

Changes in species diversity following habitat disturbance are dependent on spatial scale: theoretical and empirical evidence

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Summary

1. Many studies have examined the impacts of tropical habitat disturbance. However, the effects of moderate habitat disturbance on species diversity show little consensus, with both increased and decreased diversity following disturbance being reported with approximately equal frequency. Previous work has shown that the spatial scale of sampling affects the reported changes in diversity following habitat disturbance, and here we present new theoretical and empirical data which explain why this is so.

2. We assume that habitat disturbance reduces the slope of the species–area relationship (SAR), and we show theoretically that this reduction in the slope results in a scale-dependent response of diversity to disturbance. Thus, following moderate habitat disturbance, diversity is reported to increase when measured at small spatial scales but declines when measured at large spatial scales. Our findings suggest that even a very small change in the SAR slope following disturbance corresponds with a scale-dependent response of diversity to disturbance.

3. We analyse new empirical data for tropical butterflies at a range of spatial scales (≈ 3 –80 ha). Our results support our theoretical findings and the notion of scale-dependence in estimates of diversity. We show that this scale-dependence occurs because α and β diversity increase with spatial scale at a significantly faster rate in undisturbed forest compared with disturbed forest. This is due to reduced habitat heterogeneity and reduced spatial autocorrelation of butterfly diversity data following disturbance.

4. *Synthesis and applications.* There is little consensus in the reported responses of species diversity to moderate tropical habitat disturbance, and the spatial scale at which studies are carried out largely pre-determines the findings. Here we demonstrate, both theoretically and empirically, the mechanisms that produce a scale-dependent response of diversity to habitat disturbance. There is little agreement among researchers about the best methods for sampling tropical species in the field, and our findings highlight the problems of using diversity changes that do not account for the spatial scale of sampling. We conclude that in the future, studies should assess spatial patterns in diversity over a range of spatial scales and should not evaluate changes in diversity at a single spatial scale.

Key-words: habitat heterogeneity, Lepidoptera, selective logging, self-similarity, species–area relationships

Introduction

Examining patterns of species diversity has been a central theme in ecological research (Peet 1974; Huston 1994). One of the most widely documented patterns is the species–area

relationship (SAR), showing that larger areas contain more species than smaller areas (Harte, Kinzig & Green 1999; Maddux 2004). Thus, measures of species richness (Palmer & White 1994; He & Legendre 2002) and many measures of species diversity vary with spatial scale (Crawley & Harral 2001; Gering & Crist 2002; Willis & Whittaker 2002). In addition, there is now increasing evidence that changes in diversity

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following habitat disturbance are also dependent upon the spatial scale at which they are measured (Hamer & Hill 2000; Kaiser 2003; Hill & Hamer 2004). Most species decline following severe habitat disturbance (Holloway, Kirkspriggs & Khen 1992), but responses of species to less severe disturbance appear to be scale-dependent. For example, studies examining changes in Lepidoptera diversity following moderate habitat disturbance (e.g. commercial selective logging) report increased diversity following disturbance when measured at small (< 1 ha) spatial scales, but decreased diversity when measured at larger (> 3 ha) spatial scales (Hamer & Hill 2000). These findings are of concern to ecologists and conservationists because such results indicate that the choice of sampling protocol may largely influence the studies outcome.

The scale-dependent response of diversity to habitat disturbance may be influenced by changes in the slope of SARs. Such changes in the slope could occur if habitat disturbance has different effects on local diversity at sampling points (α diversity) compared with species turnover between sampling points (β diversity; Condit *et al.* 2002). For example, disturbance is known to create new habitats for species not found in undisturbed areas (Connell 1978) but may also reduce β diversity through reduced habitat heterogeneity (Hill & Hamer 2004). These effects could explain why empirical studies of habitat disturbance have reported qualitatively different impacts on diversity at small and large spatial scales, but studies explicitly examining relationships between habitat disturbance, habitat heterogeneity and diversity are lacking.

In this study, we examine relationships between diversity, spatial scale and disturbance using both theoretical and empirical approaches. First, we describe an algebraic model that examines how changes in the slope of SARs influence estimates of diversity at different spatial scales. We focus on the impacts of relatively small changes in the slope as these would be more typical of moderate habitat disturbance (Rosenzweig 1995). Second, we compare our theoretical findings with those from new field data examining the impacts of moderate habitat disturbance (commercial selective logging) on tropical butterflies. We investigate how SARs are affected by habitat disturbance, and quantify changes in butterfly diversity following disturbance over a range of spatial scales (3.14–78.5 ha).

Materials and methods

THEORETICAL APPROACH

In order to examine how changes in SARs are mechanistically linked to scale-dependent responses of diversity to habitat disturbance, we developed the following algebraic model. The relationship between species number and area is usually described by the equation:

$$S = cA^z, \quad \text{eqn 1}$$

where S is the number of species at a location with area A , and where c (intercept) and z (slope) are constants that depend on the habitat and taxon being sampled (Rosenzweig 1995). Equation 1, a power function, is widely used to model SARs, and hence, we use it in this

study, but it is not the only plausible mathematical function. Harte *et al.* (1999) suggested that this power law arises from a probability rule and self-similarity. If an area of size A_0 containing S_0 species is bisected into two identical self-similar sub-areas A_1 , with a fixed (i.e. scale independent and species independent) probability a that a species present in A_0 will be present in a given A_1 , then equation 1 will hold with a z value given by $a = 2^{-z}$. Thus, arguing inductively, if A_n is an area obtained by n successive bisections of A_0 , then the expected number of species in A_n is given by:

$$S_n = a^n S_0. \quad \text{eqn 2}$$

This link between z and a , together with the empirical observation that disturbance tends to decrease the value of the slope z (Rosenzweig 1995), can then be further exploited as follows. Consider a large area A_0 of undisturbed habitat, containing a total of S_u species, and which follows a SAR of the form of equation 1 with parameter z_u at spatial scales smaller than A_0 . Consider also an ostensibly identical area of disturbed habitat containing S_d species with SAR parameter z_d . We assume that $z_u > z_d$ (so that $a_u < a_d$ in the obvious notation, using the fact that $a = 2^{-z}$). Equation 2 implies that at the smallest spatial scale (i.e. with a large number of bisections n), fewer species are observed in the undisturbed habitat compared with the disturbed habitat, because a_u^n / a_d^n tends towards zero for large n . If $S_u \leq S_d$ at the largest spatial scale A_0 , then the undisturbed habitat will appear less diverse than disturbed habitat at all spatial scales. However, if $S_u > S_d$, then it is easy to identify the intermediate spatial scale at which undisturbed and disturbed habitats have equal species richness/diversity. The spatial scale at which the two habitats have equal diversity is given by solving $a_u^{n^*} S_u = a_d^{n^*} S_d$ (from equation 2), resulting in

$$n^* = \frac{\ln\left(\frac{S_d}{S_u}\right)}{\ln\left(\frac{a_u}{a_d}\right)} = \frac{\ln\left(\frac{S_d}{S_u}\right)}{(\ln 2)(z_d - z_u)} \quad \text{eqn 3}$$

In equation 3, n^* refers to the number of times the original area has been bisected, so that the actual area at which undisturbed and disturbed habitat appear equally diverse is $A_e = A_0 / 2^{n^*}$.

This model, whilst appealing in its simplicity, equates diversity with species richness at any given scale. However, this is an incomplete description of diversity because it ignores issues of species abundance within a community. We can address issues of relative abundance within our theoretical context, but only by imposing further assumptions on the way individuals are distributed among species (i.e. by imposing species-abundance relationships on the community). For example, if we assume that when a species is present in both halves of a given bisection it is equally abundant in each half, then we can calculate modified estimates for n^* using Margalef's diversity index (D_{Mg} ; Magurran 2004). This index is one of several commonly used indices which combine species richness and evenness into a single measure, and is calculated as:

$$D_{Mg} = \frac{S - 1}{\ln N}, \quad \text{eqn 4}$$

where S is the total number of species recorded and N the total number of individuals recorded. Values for n^* are then given by substituting $S = a_u^{n^*} S_u$ (from equation 2) and $N = N_u / 2^{n^*}$ (from the assumption of equal abundances in each bisection) into equation 4, substituting similarly for d subscripts, and equating the two expressions. This results in

$$\frac{2^{-n^*z_d} S_d - 1}{-n^* \ln 2 + \ln N_d} = \frac{2^{-n^*z_u} S_u - 1}{-n^* \ln 2 + \ln N_u}, \quad \text{eqn 5}$$

where N_u and N_d are the total number of individuals in the undisturbed and disturbed habitats, respectively. Alternative formulations of species abundance relationships such as Shannon–Wiener and Simpson's indices are not mathematically tractable (Maddux 2004) and so are not considered here. We used equation 3 (richness) and equation 5 (diversity) to examine how changes in the slope (z -value) of SARs affect the perceived response of diversity to habitat disturbance at different spatial scales. We solved these equations numerically using parameters based on new empirical data (see below).

EMPIRICAL APPROACH

We compared the findings from our algebraic model with new field data for butterflies from undisturbed and moderately disturbed tropical forest habitats.

Study site

Field work was conducted during June 2003, from March to April 2004, and from October to December 2004 at the Danum Valley Field Centre (DVFC) and the surrounding Ulu Segama Forest Reserve (USFR) in Sabah, Malaysian Borneo (5°N, 117°30'E; site details in Marsh & Greer 1992). DVFC is located within a conservation area of approximately 428 km² of protected lowland dipterocarp rainforest, and is surrounded by extensive areas of selectively logged forest (area of USFR ≈ 9730 km²). Butterfly sampling in this study was conducted in the conservation area (= undisturbed habitat), and in an adjacent logging coupe that was selectively logged in 1988 (= disturbed habitat). Logging extraction data for this coupe indicate that approximately 170 000 m³ of timber were extracted over an area of approximately 2300 ha using tractor and high lead extraction methods (Innoprise Corporation, unpublished report). The study area has temperature (annual mean = 26.7 °C) and rainfall (annual mean = 2669 year⁻¹) typical of the humid tropics (Walsh & Newbery 1999).

Butterfly sampling

Identification of butterflies in flight in very diverse areas such as Borneo can be problematic (Walpole & Sheldon 1999), and thus, we focused on species that can be sampled using fruit-baited traps (Dumbrell & Hill 2005). We assumed that traps had equal sampling efficiency in different habitats, and the use of traps may avoid potential sampling bias that may influence visual sampling methods due to differences in visibility between habitats. Approximately 75% of nymphalid butterfly species on Borneo belong to the fruit-feeding guild (Hamer *et al.* 2003).

In each habitat, butterfly traps were hung approximately 2 m above the ground every 200 m in a five-by-five trap arrangement (total = 25 traps per habitat; 100 ha sampled per habitat). Both trapping grids were within large tracts of continuous forest, and each grid was located at least 200 m from small areas of non-forest (rivers and logging roads) to minimise any edge effects. This 'grid' design allowed us to estimate α and β diversity over a range of spatial scales in each habitat (from a single trap to the entire 100 ha grid), and thus allowed us to examine how diversity changes were associated with changes in z -values between habitats. Traps were baited with banana and sampled daily for 12 consecutive days each month in each

habitat over the six-month study period (1800 trap-days per grid). All butterflies caught were identified to species, marked with a permanent marker and released. Recaptures were excluded from subsequent analyses.

Butterfly diversity and spatial scale

The area over which fruit-baited traps sample butterflies is not known. In this study, traps were placed 200 m apart and we assumed that each individual trap sampled over a radius of 100 m, resulting in each trap having a sampling area of 3.14 ha (Hamer & Hill 2000). However, the precise area over which traps sample butterflies is not crucial to our findings, where we are primarily interested in the relative differences between disturbed and undisturbed habitats. In subsequent analyses of the relationships between diversity and spatial scale, our measures of spatial scale refer explicitly to the spatial scale of sampling. In each habitat, we calculated three indices of α diversity (Margalef, Shannon–Wiener and Simpson; following methods in Magurran 2004) over a range of spatial scales. All indices are quoted such that an increase in index value corresponds with an increase in diversity.

First, we calculated α diversity per trap (area = 3.14 ha). We then calculated diversity at a larger spatial scale by selecting a second trap at random from the grid and recalculating diversity by combining data from both traps. This process continued by sequentially adding additional traps selected at random until all traps had been included (resulting in the largest spatial scale of 78.5 ha). The entire process was then randomized 50 times to remove any effect of trap order on diversity estimates and confidence intervals were computed. This provided a robust estimate of the relationship between α diversity and area in each habitat.

In order to examine how β diversity might influence SARs, we used the complement of Morisita–Horn's index to examine patterns of β diversity in the two habitats (Magurran 2004). β diversity values were calculated for every pairwise combination of traps in each habitat ($n = 300$ pairwise combinations per habitat). Relationships between spatial scale and diversity (α and β) in undisturbed and disturbed habitats were examined by linear regression, ANCOVA (α diversity) and Mantel tests (β diversity).

Differences in species turnover between habitats may be affected by spatial autocorrelation in diversity measures. Thus, we used geostatistics to examine patterns of spatial autocorrelation in α diversity measures (Margalef, Shannon–Wiener and Simpson's indices) in undisturbed and disturbed habitats. Patterns of spatial autocorrelation were examined using semivariograms that were calculated from α diversity values estimated per trap. Model accuracy in describing the distribution of semivariogram values was assessed using the Indicative Goodness of Fit (IGF) function of the VARIOWIN 2.2 package (Pannatier 1996). The closer the IGF value is to zero, the better the fit of the semivariogram model to the distribution of the data, with a significance level usually set at IGF = 0.05 (Pannatier 1996).

Forest structure and habitat heterogeneity

In order to examine how habitat heterogeneity might affect butterfly diversity patterns, we assessed the structural composition of the vegetation at each location where we placed a butterfly trap ($n = 50$ trapping stations). Each trapping station was divided into four quadrants centred on the trap, and the following variables were recorded in each quadrant within a 30 m radius of the trap: height, girth at breast height, point of inversion (whether the first major

Table 1. Species richness, abundance, and diversity of nymphalid butterflies sampled from 25 fruit-baited traps in undisturbed and disturbed habitats. Diversity indices are shown with 95% confidence intervals (grid data) or mean values and SEs (trap data). Indices were compared between habitats using a pairwise randomisation test based on 10 000 re-samples of species abundance data, following Solow (1993). Values in bold were significantly different at the 5% level. Underlined values were approaching significance ($P = 0.056$) between habitats

	Data analysed per trap (small spatial scale)		Data analysed per grid (large spatial scale)	
	Undisturbed forest	Disturbed forest	Undisturbed forest	Disturbed forest
No. of species	14.64 (0.72)	13.44 (0.68)	56	51
No. of individuals	46.00 (3.42)	43.76 (3.30)	1150	1094
Shannon–Wiener	2.28 (0.06)	2.20 (0.06)	3.09 (0.07)	3.00 (0.08)
Simpson	9.25 (0.60)	9.16 (0.70)	<u>14.98</u> (1.06)	<u>13.43</u> (1.07)
Margalef	3.59 (0.16)	3.33 (0.15)	7.80 (0.57)	7.15 (0.05)

branch was above or below the midpoint of the tree), distance from trap, and identity (family Dipterocarpaceae, pioneer *Macaranga* spp., or other) of the two trees (> 0.6 m girth) nearest to the trap ($n = 8$ trees per station). The distance from the trap, girth at breast height, and identity of the nearest two saplings (0.1 – 0.6 m girth) were also recorded in each quadrant ($n = 8$ saplings per station). The percentage cover of ground, low level (> 2 m from ground), understorey and canopy vegetation were estimated within a 10 m radius of the trap. Overstorey vegetation cover was also estimated using a densiometer (Lemmon 1957). We used Levene's test and t -tests to compare differences in the variance and mean values of vegetation variables between the two habitats.

Results

THEORETICAL APPROACH

We determined the spatial scale at which estimates of diversity were numerically equal in undisturbed and disturbed habitats (A_e) by solving equation 3 (species richness) and equation 5 (Margalef's diversity index) for decreasing values of z (the slope of SARs; Fig. 1). In order to do this, data on species richness and number of individuals in disturbed and undisturbed habitats were obtained from our empirical data for butterflies (undisturbed habitat; $S_u = 56$ species, $N_u = 1150$ individuals; disturbed habitat, $S_d = 51$, $N_d = 1094$; Table 1).

For both species richness (equation 3) and diversity (equation 5), the spatial scale at which the measure of diversity was equal between habitats was highly sensitive to small changes in the value of z , and the larger the decrease in z -values following disturbance, the greater the spatial scale at which diversity was equal in the two habitats (Fig. 1). These results show that empirical studies carried out at spatial scales smaller than values for A_e will report increased diversity following habitat disturbance, whereas those carried out at spatial scales larger than A_e will report decreased diversity following disturbance for a given decrease in z .

We explored possible values of A_e in the field by incorporating observed z -values of SARs from our empirical butterfly data. In order to do this, we produced plots of SARs and modelled them to a power function using linear regression (Fig. 2). We subdivided data from the two study grids using a rectangular bisection method (Harte *et al.* 1999) by first dividing the grid into two non-equal rectangles and then

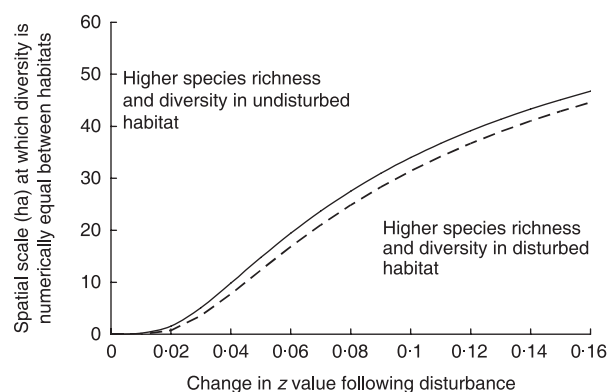


Fig. 1. Changes in the spatial scale at which species richness (dashed line) and diversity (solid line) were observed to be numerically equal between habitats with a decrease in z -values (slope of SARs) following habitat disturbance. Values of $S_u = 56$ and $S_d = 51$ were used to solve equation 3 (species richness). Values of $S_u = 56$; $S_d = 51$; $N_u = 1150$ and $N_d = 1094$ were used to solve equation 4 (Margalef's index of diversity) $A_0 = 78.5$ ha for both. The relationship between the spatial scale at which diversity is numerically equal between habitats and changes in z -values is the same regardless of absolute values of z from each habitat.

continuing to bisect areas until the smallest spatial scale was reached (a single trap), resulting in nine different spatial scales. SARs in the two habitats (Fig. 2) were described by the following equations: (i) undisturbed forest, $\log S = 0.420$ (SE = 0.024) $\times \log A + \log 0.988$ (SE = 0.031), (linear regression, $F_{1,7} = 315.55$, $P < 0.001$, $R^2 = 0.98$); (ii) disturbed forest, $\log S = 0.400$ (SE = 0.027) $\times \log A + \log 0.975$ (SE = 0.035), (linear regression, $F_{1,7} = 230.43$, $P < 0.001$, $R^2 = 0.97$).

Thus, our empirical data indicate similar z -values between habitats, with only a small decrease in z -value reported following disturbance (decrease in $z = 0.020$). These z -values were very similar regardless of how study grids were bisected and regardless of whether or not species richness values were rarefied (to account for the effects of abundance on species richness) prior to analysis (range of z -values, undisturbed forest $z = 0.321$ – 0.424 ; disturbed forest $z = 0.301$ – 0.410 ; change in $z = 0.014$ – 0.020). Incorporating these z -values into equation 3 (species richness) gave values of $n^* = 6.75$ which shows species richness to be numerically equal between habitats at a spatial scale (A_e) of 0.73 ha. Numerical solutions

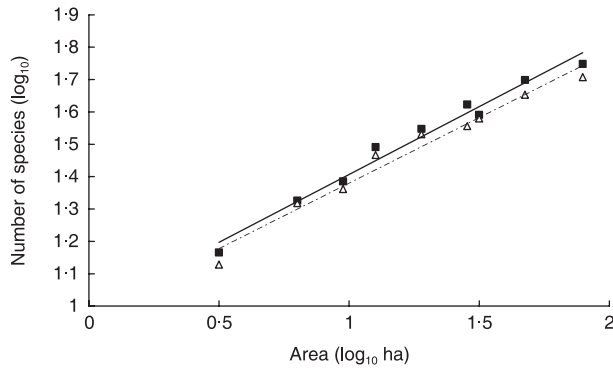


Fig. 2. Species–area relationships for fruit-feeding nymphalid butterflies in undisturbed (squares and solid line, $z = 0.42$) and disturbed habitats (triangles and dashed line, $z = 0.40$).

to equation 5 (Margalef's index) revealed similar values of n^* to those predicted by species richness ($n^* = 5.69$; $A_c = 1.53$ ha).

EMPIRICAL APPROACH

There were significant positive linear relationships between spatial scale and both species richness and α diversity (Shannon–Wiener, Margalef and Simpson's indices) in undisturbed and disturbed forests ($F_{1,23} \geq 107.60$, $P < 0.001$, $R^2 \geq 0.82$ for all regressions). However, measures of species richness and diversity increased at a significantly faster rate in undisturbed forest than in disturbed forest (ANCOVA of species richness or diversity in undisturbed and disturbed forests with spatial scale as a covariate; habitat by spatial scale interaction; species richness, $F_{1,46} = 8995.79$, $P < 0.001$; Margalef index, $F_{1,46} = 29.58$, $P < 0.001$; Simpson's index, $F_{1,46} = 19.01$, $P < 0.001$; but there was no significant interaction effect with Shannon–Wiener's index, $P = 0.95$). As a consequence, butterfly diversity generally decreased following disturbance when data were analysed at a large spatial scale by combining data from all traps on the study grid, whereas little difference in diversity was observed when data were analysed at a small spatial scale per trap (Table 1). These differences in α diversity patterns between habitats were supported by analyses of β diversity which showed that Morisita–Horn's index was significantly positively correlated with geographical distance in undisturbed forest but not in disturbed forest (Fig. 3; Mantel test, using 10 000 randomizations; undisturbed habitat, $r = 0.23$, $P = 0.001$; disturbed habitat, $r = 0.04$, $P = 0.3$).

Thus, higher z -values from SARs in undisturbed forest were associated with higher species turnover and greater increases in α diversity with increasing spatial scale in undisturbed forest, compared with disturbed habitat. These findings were supported by semivariogram analyses which showed that measures of Simpson's index were positively spatially autocorrelated in undisturbed forest but not in disturbed forest (Fig. 4). The distribution of semivariogram values fitted a Gaussian model best (IGF = 0.0007) and produced the following values: nugget = 2.49 (22% of the variance attributed to error); sill = 8.93 (78% of the variance

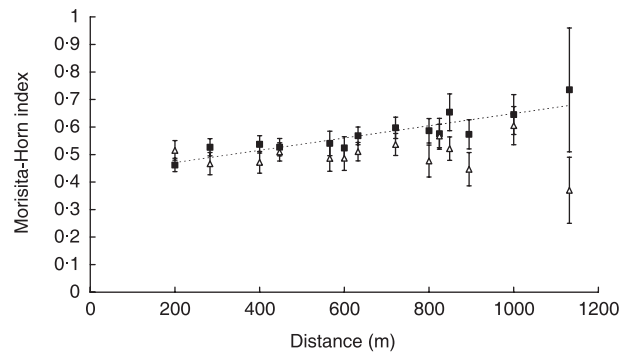


Fig. 3. Relationship between spatial scale and β diversity (means \pm SEs) in undisturbed (squares) and disturbed (triangles) habitat. A significant relationship was detected only in undisturbed forest (dashed line).

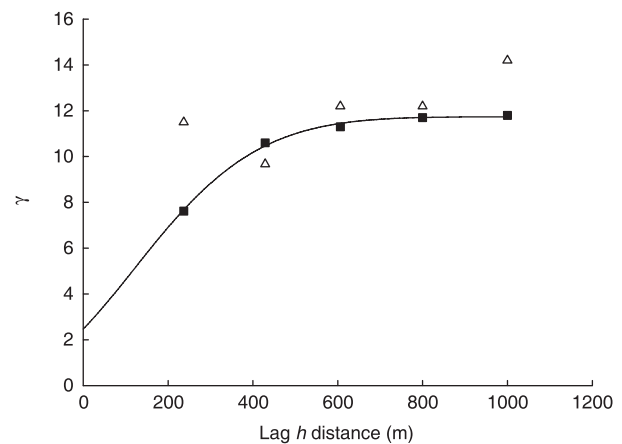


Fig. 4. Semivariogram of Simpson's index in undisturbed (squares) and disturbed (triangles) habitat. Line shows significant fit of semivariogram values to a Gaussian model in undisturbed habitat. γ is the semivariogram value, or mean difference, between pairs of samples separated by a distance or lag, h .

attributed to spatial autocorrelation); and range = 345.4 m (distance at which samples become spatially independent). The high proportion of the variance explained by the sill (78%) suggests that Simpson's index in undisturbed forest was strongly positively spatially autocorrelated between pairs of sampling points separated by distances smaller than 345.4 m. Semivariogram values for the other diversity indices (Margalef and Shannon–Weiner) were all shown to exhibit a pure nugget effect in both undisturbed and disturbed forest, and thus, there was no detectable spatial autocorrelation in these data.

FOREST STRUCTURE AND HABITAT HETEROGENEITY

Habitat structure and heterogeneity differed between habitats. Undisturbed forest had significantly taller, larger trees and higher overstorey, ground and canopy cover compared with disturbed forest (Table 2; t -test assuming unequal variance; tree height, $t_{36.73} = 6.92$, $P < 0.001$; tree girth, $t_{38.81} = 2.67$, $P = 0.01$; overstorey cover, $t_{34.61} = -2.35$, $P = 0.024$; ground cover, $t_{47.60} = 2.74$, $P = 0.01$; canopy cover $t_{26.36} = 4.99$, $P < 0.001$).

Table 2. Vegetation structure in undisturbed and disturbed habitats. Mean values and standard errors are shown. Asterisks denote significant differences between habitats using *t*-tests. Values in bold denote significant differences in variance of variables between habitats using Levene's tests

Variable	Undisturbed forest		Disturbed forest	
	Mean	SE	Mean	SE
Trees				
Number of trees	7.76	0.12	7.72	0.14
Proportion branching above mid point	0.83	0.03	0.78	0.06
Height (m)***	27.80	0.89	20.80	0.47
Girth (m)**	1.55	0.12	1.18	0.07
Density	84.34	12.77	71.20	8.41
Proportion of Dipterocarps***	0.63	0.03	0.16	0.03
Proportion of <i>Macaranga</i> spp.***	0.00	0.00	0.48	0.05
Saplings				
Number of saplings	8.00	0.00	8.00	0.00
Girth (m)	0.20	0.01	0.20	0.01
Density	3.80	0.29	3.91	0.44
Proportion of Dipterocarps***	0.57	0.03	0.27	0.04
Proportion of <i>Macaranga</i> spp.**	0.00	0.00	0.11	0.03
Percentage covers				
Densiometer*	87.80	0.56	84.71	1.17
Ground**	39.10	2.97	27.80	2.76
Low level (2 m)	45.50	2.34	43.10	2.72
Understorey	45.50	2.31	44.30	2.98
Canopy***	25.80	4.36	2.80	1.04

Undisturbed forest also had a significantly higher proportion of Dipterocarp trees and saplings and a significantly lower proportion of trees and saplings of the pioneer genus *Macaranga* (Table 2; Dipterocarp trees, $t_{46.44} = 9.87$, $P < 0.001$; Dipterocarp saplings, $t_{45.65} = 5.38$, $P < 0.001$; *Macaranga* spp. trees, $t_{24.00} = -7.39$, $P < 0.001$; *Macaranga* spp. saplings, $t_{24.00} = -3.35$, $P < 0.001$). Measures of tree height, tree girth and canopy cover had significantly greater variance in undisturbed forest than in disturbed forest, indicating more homogeneous vegetation following disturbance (Table 2; Levene's test for equality of variances, tree height, $F_{1,48} = 7.51$, $P = 0.009$; tree girth, $F_{1,48} = 9.80$, $P = 0.003$; canopy cover, $F_{1,48} = 41.42$, $P < 0.001$).

Discussion

DIVERSITY AND SPATIAL SCALE

Our theoretical approach produced a novel mathematical explanation for how a decrease in the slope of SARs can produce a scale-dependent response of diversity to habitat disturbance. Our theoretical model predicted numerically equal species richness and diversity in undisturbed and disturbed habitats at spatial scales of approximately 0.73–1.55 ha, with increased diversity following disturbance at smaller spatial scales and decreased diversity following disturbance at larger spatial scales. These findings were supported by our empirical data for butterflies showing significantly lower diversity in the disturbed habitat at large (78.5 ha) spatial scales but little

difference between habitats at smaller (3.14 ha) spatial scales. However, by contrast with the model, our empirical data did not provide any evidence of increased diversity following logging at very small spatial scales. This is probably because even the smallest spatial scale we sampled (3.14 ha) was relatively large compared with our predicted A_e ; other published studies carried out at much smaller spatial scales using walk-and-count transect methods (0.1–0.9 ha) have shown increased diversity of Lepidoptera following disturbance (Hill & Hamer 2004).

Ideally, we should have tested our theoretical findings with empirical data spanning a wider range of spatial scales than those we considered here, and including spatial scales well above and below the value at which diversity is numerically equal (Fig. 1). However, no single field study has yet been carried out over a sufficiently wide range of spatial scales to test this; most single-taxon studies generally use a single sampling method (e.g. walk-and-count transects or baited traps for butterflies), resulting in studies generally being either at small (i.e. transects) or large (i.e. traps) spatial scales (Hamer & Hill 2000). In addition, a thorough testing of our model not only requires data to be collected over a range of spatial scales from different habitats, but samples need to be contiguous and follow a spatially explicit design that allows species–area relationships to be examined. The empirical data presented in this study are from a comparison of only two sites, and thus, further data are required to test the robustness of our findings. Nonetheless, our data indicate that not only may the sampling method chosen by researchers have an impact on

whether or not diversity is reported to increase or decrease following disturbance, but the way in which data are subsequently analysed may affect whether these diversity changes are significant. Other published studies (Tittensor *et al.* 2007), support our theoretical explanation for how a decrease in the slope of SARs may be associated with a scale-dependent response of diversity to disturbance.

METHODOLOGICAL ISSUES

There are some caveats to our theoretical explanation. Importantly, Harte *et al.*'s (1999) bisection algorithm, which forms the basis of our algebraic model, is not universally accepted. For example, Maddux (2004) demonstrated that Harte *et al.*'s (1999) probability rule for producing power law SARs only works when certain types of 'well-shaped' rectangles are bisected. However, arguments used for equation 3 (species richness), although derived using the bisection method, do not rely on this method and the same result can be derived by considering the intersection of two continuous species area curves in log-log space. Thus, potential problems associated with the bisection method only affect equation 5 (diversity index). Nonetheless, Harte *et al.*'s (1999) bisection algorithm is one of very few robust methods with which to produce power function SARs that can be used to test further hypotheses. In addition, SARs derived from empirical data in this study were fitted to a power function and results were qualitatively the same regardless of whether sub-divisions of the study grids followed a rectangular bisection method or not (see Maddux 2004). Perhaps more importantly, changes in z -values following disturbance were similar regardless of how data were combined across study grids to construct SARs. Thus, we are confident that using Harte *et al.*'s (1999) bisection algorithm to produce power function SARs provides a robust method on which to test further hypotheses.

In this study, our theoretical model assumes that habitat disturbance reduces the slope of SARs (z -values). This assumption is supported empirically across a range of disturbance types and taxa (Cannon, Peart & Leighton 1998; Reilly, Wimberly & Newell 2006). Nonetheless, increases in z -values following disturbance may occur (Reilly *et al.* 2006). For example, habitat disturbance could increase z -values if the frequency and intensity of disturbance was such that it produced a mosaic of habitat types and thus increased habitat heterogeneity. In our study, incorporation into our algebraic model of increased z -values following habitat disturbance would produce results opposite to those presented. Thus, we would have reported decreased diversity following disturbance when measured at small spatial scales, but increased diversity when measured at larger spatial scales. Although this was not observed in our study, such effects may occur in other taxa (Hill & Hamer 2004) and deserve more study.

IMPACTS OF SPATIAL SCALE AND DISTURBANCE

Butterfly species richness and α diversity were positively related with spatial scale in both undisturbed and disturbed

habitats, although these relationships increased at a significantly faster rate in undisturbed forest compared with disturbed forest. β diversity was also positively correlated with increasing distance between samples in undisturbed forest but not in disturbed forest. In addition, measures of α diversity (Simpson's index) were spatially autocorrelated in undisturbed forest, but not in disturbed forest. As a consequence of these relationships between diversity and spatial scale, there was a significant decrease in butterfly α diversity following disturbance when measured at a large spatial scale but no significant change in diversity at a small spatial scale (Table 1). Thus, higher z -values in undisturbed forest were associated with higher β diversity and greater increases in α diversity with increasing distance in undisturbed forest, compared with disturbed forest.

These patterns of butterfly diversity were associated with changes in habitat structure following disturbance. Analysis of vegetation data showed that the variance of some variables was higher in undisturbed forest compared with disturbed forest, indicating a reduction in the structural heterogeneity of forests following disturbance. For example, undisturbed forest had significantly greater heterogeneity in canopy cover and tree size, which in turn is likely to affect the amount of light penetrating the forest, and thus the distribution of butterflies throughout the forest (Hill *et al.* 2001). In this study, the reduction in habitat heterogeneity following disturbance was associated with a reduction in the rate at which α and β diversity increased with distance between samples in disturbed habitats, and affected patterns of spatial autocorrelation. These diversity changes resulted in a reduction in the slope (z -value) of SARs in disturbed habitats (Drakare, Lennon & Hillebrand 2006), which our model showed was sufficient to result in scale-dependent estimates of diversity changes following disturbance. Thus, for butterflies, changes in habitat heterogeneity were associated with changes in α and β diversity, consistent with the observed reduction in z -value following disturbance, which in turn resulted in a scale-dependent response of diversity to disturbance in both our theoretical and empirical studies. Thus, understanding habitat heterogeneity and how it affects SAR z -values appears crucial to understanding responses of species to disturbance.

DIFFERENCES AMONG TAXA IN SCALE-DEPENDENCE

This study suggests that responses of butterflies to habitat disturbance are scale-dependent, but the role of spatial scale may differ among taxa. For example, the responses of birds to moderate tropical forest disturbance are scale-dependent, but bird studies at large spatial scales report increased diversity following disturbance and decreased diversity at small spatial scales, the opposite response to that for Lepidoptera (Hill & Hamer 2004). Part of the reason for this difference may be that birds are usually sampled over much larger spatial scales than Lepidoptera, and the higher dispersal ability of birds may result in them experiencing habitat structural characteristics differently from Lepidoptera, even when the spatial scale of studies are apparently similar (Loreau 2000; Hill &

Hamer 2004). Overall, conclusions from bird and Lepidoptera studies indicate that we might expect increased diversity following disturbance at both very small and very large spatial scales and decreased diversity following disturbance at intermediate spatial scales, although the precise values for spatial scale are likely to vary among taxa. The challenge now is to determine the conditions under which our algebraic model might support these conclusions; non-linear relationships between spatial scale and diversity might arise from non-linear relationships between z -values and spatial scale (Crawley & Harral 2001; but see Smith *et al.* 2005), and more empirical and theoretical studies clearly are needed.

SENSITIVITY OF RESPONSE TO SMALL CHANGES IN SARs

This study suggests that only very small changes in z -values from SARs following disturbance were sufficient to result in qualitatively different responses of diversity to disturbance at large and small spatial scales. This apparent sensitivity to very small changes in SARs and diversity-area relationships (Figs 2 and 3) highlights that no matter how minor the habitat disturbance, quantifying the effect of that disturbance on diversity is likely to be dependent on the spatial scale of analyses. A far broader ecological implication is that when comparing the diversity of any two communities, if there is even a minor difference in SARs between communities, then the estimated difference in diversity may be dependent on the spatial scale of sampling. Techniques that assess differences in community composition, rather than diversity, overcome these problems, but this does not mean that measures of diversity should be ignored, and such measures are likely to continue to be useful in highly diverse areas such as tropical forests.

Conclusions and applications

Results from this study demonstrate, both theoretically and empirically, the mechanisms that can produce a scale-dependent response of diversity to habitat disturbance. Changes in the slope of SARs reflect species responses to changes in the pattern and scale of habitat heterogeneity, which results in changes in the spatial patterns of α and β diversity. This study highlights the link between spatial scale and estimates of diversity change following habitat disturbance, and indicates that only a relatively small change in SARs and diversity-area relationships may be needed to produce a scale-dependent response of diversity to disturbance. This highlights a major problem with using diversity metrics to assess ecological impacts of disturbance. Thus, future studies may choose to assess changes in spatial patterns of diversity or sample over a range of spatial scales following disturbance rather than just evaluating changes in a single metric of diversity at a single spatial scale.

Acknowledgments

Field work was carried out at Danum Valley Field Centre and we thank all the staff, especially Glen Reynolds and Nasir Abdul Bin Majid, and our Malaysian collaborators Professor Dr Maryati and Dr Chey Yun Khen. We also thank

Yayasan Sabah (Forestry Division), the Danum Valley Management Committee, Sabah Chief Minister's Department, and the Economic Planning Unit of the Prime Ministers Department, Putra Jaya for granting permission to conduct research. We also thank Mark Williamson and an anonymous referee for comments that helped improve this paper. This paper is based on research carried out within the Royal Society's SE Asia Rainforest Research Programme, and was supported by NERC PhD (A.J.D.) and MRes studentships (E.J.C., G.A.F., T.E.R.).

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Received 15 January 2007; accepted 7 July 2008

Handling Editor: Andreas Erhardt