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Research article

Historical data reveal contrasting habitat amount relationships with plant biodiversity

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Assessing habitat loss effects on biodiversity is a major focus of ecological research. The relationship between habitat amount and biodiversity, postulated in the habitat amount hypothesis, is usually assessed at one point in time, which does not account for habitat loss as a temporal process. We examined habitat amount effects at two time periods, 1930s and 2010s, using plant data from three semi-natural habitats: calcareous grassland, heathland and broadleaved woodland, across Dorset, southern England. Woodlands, which changed little in area over the time period, showed minimal effects of habitat amount on species occurrence in both time periods. For grassland and heathland, which had undergone severe losses over the study period, we found the expected positive relationship in the 2010s, but the relationship was negative for these habitats in the 1930s. We explored possible reasons for this result. Total perimeter-to-area ratio (TPAR) showed positive effects in the 1930s for grassland and heathland, suggesting effects of habitat configuration, specifically edge. However, TPAR was highly correlated with habitat amount so this finding is speculative. One possible explanation for the relationships with habitat amount, and the change between the two periods could be the quality of the surrounding matrix. In the 1930s, the landscape was less intensified and was dominated by semi-natural habitats, whereas by the 2010s much had been converted to arable and intensive grasslands. We speculate that species could likely utilise the matrix to a greater degree in the 1930s compared with the 2010s when the matrix was more hostile, thereby decreasing the importance of habitat amount in the 1930s compared with the 2010s. These findings have important implications for conservation, as they show the importance of context (i.e. matrix quality) in determining the relationship between habitat amount and biodiversity.

Keywords: calcareous grassland, habitat area, habitat edge, heathland, landscape, species–area-relationship, species occurrence, woodland

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Introduction

The loss and degradation of habitats is one of the main drivers of biodiversity declines across the globe (IPBES 2019). Over the last century, processes including agricultural intensification and urbanisation have led to major changes in land cover, with the direct loss of habitats and the fragmentation of those that remain (Haddad et al. 2015). Habitat destruction is predicted to continue to be a major driver of biodiversity decline (Powers and Jetz 2019), and so there is a need to understand if and how the effects of habitat area vary over time.

Habitat loss leads to a reduction in the area of habitat available, but also changes the configuration of habitats. While the relative importance of habitat area and configuration is debated (Fahrig 2013, 2019, Hanski 2015), the majority of habitat configuration metrics are correlated with habitat area in the landscape (Fletcher and Fortin 2018). This makes it challenging to assess which of area and configuration is more important for understanding changes in species occurrence, abundance and richness. Recently, the research focus has shifted to assessing whether the amount of habitat in the landscape is the most important predictor of species richness, as proposed by the habitat amount hypothesis (HAH) (Melo et al. 2017, Watling et al. 2020), although this is contested (Haddad et al. 2017, Lindgren and Cousins 2017). Two dominant approaches to testing the effects of habitat amount are at patch-level and landscape-level (McGarigal and Cushman 2002). Patch-level approaches measure habitat metrics within focal patches, while landscape-level approaches quantify the influence of the spatial character and distribution of surrounding habitat patches, typically at multiple scales. Whichever approach is used, much context-dependence is apparent, with the effects of habitat amount on species richness depending on habitat type (Tu et al. 2020), the habitat specialisms of the species considered (Matthews et al. 2014), the quality of the habitat and surrounding matrix (Ricketts 2001, Kupfer et al. 2006, Chetcuti et al. 2021) and the study design (Eigenbrod et al. 2011).

The effect of habitat amount can vary depending on the habitat evaluated, since different habitats experience different degradation histories and contain different sets of species. Many habitat amount studies consider a single habitat type, often forest (Watling et al. 2020, Rios et al. 2021). However, if the general effects of habitat amount on species richness are to be evaluated, this needs to be examined across multiple habitat types, ideally within the same landscape. In general, habitat specialists respond more strongly to habitat loss, since they strongly depend on resources in their associated habitat (Olsen et al. 2018). On the other hand, generalists are more able to utilise resources in surrounding matrix habitats, and are therefore likely less responsive to the amount of a single habitat type in the landscape (Öckinger et al. 2010). The character of the surrounding matrix can modify habitat amount-richness relationships (Ricketts 2001, Kupfer et al. 2006, Chetcuti et al. 2021), since its condition or quality can influence a landscape's overall resource availability and the degree of permeability to movement (Eycott et al. 2012). A very high-quality matrix may, in effect, increase the amount of habitat if species of that habitat are also able to live and reproduce in parts of the matrix.

Habitat loss is a temporal process (Ridding et al. 2020c), yet since historical biodiversity data are rare, the effects of habitat loss are most often evaluated using space-for-time substitution. Although such studies improve our understanding of biodiversity variation across habitat amount gradients, they are vulnerable to the confounding of habitat amount with abiotic gradients, owing to non-random patterns of habitat loss (Simmonds et al. 2017). This could lead to the prescription of erroneous area-based conservation targets in human-modified environments (Lindenmayer and Luck 2005, Simmonds et al. 2017). Furthermore, present-day biodiversity is presumed to be in equilibrium with the present-day habitat amount, even though this is often not the case (Kuussaari et al. 2009). Instead, many species have a delayed response to habitat loss, leading to extinction debts and colonisation credits (Haddou et al. 2022). The quality of the matrix can also vary over time, so that the current matrix is unlikely to represent that of the past, and the changing character of the matrix might obscure our understanding of habitat amount effects. As a consequence, rather than comparing landscapes with varying levels of habitat loss and fragmentation at a single point in time, having both species and landscape data, as well as information on the matrix, from two or more time periods might facilitate a more rigorous assessment, with habitat loss recognised as a temporal process.

In this landscape-scale study, we examine if and how the effects of habitat amount on biodiversity changes between two time periods, using presence/absence plant data sampled from three semi-natural habitats: calcareous grassland, heathland and broadleaved woodland, across Dorset, southern England, in the 1930s and 2010s. Like much of western Europe, Dorset underwent considerable intensification of land use between 1930 and 2010, with large amounts of semi-natural habitats lost to agricultural intensification (Hooftman and Bullock 2012). This unique dataset provides the opportunity to explore three habitats that have contrasting changes in extent (broadleaved woodland increased slightly in extent, calcareous grassland declined greatly and heathlands also declined, but to a lesser extent) and a matrix that was considerably less intensive in the 1930s. We hypothesised that the probability of species' occurrences would be greater with an increase in habitat amount and that this would be evident at both time points. We hypothesised that the relationship would be weaker for generalists compared with specialists. We also hypothesised that the habitat amount effects would be stronger in the 2010s given that the matrix was more intensive and thus more hostile in the 2010s compared with the 1930s.

Material and methods

Study landscape

Dorset is a predominantly rural county in southern England, which covered ca 2500 km^2 in 1930 (Hooftman and Bullock

2012) (the contemporary county is larger, but the historical data sit within the old boundary (Fig. 1)). Dorset underwent considerable intensification of land use over the last century, whereby large areas of semi-natural habitats were lost to agricultural intensification, afforestation and urbanisation (Hooftman and Bullock 2012, Ridding et al. 2020b, c). The three habitats examined in this study experienced different patterns of change between the 1930s and 2015. Ridding et al. (2020c) determined the habitat type of over 3700 locations that were derived from the original Good (1937) survey sites between the 1930s and 2015. They found the greatest losses were evident in calcareous grassland (70% of sites lost) followed by heathland (50%), whereas broadleaved woodland increased very slightly (3%) due to tree planting over the same time period.

Species data

Over 7000 sites were surveyed for vascular plant species by Professor Ronald Good across Dorset between 1931 and 1939. Sites were selected to be somewhat evenly scattered across the county to represent different habitat types, which were described as 'reasonably distinct topographical and ecological entities' (Good 1937). A subset of these sites was re-surveyed between 2008 and 2010 for three habitat types: calcareous grassland, heathland and broadleaved woodland. These sites ranged in size from 0.18 ha to 32.24 ha (median = 3.18 ha), and were re-surveyed using the same methodology. Only re-surveyed sites that persisted as their original habitat type as determined in the 1930s were included in this analysis; 88 calcareous grasslands (Newton et al. 2012), 65 heathlands (Diaz et al. 2013) and 86 woodlands (Keith et al. 2009, 2011). Although most studies (Watson et al. 2020) use plots of the same size, this was not possible in this study, so instead we controlled for the effect of survey site area in all analyses (Statistical analysis).

We classified species as specialist or generalist using the habitat preferences of Hill et al. (2004). Where a species was associated with the relevant habitat (calcareous grassland, heathland or broadleaved woodland) and any other habitat, these were defined as 'specialists'. 'Generalists' were species that had no association with the relevant habitat at all.

Habitat data

The area and slope of the survey site were calculated using ArcGIS v10.4 (© ESRI, Redlands, CA). Slope was calculated using a 5 m resolution Digital Elevation Model (Intermap Technologies 2007). To determine the past and present habitat amount for calcareous grassland, heathland and broadleaved woodland, we utilised 25 m rasters of the 1930s land cover map created by Hooftman and Bullock (2012)

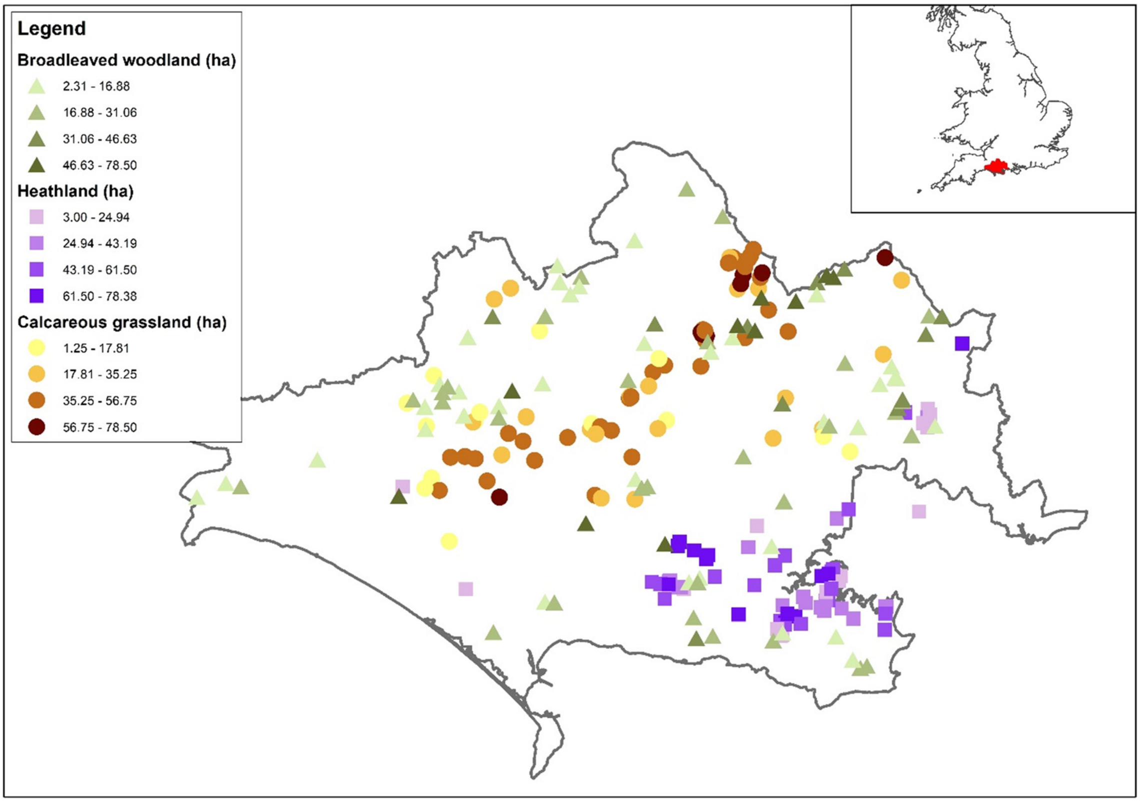

Figure 1. Calcareous grassland (orange), heathland (purple) and broadleaved woodland (green) sites surveyed for plant species across Dorset (historic boundary), southern England in the 1930s and 2010s, shaded by the area of the same habitat in a 500m buffer around the site centroid in the 1930s.

and Natural England's Priority Habitats' Inventory (Natural England 2015), respectively. The 1930s map was an adapted version of the Dudley Stamp Map which was created from the 1930s Land Utilisation Survey of Britain, for which volunteers mapped six land uses onto Ordnance Survey maps based on field surveys (Stamp 1931). The Priority Habitats' Inventory provides the geographic extent and location of 27 Natural Environment and Rural Communities Act (2006) Section 41 'habitats of principal importance' across England. The data are based upon Ordnance Survey MasterMap, individual habitat inventories, ENSIS (Natural England's database of Sites of Special Scientific Interest, SSSIs), aerial photography and other data sources (Natural England 2015). There is a slight time difference between the present habitat data (2015) and species data (2008–2010); however, it is unlikely that there were any significant habitat area changes during this time, as only a small number of semi-natural habitat sites were lost or gained between 1990 and 2015 across Dorset (Ridding et al. 2020c). We used a focal patch approach to quantify the effects of habitat amount at the landscape scale. Focal patch studies are empirical field-based studies that examine species responses (e.g. presence–absence) within discrete focal patches, and then relate these to characteristics of the focal patches and the surrounding landscape (Thornton et al. 2011). Habitat amount was calculated in four buffer sizes; 250, 500, 1000 and 1500 m, for each of the three habitats in the 1930s and 2015 using R package 'landscapemetrics' (Hesselbarth et al. 2019). The buffer was created around the centroid of the site, meaning the amount calculation also included the area of the survey site itself (the area in which plant species were recorded).

Statistical analysis

Habitat amount analysis

To ensure survey sites included in the analysis were spatially independent, we used information on the dispersal distances of plant species found within calcareous grassland, heathland and broadleaved woodland in the 1930s. The dispersal syndrome, growth form and terminal velocity for each species were used to calculate the maximum dispersal distance using linear models from the 'dispeRsal' package (Tamme et al. 2014) in R ver. 4.0.3 (www.r-project.org). The median values of this maximum dispersal distance were less than 10 m for all three habitats (Supporting information). The 75% quartile in all three habitats was ca 220 m, and we used this as the basis for a cut-off distance of 250 m. Thus, any sites within the same habitat type that were within 250 m of one another were allocated at random into two separate datasets (Supporting information). If more than two sites were found within 250 m of each other, the extra sites were randomly eliminated, which resulted in the loss of three calcareous grassland and two heathland sites. Thus, two datasets were generated. Both had the same set of spatially independent sites, but the first dataset also contained the first subset of the sites that originally were within 250 m of another. This was used for the main analysis. The second dataset, by contrast, also contained the second set of sites within 250 m of another, and was used to check for consistency between results. The number of sites for calcareous grassland, heathland and woodland for dataset 1 was 62, 50 and 82, respectively. The same was true for dataset 2, minus one heathland site.

We modelled species' occurrences with presence/absence data using multilevel models (Pollock et al. 2012, Jamil et al. 2013, Miller et al. 2019). We used occurrences rather than metrics such as species richness or diversity, since this was less dependent on the area surveyed for plant species. To quantify the relationship between species' occurrences and habitat amount in the 1930s and 2010s (we use these time periods hereafter, which accounts for the slight difference between land cover and species data during the two time points), we constructed generalised linear mixed models (GLMM) with a binomial distribution, separately for each habitat type: calcareous grassland, heathland and broadleaved woodland. All models were fitted using the 'lme4' package (Bates et al. 2014). Fixed effects comprised habitat amount, year and whether the species was classified as a habitat specialist or not (binary variable, hereafter specialism). We fitted an interaction between habitat amount, year and specialism, to represent our hypotheses that species were more likely to occur with increasing habitat amount and that this effect would be stronger in the 2010s. Specialism was included since habitat loss can lead to the loss of specialists, but also an influx of generalists, so considering all species together could mask potential effects of habitat amount (Matthews et al. 2014). For the calcareous grassland model, the topographic slope of the site was also included, since this is known to be an important variable influencing species composition in this habitat (Bennie et al. 2006). There were no strong correlations between slope and habitat amount (Supporting information). The model for each habitat type also included the area of the survey site, to account for differences in the area surveyed for plant species (Arrhenius 1921). The survey site area was not strongly correlated with the habitat amount for any of the buffer sizes for all three habitat types (calcareous grassland Spearman's Rho < 0.22; heathland Spearman's Rho < 0.53; woodland Spearman's Rho < 0.64) (Supporting information).

Species and survey site were included in the model as random effects, because the species × site data points were not independent, since species occur at multiple sites. Including species and site as random effects allows them to have unique responses to the other interactions terms, as follows:

Species' occurrence ~ Habitat amount × Year × Specialism + Survey site area (+ Slope) + (1|Survey site) + (1|Species)

We excluded species that occurred in less than 10% of sites for each of the three habitat types, since they may add noise to the analysis (McCune et al. 2002, Kent 2012). All continuous variables were centred and standardised by one standard deviation prior to analysis (Schielzeth 2010). We checked for survey site area outliers with the aim to remove very large sites and reduce skew. This eliminated two grassland and six woodland sites from the 1930s and 2010s. We also ensured the range of habitat amounts for the 1930s and 2010s were similar, also to reduce skew. For calcareous grassland and broadleaved woodland this involved removing any sites that fell over the 90th and 95th quantile of habitat amount in the 1930s and 2010s, respectively. Since the habitat amount range was much greater in the 1930s compared with the 2010s (Supporting information), this removed a small number of sites in the 1930s only (calcareous grassland = 12, woodland = 7). These refinements had little effect on the species' pool in the 1930s and 2010s. The final number of sites included in the analysis for calcareous grassland, heathland and broadleaved woodland for all of the models was 60, 50 and 76, respectively.

Habitat amounts within different buffer sizes (250, 500, 1000 and 1500 m) were strongly correlated (Supporting information), so we fitted separate models for each buffer size. We retained the buffer size in the model with the lowest second-order Akaike information criterion (AIC) (Burnham and Anderson 2002).

Analysis of alternative explanatory variables to habitat area

The results of the habitat amount analysis yielded unexpected results that were contrary to our predictions, whereby the relationship of habitat amount with species occurrence was negative for calcareous grassland and heathland in the 1930s, rather than positive (Results). To examine these findings, we performed additional exploratory analyses. We proposed three possible explanations for the negative relationship: (1) Environmental conditions, such as soil fertility, which is known to influence semi-natural habitat communities (Marrs 1993) may relate negatively with occurrence probabilities of many species that are positively confounded with habitat amount. (2) Communities found at sites with larger amounts of habitat in surrounding landscapes may differ from those with smaller habitat amounts. Alternatively, (3) habitat configuration, specifically the amount of edge exposed, is confounded with habitat amount, but may provide a better explanation of the variation in species' occurrence. The presence of edges within landscapes is known to influence species' occurrences; for example, generalists, edge specialists and invasive species can be more likely to occur within habitat boundaries compared to interiors (Ries et al. 2004, Watling and Orrock 2010).

To explore explanation (1) we checked for correlations between habitat amount and the community weighted mean (CWM) Ellenberg indicator values for soil N (Hill et al. 2004) to understand whether differences in soil fertility existed in the 1930s. These differences may arise naturally or as a consequence of management, for example through the traditional use of farmyard manure (Fussell 1948). For explanation (2), to assess if there were differences in species composition between sites with larger habitat amounts compared with smaller habitat amounts, we used non-metric multidimensional scaling (NMDS). Species data from the 1930s were used to establish if a difference was already present before the landscape was intensified; the 1930s was also the time period which revealed the unexpected result. The analysis was performed using the 'vegan' package (Oksanen et al. 2007). For explanation (3) we calculated the total perimeter-to-area ratio (TPAR), to represent the amount of exposed edge, whilst accounting for area. TPAR was calculated within a 500 m buffer by dividing total edge by total habitat area, which were determined using the 'landscapemetrics' package (Hesselbarth et al. 2019). Since TPAR was correlated with habitat amount (Supporting information), we considered TPAR in a separate model, by substituting habitat amount in the previous model (see Statistical analysis – Habitat amount analysis) with TPAR. Again, rare species were removed and variables were centred and standardised. Sites that fell over the 90th, 85% and 95th quantile of TPAR for calcareous grassland, heathland and woodland, respectively, were removed to ensure the range of TPAR was even in both survey periods.

Results

Habitat amount relationships with species' occurrence

The direction of the effect of habitat amount changed with year for specialists and generalists in all three habitat types (Fig. 2). The patterns were consistent across all four buffer sizes, with the exception of woodland, which showed greater variation between sizes (Supporting information). Habitat amount in the 250 m buffer was the best model (lowest AIC) for occurrences in heathland and woodland (Table 1), whereas the 500 m buffer was the best for calcareous grassland and had second lowest AIC for heathland. We elected to present results using habitat amount within the 500 m buffer for all three habitats, since this had low AIC values for all habitats whilst also showing patterns consistent with other buffer sizes. The 500 m buffer had the additional benefit of ensuring a reasonable range was obtained for habitat amount across both survey periods, since the practicality of the 250 m buffer was constrained by the smaller number of 25 m raster cells. The conditional R^2 (variance explained by fixed and random effects) was higher for calcareous grassland and heathland compared with broadleaved woodland (Table 1), with the former values consistent with other habitat amount studies ($R^2 = 0.350$ (Vieira et al. 2018); $R^2 = 0.37/0.33$ (Merckx et al. 2019)).

Similar patterns were identified for calcareous grassland and heathland, whereby species were more likely to occur with an increase in habitat amount within a 500 m buffer in the 2010s, as expected. However, we found a counter-intuitive pattern in the 1930s, whereby the relationships with habitat amount were negative (Fig. 2, Supporting information). The same pattern was evident for both specialists and generalists. Conversely, in broadleaved woodland, there was little effect of habitat amount for the occurrence of specialists or generalists in the 1930s and 2010s. These results were confirmed by the second datasets (Supporting information).

Alternative explanatory variables

In our exploration of possible causes of the counter-intuitive negative relationships between habitat amount and species'

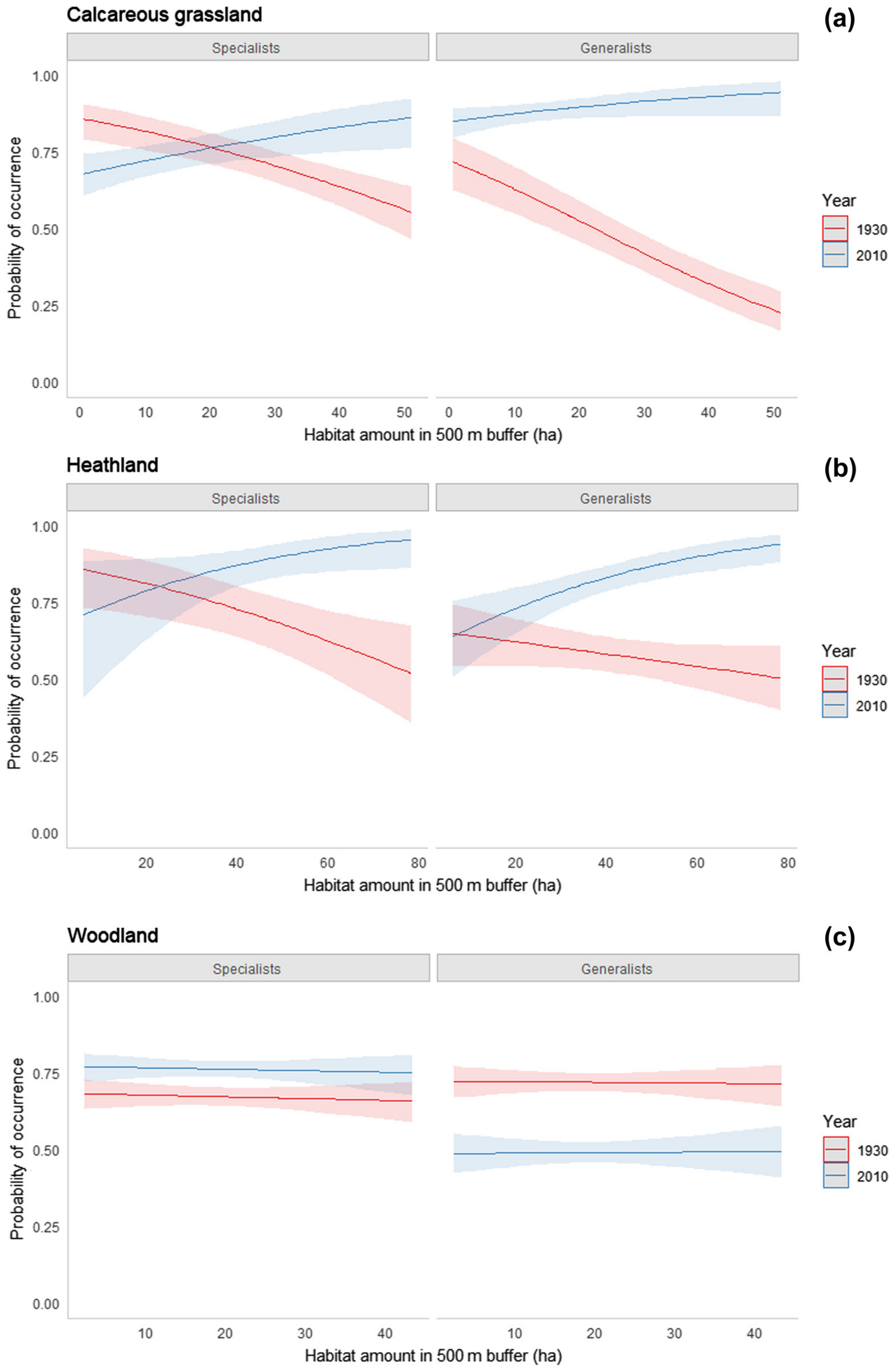

Figure 2. The effect of habitat amount (ha) within 500 m of a site depended on the survey year (1930s (red) and 2010s (blue)) and specialism (specialist (left), generalist (right)) on species' occurrence in calcareous grassland (a), heathland (b) and broadleaved woodland (c) in Dorset. Shaded areas show confidence intervals for fixed effects.

Table 1. The marginal (R^2m) and conditional (R^2c) R^2 values and ΔAIC for generalised linear mixed models (binomial) of species' occurrence with year (1930s and 2010s), specialism (specialist, generalist) and habitat amount within four buffers sizes (250, 500, 1000 and 1500 m) as interaction terms. This was modelled for each of the three habitats across Dorset: calcareous grassland, heathland and broadleaved woodland.

Habitat	Buffer	ΔAIC	R^2m	R^2c
Calcareous grassland	500 m	0	0.17	0.29
	250 m	10.62	0.17	0.28
	1000 m	44.79	0.15	0.26
	1500 m	62.92	0.15	0.25
Heathland	250 m	0	0.17	0.27
	500 m	21.39	0.14	0.23
	1000 m	33.05	0.13	0.21
	1500 m	39.22	0.12	0.20
Broadleaved woodland	250 m	0	0.05	0.12
	1500 m	1.53	0.05	0.12
	1000 m	6.10	0.05	0.11
	500 m	7.69	0.05	0.11

occurrence, we found little evidence of relevant environmental conditions being confounded with habitat amount (explanation 1). No strong correlations were found between CWM Ellenberg N and habitat amount for all three habitats (Supporting information), suggesting soil fertility was not collinear with habitat amount. Species composition in the 1930s appeared to vary with habitat amount for calcareous grassland and – to a lesser extent – woodland, but no clear pattern was identified for heathland (explanation 2) (Supporting information). For calcareous grassland, species located towards the right-hand side of the NMDS plot near sites with high habitat amount tended to be calcareous grassland specialists (e.g. *Briza media*, *Campanula glomerata* and *Pimpinella saxifraga*), whilst those associated with sites with a low habitat amount on the left-hand side were not typically associated with the habitat (e.g. *Lolium perenne*, *Ranunculus repens* and *Hypochaeris radicata*) (Supporting information). A similar pattern was identified for woodland, whereby species typically associated with broadleaved woodland were located near sites with high habitat amount on the NMDS plot (e.g. *Arum maculatum*, *Acer pseudoplatanus* and *Dryopteris dilatata*), whilst those located near sites with low habitat amount were generalists (*Crepis capillaris*, *Bellis perennis* and *Anthoxanthum odoratum*) (Supporting information).

With regard to the third possible explanation (the amount of edge exposed may provide a better explanation of the variation in species' occurrence), we found the relationships of species' occurrence with TPAR (Fig. 3) were the converse of those for habitat amount. These opposing relationships are not surprising, given the strong negative correlation between habitat amount and TPAR (Supporting information). The TPAR models produced higher AICs (i.e. with poorer fit) than those using habitat amount for calcareous grassland (ΔAIC = +18.10) and heathland (ΔAIC = +15.73), whilst the AIC for broadleaved woodland was lower for the TPAR model (ΔAIC = −25.51).

Discussion

Counter-intuitive relationships between habitat amount and species' occurrence

In two of the three habitats (calcareous grassland and heathland) examined in this study, species were less likely to occur with an increase in habitat amount in the 1930s. Even in broadleaved woodland the effect of habitat amount was minimal during both time periods. This does not support our first prediction, that species were more likely to occur with an increase in habitat amount, nor is it consistent with many studies that report an increase in species richness with habitat amount (Krauss et al. 2004, De Camargo et al. 2018, Merckx et al. 2019, Watling et al. 2020). These findings cast doubt on the importance of the habitat amount hypothesis, and this is not the first time a negative relationship with habitat amount has been detected. For example Lindborg et al. (2012) found the occurrence of clonal plant species decreased with habitat area, and long-lived plant species decreased with grassland area in north-central Europe. Lecoq et al. (2022) also reported a negative relationship between the functional diversity of grassland plant assemblages and habitat amount. They suggest two reasons for this. First, it may be because sites with high grassland amount have a lower proportion of other land uses which shelter immigrating non-grassland species. Second, these high grassland amount areas may be managed through homogenous practices, such as through grazing. The latter could also be important in our study, since even to this day Dorset is dominated by large estates which are likely to employ standardised management practices (Who owns England? 2020). In this same landscape we found evidence of extinction debts in the 2010s in relation to the 1930s (Ridding et al. 2020a). This suggests time lags in response to habitat loss might have had a role in the 1930s, although it is hard to conceive how this would lead to the negative relationships with habitat amount.

Counter-intuitive results might raise questions about data quality, in particular that of the historical data. However, the 1930s land cover map was validated by Hooftman and Bullock (2012) using the original vegetation survey of 2670 sites (full set, not just those resurveyed). This showed a 90.4% concordance with the assigned land cover. Thus, we have a high level of confidence in this dataset. Although the exact details of how the survey sites were originally selected were not reported, the survey was extensive across the whole of Dorset with 5–6 sites surveyed per square mile. Thus, it is unlikely that there was any bias in the selection of sites. Furthermore, if there had been any bias in the selection of the survey sites, it is unclear how this would result in a negative relationship between species occurrence and habitat amount.

We speculated that additional exploratory analysis might explain the negative relationship and the differences in habitat amount effects between the two survey periods. We did not identify any consistent strong co-variation between habitat amount and likely important biophysical factors comprising nutrient availability and species composition across all three

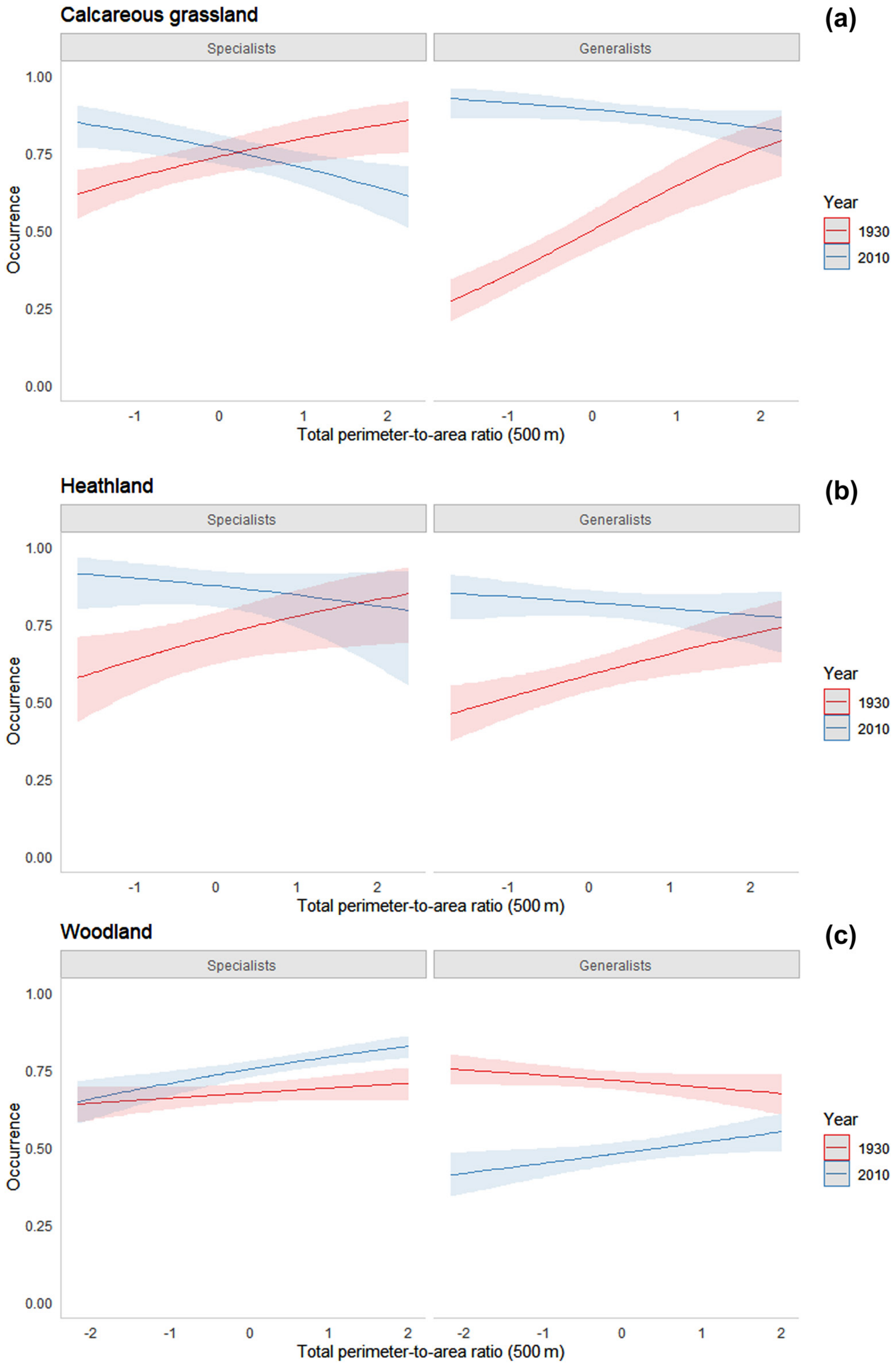

Figure 3. The effect of total perimeter-to-area ratio (TPAR) within 500 m of a site depended on the survey year (1930s (red) and 2010s (blue)) and specialism (specialist (left), generalist (right)) on species' occurrence in calcareous grassland (a), heathland (b) and broadleaved woodland (c) in Dorset. TPAR has been centred and scaled. Shaded areas show confidence intervals for fixed effects.

habitats. There were differences in species composition with varying habitat amount in the 1930s for calcareous grassland and to a lesser extent woodland. Species associated with sites surrounded by high amounts of habitat tended to be species typically associated with that specific habitat type, whereas species associated with sites with low habitat amounts were usually generalists, found across a range of habitats. It may be possible that, at varying habitat amounts, certain combinations of species are more or less likely to occur. However, this does not explain the counter-intuitive results we find, where occurrence is examined across all sites and such patterns of increased or decreased occurrence per species would be averaged overall. A difference in composition was not found for heathland, which suggests that biophysical factors alone did not explain the counter-intuitive results for this habitat. The relationship with TPAR was the converse to that identified for habitat amount; however, owing to the lack of independence with habitat amount it was not possible to disentangle the two effects.

The relationship between habitat amount, TPAR and species' occurrence in two time periods

Our analysis revealed quite different relationships between species' occurrences and habitat amount for all three habitats during the two time periods. For calcareous grassland and heathland, habitats that have undergone the greatest loss over time, negative relationships between species' occurrences and habitat amount in the 1930s were apparent, whilst in the 2010s, relationships were positive. Our prediction of positive effects that were stronger in the 2010s was therefore difficult to support given the negative effects found in the 1930s. The patterns for specialist and generalists were very similar for each habitat type, which is inconsistent with our prediction of a stronger effect for specialists.

The direction of the relationships with TPAR were the converse, with species more likely to occur with an increase in TPAR in the 1930s. This might suggest that species were more likely to occur where the habitat had more edge per unit area in the 1930s whilst, in the 2010s, species' occurrences decreased with the amount of edge. However, owing to the strong correlation between TPAR and habitat amount, the effects of both variables cannot be disentangled. Despite this, one explanation for the negative relationship with habitat amount could be the state of the surrounding matrix. In the 1930s the Dorset landscape, like that of much of southern England, was dominated by semi-natural habitats, characterised by low-intensity (by modern standards) management and high species richness (Hooftman and Bullock 2012, Jiang et al. 2013). Between 1930 and 2000 the area of these semi-natural habitats in Dorset declined considerably; calcareous (−83% area loss), mesotrophic (−97%) and acid grasslands (−61%), as well as heathlands (−56%) (Hooftman and Bullock 2012), with the majority converted to arable land or agriculturally improved grasslands (Ridding et al. 2020b). Not only did this increase the area of intensive land uses (arable land or agriculturally improved grasslands) which often have low species richness and a preponderance of generalists (Auffret et al. 2018), but the management of these agricultural areas also became increasingly intensive after the Second World War. Since 1945 there has been a fourfold increase in yields, over a time during which the number of farms declined by 65% and farm labour by 77% (Robinson and Sutherland 2002). Farms became more specialised, with an increase in machinery but also the use of pesticides and fertiliser, which has increased across Britain since 1960 (Robinson and Sutherland 2002), making the landscape more hostile for wild species.

Our rationale is that, as the surrounding matrix was less intensively used and therefore less hostile in the 1930s, species were able to move through the matrix more easily and use it as habitat, thus reducing the reliance on habitat amount. Reviews have reported that movement through the matrix was greater where the matrix structure was more similar to the species' habitat (Prevedello and Vieira 2010, Eycott et al. 2012). On the other hand, in the 2010s when the surrounding matrix was dominated by agriculturally improved land that was more intensively used, and therefore harsher, species associated with our habitats likely found it more difficult to disperse between habitat patches and could likely not use it as habitat. This coincides with much of the habitat fragmentation research which confirms that the quality of the matrix matters (Ricketts 2001, Prugh et al. 2008, Prevedello and Vieira 2010), although further research is required to investigate what high-quality means and how this has changed over time. There could be important implications for conservation, whereby reducing the harshness of the matrix could be as useful as increasing habitat amount. It is important to emphasise that these ideas are somewhat speculative, as the counter-intuitive relationships we have described are not easily explained.

In broadleaved woodland, we found little effect of habitat amount in the 1930s and 2010s, by comparison to the effect for heathland and calcareous grassland. This suggests that other factors are important for influencing the occurrence of species in woodland. Keith et al. (2009) suggested that plant communities had reorganised between 1930 and 2010 in Dorset, in response to eutrophication and increasingly shaded conditions due to a decline in traditional management.

Conclusion

Using a unique historical dataset, this study highlights that species' occurrence does not necessarily increase with habitat amount, contradicting many previous studies. Most studies utilise space-for-time comparisons which do not account for temporal change, by contrast to this study. This approach could lead to an overestimation in the literature of the importance of habitat amount, as other potential drivers are overlooked. We suggest that habitat context is also an important consideration and in particular the quality of the matrix may be a key driver. The findings have implications for conservation, suggesting that remedial action should focus not only on increasing habitat area alone, but also on appropriate management of the habitat and increasing the quality of the matrix.

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Data availability statement

The Priority Habitats' Inventory is available from www.data.gov.uk/dataset/4b6ddab7-6c0f-4407-946e-d6499f19fcde/priority-habitat-inventory-england. Plant occurrence data can be requested from The Good Archive https://derc.org.uk/the-good-archive/.

Supporting information

The Supporting information associated with this article is available with the online version.

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