Received: 13 December 2022 | Accepted: 17 August 2023

DOI: 10.1111/icad.12685

ORIGINAL ARTICLE

Insect Conservation and Diversity

Idiosyncratic trends of woodland invertebrate biodiversity in Britain over 45 years

Diana E. Bowler[1] | Charles A. Cunningham[2,3] | Colin M. Beale[2,3,4] | Lisa Emberson[5] | Jane K. Hill[2,3] | Merryn Hunt[6] | Lindsay Maskell[6] | Charlotte L. Outhwaite[7] | Piran C. L. White[4,5] | Michael J. O. Pocock[1]

[1]UK Centre for Ecology & Hydrology, Wallingford, Oxfordshire, UK

[2]Department of Biology, University of York, York, UK

[3]Leverhulme Centre for Anthropocene Biodiversity, University of York, York, UK

[4]York Environmental Sustainability Institute, University of York, York, UK

[5]Department of Environment and Geography, University of York, York, UK

[6]UK Centre for Ecology & Hydrology, Lancaster Environment Centre, Bailrigg, UK

[7]Centre for Biodiversity and Environment Research, University College London, London, UK

Correspondence
Diana E. Bowler, UK Centre for Ecology & Hydrology, Wallingford, Oxfordshire OX10 8BB, UK.
Email: diana.e.bowler@gmail.com

Funding information
UKRI Future of UK Treescapes Research Programme, Grant/Award Number: NE/V02020X/1; UK Natural Environment Research Council, Grant/Award Number: NE/V006533/1

Editor: Raphael K. Didham and Associate Editor: James Bell

Abstract

1. Woodland cover in Britain has increased over the past century and is set to increase further through woodland creation schemes aiming to tackle climate change. Nonetheless, the wider repercussions of increasing woodland cover for species, especially invertebrates, have not been comprehensively assessed.
2. Here, we quantified the woodland associations of 2762 invertebrate species in Britain across 21 broad taxon groups using species occurrence records collected by specialist recording societies. We then related the strength of species' woodland associations to published estimates of their long-term national distribution trends between 1970 and 2015.
3. Across all taxa, 29% of species were positively associated with broadleaf woodland cover, whereas 27% of species were negatively associated. There was a slight tendency for species associated with broadleaf woodland to have more positive long-term distribution trends, but the effect had little explanatory power. For 15% of species, we detected a non-monotonic association with broadleaf woodland cover, such that their occurrence peaked at intermediate levels of cover. Intermediate-cover species had more positive long-term distribution trends than species with monotonic positive or negative woodland associations.
4. Our findings suggest that woodland invertebrates have not consistently increased, despite the increases in woodland cover. While some caution is warranted owing to our use of heterogeneous occurrence records, the considerable variation in distribution trends of woodland-associated species could be explained by the high diversity of woodland species and ways in which they use woodland habitat. Woodland creation, or increasing tree cover in general, could have idiosyncratic impacts on species, depending on how new woodlands are created and managed.

KEYWORDS
forests, insects, long-term trends, reforestation, tree-planting

INTRODUCTION

Woodland cover in Britain has fluctuated throughout the Holocene (Fyfe et al., 2013; Woodbridge et al., 2014) but by the beginning of the 20th century comprised only ca. 4.7% of the land surface (Forest Research, 2021). Over the 20th century, woodland cover increased, largely due to conifer plantations for timber production (Harmer et al., 2015; Mason, 2007), but more recently also benefiting from broadleaf tree-planting, resulting in the 13% coverage present today (Forest Research, 2021; Raum, 2020). Over a similar time frame, forest cover has increased in many other countries across Europe (Gerard et al., 2010) and other temperate regions (Keenan et al., 2015), with land abandonment and natural expansion contributing to the broader trend. Woodland cover in Britain is set to increase further over the coming decades as part of the nature-based strategy to offset carbon emissions and mitigate climate change, while also restoring and rewilding ecosystems (Bateman et al., 2022; Committee on Climate Change, 2019; Pörtner et al., 2021). The broader ecosystem consequences of these changes for different taxa associated with woodlands remain unclear, making it uncertain if tree-planting schemes will help reverse biodiversity loss.

Insect populations have been reported to be in decline (Fox et al., 2015; Hallmann et al., 2017), but a complex picture of community turnover with winners and losers is typically found (Bell et al., 2020; van Klink et al., 2020). Due to limited data, inferring large-scale patterns of decline across taxa and habitats should be treated with caution (Montgomery et al., 2020). Specifically, in terms of woodland, despite increases in cover, the evidence so far suggests that the population or distribution trends of woodland species have not followed the same pattern (Defra, 2021). Woodland birds show, on average, stable trends across Europe (Gregory et al., 2019), but specialist woodland species tend to be declining in the United Kingdom (Harrison et al., 2016; Hewson et al., 2007). A multi-taxa study of insect trends in German forests found declines in the majority of sites, species and trophic groups (apart from herbivores) over a 10-year period (Staab et al., 2023). In the United Kingdom, woodland moths, especially those associated with coniferous woodland, have increased (Tordoff et al., 2022), but, overall, moth species have declined faster in wooded landscapes (Blumgart et al., 2022; Macgregor et al., 2021). Based on these well-studied taxonomic groups, it is far from clear whether there are any general patterns in the trends of woodland-associated species.

Diversity in the findings of previous studies might be partly explained by differences in how the woodland association of species was classified. Indicators of species trends within specific habitats are known to be sensitive to decisions about species' habitat associations, which can be subjective (Gregory et al., 2019). Previous studies are also limited to the most well-sampled taxonomic groups—especially birds, butterflies and moths—taxa whose responses may not be representative of other organisms with a diverse range of life cycles, specialisms and dispersal abilities. Hence, identifying any general patterns and systematic differences requires examining a broader range of taxonomic groups, with a greater diversity of life histories and habitat use, and a consistent approach to classifying species' woodland associations. Cross-taxa analysis that uses a consistent methodology to analyse multiple groups will help understand better how different taxa are affected by environmental changes (Bowler et al., 2015; Daskalova et al., 2020).

Here, we assessed the trends of woodland invertebrate species (21 taxon groups of insects, spiders, centipedes, and molluscs) in Britain over a 45-year period (1970–2015). We focused on invertebrates since their trends are especially poorly documented, but many are found in woodland habitats performing key ecosystem functions. We use the term 'woodland' rather than forest because the former is more typically used in the British context because of lower canopy cover in Britain woodlands compared with forest elsewhere. Our analysis comprised two main parts. First, we characterised the woodland association of all species using a standardised model-based approach, based on the relationship between woodland cover and species' occurrence. We contrasted models of linear or non-linear woodland associations (i.e. whether occurrence peaked at intermediate woodland cover) to assess the prevalence of different types of woodland associations across species. To validate our approach and obtain more detailed information on woodland use, we also extracted woodland association information from a trait database. Second, we tested whether woodland-associated species have increased, which would be consistent with them benefiting from increase in woodland cover, using distribution trend estimates from a previous study (Outhwaite et al., 2019; Outhwaite et al., 2020). We used this analysis to also identify declining and increasing woodland invertebrate species of conservation concern. We focused the majority of the analysis on broadleaf woodland associations, because this is the dominant native tree type, but compared the strength of associations with those of coniferous woodland, as well as association with ancient woodland cover, as a measure of woodland quality.

MATERIALS AND METHODS

Species occurrence data

Species occurrence records were collated from various UK and GB recording schemes (Pocock et al., 2015) to characterise species' woodland associations. We use the same data as had been used to estimate species' distribution trends (Outhwaite et al., 2019). These records are opportunistic recordings of species, usually collected by volunteers, but were verified as a plausible observation by members of the respective specialist recording societies who typically have strong taxonomic identification (ID) skills. We included data from 21 recording schemes for ants, aquatic bugs, bees, caddisflies, centipedes, craneflies, dragonflies, empid flies (and hybotids and dolichopodids), Gelechiids, grasshoppers/crickets, ground beetles, hoverflies, ladybirds, mayflies, molluscs, moths (macro moths), plant bugs, shield bugs, soldierflies, spiders and wasps (see Table S1 for a list of associated recording schemes). Each occurrence record reports an observation of a specific species in a specific place and time. The temporal and spatial precision of these records can vary considerably. Here, we only used those records where the specific date (i.e. day, month and year) of the

record is known and where the location of the record can be identified to a 1 km Ordnance Survey grid cell or finer resolution. We used all data from Britain (i.e. England, Scotland and Wales) since records for Northern Ireland were sparse for many taxa.

Data from each recording scheme were analysed separately using the same standardised workflow. We organised the occurrence records into detection–non-detection data. To do this, we defined unique 'visits' in our data frame based on the sets of species records collected on the same date in the same 1 km Ordnance Survey grid cell. Each record provides detection data for a specific species on a given visit. Non-detection data were inferred from the detection data. For instance, if there was a detection for species A on a given visit, then non-detections were inferred for species B and C (i.e. any other species reported by the same recording scheme). Through these steps, we created a detection–non-detection variable with values of 1 when the species was detected/reported on a visit and a value of 0 when it was not detected/reported, but other species of the same taxonomic group were. Grid cells where no species were recorded for any species within the taxonomic group were not included in the analyses. We used species data between 1990 and 2015 to match the time frame of available woodland cover data.

We subsampled this detection–non-detection data to reduce the spatial bias in recording (i.e. the large skew in number of visits per grid cell) and high imbalance in species records (i.e. for most species, there were a small number of detections vs. a large number of non-detections), following recent recommendations (Gaul et al., 2022; Robinson et al., 2020). To do this, we first retained all the detections for each species (i.e. all the data associated with a response of value 1). Next, we subsampled the non-detection data for each species separately (i.e. all the data associated with a response value of 0 for a given species). Subsampling non-detection data involved: (1) removing non-detection data for a species that was outside the period of year when the species was ever reported and (2) sampling one non-detection record each year from all those available within the surrounding 10 km grid of a detection of the species. We compared this approach with a simpler filtering method (randomly sampling one visit per 1 km grid cell and year, regardless of whether the species was detected), but similar results were found (Figure S1). The advantage of only subsampling the non-detection data was that more rare species passed the threshold for inclusion in the analysis, since all detections were retained, and that we could better model species' phenology and account for variation in sampling dates. Because of the subsampling, we refer to our modelled response as relative occurrence probability.

We only analysed species with at least 50 detections across at least 20 different 1 km grid cells so that records were sampled across an environmental gradient with reasonable sample size. Many rare species (1969) failed to pass this threshold. We initially analysed data for 3072 species.

Woodland cover data

We used the UK Land Cover Map in which woodland is classified as either broadleaf or coniferous woodland (Fuller et al., 2002; Morton et al., 2014; Rowland et al., 2017; Rowland et al., 2020). In this map, broadleaved woodland is defined as stands >5 m high with tree cover >20% or scrub (<5 m) with a cover >30%. Coniferous woodland is defined as semi-natural stands and plantations, with cover of coniferous trees >20%, as well as felled areas that are likely to be replanted. These woodland data are available for 1990, 2000, 2007 and 2015 during our study period. We extracted information on the percentage broadleaf and percentage coniferous woodland cover in each Ordnance Survey grid cell of Britain at 1 km resolution. We matched the species data to the corresponding woodland cover value of the associated 1 km grid cell using the woodland data nearest in time to the year of the species sampling visit. Since woodland cover change tends to be slow, in annual terms, any slight mismatch between the year of species observation and the year of woodland cover should not have a large effect on our results.

As a potential measure of woodland habitat quality, we also extracted data from the Ancient Woodland Inventory (AWI) for England, Scotland and Wales (Spencer & Kirby, 1992). These data comprise the boundaries of Ancient Woodland Sites in each country (woodland that has persistence since 1600 in England, Wales and Northern Ireland, and 1750 in Scotland), identified using presence or absence of woods from old maps, ground survey, aerial photography, information about the wood's name, shape, internal boundaries and location relative to other features. From the AWI vector data, we created 25 m resolution rasters to match up with the UK land cover map data. As the AWI categories vary among England, Scotland and Wales, the data were reclassified to simply indicate whether a pixel contained ancient woodland and then combined to provide a single AWI dataset covering Britain. From these data, we extracted the percentage ancient woodland in each 1 km grid cell.

Species' woodland associations

As the simplest metric, we first calculated woodland association based on the strength of the linear association between species' relative occurrence probabilities and percentage of woodland cover of 1 km grid cells within Britain. Species responses to any environmental gradient are often non-linear with peak responses at intermediate values of the environmental variable. To investigate this, we also quantified woodland associations in more flexible models that allowed for non-linear associations to emerge, which identified species associated with intermediate woodland cover.

Linear associations

We first built a model to quantify the linear association between the relative occurrence probability of a species (logit-scale) and percentage woodland cover and used the slope of this relationship as a continuous metric of woodland association. For this, we used a generalised additive mixed model (GAMM) to predict species relative occurrence (whether a species was recorded on a visit) based on

percentage broadleaf woodland cover within the 1 km grid cell, included as a linear term. We included the geographic coordinates of the grid cell centroids as a bivariate spatial spline to account for any geographic gradients in occurrence. Year was also included as a random effect. To account for variation in sampling effort, we included additional covariates for list length, following previous analysis (Bowler et al., 2021; Outhwaite et al., 2019). List length refers to the number of species from the same taxonomic group reported on a visit and was included as a factor to separate opportunistic records (list length of one), from short surveys (list length of two to three species) and more comprehensive surveys (list length of four or more). We additionally included day of year, as a spline-based smooth term, in the detection model to account for variation in sampling days of separate visits (Bowler et al., 2021). Each species was modelled individually (i.e. 3072 GAMMs). We use the regression coefficient for the effect of broadleaf cover as our measure of woodland association. In subsequent analyses, we excluded species with highly uncertain woodland association estimates, assessed as those with a standard error greater than 1.5 times the interquartile range of the standard error values above the third quartile of the standard error values (310 species were excluded on this basis, leaving 2762 species in total). We repeated this analysis also to test for coniferous woodland association using the same methodology, which was used to compare broadleaf and woodland associations (see the section '*Broadleaf vs. coniferous specialism*').

Allowing for non-linearity

Species' responses to many environmental gradients are non-linear, causing species occurrence peaks at intermediate values of the gradient (Citores et al., 2020). In our case, this could represent species adapted to heterogeneous landscapes comprising both woodland and open habitats, whose occurrence probability is the highest at an intermediate level of woodland cover within the 1 km grid cell. To allow for more complex (i.e. non-linear) woodland associations, we ran another set of GAMM models in which the effect of percentage broadleaf woodland cover was modelled with a penalised thin plate regression spline rather than included as a linear term, using the mgcv package. To avoid overfitting the curve to the data and ensure biologically reasonable uni-modal response curves, the spline was constrained to a low dimension ($k = 4$, where k is the dimension of the base of the spline function). Along with broadleaf woodland cover, we included the same set of covariates as in the previous set of models (i.e. day of year of visit, list length and the geographic coordinates as a bivariate spatial spline and year as a random effect). Using these models, we then derived a response curve for each species by predicting relative occurrence probabilities over the full range of possible broadleaf woodland cover values (0%–100%), setting all other covariate values to their median. From each model, we extracted the % broadleaf woodland cover at which this occurrence probability was maximised.

We simplified the species-specific response curves into a smaller characteristic set using a cluster analysis. For this, we first calculated the derivatives of the species response curves, that is, how much occurrence changes per 1% increase in woodland cover, along the full possible gradient between 0 and 100%. As input data, we used the predictions of the GAMMs based on the best estimates. We did not explicitly include the uncertainty of the GAMM, but excluded species whose predictions were highly uncertain (as above, based on whether the mean standard error of the predictors was >1.5 times the interquartile range above the third quartile). We then created a distance matrix that quantified how much the derivatives differed among species at different points along the gradient, using Manhattan distances (Simpson, 2022). Finally, we grouped together species with similar sets of derivatives over the gradient used partitioning around medioids ('pam') clustering (Maechler et al., 2022). We selected the optimum number of clusters based on the average silhouette width, using the *pamk* function in the *fpc* package (Hennig, 2020). To account for uncertainty in cluster membership, we calculated the silhouette width for each species and removed those that had a negative silhouette width (i.e. not assessed to be typical of the cluster, 15% of species) from subsequent analysis with the clusters, but similar results were made without this exclusion step.

Broadleaf versus coniferous specialism

We used outputs from the first set of GAMMs estimating linear associations of species with broadleaf and coniferous woodland to calculate a measure of specialism towards one woodland type or the other. This was calculated as the log-ratio of the linear woodland association coefficients for each woodland type. Positive values reflected a greater association of broadleaf over coniferous woodland; zero reflected equivalent associations and negative values reflected a greater association of coniferous over broadleaf woodland. For simplicity, we defined broadleaf specialists as those with log-ratio >2 and coniferous specialists as those with log-ratio smaller than −2.

Species' distribution trends

Our estimates of species' woodland association were related to their trends in national-scale annual occupancy estimates from 1970 to 2015 in Britain available for our study species from a previous study (Outhwaite et al., 2019). These annual occupancy estimates are the predicted proportion of 1 km grid cells in which a species was present (out of the total number of sampled 1 km grid cells) and were produced using Bayesian occupancy-detection models applied to the same species occurrence data that were used to determine woodland associations in the present study. Previously, these estimates were used to assess general patterns of invertebrate change in the United Kingdom (Outhwaite et al., 2020). These annual estimates are available from Outhwaite et al. (2019) as samples from the posterior distributions of each annual occupancy estimate for each species.

For the present study, we took 999 samples of the posteriors for each species and year and used these to calculate species' long-term

distribution trends. Distribution trends were summarised by comparing the occupancy estimate of the first and last years, following Outhwaite et al. (2019):

$$\text{Distribution trend} = \left(\left(\frac{f}{s}\right)^{\frac{1}{nyear-1}} - 1\right) \times 100.$$

Here, f and s were predicted annual occupancies in the final and starting years, respectively, and *nyear* was the number of years over the study period (1970–2015). Species' distribution trends were calculated separately for each random sample from the posteriors and then summarised across the 999 samples as the mean, standard deviation and 95% quantiles. Some species had extreme and highly uncertain trend estimates. We excluded species ($n = 128$ species) if the standard error of the trend estimate was an outlier based on the same approach we used to deal with uncertainty of woodland association estimates.

To investigate the overall relationships between species' distribution trends and woodland associations, we used meta-analysis mixed effects models to combine data for all species across all taxonomic groups, with woodland association as the predictor and species distribution trend as the response. Woodland association was tested, in separate models, as both the continuous linear association (scaled to units of standard deviation) and as the categorical woodland association cluster, as estimated from the above models. These models accounted for the uncertainty in the estimated distribution trends using the standard error of the estimated distribution trends in the model weights (inverse variance) and in the overall 95% confidence interval (Viechtbauer, 2010). Taxon was included as a random intercept to account for differences in the mean distribution trends of each taxonomic group. These models were run using the *metafor* package and rma.mv function (Viechtbauer, 2010). Significance was tested at the 5% level based on the frequentist interpretation of probability.

Finally, to visualise the annual time-series, we also calculated multi-species indicators by calculating the geometric mean of the annual occupancies of species within each forest association cluster for each taxon group, similarly summarising across the 999 sample as mean and 95% quantiles.

Relationship with other habitat classifications and conservation status

To confirm the accuracy of our woodland association measures, we extracted information on species woodland use from the Pantheon trait database (Webb et al., 2018). This database listed 79% of our species and provided habitat classification data for 73%. We note, however, that some taxonomic groups were poorly represented by this database (50% or fewer species represented for aquatic bugs, bees, centipedes, ground beetles, molluscs, and plant bugs), but we used all the data that were available. We mapped our estimates of woodland association with the 'tree-associated' habitat classification from this database and used a linear model to test whether tree-associated species had higher woodland association estimations. To investigate differences in the trends of species using woodland in different ways, we extracted more detailed information on woodland use available within the Pantheon database, which could not be calculated from the occurrence records. Specifically, we extracted information on whether species were classified as using the following woodland strata: arboreal, decaying wood or shaded woodland floor. We selected only species that were classified as using one of these woodland strata and not any others, that is, specialist woodland species of these strata. We then repeated a similar trend analysis above, using meta-analysis models, to calculate the mean trends of species within each of these groups.

Finally, we investigated the trends of species of conservation concern to identify whether and which woodland species are particularly at risk, given the low woodland cover of the United Kingdom. We used official conservation designations that reflected broad-level designations such as UK Biodiversity Action Plan priority species list, national red lists and NERC Section 41 species (see Table S2 for full list of included designations). We used a simple Chi-square test (χ^2) to ask whether woodland species were more likely to have a conservation designation than other species. We note that some species might not have a designation due to insufficient data or assessment.

All analysis was run in R version 4.1.2 (R Core Team, 2021). Boxplots in the Results section show the median (central line within the box), lower and upper quartiles (the border of the box) and the range (the full line or 'whiskers', minus outliers).

RESULTS

Species' woodland associations

We characterised the woodland association of 2762 species across 21 taxonomic groups. Our first approach to assess woodland association was based on the linear association between percentage broadleaf cover and species relative occurrence (Figure 1a,b). Based on these estimated linear associations, 791 (29%) species across all taxa had a significantly positive association with broadleaf woodland cover, 753 species a negative relationship (27%) and 1218 species (44%) a non-significant relationship. Taxa with the highest proportion of significant woodland-associated species were moths and grasshoppers/crickets, whereas mayflies and aquatic bugs had the least.

Our woodland linear association estimates showed some consistency with habitat data available in the Pantheon database, with our estimates generally separating 'tree-associated' species from 'other habitat' species (p-value of mean difference < 0.001; see Figure S2). Deviations are likely because our estimates were based on the statistical association between occurrence and woodland cover at a large spatial scale (1 km) rather than based on species' ecology as considered by Pantheon. Species' associations with broadleaf woodland were also strongly correlated with their estimated associations with ancient woodland cover (median correlation coefficient across taxa = 0.84, Figure S3).

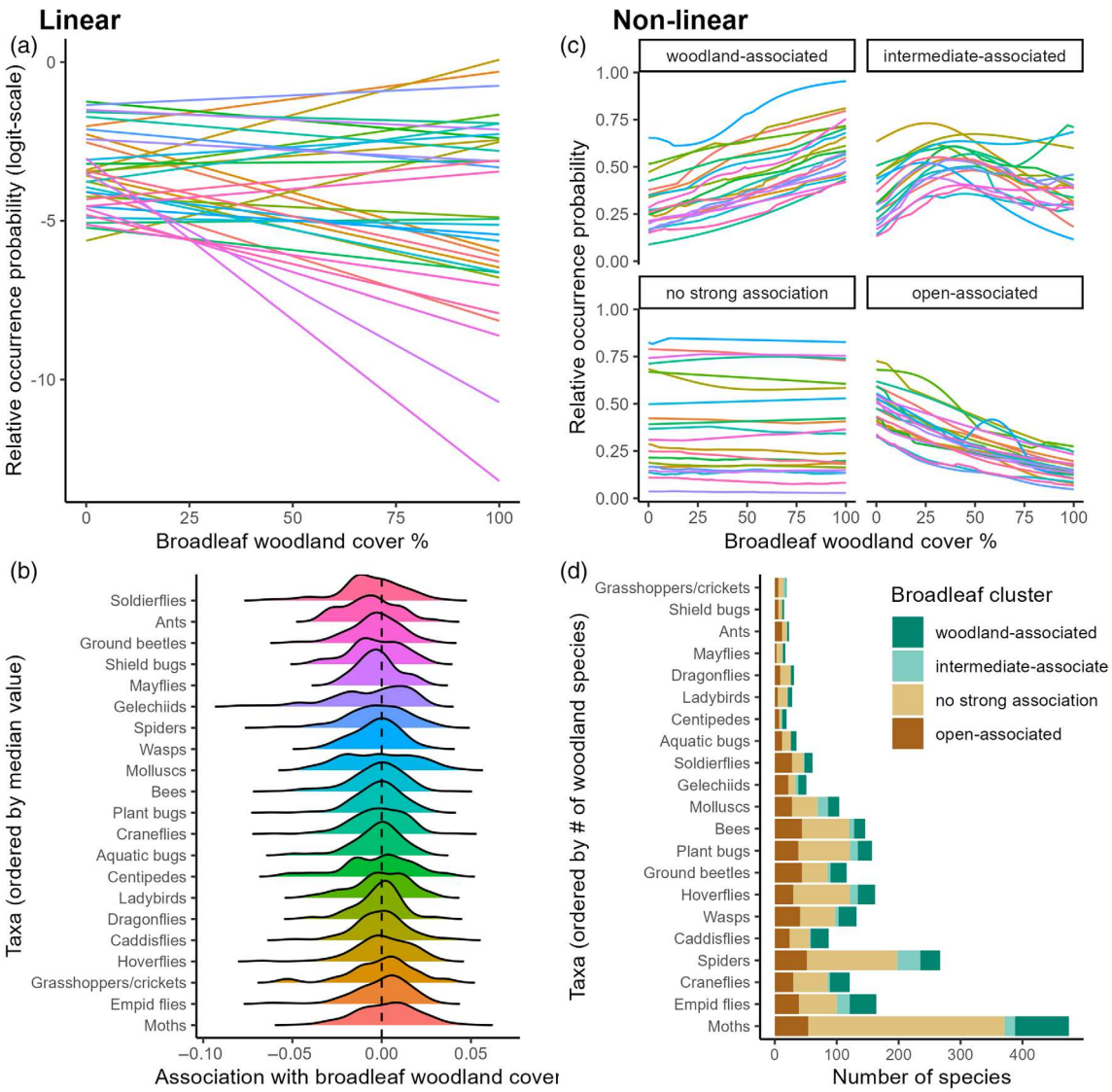

FIGURE 1 Linear: (a) Example linear relationships between broadleaf woodland cover percentage and (logit-scale) relative occurrence probability to a grid cell in Britain—shown for ant species. (b) Density plots of these species-specific linear woodland associations across all taxa. Taxa are ordered by the median value. The vertical dashed zero line reflects the line of no association. Nonlinear: (c) Cluster analysis of woodland non-linear response curves in Britain—shown are the mean response curves of species within each taxa (i.e. shown are 21 response curves for each cluster) and (d) the number of species falling into each cluster for each taxa. Taxa are ordered by the number of woodland-associated species. See Figure S5 for example species response curves.

Our second approach allowed for more complex, non-linear relationships between broadleaf woodland cover and species relative occurrence. When comparing the woodland association estimates based on linear relationships with the clusters based on the non-linear relationships, the two approaches largely agreed in separating species associated with woodland and those associated with open habitat (Figure S4). The fitted non-linear relationships were still broadly flat or monotonic for most species (85%). For the remaining 15% of species, relative occurrence probability peaked at intermediate woodland cover (median of the peak for these species was 37% woodland cover, interquartile range = 30%–45%).

Cluster analysis of these species response curves identified four main clusters (Figure 1c): species with an increase in relative occurrence with increasing woodland cover (labelled 'woodland-associated'); species whose relative occurrence decreased with increasing woodland cover (labelled 'open-associated'); species whose relative occurrence peaked at an intermediate woodland cover value (labelled 'intermediate-associated') and species whose relative occurrence did not strongly change along the woodland cover gradient (labelled 'no strong association'). After excluding species with uncertain cluster membership, 26% of species were included in the woodland-associated cluster—associated with either intermediate (7%) or high woodland cover (19%) (Figure 1b,c). The remaining species were in the open habitat association cluster (24%) or no strong association cluster (50%). Taxa with the most woodland species were moths and empid flies (Figure 1d).

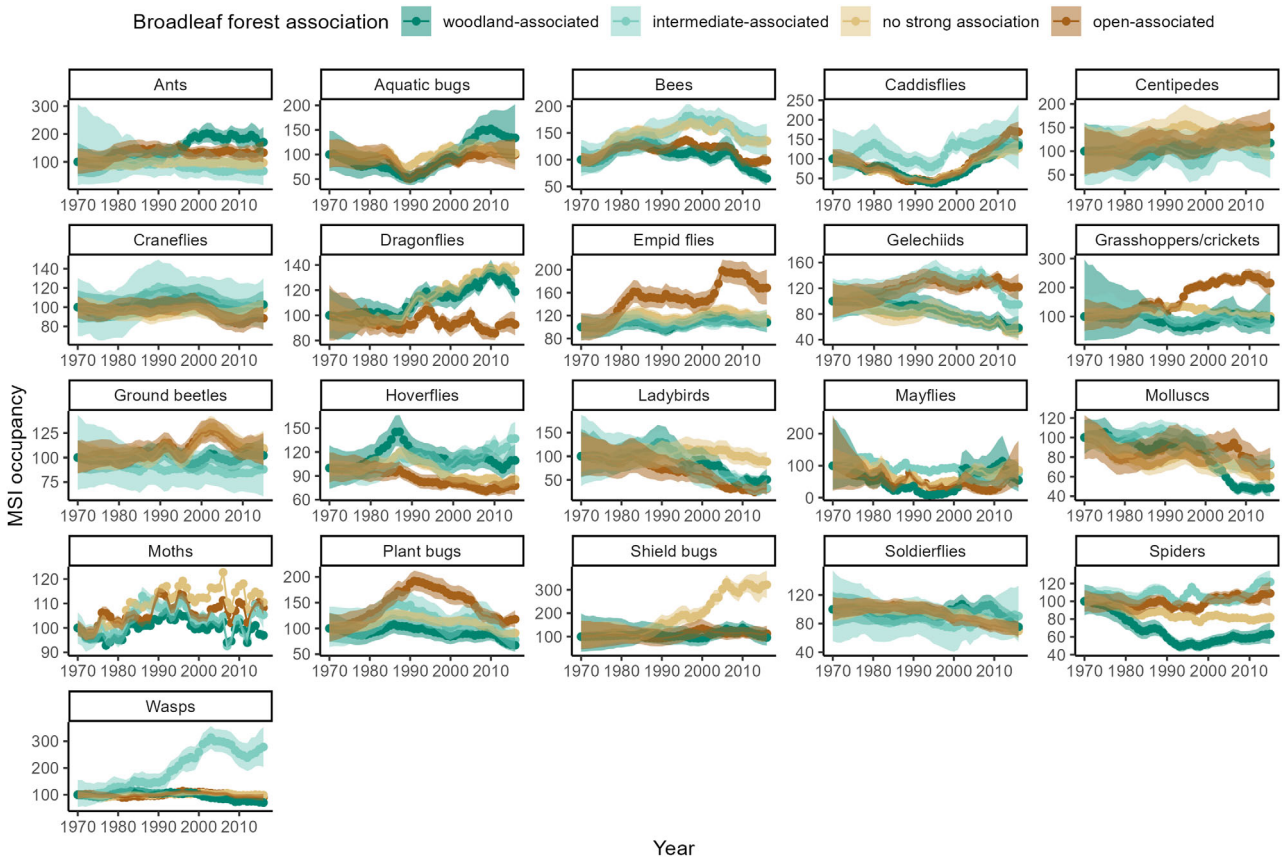

FIGURE 2 Multi-species indicators (MSI): each ribbon shows the 95% CI of the mean annual occupancy of species in Britain within each taxon group, according to their assigned woodland-association cluster (labelled by the colours). Time-series are standardised to 100 in year 1 to facilitate comparison.

Relationships between broadleaf woodland association and distribution trends

The predicted time-series of mean annual occupancy of species in each of the four woodland-association clusters varied among taxa (Figure 2). To facilitate comparison, the annual time-series for each species were summarised by a single distribution change metric based on the change in occupancy for species between 1970 and 2015 (Figure 3).

Across all species and taxa, there was a slightly positive effect of broadleaf woodland association (the linear association; Figure 1a) on species' distribution trends (Figure 3a, meta-analysis: slope of the relationship = 0.049, 95% CI = 0.032, 0.066), suggesting that species with stronger positive associations with broadleaf woodland had slightly more positive trends, on average. Woodland association, however, only explained 0.3% of the variation in trends among species and so has little biological significance. Similar positive but heterogeneous effects were found between distribution trends and ancient woodland cover association (Figure S6, meta-analysis: slope of the relationship = 0.047, 95% CI = 0.030, 0.065). For both broadleaf cover and ancient woodland cover, the pattern was not consistent within taxon groups: only two groups had significant positive relationships (hoverflies, mayflies), whereas two other groups had significant negative relationships (empid flies, Gelechiids).

Among the four woodland-association clusters, species in the woodland-associated cluster did not differ in mean trends from those in the open habitat-associated cluster (meta-analysis 95% CI of mean difference = −0.09, 0.02). Species in the intermediate-associated cluster had more positive trends than those in the woodland-associated cluster (95% CI of mean difference = 0.11, 0.32) or the open habitat-associated cluster (95% CI of mean difference = 0.08, 0.28) and slightly more than those in the no strong association cluster (95% CI of mean difference = 0.03, 0.22).

But, again, despite these differences in mean trends, there was considerable variation among species in each woodland cluster across the taxonomic groups, with increases and decreases in all clusters (Figure 1c,d). Based on the Pantheon database habitat classification, tree-associated species had a similar diversity of trends (Figure S7).

Differences in the trends of coniferous- versus broadleaf-associated species

Species' linear associations with broadleaf woodland cover and coniferous woodland cover were generally correlated (median correlation across taxa = 0.48, Figure S8). More species had significantly positive

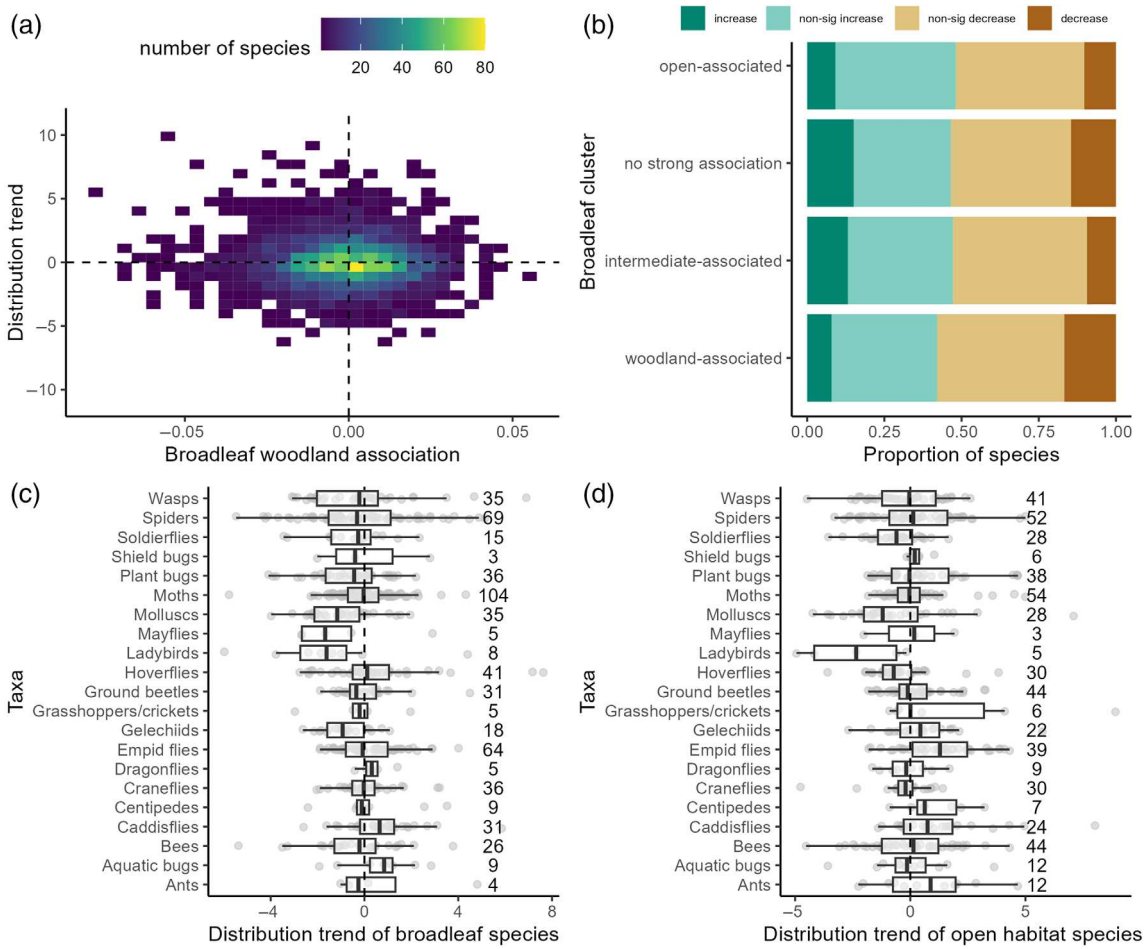

FIGURE 3 Long-term distribution trends in relation to species broadleaf woodland association in Britain, when assessing woodland association based on the linear relationship between relative occurrence probability and broadleaf woodland cover (a) or as a categorical woodland association cluster based on non-linear relationships (b), across all taxa. Boxplots show the distribution of species' distribution trends separately for each taxon group, for those species in either (c) the 'woodland-associated' or 'intermediate-associated' cluster or (d) species in the 'open-associated' cluster. The vertical dashed line shows the line of no change in distribution size between 1970 and 2015. Grey points are the underlying species, and numbers indicate the number of species for each boxplot.

associations with broadleaf woodland than with coniferous woodland (29% vs. 21% of species). Species associated with broadleaf woodland had, on average, slightly more positive trends (or rather less negative trends) than species associated with coniferous woodland (Figure 4a, 95% CI of mean difference = −0.69, −0.43), but trends of both woodland groups varied substantially among taxa (Figure 4b).

Effects of woodland stratum on species trends

Of the species with data in the Pantheon database (71% of study species), 19% of species are arboreal (i.e. occurring in and on trees, including the canopy, trunks and branches), 6% are associated with decaying wood (i.e. decay within a tree's heartwood) and 15% occur on shaded woodland floor (i.e. found in closed canopy woodland and scrub). Both arboreal and shaded woodland floor species had mean negative trends (Figure 5, meta-analysis: arboreal 95% CI of trend = −0.73, −0.24, shaded floor 95% CI of trend = −0.58, −0.08), whereas species associated with decaying wood had no consistent mean trend (95% CI = −0.41, 0.20).

Conservation priority species

A total of 468 (17%) of our study species had a conservation designation. Across these species, more species were declining (72 or 15%, based on significant trends only) than increasing (24 or 5%; Figure 6). Most of the species with significant declining trends were placed in the no strong association woodland cluster (41 or 63%), but this cluster contained the largest number of species in total. Overall, there was no association between woodland association cluster and the direction of significant trends for species with a conservation designation (chisq = 1.75, $df = 3$, $p = 0.63$; Figure 6). Declining species with a conservation designation and a woodland association include

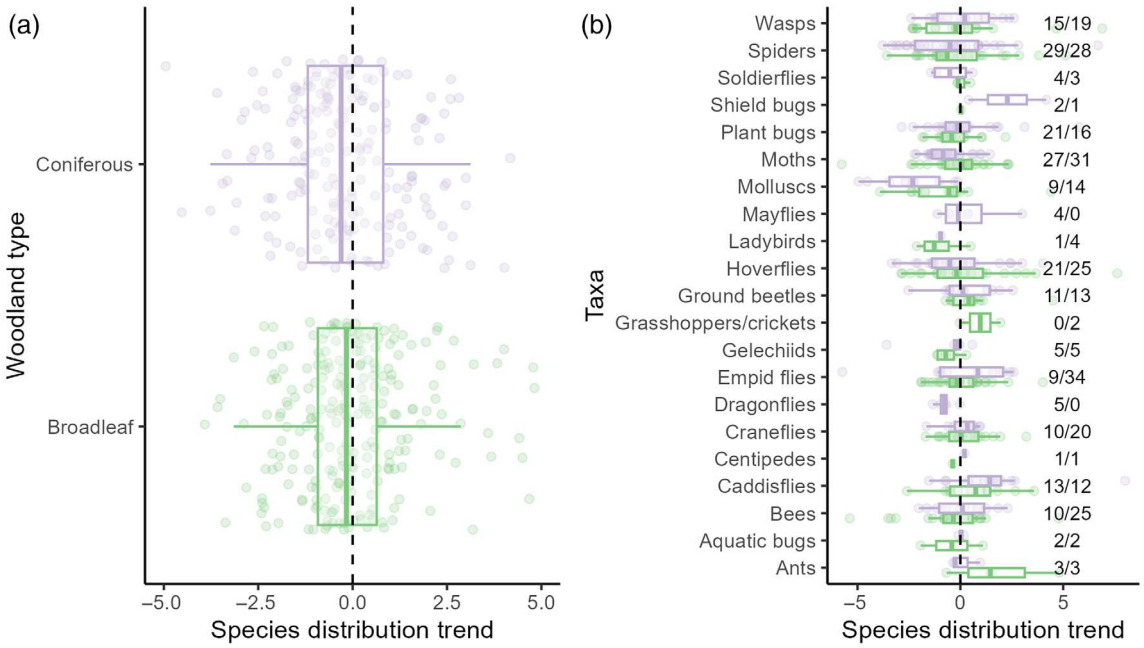

FIGURE 4 (a) Boxplots show the distribution of species' distribution trends in Britain for those associated with broadleaf or coniferous woodland, across all species. The vertical dashed line is the line of no change in distribution size between 1970 and 2015. The grey points show the underlying data points for each species. (b) Boxplots are the same as (a) except split for each taxon group. Numbers indicate the number of species in the coniferous/broadleaf boxplots.

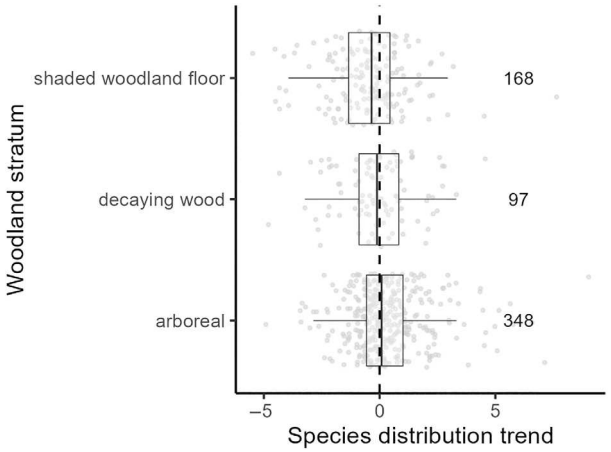

FIGURE 5 Boxplots show the distribution of species' distribution trends in Britain using different woodland strata, for each taxon group. The vertical dashed line is the line of no change in distribution size between 1970 and 2015. The grey points show the underlying data points for each species, and the numbers indicate the number of species in each group.

species of moths (*Macaria wauaria*, *Brachylomia viminalis*, *Mniotype adusta*), bees (*Andrena coitana*, *Eucera longicornis*), molluscs (*Acicula fusca*, *Azeca goodalli*), soldierflies/horse flies (*Sargus flavipes*, *Hybomitra bimaculata*), spiders (*Hypselistes jacksoni*) and wasps (*Ectemnius ruficornis*). By contrast, increasing species with a conservation designation and a woodland association include species of spiders (*Xerolycosa nemoralis*, *Dolomedes fimbriatus*, *Marpissa muscosa*), bees (*Osmia bicolor*) and ants (*Lasius brunneus*).

DISCUSSION

Despite ongoing increases in woodland cover in the United Kingdom, a few studies have assessed the impacts of increasing woodland cover on species (Burton et al., 2018; Spake & Doncaster, 2017). Our study reveals considerable variation in species' woodland associations and the long-term trends of invertebrates in Britain. Depending on the method, we estimated between 26% and 29% of species are positively associated with broadleaf woodland cover (including those associated with intermediate levels) across our focal taxon groups. On average, species associated with broadleaf woodland had slightly more positive distribution trends between 1970 and 2015, but the relationship only explained 0.3% of the variation in trends, and the direction and magnitude of this effect varied among different taxon groups. Since we do not find strong evidence of a consistent increase of woodland invertebrates across all taxa, our findings suggest that increased woodland cover over recent decades in Britain has not provided the appropriate conditions for most woodland invertebrate species to thrive. Moreover, our findings indicate the complexity of invertebrate biodiversity change, with both loss and gains expected according to species' woodland associations, as a result from future woodland creation for climate change mitigation, a pattern already predicted for vertebrate taxa (Douglas et al., 2020).

Woodland invertebrates might not have consistently benefited from increases in woodland cover because of a combination of the state of existing woodlands and insufficiency of new woodlands. Most woodlands in Britain are in a poor ecological condition (only 7% are classified 'favourable') and lack many habitat quality indicators,

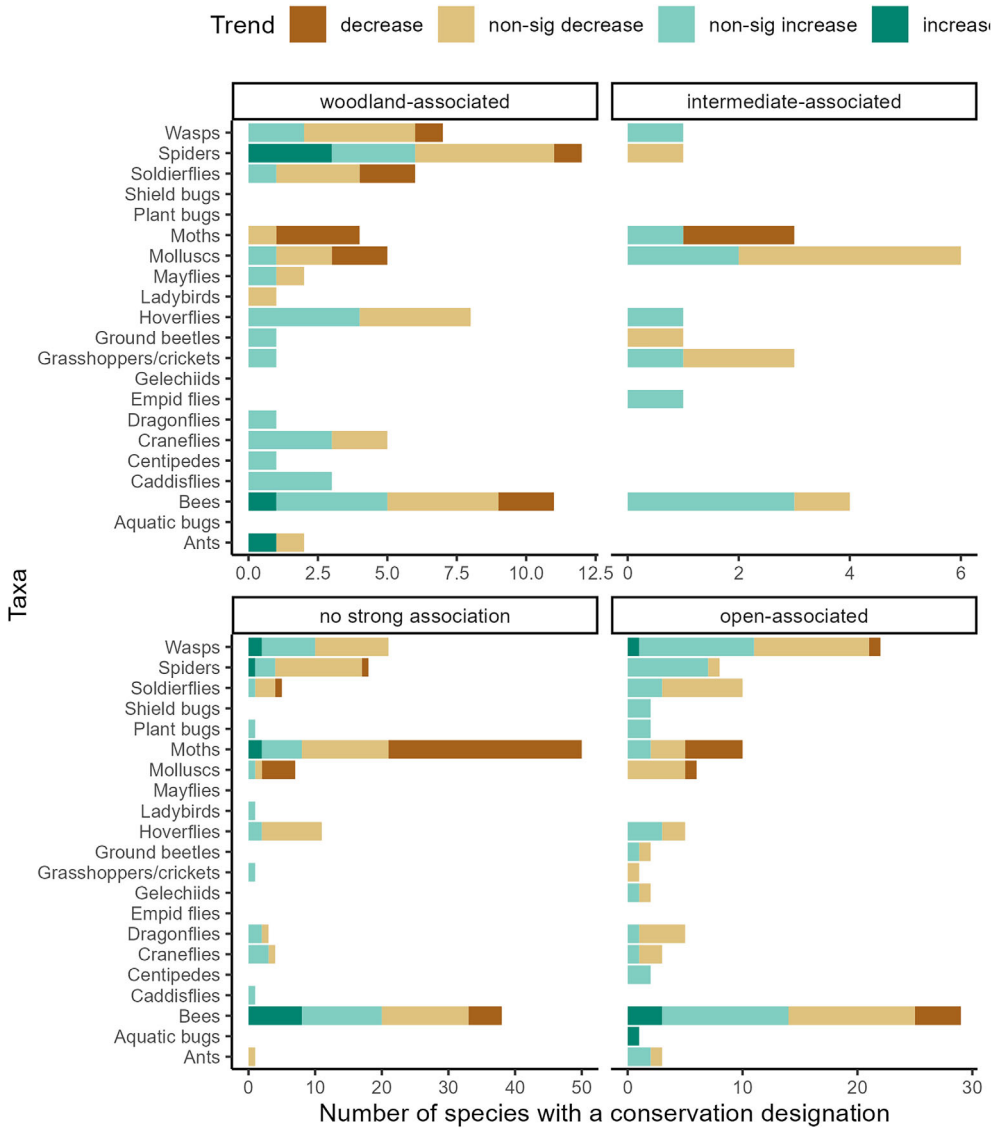

FIGURE 6 Number of species with a conservation designation according to the direction and significance of their distribution trends between 1970 and 2015 in Britain (shown by the colours) and their assigned broadleaf woodland association cluster (shown in the separate panels). Note the different y-axis scales.

including deadwood, structural heterogeneity and diverse ground vegetation that are important for invertebrates (Ditchburn et al., 2021; Fuller et al., 2018). While tree-planting schemes have created new woodlands, there has probably been insufficient time for them, in most cases, to become established with a diversity of structure/form (Fuentes-Montemayor, Watts, et al., 2022). Also, other factors that contribute to the poor condition of existing woodlands, such as grazing and browsing damage from herbivores and eutrophication, may be limiting the development, and biodiversity value, of new woodlands. In general, woodland habitats in Britain have tended to become more structurally homogeneous with more dense canopies and fewer clearings, with management practices limiting the development of old-growth features (Quine et al., 2011; Reid et al., 2021).

Invertebrate species can be associated with trees or woodland cover in diverse ways, but the low heterogeneity of British woodlands and associated low habitat quality has probably offered few opportunities for many species except the most generalist. Indeed, we found overall declines of woodland specialists of specific strata, occurring on woodland floor or arboreal habitats, although habitat classification data were not available for all species. Previous studies have especially highlighted the loss of open clearings and early succession areas in British woodlands due to a cessation or reduction of management practices such as coppicing, thinning and wood pasture (Thomas et al., 2015). Loss of coppiced woodlands has been linked with declines of specific woodland species such as the High Brown Fritillary butterfly (*Argynnis adippe*). Similarly, we found declines of the Little Emerald moth (*Jodis lactearia*), which favours open woodland. Thomas et al. (1994) found that many declining or threatened invertebrate species in the United Kingdom were associated with the earliest and latest seral stages of habitats including woodland clearings and

ancient trees. A more recent synthesis of invertebrate trends in the United Kingdom found evidence of widespread declines of species that specialise on early seral stages within woodland (Thomas et al., 2015), but their trends were not compared with those of other woodland habitats.

Broadleaf expansion has generally resulted in small, scattered woodlands rather than large blocks of woodland (Quine et al., 2011). This may explain why we found more positive increases of species that were associated with intermediate woodland cover—these species are likely those adapted to a heterogeneous landscape of small woodland patches within an open landscape. The fragmentation of existing woodlands and woodland species populations would also explain a slow recovery of woodland ecosystems and associated fauna. Even for highly mobile organisms such as birds, there can be large temporal lags before newly created habitat is colonised (Whytock et al., 2018). While evidence suggests that some woodland species colonise newly created sites (Fuller et al., 2018; Warner et al., 2021), generalists are usually the first to establish (Fuentes-Montemayor, Park, et al., 2022; Whytock et al., 2018). For woodland specialists, including saproxylic species, colonisation and recovery may be slow even if suitable habitat, such as dead wood, is available. Many studies agree on the importance of creating woodland in the right places, for instance, near ancient woodland, to facilitate the colonisation of woodland species, especially specialists (Burton et al., 2018). For some warm-adapted woodland species, climate change may foster their expansion and colonisation if woodlands are well-connected. For instance, we found positive trends of the jumping spider, *Ballus chalybeius*, a species with a conservation designation ('Nationally Scarce') that is especially associated with oak woodland, but its distribution has been so far mostly limited to southern England.

We focused on species' associations with woodland using land cover data at a coarse spatial-scale. Species' habitat associations, however, do not necessarily map onto vegetation types such as grassland or woodland (Dennis et al., 2014; Platts et al., 2019). Species' habitat use can also be defined in a broader sense by resource availability and environmental conditions. We were not able to capture many of the nuanced ways in which species use woodland habitats and the resources within them, at smaller spatial scales. Expert knowledge could help unpack some of these nuances, by defining the specific microhabitats, resource use and biotic interactions of species, which may help explain some of the variation in the trends of different woodland species that we observed. Better understanding of the diversity of woodland associations among species could help inform conservation action, not just in terms of land cover but also in terms of species' resource requirements (Dennis et al., 2006; Dennis et al., 2014).

Analysis at a final spatial-scale, lower than the 1 km of our study, could also help understand the effects of specific woodland attributes and proxies of woodland quality, although there is a lack of spatio-temporal data on different aspects of woodlands over our study period. Further work could also seek to understand interactions between woodland changes and other drivers of change. Invertebrate species trends are not solely affected by habitat cover (Wagner et al., 2021). A diverse range of drivers, including urbanisation, agricultural intensification and associated practices, climate change and pollution, contribute to observed insect declines. The absence of an increase in woodland invertebrates, despite increases in woodland cover, could be explained by overriding effects of these other drivers of change.

We analysed a large number of species of different taxa over nearly five decades, but our findings still have several limitations. First, our analysis was based on occurrence data not collected with a standardised protocol. Hence, some caution is needed when interpreting both our forest association estimates and the distribution trend estimates. To account for variation in sampling effort, we included a number of detection covariates in models (day of year and list length) (Bowler et al., 2021; Outhwaite et al., 2020) with these types of data. Nonetheless, the trend estimates could still be affected by changes in sampling effort through time that is unexplained by these covariates. Our estimates of forest association could be affected by spatial sampling biases: broadleaf woodlands tend to be sampled more than other habitats, while coniferous woodlands are under-sampled (Border et al., 2019). Scotland is generally under-recorded for invertebrates but has some of the highest woodland cover, and cover change, in the United Kingdom especially in coniferous woodland. Clearly large-scale standardised data would be preferable, but such data are not available for most invertebrates, except Lepidoptera. In the absence of standardised data, our analysis uses a common statistical approach to account for variation in recorder effort, and we expect that our general conclusions across our wide range of species and taxa are robust.

Our analysis highlights the diversity of woodland invertebrate species and their distribution trends. Despite general increases in woodland cover, several studies have already highlighted the lack of deadwood, ancient trees, open areas and structural diversity in British woodlands. Increases in woodland cover so far have probably not provided suitable new habitat for many woodland invertebrates. Currently, the United Kingdom has a target for 17% of woodland cover by 2050, but planting new woodlands will not instantly produce diverse structural forms of woodland that invertebrates need, even if managed appropriately. Careful spatial planning is needed to ensure that any future woodland creation balances the needs of both woodland and open habitat specialists, as well as carbon sequestration goals. Moreover, existing and new woodlands need to be carefully managed to ensure they have the habitat and resource heterogeneity to meet the diverse requirements of different woodland invertebrate species.

AUTHOR CONTRIBUTIONS

Diana E. Bowler: Writing – original draft; conceptualization; methodology; investigation. **Charles A. Cunningham:** Writing – original draft; writing – review and editing; conceptualization. **Colin M. Beale:** Conceptualization; writing – review and editing. **Lisa Emberson:** Writing – review and editing; conceptualization. **Jane K. Hill:** Writing – review and editing; funding acquisition; conceptualization. **Merryn Hunt:** Writing – review and editing; conceptualization. **Lindsay Maskell:** Writing – review and editing; conceptualization.

Charlotte L. Outhwaite: Writing – review and editing. **Piran C. L. White:** Writing – review and editing; funding acquisition; conceptualization. **Michael J.O. Pocock:** Writing – review and editing; conceptualization; methodology.

ACKNOWLEDGEMENTS

We thank the following recording schemes and societies for contributing data to the dataset underlying this study: Aquatic Heteroptera Recording Scheme; Bees, Wasps and Ants Recording Society; British Arachnological Society - Spider Recording Scheme; British Dragonfly Society - Dragonfly Recording Network; British Myriapod and Isopod Group - Centipede Recording Scheme; Conchological Society of Great Britain and Ireland; Cranefly Recording Scheme; Empididae, Hybotidae and Dolichopodidae Recording Scheme; Gelechiid Recording Scheme; Grasshoppers and Related Insects Recording Scheme; Ground Beetle Recording Scheme; Hoverly Recording Scheme; Butterfly Conservation - National Moth Recording Scheme; Riverfly Recording Schemes - Ephemeroptera, Soldierflies and Allies Recording Scheme; Riverfly Recording Schemes - Trichoptera; Terrestrial Heteroptera Recording Scheme - Plant bugs and allied species; Terrestrial Heteroptera Recording Scheme - Shield bugs and allied species; UK Ladybird Survey. We would like to thank Martin Harvey for advice on the datasets.

FUNDING INFORMATION

This work was supported by a project grant (NE/V02020X/1) within the UKRI Future of UK Treescapes Research Programme. The programme is funded by the Natural Environment Research Council (NERC), the Economic and Social Research Council (ESRC) and the Arts and Humanities Research Council (AHRC), with additional support from UK Government bodies—the Department for Environment, Food and Rural Affairs (Defra), Forestry Commission and the Scottish and Welsh Governments. CLO is funded by a UK Natural Environment Research Council grant (NE/V006533/1).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The occupancy-detection model predictions (annual occupancies) are available from Outhwaite et al. (2019). Code for analysis and data on species' woodland estimates are available at: https://doi.org/10.5281/zenodo.8298056.

ORCID

Diana E. Bowler https://orcid.org/0000-0002-7775-1668
Charles A. Cunningham https://orcid.org/0000-0001-7292-3144
Colin M. Beale https://orcid.org/0000-0002-2960-5666
Lisa Emberson https://orcid.org/0000-0003-3463-0054
Jane K. Hill https://orcid.org/0000-0003-1871-7715
Merryn Hunt https://orcid.org/0000-0003-4435-3644
Lindsay Maskell https://orcid.org/0000-0003-4006-7755
Charlotte L. Outhwaite https://orcid.org/0000-0001-9997-6780
Piran C. L. White https://orcid.org/0000-0002-7496-5775
Michael J. O. Pocock https://orcid.org/0000-0003-4375-0445

REFERENCES

Bateman, I.J., Anderson, K., Argles, A., Belcher, C., Betts, R.A., Binner, A. et al. (2022) A review of planting principles to identify the right place for the right tree for 'net zero plus' woodlands: applying a place-based natural capital framework for sustainable, efficient and equitable (SEE) decisions. *People and Nature*, 5, 271–301.

Bell, J.R., Blumgart, D. & Shortall, C.R. (2020) Are insects declining and at what rate? An analysis of standardised, systematic catches of aphid and moth abundances across Great Britain. *Insect Conservation and Diversity*, 13, 115–126.

Blumgart, D., Botham, M.S., Menendez, R. & Bell, J.R. (2022) Moth declines are most severe in broadleaf woodlands despite a net gain in habitat availability. *Insect Conservation and Diversity*, 15, 496–509.

Border, J., Gillings, S., Newson, S.E., Logie, M., August, T., Robinson, R.A. et al. (2019) The JNCC Terrestrial Biodiversity Surveillance Schemes: An Assessment of Coverage. JNCC Report No. 646, JNCC, Peterborough, ISSN 0963–8091.

Bowler, D.E., Eichenberg, D., Conze, K.J., Suhling, F., Baumann, K., Benken, T. et al. (2021) Winners and losers over 35 years of dragonfly and damselfly distributional change in Germany. *Diversity and Distributions*, 27, 1353–1366.

Bowler, D.E., Haase, P., Kroncke, I., Tackenberg, O., Bauer, H.G., Brendel, C. et al. (2015) A cross-taxon analysis of the impact of climate change on abundance trends in Central Europe. *Biological Conservation*, 187, 41–50.

Burton, V., Moseley, D., Brown, C., Metzger, M.J. & Bellamy, P. (2018) Reviewing the evidence base for the effects of woodland expansion on biodiversity and ecosystem services in the United Kingdom. *Forest Ecology and Management*, 430, 366–379.

Citores, L., Ibaibarriaga, L., Lee, D.J., Brewer, M.J., Santos, M. & Chust, G. (2020) Modelling species presence-absence in the ecological niche theory framework using shape-constrained generalized additive models. *Ecological Modelling*, 418, 108926.

Committee on Climate Change. (2019) Net Zero: The UK's contribution to stopping global warming.

Daskalova, G.N., Myers-Smith, I.H., Bjorkman, A.D., Blowes, S.A., Supp, S.R., Magurran, A.E. et al. (2020) Landscape-scale forest loss as a catalyst of population and biodiversity change. *Science*, 368, 1341–1347.

Defra. (2021) Biodiversity 2020: a strategy for England's wildlife and ecosystem services. Indicator.

Dennis, R.L., Dapporto, L. & Dover, J.W. (2014) Ten years of the resource-based habitat paradigm: the biotope-habitat issue and implications for conserving butterfly diversity. *Journal of Insect Biodiversity*, 2, 1–32.

Dennis, R.L.H., Shreeve, T.G. & Van Dyck, H. (2006) Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodiversity and Conservation*, 15, 1943–1966.

Ditchburn, B., Wilson, T., Henderson, L., Kirby, K. & Steel, P. (2021) Woodland ecological condition in Britain, National Forest Inventory, Forestry Commission.

Douglas, D.J.T., Groom, J.D. & Scridel, D. (2020) Benefits and costs of native reforestation for breeding songbirds in temperate uplands. *Biological Conservation*, 244, 108483.

Forest Research. (2021) Forestry Statistics. https://www.forestresearch.gov.uk/tools-and-resources/statistics/forestry-statistics/forestry-statistics-2021

Fox, R., Brereton, T.M., Asher, J., August, T.A., Botham, M.S., Bourn, N.A.D. et al. (2015) The State of the UK's Butterflies 2015, Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, Dorset. Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset BH20 5Q.

Fuentes-Montemayor, E., Park, K.J., Cordts, K. & Watts, K. (2022) The long-term development of temperate woodland creation sites: from tree saplings to mature woodlands. *Forestry*, 95, 28–37.

Fuentes-Montemayor, E., Watts, K., Sansum, P., Scott, W. & Park, K.J. (2022) Moth community responses to woodland creation: the influence of woodland age, patch characteristics and landscape attributes. *Diversity and Distributions*, 28, 1993–2007.

Fuller, L., Fuentes-Montemayor, E., Watts, K., Macgregor, N.A., Bitenc, K. & Park, K.J. (2018) Local-scale attributes determine the suitability of woodland creation sites for Diptera. *Journal of Applied Ecology*, 55, 1173–1184.

Fuller, R.M.S., G.M., Sanderson, J.M., Hill, R.A., Thomson, A.G., Cox, R. et al. (2002) *Land cover map 2000 (1km percentage aggregate class, GB)*. NERC Environmental Information Data Centre, UK. https://eidc.ac.uk/

Fyfe, R.M., Twiddle, C., Sugita, S., Gaillard, M.J., Barratt, P., Caseldine, C.J. et al. (2013) The Holocene vegetation cover of Britain and Ireland: overcoming problems of scale and discerning patterns of openness. *Quaternary Science Reviews*, 73, 132–148.

Gaul, W., Sadykova, D., White, H.J., Leon-Sanchez, L., Caplat, P., Emmerson, M.C. et al. (2022) Modelling the distribution of rare invertebrates by correcting class imbalance and spatial bias. *Diversity and Distributions*, 28, 2171–2186.

Gerard, F., Petit, S., Smith, G., Thomson, A., Brown, N., Manchester, S. et al. (2010) Land cover change in Europe between 1950 and 2000 determined employing aerial photography. *Progress in Physical Geography-Earth and Environment*, 34, 183–205.

Gregory, R.D., Skorpilova, J., Vorisek, P. & Butler, S. (2019) An analysis of trends, uncertainty and species selection shows contrasting trends of widespread forest and farmland birds in Europe. *Ecological Indicators*, 103, 676–687.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H. et al. (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, 12, e0185809.

Harmer, R., Watts, K. & Ray, D. (2015) A hundred years of woodland restoration in Great Britain: changes in the drivers that influenced the increase in woodland cover. In: *Restoration of boreal and temperate forests*, Vol. 2nd Edition. CRC Press, p. 22.

Harrison, P.J., Yuan, Y., Buckland, S.T., Oedekoven, C.S., Elston, D.A., Brewer, M.J. et al. (2016) Quantifying turnover in biodiversity of British breeding birds. *Journal of Applied Ecology*, 53, 469–478.

Hennig, C. (2020) Flexible Procedures for Clustering. In R package version 2.2-9. https://cran.r-project.org/package=fpc

Hewson, C.M., Amar, A., Lindsell, J.A., Thewlis, R.M., Butler, S., Smith, K. et al. (2007) Recent changes in bird populations in British broadleaved woodland. *Ibis*, 149, 14–28.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A. & Lindquist, E. (2015) Dynamics of global forest area: results from the FAO global Forest resources assessment 2015. *Forest Ecology and Management*, 352, 9–20.

Macgregor, C.J., Williams, J.H., Bell, J.R. & Thomas, C.D. (2021) Moth biomass has fluctuated over 50 years in Britain but lacks a clear trend. *Nature Ecology & Evolution*, 5, 865–883.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M. & Hornik, K. (2022) cluster: Cluster Analysis Basics and Extensions. In R package version 2.1.4. https://cran.r-project.org/package=cluster

Mason, W.L. (2007) Changes in the management of British forests between 1945 and 2000 and possible future trends. *Ibis*, 149, 41–52.

Montgomery, G.A., Dunn, R.R., Fox, R., Jongejans, E., Leather, S.R., Saunders, M.E. et al. (2020) Is the insect apocalypse upon us? How to find out. *Biological Conservation*, 241, 108327.

Morton, R.D.R., C.S., Wood, C.M., Meek, L., Marston, C.G. & Smith, G.M. (2014) *Land Cover Map 2007 (1km percentage aggregate class, GB) v1.2*. NERC Environmental Information Data Centre, UK. https://eidc.ac.uk/

Outhwaite, C.L., Gregory, R.D., Chandler, R.E., Collen, B. & Isaac, N.J.B. (2020) Complex long-term biodiversity change among invertebrates, bryophytes and lichens. *Nature Ecology & Evolution*, 4, 384–392.

Outhwaite, C.L., Powney, G.D., August, T.A., Chandler, R.E., Rorke, S., Pescott, O.L. et al. (2019) Annual estimates of occupancy for bryophytes, lichens and invertebrates in the UK, 1970-2015. *Scientific Data*, 6, 259.

Platts, P.J., Mason, S.C., Palmer, G., Hill, J.K., Oliver, T.H., Powney, G.D. et al. (2019) Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. *Scientific Reports*, 9, 15039.

Pocock, M.J.O., Roy, H.E., Preston, C.D. & Roy, D.B. (2015) The biological records Centre: a pioneer of citizen science. *Biological Journal of the Linnean Society*, 115, 475–493.

Pörtner, H.O., Scholes, R.J., Agard, J., Archer, E., Arneth, A., Bai, X. et al. (2021) *IPBES-IPCC co-sponsored workshop report on biodiversity and climate change*. IPBES and IPCC. https://doi.org/10.5281/zenodo.4782538

Quine, C.P., Cahalan, C., Hester, A., Humphrey, J., Kirby, K., Moffat, A. et al. (2011) National Ecosystem Assessment – woodlands chapter. In: The UK National Ecosystem Assessment Technical Report. UK National Ecosystem Assessment, UNEP-WCMC, Cambridge.

R Core Team. (2021) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raum, S. (2020) Land-use legacies of twentieth-century forestry in the UK: a perspective. *Landscape Ecology*, 35, 2713–2722.

Reid, C., Hornigold, K., McHenry, E., Nichols, C., Townsend, M., Lewthwaite, K. et al. (2021) *State of the UK's woods and trees 2021*. Woodland Trust.

Robinson, O.J., Ruiz-Gutierrez, V., Reynolds, M.D., Golet, G.H., Strimas-Mackey, M. & Fink, D. (2020) Integrating citizen science data with expert surveys increases accuracy and spatial extent of species distribution models. *Diversity and Distributions*, 26, 976–986.

Rowland, C.S.M., R.D., Carrasco, L., McShane, G., O'Neil, A.W. & Wood, C.M. (2017) *Land cover map 2015 (1km percentage target class, GB)*. NERC Environmental Information Data Centre, UK. https://eidc.ac.uk/

Rowland, C.S.M., C.G., Morton, R.D. & O'Neil, A.W. (2020) *Land Cover Map 1990 (1km percentage target class, GB) v2*. NERC Environmental Information Data Centre, UK. https://eidc.ac.uk/

Simpson, G. (2022) gratia: Graceful ggplot-Based Graphics and Other Functions for GAMMs Fitted using mgcv. In R package version 0.7.3. https://gavinsimpson.github.io/gratia/

Spake, R. & Doncaster, C.P. (2017) Use of meta-analysis in forest biodiversity research: key challenges and considerations. *Forest Ecology and Management*, 400, 429–437.

Spencer, J.W. & Kirby, K.J. (1992) An inventory of ancient woodland for England and Wales. *Biological Conservation*, 62, 77–93.

Staab, M., Gossner, M.M., Simons, N.K., Achury, R., Ambarli, D., Bae, S. et al. (2023) Insect decline in forests depends on species' traits and may be mitigated by management. *Communications Biology*, 6, 338.

Thomas, J.A., Edwards, M., Simcox, D.J., Powney, G.D., August, T.A. & Isaac, N.J.B. (2015) Recent trends in UK insects that inhabit early successional stages of ecosystems. *Biological Journal of the Linnean Society*, 115, 636–646.

Thomas, J.A., Morris, M.G. & Hambler, C. (1994) Patterns, mechanisms and rates of extinction among invertebrates in the United-Kingdom. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 344, 47–54.

Tordoff, G.M., Dennis, E.B., Fox, R., Cook, P.M., Davis, T.M., Blumgart, D. et al. (2022) Inconsistent results from trait-based analyses of moth

trends point to complex drivers of change. *Biodiversity and Conservation*, 31, 2999–3018.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A. & Chase, J.M. (2020) Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, 368, 417–420.

Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R. & Stopak, D. (2021) Insect decline in the Anthropocene: death by a thousand cuts. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2023989118.

Warner, E., Hector, A., Brown, N., Green, R., Savory, A., Gilbert, D. et al. (2021) The response of plants, carabid beetles and birds to 30 years of native reforestation in the Scottish highlands. *Journal of Applied Ecology*, 58, 2185–2194.

Webb, J., Heaver, D., Lott, D., Dean, H.J., van Breda, J., Curson, J. et al. (2018) Pantheon – database version 3.7.6.

Whytock, R.C., Fuentes-Montemayor, E., Watts, K., De Andrade, P.B., Whytock, R.T., French, P. et al. (2018) Bird-community responses to habitat creation in a long-term, large-scale natural experiment. *Conservation Biology*, 32, 345–354.

Woodbridge, J., Fyfe, R.M., Roberts, N., Downey, S., Edinborough, K. & Shennan, S. (2014) The impact of the Neolithic agricultural transition in Britain: a comparison of pollen-based land-cover and archaeological C-14 date-inferred population change. *Journal of Archaeological Science*, 51, 216–224.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

How to cite this article: Bowler, D.E., Cunningham, C.A., Beale, C.M., Emberson, L., Hill, J.K., Hunt, M. et al. (2023) Idiosyncratic trends of woodland invertebrate biodiversity in Britain over 45 years. *Insect Conservation and Diversity*, 1–14. Available from: https://doi.org/10.1111/icad.12685