Original article

# Landscape effects in the intertidal around the coastline of Great Britain

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## ABSTRACT

**Aim** We tested whether the size of habitat patches along the coastline of Great Britain influences molluscan species richness.

**Location** Coastline of Great Britain.

**Methods** Intertidal mollusc data were compiled from the National Biodiversity Network to derive a matrix of species presence/absence in 10 km × 10 km squares (hectads). Major groupings within the coastal fauna were identified using clustering based on Simpson's dissimilarity index. Contiguous hectads assigned to the same cluster were considered as patches. Potential island biogeographical effects were investigated using regressions of species density against patch size.

**Results** 598 hectads were clustered into 15 groups, with the three largest groups (94% of hectads) having broad associations consistent with hectad dominance by rocky shore habitat, sheltered sediment or sediment on exposed coasts. For all three main groups, there were fewer species in larger patches than would be expected from a random sampling of hectads. Species densities (species hectad$^{-1}$) increased with patch size in rocky shore-dominated habitat. There was no support for a similar effect in sedimentary habitats, with higher than expected species richness in isolated hectads of sheltered habitat.

**Main conclusions**

The increases in mollusc species density with patch size in rocky shore dominated habitat are consistent with island biogeographical processes. The absence of similar effects in sedimentary habitats may reflect more overlap between the species of intertidal and subtidal in these habitats. Subtidal habitat may therefore act to change the hostility of the matrix between intertidal patches of sedimentary habitat, diluting any island effects. As landscape effects may change species richness at the scale examined, concerns that increased building of artificial habitats will change the local patterns of species richness may be justified for rocky habitats.

**Keywords:**

Beach, British Isles, cluster, inter-tidal, mollusc, rocky shore, patch size, sediment, species area, species richness

# INTRODUCTION

Several different processes may cause variation in the species richness of differently sized patches of habitat. Larger segments of habitat may have greater species richness than smaller areas of similar habitat as a consequence of holding more individuals (Preston, 1962). Larger patches of habitat may also be associated with higher species richness as the increased area samples a greater amount of environmental heterogeneity (Stein *et al.*, 2014). If the number of species in comparable areas (e.g., same-size plots) within small patches and large patches differs, this requires further explanation (Fahrig, 2013). One of the most widely known explanations for an increase in species density (species per unit area) in larger fragments is the theory of island biogeography (MacArthur & Wilson, 1967): larger islands have lower extinction rates and/or higher species immigration rates than smaller islands, resulting in more species at the equilibrium point between species extinction and species immigration. Island biogeography has often been applied to habitat mosaics, where the matrix is not as hostile as the sea is to inhabitants of true islands. Matrix effects can alter island biogeographical processes by obscuring patterns of habitat specialists (Cook *et al.*, 2006). The edge of habitat fragments can be areas of increased richness as ‘mass effects’ allow species to persist in unfavourable habitats due to immigration from an adjacent favourable matrix (Kunin, 1998). Positive or negative edge effects may arise from altered or intermediate habitats around the perimeter of patches (Ewers & Didham, 2006).

Despite the wealth of theory related to patch, island and landscape effects, it is not always clear how the different potential processes may be evident in different systems. This of course reflects both scale-dependent differences across studies, variations in species traits such as dispersal capacity and differences in the composition and heterogeneity of landscapes (Sólymos & Lele, 2012). Studies of landscape effects in marine systems lag behind the terrestrial literature (Boström *et al.*, 2011), and yet there are many concerns about changes in marine habitats due to sea level rise, habitat loss and habitat modification (e.g., Bulleri & Chapman 2010; Jackson & McIlvenny, 2011; Hawkins, 2012). Landscape effects on species richness (e.g., Steffan-Dewenter, 2003) have implications for managing habitat change and conservation planning.

To investigate how intertidal species richness may be linked to landscape structure we used a clustering approach to identify the broad-scale structure of intertidal molluscan diversity around Great Britain. Structure was defined at the grain scale of 10 km × 10 km squares (hectads). Having identified a parsimonious description of heterogeneity at the hectad scale, the links between patch size (based on neighbouring hectads of the same cluster) and species richness were examined using null models (Gotelli, 2001). Null models, in the current study as random selections of hectads into patches, can be used to generate an expectation for patches in the absence of spatial structuring processes. For example, if there are Allee effects (Gascoigne & Lipcius, 2004) or colonization–extinction dynamics that require local (within patch) population sources, then larger patches may have more persistent populations and higher species richness as envisioned by MacArthur & Wilson (1967). If edge or isolation effects restrict the colonization and persistence of populations in small patches, then there should be fewer species than expected in small groups of hectads.

The observed diversity of patches of habitat will be influenced by a number of processes. Ideally these could be controlled by a standardized sampling programme, but it is not feasible to generate contiguous coverage along extensive coastlines using such an approach. The patterns of diversity in habitat patches were therefore examined using a proxy for collection effort. An indented coastline may also reflect greater intertidal area or habitat heterogeneity, for example by creating variance in wave exposure. This proxy was also examined using coastline length as a possible influence on species richness. Considering the two additional predictor variables led to a more robust test of the central question: whether species density increased in larger patches of intertidal habitat. This was supplemented by a test of species accumulation to test whether total species richness in patches was greater or lesser than expected by chance selection of hectads.

## MATERIALS AND METHODS

### Broad scale habitat structure

Existing shoreline maps (Fig. 1) were used to help identify likely habitat associations of clusters identified separately using species presence–absence in hectads. The available shoreline maps are based on digitized coastlines, cross-referenced with satellite images; http://www.eurosion.org. One of the major habitat distinctions is between sedimentary shores (beaches) and rocky shores. The Eurosion categories emphasize a further group of habitats generally found in estuaries. The category of 'conglomerates and/or cliffs with rock and sediment on shore' is intermediate between sedimentary and rocky shores. The match to rock or sediment dominance for the conglomerates category is dependent on local factors.

### Clustering of species assemblages

Species presence records in 10 km × 10 km hectads in the UK National grid system were extracted from the National Biodiversity Network (NBN; http://data.nbn.org.uk; records accessed 19/11/2008). The data were examined to remove ambiguous records (e.g., those with genus name only) and filtered to include intertidal records only, as described in Blight *et al.* (2009). Molluscs were used as a suitable indicator phylum for distributional patterns as this group is relatively widely collected and identified, occurs in both hard and soft shore habitats and has been found to act as a surrogate for other littoral species (Smith, 2005). Species authorities follow the World Register of Marine Species (WoRMS Editorial Board, 2015).

There were 598 hectads with data on mollusc presence. It is not possible to extrapolate the existing habitat classification for the UK intertidal (JNCC biotopes, Connor *et al.*, 2004) to hectads as this would require a greater coverage of biotope maps than currently exists and additional decisions on how to deal with mixtures of biotopes at the 10 km × 10 km grain size of the available species data. Clustering was therefore applied directly to the matrix of species records to define groups of hectads with similar species (Kreft & Jetz, 2010). Dissimilarities between hectads were calculated using Simpson's dissimilarity index ($\beta_{sim}$, Koleff *et al.*, 2003). The advantage of Simpson's index in this context is that it summarizes information on the turnover element of beta diversity (Baselga, 2010). In cases such as the NBN data, where details of collection effort are variable and often unknown, a reduced species list for a hectad is more likely to represent under-collection than an absence of species. We are interested in fairly broad habitat classifications so that, on balance, a hectad with just the most common species for, say, rocky shores will cluster with a hectad with a longer species list containing the same common species. In such cases, Simpson's index is preferable to other common indices like Sørensen's, which are also influenced by the change in species number, even if all species in the species-poor hectad are also found in the species-rich area.

The matrix of Simpson's dissimilarities among hectads was clustered using average dissimilarities among groups (UPMGA) using the HCLUST package in R (R Development Core Team, 2013). A stopping rule is needed to judge the number of clusters that represents a parsimonious description of structure in the data. Methods for finding an ‘elbow’ in cluster dispersion data (Kreft & Jetz, 2010) did not work satisfactorily in this study: the decline in within-cluster dispersion with group number was too smooth.  We attempted to find a cluster number using a technique based on resampling the locations to create a null expectation of cluster structure (cf. Dudoit & Fridlyand, 2002). A conventional $r^2$ statistic was used to judge the degree to which clusters represent the distances between hectads. The squared distances from cluster centroids required to calculate $r^2$ can be obtained from the sum of squared distances between cluster members divided by the number of sites in the cluster (Anderson & Thompson, 2004). The expectation is that $r^2$ will rise more or less asymptotically to 1 as the number of clusters approaches the number of hectads. This will occur even as hectads are randomly assigned to clusters of the same size as those defined from hierarchical clustering. The difference between the $r^2$ from hierarchical clusters defined by group averaging and clusters assembled randomly gives an estimate of the degree of structure for any given number of groups. To estimate the expectation from random allocation of hectads to clusters, the average $r^2$ was calculated after 100 randomizations for each node in the hierarchical clustering using the ‘sample’ command in R to reallocate cluster membership.

## Patch size effects

By defining an informative clustering of hectads, the spatial structure within cluster groups could be examined. Hectads from the same cluster group were considered to form patches when they were contiguous (using an eight cell neighbourhood). For the most common clusters, this led to a relatively large number of fragments (patches), separated by areas of different habitat. The number of hectads of the same cluster in each patch defines the patch size hereafter.

In any heterogeneous system, species richness will increase with an increasing sample area or number of independent sample quadrats, reflecting the increased effort. The term species accumulation is used to refer to this effect (Gotelli & Colwell, 2001). We therefore expect overall species richness to be linked to patch size. An appropriate null model of species accumulation is needed to test for the presence of additional influences on species richness in patches. A null model for the expected rate of increase of species in the absence of spatial structure can be estimated from a random resampling process. Hectads within each habitat group were randomly reassigned to patches to generate a species accumulation in the absence of any island biogeographical effects. Simulations were carried out using POPTOOLS (Hood, 2010). The size of any observed departure from the null expectation was expressed using *z*-scores, the difference between observed and mean resampled species number for each patch divided by the SD from 100 randomizations. Extended tests indicated that the null expectations were stable at 100 simulations and larger resampling trials were not needed. If there are no patch effects, then the *z*-scores should lie close to zero with no trend associated with changes in patch size.

An alternative means of examining the patch size effect is to test the average number of species for a fixed area in different sized fragments (Fahrig, 2013; called D-SAR in Giladi *et al.*, 2014). This was tested using regressions of the mean species richness hectad$^{-1}$ in patches, as a function of the patch size for different habitats. If patch-related processes help species establish or persist at the hectad scale, then the regression of mean hectad richness should have a positive slope.

Alongside any landscape effects at the patch scale, two alternative predictors were also examined to evaluate other potential influences on average richness hectad$^{-1}$ in patches. The collection effort in the NBN database is uneven as the data reflect the amalgamation of different surveys. Details like the number of individuals examined or survey effort in different contributions to the NBN data are generally not known. Blight *et al.* (2009) found that the number of survey records in a hectad helped explain variation in species richness. ‘Survey records’ in this context includes repeat observations of the same species so that data of this sort includes information on the total effort expended in the hectad. A further variable that may influence species richness in patches of hectads is the length of coastline found there. A heactad containing a relatively longer fragment of coastline may contribute more species to a patch if a longer coastline implies a more convoluted shoreline where habitat heterogeneity results in increased species richness. A longer coastline also implies a greater intertidal area within a hectad. Greater area within a hectad may also boost species richness if island biogeographical processes operate at this scale. The average coastline length per hectad within a patch was therefore examined as a third potential predictor of patch species richness.

**Analysis of patch effects**

The species accumulation (*z*-scores) relationships with patch size were examined using ANCOVA with group as a fixed factor and patch size as the covariate. Residual plots were examined for departures from normality and homoscedasticity and these assumptions were supported by the diagnostic plots. Full ANCOVA models (including the group × patch size interaction term) were fitted and compared with models containing the main effects only. The optimum model to descried the data was subsequently chosen on the basis of the lowest small sample corrected Akaike Information Coefficient ($AIC_c$). Akaike weights were used to compare candidate models. The Akaike weight indicates the relative support for a model, while the ratio between the weights of different models (the evidence ratio) indicates the likelihood that one model is a better fit to the data than the comparator (Burnham and Anderson, 2002).

Calculating the mean species hectad$^{-1}$ involved estimates with varying precision (dependant on the number of heactads in a patch). Estimates from patches with low numbers of hectads were more variable. This heterogeneity creates an issue for ordinary least squares regression and was addressed by using weighted regression: based on the variance in a patch size of $n$ hectads being $s^2/n$, where $s^2$ is the variance of species richness across all hectads in a habitat group. The relative influences of competing models using combinations of the three predictor variables (patch size, average coastline length of hectads in patch and total records in patch) were also compared using $AIC_c$ values from competing linear regression models.

The influence of patch size on species identity was estimated using the matrix of Simpson's dissimilarities for each habitat type. The null hypothesis here is that hectads drawn from patches of similar sizes will be more similar than hectads from differently sized patches. This was tested using the RELATE test within the PRIMER package, which calculates the rank correlation between the matrix of dissimilarities and a distance matrix of difference in patch size, using a randomization equivalent to a Mantel test to evaluate the significance of the observed correlation (Clarke & Gorley, 2006).

The presence of edge effects on isolated hectads can also be tested by examining the structure in the Simpson's dissimilarity matrix. Under the null hypothesis of no edge effects, the average dissimilarity between a hectad and all hectads not in the same habitat group should not change when comparing means from isolated hectads with means from hectads contiguous with at least one hectad of the same habitat group. If the species composition in isolated hectads is influenced by the surrounding habitat, then isolated hectads should be more similar to hectads from other habitat groups than is the case for hectads from larger patches.

## RESULTS

The relationship between group number in the cluster analysis and explanatory power ($r^2$) rose to an asymptote, but the profile contained jumps, with a pronounced plateau (Fig. 2). The difference between the observed $r^2$ and the average profile from resampling also reached a plateau, indicating that much of the pattern in the data could be explained by relatively few groups. The most informative division was therefore taken to occur at 15 clusters, the inflection point in the profiles.

With 15 clusters providing a parsimonious description of structure in the dataset, the three largest identified clusters contained 94% of the 598 hectads with data. These three groups were used to examine patch effects after identifying contiguous hectads with the same cluster type. Although cluster members were found all around the coastline of Great Britain (Fig. 3), there appeared to be some general associations with broad-scale habitat conditions. Hectads in group A ($n$ = 358) were generally found on open coasts and in positions consistent with the likely presence of at least some rocky shore (including what Eurosion classed as ‘conglomerates’). Group B (130 hectads) was concentrated around sheltered areas, particularly estuarine areas like the Wash in the east of England, the Solent on the south coast and the Solway Firth. The 73 hectads of group C seemed to be associated with predominantly sedimentary shores in open coast areas. A cross referencing of hectads in separate clusters with the nearest Eurosion category showed strong associations (G-test of association, $G_6$ = 338, $P < 0.001$, clusters not random across Eurosion habitat types).

The total species lists in the three largest groups were overlapping in content, with an average intergroup Simpson's dissimilarity of 6%. Within the small number of species exclusive to each group, there was some evidence to support the broad-scale environmental associations suggested from Fig. 3. For example, the saltmarsh and seagrass specialists *Assiminea grayana* and *Haminoea navicula* were found exclusively in group B. Relative frequencies of species in the separate groups were also suggestive of a coarse separation into dominant shore types: characteristic rocky shore species such as *Patella vulgata*, *Nucella lapillus*, *Melarhaphe neritoides* and *Gibbula umbilicalis* were more than four times more likely to be found in group A than in the other two groups.

Pairs of hectads within the same habitat group became more dissimilar with distance (Fig. 4). In contrast, distances between hectads within a patch were relatively small, reflecting the sizes of patches overall. This meant that the average beta dissimilarity between hectads was greater than the dissimilarities within patches. Observed species lists in patches are therefore accumulated from less distinct species lists than is the case for random allocations: as patches are made up of neighbouring hectads more similar than the average for the coastline as a whole. This phenomenon was reflected by larger habitat patches having fewer species than would be expected on the basis of random allocation of hectads to patches (Fig. 5, Table 1). The model with an interaction between patch size and habitat type had an evidence ratio suggesting that it was more than twice as likely as more simple models. The relative decline in accumulated species was greatest in habitat B, associated with estuarine habitats. This grouping also had a standardized species number above one for single hectad patches: indicating that single hectad patches were richer than might be expected by chance (mean standardized species richness for single hectad patches = 0.65, SE 0.288). By comparison, single hectad patches of habitat C had close to the expected number of species (mean standardized richness -0.09, SE 0.1176). Single hectad patches of habitat A had fewer species than would be expected from random selection of single hectads (mean score -0.42, SE 0.173).

Unsurprisingly, the proxy for collection effort, number of records, was a consistent predictor of the average species richness hectad$^{-1}$ in different patches (Fig. 6). Patch size was also supported as a predictor for species density, although the effects were not consistent in different habitat groups (Table 2). For group A, the evidence ratio suggests that the optimum model was over three times as likely as the next best alternative. For this habitat, consistent with rocky shore dominated areas, species density increased with patch size (slope 0.00254, SE 0.000781). In contrast, species density declined with patch size in habitat group B (estuarine areas). The optimum model for habitat group B had overwhelming support compared to competing models and included all three predictor variables. This habitat group therefore had evidence for an additional effect of coastline length. Species density was higher in more convoluted estuarine areas. The final habitat group had less support for an optimum model, although the effect of species record number was still positive for species density. The weakly supported alternative model ($w_i\mathrm{AIC_c} = 0.298$) had a negative relationship between patch size and species density, although the estimated error around the slope was relatively high (habitat C, model averaged slope for patch size = -0.03, SE 0.023).

The dissimilarity between hectads did not seem to be a function of the relative patch size for habitat A (RELATE test, correlation between dissimilarity matrices = 0.001, $P > 0.05$). In contrast, greater differences in patch size were related to the degree of difference in species composition within habitat B (correlation 0.039, $P < 0.05$) and habitat C (correlation = 0.084, *P* < 0.05). Aside from intra habitat changes in dissimilarity, inter habitat dissimilarity was also affected by patch size for two habitat groups (Table 3). Isolated hectads of both habitat groups B and C were more similar to hectads from other groups when compared to the means from larger patches. In contrast, isolated hectads of habitat A were no less dissimilar to non-A habitat than larger patches.

## DISCUSSION

There were habitat-specific differences in the way species accumulated in patches of different size and in the influence of patch size on species richness hectad$^{-1}$. In the case of habitat group A (rocky shore dominated), the increase in species density with patch area in larger patches of group A habitat is an effect consistent with patterns seen in island biogeography. An island effect is also suggested by the pattern for single hectad fragments of habitat A to have fewer species than expected from a random selection of hectads. Habitat B had the opposite pattern, relatively species rich single hectads, with a decline in species density in larger patches. In contrast, there was less evidence for patch size effects on species richness in the third habitat grouping (associated with sedimentary shores in open coast areas).

It is not clear why the habitat group consistent with rocky shores had an island biogeographical effect of increasing species density in hectads from larger patches. The inference from island biogeography is that species extinction is lower and/or immigration to hectads is higher in larger patches. Immigration of molluscan species to areas of newly established artificial hard shores far smaller than hectads seems relatively rapid (Dethier *et al.*, 2003; Krone *et al.*, 2013). Other studies, however, suggest that recolonization can take decades for species with direct development (Johnson *et al.*, 2008). The converse of a positive effect of patch size on the supply of colonists to individual hectads would be an increase in extinction in small fragments of rocky shore. For example, if being surrounded by sedimentary areas increases stress on rocky shores (e.g., by sedimentation or scouring, Airoldi, 2003), this may cause greater local extinction rates with lower associated mollusc diversities.

Both greater immigration to larger patches and greater loss of species in isolated hectads can affect the species density–patch size relationship in the same way:  it is therefore difficult to separate these potential effects in the current study. Little is known about the extinction–colonization dynamics of intertidal species at the scale of hectads. Considerable turnover has been observed in areas of 4 $m^2$ monitored over a decade (Dye, 1998); for reasons of tractability, most monitoring occurs at a similar scale. If larger patches reflect an increased potential for source populations to supply colonists for recovery of local extinctions, this may lead to greater local species densities. As the habitats are large relative to the movement capacity of intertidal molluscs, a link between habitat extent and hectad-scale extinction colonization dynamics would require a metapopulation effect with local populations linked by larval dispersal or rafting. Repeated surveys of areas with different habitat extents could test a recolonization rate and local extinction rate hypotheses, but this would be a challenging project and not one that appears to have been attempted as yet.

The lower species richness $hectad^{-1}$ in larger patches of estuarine habitat (group B) is not surprising given the general tendency for estuarine habitats to be species poor (Attrill, 2002). However, this alone does not explain why a landscape effect similar to rocky shores does not seem to be present in habitat B. The positive influence of average coastline length implies that more convoluted coastlines promote species richness. A more convoluted coastline could promote species richness $hectad^{-1}$ by an effect of habitat area, but this is not consistent with the decline in species density in larger patches of habitat B. It therefore seems more likely that the positive effect of coastline length reflects greater habitat heterogeneity. As single hectads of habitat B had higher species richness than expected by chance alone (Fig. 5), this implies an edge effect of enrichment from surrounding, non-estuarine, habitat or that the isolated fragments have a greater chance of including diverse habitat types, with larger patches being more homogenous. Such edge effects are supported by the observation that isolated hectads of habitat B are more similar to the surrounding habitat than is the case for hectads from larger patches (Table 3).

Habitat C seemed to have few influences of patch size on species richness. The decline in accumulated species in larger patches is consistent with patches undersampling the available diversity among hectads in the dataset, as occurred for the other habitat groups. Similar to Habitat B, there was some suggestion for enrichment from surrounding habitat in isolated hectads of Habitat C, along with some patch size related changes in assemblage composition.

A distinction that may explain the differences between predominantly hard (group A) and soft habitats (groups B and C) is that relatively more species in soft habitats are also found subtidally. For example, the sediment dwelling genera *Abra*, *Cerastoderma* and *Mya* are given as characteristic components of both littoral and subtidal biotopes in the marine habitat classification for Britain and Ireland (Connor *et al.*, 2004). In contrast, *Littorina* species occurred more frequently in habitat A than any other habitat group, are listed as components of over 50 interdidal biotopes, but only mentioned in one uncommon subtidal biotope (Connor *et al.*, 2004). With additional source areas available, patch size may not be such a good proxy for potential source populations in sedimentary habitats as it is in rocky habitats.

The theory of island biogeography relies on changes in colonization–extinction dynamics related to island size. Colonization and extinction are also related to life history traits, with the presence or duration of a pelagic dispersal stage potentially influencing molluscan species distributions at a number of scales (Johnson *et al.,* 2001). The absence of a larval stage generally restricts the estimated average dispersal distance of marine species (Kinlan and Gaines, 2003). Under the inference that direct developers are poor dispersers, one might expect this group of species to benefit more from the presence of alternative source populations in a larger habitat patch. This idea was examined by calculating the average patch size where each species was found and then comparing means between the different dispersal modes. If large patches favour direct developers, this group should have a higher average patch size than planktonic dispersers. The result of this comparison was not significant (e.g., average patch size where direct developers found in habitat A = 28.6 hectads (SE 1.31), *n* =54; equivalent values for planktonic dispersers: mean 26.4 hectads (SE 0.69), *n* = 214). It is difficult, however, to interpret the lack of a difference between dispersal modes in the face of examples where direct developing species have been shown to reach isolated habitat patches (Johannesson, 1988; O'Foighil, 1989); observations that undermine the assumption behind a simple distinction in colonization range between dispersal modes. The RELATE test makes a further point with respect to the differences between patch sizes: there was not a clear pattern for different assemblages on different sized patches of habitat A. Some influence of patch size on species turnover was evident in habitat types B and C. This may reflect the influences of surrounding habitat on patches of different sizes, particularly the edge effects proposed for habitats B and C earlier.

As emphasized by Giladi *et al.* (2014), the different techniques of species density and species accumulation applied in the current study emphasize separate mechanisms affecting species richness. The patterns are also likely to be grain-size dependent. Experience of resampling species occurrence grids at different scales suggests that measures of turnover decrease as grain size increases (Lennon *et al.*, 2001). By collating the information at larger scales, the turnover of species at smaller scales is lost, in the same way that widely spaced temporal sampling can miss species turnover (the residency effect, Burns, 2014). If the data were available to subdivide hectads, larger levels of turnover would therefore be expected. This might be expected to lead to greater definition of habitat classes and a wider diversity of landscape effects ranging from none to strong effects depending on target habitat and context.

It is possible to move to analyses at larger grain scales. As predicted, this decreases the average turnover among locations (e.g., mean Simpson's dissimilarity declines from 0.47 among hectads to 0.33 when using 50 km × 50 km cells). Lower discrimination between locations results in the definition of fewer groups that explain less of the observed structure (compare 15 groups with a difference of 0.45% between observed and resampled $r^2$ in Fig. 2 to a difference of 0.19% for five groups with 50 km × 50 km cells, results not shown). A consequence of moving grain size is that different habitats are identified. This restricts the comparisons that can be done across scales. For example, Habitat C is split almost evenly across the two largest groupings of 50 km × 50 km cells.

The effect of patch size on hard-shore communities suggests that increased use of shore armouring and artificial structures will affect biogeographical patterns by increasing hard shore habitat. One of the concerns about novel structures in the sea is that this will facilitate the establishment of invasive species (Mineur *et al.*, 2012). The inferred island biogeographical effects from species density are consistent with this hypothesis, although the pattern is likely to be a positive relationship between native and introduced species density

(Mineur *et al.*, 2008) unless the novel structures lead to a greater degree of habitat homogeneity at the patch scale.

For conservation planning, the results suggest that reserve spacing and sizes should be considered differently for the different habitat groups. Soft sediment areas maintain species richness in small fragments, so relatively small protected areas (1 hectad) may be functional, with the highest diversity achieved by spacing around the coastline. In contrast, the more rocky shore dominated areas have landscape effects, suggesting that landscape context should also be considered when selecting areas for protection.

Overall, the results suggest that the presence of landscape and edge effects depends on the type of habitat defined at the scale of analyses. The patch size of rocky habitat appears to promote mollusc species density, possibly by increasing the pool of potential local source populations and/or by reducing local extinction rates. This does not appear to result in a different assemblage in larger patches of rocky habitat, so the majority of associated species appear to benefit. In contrast, species density in soft sediments appears to benefit most from heterogeneity of habitats in adjoining hectads. Intertidal molluscs associated with rocky and sedimentary habitats have different relationships to potential source habitat. The results are consistent with the observation of stronger island effects when species have a higher degree of specialization on the focal habitat (cf., Cook *et al.*, 2006, Lövei *et al.*, 2006). It is likely that other intertidal groups will have different responses, reflecting other relationships with potential source habitats, including variation in the fidelity of species to particular habitats.

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## Biosketch

**Mark Johnson** is a marine ecologist with interests in the spatial ecology of benthic and pelagic systems.

Author contributions: M.J., C.A.M. and A.L.A conceived the project. A.J.B. collated the data and was involved with the other authors in discussions over the patterns within the data. M.J. carried out the final analyses and wrote the first draft with subsequent contributions from the other authors.

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**Table 1.** Ranking of alternative models for the change in standardized intertidal molluscan species richness in patches of different sizes, with habitat type considered as a categorical variable. Records were extracted in 2008 for the coastline of Great Britain with habitats defined by clustering (distributions shown in Fig. 3). Variables shown as Patch: log number of hectads in patch and Habitat: Habitat group. The small sample corrected AIC ($AIC_c$) was used to compare models. $\Delta AIC_c$ is the difference between the model with the lowest $AIC_c$ and other models, $w_i AIC_c$ are Akaike weights used to compare the support for different models.

| **Predictor variables in model** | **$r_{adj}^2$ (%)** | **$AIC_c$** | **$\Delta AIC_c$** | **$w_i AIC_c$** |
|---|---|---|---|---|
| Habitat, Patch, Habitat × Patch | 15 | 445.2 | 0.00 | 0.585 |
| Habitat, Patch | 13 | 447.1 | 1.88 | 0.229 |
| Patch | 11 | 447.5 | 2.30 | 0.186 |
| Habitat | 4.4 | 458.3 | 13.16 | 0.001 |

**Table 2.** Evaluation of alternative models for the average intertidal molluscan species richness hectad$^{-1}$ in patches of different size around the coast of Great Britain. Predictor variables are the average coastline length of hectads in a patch (coastline), the log of the total number of species records in the patch (Records) and the number of hectads in the patch (Patch). The small sample corrected AIC ($AIC_c$) was used to compare models. $\Delta AIC_c$ is the difference between the model with the lowest $AIC_c$ and other models, $w_i AIC_c$ are Akaike weights used to compare the support for different models. Colinearity of predictor variables was minimal, variance inflation factors (VIFs) were below 1.4

a) Habitat group A

| **Coastline** | **Records** | **Patch** | **$r_{adj}^2$ (%)** | **$AIC_c$** | **$\Delta AIC_c$** | **$w_i AIC_c$** |
|---|---|---|---|---|---|---|
| | x | x | 70 | -14.4 | 0.00 | 0.737 |
| x | x | x | 70 | -12.1 | 2.31 | 0.233 |
| x | x | | 66 | -6.8 | 7.63 | 0.016 |
| | x | | 65 | -6.5 | 7.94 | 0.014 |
| | | x | 15 | 47.9 | 62.29 | 0.000 |
| x | | x | 14 | 50.2 | 64.59 | 0.000 |
| x | | | 2 | 56.8 | 71.24 | 0.000 |

b) Habitat group B

| **Coastline** | **Records** | **Patch** | **$r_{adj}^2$ (%)** | **$AIC_c$** | **$\Delta AIC_c$** | **$w_i AIC_c$** |
|---|---|---|---|---|---|---|
| x | x | x | 81 | -1.6 | 0.00 | 0.946 |
| | x | x | 78 | 5.1 | 6.76 | 0.032 |
| x | x | | 77 | 5.9 | 7.52 | 0.022 |
| | x | | 71 | 15.0 | 16.64 | 0.000 |
| x | | | 28 | 55.2 | 56.81 | 0.000 |
| x | | x | 26 | 57.6 | 59.23 | 0.000 |
| | | x | -2 | 70.6 | 72.19 | 0.000 |

c) Habitat group C

| **Coastline** | **Records** | **Patch** | **$r_{adj}^2$ (%)** | **$AIC_c$** | **$\Delta AIC_c$** | **$w_i AIC_c$** |
|---|---|---|---|---|---|---|
| | x | | 55 | 16.3 | 0.00 | 0.413 |
| | x | x | 56 | 17.0 | 0.65 | 0.298 |
| x | x | | 55 | 17.8 | 1.51 | 0.195 |
| x | x | x | 55 | 19.3 | 2.95 | 0.094 |
| x | | | 3 | 42.9 | 26.57 | 0.000 |
| | | x | -1 | 44.3 | 28.03 | 0.000 |
| x | | x | 0 | 45.3 | 28.93 | 0.000 |

**Table 3.** Mean hectad dissimilarities between each of the three main habitat groups defined for intertidal molluscs and all hectads not in the focal habitat group. Records were collated for hectads around the coast of Great Britain, as described in the text. Dissimilarities were calculated with the Simpson's index, where larger values indicate greater species turnover bwteen the hectads being compared. Means were calculated for single hectad patches and for all larger patches of the same habitat. Differences between means within a habitat were examined with t-tests (equal variances not assumed).

| | **Mean dissimilarity between habitat group and hectads not in same group (SE)** | | | |
|---|---|---|---|---|
| **Habitat group** | **Isolated hectads** | **Patches with more than one hectad** | **t value (df)** | **p** |
| A | 0.57 (0.024) | 0.58 (0.006) | 0.32 (26) | >0.05 |
| B | 0.51 (0.034) | 0.62 (0.016) | 3.03 (33) | <0.01 |
| C | 0.48 (0.018) | 0.57 (0.023) | 3.04 (60) | <0.01 |

## Figure legends

**Figure 1.** Simplified shoreline types for Great Britain derived from the Eurosion dataset (http://www.eurosion.org/) hosted by the European Environment Agency. For simplicity, the 20 morpho-sedimentological codes of Eurosion have been amalgamated into rocky shores (including artificial substrate), sedimentary shores (beaches), estuarine-type habitats and conglomerates/cliffs with rock and sediment on the shore. The latter category is intermediate between rocky and sedimentary shore. Locations mentioned in the text are labelled.

**Figure 2.** Degree of variation accounted for (as $r^2$) as a function of the number of clusters defined in the hectad data for intertidal molluscs around the coast of Great Britain. The observed pattern is derived from clusters defined by UWPGA averaging of the matrix of dissimilarities among hectads. The random group allocation line is generated by permuting the group labels randomly across hectads (mean of 100 randomizations for each group number). The dotted line for observed-random indicates the information content over and above the expected increase in $r^2$ with group number. Profiles show a sharp inflection at 15 groups, which was taken to give a parsimonious description of structure in the data.

**Figure 3.** Distribution of hectads allocated to the three most common habitat groups (A, B, C) defined by clustering of intertidal mollusc data for Great Britain. The three groups contain 94% of the 598 hectads with data and were defined in the most informative grouping based on the proportion of variance explained ($r^2$).

**Figure 4.** Comparison between (a) the distribution of separation distances between hectads within patches and (b) the average turnover of mollusc species between hectads separated by different distances (as mean Simpson's dissimilarity, error bars SE). The majority of within-

patch separations are less than 25 km, at which point turnover is lower than the asymptotic value. Data are shown for habitat group A only, but the patterns are similar in groups B and C.

**Figure 5.** Relationship between patch size and the accumulated number of intertidal mollusc species found in the patch. The species list for each patch is expressed as a standardized score with reference to the mean and standard deviation from a random allocation (within each habitat group) of hectads to patches. If species richness is unaffected by landscape-related processes, the data are expected to have a mean of 0 and no slope. The separate lines represent the patch size × habitat group interaction found in the best supported model ($r_{\mathrm{adj}}^2$ 15%).

**Figure 6**. Residual variation in mollusc species density (species hectad$^{-1}$) as a function of predictor variables in the optimum model (identified using AIC$_c$ in a multiple regression analysis). Plots separate the influence of variables controlled for the influence of other predictors. Rows in the figure show the patterns for different habitats, distinguished as open circles (habitat A), filled triangles (habitat B) and shaded squares (habitat C). Each column relates to a separate predictor variable. As only the variables contained in the optimum model for each habitat are shown, gaps in the figure indicate where a no contribution was estimated for a predictor of variation in mollusc species density for a particular habitat.

Fig. 1

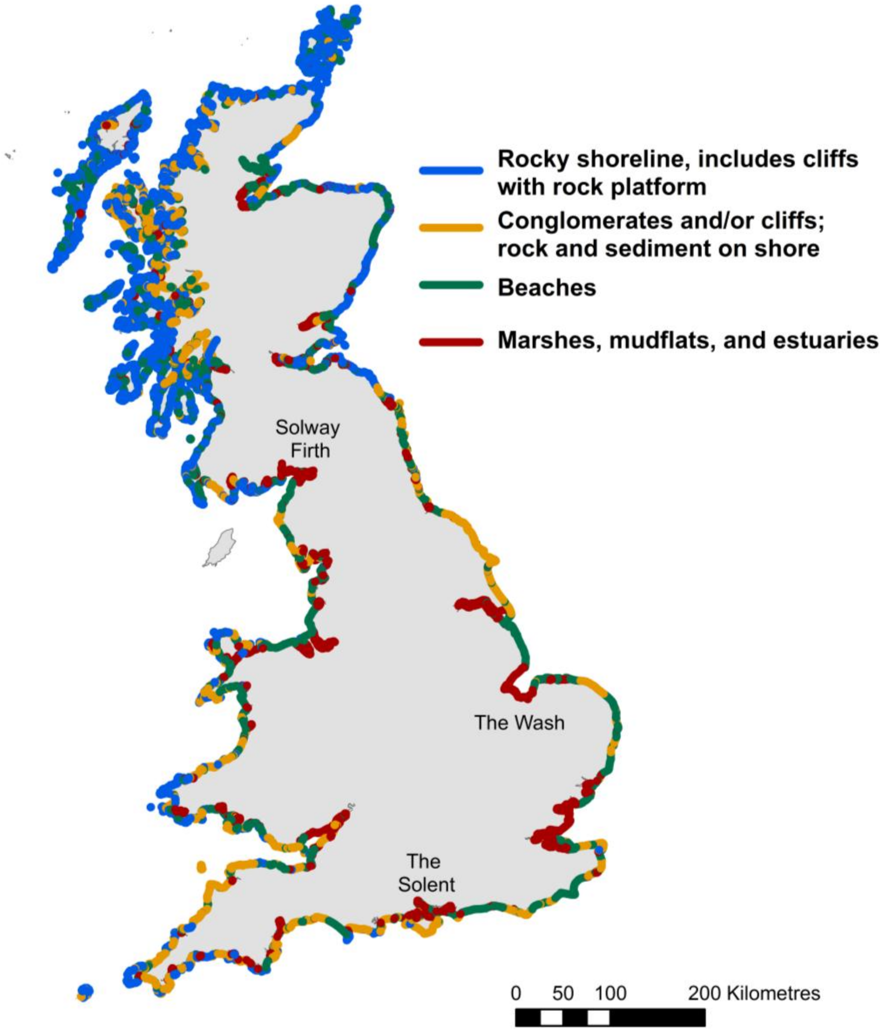

Rocky shoreline, includes cliffs with rock platform
Conglomerates and/or cliffs; rock and sediment on shore
Beaches
Marshes, mudflats, and estuaries
Solway Firth
The Wash
The Solent
0 50 100 200 Kilometres

Fig. 2.

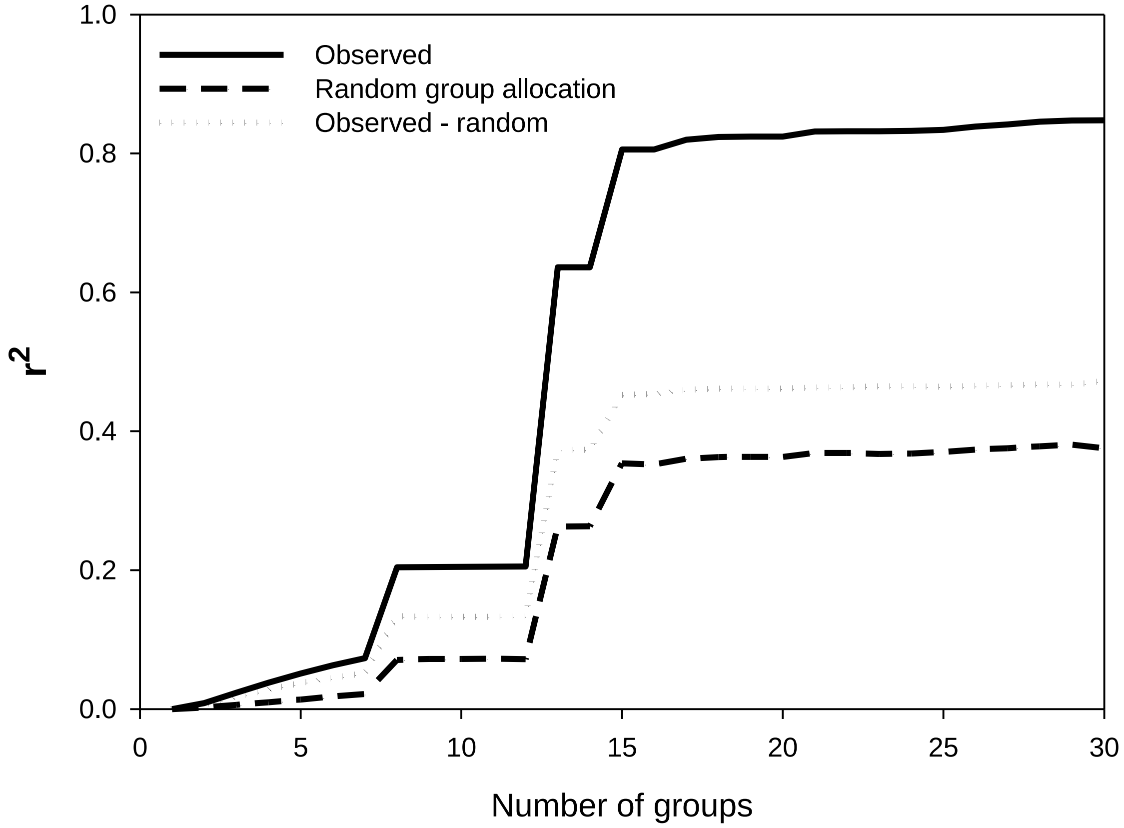
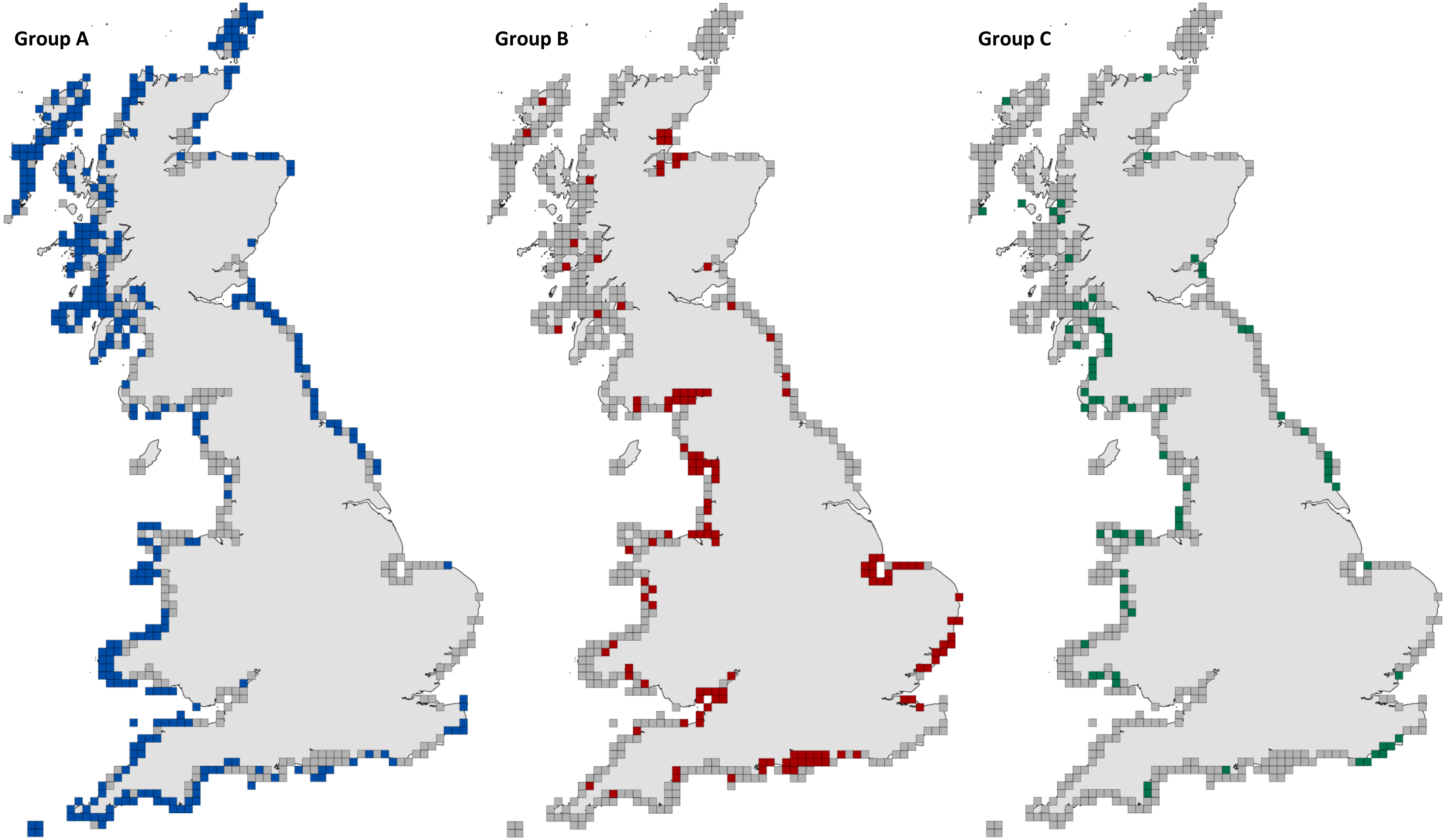

1.0
0.8
0.6
0.4
0.2
0.0
$r^2$
0
5
10
15
20
25
30
Number of groups
Observed
Random group allocation
Observed - random

Fig. 3.



Group A

Group B

Group C

Fig. 4.

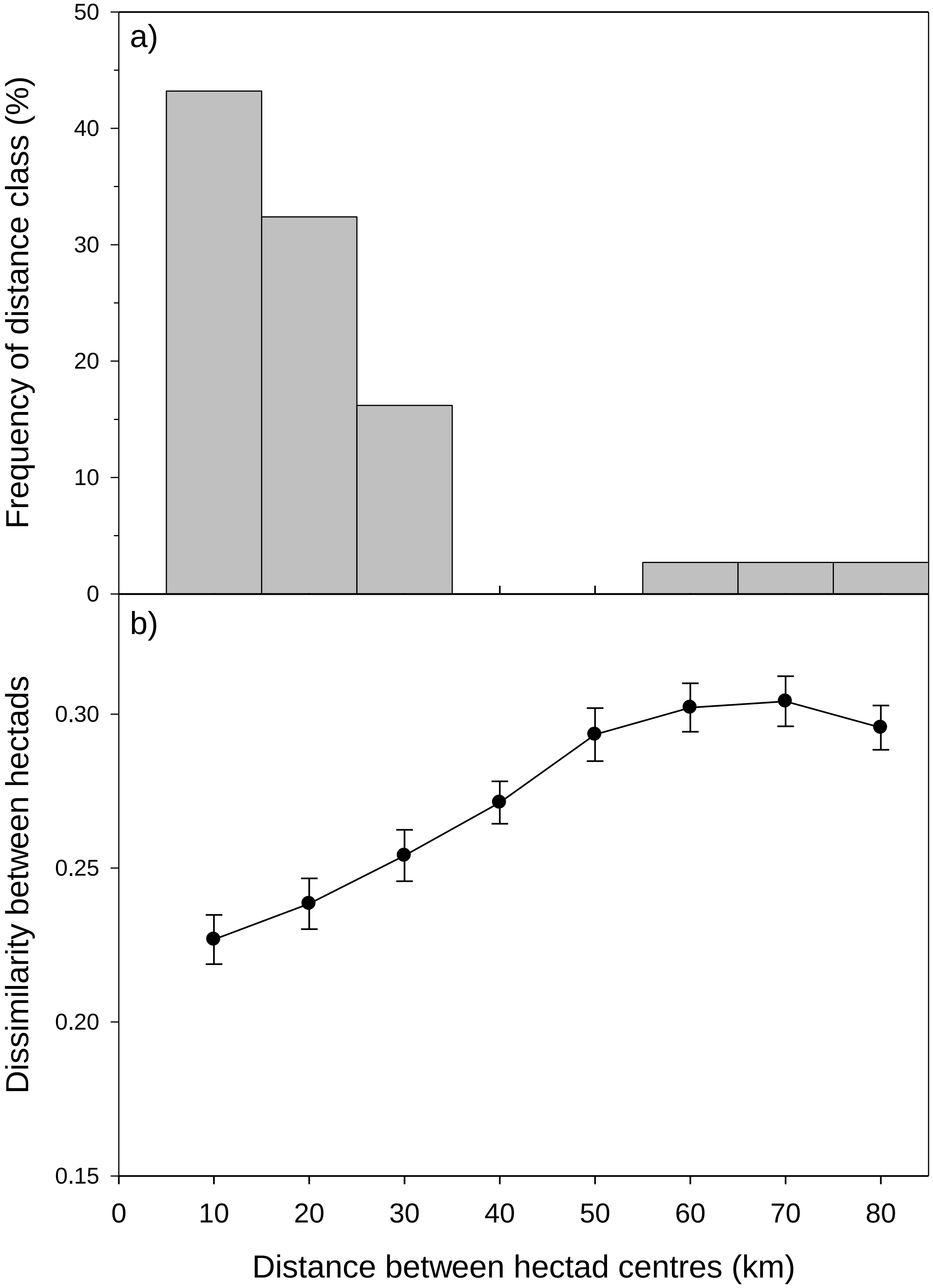
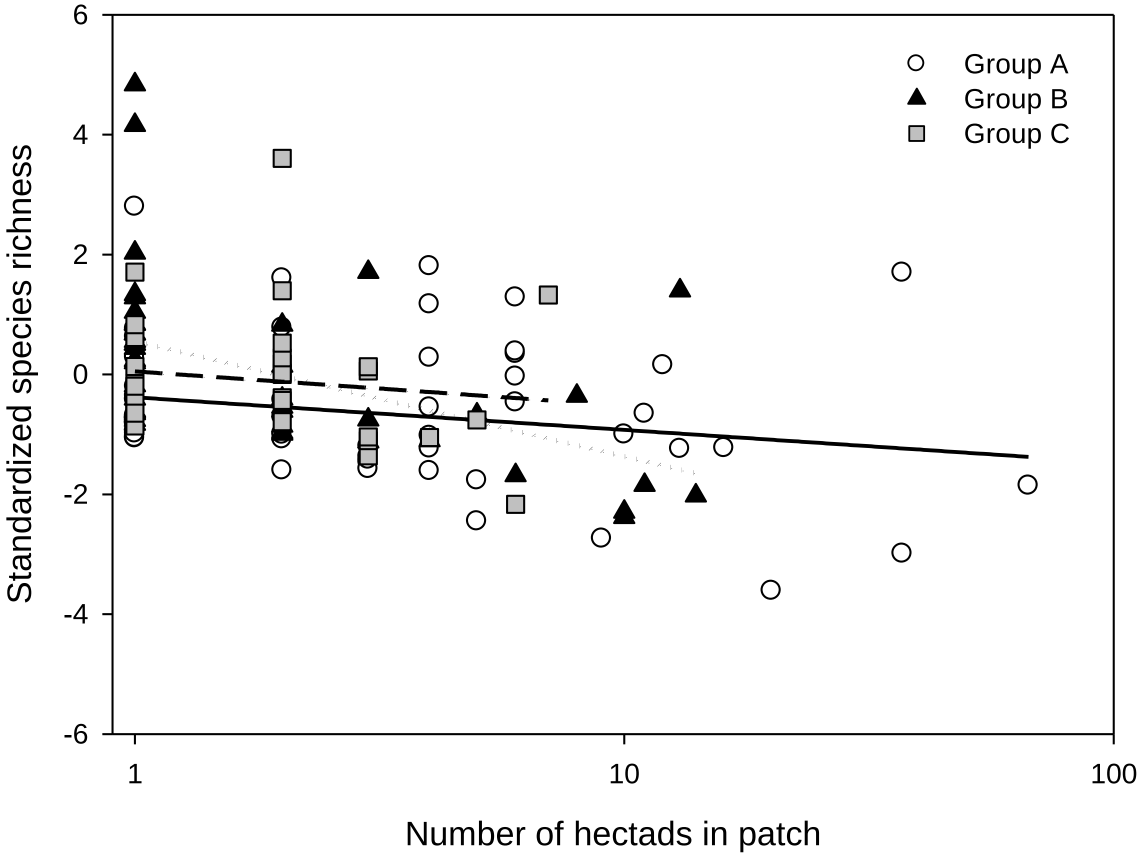

a)
b)
Frequency of distance class (%)
0
10
20
30
40
50
Dissimilarity between hectads
0.15
0.20
0.25
0.30
0
10
20
30
40
50
60
70
80
Distance between hectad centres (km)

Fig. 5.


6
4
2
0
-2
-4
-6
Standardized species richness
1
10
100
Number of hectads in patch
○ Group A
▲ Group B
▨ Group C

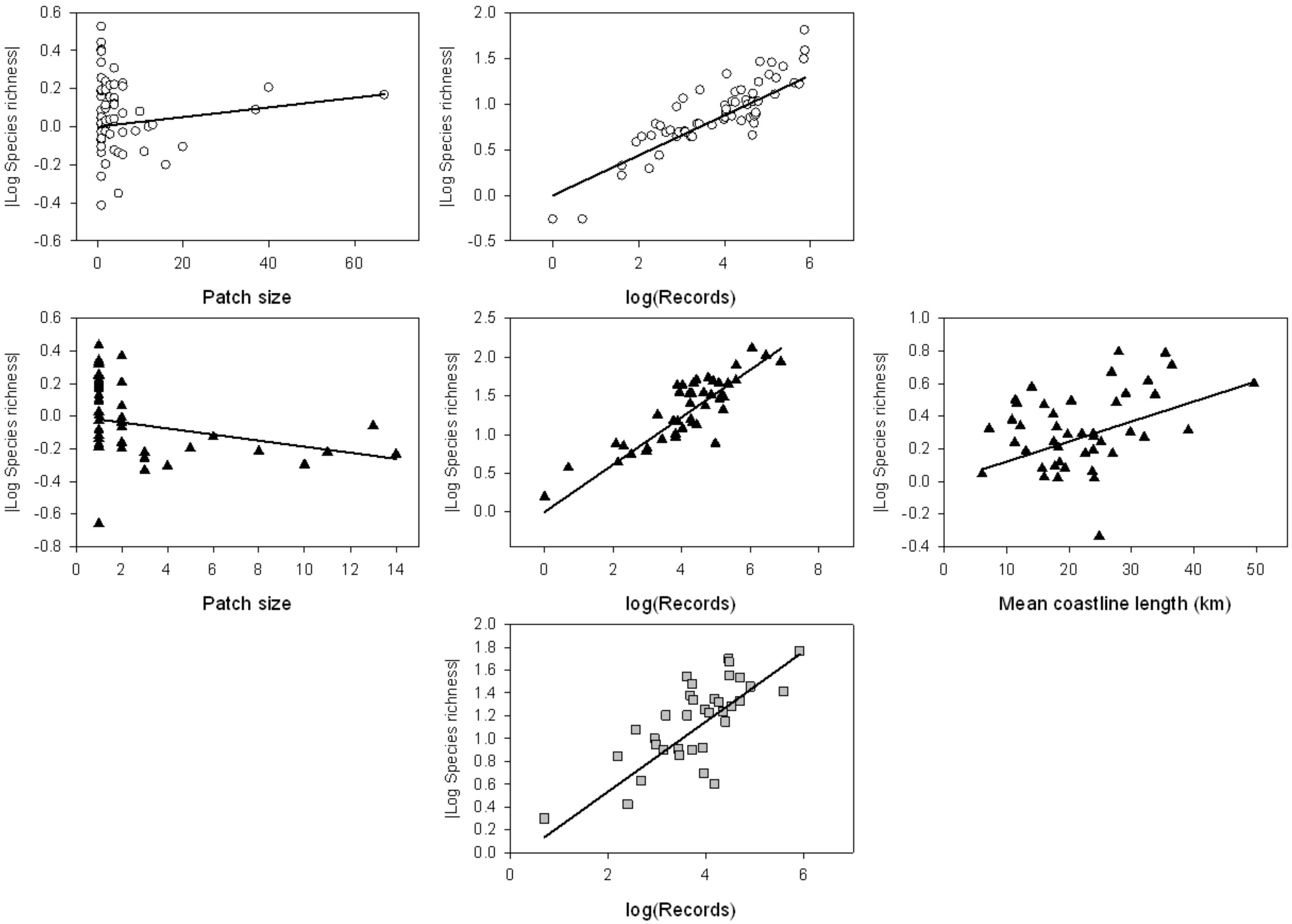

|Log Species richness|
Patch size
log(Records)
Mean coastline length (km)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
0
20
40
60
2.0
1.5
1.0
0.5
-0.5
2.5
2
4
6
8
10
12
14
1.0
0.8
30
50
1.8
1.6
1.4
1.2

Fig 6.