JNCC Report
No. 722

Representation of specialist bryophytes, centipedes, dragonflies and hoverflies in the United Kingdom's protected area network

Research and Review report

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September 2022

ISSN 0963 8091

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This report was produced for JNCC under C16-0301-1073 with additional input and expertise from the co-authors.

This report should be cited as:
Boyd, R., Wright, E., Pescott, O., Morris, R., Preston, C., Hassall, R. & Isaac, N. 2022. Representation of specialist bryophytes, centipedes, dragonflies and hoverflies in the United Kingdom's protected area network. *JNCC Report No. 722 (Research and Review Report)*, JNCC, Peterborough, ISSN 0963-8091.
[https://hub.jncc.gov.uk/assets/c0886a17-1745-439e-a7cb-dd61e728ffd8]

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Acknowledgments:
We would like to thank Pam Taylor and Tony Barber for their expert assessments of the species distribution models for the dragonflies and centipedes, respectively. This work was supported by the Terrestrial Surveillance Development and Analysis partnership of the UK Centre for Ecology & Hydrology, British Trust for Ornithology and the Joint Nature Conservation Committee, and by the Natural Environment Research Council award number NE/R016429/1 as part of the UK-SCAPE programme delivering National Capability.

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Summary

- Habitat specialists have a limited ability to respond to environmental perturbations so their habitat must be protected. Protected areas (PAs) may offer some refuge but only to species whose habitat they overlap with geographically.

- We assessed the extent of overlap between species' potential geographic distributions and PAs in the United Kingdom (UK). We focused on 1,083 species of bryophyte, centipede, dragonfly and hoverfly (adult phases for the latter two). We began by defining each species' level of specialism based on the number of land cover classes in which it has been recorded. We then mapped areas of suitable habitat for each species using two methods. To measure representation, we calculated the proportion of each species' suitable habitat that falls in 1km grid cells that have ≥ 10% PA coverage. Taxon experts assessed the realism of our habitat suitability estimates and the extent to which the records of each species cover its environmental niche. We used these assessments to categorise our estimates of species' levels of specialism, and habitat suitability, as "reasonable" (294 species), "poor" (107 species) or unassessed (682 species).

- We found that specialists are better represented in the UK's PA network than generalists. This finding is robust to the choice of method used to categorise habitat as suitable or unsuitable. However, the extent to which specialists are better represented than generalists depends on the species considered: specialists appear relatively better represented when considering all species than when focusing on the species which were assessed to be "reasonable". This suggests that our findings for the "reasonable" species should not be generalised. We also found that bryophytes are best represented of the taxonomic groups considered, and centipedes are the least; this finding is robust to the choice of method used to estimate habitat suitability and to the species considered.

- Our results demonstrate the need for conservation actions that consider all taxa rather than a select few. Going forward, it would be useful to consider additional habitat features, such as geology and soil type, which are likely more important for some taxa than those used here. It would also be useful to consider alternative measures of vulnerability such as rarity.

Contents

1 Introduction

All species are not equal when it comes to their risks of extirpation and extinction. For example, habitat specialists – that is, narrowly adapted species which exploit relatively few niches – tend to be more vulnerable than generalists (McKinney 1997). This tendency has been demonstrated for many taxa including birds, fish, mammals, plants and reptiles (Munday 2004; Rooney *et al.* 2004; Segura 2007; Correll *et al.* 2019) – although far less attention has been paid to invertebrates. One explanation for specialists' vulnerability is that their narrow environmental niches impede their ability to adapt to environmental perturbations such as habitat loss and climate change (Clavel *et al.* 2011). Measures to prevent habitat loss are therefore essential but must also ensure that the physical conditions favoured by specialists are preserved.

The most direct way to safeguard habitat is through the establishment of protected areas (PAs); that is, "clearly defined geographical spaces, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (Dudley & Stolton 2008). Whilst generally considered to be beneficial, there has been some debate over the effectiveness of PAs from an ecological perspective (Rodrigues *et al.* 2004; Gaston *et al.* 2006). The ecological effectiveness of a PA can be decomposed into i) the level of protection afforded to species found within its bounds, and ii) the representation of species within its bounds (Gaston *et al.* 2006). The level of protection afforded to a species by a PA is clearly contingent on its representation; for example, a PA provides no direct protection to a species with which it does not overlap geographically. It is therefore crucial to understand the extent to which PA networks capture specialists, or habitat that is suitable for specialists, within their bounds.

In the United Kingdom (UK), 70,458 km^2 of land has some form of protection, representing >28% of its terrestrial surface. However, there is substantial variation among protected sites in terms of how much protection they afford to species within their boundaries. Lawton (2010) proposed a three-tier categorisation for England, in which tier one sites are those whose primary purpose is nature conservation and which receive a high level of protection. Tier one PAs include Sites of Special Scientific Interest (SSSI), Ramsar sites, Special Areas of Conservation (SACs), Special Protection Areas, National Nature Reserves (NNRs), and local nature reserves (Lawton 2010). It is crucial that habitat specialists are adequately represented in tier one PAs.

Here, we assessed the representation of 1,083 species of bryophyte, centipede, dragonfly and hoverfly in tier one PAs in the UK. We began by defining each species' level of specialism based on the number of land cover classes in which it has been recorded. Then, for each species, we mapped relative habitat suitability across the UK using species distribution models (SDMs). We used two methods to categorise the models' estimates of relative habitat suitability, originally expressed on a continuous scale, as "suitable" or "unsuitable". To measure representation, we calculated the proportion of each species' suitable habitat that falls within the boundaries of PAs. Taxon experts assessed the realism of our habitat suitability estimates and the extent to which the records of each species cover its environmental niche. This enabled us to categorise our estimates of species' levels of specialism, and habitat suitability, as "reasonable" (294 species), poor (107 species) or unassessed (682 species). We assessed species' representation by level of specialism and taxonomic group, and assessed the sensitivity of our finding to the set of species included (reasonable vs all) and the method used to discretize the SDM predictions.

2 Methods

2.1 Protected areas

The first step in our analysis was to delineate the portion of the UK's PA network that receives a high level of protection. We extracted data on the UK's PAs from the World Database on Protected Areas (WDPA; https://www.protectedplanet.net/en). We then filtered these data to include only tier 1 sites (described above). The PA data were provided as spatial polygons; we reprojected these onto a 1 km^2 grid to match our habitat suitability predictions (see below). Specifically, we gridded the data by calculating the percentage of each 1km grid cell's land area that was covered by a PA spatial polygon. For ease of analysis, we then categorised each cell as "protected" or "unprotected". Each grid cell was designated based on its PA coverage: if its coverage was ≥ 10% we classed it as "protected" and unprotected otherwise (Figure 1). The 10% threshold, whilst subjective, seems like a reasonable starting point given that the median size of English SSSIs is 25 ha (Lawton 2010). In other words, our definition excludes very small protected areas (unless there are several in the same 1 km^2 grid cell): we justify this on the basis that very small PAs are unlikely to be viable in the long term (Lawton 2010). However, it is important to recognise that our results are dependent upon this definition. Using our criterion 4.6% of 1 km grid cells were classed as protected (Figure 1).

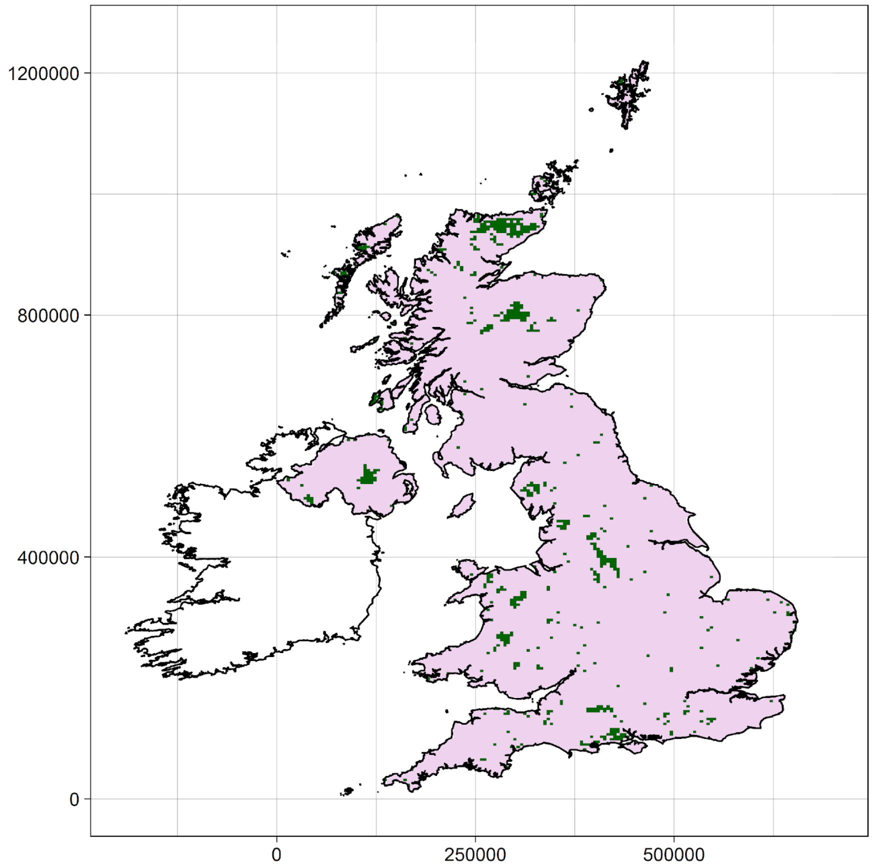

Figure 1. Protected area network (green areas) as defined in this study. See text for details.

2.2 Designation of specialised species

We used presence-only species occurrence data to calculate a specialisation index for each of the 1083 species considered. These data were supplied by the British Bryological Society, the Centipede recording scheme, the British Dragonfly Society and the Hoverfly Recording Scheme. We used the records of each species to create a vector of 1s (occupied) and 0s (unoccupied) for each of the 26 land cover classes as classified for the UK CEH land cover map (Morton *et al.* 2011). The specialisation index is calculated as the Gini coefficient of inequality across all 26 landcover classes (Morelli *et al.* 2019). Using this method, the SSI falls on a scale between 0 and 1, with 0 indicating a highly generalist species recorded in all 26 landcover classes and 1 indicating a highly specialist species recorded in only a single landcover class. We considered species in the upper quartile of the SSI to be true habitat specialists and species in the lower quartile to be true generalists.

We have taken a fairly standard approach to estimate species' levels of specialism; however, we acknowledge that the use of macro-scale habitats is overly simplistic for some taxa whose habitat requirements are more nuanced. We expand on this limitation in the Discussion section below. It should also be noted that the vast majority of dragonfly and hoverfly records pertain to the adult or dispersive phases; hence, our definition of specialism does not include the requirements of the larval phases.

2.3 Mapping habitat suitability

We used SDMs to predict areas of suitable habitat for each species. In this section, we briefly outline the SDM workflow, but refer the reader to the ODMAP (Overview, Data, Model, Assessment and Prediction) document in supplementary material one for full details. We used three SDM algorithms to estimate species' habitat suitability: Maxent, regularized GLMs and random forests. We used the species occurrence data described above, and pseudo absences generated according to the "target group" approach (Phillips *et al.* 2009), as response variables. Twenty-five climate, land cover and topographic data were used as predictors. (Recall that the vast majority of the records of dragonflies and hoverflies pertain to the adult or dispersive phases, so the SDMs do not estimate habitat that is suitable for the larval phase.) The models were fitted at a spatial resolution of ~ 1 km^2 on the British ordnance survey grid. Ensemble predictions were generated for each species by taking a weighted average (based on AUC, a measure of skill) of the three algorithms' predictions.

The ensemble SDM predictions are expressed on a continuous scale as habitat suitability. To enable assessment of the overlap between species' suitable habitat and the PA network, we discretized the continuous predictions to obtain binary predictions whereby each cell is classed as suitable or unsuitable for a given species. This requires the definition of a threshold habitat suitability score above which a grid cell is classed as suitable and vice versa. Many methods have been proposed to optimise this threshold (Liu *et al.* 2005). We use the "Lowest Presence Threshold" (LPT) method (Pearson *et al.* 2007), whereby the threshold is set at the lowest suitability score encompassing a fixed fraction of the presence data. The LPT method is appropriate for our analysis because, unlike other methods, it does not require information on where species are absent (which we do not have).

We used two variants of the LPT method to discretize the SDM predictions. The first is simply to set the threshold at the lowest habitat suitability score encompassing all of the presence data (the 100% threshold hereafter). This method tends to produce large areas of suitable habitat because every presence point must be predicted to be suitable. The second variant is the lowest habitat suitability score encompassing 95% of the presence data (hereafter the 95% threshold). This method tends to give more conservative estimates of the area of suitable habitat.

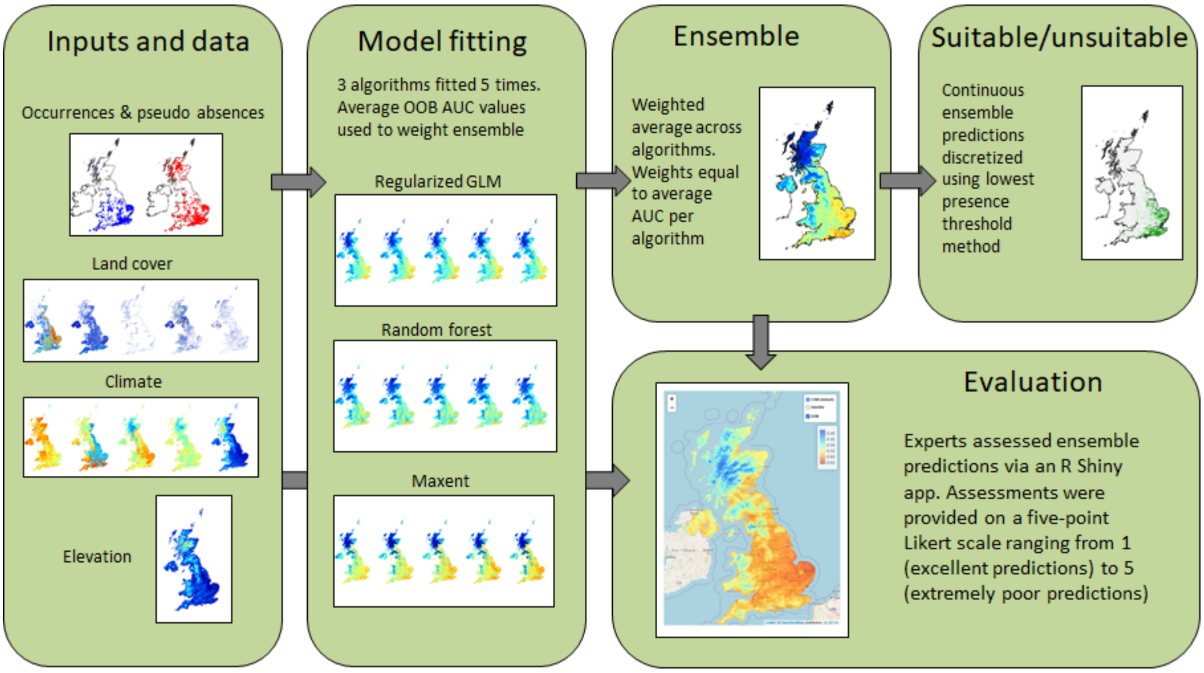

Figure 2. Species distribution modelling workflow. See the supplementary ODMAP document for full details. OOB = Out-Of-Bag data.

2.4 Incorporation of expert knowledge

As part of a separate exercise, taxon experts assessed the available records and SDM predictions for all species in their group of interest (or a random subset in the case of the bryophytes; Table 1). Amongst other questions, they were asked 1) whether the available records for each species cover its environmental niche; and 2) whether the map of habitat suitability (continuous predictions from the ensemble model) for each species reflects reality. The experts provided their answers to these two questions on a Likert scale ranging from 1 (excellent coverage of a species' niche/excellent habitat suitability predictions) to 5 (extremely poor coverage of a species' niche/extremely poor habitat suitability predictions). The answer to the first question indicates whether it is appropriate to use the number of land cover classes on which a species has been recorded as an indicator of its specialism (but see the Discussion for caveats). The answer to the second question indicates whether estimated habitat suitability is reasonable.

Table 1. A taxonomic breakdown of the number of species modelled, the number of species for which models and data were assessed by experts, and the number of species for which the models and data were assessed to be reasonably good (defined in the text).

Taxonomic group	Number of species modelled	Number of species assessed	Number of species with reasonable models and data (% of assessed species)
Bryophytes	782	100	77 (77%)
Centipedes	29	29	19 (67%)
Dragonflies	46	46	34 (74%)
Hoverflies	226	226	164 (73%)
Total	1083	401	294 (73%)

Using the expert scores described above, we defined species about whose level of specialism and habitat suitability we were reasonably confident as those who scored ≤ 3 on both questions. We were not confident about species which did not meet this criterion, whether because the records or models for those species were poor, or because they were not assessed.

2.5 Overlap between protected areas and species' potential distributions

To assess the overlap between specialists' potential distributions and PAs, we calculated the proportion of grid cells with suitable habitat for each species that have protected status (defined above). We broke the results down by level of specialism (quartiles of the specialisation index) and taxonomic group. When comparing the results between taxonomic groups, in addition to defining true habitat specialists as those species in the top quartile of the SSI *across* groups, we also calculated those species in the top quartile *within* each group.

To account for two potential sources of uncertainty outlined above, we repeated our analysis four times: once for each combination of habitat suitability threshold (95% or 100%) and degree of expert confidence in the SDMs and data (i.e., assessed to be reasonable vs all modelled species). We refer to the results of these "methodological scenarios" using the following codes: all_95 (all species, 95% threshold), all_100, reasonable_95 (species for which the data and models were assessed to be reasonable, 95% threshold) and reasonable_100. One might argue that it is best to focus solely on the species for which we have reasonable estimates of habitat suitability and level of specialisation. This is essentially an argument of internal vs external validity: the results for the subset of species that were assessed to be reasonable are most likely to be true (internally valid); however, there is no reason to suppose that we can generalise these results to all species (external validity). Contrasting the results obtained for the subset of species with those obtained for all species allowed us to gauge the external validity of our findings.

3 Results

3.1 Representation by level of specialism

Generally, specialists appear to be better represented in the UK's PA network than generalists. In three of the four methodological scenarios (all_95, all_100 and reasonable_95), there is very strong evidence that species in the upper specialism quartile are better represented than those in the lower quartile (Mann-Whitney U test; $p < 0.001$ in all cases; Figure 3). In the reasonable_100 scenario, however, there is little evidence that specialists are better represented than generalists (Mann-Whitney U test; $p = 0.1663$). Note that we intentionally avoid the terminology of statistical significance following (Muff *et al.* 2021).

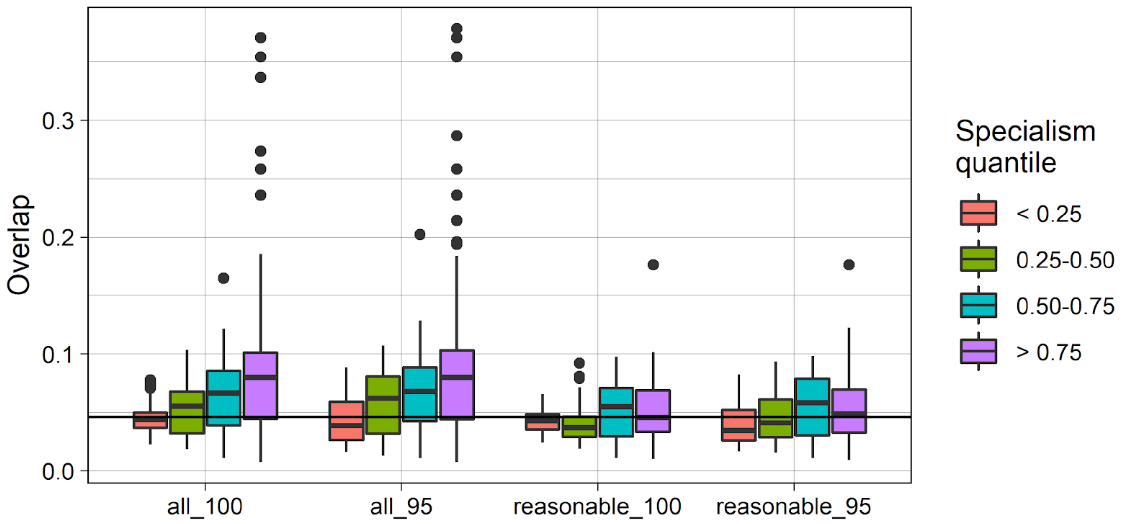

Figure 3. Proportion of species' suitable habitat overlapping PAs by specialism quartile "methodological scenario" (see text). The horizontal black line indicates the null expectation if species were randomly distributed; that is, the proportion of the UK covered by PA as defined here.

To establish whether species are better represented than would be expected by chance (i.e., if they were randomly distributed across the UK), we can compare the level of representation with the proportion of grid cells in the UK that are classed as protected (horizontal black line in Figure 3). In the all species scenarios, specialists are, on average, better represented than would be expected by chance, whereas generalists are not. This pattern is not evident in the reasonable species scenarios.

3.2 Representation of specialists by taxonomic group

There appears to be substantial taxonomic variation in representation of specialists (Figure 4). This is most pronounced in the all species scenarios, where Bryophytes are best represented. In all scenarios, centipedes are poorly represented. Dragonflies appear to be much better represented in the reasonable species scenarios. Note that statistical analysis would not be meaningful here due to the very low sample sizes per group (e.g. one species of dragonfly in the all species scenarios). Hence, we only compared the group medians.

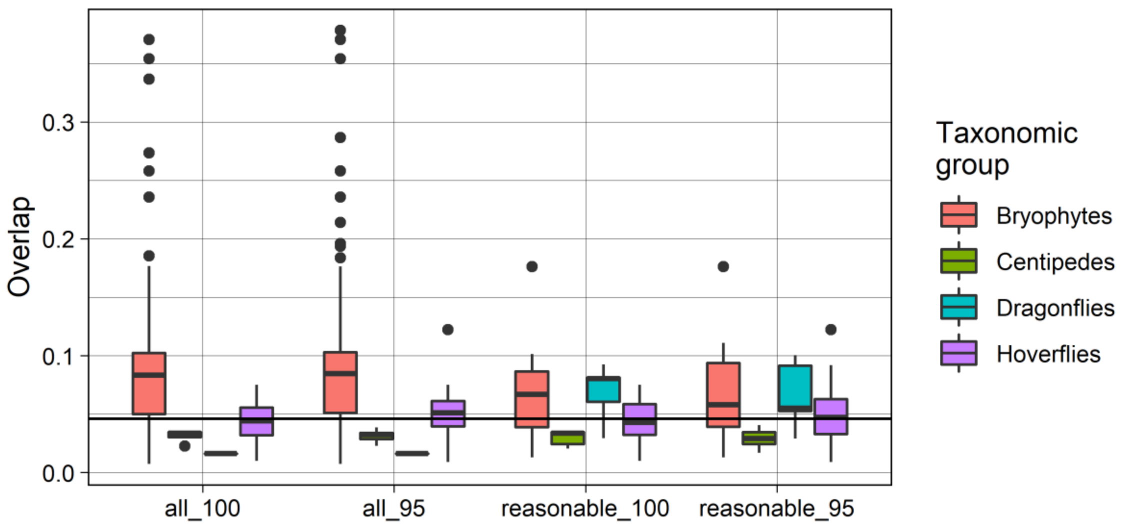

Figure 4. Proportion of specialists' (top quartile in each taxonomic group) suitable habitat overlapping PAs across the UK for each "methodological scenario" (see text).

Figure 4 is challenging to interpret because the taxonomic groups vary in terms of their SSIs and the number of constituent species. Whether considering all species or just the “reasonable” species, bryophytes tend to be most specialised and dragonflies tend to be the least (Figure A1). Likewise, bryophytes are considerably more speciose than the other groups (Table 1). Hence, there is considerable variation among groups in the number of species that make it into the top quartile of the SSI. In the all species scenarios, for example, there are 220 bryophytes in the top quartile and only one dragonfly.

As an alternative to defining true habitat specialists across taxonomic groups, we also defined true specialists as those species in the top SSI quartile *within* each group. Using this definition, five species of dragonfly were classed as true habitats specialists (rather than the one species above); hence, we were able to test for a difference among groups statistically.

There is very strong evidence for variation in representation among taxonomic groups in the “all species” scenarios (Kruskal-Wallis rank sum tests; $p < 0.001$), and strong evidence in the “reasonable species” scenarios (Kruskal-Wallis ranks sum tests; $P < 0.01$). On average, specialist bryophytes are best represented and specialist centipedes are least–and indeed poorly– represented (Figure 5).

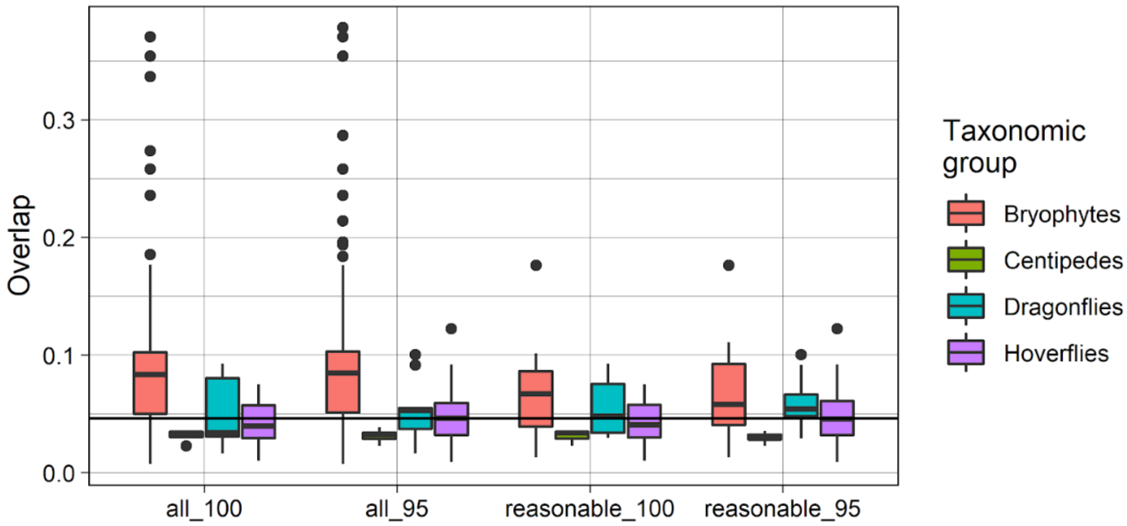

Figure 5. Proportion of specialists’ (top quartile in each taxonomic group) suitable habitat overlapping PAs across the UK for each “methodological scenario” (see text). Note that here specialists were defined as those species in the top quartile of the specialisation index within taxonomic groups rather than across taxonomic groups in Figs. 3 and 4.

The results obtained when defining specialists within groups (Figure 5) are very similar to those obtained when defining specialists across all taxon groups (Figure 4). Dragonflies are the only group to differ appreciably; this is not surprising given that only one species of dragonfly made the top quartile in the all species scenarios when specialists were defined across groups.

4 Discussion

Habitat specialists have a limited ability to respond to environmental perturbations so their habitat must be protected. In this report, we assessed the geographic overlap between habitat that is suitable for specialists and tier 1 PAs in the UK. We repeated our analyses four times to assess the sensitivity of the results to methodological decisions. These “methodological scenarios” included all combinations of method used to categorise habitat as suitable or unsuitable (thresholds), and the taxa included (all species vs only those for which the experts assessed the models and data to be reasonable). We found that habitat specialists appear to be better represented than generalists. This finding is robust to the choice of method used to categorise habitat as suitable or unsuitable, but is more sensitive to the set of taxa included. Breaking representation down by taxonomic group, we found that bryophytes are the best represented of the taxa considered, and centipedes are the least. This result is robust to both the choice of method used to categorise habitat as suitable and unsuitable and the species included.

Our findings that specialists appear better represented than generalists (Figure 3), and that bryophytes and dragonflies appear better represented than other taxa (Figure 4), could be explained by the rationale for designating PAs in the first place. Whilst most SSSIs were designated on the basis that they captured important habitats, the intention was also that they captured rare species (Ratcliffe 1977; Bainbridge *et al.* 2013). Rarity is often closely associated with specialism (Williams *et al.* 2009), so there may be a bias towards protecting specialist species. Similarly, bryophytes and dragonflies were more likely to be considered during the process of designation (among other taxa) than centipedes or hoverflies based on the knowledge of the time (Ratcliffe 1977; Bainbridge *et al.* 2013). Our results suggest that the initial aims of these PAs have been fulfilled, at least to some extent, but more needs to be done to protect taxa which were not borne in mind when designating PAs historically.

Unlike most studies of the representation of species in PAs–which have focused on charismatic taxa such as birds, mammals and butterflies (Duran *et al.* 2016; Beresford *et al.* 2011; Jackson *et al.* 2019)– we focused on lesser-studied groups. We found that there is substantial variability among the habitat specialists in these groups in terms of their representation, and that some are very poorly represented (e.g. centipedes). This demonstrates the need for conservation action that protects as wide a set of taxa as possible in future. Actions that protect many taxa simultaneously might not be as infeasible as they first seem. For example, Critchlow *et al.* (2021) performed a gap analysis to determine where best to place PAs in the UK in future; they found that, despite large differences in the geographic distributions of the taxa considered, priorities for PA designations among groups were fairly congruent.

Whilst our analysis suggests that specialists are better represented in the UK's PAs than generalists, it is important to note that ours is not necessarily the best approach for estimating species' levels of specialism for all taxa considered. Following earlier studies of vertebrates (Julliard *et al.* 2006; Correll *et al.* 2019; Morelli *et al.* 2019), we defined species' levels of specialism based on the number of broad land cover classes in which they have been recorded. However, for many of the taxa considered here, the most important habitat requirements might be finer scale and not evident in broad land cover classes (e.g., vegetation, underlying substrate). To illustrate this point, consider the hoverfly *Criorhina asilica*: this species is a specialist in that its larva requires decaying timber from certain tree species (http://hoverfly.uk/hrs/taxonomy/term/500); however, it has been recorded in 13 land cover classes, so appears relatively generalist according to our definition. This issue is most likely to be problematic for the invertebrates whose habitat requirements are less tightly coupled to land cover.

In addition to the problem of scale, the task of defining invertebrates' habitat requirements is further complicated by the fact that they vary with ontogeny. The vast majority of available records for dragonflies and hoverflies pertain to the adult or dispersive phases; hence, we have essentially defined species' levels of specialism in those phases. The requirements of the larval stages may be very different—for example, dragonflies are aquatic in the larval stage and terrestrial thereafter. Other than obvious examples like the dragonflies, we simply do not know whether most species' levels of specialism in the adult phase are representative of those at larval stage.

A key question that we have tried to address is whether our findings should be generalised beyond the taxa about whose data and models we are confident. To answer this question we conducted our analysis both for the “reasonable” species and again for all species. Our finding that specialist bryophytes are best represented, and centipedes are the least, is fairly robust to the set of species included. It is also fairly robust to the definition of true specialist (i.e. top quartile across groups vs within groups). However, our finding that specialists might be better represented than generalists is highly sensitive to the set of species included: when all species are included it is much more apparent.

One explanation for the sensitivity of our finding that specialists are better represented than generalists (Figure 3) to the set of species included could be that bryophytes are the most speciose group by some distance. In the all species scenarios, bryophytes dominate the upper specialism quartile (e.g. 220 bryophytes vs 20 hoverflies), whereas in the “reasonable” species scenario there is a more even distribution of species among taxonomic groups (e.g. 22 bryophytes vs 36 hoverflies). There is strong evidence that specialist bryophytes are better represented than the other groups (Figure 4), which could explain why specialists appear much better represented when considering “all” species (most of which are bryophytes). Whilst this is clearly an artefact of our methodology – only a subset of bryophytes were assessed by the expert – it is our view that it would not be appropriate to give higher weighting to species in less speciose groups in our analysis: why should one species be given more weight than another?

In addition to the proportion of species in each group that was assessed, biases in which species were assessed to be “reasonable” could also explain the discrepancy between the results for “all” and “reasonable” species. For example, models for species associated with some land cover type might have been poorer than the rest, and therefore not included in the “reasonable” species scenarios. If this land cover type was relatively well or poorly represented in PAs, then this could explain the difference in the results for the reasonable and all species scenarios.

4.1 Next steps

There are several ways in which we can build on the analysis presented here in future. First, we could consider alternative measures of species’ vulnerability. Defining habitat specialism based on land broad land cover classes might not be appropriate for many species considered here. As an alternative, we could consider rarity, which would be calculated as the number of hectads (10 x 10 km squares) in which each species has been recorded. Second, pursuing the current line of investigation around species’ levels of specialism, we could conduct a scoping exercise to try and tease out invertebrate specialisms not evident in land cover data. Finally, we could expand the analysis to include additional taxa. We are currently working with experts from recording societies across the UK to assess SDMs for many more taxa; these could be included in future iterations of this analysis.

5 Code availability

The R code used to conduct this analysis can be found at https://github.com/robboyd/tsda_protected_area_analysis.

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Appendix

Figure A1 shows the distribution of the specialisation indices per taxonomic group, both across all species and the reasonable species.

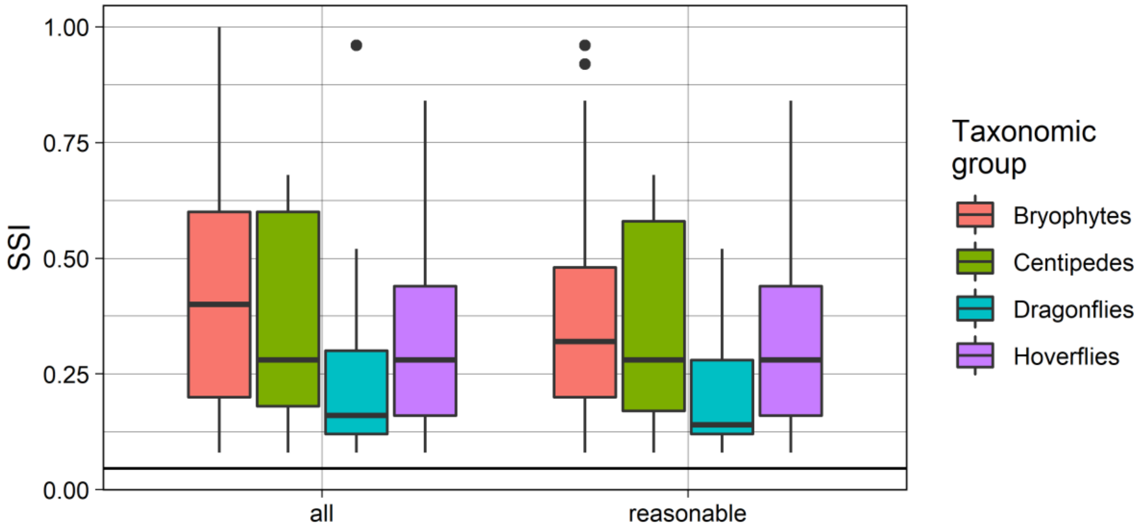

Figure A1. Distribution of SSIs in each taxonomic group, both across the reasonable species and all species.