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Assessing species' habitat associations from occurrence records, standardised monitoring data and expert opinion: A test with British butterflies

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Abstract

Accurate knowledge of species' habitat associations is important for conservation planning and policy. Assessing habitat associations is a vital precursor to selecting appropriate indicator species for prioritizing sites for conservation or assessing trends in habitat quality. However, much existing knowledge is based on qualitative expert opinion or local scale studies, and may not remain accurate across different spatial scales or geographic locations. Data from biological recording schemes have the potential to provide objective measures of habitat association, with the ability to account for spatial variation. We used data on 50 species of British butterfly as a test case to investigate the correspondence of data-derived measures of habitat association with expert opinion, from two different butterfly recording schemes. One scheme collected large quantities of occurrence data (c.3 million records) and the other, lower quantities of standardised monitoring data (c.1400 sites). We used general linear mixed effects models to derive scores of association with broad-leaf woodland for both datasets and compared them with scores canvassed from experts.

Scores derived from occurrence and abundance data both showed strongly positive correlations with expert opinion. However, only for occurrence data did these fell within the range of correlations between experts. Data-derived scores showed regional spatial variation in the strength of butterfly associations with broad-leaf woodland, with a significant latitudinal trend in 26% of species. Sub-sampling of the data suggested a mean sample size of 5000 occurrence records per species to gain an accurate estimation of habitat association, although habitat specialists are likely to be readily detected using several hundred records. Occurrence data from recording schemes can thus provide easily obtained, objective, quantitative measures of habitat association.

Key words: spatial variation, recording scheme, citizen science, latitudinal gradient, biological indicators

1. Introduction

Associations between species and habitats are one of the basic principles of ecology (Aarts et al. 2013; Yapp 1922). As habitat loss remains the primary cause of global biodiversity declines (Brooks et al. 2006; Thomas et al. 2004) identifying such associations accurately is important for conservation planning, policy and research. Where species are in decline, accurate information on habitat associations is required so that investigations into likely causes, and subsequent implementation of conservation efforts, can be targeted correctly. Likewise, if a particular habitat is undergoing change, well characterised associations enable predications to be made about which species are most likely to be affected. Accurate knowledge of associations is also vital to selecting appropriate indicator species for use in prioritizing sites for conservation, monitoring environmental conditions or assessment of habitat quality (Carignan and Villard 2002).

Although the habitat associations of some taxa are well characterised, most species are poorly studied. Even for well-studied taxa there may be limitations to our understanding of habitat associations at large spatial scales (Gregory and Baillie 1998) as many studies are carried out at a local level in response to specific conservation issues (e.g. Knight and Arthington 2008; Loeb et al. 2000; Rouquette and Thompson 2005). As a result, information on wider scale habitat associations, including that which forms the foundations of much conservation policy, is often extrapolated from such studies or from qualitative descriptions based on expert opinion (Reif et al. 2010). This is potentially problematic, as both habitat associations and expert perceptions of them have been demonstrated to vary with location (O'Leary et al. 2009; Oliver et al. 2009), spatial scale (Mayor et al. 2009) and environmental change (Pateman et al. 2012). It is thus important to test existing knowledge on habitat associations against quantitative methods. These have the potential to operate at a range of spatial scales, and to take into account spatial or temporal variation. Such methods also have the potential to uncover cryptic requirements or previously unknown plasticities in habitat association.

National or international biological recording and monitoring schemes provide a valuable source of data for analysing large scale patterns in time and space (Bishop et al. 2013; Thomas 2005). Large sample sizes and extensive spatial coverage make them well suited to use in detecting habitat associations. However, monitoring scheme data vary in quality and quantity, from simple occurrence data (i.e. georeferenced records of species' presence) to detailed demographic data from standardised protocols. Whilst datasets at all points along this spectrum have their value for specific applications, it is important to test which are most suitable for detecting habitat associations, especially as increasing levels of information come at a cost of time and effort in collection, and, consequently, in the number and spatial coverage of records (Bishop et al. 2013).

This study used two different butterfly recording scheme datasets - one comprising large quantities of occurrence data and the other, lower quantities of abundance data from a standardised monitoring scheme - alongside data on the extent of British broad-leaf woodland. Butterflies are a useful test case for determining habitat associations. They are frequently used as indicator species (Thomas 2005) as their host plant specificity and temperature-dependent development and behaviour make them sensitive to environmental changes, whilst their short life cycles ensure that they respond quickly (Oliver et al. 2009; Pateman et al. 2012; Warren et al. 2001). In Britain, they are well recorded, giving sufficient data for analyses, and well-studied, such that expert opinions are likely to be well-founded and consistent and thus a good yardstick by which to measure the performance of data-derived measures of habitat association. We compared data-derived methods for calculating metrics of habitat association from the two butterfly datasets with expert opinion, including their ability to account for spatial variation in association, and assessed the applicability of these methods to other taxa for which data-derived methods might form the only means by which to assess species' habitat associations.

2. Methods

2.1. Species data

We obtained data on 50 butterfly species in Great Britain (GB) from two monitoring schemes – Butterflies for the New Millennium (BNM) and the UK Butterfly Monitoring Scheme (UKBMS). Species nomenclature follows Agassiz et al. (2013).

BNM is a national scheme which collates butterfly records (i.e. species occurrence at a location), with the aim of maintaining an up-to-date database of butterfly distributions (Asher et al. 2001). This study included only BNM records with spatial resolution of 1 km x 1 km Ordnance Survey grid cell or finer. Duplicate records of the same species in the same cell were removed, resulting in a dataset of approximately 3 million butterfly occurrence records. The study used records from 1990 - 2010, to decrease the likely effect of changes over time in woodland extent or habitat association on the results.

The UKBMS differs from BNM in aiming to monitor population trends through a standardized survey method involving weekly visits between April and September (Pollard and Yates 1993). Although this allows calculation of abundance throughout each survey year and thus analysis of population trends and phenology, it is relatively labour intensive and there are records from far fewer sites than in BNM (data from 1433 sites were included in our analysis).

Although the spatial scale of GB reflects an artificial imposition onto an ecologically meaningful hierarchy of scales, being neither the full range of a species nor of an individual butterfly, it reflects the scale at which national policy for particular species and habitats tends to be formulated (Roy et al. 2007) and at which biological recording schemes tend to be coordinated.

2.2. Habitat data

Broad-leaf woodland data were obtained from the Land Cover Map 2007 (LCM2007, Morton et al. 2011). We chose this habitat because it is well characterised in LCM2007 and includes various habitats which are prominent in UK planning and policy (e.g. ancient broad-leaf woodland, DEFRA 2011). The proportion of broad-leaf woodland was calculated for every 1 km grid cell in mainland GB and for a 500 m radius around each UKBMS site centroid, giving a consistent scale of analysis between datasets. This scale also reflects the relatively coarse resolution at which much large scale habitat data is readily available. These analyses were performed in ArcGIS (v 9.3.1 © 2010 ESRI, Redlands, California).

2.3. Scoring habitat association from biological recording data

Analyses were performed independently. To distinguish 'genuine' absences for each species from a 1 km cell in the BNM data, as opposed to pseudoabsence generated by lack of recorders or non-detection (Prendergast et al. 1993), we applied a threshold of species detection. Cells in which more than five butterfly species were recorded (i.e. c. 10% of the total UK species pool, following Hickling et al. (2006)) but which lacked a record of the species in question were assumed to be genuine absences, whilst others were removed from all further analyses. We did not use more analytically complex methods of accounting for recorder effort (e.g. Hill 2012; Isaac et al. 2014; Mason et al. 2015) because UK butterflies are generally well recorded, not particularly speciose, and have several ubiquitous species which are well recorded across the entire of the country. Therefore, although there is a latitudinal gradient in butterfly species richness in the UK, the 5 species threshold is met by a relatively consistent proportion of cells per region supplementary material, Table S2). Whilst butterfly species have been shown to vary in detectability (Isaac et al. 2011) there is little evidence for a systematic bias whereby the detectability of individuals varies with woodland area and where this relationship varies between species, which would be the only situation in which detectability would automatically influence relative habitat association scores. To account for potential variation in species' habitat associations across GB, data were analysed on a regional basis, splitting the dataset into 100 km by 100 km cells (from here on referred to as a 100 km region). Regions where a species had less than 30 of each of presence and 'genuine' absence records were unlikely to provide robust estimates and were excluded. We also limited analyses to species that were recorded on a minimum of ten UKBMS sites.

General linear mixed effects models (GLMM) were used to model the relationships between habitat and butterflies, using the *lme4* (Bates et al. 2013) package in R (R Core Team 2013). For the BNM data, we fitted species presence/absence to proportion of broad-leaf woodland cover in the 1 km grid cell, with a binomial error structure. For UKBMS data the fixed explanatory variable was proportion of woodland in the 500m radius buffer whilst the response variable was total annual count, adjusted for missing visits (Rothery and Roy 2001); therefore, a Poisson error structure was specified. Due to the presence of zero counts for some species, we also tested analyses using zero-inflated Poisson models or summing data across all years to reduce zero counts, but the species' habitat association scores resulting from these models showed lower correlation with independent data from expert opinion (see section 2.4). For all models, 100 km region (BNM data) or Site ID (UKBMS data) was included as a random intercept, in order to account for spatial variation in the mean frequency of butterflies and multiple measurements across years from the same site. Preliminary analyses, comparing AIC of models with different random effect structures, also supported the inclusion of a random slope whereby the relationship between proportion of woodland and butterfly occurrence could vary by 100km region. For both datasets, the slope of the GLMM was then designated to represent the mainland GB habitat association score, set to zero where the p value was greater than 0.05.

To further investigate variation in habitat association by 100km region, we ran independent general linear models in each region. This is more appropriate than extracting the corresponding random slopes from the GLMM because of the issue of shrinkage towards the expected mean slope in regions where the sample size is lower (Gelman and Hill 2007). A possible driver of spatial variation in scores was investigated by performing linear regression of regional score against latitude, as latitudinal gradients affect many aspects of British butterfly ecology (Oliver et al. 2009; Oliver et al. 2012; Oliver et al. 2014; Thomas et al. 1994; Turner et al. 1987).

2.4. Scoring habitat association from expert opinion

To test the performance of the data-derived scores against established opinion, five butterfly experts from research or conservation organisations (including authors TB and RF) were asked to rank the species in order of woodland association, from one (strong negative association) to 50 (strong positive association), such that each of the 50 species could be assigned a unique rank if experts deemed this suitable. Experts were requested to base rankings on where adult butterflies might be expected to be encountered, rather than limiting association to breeding habitat. The mean and median rankings of each species were then taken to represent average expert-derived association scores for comparison with data derived scores.

2.5. Determining minimum sample size for estimating habitat association

In order to investigate the number of samples required to detect habitat associations via the data-derived methods we took random samples of presence records at a range of sample sizes, for each species. Abundance data was not re-sampled, as it showed lower correlation with expert scores (see results, section 3.2). Sample sizes analysed ranged from 100 to 1000 at intervals of 100, and from 1000 to 50000 at intervals of 500, with random sampling of occurrence records being repeated 100 times for each sample size. Each sample was then used to score habitat association using the GLMM, and the resultant scores for each sample size and species compared to expert scores. The sample size required for the ranking of the mean score from the 100 re-samplings to fall within the mean range of expert scores was then held to be the minimum sample size required for estimation of habitat association for that species (i.e. the sample size at which the ranked score is no more variable than expert scorings are from one another). We then compared these minimum sample sizes between species, and to the sample sizes typically available for species from other British taxa, applying the same selection criteria to these records as to those drawn from the BNM data (i.e. the year 1990 onwards, with 1 km precision).

3. Results

3.1. Variation in expert scores

Correlation between the habitat association scores from the two data-derived methods was significant and positive (Pearson's r, r = 0.727, p < 0.001) but with much variation in the degree of association assigned to individual species (see supplementary material, Table S1, for full table of association scores). Correlations between expert scores were always significant and strongly positive (p < 0.001). However, expert opinions also showed a considerable amount of variation in ranking of individual species (Figure 1). There was complete consensus in ranking only for the two highest ranked species, Purple Emperor *Apatura iris* and White Admiral *Limenitis camilla*, although other species also showed little variation in ranking - for example, Brown Hairstreak *Thecla betulae,* Silver-washed Fritillary *Argynnis paphia* and Adonis Blue *Polyommatus bellargus*.

3.2. Comparing data-derived scores with expert scores

All correlation coefficients between each expert's rank score and the ranked score from occurrence data (r = 0.646 to 0.849) were significantly positive (p < 0.001) and lay within the range of correlations between experts (r = 0.626 to 0.909), suggesting that this method produces rankings which are no more variable from expert opinion than variation between experts. However, correlation coefficients between expert rank scores and the score from abundance data (0.554 to 0.611) were lower than all correlations between experts, suggesting that this method produced rankings which varied more from expert opinion than the least concurrent pair of experts. Correlations between the occurrence derived score and the mean and median expert scores (r = 0.794, r = 0.748, respectively) were higher than for the abundance-derived scores (r = 0.724, r = 0.699, respectively). The abundance-derived score also showed a greater number of species where the data-derived ranked score fell outside the range of all expert scores (Figure 2b). These included White-letter Hairstreak *Satyrium w-album*, which was given only an intermediate ranking by the abundance data but was amongst the highest ranked (i.e most strongly woodland associated) by experts, and Large Heath *Coenonympha tullia*, which was also assigned an intermediate ranking by the abundance data despite expert opinion giving it one of the lowest rankings. The occurrence data-derived score showed fewer outliers (Figure 2a) although some species were still given rankings which differed substantially from those given by experts. For example, Brown Hairstreak was ranked higher by all experts than by occurrence data, whilst Marsh Fritillary *Euphydryas aurinia* was ranked lower.

Most species showed variation in habitat association scores between 100km regions, which was in many cases significantly correlated with latitude (see supplementary material, Table S1). Such variation usually affected the strength of association, rather than reversing the direction of the relationship. An example, for Ringlet *Aphantopus hyperantus*, is shown in Figure 3, where associations were stronger in the south of GB and declined in strength with increasing latitude.

3.3. Re-sampling to determine minimum sample size for estimating habitat association

The re-sampling of occurrence records showed that, across all species, the minimum sample size for which the mean data-derived score fell within the range of expert scores had a mean of 5480 (standard error = ± 1750), equivalent to a mean of 223 occurrence records per 100km region. However, this required minimum sample size showed considerable variation between species (see supplementary material, Table S1). Species at either extreme of woodland association as determined by the full-sample score and by expert opinion (i.e. with low or no significant woodland association, or with high woodland association), tended to require comparatively low sample sizes (100 - 1000) to come within the range of expert scores. Those species with moderate woodland association scores frequently required higher sample sizes to come within the range of expert scores. The mean across species was thus heavily influenced by a few species which required large sample sizes, such that the mean required sample size for the ten species which showed the strongest woodland associations (highest full-sample scores) was reduced to 1155 (standard error = ± 815). The five most strongly woodland associated species which were suitable for analysis by re-sampling (*Limenitis camilla, Argynnis paphia, Apatura iris, Favonius quercus, Leptidea sinapis*) required even lower sample sizes, with a mean of 400 (standard error = ± 109).

4. Discussion

Our results showed that occurrence data have the potential to generate objective, quantitative habitat association scores which correlate strongly with expert opinion. Scores from occurrence data showed fewer deviations from expert opinion than did those from abundance data, especially for specialist species (i.e. those at either extreme of the spectrum of woodland association). For abundance data, the appearance of more scores which are strongly counter to expert opinion and a lesser correlation with expert rankings, suggests that, invaluable though these data are for monitoring population trends, they are less suitable for estimating habitat associations for certain species. This may in part be an issue of statistical power, with the number of data points for occurrence data (i.e. geographical locations) being orders of magnitude greater than for abundance data, especially for less widespread, specialist species (e.g. Large Heath, see supplementary material, Table S1). This difference in sample sizes is due to the fact that it is less intensive in terms of time and effort, both in design of the monitoring scheme and in actual data collection, to acquire additional occurrence data than to set up additional standardised population monitoring sites (Bishop et al. 2013). There are also other issues including potential bias in the selection of locations for standardised monitoring transects toward the highest quality or most accessible habitats. It thus appears that in the case of assessing habitat associations, it may be better to use large quantities of simple occurrence data than more detailed standardised monitoring datasets.

Existing, and widely used, data-derived metrics of habitat association such as IndVal (Cáceres and Legendre 2009; Dufrene and Legendre 1997) compare abundance or frequency of species between sites showing known differences in habitat. These rely on the location at which the organism is recorded being a true reflection of the habitat with which it is associated. This is likely to be true at larger spatial scales, and for sessile organisms or extensive habitats. However, many recording schemes vary in the accuracy with which locations are recorded, so that the exact habitat in which the species was observed is not known. In addition to this, the habitat where a species is primarily found may only partly reflect the full range of resources required to complete its life cycle. In the case of butterflies these include host plants, nectar plants and roosting sites (Dennis et al. 2003). Our approach thus has the advantage of increasing the likelihood of capturing all essential resources by testing the importance of the total proportion of a given habitat type at the landscape-scale.

There are still obvious limitations to this method, as not every important factor determining habitat suitability is well represented by cover of a readily mapped habitat type. Such factors for butterflies may include microclimates for egg laying, pupation and shelter, the presence of parasitoids or larval hosts and specific resources for larval and adult feeding (Dennis et al. 2006; Dennis et al. 2003; Krämer et al. 2012). Also, species are rarely restricted to only one type of habitat, and there is the possibility that individuals, populations or species may adapt their habitat affinities if the primary habitat is depleted or degraded (Merckx et al. 2003; Merckx and Van Dyck 2006; Proença and Pereira 2013). Even where this does not occur, species may also receive benefits from habitats other than the one which primarily determines their occurrence. For example, Villemey et al. (2015) found that grassland butterfly richness and abundance were affected to a greater extent by local woodland cover than by connectivity of the primary grassland habitat. For these reasons, the data derived scores reported here should not be assumed to have captured all the information required for successful species conservation. However, they should provide a robust method for assessing which species are most strongly associated with a particular habitat of concern and *vice versa*, a vital preliminary step in much conservation planning and policy.

Studies comparing or combining expert opinion with data-derived methods to optimise habitat association models have shown varied results (e.g. Clevenger et al. 2002; Kuhnert et al. 2005; O'Leary et al. 2009; Pearce et al. 2001; Reif et al. 2010; Seoane et al. 2005). This variation is potentially driven by differences in the accuracy of expert knowledge across different locations and taxa, as well as differences in the interpretation of a particular habitat type (O'Leary et al. 2009). The latter probably accounts for some of the observed differences between expert opinion and occurrence data in this study. For example, Purple Emperor and Brown Hairstreak are both specialists of specific woodland types which comprise only a small part of the LCM2007 land cover map broad-leaf woodland class - the former of extensive, mature woodlands with a tall canopy and the latter of scrub and wood edge habitats, as well as hedgerows, which are not detected by LCM2007.

Unlike many other taxa, GB butterflies are likely to be sufficiently well studied that expert opinion should be well-founded, and thus a good yardstick by which to measure the performance of data-derived methods. Despite this, scores varied to some extent between experts. This illustrates the difficulty of using expert opinion to move beyond qualitative descriptions, even to a simple, ordinal ranking for such a well-studied taxon as British butterflies. Variation amongst experts was especially notable for common, widespread or mobile generalist species which received intermediate rankings (Figure 1). Ranking the association of such species with a particular habitat is particularly challenging, so data-derived methods may be better able to detect subtle differences in habitat association between species, especially where environmental change has created differences in habitat use which are not immediately apparent or where expert opinion is likely to be less well informed or less up to date than for such a well monitored group as UK butterflies (Pateman et al. 2015; Pearce et al. 2001; Seoane et al. 2005). Experts are also likely to be most familiar with a particular geographic area and base their scorings upon this knowledge. However, our results

(Figure 3), along with previous studies (Mayor et al. 2009; O'Leary et al. 2009; Oliver et al. 2009) show the existence of spatial variation in habitat association for some species. Thus, expert opinion is not necessarily transferable between geographic locations or spatial scales (Pearce et al. 2001), so it may be advantageous to employ data-derived methods on data gathered over large spatial scales to allow variation in habitat associations to be assessed, unless a range of experts can be canvassed whose expertise cover the entire geographic area of interest. The observed spatial variation in habitat association also has important implications for conservation. The Ringlet, as shown in figure 3, has previously been shown to exhibit shifts to core habitats under drought conditions (Sutcliffe et al. 1997), so it is possible that sensitivity to drought drives the stronger affinity with woodland in warmer, drier (i.e. Southern) areas of Britain, as has been demonstrated for this and other species (Oliver et al. 2009; Oliver et al. 2015; Pateman et al. 2015; Suggitt et al. 2012). Such interactions between habitat and climatic variables are important to consider in the light of ongoing environmental change and conservation efforts to mitigate its effects (Fox et al. 2014; Oliver et al. 2015).

Examining the association with a single habitat does have the disadvantage that it is difficult to imply causation – for example, a species showing a positive association with broadleaved woodland could, in theory, be using a different habitat type which co-varies with woodland area (Botham et al. 2015). However, whilst some significant correlations between broad habitats occurred at the regional level (supplementary material, table S2), across 100km regions, there were no consistently strong correlations between broadleaved woodland and any other land cover class (see supplementary material, table S2), suggesting that there is no overall issue with broadleaved woodland simply being a measure of some other habitat. Although this study focussed on woodland as a test case, the methodology is equally applicable to any habitat (or, potentially, other environmental variables) with information on spatial coverage. Analyses could thus be run for a range of land cover types to find those with the highest association for each species, or by comparing scores from independent models with increasing levels of habitat specificity (e.g. broad-leaf woodland, ancient broad-leaf woodland, ancient oak woodlands).

The use of occurrence data to detect species habitat associations is likely to be most valuable for other taxa for which expert opinions are likely to be more region specific, or for which there is no consensus or insufficient study to form reliable expert opinions (Seoane et al. 2005). In such cases, occurrence data can be relatively easily gathered from a range of sources (historical records, casual species observations or national recording schemes) and so useable sample sizes may well be available for a comparatively large number of species. Occurrence data also have the advantage that the data collected is consistent (a species, a date and a geographical location), rather than the broad range of methodologies employed in standardised monitoring schemes for different taxa, such that the methods described in this study are likely to be applicable across taxa. Of course, such data is only useful alongside contemporaneous environmental data, but this is becoming increasingly plausible given the increasing availability of spatial environmental datasets, including digitized historic mapping. Other issues associated with the use of occurrence data, particularly the need to account for biases introduced by spatial and temporal accounting for recorder effort, have also developed an extensive literature, with a range of methods now available (Hill 2012; Isaac et al. 2014; Mason et al. 2015). Such methods are likely to be a vital prerequisite in using the methods described here to estimate habitat associations for poorly recorded or highly speciose groups, or those with complex patterns of species richness or recorder effort.

The differences in the number of occurrence records required to derive habitat association scores which fall within the range of those given by experts are unsurprising. It is highly likely to be easier to detect stronger habitat associations at lower sample sizes. Those species requiring the largest sample sizes for convergence with the expert scores were, accordingly, mostly widespread generalists with moderate woodland association from the full-sample scores and expert ranking (e.g. the Comma *Polygonia c-album*). Not only are larger sample sizes required to detect weak relationships, but these species often showed significant spatial variation in their association scores (see supplementary material, Table S1). So, whilst 5000 records might be required to ensure accurate detection of subtle or cryptic habitat associations, detecting those species with strong associations is likely to be possible with several hundred to 1000 records. Such species are frequently those which habitat association analyses seek to identify, as being most vulnerable to predicted habitat change or as potential indicators. It is also likely that robust results could be obtained from lower sample sizes if there was no reason to suspect spatial variation in habitat association, and therefore no reason to include a term allowing regional variation in the model. However, the fact that 26% of the species analysed here showed a relationship with latitude, let alone the potential for other spatial variation, suggests that accounting for spatial variation is most likely necessary at all but the smallest spatial scales (Pateman et al. 2015; Pearce et al. 2001).

Comparing the sample sizes required to detect woodland association for butterflies with the number of records for other taxa in Britain (figure 4), it is clear that butterflies are a particularly data rich group (hence their use in this study as a test case). Few other taxa are as well recorded, although around 30% Odonata and 10% of macro-moths meet the 5000 record threshold. For other groups, although there is likely to be insufficient data to detect subtle or cryptic habitat associations, comparatively large numbers of species have sufficient data to apply this method with a strong probability of obtaining robust, quantitative scores for those species most reliant on a particular habitat. These could then be used in a wide variety of ecological applications including the selection of indicator species, the development of indices of habitat quality by weighting aggregate species' population trends by degree of habitat specialisation or prediction of the extent to which each species may be affected under scenarios of land-use change. Ultimately, such analyses form the basis of much conservation policy at the species, habitat and ecosystem level.

4.1. Conclusions

This study has shown that analysis of recording scheme data can produce measures of habitat association which support expert opinion, whilst offering several advantages over reliance on the latter in terms of objectivity and the ability to detect spatial variation. The better performance of readily available occurrence data over abundance data in this context confirms the value of large scale volunteer recording schemes in the light of recent discussion on their comparative strengths and weaknesses (Bishop et al. 2013; Dickinson et al. 2010; Tulloch et al. 2013). Although further work is required to confirm the transferability of the methods detailed in this study for different taxa, habitats and spatial scales, the quantitative association scores derived by the methods in this study have multiple applications in conservation research.

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Data Accessibility

- The UK Land Cover Map 2007 is archived on the EIDC: Morton, R.D., Rowland, C.S., Wood, C.M., Meek, L., Marston, C.G., Smith, G.M. (2014). Land Cover Map 2007 (vector, GB) v1.2. NERC-Environmental Information Data Centre doi:10.5285/2ab0b6d8-6558-46cf-9cf0-1e46b3587f13
- UKBMS and BNM data are held by Biological Records Centre on behalf of Butterfly Conservation and are available on request for research purposes:
  - UKBMS data: http://www.ukbms.org/Obtaining.aspx

- BNM data: https://data.nbn.org.uk/Datasets/GA000832

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Figures

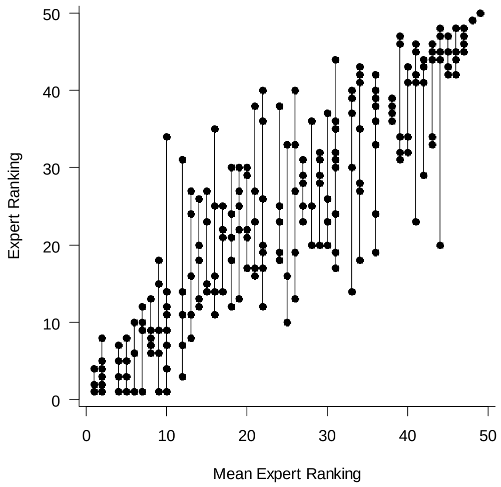

Fig.1 Plot of variation in expert rankings of butterfly woodland association scores. The mean expert ranking is plotted on the x axis, with the associated rankings given by each expert plotted on the y axis. Vertical black lines indicate the range of rankings across all five experts for each species.

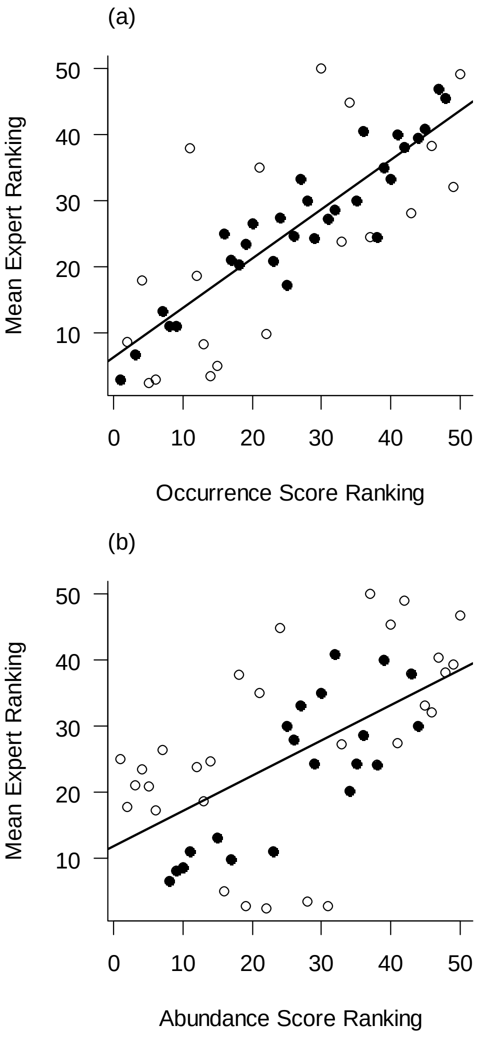

Fig. 2 Plots of a) Rank score from occurrence data and b) Rank score from abundance data against mean expert ranking. Open circles are species for which the ranking of the data-derived score did not lie within the range of the rankings assigned by experts.

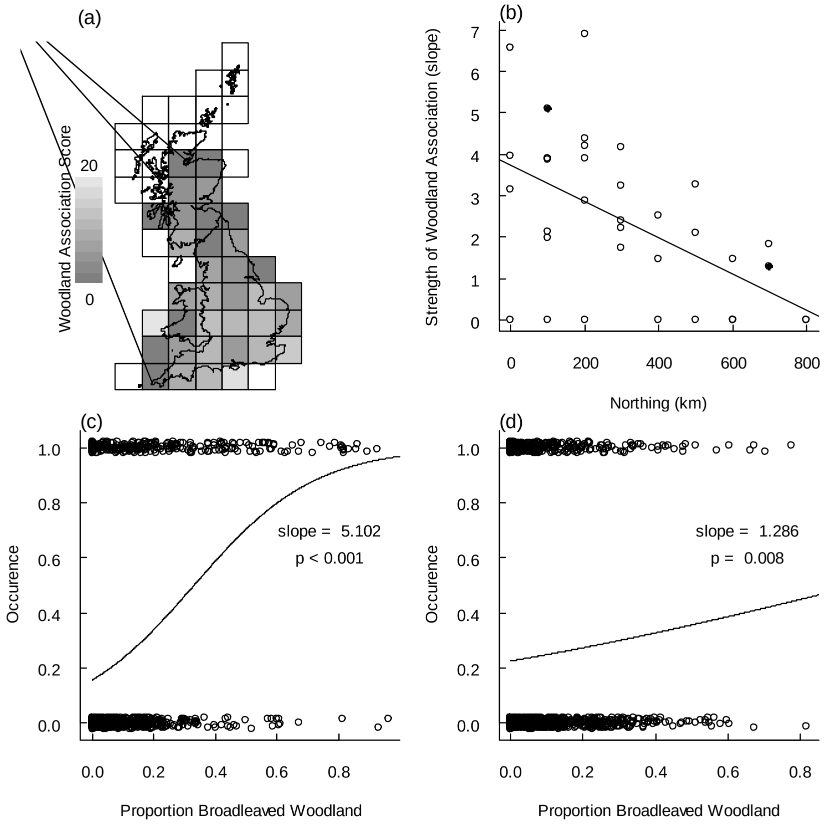

Fig.3 Regional variation in the association of the Ringlet butterfly *Aphantopus hyperantus* with broad-leaf woodland across Great Britain (GB), as detected from occurrence data. (a) Map of GB showing relative strength of association in 100 km regions. Unshaded regions had insufficient data for analysis. (b) Plot of association scores against latitude, measured as distance north from grid origin (Northing). Filled points indicate example regions where the relationship is shown in panel (c), an example of a strong, positive relationship with broad-leaf woodland and panel (d), an example of a weaker relationship with broad-leaf woodland.

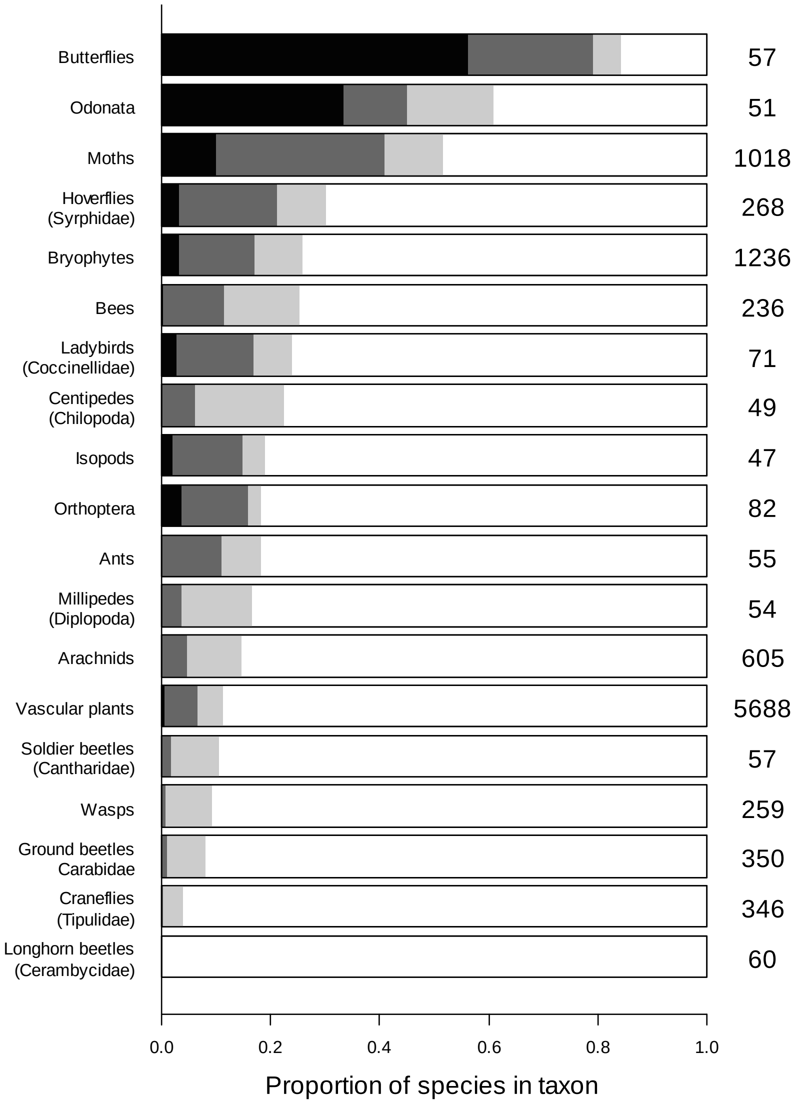

Fig 4. Comparisons of proportions of species in different GB taxa which meet various thresholds in number of unique occurrence records with 1 km or better precision. Numbers to the right of bars indicate total number of species within each taxon. Sections of bars are shaded by number of species meeting thresholds: black sections = 5000 records, dark grey sections = 1000 records, light grey sections = 500 records.

Supplementary material

Additional supplementary material may be found in the online version of this article:

Table S1 Results of scoring species association with broad-leaf woodland for 50 butterfly species in mainland GB, from abundance data, occurrence data and expert opinion.

Table S2 Pearson's correlation coefficients from correlations between broadleaved woodland and other land cover classes from the UK land cover map 2007, by 100 km x 100 km region.