal or crepuscular) and habitat preferences, but that the relationships were complicated, inter-linked and sometimes conflicting.

Here, we use long-term monitoring data and ecological trait information to investigate moth declines using a predictive framework. We collated and analysed data on ecological characteristics of individual species linked with population decline in moths, such as habitat preferences, larval food requirements, temporal activity, wingspan (a proxy for body size [see Mattila et al., 2006, 2008]), and seasonality (see Mattila et al., 2006, 2008). We also evaluated other potential drivers including habitat specialism, overwintering behaviour and voltinism (number of broods per year, Altermatt, 2010; Broome et al., 2011; Valtonen et al., 2011). Our aim was to investigate the utility of ecological indicator traits in predicting population trends in individual taxa, with specific objectives to: 1) identify key factors associated with long-term change in species incidence, 2) develop a predictive machine-learning model of future trends in species incidence, and 3) test the predictive model with observed trend categories.

2. Methods

Our moth population data came from the Rothamsted Insect Survey, a long-term study of insect abundance and diversity conducted across the UK (Fox et al., 2013; Storkey et al., 2016). Under this scheme moths are surveyed using light traps at 430 sites, and the data includes 337 'macro-moth' species (Fox et al., 2013; Conrad et al., 2006) monitored between 1974 and 2014 consisting of a total of 541,042 records. The data represent nine Lepidoptera families and 31 sub-families, from species which were trapped regularly enough across the country to allow for the analysis of abundance and occurrence through the duration of the study period (see criteria set out in Conrad et al., 2006), and so are all classed as 'common and widespread' species.

Ecological traits for all moth species were collated from a variety of sources detailed in Table 1, including field guides and websites (regional and national moth websites populated by experts). Data were collated for wingspan (as a proxy for body size: see Mattila et al., 2006, 2008 and Merckx et al., 2018), photoperiod activity (i.e. nocturnal/diurnal), larval and adult food source (i.e. herbaceous, woody etc.), habitat preferences, flight season, voltinism and overwintering behaviour.

The national population change for species in our dataset was estimated by using TRIM analysis (TRends and Indices for Monitoring data) and included data from a 40-year period (see Conrad et al., 2004 and Fox et al., 2013 for a detailed account of original data analysis used to create the population trend data used in this paper). TRIM analysis takes into account issues with observer bias and missing data in large,

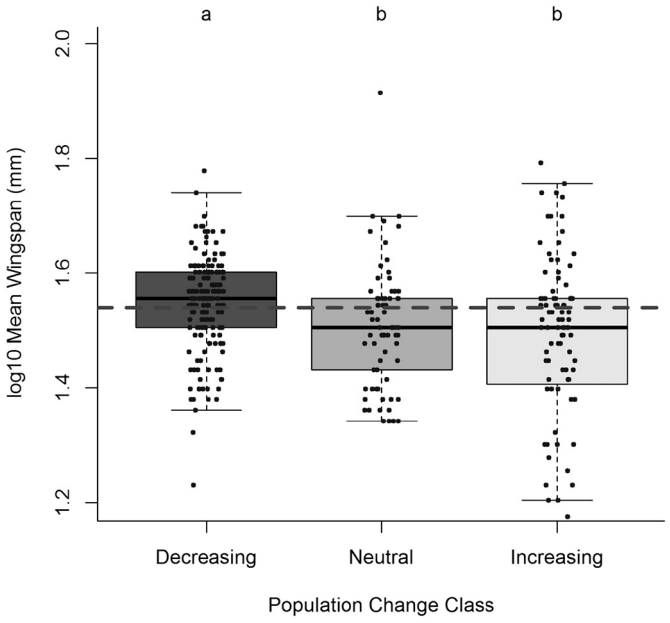

Fig. 1. Mean wingspan (log10) across the three population change classes (Declining, Increasing, Stable) (Results of the Wilcoxon test are presented; means that share a superscript [a/b] do not differ significantly). Grey dashed line is the log10 mean wingspan from the three groups pooled.

ecological datasets (Pannekoek and Strien, 2005). Detailed analysis of population trends and range shifts for particular species has previously been carried out (Fox et al., 2013), and is therefore not discussed here. Population classes of 'Decreasing', 'Increasing' and 'Stable' were created from the trend data using the thresholds of +/− 10%, 20%, 25% and 30% change (over the 40 year period), based on the IUCN criteria for Vulnerable (> 30% population decline over 10 years is one of the threshold criteria set by the IUCN for the Vulnerable category, IUCN, 2012). Analyses were run with each of these thresholds, and the final model was run using the threshold of 30%. Further analyses were run using these dependent variables, with 'Stable' species removed (classified as above). Chi-square was used to test for associations between population trend classes and ecological traits. A Kruskal-Wallis rank sum test was used to test for a difference in wingspan across population trend class and a pairwise Wilcoxon rank sum test with Holm-Bonferroni correction for multiple comparisons to test for differences between the classes.

To identify variables in the dataset with high importance in predicting population trends, we used Random Forest in R (package: *'randomForest'*, Liaw and Wiener, 2015, R Core Team, 2013). Random Forest is a machine learning classification and regression tree method (Howard and Bickford, 2014). Random Forest analysis fits many classification trees to a dataset and then combines predictions from these trees to produce a model for classification predictions based on variables ranked by predictive value (Cutler et al., 2007). We allowed each model run to generate 5000 trees (according to methods described in Huhn 2008). A total of 41 variables were included in the analysis, with many of these being different measurements of the main ecological traits. Each model was run ten times (creating 50,000 trees) to obtain an estimate variation in variable importance. The packages *'rpart'* (Therneau and Atkinson, 2018) and *'partykit'* (Zeileis et al., 2008) were used to build a decision tree as a result of the consensus random forest model run.

To test the possible effect of phylogenetic relatedness on abundance trends between closely related species, we utilized available DNA sequence data from GENBANK. We identified available sequences at the cytochrome oxidase I (COI) locus for all 327 moth species. The sequences were aligned in MEGA7 (Tamura et al., 2013) using clustalW and pairwise distances were estimated using the Maximum Composite Likelihood model (Tamura et al., 2004). All positions containing gaps and missing data were eliminated from analysis, resulting in a total of 640 nucleotide positions in the analysis. A Mantel test was used to compare pairwise differences between the genetic distance matrix and the distance matrix for change in national occurrence records for each species using the '*ade4*' package in R (Dray and Dufour, 2007).

3. Results

Overall, our genetic distance estimate for the entire dataset was 0.13 ± 0.03 (mean ± s.d). We found no correlation between our genetic distance estimates and our abundance change estimates (Mantel obs. = 0.0026, $p = 0.42$). As a result of this, variables relating to phylogeny(subfamily, family) were removed from the random forest analysis. Random forest analysis using regression produced very low variance explained for these data. Classification models were successful however using a range of classification thresholds. When the threshold of 30% change was used to classify species, the Out of Bag (OOB) error rate was 24.4%, with successful prediction of decreasing species on 89.9% of occasions. Prediction of increasing species was not so good, with an accuracy of only 46.6%.

We identified wingspan to be the most important variable in predicting a decrease in populations by a substantial amount (see Fig. 2). Following from this, larval food plants, photoperiod activity (nocturnal or crepuscular), and number of habitats occupied were also top predictors respectively (Fig. 2). Although all other variables also contributed to the accuracy of the model overall, they were not, however, as important in predictions.

Based on the final run of the random forest, 178 species (52%) were classified as 'Decreasing' over the data period, 71 species (21%) were 'Stable', and 88 species (26%) were 'Increasing' (See Methods section for criteria on classes). The mean wingspan for declining moths was 35.8 mm (mean ± s.d 6.5), for increasing 32.1 mm (mean ± s.d 10.8), and for stable species 33.2 mm (mean ± s.d 9.2) (Fig. 1). Wingspan was significantly different between these three population change trend groups (Kruskal-Wallis: $\chi^2 = 18.9$ df = 2, $p < 0.001$), driven by the difference between the decreasing group and both the increasing and stable groups (Wilcoxon: $p = 0.001$). Total months in flight and number of habitats occupied were not found to be significantly different between the population classes ($p > 0.05$).

An association was found between photoperiod activity (nocturnal or crepuscular), habitat specialism, and larval food source, and population status (Pearson Chi-squared test cross-tabulation for photoperiod activity [$\chi^2 = 37.3$, df = 2, $p < 0.001$], habitat specialism [$\chi^2 = 44.5$, df = 2, $p < 0.001$], and larval food source [$\chi^2 = 16.9$, df = 2, $p < 0.01$]). Of the declining moth species, 93% were nocturnal and the remaining species crepuscular. Our data represented species with a mixture of larval food requirements, with 50% of declining species being woody larval feeders, 28% herbaceous, and the remainder feeding on other sources. The majority (78%) of declining species were also larval specialists, although this was not found to be significant.

Decision trees created using the variables from the random forest revealed wingspan, photoperiod activity, primary habitat and larval food source to be the most important factors in determining the population trends of species (Fig. 3). For the node which explained the largest amount of the data ($N = 199$), moths with decreasing population trends had larger wingspans (> 20.5 mm), and fed on plant sources (Node 5, $N = 209$). With regards the rest of the species, the picture was more complicated. Species within the increasing group had smaller mean wingspan (< 20.5 mm, Node 11, $N = 17$), or much larger wingspan [> 48.5 mm, Node 6, $N = 10$], were often crepuscular ($N = 33$), and had larval food sources such as lichens or fungi (Node 7, $N = 7$). These associations however were not as clear as with regards to the declining species, and nodes revealed only small numbers of species (Fig. 3).

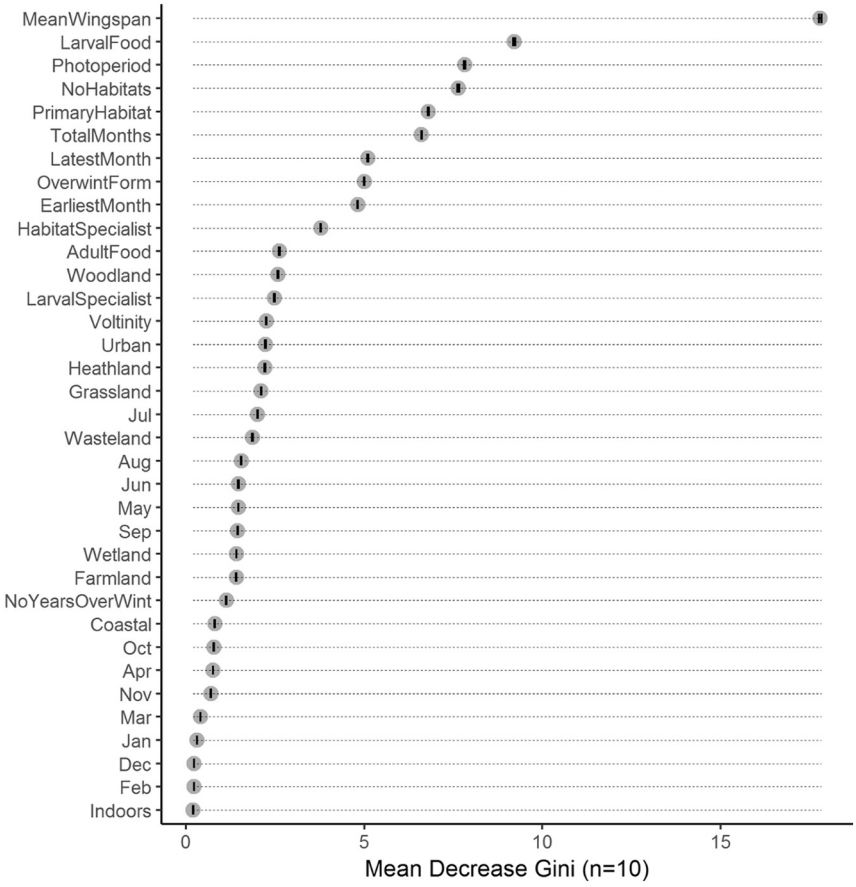

Fig. 2. Random forest variable importance plot using mean (+/− SE) decrease in Gini using $N = 10$ ensemble of trees (50,000 trees).

4. Discussion

Using long term moth trend data and a predictive machine learning framework, our analyses revealed that long term national declines can be predicted in moths using ecological trait data. Extinction risk predictions using machine learning are a useful means of identifying at-risk species, essential for prioritisation of conservation action (Howard and Bickford, 2014; Bland et al., 2015), so these results are positive for moth conservation. Our model was able to accurately classify declining species 89.9% of times, reducing to a success rate of 46.6% for increasing species, something which may not be a problem in conservation, but warrants further investigation with a larger dataset. The model and subsequent trees revealed wingspan to be by far the best predictor for declines. However, photoperiod activity, larval food preferences and the number of habitats occupied all also significantly contributed to the model. Comparative analyses revealed that mean wingspan, photoperiod activity and larval food source were significantly different between increasing, declining and stable groups identified in the initial analysis. Initial phylogenetic analyses did not reveal any significant relationship between phylogenetic relatedness and population trends; which is not altogether surprising, as it is considered that many traits such as dispersal ability may be independent of phylogeny (Nieminen et al., 1999; Slade et al., 2013).

Larger, longer-winged moths, which our analysis revealed to be declining more significantly, are generally considered to have better flight speeds and dispersal abilities (Jones, 2014), and thus to be less susceptible to habitat fragmentation (Usher and Keiller, 1998). Recent research into the effects of urbanisation on moth communities has also found that larger moths are more frequent in urban areas (Merckx et al., 2018). Analysis of life-history traits in European moths however found that larger woodland species were more likely to be in decline (Potocký et al., 2018). In our dataset, the species found to be increasing tended to have smaller wingspans. This fits the trend that generally, independent of fragmentation and dispersal effects, larger-bodied species tend to decline faster than smaller species due to their larger area requirements (Slade et al., 2013), particularly in woodland species, whose dispersal abilities may be lower. These declines are also likely to have an effect on the overall available biomass of night flying invertebrates. Decision trees revealed a relationship between wingspan, photoperiod activity and primary habitat preference for declining species.

Habitat breadth was an important predictor, however no significant differences were found in comparative analysis between the three classes and the number of habitats occupied. On interrogation of decision trees however, the direction of this relationship was not clear, but many declining species were found across more habitats. Habitat preference, although not ranked so highly, was also pulled out by decision trees as a splitting factor for classification. A significant number of declining species were associated with grassland, heathland or wetland habitats. These findings agree with those from Sweden (Franzén and Johannesson, 2007), where non-woodland species were more likely to decline, and those from Central Europe (Potocký et al., 2018), where woodland species were found to be more common. Despite existing evidence that specialist species are at increased risk of extinction (Koh et al., 2004; Kotiaho et al., 2005; Mattila et al., 2006; Mattila et al., 2008), we could not confirm this in any clear way for the species studied, but this may be a reflection of the species included in the analysis (i.e. only common and widespread species).

As with habitat specificity, we did not find any link between larval specificity and population trends, however for the majority of declining moths, larval food preferences were for woody or herbaceous plants rather than grasses, lichens or other food sources. This may reflect the declines or local extinction of key food plants (Mattila et al., 2009), and

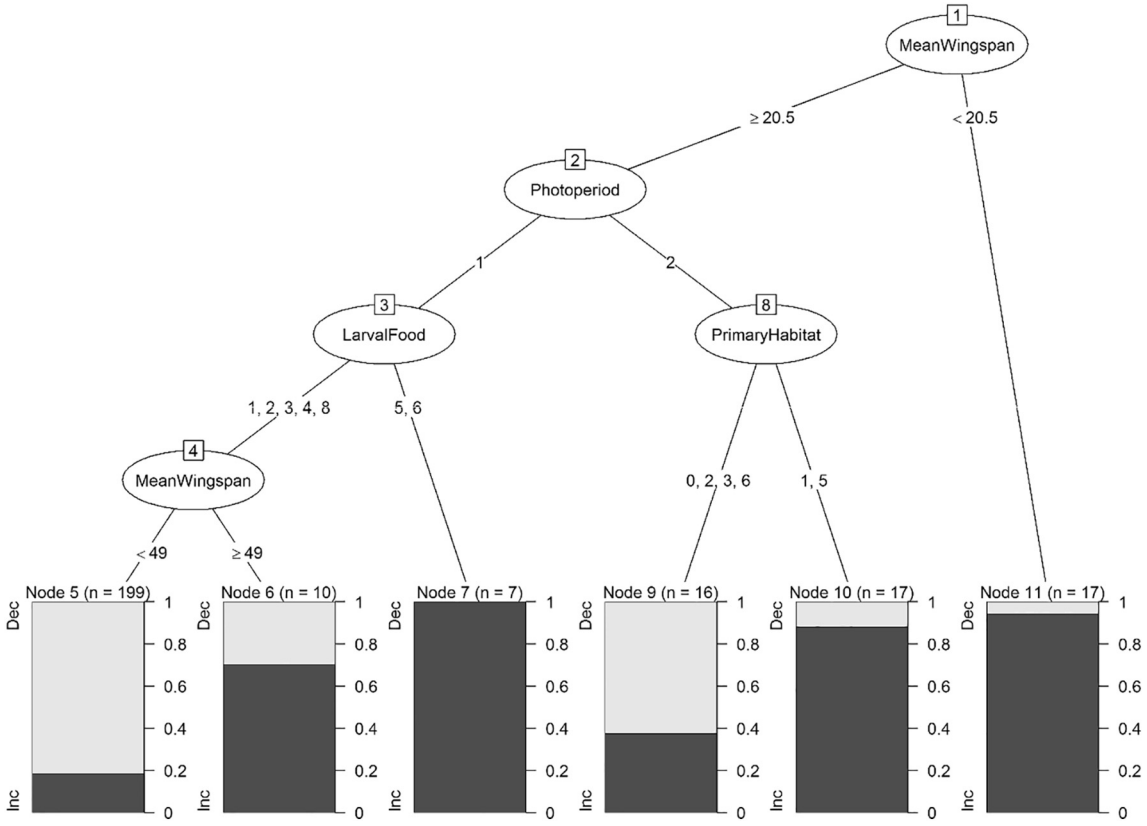

Fig. 3. Decision tree showing population change of moth species according to their ecological and morphological traits. Within the tree wingspan relates to thresholds in size (mm), photoperiod (1 = Nocturnal, 2 = Crepuscular), larval food (1 = Herbaceous, 2 = Woody), and primary habitat (0 = No association, 1 = Woodland, 2 = Grassland, 3 = Heathland, 4 = Urban, 5 = Coastal, 6 = Wetland). For each node of the tree, the N indicates the number of species at each node and the bar indicates the proportion of each species in a node that are increasing (dark grey) or decreasing (light grey) in population. Nodes 5 and 9 are made up of moths that are primarily decreasing (light grey), whereas nodes 6, 10 and 11 contains moths that are primarily or, in the case of node 7, all increasing (dark grey).

such co-declines reinforce their utility as bioindicators, as plant predators may be used to indicate overall habitat health (Ricketts et al., 2002; Thomas, 2005). One factor significantly affecting invertebrate populations is increased nitrogen deposition, which is known to negatively affect nitrogen-sensitive plant species (Stevens et al., 2010), likely leading to cascading losses of plant predators. Some moth species may however have benefited from nitrogen deposition, with increased nitrogen leading to larger individuals and increased broods of some species depending on host plants (Pöyry, et al., 2016). One taxa potentially benefiting from these changes may be the Footman moths (Euarthropoda), a group of lichen feeding moths for which three species (*Eilema griseola, E. depressa and E. complana*) have increased by over 1000% in last 40 years, possibly as result of increases in nitrophilic lichens in agricultural landscapes. These 'winners' however are in the minority, with only one third of so called 'common and widespread' species increasing at all over the last 40 years.

Nocturnal activity is known to be linked strongly with moth declines due to the negative impact of light pollution, principally street lighting, which is thought to significantly negatively impact navigation and feeding behaviour (MacGregor et al., 2015, 2017). In the UK, about 90% of 'macro' species are nocturnal, so this is by far the most common behaviour, although many are crepuscular and fly at dawn and dusk (Newland et al., 2013). We found that almost all declining moths in this analysis were nocturnal, which is not surprising in light of the research and the scale of light pollution as a threat to nocturnal species. In 2001, around 18% of the Earth's terrestrial surface was significantly polluted by unnatural light (Longcore and Rich, 2004), and all natural ecosystems have experienced increases in light pollution, with effects on the phenology of many seasonal taxa (Bennie et al., 2015). This suggests that the threat from unnatural lighting will only continue to significantly affect moth populations.

Our data comes from a long-term monitoring scheme for macro-moths, and in order for long-term trends to be calculated accurately, the species used in the population analysis were those trapped regularly enough to yield sufficient data. As a result, the 337 species included in our analysis are those which might be considered to be 'common and widespread'. Despite this bias, our findings and those of previous researchers (Conrad et al., 2004; Fox et al., 2013) still indicate that these ostensibly common species are still suffering significant losses, and that due to the diversity of moth life-history traits, the relationship between population trends and ecological traits is not straightforward. There are thousands of rarer or more difficult to sample or identify species for which population trends are unknown, and may be declining. Potential issues may also exist where ecological trait information is incorrect or out of date, and our model will be updated accordingly.

Our findings highlight the concerning evidence that even so called 'common and widespread' moth species are in significant decline, and those in decline exhibit a range of life-history traits, with relationships not always as expected from interpretation of the literature. This research also shows the importance of good longitudinal data for understanding the drivers for population change (Hallmann et al., 2017). With over 2000 Data Deficient moth species in the UK alone, we intend that our model be applied to emerging ecological traits databases in order to help identify potential at-risk species. We suggest that making predictions purely based on previous research on ecological traits, may not be effective, and that this machine-learning framework be used to predict declines in Data Deficient species in order that conservation management and research be targeted appropriately. Work is currently being carried out to compile databases of ecological traits for moths, and this will be used in further models to identify at-risk species, from

the vast numbers of understudied and under-recorded moths. We suggest that other large and diverse invertebrate groups such as hoverflies and beetles may be also good taxa for further analysis, where population data is available.

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