Land-cover gradients determine alternate drivers of mammalian species richness in fragmented landscapes

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Abstract

Context Understanding habitat fragmentation is a critical concern for nature conservation and the focus of intense debate in landscape ecology. Resolving the uncertainty around the effects of habitat fragmentation on biodiversity remains an ongoing challenge that requires the successful delineation of multiple patch-landscape interactions.

Objectives We carried out a regional analysis on species richness of woodland mammals to determine the relative influence of structural, compositional and functional characteristics related to woodland habitat across different land-cover gradients.

Methods We calculated the Edge-weighted Habitat Index, an area-weighted measure of functional connectivity that incorporates a mechanistic estimate of edge-effects, for interior woodland habitat. We compared its influence on mammalian species richness to that of increasing edge and patch density, landscape diversity, and a habitat-only model, in different contexts of matrix hostility across Northern England in the UK.

Results Our results demonstrate the relevance of alternative drivers of species richness resulting from patch-landscape interactions across gradients of matrix hostility. Evidence is provided for positive and negative effects of increasing structural (edge density), functional (connected interior habitat) and compositional (landscape diversity) attributes, varying according to matrix type and intensity. Results were sensitive to dominant land-cover types in the matrix and the scale of observation.

Conclusion This study provides new insights into fragmentation effects on biodiversity and clarifies assumptions around the relative influence of structural, compositional and functional habitat characteristics on landscape-level species richness. We highlight the presence of thresholds, related to matrix hostility, that determine alternative drivers of species richness in woodland mammals. These drivers, and related thresholds, were sensitive to the scale of observation and landscape context. Landscape decisions aimed at promoting biodiversity should

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consider sources of matrix hostility and homogeneity at scales relevant to ecological processes of interest.

Keywords Fragmentation · Edge effects · Species Richness · Woodlands · Mammals · Functional Connectivity

Introduction

Fragmentation in biodiversity studies

Habitat fragmentation is frequently cited as a major driver of the modern biodiversity crisis (Haddad et al. 2015; Betts et al. 2019; Ramírez-Delgado et al. 2022; Ma et al. 2023). Fragmentation is often associated with loss (of habitat quality and species) and its occurrence is commonly measured and conceptualised through the geometric lens of landscape indices (Wang et al. 2014; Kumar et al. 2018). While the field of landscape ecology offers a diverse set of metrics to quantify the influence of fragmentation-related properties such as patch size and shape on species richness, the complexity of ecological systems often results in inconclusive findings (Rybicki et al. 2020). Resolving the puzzle of conflicting reports concerning the impacts of landscape composition and configuration on biodiversity (Fletcher et al. 2018; Fahrig et al. 2019) remains an ongoing challenge. The situation warrants further research and refinement of methodologies to understand the reliability of fragmentation metrics and the role of structural versus functional characteristics in determining biodiversity in fragmented landscapes.

Improving these lines of evidence would further clarify current debates focussed on whether fragmentation per se (Fahrig 2020; Urban 2023) should promote or reduce biodiversity. For example, a major review by Fahrig (2017) of SLOSS (Single Large Or Several Small) studies suggested a seeming prevalence of SS > SL (i.e., several small patches supporting greater species richness than single/fewer larger patches) found in the literature. This claim is at the centre of what has since become known as the habitat fragmentation and biodiversity debate (Valente et al. 2023). Opposing views cite empirical studies demonstrating the importance of patch size and isolation on species richness, (e.g. Fletcher et al. 2018; 2023). Fahrig et al. (2019) responded to these claims

by highlighting that fragmentation effects (on species richness as a function of the spatial configuration of habitat) should be made at the landscape level, not extrapolated from patch-based observations. They reference edge-effects and patch isolation, alongside patch size, as specific attributes that have an influence on species richness at the landscape-scale. Edge and edge-effects are of particular interest given the often-assumed association between increasing fragmentation, increasing edge length and habitat degradation resulting in species loss (Haddad et al. 2015; Willmer et al. 2022). Fahrig et al. (2022) propose a number of mechanisms, drawing on geometric properties of habitat patches in the landscape that may promote species richness. These include increased heterogeneity, risk spreading and between-patch movement (dispersal) rates that result from a greater number of patches and higher amounts of habitat edge in the landscape. The likelihood that habitat fragmentation will lead to greater or lower biodiversity, as a function of the interaction of these mechanisms, has been conceptualised through a three-dimensional heuristic, which the authors refer to as the "SLOSS Cube". These mechanisms have subsequently been adopted to estimate optimal configuration for habitat within a matrix of human land-use (Arroyo-Rodríguez et al. 2020). A key prediction of the SLOSS Cube is that fewer larger patches should only promote higher species richness in scenarios where dispersal events (movement between patches) and landscape-scale heterogeneity are generally low. An effective evaluation of the prevalence and behaviour of these mechanisms, therefore, requires an appreciation of patch-landscape interactions as a function of matrix properties. For example, functional connectivity is a crucial process in fragmented landscapes (Grander et al. 2020) with patch size and isolation informing expectations around the likelihood of successful dispersal (Ovaskainen and Hanski 2001; Chandler et al. 2015; Bonte and Bafort 2019).

In this context, matrix composition influences patch isolation as a function of landscape permeability, habitat availability, edge-effects and land-cover diversity (Watts and Handley 2010; Barros et al. 2019). Though attention has been given to the influence of habitat connectivity on species richness in fragmented landscapes (Uroy et al. 2019), few studies have compared the relative role of increasing habitat edge, land-cover diversity and functional

connectivity. Though Watling et al. (2020) consider the influence of patch isolation on species richness, they tested only landscape structure (spatial distribution of patches) as opposed to functional connectivity. Herrera et al., (2017) considered the importance of small habitat patches from a functional connectivity perspective, but did not directly test the influence of connectivity on species richness. Regolin et al., (2020) compared the influence of composition (quantified as woody cover), configuration (quantified as patch and edge density) and land-cover diversity on mammalian species richness. They highlighted better explanatory power of configuration over composition and environmental heterogeneity. However, structural measures such as edge and patch density, without consideration of functional connectivity, do not offer a full picture of landscape configuration. One advantage of properly integrating functional connectivity into configuration assessments is the opportunity to incorporate several ecologically meaningful attributes including matrix permeability and edge effects. For example, Dennis et al. (2024) recently demonstrated the importance of adopting a mechanistic approach to understanding edge-effects as a patch-landscape interaction influencing habitat connectivity. This is a promising step forward given the general lack of studies that properly, and in a consistent way, disentangle the influence of structural attributes (i.e. geometric properties of patches), land-cover composition, and more functional considerations (i.e. patch-landscape interactions) on species richness. Direct comparisons of structural, compositional and functional measures in the same study landscape are, surprisingly, also largely absent from fragmentation-biodiversity studies, despite the obvious relevance of patch and edge density, connectivity and land-cover diversity to the central question of whether fragmentation should inhibit or encourage species richness.

Patch-landscape interactions relevant to landscape-scale biodiversity outcomes

Previous work suggests that the effects of fragmentation per se may be moderated by the amount of habitat within a given landscape (Fahrig 2013; Villard and Metzger 2014; Melo et al. 2017). We extend this proposition by suggesting that the context (i.e., the matrix) within which biodiversity outcomes are measured is also a crucial factor. Specifically, we argue that the degree to which edge effects are exerted on habitat patches should modify their size, shape and quality. Note that this has particular importance for area-weighted assessments of connectivity, including many popular graph-theoretic approaches in the Hanski lineage (Dennis et al. 2024). Landscape permeability is also closely modified by matrix quality, with a subsequent impact on patch connectivity (Watts and Handley 2010). Overall, these patch-landscape interactions can lead to different outcomes for the same spatial configuration when matrix hostility differs between landscapes (Fig. 1). Spatial context, as well as amount of habitat, therefore, seem to be logical elements to include in assessments of landscape-scale biodiversity outcomes. The role of functional connectivity and patch geometry in landscape-scale biodiversity assessments should therefore be explored across different levels of fragmentation, matrix hostility and habitat availability.

To explore the roles of edge, land-cover diversity and functionally connected habitat in landscape-scale species richness outcomes across a range of matrix contexts, we undertook a comprehensive large-scale assessment of mammalian species richness for a region in the United Kingdom (UK) that is undergoing considerable afforestation measures. The potential for landscapes within this zone to contribute to major biodiversity goals (e.g., 30×30; IUCN, 2021) depends on a better understanding of how the distribution of habitat patches relates to changes in species richness. We focussed on mammalian species richness as this group is thought to be particularly sensitive to changes in landscape composition and configuration (Haddad et al. 2015; Melo et al. 2017; Regolin et al. 2020). Mammalian groups are also suitable for large landscape-scale studies given their generally high dispersal capacities and sensitivity to matrix permeability and associated edge effects (Benítez-López et al. 2010). We specifically targeted mammals that are dependent on temperate broadleaf woodland, given that the restoration of native woodland has been identified as an environmental priority with recent UK government pledges related to policy, funding and research (Environment, Food and Rural Affairs Committee 2022).

We approached the study with several expectations. 1. Given the long history of habitat fragmentation in UK landscapes, and subsequently high proportion of edge habitat, prevalent species
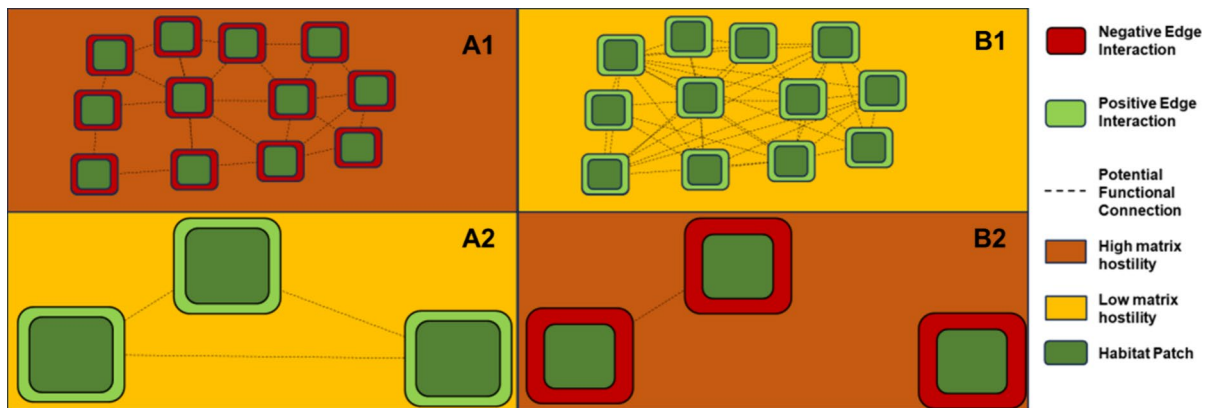
Fig. 1 Schematic example of patch-landscape interactions modelled in this study. Both A1 and B1 panels represent the same spatial configuration of small patches (high fragmentation, high edge length). In B1 generally positive edge-matrix interactions are seen compared to negative "edge effects" in panel A1. Similarly, positive and negative edge interactions are represented by panels A2 and B2 respectively (represent-ing low fragmentation, low edge length scenarios). The differ-ent outcomes for the same spatial configuration are a function of different levels of matrix hostility such that the high frag-mentation scenario in B1 can achieve higher connected inte-rior habitat than the low fragmentation scenario in B2. For the same reason, A2 achieves less positive edge-matrix interaction than B1 but greater than that exhibited by A1

should be edge-adapted and able to persist in land-scapes dominated by edge-habitat. Recent evi-dence that greater species richness generally occurs within edge habitats in temperate latitudes adds confidence to this prediction (e.g., Wilmer et al. 2022). 2. Functional connectivity should influence species richness, given its importance for meta-population capacity. 3. Land-cover diversity should generally promote species richness, following assertions elsewhere (e.g., Regolin et al. 2020). 4. Landscape context (matrix hostility) should modify the relative importance of expectations 1–3 for spe-cies richness.

Our study focussed on the recently proposed Northern Forest in the UK, an ambitious reforesta-tion project pledging to plant at least fifty million trees across the North of England covering just over ten thousand square miles (IALE 2018). The area covers multiple gradients of urbanisation, agricultural intensity and tree cover. The Northern Forest, therefore, presents a promising context for a study on woodland configuration and species rich-ness given the range of conditions present and the practical implications of potential findings for the implementation of new woodland.

Methods

To test expectations 1–4, we explored the relative influence of habitat edge, land-cover diversity and connected interior habitat across several landscape gradients related to different land-covers; one urban and two agricultural (arable and grassland). We used the 10 m resolution UK Landcover Map 2021 (Marston et al 2022) to characterise the study area landscapes and delineate habitat (broadleaf wood-land) from non-habitat. We assigned values for edge effects (as Euclidean distance) and movement costs associated with matrix land-cover types according to a Delphi review carried out by Eycott et al. (2011) for the same land-cover classification. From these data, we determined functional connectivity within regu-lar hexagonal cells with widths of 10, 15 and 20 km, approximating the Northern Forest zone, created in QGIS 3.32.3 (Fig. 2). The minimum width of 10 km was informed by a previous analysis on mammal dis-tribution within the boundary of the study area that demonstrated poor model performance below this scale (Dennis et al. 2024). Any analysis comprising zonal aggregation is liable to exhibit the Modifiable Areal Unit Problem (MAUP, Jelinski and Wu 1996),
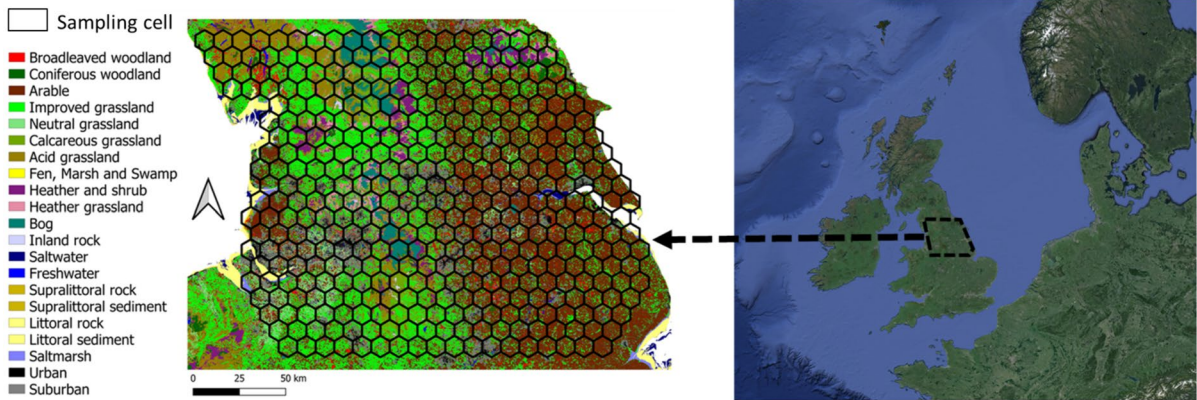
Fig. 2 Study area tessellation (10 km width hexagonal grid cells) overlaid onto the UK Land-cover Map

in which the zone geometry can influence the resulting values and inferences. The MAUP comprises two components: the scale problem, which arises from aggregation into units of different sizes leading to different values; and the zoning problem, which arises from aggregation into units of the same size but a different shape, location or orientation, leading to different values. In order to address the scale problem, we used additional sampling scales of 15 km and 20 km to test the sensitivity of subsequent modelling to scale effects. In order to address the zonal problem, we ran a sensitivity analysis using rectangular and diamond-oriented grid cells, approximating the size of the hexagonal cells at the scale (10, 15 or 20 km) that produced best model performance.

To assess functional connectivity, we used a graph-theoretical connectivity network method developed by Dennis et al. (2024). This method combines effective (least-cost) distance with landscape-level estimations of interior-edge habitat transitions, allowing us to delineate functional connectivity for edge and interior habitat as well as scenarios for true generalists (i.e., where the whole patch is considered viable habitat). Briefly, this method employs land-cover specific values for the extent of edge-effects exerted by the matrix, which are combined in a function with the area of contiguous land-cover types in the matrix to generate an edge surface. The resulting surface is used to determine the degree to which different locations within habitat patches are affected by edge, establishing an "edge gradient" for each patch. This gradient can then be used in an edge- and

area-weighted graph-theoretic framework to model functional connectivity for interior, edge and generalist habitat. The resulting connectivity value is the Edge-weighted Habitat Index (EHI), so called as it refers to the amount of connected habitat (as a percentage of the total landscape area) after accounting for landscape permeability and edge-effects.

We computed EHI connectivity for interior habitat (hereafter "connected interior habitat" or "Int") with dispersal distances of 10, 15 and 20 km (distances at which a negative-exponential function predicts dispersal success of 0.05). Again, these distances were based on model performance observed in Dennis et al. (2024) in which modelled dispersal distances ≥ 10 km were optimal. To test the effect of matrix permeability on patch isolation, we compared the use of least-cost path and Euclidean distance to measure patch isolation. To assess the relative importance of a functional measure of edge-effects (computed using the EHI method) we also computed the probability of connectivity (PC) metric (Saura and Pascual-Hortal 2007) for comparison. The PC metric is an area-weighted graph-theoretic connectivity measure and is a special case of the EHI where no consideration of edge-effects is given. Mean patch area (MPA) was computed as an added structural (i.e. non-functional) measure of connectedness. Within the same sampling grids, we also computed two fragmentation-sensitive landscape metrics for temperate broadleaf woodland: edge density (ED) and patch density (PD). Total habitat amount as a percentage (pcArea) was also determined along with land-cover

diversity (LC). The latter was calculated by applying the Shannon's Index to land-cover types using the Vegan package in R (Oksanen et al. 2012). Within this framework, we defined MPA, ED and PD as structural attributes (of habitat patches), Int and PC as functional attributes, and pcArea and LC as composition (of land-cover) attributes.

To set up the gradient analysis, we calculated percentage cover by arable, urban and grassland (aggregating all grassland types) land-covers within the UK Land Cover Map. A full list of candidate predictor variables is given in Table 1.

We downloaded occurrence data for all mammal species from the UK National Biodiversity Network Atlas (NBN Trust 2023) recorded since the year 2000 and filtered records for mammals with broadleaf woodland associations and "accepted" accuracy status. We then calculated species richness for all grids across the study area. A list of all species records

entered into the analysis, with counts, is available in Table S1.

Statistical analysis

For analysis, we set mammalian species richness as the response variable and fragmentation-connectivity measures (Table 1) as explanatory variables. To account for the influence of spatial location, we built autoregressive models with a spatial random effect (after Besag et al. 1991) using the INLA package in R (Lindgren and Rue 2015), adding cell centroid coordinates as model covariates and setting the adjacency matrix according to the mean distance between centroids. To analyse the influence of gradients of urban, arable and grassland land-cover we ran a series of models, sequentially removing sampling cells (i.e. the 10, 15 and 20 km grid cells) from the analysis based on their percentage cover

Table 1 Candidate explanatory variables for analytical models (response variable = species richness)

Variable	Landscape attribute	Abbreviation	Description	Process: increasing values =	Units
Connected interior habitat	Functional	Int	Percentage of landscape that is functionally connected interior habitat computed using the Edge-weighted Habitat Index	Increasing functional connectivity	%
Probability of connectivity	Functional	PC	Functional connectivity for true generalists (no consideration of edge effects)	Increasing functional connectivity	Dimensionless (range 0–1)
Mean patch area	Structural	MPA	Mean area of broadleaf woodland patches in each sampling unit	Increasing structural connectivity	m^2
Edge density	Structural	ED	Amount of habitat patch edge within each sampling unit	Increasing fragmentation	$m\ ha^{-1}$
Patch density	Structural	PD	Number of spatially discrete patches of woodland in a sampling unit	Increasing fragmentation	Count
H' Land-cover	Compositional	LC	Shannon's Index of Land-cover Diversity	Increasing diversity of landscape composition	Dimensionless (range 0-infinity)
Woodland cover	Compositional	pcArea	Percentage of the sampling cell that consists of broadleaf woodland cover	Increasing proportion of landscape composition as woodland habitat	%

of the target gradient. We iterated over land-cover thresholds (ranging from 0 to 20% cover) which increased by one percent (starting from zero) for every iteration of the modelling. With each iteration, sampling cells were removed if cover by the target gradient was below the threshold. Hence, with each model iteration, a sub-sample of the data is produced that is increasingly dominated by the target land-cover. For consistency, we set the maximum proportion of all land-covers to 20 percent to ensure that enough sampling points remained for model building at all analysis scales and gradients. At each point along these gradients, we recorded the mean posterior model estimates (coefficients) for all explanatory variables in the corresponding model. To establish which covariates should be entered into these gradient-based analyses, we ran univariate models for each candidate variable in Table 1 with species richness as the response. We identified the best performing variables related to the processes of (a) increasing fragmentation (variables ED and PD, Table 1) and (b) increasing connectivity (variables Int, PC and MPA, Table 1) at scales of 10, 15 and 20 km. We entered the best performing variables (exhibiting the lowest Wattanabe-Akaike Information Criterion (WAIC) in univariate models) along with land-cover diversity (LC, Table 1) into subsequent multivariate gradient-based models at the corresponding scale. We additionally ran global models (all sampling cells included) using the same variable selection process for comparison. All predictor variables were centred and scaled in order to bring effect sizes into the same range for ease of comparison. We tested for collinearity between predictor variables in multivariate models by calculating the Variance Inflation Factor for each with the CAR package (Fox and Weisberg 2019) in R. To assess whether the influence of explanatory variables was simply a surrogate for the effect of habitat amount, we also ran global habitat-only models (all sampling cells) at each scale with the proportion of habitat cover per sampling cell (pcArea) as a single explanatory variable. This served as a null model where we considered other models to be statistically relevant only if they achieved better performance than the habitat-only model. We ran diagnostic tests on model outputs by calculating Moran's I on model residuals based on the same adjacency matrix used in model building. All spatial and statistical

analyses were carried out in the R environment (R 4.3.1 Core Team, 2023). A diagrammatic representation of the work flow is given in Fig. 3.

Results

Full and univariate models

Our results highlight the presence of alternative drivers of species richness as a function of patch-landscape interactions. Of the connectivity-related covariates, Mean Patch Area (MPA) produced best model performance at scales > 10 km and connected interior habitat (Int) produced best model performance for all gradients at the 10 km scale. Table S2 gives descriptive statistics for all variables considered in the modelling approach. The models did not exhibit issues related to spatial autocorrelation (see Figure S1 for Moran's I plots across all gradients).

Models at the 10 km scale exhibited the highest correlation between observed and fitted values (Table 2). PC exhibited very high collinearity with ED and habitat cover and produced unacceptable VIF values (> 5) in multivariate models so was removed from further analysis. At the 20 km scale, the habitat-only model produced the best model performance. At 15 and 10 km scales of analysis, ED univariate and full (multivariate) models performed best, respectively. There was no significant difference between models parameterising isolation based on least-cost path versus Euclidean distance. Table 2 shows model performance for multivariate ("Full model") and univariate models. Estimated posterior distributions of regression coefficients for the "full" (i.e. all fragmentation-connectivity metrics considered) and "habitat-only" (pcArea) models are given in Table S3.

R-squared values refer to the full-model performance (based on fitted versus observed values). Bold font denotes the best performing model at each scale. The full model contains the best performing variables representing (a) fragmentation (ED or PD) and (b) connectivity (Int, PC or MPA) in addition to land-cover diversity (LC).

Gradient-based models

Explanatory variables varied significantly in their strength and direction of association with species
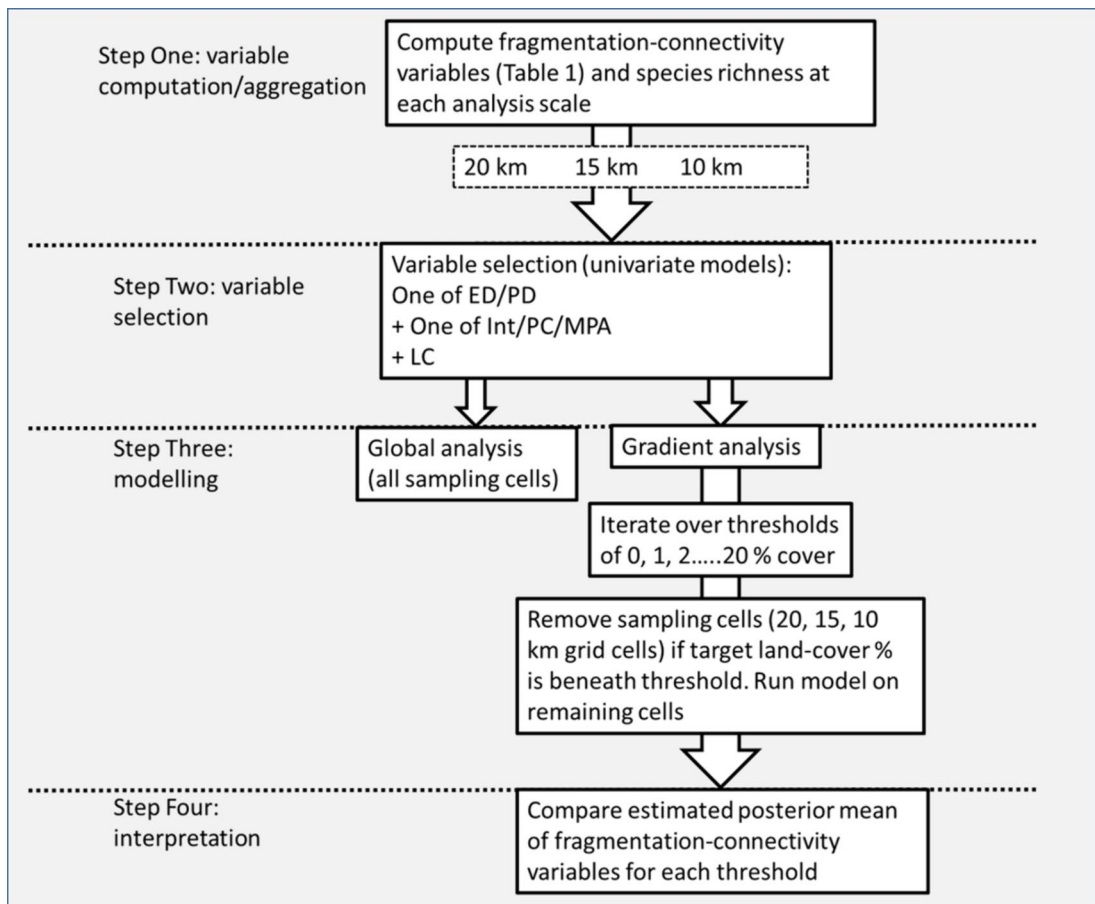
Fig. 3 Work flow used in this study. Note all models are run as autoregressive models with a spatial random effect where mammalian species richness is the response variable (see Sect. "Statistical analysis")

richness across the different gradients (Fig. 4). At all scales and at all threshold values, edge density (ED) presented the strongest positive relationship with species richness along the grassland gradient and generally exhibited stronger effect sizes in other land-cover contexts where the gradient value was low (Fig. 4). Connectivity measures were most relevant along the urban gradient and land-cover diversity (LC) exhibited strongest positive effects at scales < 20 km along gradients of arable land-cover. Grassland was the only gradient that did not produce obvious threshold effects, i.e. where variables changed rank as a function of gradient increase. Figure 4 shows the relative effect size of each predictor variable in the full model (Table 2) for each gradient and scale of analysis. Note for the full models > 10 km MPA was the better performing

connectivity metric whereas, at the 10 km scale, Int performed best (see figure legend).

The relative standing of ED, Int and LC were comparable when results were reproduced based on rectangular and diamond shaped grid cells. Figure S2 shows the comparison for rectangular and diamond-oriented cells of the same size as the 10km scale hexagons in Fig. 2. Trends were similar across the sampling cell types (Figure S2).

Discussion

Our findings bring together several insights into functional, structural and compositional characteristics that appear to influence species richness in fragmented landscapes. Considering the entire

Table 2 Results at 10, 15 and 20 km scales (all sampling cells)

Scale	Model	Effective number of parameters	WAIC	Marginal log likelihood	Pearson's R
20 km	**Habitat-only (pcArea)**	4.86	453.58	− 867.26	0.82
	ED	3.77	454.30	− 867.53	
	Full model (ED + MPA + LC)	3.12	455.36	− 880.80	
	MPA	2.52	456.21	− 868.51	
	PD	2.61	456.84	− 868.68	
	Int	2.92	458.97	− 869.89	
	LC	4.49	463.80	− 871.98	
15 km	**ED**	4.73	843.59	− 609.25	0.77
	Full model (ED+MPA+LC)	6.09	846.57	− 632.71	
	PD	4.86	850.41	− 612.59	
	Habitat-only (pcArea)	6.43	851.92	− 612.45	
	MPA	6.11	864.45	− 619.11	
	Int	7.02	865.10	− 618.74	
	LC	5.63	869.81	− 621.95	
10 km	**Full model (ED+Int+LC)**	142.55	2544.47	− 2013.77	0.92
	ED	145.77	2550.72	− 2005.96	
	PD	151.40	2555.38	− 2012.41	
	Habitat-only (pcArea)	152.44	2556.49	− 2014.53	
	LC	202.42	2561.43	− 2026.09	
	Int	160.30	2563.53	− 2025.18	
	MPA	186.84	2568.28	− 2030.30	

Fig. 4 Model variable estimates for increasing land-cover gradients at (moving left to right) 20 km, 15 km and 10 km scales. X axis denotes percentage cover by the focal land-cover type. Y axis values correspond to effect sizes for each predictor variable. Error represents 95% confidence interval around the mean estimate
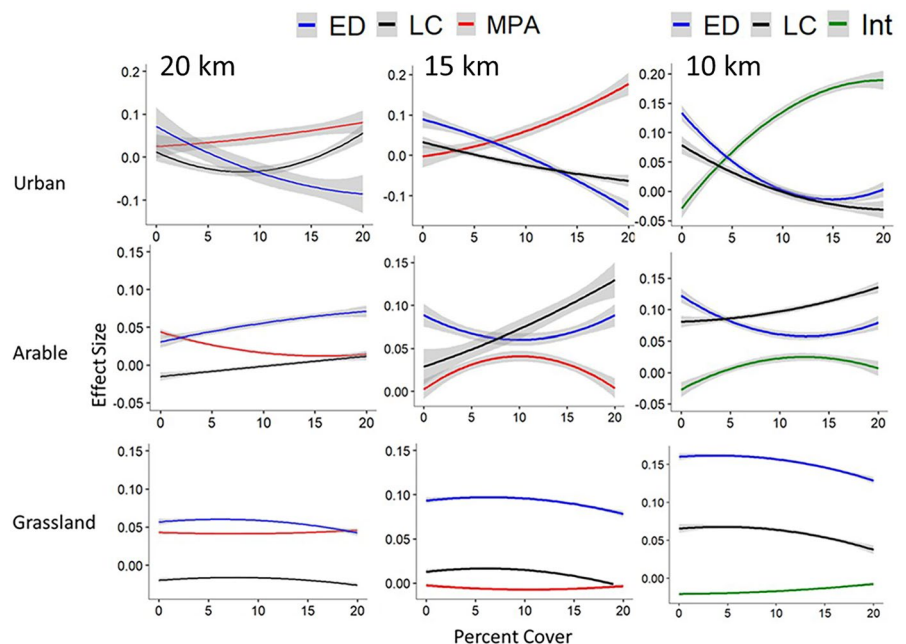
landscape (all sampling cells), our results suggest that species richness measured at broad scales (20 km cells) over a large regional extent was best explained by habitat amount. However, at scales below this, fragmentation-connectivity related variables were more relevant, outperforming the habitat-only model (Table 2). The influence of connected interior habitat (Int) on species richness in the urban context was most pronounced at the 10 km analysis scale (Fig. 4). Similarly, the strength of association between land-cover diversity (LC) and species richness increased as scales of analysis moved from largest to smallest. Variance (standard deviation) of the response variable and land-cover diversity were relatively stable across analysis scales, though, as should be expected, mean species richness did increase with sampling cell size (Table S2). Therefore, whether the sensitivity of LC to the scale of analysis is the result of landscape processes or artefacts of the data aggregation requires further research. Results for rectangular and diamond-shaped cells were comparable (Figure S2) suggesting that the observed trends were robust to different spatial sampling approaches and not noticeably affected by the zonal component of the Modifiable Areal Unit Problem (Jelinski and Wu 1996). The PC metric produced VIF values > 5 and was not entered into the gradient analysis as a result. This implies that the use of area-based connectivity metrics that do not incorporate functional considerations such as edge-effects may be limited in studies of fragmentation per se due to their potential redundancy on overall habitat amount.

The relevance of edge, interior habitat and land-cover diversity varied across the different land-cover gradients considered. In these different contexts, we observed thresholds that determined alternative drivers of species richness (Fig. 4). This suggests that local variability may play a significant role in our understanding of the influence of composition and configuration on species richness in fragmented landscapes. For example, we observed relatively stronger positive associations between edge density and species richness in all cases where matrix hostility (i.e. the gradient value) was low. That edge density was a principal driver of species richness in low-urban contexts, and exhibited consistent positive associations with species richness across agricultural gradients, implies that edge density is a critical component influencing species richness.

In addition to positive effects of edge density, our results provide particularly strong evidence that deleterious edge-effects are also a key mediating process for habitat-landscape interactions that drive species richness. These effects appeared to be strongest along urban rather than agricultural gradients. In the latter case, increasing arable cover was strongly negatively correlated with LC (Tables S4–S6). This land-cover type also exhibited weak negative correlations with all other land-cover types (Tables S4–S6) and was the only type that exhibited a negative correlation with broadleaf woodland cover. This implies that, for our study area, increasing arable land-cover disproportionately drives landscape homogeneity. Local gradients and the dominance of particular land-cover types (e.g. urban versus arable) within the matrix may, therefore, determine to a large degree the ascendency of alternative drivers of species richness. For example, in the case of arable-dominated landscapes, increasing land-cover diversity appeared to be more relevant to gains in species richness than buffering against edge effects.

Relevance to wider research

In recent literature, several mechanisms have been proposed to elucidate biodiversity outcomes in relation to landscape configuration. These proposals have predominantly focused on patch geometry, specifically emphasising the significance of properties such as patch size and edge, and their interaction with extinction-colonisation processes and heterogeneity (Fahrig et al. 2022). Our results give some support to the supposition that landscapes with a greater amount of edge should contain higher species richness given that increasing edge density exhibited clear positive associations with species richness (Table 2, Fig. 4). These observations align with other findings demonstrating the importance of patch density and edge for landscape-scale species richness (Riva and Fahrig 2022). However, our results suggest that this may only hold under certain thresholds of matrix hostility. For example, in situations where edge effects are extensive and severe (i.e. where urbanisation levels are high), well-connected interior habitat may be a more reliable determinant of species richness. The relative ascendency of interior over edge in promoting species richness was most pronounced (Fig. 4) at the 10 km level. This scale of analysis also showed the best

model performance in terms of predicting observed values (Table 2). Therefore, at the scale at which the phenomenon was best explained, connected interior habitat is a key driver of species richness along urbanisation gradients. Notably, neither connectivity nor fragmentation best explained species richness at the 20 km scale in the global analysis (Table 2) where habitat amount performed best. Therefore mechanisms related to key questions in landscape ecology around habitat amount (Fahrig 2013) and fragmentation (Valente et al. 2023) may be revealed at different scales of observation.

That connected interior habitat was highly significant over edge and land-cover diversity in environments with high matrix hostility is relevant to assertions put forward in recent fragmentation-biodiversity research (Fahrig et al. 2022). The SLOSS Cube proposes high matrix hostility as a condition that can lead to negative biodiversity outcomes as a function of fragmentation and our results confirmed the importance of interior habitat in more urban environments. However, though connected interior habitat appeared to promote species richness in high urbanisation contexts, we did not find evidence that matrix permeability was a key driver, given that the use of both Euclidean distance and least-cost path measures of isolation in functional connectivity assessments produced identical model outcomes. This implies that matrix effects on patch characteristics (i.e. edge effects) that effectively reduce interior patch size in area-weighted functional connectivity measures may be more relevant to species richness than permeability effects in highly anthropogenic environments.

Notwithstanding the evidence for the importance of edge-related factors, simple measures such as patch size and number may not be sufficient in themselves to characterise the underlying functional drivers of species richness in fragmented landscapes. Rather, this study supports a shift towards giving greater attention to patch-landscape processes (i.e. connectivity, land-cover diversity, and edge effects). Our findings suggest that patch-landscape interactions drive species richness, rather than patch size or number per se. The relevance of functionally connected interior habitat, edge length and land-cover diversity imply that habitat amount alone may be insufficient to understand processes affecting species richness across environmental gradients. Our study therefore sits alongside other recent work aiming at a more

functional delineation of habitat. For example, Halstead et al. (2019) used stacked species distribution models (SDMs) to estimate community-level habitat availability. They report improved model performance when predicting species richness as a result of using a more species-specific (i.e. functional) measure of habitat. However, we note that species distribution modelling is more closely aligned with the niche concept (especially when including climatic and topographic information) than with delimiting biodiversity supporting land-cover. In contrast, our approach, by modelling the interaction between alternative land-covers, as a function of their expected influence of species groups, provides a practical means to estimate how complex land-use mosaics may contribute to species richness. Our work should therefore inform existing research agendas, such as the fragmentation-biodiversity debate, that would benefit from a focus on patch-landscape interactions.

Our results do not refute predictions based on the SLOSS Cube. However, they do suggest that a re-framing of habitat availability as a function of patch-landscape interactions, might provide a more effective basis for landscape comparisons than simple measures of patch size at scales best reflecting fragmentation effects. While fixing attention on area-based evaluations of landscapes and species richness may provide a basis for exploring patterns at large scales, a re-orientation towards a process-based view may be a promising route forwards for context-specific landscape research. For example, our findings imply that landscape context can modify the relevance of different patch attributes for species richness. As such, this perspective may help to reconcile opposing views on the importance of patch-versus-landscape processes in fragmentation-biodiversity studies, as called for in recent prominent publications on this topic (Valente et al. 2023).

Implications for landscape decision-making

Together, these findings related to connectivity, edge and landscape composition have implications for our understanding of the effects of structural, compositional and functional attributes on species richness. For example, we identified that the influence of compositional (e.g., landscape diversity) and functional (e.g. connectivity) factors on species richness can alternate according to environmental contexts. In so

doing, we update recent suppositions around patch number, size and configuration (Fahrig et al. 2022) to include the acknowledgement of more formal patch-landscape processes that can lead to, and modify, the proposed mechanisms driving species richness found in recent debates (Fletcher et al. 2018; Fahrig et al. 2019). As a result, our findings have direct relevance to landscape decision-making. Though we acknowledge that such decisions are often made on a land-area basis, we propose that our findings could be implemented into restoration and conservation planning with more holistic management aims. For example, in landscapes subject to a highly hostile matrix, well connected patches that provide greater connected interior habitat (i.e., minimally impacted by edge effects) should be prioritised, rather than simply favouring more or larger patches without consideration of edge-effects and configuration. Likewise, in landscapes where the matrix is less hostile but more homogenous, diversity of non-habitat land-cover may be an important consideration in addition to habitat patch attributes and distribution. Moving towards context- (i.e. the matrix) and process- (i.e. patch-landscape interactions) rather than area-based (i.e. simply considering habitat size or amount) perspectives could help clarify the role of landscape pattern, and associated metrics, for species richness and reap substantial rewards in nature recovery efforts.

Conclusion

This study provides new insights into assumptions around the relative influence of structural, compositional and functional characteristics of habitat on species richness. Our results highlight the need to consider patch-landscape interactions such as those concerning edge effects, land-cover diversity and connectivity in assessments of species richness in addition to geometric or patch-level properties. The importance of structural and functional characteristics may be subject to thresholds related to matrix hostility and, under these different conditions, alternative configurations may better promote species richness. Therefore, the answer to the question as to whether fragmentation per se reduces or encourages species richness at the landscape-level may lie in the context in which fragmentation effects are observed. Specifically, we identified a clear distinction between

the importance of connected interior habitat and edge density in areas with high and low edge-effects, respectively. In addition, we found that drivers of species richness in woodland mammals may be sensitive to the scale of observation. Addressing scale-effects in fragmentation studies wherever possible should therefore become a standard approach. The identification of thresholds that determine alternative drivers of species richness in fragmented landscapes should consider matrix hostility and homogeneity at scales relevant to decision making or ecological processes of interest. Such thresholds could serve as valuable guidance for making conservation decisions across gradients of human-induced impacts in fragmented landscapes.

Declarations

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