

REPORT

## The area-independent effects of habitat complexity on biodiversity vary between regions

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### Abstract

Potential explanatory variables often co-vary in studies of species richness. Where topography varies within a survey it is difficult to separate area and habitat-diversity effects. Topographically complex surfaces may contain more species due to increased habitat diversity or as a result of increased area *per se*. Fractal geometry can be used to adjust species richness estimates to control for increases in area on complex surfaces. Application of fractal techniques to a survey of rocky shores demonstrated an unambiguous area-independent effect of topography on species richness in the Isle of Man. In contrast, variation in species richness in south-west England reflected surface availability alone. Multivariate tests and variation in limpet abundances also demonstrated regional variation in the area-independent effects of topography. Community composition did not vary with increasing surface complexity in south-west England. These results suggest large-scale gradients in the effects of heterogeneity on community processes or demography.

### Keywords

Fractal, heterogeneity, lottery, spacing, topography.

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### INTRODUCTION

A traditional focus for studies of species richness is the increase in species number with area: the species–area relationship (Lomolino 2001). The slope of the species–area relationship varies between studies (Williamson 1981) and with spatial scale (Crawley & Harral 2001; Hubbell 2001). Despite the long history of research on species–area curves, a mechanistic understanding of the variation in slope is lacking. For example, it is not currently possible to predict how species number will decline following habitat fragmentation (Gonzalez 2000).

Investigations of spatial variation in species richness are often undermined by the extensive covariation between potential explanatory variables (Kerr 2001). For example, the effects of increasing area and habitat heterogeneity can be particularly difficult to separate (Ricklefs & Lovette 1999; McGuinness 2000). A 'habitat diversity' hypothesis proposes that larger areas contain more species when new habitat types are included as a greater area is sampled (Whittaker 1998). An alternative is that there may be little effect of habitat heterogeneity: an area *per se* effect exists. Larger areas may have more species simply as a reflection of finding

additional species when the sampling effort increases (Williamson 1981; Ricklefs & Lovette 1999). Area-related effects may also be associated with changes in the rates of local extinction and colonization of species (island biogeography, MacArthur & Wilson 1967). At larger scales both area and heterogeneity may facilitate increased speciation (Losos & Schluter 2000; Rahbek & Graves 2001).

A particular case of confounded variables exists when topographic complexity generates habitat diversity. Topographic complexity is positively related to species diversity in many ecological communities (MacArthur & MacArthur 1961; McCormick 1994; Kostylev 1996; Petren & Case 1998). Often the species richness associated with topographic variation is linked to an increased range of ecological niches: a habitat diversity hypothesis (e.g. Debski *et al.* 2002). Examples from rocky shores demonstrate a role for topographic complexity in creating microclimate variation, concentrating biological interactions (predation haloes; Fairweather 1988; Johnson *et al.* 1998) and providing refuges from physical and biological disturbance (Menge *et al.* 1985; Bergeron & Bourget 1986). Despite the apparent correlation between habitat diversity and topographic complexity, separating the habitat diversity and area *per se*

hypotheses is difficult. Surface area also increases as a function of topographic complexity. Hence indices of habitat heterogeneity, such as elevation variability (Kerr & Packer 1997), are ambiguous, as more complex landscapes also have increased surface areas.

Whereas it is easy to appreciate that increasingly complex topographies have a greater surface area, the fractal nature of complex surfaces is not always considered. On a fractal surface, estimates of surface area are scale dependent: increasing when measurements are made at finer scales (Mandelbrot 1967). A complex surface therefore has no single property of 'area' and measurements of species richness per unit area are also scale dependent (Pennycuik 1992). Measurements taken on different fractal surfaces can be transformed to allow scale-invariant comparisons of organism density or species richness (Pennycuik 1992). Not only does this provide a valid way of comparing between densities on surfaces of differing complexity, it facilitates separation of the area *per se* and habitat diversity effects. With an area *per se* effect, increases in species number with greater surface complexity will reflect surface availability alone. The habitat diversity hypothesis predicts more species on complex surfaces than would be expected from surface availability alone. This can be thought of as an increase in species packing in response to increased habitat diversity.

We used scale-invariant measures of species richness to separate the effects of habitat diversity and increased surface availability in areas of differing surface complexity. The generality of any habitat diversity effects was tested by comparisons between sites, shores and regions. Fixed quadrat sizes were used to control for other variables confounded with area. Quadrat sizes were small relative to dispersal distances. Hence variation in species richness between quadrats was not confounded by local speciation events.

## MATERIALS AND METHODS

### Fractals and the spacing of species on surfaces

Many natural structures have fractal properties (Mandelbrot 1967). A fractal line has a non-integer dimension ( $D$ ) of between one and two and does not have a single identifiable property of 'length'. The same logic applies to complex surfaces. Fractal surfaces have a dimension between two and three, with estimates of surface area changing as a function of the measurement scale (Pennycuik 1992). A more complex surface will have a higher fractal dimension than a smooth surface. Comparisons of species richness ( $N$ ) between regions of different complexity are problematic because they involve comparisons of measurements with different dimensions (e.g.  $m^{-2.1}$  and  $m^{-2.4}$ ). A solution to this is to use estimates of 'spacing' ( $S$ ) to convert measures

of species richness on different surfaces to the same dimension (Pennycuik & Kline 1986; Pennycuik 1992):

$$S = (E/N)^{1/D} \quad (1)$$

$E$  is a scale-invariant measure of the surface extent, defined by:

$$E = ns^D, \quad (2)$$

where  $n$  is the number of steps (or surface 'tiles') with a length (or area) of  $s$  required to measure a line (or surface) with a fractal dimension of  $D$ . Tiles are flat surfaces of the same area. Pennycuik (1992) also gives an approximation method for estimating fractal extent from contour maps. The derivation of spacing reduces measurements made at a range of different dimensions to a single linear quantity, and therefore allows comparisons between surfaces with different degrees of complexity.

Spacing was originally used to describe the occurrence of nests on different coastlines (Pennycuik & Kline 1986). Along a linear coastline, the spacing represents the average distance between nests (km in Pennycuik & Kline 1986). The reciprocal of spacing gives an estimate of density, which can be squared to give a value per unit area. The value for spacing describes the separation distance between objects on an idealized flat surface. When comparing species richness between quadrats, the spacing represents the average distance between different species on an idealized flat surface.

If species richness reflects the availability of colonizable surface, the expected number of species will be greater in topographically complex regions. However, if surface availability is the only factor controlling species number, the spacing of species will not change with increased surface complexity. Conversely, if topographic complexity increases species richness independently of area (an 'area-independent' effect of habitat complexity), then the spacing between species should decrease on more complex surfaces. This can be interpreted as an increase in the packing of species in regions where there is greater habitat (niche) diversity.

### Data collection and analysis

Estimates of species richness and topographic complexity were made in  $0.0625 \text{ m}^2$  quadrats separated by a hierarchical series of scales on rocky shores. Surveys were carried out in April 2000. The largest spatial scale was a regional comparison between shores on the Isle of Man and shores in south-west England (approximately 450 km separation between regions). Two shores were chosen at random from those accessible in each region, with separation between shores ranging from 3.5 to 15 km. Samples within a shore were from two haphazardly selected sites separated by 50–100 m. Shores used in

south-west England were Heybrook and Port Wrinkle. Port St Mary and Poyll Vaaish were sampled in the Isle of Man. Topographic complexity varied within shores, ranging from relatively smooth horizontal surfaces to rougher areas containing a variety of crevices and cracks. All the shores are composed of sedimentary rock types. Poll Vaaish and Port St Mary are both Carboniferous Limestone, although there are differences between the shores in rock origin, erosion patterns and topography. The shores in south-west England are composed of Devonian siltstones and slates. Port Wrinkle has a greater prevalence of slate than Heybrook, with some hard grit outcrops.

A total of 20 haphazardly thrown quadrats were surveyed in the mid shore at each site, with 1–10 m between replicates. All species greater than 1 mm in sample quadrats were recorded. It was not always possible to count the number of individuals in quadrats, as identification of individuals in colonial, encrusting or turf forming species is difficult. The percentage cover of standing water, barnacle cover and number of limpets were, however, recorded for each quadrat. Sessile organisms potentially increase the available settlement area for new species. The effect of such additional species was controlled for by excluding organisms not found on the rock surface. Topographic complexity was measured by pressing a plastic profile gauge made up of 300 1 mm plastic sliders into the rock surface. With the exception of barnacles, species were moved aside to allow the profile gauge to follow the rock surface. Destruction of barnacles was not necessary as the presence or absence of individuals made little difference to estimates of surface complexity given the minimum grain of the study (1 mm). Barnacle cover was not positively related to quadrat fractal dimension or species richness ( $r < 0.087$ ,  $P > 0.05$ ). Profiles were traced on to a sheet of paper in the field and subsequently scanned and converted to a digital image. Fractals were estimated using the divider method (Sugihara & May 1990; Cox & Wang 1993) with a geometrically increasing series of step lengths. Topographic complexity values were estimated using three profiles from each quadrat and assumed that linear measurements could be transformed into a surface fractal dimension (Petigen & Saupe 1988).

Estimates of spacing from fractal geometry were used to examine whether increases in species richness with surface complexity reflected surface availability alone. Before carrying out analyses of spacing and community composition, the appropriate level of data aggregation was derived. The nested design was used to examine within-shore, between-shore and regional variation in the slope of the species richness–habitat complexity relationship. The null hypothesis in this hierarchical comparison was that the slope was the same across all locations. Slopes of the relationship

between species richness and quadrat fractal dimension were compared at the different spatial scales using a homogeneity of slopes test within a nested ANCOVA design. In contrast to the use of ANCOVA to correct for the effects of a covariate on experimental treatments, the focus on this study was on the homogeneity of slopes (Zar 1996). For this reason interaction terms are left in the model as a test for homogeneity of slopes (Quinn & Keough 2002). The design planned for tests of slopes across each level of nesting, so interaction terms were tested against the residual term in the model (Quinn & Keough 2002). If the null hypothesis of homogeneous slopes is accepted (no interactions between slope and spatial scale), then it is possible to compare locations having corrected for variability associated with quadrat surface complexity.

Application of ANCOVA was supported following examination of residuals plots (Sokal & Rohlf 1995; Quinn & Keough 2002). More rigorous testing of ANCOVA assumptions included normality tests for residuals (Sokal & Rohlf 1995), linearity tests on the species richness–fractal dimension relationship ( $H$  statistic, Thornby 1972) and homogeneity of variance tests (Huitema 1980). An assumption of ANCOVA designs, as in all Model I linear regression, is that the independent variable is measured without error. The sampling and measurement of fractal dimension for each quadrat is likely to have introduced some degree of random error. Uncertainty in covariate values tends to reduce the estimates of slope in ANCOVA. However, the most serious issue with covariate uncertainty is when comparing adjusted response variables where the mean covariate differs between treatments (Huitema 1980). This latter problem does not arise in a test of homogeneity of slopes where covariate values are random, although there may be some loss of statistical power (Huitema 1980).

The effect of topographic complexity on community structure was clarified using multivariate tests. The RELATE procedure in the PRIMER community analysis program (Clarke & Warwick 1994) was used to compare a matrix of the similarities between sample quadrats based on their species composition and a matrix of similarities based on the Euclidean distance between sample fractal dimensions. Multivariate distances between samples based on species presence or absence were calculated using the Sorenson coefficient. A test statistic is generated for the non-parametric correlation between community and fractal dimension matrices. Significance values of the observed correlation are assigned following a procedure that randomly permutes one of the matrices in a manner equivalent to a Mantel test (Sokal & Rohlf 1995). The null hypothesis of no association between the separate distance matrices is rejected if fewer than 5% of randomly generated associations exceed the observed value.

## RESULTS

There was a positive relationship between the species richness and surface complexity in quadrats (Fig. 1). The slope of the species richness–complexity relationship differed between regions (significant region-by-complexity interaction in an ANCOVA, Table 1). At the level of shore or site within shore, there were no significant interactions between species richness and fractal dimension: the slope of the relationship between species richness and surface roughness did not vary significantly within shores or between shores within a region.

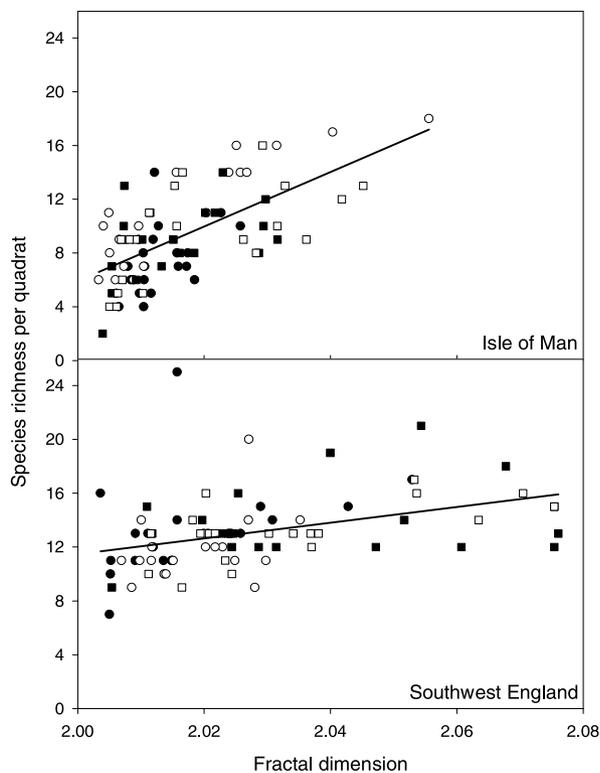
The tests of homogeneity of slopes suggested that the appropriate comparisons of the area-independent effect of surface complexity should be between regions. There was no correlation between species spacing and the surface fractal dimension in south-west England (Fig. 2,  $r = -0.147$ ,  $P > 0.15$ ). This implies that the increases in species richness on more complex surfaces in south-west England reflect a simple response to increases in surface availability. In contrast, estimates of spacing decreased with

complexity in the Isle of Man ( $r = -0.486$ ,  $P < 0.001$ ), indicating an area-independent enhancement of species richness.

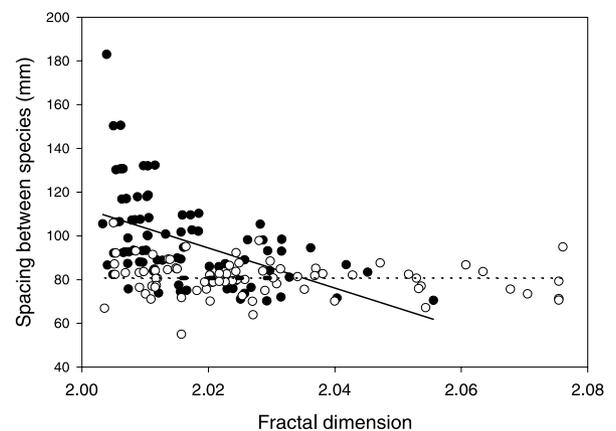
Spacing of adult *Patella vulgata* L. repeated the pattern seen with species richness. Numbers reflected surface availability in south-west England (no significant correlation between limpet spacing and complexity,  $r = 0.099$ ,  $P > 0.4$ ) but there appeared to be additional benefits to topographic complexity in the Isle of Man (correlation between limpet spacing and complexity,  $r = -0.318$ ,  $P < 0.05$ ). Average

**Table 1** Homogeneity of slopes ANCOVA for the variation in species richness associated with fractal dimension of the sample quadrat at different levels of spatial scale. Application of ANCOVA was supported following acceptance of the null hypotheses for linear trends, normally distributed residuals and homogeneity of variances at  $P > 0.05$ . No test of region, shore or site is given due to differences in slope between regions.  $P$ -values shown as \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , NS not significant

Source of variation	d.f.	MS	$F$	$P$
Fractal dimension ( $D$ )	1	248.14	39.95	***
Region	1	42.18	—	—
Shore(Region)	2	10.08	—	—
Site(Shore(Region))	4	1.48	—	—
$D \times$ Region	1	41.10	6.62	*
$D \times$ Shore(Region)	2	10.11	1.63	NS
$D \times$ Site(Shore(Region))	4	1.47	0.24	NS
Residual	144	6.21		



**Figure 1** Changes in species richness with quadrat fractal dimension. Separate shores within a region are shown as different shapes with filled and open symbols indicating different sites within a shore. Pooled regression slopes are shown for each region (both lines significant at  $P < 0.001$ ,  $r^2 = 0.42$  for the Isle of Man, 0.16 for south-west England).



**Figure 2** Measurements of species spacing in quadrats of different complexity. Following the homogeneity of slopes test, measurements are identified by region only, with filled circles for data from the Isle of Man and open circles for south-west England. A regression slope is drawn for the Isle of Man data ( $P < 0.05$ ). The dotted line shows the mean spacing for south-west England quadrats as the least squares regression slope was not significantly different from zero.

**Table 2** Correlation between the distances between samples based on species presence/absence and the distances between the fractal dimensions of sampled quadrats. *P*-values shown as \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001, NS not significant

Region	Correlation†	Number of randomizations‡	<i>P</i>
Isle of Man	0.133	10	*
South-west England	0.033	254	NS

†Correlation between community and fractal matrices.

‡Number of randomizations exceeding the observed correlation (maximum = 999).

limpet density did not differ between regions (nested ANOVA,  $F_{1,2} = 3.37$ ,  $P > 0.05$ ).

Multivariate comparisons of the similarity between quadrats suggested that the observed community changed in response to measured fractal dimension in the Isle of Man but not in south-west England (Table 2). The differences between regions were not due to different species identities. Analyses using only the species found in both regions produced similar results in ANCOVA and multivariate tests. Spacing of species in common between regions decreased with increasing complexity in the Isle of Man ( $r = -0.462$ ,  $P < 0.001$ ). There was no relationship between spacing of species in common and fractal dimension in south-west England ( $r = -0.06$ ,  $P > 0.5$ ).

## DISCUSSION

As has been reported in other studies, there were positive relationships between species richness and surface complexity. Analyses of the spacing between species allowed an assessment of the habitat diversity effect, while controlling for increased surface availability on complex surfaces. Previous attempts to separate the effect of habitat heterogeneity from that of area have used stepwise regressions, despite the correlation between variables that can make application of this method ambiguous (Sokal & Rohlf 1995; Ricklefs & Lovette 1999). An area-independent effect of topographic complexity on species richness was demonstrated after correcting for the increased surface availability on more complex surfaces. The strength of this effect did not vary between shores within a region but did vary between regions. Many field studies of the effect of habitat heterogeneity look at single sites or locations separated by only a few km (Douglas & Lake 1994; Downes *et al.* 1998). The results presented here suggest that such studies have limited generality, because the strength of the habitat-heterogeneity effect can vary at regional scales.

Given the prediction that habitat heterogeneity enhances species coexistence (Pacala 1987), the surprising result is

that species richness reflects surface area alone in south-west England. This absence of a habitat effect suggests that coexistence of the mostly sessile rocky shore species could occur by a lottery effect (Chesson & Warner 1981; Sale & Douglas 1984). Under the lottery model, increases in surface area represent additional opportunities for a species to recruit to the community. An important proposition of lottery systems is a decoupling of recruitment and the local density of adults. As recruits are drawn randomly from a diverse larval pool, the expected species richness increases with the number of recruitment sites. The lack of a relationship between community structure and fractal dimension in the RELATE test for south-west England supports the idea that species are recruiting to the shore in a lottery system. Tokeshi (1999) emphasizes that lottery processes are likely at local scales in variable recruitment (e.g. Gaines & Bertness 1992) systems such as rocky shores. Various mechanisms, such as frequency dependent predation or intraspecific aggregation, can also facilitate species coexistence (Tokeshi 1999). The lottery model appears to be the most parsimonious explanation of the constant spacing in quadrats from south-west England. Additional assumptions are generally required to explain how processes such as frequency dependent selection could lead to increased diversity with greater surface availability. The mechanisms underlying coexistence could be investigated further with manipulative experiments on species abundances and spatial patterns at the quadrat scale.

The contrast between regions suggests that the value of surface complexity in generating habitat diversity changes between regions. Regional variations in demographic processes have been reported for rocky shores (e.g. Jenkins *et al.* 2001). This implies that regional variability in the effects of complex surfaces may not be unusual. Habitat diversity is created by topographic complexity in the Isle of Man, but not in south-west England. The change in value of surface complexity may be related to wave exposure (Raffaelli & Hughes 1978). However, regional differences in wave climate seemed small, all shores could be classed as 'moderately exposed' (Ballantine 1961). The utility of topographic features such as crevices is related to local environmental conditions (Johnson *et al.* 1998). The warmer weather of south-west England may remove the habitat variation associated with centimetre scale topographic features in the Isle of Man. For example, a crevice may maintain a microclimate throughout a tidal cycle in the Isle of Man while a feature of the same dimensions dries out in south-west England. This desiccation-related hypothesis is supported by an examination of the relationships between standing water and species richness in the two regions. Species richness was not related to the cover of standing water in the Isle of Man ( $r = 0.064$ ,  $P > 0.05$ ) whereas species richness increased with standing water in south-west

England ( $r = 0.342$ ,  $P < 0.05$ , no significant difference between regions in prevalence of standing water and no significant correlations between fractal dimension and the amount of standing water). Behaviour or activity of species may also differ at large spatial scales. A possibility currently being investigated is that the activity of the dominant grazers, limpets, varies between regions.

One-dimensional measurements of surface complexity, such as fractal dimension, may obscure details of the structural components of a surface (e.g. particular size classes of pits, Hills *et al.* 1999; Beck 2000). The differences between regions may thus reflect the availability of particular features on Isle of Man shores. Although confounding variation in surface structures remains a possibility, there were no obvious sets of surface features differing in abundance between regions. In addition, the difference between regions appears to be generated by relatively fewer species on smooth surfaces in the Isle of Man.

Species–area curves typically span several spatial scales. However, scaling up results to areas larger than the quadrat scale is not straightforward. Although fractal estimates were consistent within quadrats, pooling of quadrats is likely to produce erroneous estimates of fractal dimension at larger scales as surfaces are often fractal over finite spatial scales (Berntson & Stoll 1997). Comparisons of quadrats of different sizes are also confounded by environmental factors that co-vary, often non-linearly, with area (Whittaker *et al.* 2001). It is such covariation between variables that is addressed by using a fixed quadrat size and scale-invariant measures of density. Clearly it would be of value to extend the approach followed in this study to surveys of species richness and heterogeneity in series of larger sample areas. The influence of different variables such as topography is considered to vary with spatial scale (Willis & Whittaker 2002). With reference to most species–area curves, the average spacing between species would be expected to increase with sample area. Archambault & Bourget (1996) suggest that topographic heterogeneity at the km scale has generally more influence on species richness than complexity at the 100 m scale. However, this conclusion is difficult to interpret as heterogeneity measurement methods also differed between scales (Archambault & Bourget 1996).

Whittaker *et al.* (2001) emphasize the confusion generated in studies of species diversity when variation in area is confounded with other variables. A possible solution is to control for area effects by comparing richness estimates in sample units of the same size (Whittaker *et al.* 2001). Where there is topographic variation between samples, it may be preferable to work with species spacing rather than richness per unit area. The results presented here suggest a further issue that may obscure an understanding of alpha (local) diversity. Species richness reflected surface availability alone in one region while there was an area-independent

complexity effect in another region. Multiple regression studies often assume that the effects of a variable are constant within a data set. This risks obscuring regional changes in the importance of different variables, such as topographic complexity. Recent large-scale studies of species richness have shown regional variation in the effect of topography (although the measurement of topography used, elevation variability, is confounded with variation in area, Kerr & Packer 1997; Rahbek & Graves 2001). Hence observations at the quadrat scale on rocky shores may be reflected in analogous processes occurring at other scales.

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