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The role of local-scale processes on terrestrial and deep-sea gastropod body size distributions across multiple scales

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ABSTRACT

Question: Does resource partitioning among body sizes at local spatial scales account for the distribution of body sizes at all spatial scales?

Hypothesis: Processes controlling regional or global patterns of species richness within size classes are scale-dependent, with regional or global patterns being influenced by macroevolutionary processes such as size-biased extinction/speciation and constraints on maximum/minimum size as opposed to local-scale interactions.

Organisms: 297 species of terrestrial and deep-sea gastropods.

Sampling sites: 838 terrestrial sites from 10 biogeographic provinces within a 2300 × 2800 km area in eastern North America, and 37 deep-sea sites from three biogeographic provinces at a depth of 196–5042 m in the western North Atlantic

Methods: Multiple parametric and non-parametric statistical tests were used to identify the presence of significant deviations between the distribution of individuals and taxa from site to regional scales in both systems.

Conclusions: The number of taxa does not always simply reflect the number of individuals across the body size spectrum with deviations becoming more prevalent with increasing spatial scale. Thus, local-scale interactions and resource partitioning alone are insufficient to explain patterns in body size at larger scales.

Keywords: biodiversity, body size spectrum, community structure, macroecology, mollusc, productivity, scale dependency.

INTRODUCTION

The key to estimating global biodiversity is identifying the body sizes that harbour the greatest wealth of species. Hutchinson and MacArthur (1959) predicted ‘a log-normal style distribution with few very small species, increasing rapidly to a modal size followed by a slow declining’, while May (1988) proposed that high species diversity might lie within the

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very smallest, undocumented organisms. Subsequent research repeatedly documents a right-skewed body size distribution (BSD) of species richness at larger spatial scales [e.g. regional, continental, and global (Kozlowski and Gawelczyk, 2002)], for faunas as diverse as nematodes (Kirchner *et al.*, 1980), insects (Siemann *et al.*, 1996), gastropods (Bouchet *et al.*, 2002), fish (Knouft, 2004), mammals (Brown and Nicoletto, 1991), and birds (Maurer and Brown, 1988). However, the richness BSD is often nearly uniform in local communities (Brown and Nicoletto, 1991; Loder *et al.*, 1997). A myriad of scale-dependent processes likely underlie these patterns, including niche partitioning (Hutchinson and MacArthur, 1959), environmental fractal dimension (Ritchie and Olff, 1999), size-biased extinction/speciation (Maurer *et al.*, 1992), trade-offs in energetic/life-history traits (Brown *et al.*, 1993), and constraints imposed by minimum size (Stanley, 1973).

Attention has also focused on the relationship between body size and abundance. However, these patterns tend to be more complicated as they represent four distinct but often confounded relationships (White *et al.*, 2007). At large spatial scales, the relationship between average body size and population density within a species (the size–density relationship, SDR) is a power law with a negative slope – that is, the smallest species possess the highest abundances (reviewed in White *et al.*, 2007). The slope of this relationship tends towards -0.75 (Blackburn and Gaston, 1997; White *et al.*, 2007), implying an invariance in energy use across body size, since metabolic rates scale at 0.75 with mass (Damuth, 1981). In contrast to their global counterparts, at local scales the SDR is either a weakly negative linear relationship or represented by a triangular constraint polygon (Blackburn and Gaston, 1996, 1997; White *et al.*, 2007). Another related but distinct relationship is the frequency distribution of individuals among size classes (abundance BSD or size spectrum), which has been analysed most often in aquatic and marine systems (Kerr and Dickie, 2001). While generally demonstrating a negative power-law relationship between abundance and body size, these relationships are often multi-modal with prominent peaks corresponding to trophic groups (Kerr and Dickie, 2001). Although the variation in these distributions across spatial scale is less documented as compared with SDRs, previous studies suggest that the abundance BSD may go from log-linear at larger spatial scales to unimodal or uniform within local communities (Kerr and Dickie, 2001; McClain, 2004).

The comparison of the richness and abundance BSD is of particular ecological interest as it helps inform about species-independent resource partitioning between body size classes (White *et al.*, 2007) and species-specific resource partitioning with a given body size (Siemann *et al.*, 1996, 1999). In particular, the documentation of statistically similar, or *coupled*, abundance and richness distributions at a given scale suggests that richness is a simple function ultimately of small-scale energetic constraints, as is suggested by the More Individuals Hypothesis (Srivastava and Lawton, 1998; Hurlbert, 2004), which posits that richness is greatest when the number of individuals and the availability of resources peaks. The most abundant and rich animal body sizes classes within a community or landscape may thus reflect the modal size distribution of potential food resources [multimodal distribution (Holling, 1992; Ernest, 2005)].

The relationship between the numbers of individuals and species within size classes also provides important information about resource partitioning. At one extreme, a few species may control resources leading to a size class consisting of a few abundant and many rare species characterized by geometric and or log-series type models (Sugihara, 1980; Magurrann, 1988). However, more equitable resource divisions will lead to abundances characteristic of broken stick, truncated log-normal, or zero-sum multinomial distributions (MacArthur, 1957; Siemann *et al.*, 1996, 1999; Hubbell, 2001; Fa and Fa, 2002; McClain, 2004; Etienne and Olff, 2004b). Although evidence is mixed whether energy use is equal across body sizes – the energetic equivalence rule of

Damuth (1981) – and the degree to which this process explains the richness BSD (Blackburn *et al.*, 1993; Blackburn and Lawton, 1994; Russo *et al.*, 2003; Ernest, 2005), a consistent pattern of coupling between the abundance and richness BSD is emerging in groups as disparate as terrestrial arthropods and marine gastropods (Siemann *et al.*, 1996, 1999; Fa and Fa, 2002; McClain, 2004).

It is unknown, however, how important local-scale processes are in determining richness across size classes at higher spatial scales (Hutchinson and MacArthur, 1959; Kozlowski and Gawelczyk, 2002), especially given the lack of scale independence for many ecological processes (Levin, 1992; Blackburn and Gaston, 2002; Denny *et al.*, 2004). Despite this, Siemann *et al.* (1996) suggested that local-scale coupling between the richness and abundance BSD could be used to predict the sizes classes harbouring the greatest global biodiversity, and Finlay *et al.* (2006) suggested that BSDs were self-similar from site to global scales. However, given that regional or global richness BSDs may be affected by large-scale macro-evolutionary processes such as size-biased extinction/speciation and constraints on maximum/minimum size (Kozlowski and Gawelczyk, 2002), the validity of these predictions remains unclear.

In this paper, we address the issues of whether the statistical coupling of abundance and richness BSDs is scale invariant, and thus examine the extent to which large-scale body size distributions are dependent on local resource partitioning. We address this issue by considering a single taxonomic class (Gastropoda) both within and across multiple spatial scales (sites, provinces, and total regions) from two highly divergent biological communities (terrestrial and deep-sea soft substrates). Potential phylogenetic confounders, typical in many cross-system comparisons, are thus minimized by limiting observations to a single taxonomic class. The identification of potential general biosphere-wide trends is aided by comparing patterns between two of Earth's most disparate environments in terms of both abiotic and biotic factors. For instance, whereas deep-sea gastropods live in an extremely food-limited environment with little organic input (McClain *et al.*, 2006), terrestrial gastropods live in almost pure organic detritus in the upper 5 cm of the soil horizon (Hawkins *et al.*, 1998).

METHODS

Sampling

Terrestrial shelled gastropods were analysed within ten geographic regions located in a 2300 × 2800 km area in east-central North America (Fig. 1a). A total of 838 sites were surveyed, from which 216 taxa were encountered, or approximately 40% of the eastern North American fauna (Hubricht, 1985). At each site, faunas were documented within representative 100–1000 m^2 areas via litter collections at places of high mollusc density (Emberton *et al.*, 1996). A constant volume (~4 litres) of litter was gathered from each site. Soil litter sampling was used as it provides the most complete assessment of site faunas (Oggier *et al.*, 1998; Cameron and Pokryszko, 2005). Additional details about collection methods, localities, and species biology can be found in Nekola (1999b, 2002, 2003, 2005).

Deep-sea gastropods from the western North Atlantic Ocean were analysed along a ~1000 km transect from Gay Head, Martha's Vineyard to Bermuda (Fig. 1b). All samples are part of the Woods Hole Oceanographic Institution's Benthic Sampling Program, and include soft-bottom benthic continental slope, rise, and abyss habitats from a depth of 196–5042 m (Sanders, 1977). A total of 81 taxa are known from the 37 sampling stations. Documentation of deep-sea gastropod faunas from each station was conducted using either

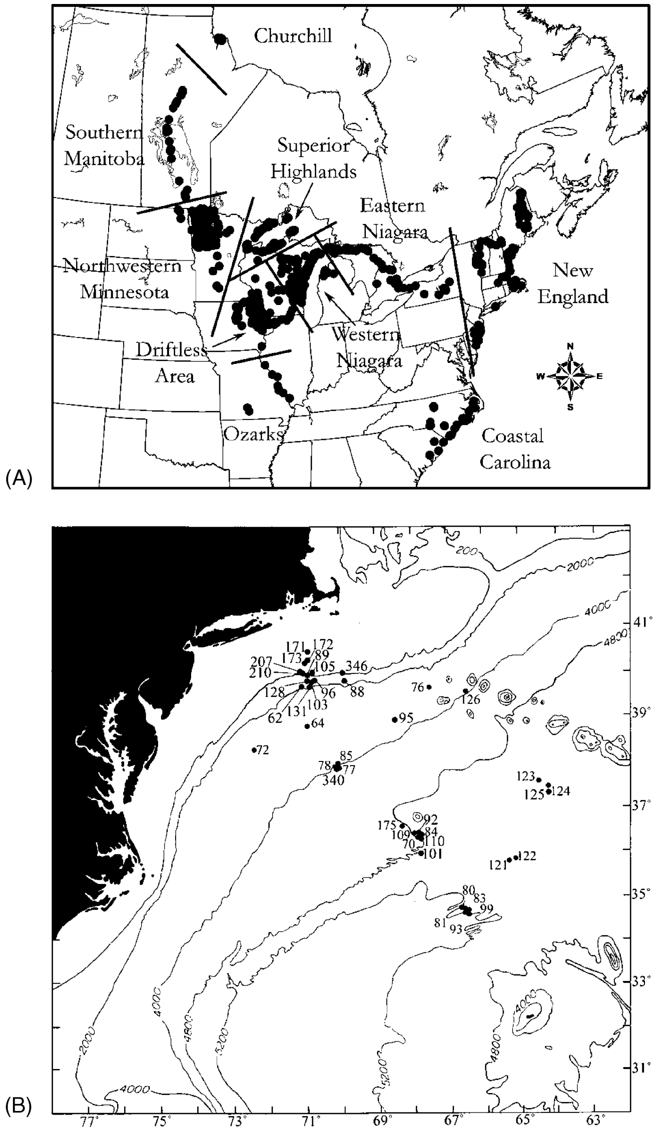

Fig. 1. (A) Location of terrestrial gastropod sample sites and metacommunities. (B) Location of deep-sea gastropod sample sites and depth contours.

epibenthic sleds (Hessler and Sanders, 1967) or anchor dredges (Sanders *et al.*, 1965). Additional details, including station maps and species biology, can be found in McClain (2004), McClain *et al.* (2005), and McClain and Crouse (2006).

In the laboratory, samples were washed through a standard sieve series, with all shells larger than 0.425 mm for terrestrial, and 0.25 mm for marine, being retained. All shells and shell fragments were removed, with all identifiable shells being assigned to species.

Estimation of body size

Approximate biovolume for adult shells was estimated from median reported species width and height (Pilsbry, 1948; McClain, 2004; McClain *et al.*, 2005; McClain and Crouse, 2006; J. C. Nekola, unpublished data). Although biovolume estimates based on shell height and width provide robust results independent of how volume is estimated (Powell and Stanton, 1985), we use two different equations given basic shell architecture differences between terrestrial and deep-sea taxa. For terrestrial gastropods, shell biovolume was calculated as a cone resting on top of a cylinder, with volume estimated using the formula:

$$V_t = (\pi r^2(1-t)h) + \left[\frac{\pi r^2 th}{3}\right], \tag{1}$$

where V_t = terrestrial shell biovolume, r = shell radius, h = shell height, and t = proportion of shell height made up of conic section, as determined through visual inspection of reference material and published illustrations.

For marine gastropods, shell biovolume was calculated as stacked cones, with volume estimated using the formula:

$$V_m = 2\left[\frac{\pi r^2(h/2)}{3}\right], \tag{2}$$

where V_m = marine shell biovolume. Note if the cones are the same radius and height, this formula simplifies to the volume of a single cone with radius r and height h. Each biovolume was $\log_2$ transformed. Each individual within a species was assigned its species-specific median biovolume.

Statistical analyses

For this paper, we define ‘decoupling’ as the lack of significant statistical correspondence between abundance and richness BSDs. To allow for robust identification of decoupling, we subjected each data set to three different tests: Kolmogorov-Smirnov test (KS), log-linear modelling (LLM), and ordinary least squares plus reduced major axis (OLS/RMA) regressions. Because of differences in these tests, discussed below, their results should be seen as complementary but not comparable. Evidence for decoupling was sought within three scales: local (individual sites, dredges, or trawls), province (summation of sites, dredges, or trawls within a given biogeographic area), and regional (summation of provinces). Biogeographic provinces were based on well-documented boundaries based on our previous and prior published works (Rex, 1977; Gage and Tyler, 1991; Nekola, 1999a, 1999b, 2002, 2003, 2005; Nekola and Smith, 1999; McClain, 2004, 2005; McClain and Etter, 2004; McClain *et al.*, 2004, 2005, 2006). Some tests were not conducted at a given scale because of a lack of statistical power, including OLS/RMA regressions for local scales. To allow for conservative estimates of decoupling rates, significance thresholds were modified using a Bonferroni correction. For the terrestrial data, graphical output was limited to five provinces representing an approximately linear latitudinal transect running from the Ozark Plateau to the southern shore of Hudson Bay.

In the first analysis, the cumulative distributions of unbinned taxa and individuals were calculated over increasing body size for both the total and province data sets.

A KS test was used to identify lack of correspondence between these distributions. As 15 tests were conducted, the significance threshold was modified to $\alpha = 0.0033$. Although the frequencies expressed in the richness and abundance distribution will always diverge to some degree because of differences in the denominators used to generate cumulative frequency, this artificial discrepancy is 5–18 times smaller in these data than the actual critical values of the KS test and are thus not a concern in these analyses. While the KS test allows for comparison of distributions without introducing artificial data bins, it is important to note that deviations are calculated along a rank order of body size. As such, when biovolumes are distributed unequally throughout the total body size spectrum, it may not provide the same results as LLM tests.

For the second analysis, distributions were binned into 34 $\log_2$ volume classes with bin centres starting at −2 and increasing by 0.5 $\log_2$ units to 14.5. The first bin value thus ranged from −2.25 to −1.75 (0.21 to 0.30 mm^3) and the last bin from 14.25 to 14.75 (19,500 to 27,000 mm^3). The numbers of species and individuals were tabulated within each $\log_2$ volume bin. As 950 total tests were conducted, the significance threshold was modified to $\alpha = 0.0000526$. Log-linear modelling was used to determine the significance of correspondence between these frequencies as the number of taxa was sparse (<5) in more than one-fifth of cells. Whereas a Pearson chi-square statistic is inappropriate in such instances, LLM tests will provide accurate results when the total numbers of observations are at least 10 times the number of cells (Haberman, 1972; Fienberg, 1980; Lunneberg and Abbot, 1983; Zar, 1984). All of our data sets easily meet this criterion (680 observations in the case when all size classes are occupied). While LLM retains the actual distribution of body sizes in its analysis, results are dependent upon the nature of binning. We obtained essentially identical results via both half $\log_2$ bins and full $\log_2$ bins, so are confident that our interpretations are robust to this factor.

Third, OLS/RMA regressions were applied to scatterplots of $\log_2$ richness versus $\log_2$ abundance per $\log_2$ volume bin for both the total and province data sets. In this test, decoupling was indicated when both variables were not significantly correlated. As 15 tests were conducted, the significance threshold was modified to $\alpha = 0.0033$. The use of RMA over OLS has been justified in previous studies because random variation in the independent variable (abundance) is likely to be equal to or more than the variance in the dependent variable (richness) (Sokal and Rohlf, 1995). We include both due to the ease of implementation and familiarity of OLS tests. A potential complication of OLS/RMA regression is that variance and degrees of freedom are minimized both from data binning and the double log transformation of bin counts. Other potential issues with OLS/RMA analyses will be outlined in the Discussion.

The null expectation of coupling due simply to the random draw of individuals from the entire pool was documented via a simple MATLAB script. For each size class, we drew m random individuals, corresponding to the empirical number of individuals observed for that size class from the total pool for a locality, province, or region. The total number of species, S, was then calculated from the randomized sample. One thousand permutations were conducted for each size class and a mean S with 95% confidence intervals calculated.

RESULTS

Within-scale comparisons

Regional

For terrestrial gastropods, cumulative distributions of abundance and richness differed greatly, with small individuals accumulating at almost twice the rate as taxa up to ~2 mm^3 ($\log_2 = 0$; Fig. 2). At volumes exceeding 64 mm^3 ($\log_2 = 6$), taxa accumulated more rapidly than individuals. The KS test demonstrated that these distributions were highly decoupled ($P < 0.000001$; Table 1). Abundance and richness across size bins were also found not to correspond (Fig. 2) with modal abundance occurring one $\log_2$ size class before modal richness. Richness largely tracked abundance from 2 to 90 mm^3 (bins 0–6.5), but at larger sizes richness greatly exceeded that expected from abundance alone. Log-linear modelling showed these differences to be highly significant ($P < 0.000001$). While these two analyses strongly imply that abundance and richness are decoupled, OLS/RMA regressions exhibit a significant correlation between $\log_2$-transformed bin values ($r^2 = 0.65$; $P < 0.0001$). Neither the OLS or RMA slopes follow the predicted 0.50 slope of the broken-stick model and only the OLS slope encompasses the predicted 0.25 slope of the canonical log-normal distribution.

For deep-sea gastropods, cumulative distributions of abundance and richness also differed greatly (Fig. 2). While abundance and richness generally corresponded up to ~8 mm^3 ($\log_2 = 3$), individuals accumulated more rapidly around 23 mm^3 ($\log_2 = 4.5$). At larger biovolumes, taxa tended to accumulate more rapidly than individuals. The KS test demonstrated that these distributions were highly divergent ($P = 0.000012$). Binned abundance and richness were also found not to correspond, again with modal abundance occurring one $\log_2$ size class before modal richness. However, abundance and richness largely tracked from biovolumes exceeding 32 mm^3. Log-linear modelling showed these differences to be highly significant ($P < 0.000001$). As for the terrestrial data, OLS/RMA regressions demonstrated a significant correlation between log-transformed binned abundance and richness data ($r^2 = 0.66$; $P < 0.0001$), with only the OLS slope encompassing those predicted by either model.

Province

For terrestrial gastropods, the KS test demonstrated four provinces exhibiting highly significant ($P \leq 0.000081$) differences in their cumulative distributions of individuals and taxa across the body size spectrum (Table 1). For these, decoupling was similar with an excess of small individuals and an excess of large taxa being observed (Fig. 3). The most northern provinces, however, showed no significant differences (e.g. Churchill, $P = 0.86$; Lake Superior Highlands, $P = 0.60$; Southern Manitoba, $P = 0.23$). Log-linear modelling demonstrated similar patterns: the two most northerly regions had coupled abundance and richness frequencies, whereas the remaining eight did not ($P \leq 0.00037$; Table 1). As before, significant decoupling was related to an excess of small (< 1 mm^3; $\log_2 = 0$) individuals and an excess of large (> 32 mm^3; $\log_2 = 5$) taxa (Fig. 3). The OLS/RMA regressions of binned abundance and richness data again largely provided conflicting results. Northern provinces demonstrated no significant ($P \geq 0.013$) correlations between log-transformed binned abundance and richness data (Table 1). Southern provinces, however, generally showed

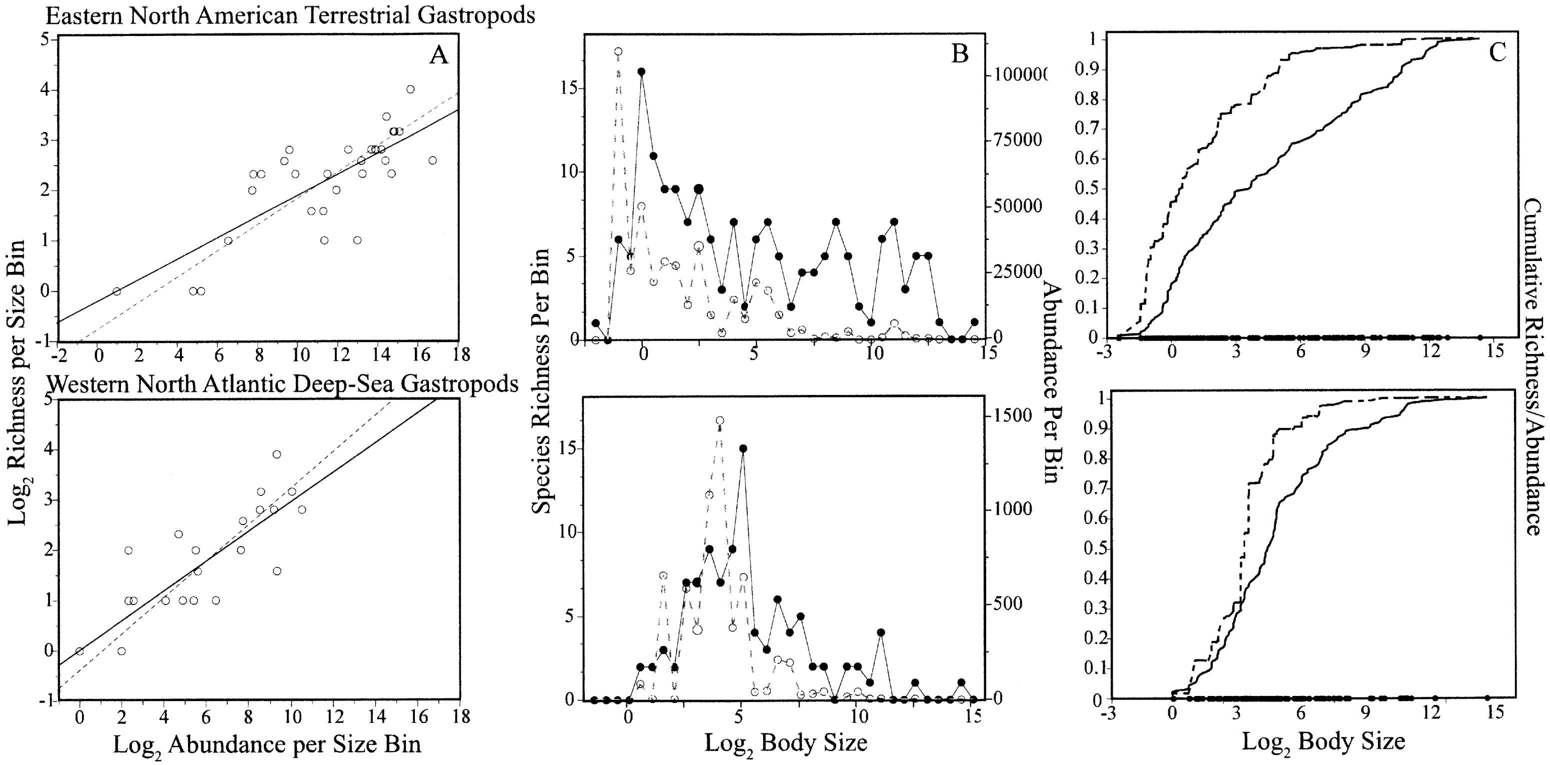

Fig. 2. Decoupling of richness and abundance for total terrestrial and deep-sea data sets, including: (A) scatterplots of log$_2$(abundance) vs. log$_2$(richness) for log$_2$ bins across the body size spectrum, with best-fit linear models for OLS (solid line) and RMA (dashed line) regressions; (B) frequency histograms of abundance (dashed lines) and richness (solid lines) within log$_2$ bins across the body size spectrum; and (C) cumulative frequency distributions of abundance (dashed lines) and taxa (solid lines) across the body size spectrum, with location of adult body sizes noted along the x-axis.

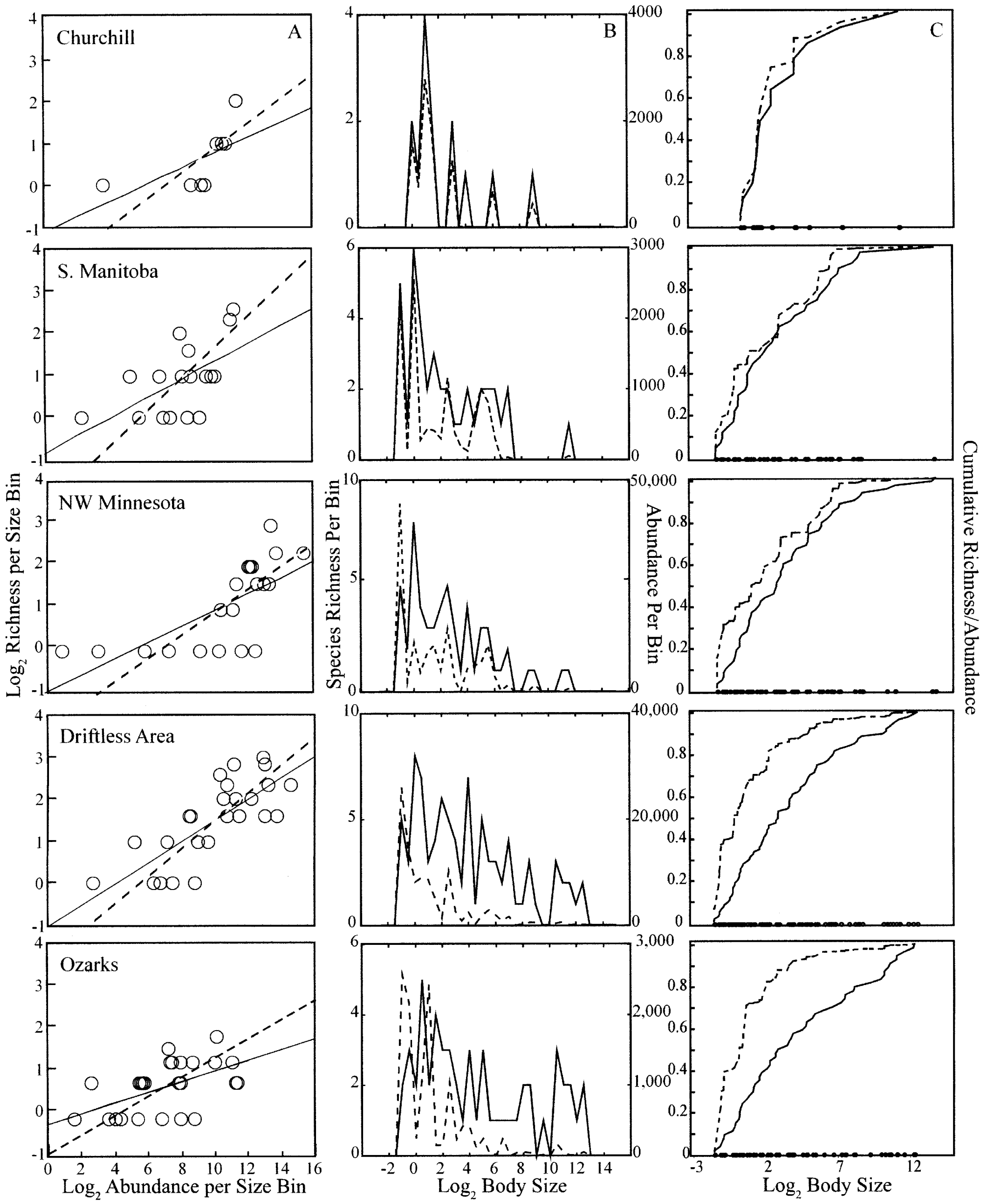

Fig. 3. Decoupling of richness and abundance for five latitudinally stratified terrestrial province data sets, including: (A) scatterplots of $\log_2$(abundance) vs. $\log_2$(richness) for $\log_2$ bins across the body size spectrum, with best-fit linear models for OLS (solid line) and RMA (dashed line) regressions; (B) frequency histograms of abundance (dashed lines) and richness (solid lines) within $\log_2$ bins across the body size spectrum; and (C) cumulative frequency distributions of abundance (dashed lines) and taxa (solid lines) across the body size spectrum, with location of adult body sizes noted along the x-axis. Graphical output was limited to five provinces representing an approximately linear latitudinal transect running from the Ozark Plateau to the southern shore of Hudson Bay.

Table 1. Within-scale decoupling of richness vs. abundance along the body size spectrum for modelling (LLM) indicates that the abundance and richness BSD are decoupled, while in contrast a

	Numbers				Within-scale decoupling of R & I			
	Non-zero bins	Species	Ind.	Sites	KS statistic	KS *P*-value	LLM χ^2	LLM *P*-value
Terrestrial								
Total	31	167	423,322	898	0.34	**<0.000001**	289.58	**<0.000001**
Churchill	8	14	9302	23	0.21	0.862200	6.60	0.472200
S. Manitoba	18	40	11,011	24	0.23	0.230700	31.67	0.016500
Superior Highlands	21	44	5023	82	0.16	0.595300	58.53	**0.000037**
NW Minnesota	21	57	142,172	192	0.23	0.088000	55.31	**0.000012**
E. Niagara	28	79	24,186	69	0.22	0.043900	92.80	**<0.000001**
W. Niagara	26	83	78,087	231	0.27	0.004200	89.81	**<0.000001**
New England	26	67	19,190	121	0.37	**0.000081**	98.99	**<0.000001**
Driftless Area	26	88	100,095	107	0.38	**0.000001**	117.10	**<0.000001**
Ozarks	26	54	12,060	11	0.46	**0.000010**	105.47	**<0.000001**
Carolina Coast	26	62	9297	38	0.41	**0.000081**	112.84	**<0.000001**
Deep Sea								
Total	23	100	6007	37	0.34	**0.000012**	119.40	**<0.000001**
Slope	17	49	4000	8	0.27	0.052000	96.62	**<0.000001**
Rise	22	56	834	11	0.21	0.133000	58.13	**0.000024**
Abyss	15	22	1173	18	0.73	**0.000006**	83.67	**<0.000001**

significant correlations ($P \leq 0.0022$), suggesting coupling between abundance and richness. None of the RMA regression slopes conformed to the predicted slopes of either the canonical or broken-stick model, while all the OLS slopes were indistinguishable from the predicted 0.25 for the canonical distribution.

For deep-sea gastropods, the KS test demonstrated significant decoupling between cumulative abundance and richness distributions only in the abyss ($P < 0.000006$; Table 1). This effect was largely due to an excess of individuals in the 8 mm^3 ($\log_2 = 3$) volume and an excess of taxa at volumes >16 mm^3 ($\log_2 = 4$, Fig. 4). Log-linear modelling demonstrated significant (maximum $P \leq 0.000024$) decoupling in all three provinces (Table 1), with an excess of individuals being noted around volumes of 8 mm^3 ($\log_2 = 3$) and an excess of taxa being noted at body sizes exceeding 32 mm^3 ($\log_2 = 5$). Again, OLS/RMA regressions of binned abundance and richness data largely provided conflicting results, with significant correlations (maximum $P \leq 0.0016$) being noted in the slope and rise (Table 1) but all OLS slopes were near the predicted 0.25 from the canonical distribution.

Sites

For terrestrial gastropods, only 71 (7.9%) sites demonstrated significant decoupling of binned abundance and richness data using LLM. Site decoupling rates were highest in the southern Western Niagara escarpment (11.3%), Driftless Area (15.7%), and Ozarks (27.3%). Conversely, site decoupling rates were lowest (0%) in Churchill and Southern Manitoba. For deep-sea gastropods, only 3 (8.1%) sites demonstrated significant terrestrial and deep-sea gastropods. Significant for Kolmogorov-Smirnov (KS) statistic and log-linear significant result for the linear regressions indicates the two distributions are coupled

Site decoupling of R & I		OLS regression				RMA	
Number (%) $P < 0.05$	Number (%) $P < 5.26 \times 10^{-5}$	Slope (95% CL)	Intercept	r^2	P-value	Slope (95% CL)	Intercept
355 (39.5)	71 (7.9)	**0.21 (0.15–0.27)**	**−0.21**	**0.65**	**<0.0001**	**0.26 (0.26–0.26)**	**0.77**
7 (30.4)	0 (0)	0.18 (0.00–0.37)	−1.09	0.39	0.0998	0.30 (0.29–0.31)	−2.13
5 (20.8)	0 (0)	0.21 (0.06–0.36)	−0.83	0.33	0.0130	0.37 (0.37–0.38)	−2.14
5 (6.1)	2 (2.4)	**0.19 (0.08–0.29)**	**−0.32**	**0.40**	**0.0022**	**0.29 (0.29–0.30)**	**−0.99**
71 (37.0)	9 (4.7)	**0.19 (0.10–0.28)**	**−0.96**	**0.49**	**0.0004**	**0.27 (0.27–0.28)**	**−1.85**
29 (42.0)	2 (2.9)	**0.24 (0.16–0.31)**	**−0.64**	**0.58**	**<0.0001**	**0.31 (0.31–0.31)**	**−1.22**
97 (42.0)	26 (11.3)	**0.25 (0.16–0.35)**	**−1.11**	**0.53**	**<0.0001**	**0.35 (0.35–0.35)**	**−2.08**
37 (34.6)	8 (7.5)	**0.21 (0.13–0.29)**	**−0.53**	**0.29**	**<0.0001**	**0.29 (0.29–0.29)**	**−1.16**
80 (66.1)	19 (15.7)	**0.22 (0.14–0.31)**	**−1.03**	**0.58**	**<0.0001**	**0.33 (0.33–0.33)**	**−1.82**
6 (54.5)	2 (27.3)	0.23(0.15–0.30)	−0.16	0.30	0.0039	0.29 (0.29–0.29)	−1.03
18 (31.6)	2 (5.3)	**0.15 (0.06–0.24)**	**−0.32**	**0.60**	**<0.0001**	**0.28 (0.27–0.28)**	**−0.74**
16 (43.2)	3 (8.1)	**0.29 (0.20–0.38)**	**0.01**	**0.66**	**<0.0001**	**0.36 (0.36–0.36)**	**0.37**
6 (75.0)	1 (16.7)	**0.19 (0.09–0.28)**	**0.28**	**0.50**	**0.0016**	**0.26 (0.26–0.27)**	**−0.10**
3 (27.3)	2 (18.2)	**0.27 (0.15–0.40)**	**0.07**	**0.49**	**0.0003**	**0.39 (0.38–0.40)**	**−0.39**
6 (39.9)	0 (0.0)	0.04 (−0.09 to 0.17)	0.26	0.03	0.5414	0.24 (0.22–0.27)	−0.41

decoupling of binned abundance and richness data. Site decoupling rates were highest in the slope (16.7%) and rise (18.2%), while no abyss sites demonstrated significant decoupling.

Null model

In both data sets at the regional and provincial levels, the three richest size bins possessed significantly more species, using a 95% confidence interval, than could be accounted for solely from the number of individuals. For example, in the regional data sets the 5th (16 species) and 14th (15 species) size bins possess the most species for the terrestrial and deep-sea data sets respectively, exceeding the upper 95% confidence bound of 14.32 and 13.29. Additionally, all of the largest size bins possessed more species than the predicted null average for these bins. Site richness BSDs were indistinguishable from the null predictions.

DISCUSSION

Despite the extreme disparity in habitat and related selection pressures experienced by terrestrial and deep-sea gastropods, analyses of both assemblages reject the hypothesis that local-scale resource partitioning among sizes classes is sufficient to explain richness BSDs across all spatial scales. Over 90% of sites in both systems exhibit coupling between the richness and abundance BSD, supporting the contention that energy utilization helps set

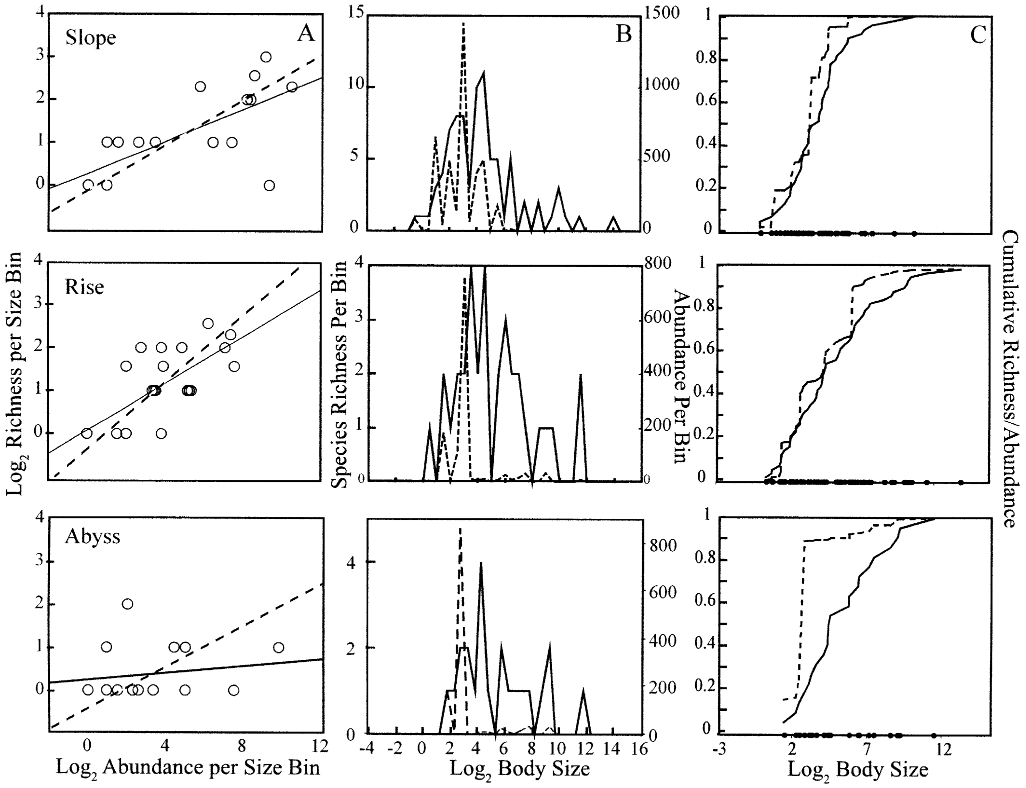

Fig. 4. Decoupling of richness and abundance for all deep-sea province data sets, including: (A) scatterplots of log$_2$(abundance) vs. log$_2$(richness) for log$_2$ bins across the body size spectrum, with best-fit linear models for OLS (solid line) and RMA (dashed line) regressions; (B) frequency histograms of abundance (dashed lines) and richness (solid lines) within log$_2$ bins across the body size spectrum; and (C) cumulative frequency distributions of abundance (dashed lines) and taxa (solid lines) across the body size spectrum, with location of adult body sizes noted along the x-axis.

interspecific size distributions within communities (Holling, 1992; Marquet *et al.*, 1995). This result is consistent with previous small-scale studies on inverterbrates (Siemann *et al.*, 1996, 1999; Fa and Fa, 2002; McClain, 2004) but contrasts with those for small mammals (Ernest, 2005). However, among biogeographic provinces coupling between the richness and abundance BSD becomes less prevalent and is non-existent at regional levels. At these larger scales, not only does modal abundance typically occur at half the biovolume as modal richness, but often the most abundant size class is not even the second or third richest (Figs. 2–4). Our data also support the existence of scale dependence in richness and abundance BSDs (for all between-scale comparisons, LLM: $P < 0.00001$) as noted by previous studies (Brown and Nicoletto, 1991; Blackburn and Gaston, 1997; White *et al.*, 2007). These results caution against general application of the conclusions of Finlay *et al.* (2006), who implied that site-scale BSDs can accurately be extrapolated to the entire globe. Rather, interactions between scale-dependent mechanisms are likely at play, with regional or global richness BSDs potentially reflecting macro-evolutionary mechanisms such as size-biased extinction/speciation and constraints on maximum/minimum size (Kozlowski and Gawelczyk, 2002).

In spite of the fact that the total energy available to deep-sea and terrestrial gastropods represent the two extremes of the productivity spectrum (Hawkins *et al.*, 1998; McClain *et al.*, 2006), patterns of richness and abundance BSD coupling at local scales are very similar in both systems (92.1% and 91.9% respectively; Table 1). It is interesting to note that the prevalence of both site/province scale richness–abundance BSD coupling appears slightly greater with lower productivity (e.g. with increasing terrestrial latitude and sea floor depth). This pattern is almost certainly driven by multiple factors, however, including the greater simplicity of regional species pools across these same gradients and the younger age of more northern terrestrial communities. As a result, time may not have been sufficient to allow size-specific extinction and speciation to generate abundance–richness BSD decoupling. Such patterns are not without precedent, as Knouft (2004) also documents latitudinal variation in the richness BSD for freshwater fish.

The stark contrast in the distribution of richness and abundance across the body size spectrum at regional and provincial scales implies differing pressures on these macroecological phenomena. While speculative and based primarily upon extrapolation from terrestrial vertebrate research, we believe that hypotheses regarding these drivers can be cautiously advanced to help promote future research. The internal abundance mode in both systems suggests that fitness decreases with extreme miniaturization. Such costs may be related to a loss of organ systems and/or reductions in the size of the neural system, which could hamper retrieval and processing of environmental stimuli and limit homeostasis ability (Hanken and Wake, 1993). The shifting of the richness mode to the right of the abundance mode indicates that these costs may extend to larger body sizes in relation to speciation. Small taxa are known to possess a reduced number of morphological and/or anatomical options, a reduction in the total DNA available for modification (Hanken and Wake, 1993), and increased population sizes (Fenchel and Finlay, 2004). While controversial, Kimura (1983) suggested that these factors can lead to substantial genetic inertia, decreased molecular diversity, and lower rates of population divergence. At biovolumes larger than the mode, both abundance and richness decrease. Numerous selection pressures may exist against larger organisms, including: increased mortality due to predation, starvation, and parasitism due to long development times; reduced agility combined with increased detectability; and higher energy requirements (Blanckenhorn, 2000). This reduction in richness and abundance of larger sizes may be due to an increase in home-range demands, decrease in population size, and increase in extinction probabilities with increasing body size (Brown and Nicoletto, 1991; Maurer *et al.*, 1992; Gaston and Blackburn, 1996a, 1996b, 1996c). The more rapid reduction in abundance may be related to greater morphological flexibility combined with smaller and potentially more isolated populations allowing for elevated speciation rates. Higher rates of allopatric speciation and competitive co-equivalency may also be expected due to increased dispersal limitation with increasing body size for passively dispersing species such as gastropods (Etienne and Olff, 2004a). This process is particularly evident in the southwestern USA, where gastropod taxa less than 5 mm in maximum dimension tend to be wide-ranging, while those greater than 10 mm tend to be single mountain endemics (Metcalf and Smartt, 1997).

Before concluding this discussion, potential methodological and sampling artifacts must also be considered. Perhaps the most important of these is the profound lack of correspondence between the OLS/RMA regressions and the KS/LLM analyses. This is most likely due to the double log-transformation of binned data in OLS/RMA, which greatly increases artificiality and decreases observed variance and available degrees of freedom, all of which will potentially obscure pattern. It is also important to remember that the existence of a significant correlation between mean abundance and richness does not necessarily indicate that all size classes are coupled. The central tendency in our data for intermediate size classes to have linked abundance and richness values cannot negate the fact that decoupling is frequent at the smallest and largest body sizes, encompassing both modal classes and over 30% of all individuals and species. Additionally, the utility of regression-type tests for these data must be questioned, as richness and abundance are not independent, given that fewer taxa are possible when the number of individuals is low. The OLS/RMA regression models are thus forced through the origin (zero individuals and zero species) and $x = 1$, $y = 1$ (one individual and one species), generating an initial slope of one irrespective of any other data. It is thus almost impossible for the OLS/RMA approach not to identify positive correlation across the body size spectrum, with the significance of this correlation being typically related to sample size or the number of occupied bins. Despite this bias towards positive correlations, we found OLS/RMA regressions to describe a relatively small proportion (often less than 50%) of doubly-log-transformed variance. As a result of these issues, we have chosen not to interpret the OLS/RMA results, even though this approach has been the only one used in previous analyses of abundance and richness across the body size spectrum (Siemann *et al.*, 1996, 1999; Fa and Fa, 2002; McClain, 2004).

For both KS and LLM, coupling may emerge from a lack of statistical power, undersampling or under certain null expectations. Given that our large-scale analyses span 10^5 individuals, 10^2 species, and 34 body size bins, the power should be sufficient to identify statistically significant decoupling. However, this issue could underlie the higher rates of coupling noted at the site scale, as these data were often limited to 10^2 individuals, 10^1 species, and perhaps only 5–10 body size bins. We are confident that power was sufficient for the LLM to correctly fail to reject the null hypothesis of correspondence between richness and abundance at this scale, given that almost all sites possessed at least 10 times the number of observations as cells. The power of the site-scale analysis was also increased by considering only the consensus result across all ~900 sites. In addition, these data clearly demonstrate that the right-skewed richness BSD is not due to undersampling of the smallest size classes as posited by Lawton (1990) and Currie (1993). Both sampling regimes utilized sieve mesh sizes well below that of the smallest known gastropods, including the terrestrial *Carychium nannodes* (Nekola, 2005) and the deep-sea *Palazzia planorbis* (Rex, 2002), both of which are included in these analyses. Additionally, in both data sets abundance peaks at a size class larger than the smallest sieve dimensions, with richness peaking at double the biovolume of modal abundance. Lastly, while it has been suggested that coupling may relate to joint constraints placed on richness and abundance by non-uniform resource distribution along the body size spectrum (Holling, 1992; Marquet *et al.*, 1995), teasing apart the exact mechanism may prove difficult given a null expectation that few species will be present as the number of encountered individuals falls (Sanders, 1968; Hurlbert, 1971; Simberloff, 1972; Palmer *et al.*, 2000). The lack of coupling at larger scales seems to argue against the rarefaction null and a simple model demonstrates that the richest size classes have far more species than expected from random draws of individuals.

These analyses indicate that within two of the most disparate environments on Earth, a general tendency exists for scale-dependent decoupling between richness and abundance across the body size spectrum. At local scales, resource partitioning among size classes may account for the fact that certain body size classes are more speciose. However, these local-scale processes cannot explain the shape of provincial and regional richness BSDs.

At larger spatial scales, macro-evolutionary processes such as size-biased extinction and speciation combined with physiological, morphological, and life-history constraints on body size may dictate the distribution of species among size classes. Thus, accurate interpolation of body size patterns between scales may be impossible. A clear need exists for further investigation of these patterns in other taxa, and for identification of the precise mechanisms underlying these phenomena.

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