

Research article

Inconsistent relationships between area, heterogeneity and plant species richness in temperate farmed landscapes

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Relationships between area, heterogeneity and species richness are fundamental concepts in ecology yet questions remain about how area and heterogeneity tradeoff (AHTO) to constrain biodiversity. Although there is growing evidence for unimodal heterogeneity diversity relationships (HDR's) and an AHTO, tests of the concept and consequences for species richness across a landscape-scale gradient of human-modified ecosystems are rare. Using data from a national (Wales) field survey we analysed relationships between environmental heterogeneity and plant species richness (α and γ). We used ordination to produce a composite metric of heterogeneity and compared this to commonly used metrics. We used niche hypervolumes to categorise the breadth of plant species' ecological preferences and analysed relationships between species richness, niche width and heterogeneity. The HDR was unimodal with α diversity at the smallest scale and positive with α and γ diversity (non-linear) at the 1 km scale although in low intensity landscapes the HDR with γ diversity was unimodal. There was a unimodal relationship between habitat diversity and γ diversity. Land use intensity was unimodally related to diversity. There were significant interactions between niche width and heterogeneity. Richness of broad niche species increased with heterogeneity with flattening of the curve at higher levels. Narrow niche species were rare and mostly unresponsive. The expected decline in narrow niche species with increasing heterogeneity was not found although they did decline with land-use intensity. Using a unique dataset, an analysis of a large-scale mosaic of ecosystems found that the shape of the HDR varies with land use intensity, the heterogeneity metric, spatial scale, diversity type and niche width. Although heterogeneity can increase species richness, there may be tradeoffs at higher heterogeneity. A fundamental constraint on realising the benefit of heterogeneity is the low availability of narrower niche species in local species pools in modified landscapes.

Key words: alpha diversity, biotic homogenisation, coexistence, configurational and compositional heterogeneity, gamma diversity, niche, plant communities



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Introduction

The relationship between spatial environmental heterogeneity (EH) and species diversity is an important topic in ecological, evolutionary and biogeographic research (Stein and Kreft 2015). The species–area relationship predicts that as area increases, the capacity for the ecosystem to support populations of species increases. Species richness is also predicted to increase with environmental heterogeneity as there is more available niche space (niche dimensionality), to meet the ecological requirements of species, so more species can co-exist and the local species pool increases (MacArthur and Wilson 1967, Rosenzweig 1995, Bar-Massada and Wood 2013, Heidrich et al. 2020). Positive heterogeneity diversity relationships (HDR's) may also result from spatial separation of species populations reducing exposure to superior competitors (Lundholm 2009, Orrock and Watling 2010, Stein and Kreft 2014, Ben-Hur and Kadmon 2020a, b). However, increasing EH must reduce the mean area of homogenous habitat space resulting in a tradeoff. The area–heterogeneity tradeoff (AHTO) is a relatively recent concept (Fig. 1).

Species richness could increase with increasing heterogeneity (green line) (Stein and Kreft 2015). As environmental heterogeneity increases, mean effective area available for individual species decreases (red line). When a threshold or inflection point is reached between species gains from heterogeneity and losses due to reductions in available area, species richness declines (Allouche et al. 2012, Ben-Hur and Kadmon 2020a, b, Heidrich et al. 2020). This results in a non-linear, unimodal relationship between heterogeneity and richness (Allouche et al. 2012, Bar-Massada and Wood 2013, Heidrich et al. 2020) (Fig. 1). Hence the positive impact of heterogeneity and the negative impact of reduced area jointly filter the species pool.

This process is hypothesised to operate non-randomly such that rarer species with smaller population sizes and narrower niche widths have higher extinction risk and are more susceptible to reduction in area (Allouche et al. 2012, Ben Hur and Kadmon 2020b) (Fig. 1 red line D). This follows because species restricted to a more limited set of conditions will be rarer if those conditions are less abundant. Mechanisms include stochastic extinction typically linked to smaller patch size

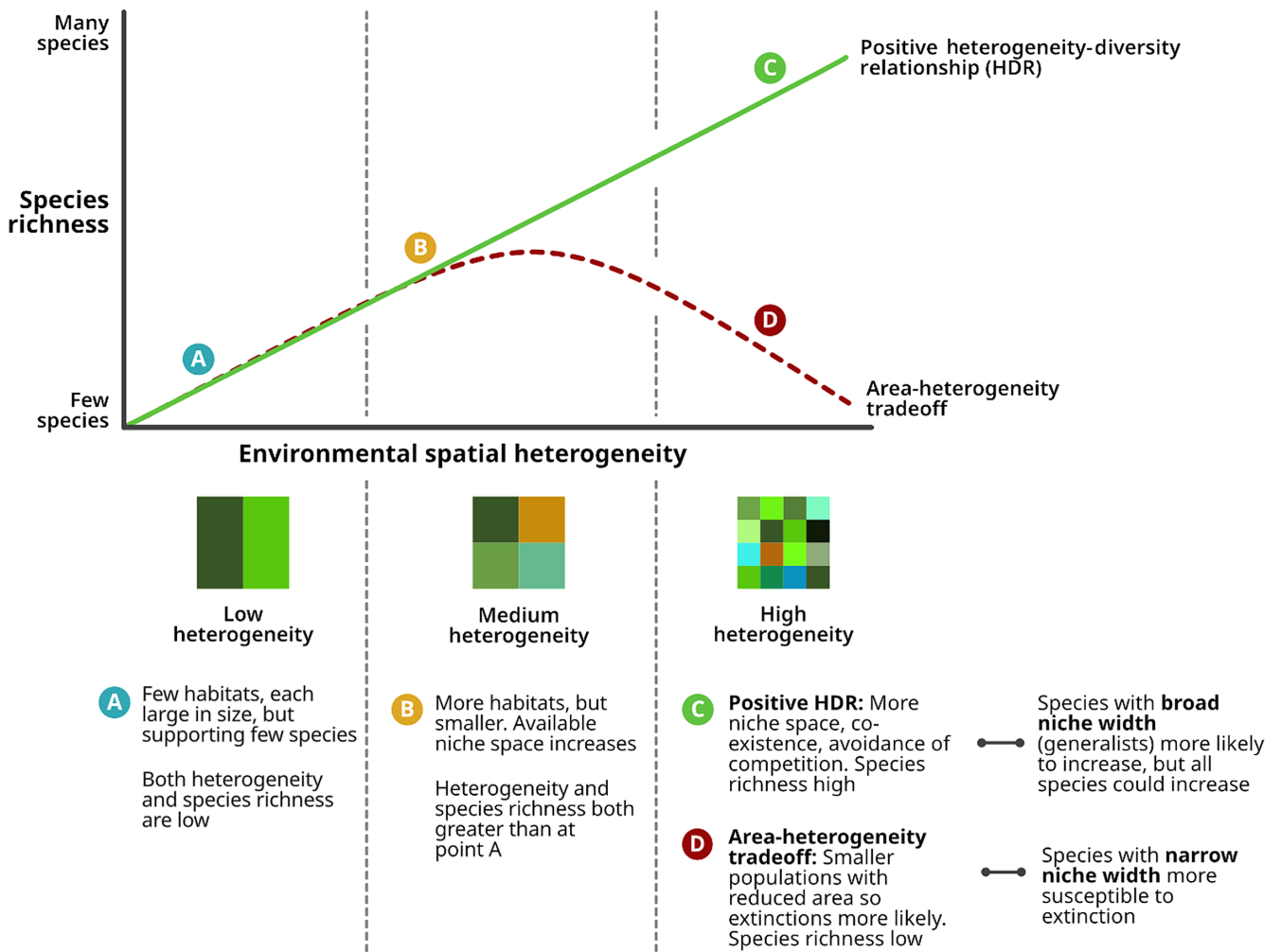


Figure 1. Conceptual diagram of relationships between heterogeneity and species richness (following Allouche et al. 2012, Orrock 2020).

and isolation (hence a fragmentation effect) and trait-based extinction reflecting changes in favourable habitat (Fahrig 2011, Ben-Hur and Kadmon 2020b).

There is evidence to support positive (Hortal et al. 2009, Stein and Kreft 2015), negative (Tamme et al. 2010) and unimodal HDR's (Allouche et al. 2012). However, explicit tests of the area–heterogeneity tradeoff and its consequences for species richness are still rare (Ben-Hur and Kadmon 2020a, Heidrich et al. 2020), especially those based on observations across landscapes that have been shaped to varying extents by a long history of human modification. This is important, because changes in land use intensity and rapid economic and social development over the last century have influenced landscape heterogeneity and changed habitat dynamics in many ecosystems (Johst et al. 2011), altering the population dynamics of species and non-randomly segregating them into 'winners' and 'losers' depending upon their trait syndromes (Smart et al. 2005, 2006, FINDERUP Nielsen et al. 2019). From a starting point of ecosystems simplified and reduced in biodiversity by intensive land-use, the tactic of increasing heterogeneity by varying the mosaic of biotic conditions is attractive because it can increase diversity from a starting point of low alpha, beta and gamma diversity. However, this relies on residual populations of responsive species persisting in the landscape (Smart et al. 2006). Not surprisingly then, increasing heterogeneity is an influential component of conservation planning, for example, the design of nature reserves (Ben-Hur and Kadmon 2020a, b), agri-environment schemes (AES) or agro-ecological farm practices, including functional agrobiodiversity (FAB) (Kleijn et al. 2011).

Environmental heterogeneity should be defined with respect to an environmental factor that is known to affect the distribution of the target species in the relevant system (Allouche et al. 2012, Bar-Massada and Wood 2013, Gavish et al. 2021). Heterogeneity diversity relationships are complicated by the many different definitions and metrics of heterogeneity resulting in substantial ambiguity in concepts and terminology (Tamme et al. 2010, Stein and Kreft 2015, Heidrich et al. 2020). Heterogeneity can be differentiated into habitat complexity or within habitat heterogeneity, for example, vertical structural heterogeneity of habitats (such as vegetation strata i.e. ground, shrub and canopy) and between-habitat, horizontal heterogeneity e.g. habitat diversity (Benton et al. 2003, Stein and Kreft 2015). Some studies have used multiple (Heidrich et al. 2020) or composite (Deuschewitz et al. 2003, Honnay et al. 2003) metrics of heterogeneity, whilst others have used relatively simple measures e.g. categorising landscapes based on the amount of semi-natural habitat (< 2% cleared landscape, 2–20% structurally simple, > 20% complex) (Tscharrntke et al. 2005, Batáry et al. 2011, Concepcion et al. 2012, Dainese et al. 2015) or the number of habitats (Ben-Hur and Kadmon 2020a, b). Stein and Kreft (2015) propose 'environmental heterogeneity (EH)' in biotic and abiotic factors including land cover (composition and configuration) (Fahrig et al. 2011, Perović et al. 2015), topography (elevation range) (Allouche et al. 2012), vegetation structure, climate and soil. The choice of heterogeneity metric

or metrics may influence heterogeneity–diversity relationships along with other factors (Batáry et al. 2011, Heidrich et al. 2020). For example, there may be different relationships with alpha diversity (α -diversity-local scale diversity) and gamma diversity (γ -diversity-total species diversity in a landscape) (Whittaker 1972). While γ should increase or be unimodal, in human modified landscapes mean α is expected to decline in smaller areas of habitat as a result of stochastic and trait-based extinction. A competing hypothesis that does not rely on spatial heterogeneity is that resource levels or other correlates of productivity should be more important than resource heterogeneity in determining plant species diversity (Lundholm 2009). Methodologically this requires that we measure heterogeneity in a way that is orthogonal to land-use intensity so as to isolate the interaction between the two (Yang et al. 2015).

Scale is likely to also be an important influencing factor on HDR's (Ma 2008, Bar-Massada and Wood 2013) and will influence the length of the heterogeneity gradient, for example, short and low resolution (large grid square) heterogeneity gradients may under-represent tradeoffs because of averaging (Bar-Massada and Wood 2013). An understanding of the potential mechanisms influencing the shape of the relationship is important to enable prediction of those conditions leading to differently shaped HDR's (Ben-Hur and Kadmon 2020a, b, Heidrich et al. 2020).

Many of the existing studies on heterogeneity and species richness have been on invertebrates and birds (Gabriel et al. 2005, Alignier et al. 2020). Here we contribute unique new understanding by examining realistic variation in plant species across a large-scale mosaic of ecosystems. We have chosen a number of metrics that reflect biotic and abiotic landscape heterogeneity and are most likely to influence plant species richness. This includes measures that directly influence plant species such as soil diversity and elevation range, and measures that reflect structural heterogeneity (e.g. the spatial pattern of woody vegetation (Bar-Massada et al. 2012, 2013)) which may indirectly influence plant diversity through variation in light availability, microclimate and soil moisture (Heidrich et al. 2020). We have used these to create a composite measure of heterogeneity using multivariate methods (Gabriel et al. 2005). We also use a simple measure of heterogeneity; habitat diversity (Ben-Hur and Kadmon 2020a) to compare to the composite metric, and also the proportion of semi-natural land (Tscharrntke et al. 2005, Batáry et al. 2011, Concepcion et al. 2012, Dainese et al. 2015). To address scale issues, we have calculated environmental variables at different spatial scales; 100 m around small quadrats versus a wider 1 × 1 km square in which quadrat samples are embedded. We expect species' responses to heterogeneity to be strongly dependent on niche width and use niche hypervolume (Blonder et al. 2018) to express where a species lies on this gradient and its interaction with heterogeneity in shaping HDR.

This study is at a national scale (Wales) and uses field data collected as part of the monitoring project (GMPE; Glastir Monitoring and Evaluation Project (Emmett et al. 2014)). This project, along with the UKCEH Countryside Survey on

which the methodologies are based, is unique in collecting fine-scaled mapping data on landscape elements alongside finely resolved vegetation plot data that can be used with remotely sensed data to measure heterogeneity.

In this study we explore relationships between plant species richness and heterogeneity and niche width. We aim to test:

- 1) Whether there is a non-linear unimodal (hump-shaped) relationship between heterogeneity and species richness and whether relationships are consistent across heterogeneity metric, context, scale and interactions with land use intensity.
- 2) Whether niche width explains variation in the response of plant species richness to heterogeneity and thus confirm its role as an influential control on HDR across human-modified landscapes, in particular, that negative impacts of reduced area will be less pronounced for species with large niche width.

Material and methods

Field survey data

We used field data from the Glastir Monitoring and Evaluation programme (GMEP) (Maskell et al. 2020a, b, c, Smart et al. 2020, Wood et al. 2021). The methodology is based largely on that of the UKCEH Countryside Survey (Norton et al. 2012). We drew vegetation data from 183 1 km squares based on an existing physiographic classification of all 1 km squares in Britain (Bunce et al. 2007). Plant responses and covariates used to define heterogeneity were all measured in each 1 km square as follows.

Habitat mapping

Within each 1 km square, a series of measurements were recorded, including habitat mapping of all features within a 1 km square. As part of the habitat mapping, areas (> 20 × 20 m) were mapped and classified to habitat type (Supporting information, Maskell et al. 2020a, Wood et al. 2021). All woody linear features (lines of trees and hedgerows) (less than 5 m wide and 20 m minimum length) and individual trees were also recorded.

Plant species richness

Up to 39 vegetation plots (mean number of plots is 18), sampling a variety of landscape features, were located within each 1 km square (Smart et al. 2020). In each vegetation plot, a list was made of all vascular plants and the more easily identifiable bryophytes. We have used species richness as our response variable in common with other studies (Lundholm 2009, Allouche et al. 2012, Heidrich et al. 2020). Five of these plots were 200 m² randomly located plots and alpha (α) diversity was calculated as the mean number of plant species recorded in these 200 m² plots in each square (Supporting information).

Other plot types sampled linear features (watercourses, hedges and field boundaries) and areal features (fields, unenclosed land e.g. upland habitats with no boundaries). Linear plots were 1 × 10 m laid out along the feature and 2 × 2 m plots were used to additionally sample habitat types within each square not already sampled by the other plot types so as to capture the full range of plant assemblage variation. Gamma (γ) diversity was calculated as the cumulative list of species recorded from all plot types in each 1 km square (Supporting information).

Calculation of niche hypervolumes

We calculated niche hypervolumes to characterise species' abilities to tolerate different ranges of environmental conditions. Occupied niche space for each species was defined by the multidimensional volume resulting from the range of the mean Ellenberg indicator scores and climate values associated with quadrats in which each species has been found in British plant communities. The database we used to calculate hypervolumes was derived from a series of vegetation surveys of all common and rare habitats across Great Britain (Smart et al. 2010). These surveys represent as accurately as possible the full range of conditions under which each species is found. Species restricted to a narrower range have a smaller hypervolume, while the opposite is true for species that occupy a broader range of ecological conditions. We calculated niche hypervolume for plant species in R (SVM machine learning algorithm) (Blonder et al. 2018). The calculations were restricted to species that had > 10 records (441 species). Species with < 10 records were excluded because their rarity means we are unlikely to have accurately sampled their niche and so hypervolumes would be biased and unreliable.

Species were classified by the size of their individual niche hypervolume into four groups (by quantiles, lowest 0–25%, to highest 75–100%). Having assigned each species to a group then mean α and γ of each group was calculated for each of the quadrats in our national sample across Wales. This enabled us to model the relationships between heterogeneity and diversity where diversity comprised either wide-ranging or narrower niche species. Mean niche width was calculated for each plot using the individual species hypervolume scores.

Heterogeneity metrics

Data were collated from the GMEP field survey, from remotely sensed data and from other third-party sources (e.g. elevation data) (Table 1, Supporting information). Data were extracted at two different spatial scales (100 m around a vegetation plot) by buffering around the vegetation plot and within the 1 km square. We include abiotic and biotic data to represent heterogeneity. Abiotic includes soil diversity, rarity, topography. Biotic elements include a measure of habitat diversity (between habitat variation) and measures to capture landscape structural complexity. Woody cover, canopy height and vegetation strata (Ma 2008, Batary et al. 2011, Bar-Massada et al. 2012, Stein et al. 2014) are used to represent structural complexity.

Table 1. Metrics used for analysis.

EH	Metric	Scale	
		100 m	1 km
Landcover	Habitat diversity (Shannon diversity)	✓	✓
	Patch size (mean area)		✓
	Land-use intensity (% semi-natural land)	✓	✓
Landcover/vegetation structure	Broadleaved woodland/woody cover (area '000 m ²)	✓	✓
Vegetation structure	Woody linear features (length '000 m)		✓
	Number of individual trees in 1 km		✓
	Sward height	✓	
	Vegetation strata	✓	
	Max canopy height	✓	
Topographic	Elevation range (max–min altitude)		✓
Soil	Soil diversity (Shannon diversity)		✓

The percentage cover of semi-natural/improved land. This was calculated from field survey data. Semi-natural was defined as all habitats excluding improved grassland, urban, arable and coniferous woodland habitats.

Habitat diversity. Shannon's diversity index was calculated from the mapped habitats in the field survey to take into account their number and the dominance among them (Maskell et al. 2019).

Patch size. Patch size was calculated as mean area of habitat per 1 km square from field survey mapping data.

Woody cover. Data from the field survey on woodland area and other woody features such as hedgerows, lines of trees and individual trees were also included in the ordination.

Other measures of vegetation structure. Each 200-m² vegetation plot was assigned to a category of ground vegetation, shrub and canopy vegetation and the number of strata was counted and included as a variable in the 100-m scale analysis.

Elevation range. A 5 m resolution raster elevation layer was provided by Welsh Government (the Nextmap Britain DTM by Intermap Technologies). We calculated elevation range to capture abiotic heterogeneity (e.g. topography, microclimate), this is an important influence on plant richness (Heidrich et al. 2020).

Soil diversity. Maxwell et al. (2017) used 98 soil associations taken from the soil survey of England and Wales in an analysis to assess spatial patterns (soil diversity) across Wales and these data were used here. Soil diversity is measured using the Shannon diversity index, similarly to the calculation for habitat diversity.

Analysis

To create a composite metric of heterogeneity, we carried out an ordination (PCA) of potential explanatory variables in R using Vegan (Oksanen et al. 2020) at the two scales 100 m and 1 km. Variables were slightly different for the two scales. At 100 m we included: habitat diversity, the area of semi-natural and improved land, the number of strata, elevation range, woodland and small woody features (Supporting information). The ordination at 1 km scale included: habitat diversity, the area of semi-natural and improved land, elevation range, soil diversity, woodland, hedgerows, trees and improved land (Fig. 2). The data fall along two axes. Axis 1

is based on the area of semi-natural and improved land and although this has often been used as a metric of complexity/heterogeneity, it appears more likely to represent a gradient of land-use intensity (100 m - 25.3%, 1 km - 31.5% of variance). Axis 2 of the ordination includes many of the other measures and appears to represent heterogeneity (100 m - 15.8%, 1 km - 18.3%) (Maskell et al. 2019). Axis 2 site scores were therefore extracted and used in subsequent analyses to represent a composite index of heterogeneity (Gabriel et al. 2005, Ma 2008). We used habitat diversity as a single metric in analyses representing between habitat heterogeneity to compare to the composite metric, it has been used as such by other authors and as is something that can be manipulated in landscape management. We have also used land-use intensity as an additional variable in subsequent analyses (correlated with axis 1), differentiating it from the overall heterogeneity measure. Axes were inverted and scores multiplied by -1 where necessary i.e. in Fig. 2 high heterogeneity has high negative value but for Fig. 3 high axis score = high heterogeneity.

Generalised additive mixed models (GAMMs) were used to allow flexibility in the shape of the response and allow testing for particular linear or quadratic responses. If the data support a unimodal relationship we would expect this to be captured by a GAMM but GAMMs could also capture more complex

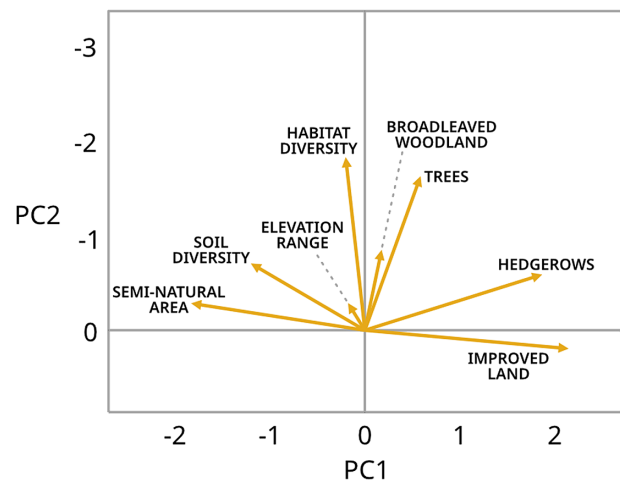


Figure 2. Ordination (PCA) diagram for variables at 1 km scale.

relationships such as an increase followed by a plateau. They were used to analyse the effects of heterogeneity metrics on 1) plot-level α -diversity, 2) square-level γ -diversity and 3) both α and γ diversity when calculated separately for species varying on niche width. We also classified the 1 km squares along a land use intensity gradient into 3 categories (0–25, 25–75 and 75–100% modified land) and re-ran the HDRs at all scales.

We used `gamm4` (Wood and Scheipl 2022) which is based on `gamm` from the R package `mgcv`, but uses `lme4` rather than `nlme` as the underlying fitting engine, because we have a random effect structure and wanted the capacity to compare AICs (Burnham and Anderson 2002). For analyses with species richness as response variable a Poisson structure was used (after testing for fit to the Poisson distribution). The 1 km square was incorporated as a random intercept in plot-level analyses. We also repeated the analyses as linear models using `glmer` in `lme4` to compare to the GAM results (Supporting information). We tested for spatial autocorrelation (SAC) (Dormann et al. 2007) by extracting the residuals and creating variograms, there was little change in semi-variance values with distance and no evidence of SAC. We also re-ran some of the models with a spatial term included and there was no difference to the output so the final models were run without a spatial term. The number of plots per square was included as a predictor in the square-level analysis.

The models were quite simple; only a single measure of heterogeneity was used (Tamme et al. 2010). We did not include additional variables, such as climate, as has been done in some studies, as climate interacts with some of the heterogeneity measures, e.g. elevation range, which represents heterogeneity. We did, however, include the scores from PC1 as a measure of land-use intensity as an interaction term when fitting heterogeneity.

Similarly to Heidrich et al. (2020), we assessed the shape of the HDR based on graphical representation (none, positive,

negative, non-linear, non-linear unimodal/hump-shaped). However, as the visual assessment of the relationships was sensitive to a) different observers and b) individual datapoints, we have 1) presented confidence intervals and explored potentially anomalous points using Cook's distance 2) recorded the estimated degrees of freedom (edf; an edf of 1 signifies a linear relationship) and 3) we analysed using linear and unimodal models and compared the AIC values, such that lower values indicated support for a model if the difference was > 2 units. Previous work has suggested identifying whether the vertex of a quadratic relationship falls within the range of the data as a way of distinguishing unimodal relationships (Chocron et al. 2015). Unlike the quadratic terms used in Chocron et al. (2015) GAMMs are more flexible and not restricted to fit unimodal relationships, therefore there is no equivalent single vertex to be identified (referred to as an inflection point in Chocron et al. 2015). Instead we have inspected the range of the data and indicated where this might influence the interpretation. To test whether niche width explains variation in the response of plant species richness to heterogeneity we tested the interaction term between niche width and heterogeneity and explored this effect at 100 m and 1 km scales.

Results

Relationships between heterogeneity and species richness

We found evidence of a potential unimodal relationship between our composite metric of heterogeneity and total plant species richness (α diversity) at a local scale (100 m) (Table 2, 3, Fig. 3, Supporting information). However, data are restricted at high heterogeneity, so confidence limits are wider and it is possible α diversity levels off rather than declines. So there is

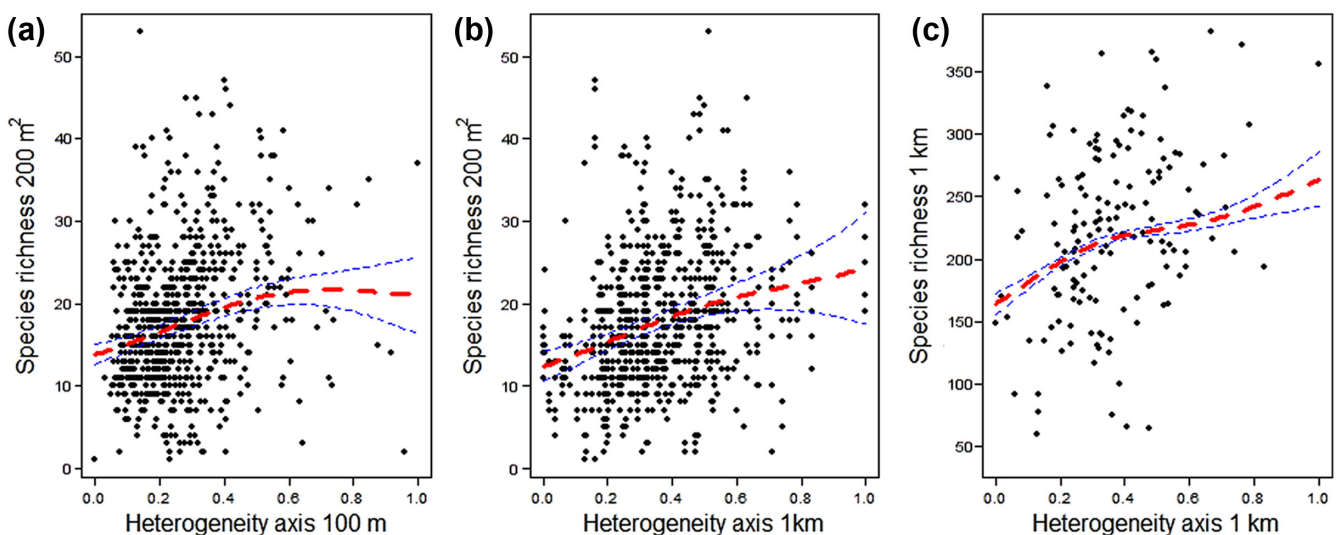


Figure 3. Heterogeneity–diversity relationship (HDR) between plant species richness and heterogeneity measured as a composite axis score in 200-m² plots (α diversity) at 100 m (a) and 1 km (b) and total species richness γ diversity in a 1 km square (c). Calculated using general additive models (`gamm4`).

potential for a unimodal relationship i.e. a downturn in the positive relationship. At the larger scale (1 km) the relationships are positive for both α diversity (although the difference in AIC values for non-linear and linear was < 2 so neither model is superior to the other) and γ (gamma) diversity although this was non-linear (Table 2, 3, Fig. 3, Supporting information).

When HDR's were analysed in three different categories of landuse intensity, in the middle category (25–75% improved land) the relationships were the same as above, however at low land use intensity there was a positive relationship at 100 m scale and potentially a unimodal relationship with γ diversity. At high land use intensity the relationship at the local scale was positive and non-significant at 1 km. This partly reflects the shorter heterogeneity gradient in these squares (Table 4, Supporting information).

If we look solely at habitat diversity (a component of the heterogeneity metric), there is again a unimodal relationship with α diversity at the smaller scale (100 m) but also with γ diversity, the relationships were non-linear and unimodal according to AIC values (Table 3, Supporting information). The relationship was positive with alpha diversity at 1 km.

We analysed relationships with land use intensity (the percentage cover of semi-natural land), which was identified as an orthogonal axis in the ordination. The relationship between species richness and land-use intensity was non-linear and unimodal for α and γ diversity at all scales (Table 3, Supporting information).

Niche hypervolume and heterogeneity

The interaction between heterogeneity and mean niche width for species richness was significant at all scales ($p < 0.001$), suggesting that change in richness with heterogeneity indeed varies with niche width. Species in the top three niche width quartiles (i.e. broadest niches), were positively related to heterogeneity at 1 km for α diversity. At the 100 m scale and for γ diversity, the relationships between broad niche species and heterogeneity were potentially unimodal although at 100 m the AIC did not differ significantly (Supporting information). As with the HDR, the confidence limits were wider at higher heterogeneity levels. Narrow niche species were

generally unresponsive to the composite heterogeneity metric (Table 2, 3, Fig. 4) although in low intensity landscapes there was a positive response from narrow niche species with γ diversity (Supporting information). Mean niche width did decline with heterogeneity at the 100 m scale (and in moderately intensive landscapes) (Supporting information).

When habitat diversity is used as the sole explanatory variable, there were positive relationships for species at all niche widths (Table 3, Supporting information). At 100 m, the narrowest niche width species were unresponsive, but at 1 km (α and γ), the narrowest niche species were positively related to habitat diversity. The interaction between habitat diversity and mean niche width was significant for α at 100 m and γ at 1 km ($p < 0.001$). Mean niche width was negatively related to habitat diversity at all scales.

The land use intensity gradient (% seminatural land) had positive effects on the species with the broadest niche width and negative effects on species with the narrowest niche width (Table 3, Supporting information) although the pool of narrow niche species was always relatively small. The two groups with intermediate niche width (25–75% quartiles) showed unimodal relationships. There were similar patterns for α and γ diversity. Interaction between niche width and land-use intensity was significant at all scales ($p < 0.001$). Mean niche width increased with land-use intensity.

Discussion

The relationships between area, heterogeneity and cumulative species number are fundamental concepts in ecology, but the inconsistencies between them have not been fully recognized nor explored. Understanding these relationships is important for restoring and reconnecting habitats, and for their biodiversity, particularly in highly modified landscapes.

Is there a unimodal relationship between heterogeneity and species richness?

There were some issues with having sufficient data at high heterogeneity, influencing uncertainty and at times limiting confidence in unimodality due to the limited range of the

Table 2. Results from general additive models (gamm4) for total species richness, richness of a niche group and niche width. += positive, -= negative, \cap =unimodal (hump-shaped), \cap l=non-linear, i.e. not unimodal but also not linear, (R) indicates that the range of the data may limit identification of unimodal effects (75–100%=broadest niche, 50–75%=upper middle, 25–50%=lower middle and 0–25%=narrowest niche). (edf=estimated degrees of freedom, dir=direction of relationship). Each row refers to a single model. (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Response var	Heterogeneity								
	100 m (α)			1 km (α)			1 km (γ)		
	edf	χ^2/F	dir	edf	χ^2/F	dir	edf	χ^2/F	dir
Species richness	2.4	79.4***	\cap (R)	1.8	28.1***	+	2.8	188.6***	+(nl)
Species richness (niche width \times heterogeneity)	9	68***		7.4	33.5***		13.9	51***	
75–100% quartile	2.5	30.6***	\cap (R)	1	27.4***	+	2.3	23.9***	\cap (R)
50–75%	2.2	60***	\cap (R)	1.6	18.6***	+	3.3	110.9***	\cap (R)
25–50%	1	39.7***	+	1	5.7*	+	2.3	23.9***	\cap
0–25%	1	1.9	ns	1	0.2	ns	1	0.04	ns
Niche width	1	31.6***	-	1	1.8	ns	1	3.1	ns

Table 3. Summary of results from Table 2 and Supporting information (Fig. 3, Supporting information) = positive, = negative, = unimodal, = unimodal but limited by range of data, = the second narrowest group 25–50% quartile and not the narrowest niche species are significant = not significant.

	α diversity 100 m				α diversity 1 km				γ diversity 1 km				
	Broad niche sp	Narrow niche sp	Niche width	Niche x Var	Broad niche sp	Narrow niche sp	Niche width	Niche x Var	HDR	Broad niche sp	Narrow niche sp	Niche width	Niche x Var
Total Heterogeneity (composite score)													
Habitat diversity (between habitat variation)													
Land-use intensity													

heterogeneity gradient. Unlike other authors (Chocron et al. 2015) we have not excluded these results but have highlighted them, suggesting that a unimodal relationship may be present but not conclusive. There appeared to be unimodal relationships between heterogeneity (composite metric and habitat diversity) and species richness at the smaller scale of 100 m around a plot. At smaller scales high heterogeneity involves effects that operate in closer proximity to each plot as well as potentially smaller areas of habitat contributing to heterogeneity because a 100 m² is being subdivided rather than a 1 km². Other authors have stressed the importance of testing multiple scales in HDRs (Lundholm 2009, Dainese et al. 2015). Tamme et al. (2010) found that negative HDRs are significantly more common at smaller spatial scales. It is likely that sampling at small spatial scales reflects biotic interactions, so that competitive sorting influences α diversity to a greater extent than across larger units with greater environmental variation and more opportunities for co-existence (Houston 1999, Tamme et al. 2010) and also because stochastic area effects are more pronounced on small scales. In a meta-analysis, Lundholm (2009) did not find a precise spatial scale threshold above which HDRs became positive, although at scales smaller than 200 m², relationships were more likely to be negative or unimodal and, above 600 m², more likely to be positive. If heterogeneity at a larger scale produces a larger species pool, then there will be more likelihood of increased species richness but there will also be a greater chance of competitive collisions between species at smaller scales.

We did not see a strong downturn in gamma (γ) diversity consistent with a clear unimodal relationship at higher heterogeneity when applying our composite metric as a covariate in the initial analysis. We might have expected that γ diversity is more sensitive to compositional heterogeneity changes because it is a summation of the differences in species composition from plot to plot. There was a unimodal relationship with γ diversity where habitat diversity was the explanatory variable. When the survey squares were classified by the degree of habitat modification, there was potentially a unimodal relationship with γ diversity in low intensity landscapes.

There were also positive HDRs indicating that diversity may be maintained at higher levels of heterogeneity at larger scales, which confirms results from other studies (Lundholm 2009, Stein et al. 2014, Ben-Hur and Kadmon 2020a).

Mechanisms for HDR's: interactions between heterogeneity and land-use intensity

Productivity/land-use intensity could be more important than heterogeneity in determining plant species diversity (Lundholm 2009). In Wales, there are large areas of semi-natural, extensively grazed land composed of heathland, semi-natural grassland, bog, bracken and scrub (Blackstock et al. 2010). There are very few natural or pristine environments as most of the land has been subjected to some degree of modification. We found unimodal relationships between

Table 4. Squares were classified into low, moderate and high land-use intensity and the HDR's with the composite heterogeneity metric analysed along this gradient (Supporting information)

⊕ = positive, ⊖ = negative, ⊙ = unimodal, ⊙ = unimodal but influenced by range of data, ns = not significant.

Land use intensity		α diversity 100 m	α diversity 1 km	γ diversity 1 km
↓	< 25% Improved land	⊕	⊕	⊙
	25–75% improved land	⊙	⊕	⊕
	> 75% improved land	⊕	ns	ns

species richness and a measure of land-use intensity (%semi-natural land) but suggest that rather than representing an HDR these may be representative of a hump-shaped species richness/productivity relationship (Fraser et al. 2015). We also found that HDRs do appear to vary along a resource/environmental severity gradient as suggested by other authors (Seiferling et al. 2014, Yang et al. 2015). Seiferling et al. (2014) suggested that in highly modified landscapes the HDR will be positive, in semi-natural; negative, and in natural landscapes mixed relationships. Yang et al. (2015) proposed that there should be positive HDR's at either end of an environmental severity gradient and unimodal HDRs at intermediate levels. They suggest that this is because there are potentially smaller regional species pools at the extreme

ends of the environmental gradient and larger species pools in intermediate environmental conditions, so in areas at the extreme ends increasing the prevalence of patches that favour intermediate conditions is likely to increase diversity (Yang et al. 2015). Our results at 100 m scale support Yang's hypothesis. In our study at larger scales (1 km) there were positive relationships in low intensity and moderate intensity landscapes suggesting some benefits of increasing heterogeneity here since a more diverse species pool exists from which to assemble greater beta diversity. Although there was a unimodal relationship with γ in low-intensity landscapes, narrow niche species were increasing so this possibly reflects environmental constraints. In highly modified landscapes there were non-significant HDR's at 1 km. It may be that a reduced species pool in more intensively farmed landscapes makes it difficult for species to respond to increasing heterogeneity at larger scales.

Mechanisms for HDR's: heterogeneity and niche width

The results show that niche width is an influential control on the HDR across temperate landscapes that vary in land-use intensity, interactions between niche width and heterogeneity as influences on species richness were significant. However, AHTO theory suggests that the unimodal relationship will be driven by a decline in narrow niche species and an increase in generalists. In our study broad niche species appear to be driving the relationships. A downturn in diversity of broader niche species could be inferior competitors winning by

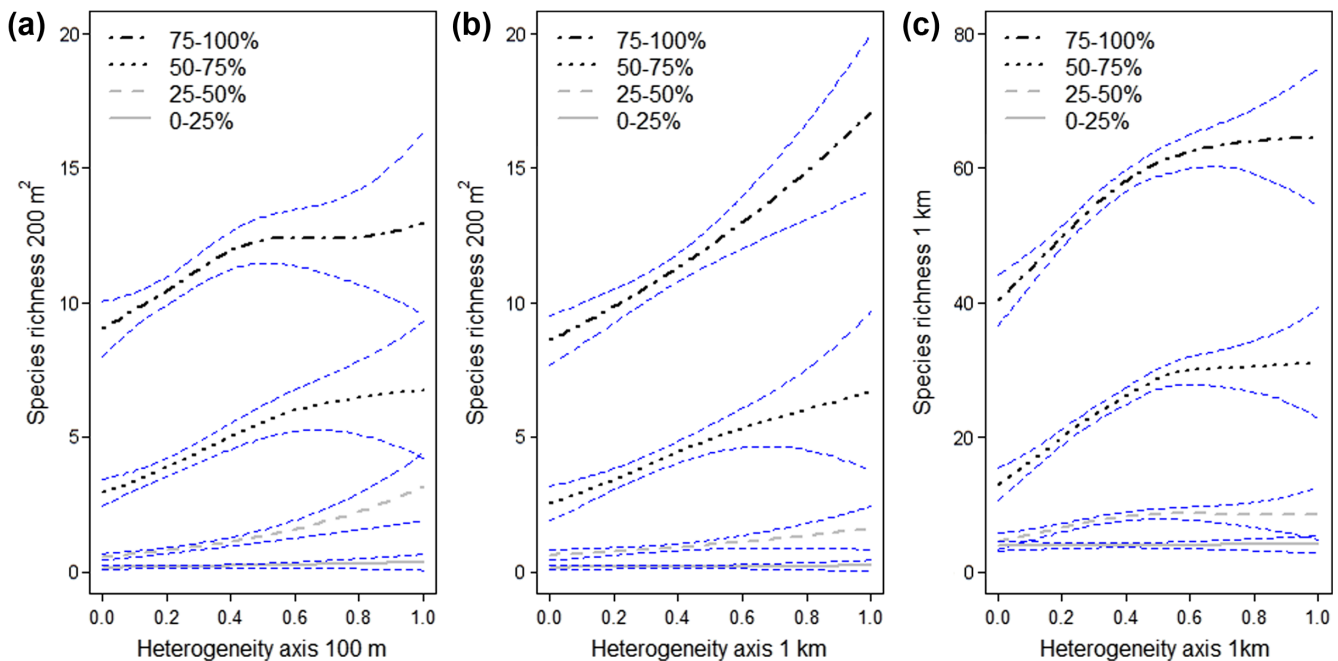


Figure 4. The relationship between the composite heterogeneity metric and species richness from classification into four niche groups (a) α species richness at 100 m, (b) α species richness at 1 km, (c) γ species richness at 1 km. The four lines represent four quartiles of niche width (75–100% = broadest niche, 50–75% = upper middle, 25–50% = lower middle and 0–25% = narrowest niche).

chance in small patches with no rescue effect such as would arise from a competition colonization tradeoff (Orrock 2020, Ben-Hur and Kadmon 2020a, b). The unimodal relationship between gamma (γ) diversity and habitat diversity and heterogeneity in low intensity landscapes also appears to be related to changes in broad niche species.

Although species with narrow niche width could benefit from EH if greater heterogeneity supports more specialised niche space (Ricklefs and Lovette 1999, Menendez et al. 2007), and there were indeed some increases in narrow niche species with habitat diversity and in low intensity landscapes, overall narrow niche width species remain at low levels despite the reduction in diversity of broader niche species and there appears to be a confounding effect with land-use intensity.

There were positive relationships between mean alpha diversity and landscape (1 km) heterogeneity which were stronger with increasing niche width whilst γ plateaued at higher heterogeneity. The implication is that beyond a certain level of heterogeneity, increases in patch level richness draw from a wider pool that no longer increases in richness beyond the inflection point. As a result species compositional similarity should increase between patches (Finderup Nielsen et al. 2019). Yet up to the inflection point heterogeneity is correlated with increased patch level richness (alpha) as well as increasing size of the wider species pool (γ).

In our study narrow niche width species were drawn from a much smaller species pool. HDR may in reality be poorly expressed across human dominated landscapes because land-use and other factors have resulted in species pools poor in narrower niche width species. Conversely, narrow niche species were found to be more responsive in less intensively managed landscapes. In many cases even if landscapes are managed to increase their heterogeneity, residual populations of specialised species are less likely to be present leading to community restoration unable to exploit residual diversity comprising a long tail of rarer species. Managing for greater heterogeneity may be more likely to benefit broad niche species while more specialised species require additional intervention to overcome dispersal constraints (Smart et al. 2006). In dynamic landscapes where management has legacy effects that have yet to fully sort the regional and local species pools, extinction debts may yet drive rarer, more specialised species to local extinction, where increasing heterogeneity has critically decreased habitat area (Kimberley et al. 2016, Ridding et al. 2020).

Defining and measuring heterogeneity

The choice of heterogeneity metric can change the observed relationships between heterogeneity, area and species richness. Using a single variable to indicate heterogeneity could misrepresent the relationship e.g. elevation range could be confounded with the species richness-altitude relationship (Hortal et al. 2013) and using only the number of habitats per unit area does not account for within-habitat complexity. In this study we used habitat diversity representing between habitat variation to contrast and compare as has been used

by other authors as a single variable (Ben-Hur and Kadmon 2020a). This is also of interest as it is a component of heterogeneity that can be manipulated. We found that using habitat diversity as a single metric did produce slightly different results to the composite metric that represents overall heterogeneity, which should be considered when implementing land management. Heterogeneity should ideally be measured using a combination of within-habitat heterogeneity metrics, such as vegetation structure, and between-habitat metrics, e.g. habitat diversity and land cover (González-Megías 2007, Heidrich et al. 2020).

Many authors (Tschardt et al. 2002, 2005, Gabriel et al. 2005, Ma 2008) have used percentage cover of semi-natural land to indicate heterogeneity and landscape complexity and it is used to identify high nature value farming areas in Europe (Paracchini 2008). We would suggest that the proportion of semi-natural land is not necessarily an indicator of landscape heterogeneity although it is a useful metric with which to study patterns of species richness. In our analysis the percentage of semi-natural land appears to represent a fertility/intensity gradient and was orthogonal to heterogeneity (Maskell et al. 2019). It is important that in testing the role of environmental heterogeneity on species richness the confounding effect of resource availability is removed (Yang et al. 2015).

Conclusions

We found that HDR's can be either positive or unimodal in the same landscape. The response depends on niche width, scale, context, definition of heterogeneity and is related to the degree of landscape modification and land-use intensity.

At smaller scales (100 m) the HDR can be unimodal suggesting that too much local heterogeneity could lead to declining species richness. There was a unimodal relationship with γ diversity in low intensity landscapes; there could be tradeoffs in species richness from increasing heterogeneity in these landscapes although it may be that species lost are not necessarily narrow niche specialists. The HDR was also unimodal with γ diversity when a single heterogeneity metric-habitat diversity representing between habitat variation but not within habitat was used.

Although percentage cover of semi-natural land has been used as a measure of heterogeneity in other studies, we believe that in this context it represents land-use intensity. Our results demonstrate that land-use intensification is implicated in the depletion of narrow-niche specialists, an impact that managed increases in heterogeneity may not easily reverse.

The area heterogeneity tradeoff proposes that the unimodal relationship results from a loss of narrow niche specialists; we found that narrow niche species were mostly unresponsive. A fundamental constraint on realising the benefits of increasing heterogeneity is therefore likely to be the low availability of narrower niche species in local species pools.

Although increasing heterogeneity may cause a tradeoff in species richness, there are positive relationships also. However, unless there is an available pool of narrow niche

species this is likely to only benefit broad niche species. More specialised species require additional interventions that conserve diversity in high quality habitats.

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Author contributions

Lindsay Maskell: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Jamie Alison:** Conceptualization (supporting); Data curation (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Neil Forbes:** Methodology (supporting); Writing – review and editing (supporting). **Susan Jarvis:** Formal analysis (supporting); Methodology (supporting); Validation (equal); Writing – review and editing (supporting). **David Robinson:** Funding acquisition (equal); Methodology (supporting); Writing – review and editing (supporting). **Gavin M. Siriwardena:** Conceptualization (supporting); Methodology (supporting); Writing – review and editing (supporting). **Claire Wood:** Data curation (supporting); Writing – review and editing (supporting). **Simon Smart:** Conceptualization (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Writing – review and editing (equal).

Data availability statement

Data are available in non-proprietary formats from the UKCEH Environmental Information Data Centre Catalogue (<https://eip.ceh.ac.uk/data>, last access: September 2021). The datasets used in this study have been assigned digital object identifiers (DOIs) <https://doi.org/10.5285/82c63533-529e-47b9-8e78-51b27028cc7f>, <https://doi.org/10.5285/9f8d9cc6-b552-4c8b-af09-e92743cdd3de>, <https://doi.org/10.5285/f481c6bf-5774-4df8-8776-c4d-7bf059d40>, <https://doi.org/10.5285/71d3619c-4439-4c9e-84dc-3ca873d7f5cc> (Maskell et al. 2020a, b, c, Smart et al. 2020). Detailed methodologies i.e. field handbooks are provided as supporting information with these datasets.

Supporting information

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

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