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North American terrestrial gastropods through each end of a spyglass

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ABSTRACT

Some suggest that because of scale independence major biodiversity metrics can be estimated at large scales from analysis of a well chosen suite of individual sites. Others have attempted to estimate individual site patterns from analysis of the continental pool. But does such cross-scale extrapolation work? This issue is addressed for the North American terrestrial gastropod fauna by comparison of family representation, species richness and body-size patterns across site to continental scales. These data demonstrate profound differences: while the continental fauna is dominated by large body-size families such as the Polygyridae, Helminthoglyptidae, Oreohelicidae, Succineidae and Urocoptidae, average site faunas are most frequently represented by small body-sized families like the Vertiginidae, Gastrodontidae, Oxychilidae, Euconulidae, Punctidae, Valloniidae, Strobilopsidae and Ellobiidae. Species richness within sites tends to be 2–7 times smaller than random draws of individuals of the same number from regional or continental pools, indicating the potential for strong bias in the construction of site faunas. And, while the body-size spectrum for average site faunas is strongly right-skewed, the continental pool is strongly left-skewed. Thus, although taxa with biovolumes >16 mm^3 dominate the continental fauna (79.4% of total), they make up only a small average fraction (4.1%) of individual site species lists. Within most regions, site faunas are overrepresented in species with biovolumes <4 mm^3 and underrepresented in species with biovolumes >128 mm^3 as compared with the regional pool. As a result, assumptions of self-similarity between observational scales in terrestrial gastropods are inappropriate.

INTRODUCTION

The search for universal patterns and simplifying assumptions is common practice among natural scientists, especially those working in complex systems such as biology. One common form taken by this search is the identification of patterns that are scale-independent, i.e. patterns that remain largely similar across all observational scales. Such relationships are often referred to as expressing ‘self-similarity’, in which large scale datasets are made up of smaller scale components possessing the same basic properties. In the realm of fractal geometry, for instance, self-similarity across multiple scales has been noted in crystals (Mandelbrot, 1983), clouds (Hentschel & Procaccia, 1984), fluids (Nittman, Daccord & Stanley, 1985) and water drainage networks (Milne, 1988). This assumption also underlies most common algorithms generating fractal artwork, lending aesthetic regularity to the generated images.

However, the assumption of self-similarity has been found to be less useful in biological systems in which the major drivers are themselves scale dependent (Wiens, 1989). For instance, none of the vegetation patterns analysed by Palmer (1988) demonstrated scale independence and self-similarity. Yet, the siren-call of self-similarity has been especially strong in biodiversity analyses as its presence would allow insights regarding patterns and parameters present at one scale to be accurately applied to adjacent scales without the need for empirical observations. Direct measurement of various diversity metrics at tractable (usually single site) scales could thus theoretically be used to generate expectations at regional to global scales where empirical observation may be logistically impossible. Finlay *et al.* (2006), for instance, claimed that self-similarity in various species composition, richness and body-size metrics allows for accurate extrapolation of insect diversity patterns at Hilbre Island and Monks Woods Nature Reserves in England to the entire globe.

Is it really the case that biodiversity patterns appear the same when peering through each end of a spyglass? Can observation of only a few sites allow for accurate estimation of regional to global scale patterns? And, is it also possible that knowledge of regional to global scale patterns informs accurately about relationships within individual sites? These questions will be empirically tested through an analysis of North American terrestrial gastropod species composition, body-size and abundance patterns across site, regional and continental scales.

MATERIAL AND METHODS

Faunistic enumeration

Site scale. Species lists and abundances were considered from 1,574 sites ranging from the Alaskan North Slope and southern California coast east to central Quebec, the Atlantic seaboard and the Florida Keys (Table 1; Fig. 1). These were sampled according to methods presented by Nekola (2010), with individual sample areas being no more than 1,000 m^2. An attempt was made to sample sites from across the entire range of habitats within a given biogeographic region and included 416 bedrock outcrops, 455 upland forests, 335 lowland forests, 126 upland grasslands/shrublands and 242 lowland grasslands/shrublands.

Regional scale. Using the maps of Pilsbry (1948), Burch (1962) and observed community composition patterns as a guide, the continent was subdivided into 21 biogeographic regions with boundaries being set to enclose areas of similar faunistic composition and to also allow each species to occur within at least one region (Fig. 1). The total faunas for each region was then determined through the county-scale distribution maps of Hubricht (1985) for eastern North America (using updates provided by Nekola & Coles, 2010 and J.C. Nekola, unpubl.), with Pilsbry (1948) and various regional lists (e.g. Metcalf & Smartt, 1997; Roth & Sadeghian, 2003; Forsyth, 2004) being used for western North America. The number of survey sites per region ranged from 8 (southern Appalachians) to 252 (western Niagaran Escarpment).

Continental scale. The total North American fauna was based on Nekola (in press). Only species having native or naturalized populations in North America north of Mexico were considered; species only occurring south of the USA boundary are considered to belong to the Central American fauna. The initial point of departure for this dataset is all terrestrial gastropods listed by Turgeon *et al*. (1998). To this were added all subsequently described species as determined via the *Zoological Record*. Additionally, all species listed by Hubricht (1985)—but not by Turgeon *et al*. (1998)—were included, as these represent dead shells limited to drift along the south Texas Gulf Coast that could easily have been sourced from local extant colonies. The list was also expanded to include all subspecies-level entities of Pilsbry (1948) that appear, based on their unique shell features, ranges and/or ecological preferences, to represent valid species-level entities. Finally, 14 undescribed new species encountered by the author during field sampling across North America have also been included, representing six *Vertigo* plus single representatives of *Columella*, *Daedalochila*, *Glyphyalinia*, *Hawaiia*, *Helicodiscus*, *Paravitrea*, *Punctum* and *Succinea*.

Taxonomy and body size

Family assignments for all species were based on those of Bouchet & Rocroi (2005), with the placement of genera into these families generally following Schileyko (2006 and previous works). Generic level assignments generally followed Turgeon *et al*. (1998). Shell/body-size dimensions for each taxon were determined from either the published literature, or in the case of undescribed taxa from lots held in the Nekola collection. Calculation of body volume (in mm^3) was then determined for each species using the formulae presented by McClain & Nekola (2008) and Nekola (in press).

Statistical analyses

All analyses were conducted in the R Statistical Environment with scripts being available upon request.

Family-level composition. The proportional representation of each family within each site was calculated by dividing the total number of species present within each family into the total species richness of that site. This process was repeated across all sites, with the mean proportion for each family then being calculated across all sites. This process was also repeated within each biogeographic region. The proportion of each family within the continental fauna was calculated by dividing the number of species within each family into the continental species richness.

Table 1. Statistical summary for the continental and regional datasets of North American terrestrial gastropods.

Region	No. of sites	Regional richness		Site richness		No. of individuals	
		Reported	Encountered	Median	Maximum	Total	Median/site
Whole continent	1,574	1,204	460	12	39	697,778	237
Churchill	23	17	15	6	12	9,303	261
Central Manitoba	24	53	41	10	21	11,014	288
Laurentian Plateau	48	80	40	8	18	9,729	131
Northwestern Minnesota	192	63	59	15	27	142,305	463
Western Superior Uplands	82	55	44	10	18	5,025	47
Eastern Niagaran Escarpment	73	149	86	16	31	26,804	305
Western Niagaran Escarpment	252	98	84	15	34	92,778	216
New England	194	133	82	13	34	84,661	217
Upper Mississippi Valley	131	103	90	20	39	105,075	587
Ozarks	35	149	88	20	34	20,601	255
Central Appalachians	22	246	86	16	35	7002	219
Southern Appalachians	8	278	42	12	33	2,181	210
Carolinas	38	131	62	8	31	9,298	132
Gulf Coast	37	156	34	3	11	2,260	43
Peninsular Florida	59	130	97	12	28	33,848	301
Southern Plains	14	154	58	12	23	3,379	128
Southern Rockies	161	308	113	7	21	72,116	230
California	30	271	51	5	10	8,219	99
Great Basin	39	76	45	7	13	12,635	206
Pacific Northwest	48	187	64	9	17	13,895	197
Alaskan Interior	64	33	32	7	16	25,644	216

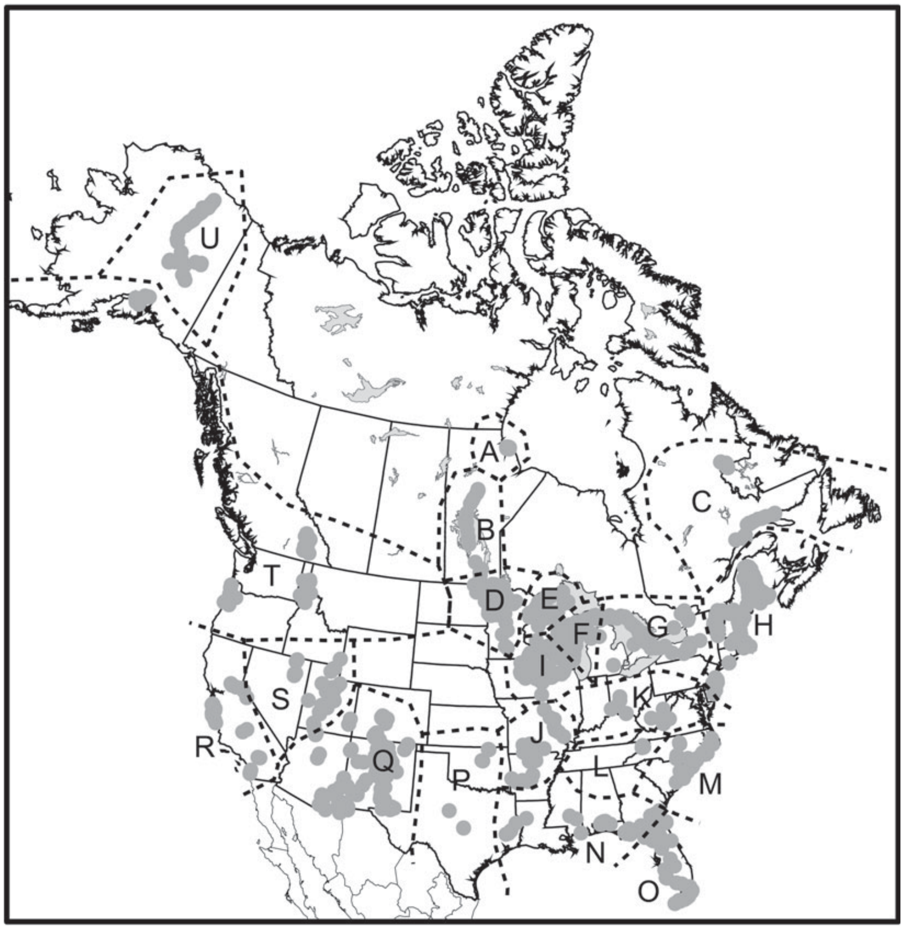

Figure 1. Location of the 1,574 sample sites and 21 biogeographic regions in North America. Regional codes are: A, Churchill; B, Central Manitoba; C, Laurentian Plateau; D, Northwestern Minnesota; E, Lake Superior Uplands; F, Western Niagaran Escarpment; G, Eastern Niagaran Escarpment; H, New England; I, Upper Mississippi Valley; J, Ozarks; K, Central Appalachians; L, Southern Appalachians; M, Carolinas; N, Gulf Coast; O, Peninsular Florida; P, Southern Plains; Q, Southern Rockies; R, California; S, Great Basin; T, Pacific Northwest; U, Alaskan Interior.

This process was also repeated at the regional level. All proportions were multiplied by 100 to give percentage representation.

Statistical significance of the difference between site and regional scale representation was calculated using a sign test for all families occurring in at least 10 regions. The number of cases in which mean site percentage was less than the regional percentage was counted, as was the number of cases in which regional percentage was less than mean site percentage. Under a null expectation of no relationship, these numbers should be equal. The P-value for deviations from this null was calculated using the binomial distribution. Because the test was repeated on 18 different families, the $P = 0.05$ significance threshold was adjusted using a Bonferroni correction to $P = 0.0028$.

Site species richness. The ratio between observed and random expected richness was calculated. Expected random richness was determined by generating a vector representing the species identities of all encountered individuals across either the entire continental dataset or a respective region. For each site, n random individuals were selected from this vector without replacement, where $n =$ the number of all identified individuals from a given site. The number of unique species in the random draw was then reported, with this process being repeated 1,000 times. The mean number of unique species across all random samples was then recorded. This process was repeated across all sites. Observed site richness was then divided into mean random richness. A box plot was then generated showing the variation in observed: random richness across all sites in the continent or respective region. Statistical significance for differences in observed *vs* randomized richness was estimated using the paired Wilcoxon rank-sum test.

Body-size spectra. Observed body-size spectra were determined across all sites by counting the number of species falling within each of 41 $\log_2$ volume classes with bins starting at -2.5 and increasing by 0.5 $\log_2$ units to 18.0. The first bin value ranged from -2.5 to -2.0 (~ 0.18 to 0.25 mm^3) and the last bin from 17.5–18.0 (185 363.8 to 262 144 mm^3). The proportion of the total site fauna found within each bin was then determined by dividing the observed bin richness by total site richness. Random expectations were then generated by randomly drawing n species, without replacement, from the continental or respective regional species pool, where $n =$ number of recorded species from that site. The proportion that each bin represented in the random draw was then calculated. This procedure was repeated 1,000 times, with the mean proportion across all randomizations being reported across all 41 bins. This process was repeated for each site. From this, body-size spectra graphs were generated showing across all bins the mean observed site representation and the minimum and maximum mean random values as drawn from the continental or respective regional pool. Regional scale patterns were illustrated through three latitudinal transects: western (Alaskan Interior, Pacific Northwest, Great Basin and southern Rockies), central (Churchill, Northwestern Minnesota, Upper Mississippi Valley and Ozarks), and eastern (Laurentian Plateau, New England, Carolinas, Peninsular Florida).

RESULTS

In all 1,204 species-level taxa are reported from North America, partitioned among 170 genera and 51 families (Nekola, in press). A total of 460 species (38% of the continental total) and 697,778 individuals were recorded from the 1,574 sites (Table 1). Regional faunistic richness ranged from 17 (Churchill) to 308 (Southern Rockies), with encountered species ranging from 15 (Churchill) to 113 (Southern Rockies). Median site richness ranged from 3 (Gulf Coast) to 20 (Upper Mississippi Valley and Ozarks), while maximum richness ranged from 10 (California) to 39 (Upper Mississippi Valley). The total number of encountered individuals ranged from 2,181 (Southern Appalachians) to 142,305 (Northwestern Minnesota), while the median number of individuals encountered per site ranged from 43 (Gulf Coast) to 587 (Upper Mississippi Valley).

Family-level composition

For the entire continental fauna (Table 2), the ten most frequently represented families were the Polygyridae (22.51%), Helminthoglyptidae (14.78%), Vertiginidae (8.64%), Oreohelicidae (6.98%), Pristilomatidae (5.40%), Oxychilidae (4.07%), Succineidae (4.07%), Gastrodontidae (2.91%), Arionidae (2.82%) and Urocoptidae (2.58%). This differs greatly from average site faunas, which were most frequently represented by the Vertiginidae (29.93%), Gastrodontidae (11.19%), Oxychilidae (7.60%), Euconulidae (7.09%), Punctidae (5.44%), Discidae (5.40%), Valloniidae (4.88%), Strobilopsidae (3.23%), Polygyridae (3.20%) and Ellobiidae (2.97%).

Regional species pools demonstrated variability in family-level representation, with the most common family ranging from the Vertiginidae (Churchill, Central Manitoba, Lake Superior Uplands, Laurentian Plateau, New England, Northwestern Minnesota, Eastern Niagaran Escarpment, Western Niagaran Escarpment, Upper Mississippi Valley and Alaskan Interior) to the Polygyridae (Southern Plains, Ozarks, Southern Appalachians, Central Appalachians, Carolinas, Gulf Coast and Peninsular Florida), Oreohelicidae (Pacific Northwest and Great Basin) and Helminthoglyptidae (California and Southern Rockies).

The sign test demonstrates that five families show significant (and another three marginally significant) differences in their representation between site and regional scales (Table 3). The Euconulidae, Punctidae and Vertiginidae all exhibited significantly (Bonferroni adjusted $P < 0.0028$) more instances of mean site fauna proportion exceeding the respective regional species pool proportion than would be expected at random. The Gastrodontidae, Oxychilidae and Strobilopsidae exhibited this pattern to only a marginal ($0.05 < P < 0.0028$) degree. However, the Polygyridae and Succineidae demonstrated significantly more instances of mean site fauna proportion being less than the respective regional pool proportion. Ten families (Agriolimacidae, Cochlicopidae, Discidae, Ellobiidae, Haplotrematidae, Helicodiscidae, Pristilomatidae, Pupillidae, Valloniidae and Vitrinidae) exhibited similar proportional representations between average site faunas and the regional species pool. Because of limited occurrence (<10 regions occupied), statistical power was too low to conduct this test on 25 families. However, among these it should be noted that in all four regions supporting members of the small body-size Thysanophoridae, percent representation within site faunas always exceeded the proportion in respective regional species pools, while in the large body-size Helicidae, Helminthoglyptidae, Humboldtianidae, Hygromiidae, Monadeniidae and Oreohelicidae site fauna representation was always less than the respective regional pool. This was also the case in 75% of the regions supporting large body-size Orthalicidae.

Site richness

Observed site richness values were approximately seven times smaller than random draws taken from the entire continental dataset (Fig. 2). The paired Wilcoxon rank-sum test demonstrated that this difference was highly significant ($P < 0.0000001$). At the regional scale, observed richness generally ranged from 1.85 times smaller than random draws (Lake Superior Uplands) to 6.3 times smaller (Southern Rockies). Observed site faunas were 2.4 and 3.6 times less rich than average random draws from the regional individual pool for Churchill and the Alaskan Interior, respectively. This number ranged from 2.7 to 3.1 for Central Manitoba, the Laurentian Plateau, New England, Northwestern Minnesota, the Eastern and Western Niagaran Escarpments and the Upper Mississippi Valley. In the Southern Plains, Ozarks and Central Appalachians, individual site faunas were 2.6–2.2 times smaller than random draws from their respective regional individual pools. This number ranged from 3.4–3.9 in the Carolinas, Gulf Coast and Peninsular Florida, and 3.1–4.7 in the Pacific Northwest, Great Basin and California. The paired Wilcoxon rank-sum test demonstrated that these differences were all highly significant ($P < 0.0000027$ with a Bonferroni-adjusted P-value threshold of 0.00238). The main exception was the Southern Appalachians, which had observed richness ranging between *c.* 1.3 times larger to 4.2 times smaller than the size of a random draw from the regional individual pool (median = 1.5 times smaller). While sites were generally less rich than random draws from the entire regional individual pool, this difference was only marginally significant ($P = 0.007813$).

Body-size spectra

Observed mean body-size spectra within sites differed strongly from random draws made from the continental species pool (Fig. 3). While observed site faunas were strongly right-skewed with a mode at the 5th $\log_2$ body-size bin ($0.71–1\ \mathrm{mm}^3$), random draws of the same richness from the continental species pool were strongly left-skewed, with modal values ranging from the 21st–24th $\log_2$ body-size bin ($181–512\ \mathrm{mm}^3$). Site faunas were greatly enriched in species with biovolumes of $5.7\ \mathrm{mm}^3$ or less, and greatly underrepresented in species with biovolumes of $90.5\ \mathrm{mm}^3$ or greater. These differences are highly significant, with the site-scale mode for species with biovolumes $<5.7\ \mathrm{mm}^3$ being more than three times larger than the maximum observed randomized mean at that same size class, and the minimum score of the randomized means for species with biovolumes $>90.5\ \mathrm{mm}^3$ being at least five times larger than observed scores for these same body-size classes. Species with biovolumes of $5.7–90.5\ \mathrm{mm}^3$ were represented at approximately equal proportions within observed and randomized site faunas.

The enrichment of small species and impoverishment of large species at site scales was also present within most biogeographic regions (Fig. 4). Among the 12 illustrated relationships in Figure 4, the Pacific Northwest, Great Basin, Southern Rockies, Upper Mississippi Valley, Ozarks, Laurentian Plateau, New England and Carolinas all strongly demonstrate this pattern. It is also more weakly exhibited in Northwestern Minnesota and Peninsular Florida. Very similar observed *vs* randomized body-size spectra were noted for the Alaskan Interior and Churchill.

DISCUSSION

These analyses clearly show that family composition, body-size spectra and species richness are not self-similar and scale independent among North American terrestrial gastropods. While the continental fauna is dominated by families with large-sized individuals like the Polygyridae and Helminthoglyptidae,

Table 2. Comparison of terrestrial gastropod family percent representation across observational scales in North America.

Family	Entire Continent		Churchill		Central Manitoba		Lake Superior Uplands		Laurentian Plateau		New England		NW Minnesota		E Niagara		W Niagara		Upper Mississippi		Southern Plains		Ozarks	
	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%
Polygyridae	22.51	3.20					5.46	0.34			12.78	0.50	1.59	0.03	12.08	3.98	8.16	2.78	10.68	6.48	32.47	18.54	29.53	18.40
Helminthoglyptidae	14.78	0.28																						
Vertiginidae	8.64	29.93	64.71	68.11	35.85	31.56	27.27	20.96	26.25	36.93	15.79	30.93	31.75	24.46	15.45	21.86	20.41	28.06	21.36	31.58	12.99	26.55	15.44	23.49
Oreohelicidae	6.98	0.37																						
Pristilomatidae	5.40	2.66			1.89	–	1.82	0.61			2.26	0.47	3.18	3.06	2.69	2.69	3.06	2.66	1.94	4.56	2.60	8.50	6.71	6.40
Oxychilidae	4.07	7.60			3.77	12.05	7.27	11.78	5.00	14.26	9.77	9.17	3.18	9.53	7.38	9.00	8.16	5.11	4.85	5.12	4.55	5.73	6.71	9.11
Succineidae	4.07	2.75	11.77	11.17	13.21	3.34	5.46	1.05	7.50	1.71	6.02	1.96	7.94	4.32	6.71	1.63	9.18	3.62	10.68	2.24	7.14	9.00	6.71	0.52
Gastrodontidae	2.91	11.19			5.66	8.02	9.09	21.71	6.25	7.53	7.52	19.70	6.35	11.92	7.38	16.63	6.12	12.61	5.83	5.66	3.25	5.81	5.37	9.75
Arionidae	2.82	–					3.64	–	11.25	–	6.02	–	3.18	–	6.04	–	4.08	–	3.88	–				
Urocoptidae	2.58	0.18																			1.95	–		
Discidae	2.24	5.40	5.88	–	3.77	13.08	5.46	12.70	3.75	8.66	2.26	3.73	4.76	6.70	4.03	7.90	4.08	7.18	4.85	5.14	1.30	0.99	3.36	2.36
Helicodiscidae	2.08	2.76			3.77	–	3.64	3.74	1.25	0.98	3.01	3.54	3.18	1.76	2.01	3.93	3.06	4.48	3.88	5.95	5.20	5.77	2.69	4.68
Phylomicidae	1.74	–									5.26	–			4.70	–	1.02	–	2.91	–	1.95	–	4.03	–
Haplotrematidae	1.33	0.44									0.75	0.09			0.67	0.29	1.02	0.07	0.97	1.13			0.67	1.70
Orthalicidae	1.33	0.23																			2.60	1.13	0.67	1.35
Monadeniidae	1.33	0.03																						
Pupillidae	1.16	1.88	5.88	2.71	1.89	–			1.25	0.28	1.50	0.41	3.18	0.08	1.34	0.92	2.04	0.05	1.94	1.77	0.65	3.73	0.67	2.50
Valloniidae	1.08	4.88			9.43	4.47	7.27	6.57	8.75	6.71	4.51	4.66	9.52	6.63	4.70	3.47	7.14	3.73	5.83	5.08	3.90	1.56	2.69	1.19
Euconulidae	0.91	7.09	5.88	13.78	3.77	10.25	5.46	5.33	2.50	12.79	3.01	7.25	3.18	7.23	2.69	5.92	4.08	6.33	3.88	5.41	1.95	3.05	2.69	4.40
Ellobiidae	0.91	2.97			3.77	3.73	3.64	2.12	2.50	–	1.50	3.68	3.18	6.33	2.01	4.45	2.04	5.08	1.94	3.98	1.30	0.48	0.67	2.21
Punctidae	0.83	5.44			3.77	6.99	1.82	4.94	2.50	2.74	1.50	7.24	4.76	6.39	2.01	6.06	3.06	5.73	2.91	5.13	0.65	2.44	1.34	4.94
Humboldtianidae	0.83	0.00																						
Helicinidae	0.75	0.63					1.82	0.15									1.02	1.65	0.97	1.73	3.25	1.13	0.67	1.08
Binneyidae	0.75	–																						
Subulinidae	0.66	0.28																			0.65	–		
Helicidae	0.66	0.05							3.75	0.14	3.76	0.03			4.03	0.59	1.02	–			2.60	–	1.34	–
Hygromiidae	0.66	0.02							3.75	–	1.50	0.14			2.69	0.06								
Megomphicidae	0.66	0.01																						
Veronicellidae	0.66	–																						
Agriolimacidae	0.50	1.30	5.88	4.24	1.89	1.96	1.82	0.10	3.75	0.15	1.50	0.96	3.18	1.69	2.01	2.56	2.04	1.73	1.94	3.27	0.65	–	1.34	0.45
Strobilopsidae	0.42	3.23			1.89	1.10	1.82	4.60	1.25	–	3.01	4.17	3.18	4.16	2.01	3.97	3.06	4.89	2.91	4.24	2.60	4.45	2.69	4.44
Thysanophoridae	0.42	0.97																			1.30	–		
Truncatellidae	0.42	0.13																			0.65	–		
Limacidae	0.42	–							2.50	–	3.01	–			3.36	–	1.02	–			1.30	–	2.01	–
Spiraxidae	0.33	0.13																			2.60	0.51		
Pleurodontidae	0.33	0.06																						
Cochlicopidae	0.25	1.99			3.77	2.37	5.46	2.54	2.50	1.77	2.26	1.24	3.18	4.05	2.01	2.84	3.06	3.67	2.91	1.25			1.43	0.22
Vitrinidae	0.17	1.43			1.89	1.10	1.82	0.76	1.25	5.36	0.75	0.15	1.59	1.65	0.67	1.23	1.02	0.42	0.97	0.11				
Pomatiidae	0.17	0.12																						
Pomatiopsidae	0.17	0.07									0.75	–			0.67	0.05	1.02	0.14	1.94	0.18			0.67	0.83
Ferrussaciidae	0.17	0.00																						
Charopidae	0.17	0.09																						
Sagdidae	0.08	0.07																						
Oleacinidae	0.08	0.07																						
Bradybaenidae	0.08	0.03																						
Streptaxidae	0.08	0.02																						
Helicarionidae	0.08	0.01																						
Cepolidae	0.08	0.00																						
Cochlicellidae	0.08	–																						
Milacidae	0.08	–							1.25	–														
Testacellidae	0.08	–							1.25	–					0.67	–								

Family	Southern Appalachians		Central Appalachians		Carolinas		Gulf Coast		Peninsular Florida		Alaskan Interior		Pacific Northwest		Great Basin		California		Southern Rockies	
	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%	R%	S%
Polygyridae	30.22	12.80	23.17	11.07	25.19	4.16	30.13	8.31	14.62	12.70			9.63	4.34			8.86	2.92	17.86	1.93
Helminthoglyptidae													1.07	–			38.75	12.12	24.35	0.51
Vertiginidae	6.12	17.73	9.76	23.49	14.50	36.83	12.82	41.36	13.08	17.53	45.46	59.09	12.30	25.66	19.74	19.83	7.75	22.23	12.66	34.17
Oreohelicidae													14.97	1.10	28.95	7.47	0.37	–	12.34	1.46
Pristilomatidae	12.95	14.39	7.32	7.34	1.53	1.83	3.21	0.52	1.54	3.27			5.88	5.14	1.32	–	2.95	5.98	0.33	4.13
Oxychilidae	12.59	13.82	10.98	11.35	9.16	18.20	8.97	14.20	4.62	4.81	6.06	3.31	3.21	6.43	3.95	1.39	2.21	0.90	1.62	5.75
Succineidae	1.80	–	4.89	1.22	7.63	–	8.33	0.39	6.93	1.30	9.09	9.94	6.42	2.03	13.16	3.59	3.69	1.94	2.27	0.57
Gastrodontidae	8.27	17.92	10.16	10.87	6.11	9.99	7.69	17.30	3.08	2.54			1.60	9.98	2.63	2.48	0.74	11.31	0.65	7.21
Arionidae			2.85	–	2.29	–							14.44	–			7.75	–	0.33	–
Urocoptidae									2.31	3.47									8.44	0.50
Discidae	5.40	0.38	2.85	1.41	2.29	0.36	1.28	–			6.06	3.55	3.21	6.52	2.63	6.94	1.48	2.64	0.65	4.13
Helicodiscidae	5.04	–	4.47	3.55	2.29	2.98	2.56	0.34	3.08	1.54			0.54	0.23			0.37	0.33	0.65	1.12
Phylomicidae	4.68	–	4.89	–	3.05	–	3.21	–	1.54	–									0.33	–
Haplotrematidae	0.72	1.91	0.41	1.94	0.76	1.40	0.64	–					1.60	3.04			4.06	5.56		
Orthalicidae	0.36	–					1.28	–	5.39	3.83									1.62	0.49
Monadeniidae													1.07	0.19			5.90	1.11		
Pupillidae	0.36	–	0.81	0.38	0.76	0.33	0.64	–	1.54	1.97	3.03	5.77	1.07	0.84	6.58	14.95	0.37	0.67	3.90	7.31
Valloniidae	1.08	–	2.03	0.64	2.29	0.64	1.28	1.68	1.54	4.31	6.06	1.34	2.14	4.17	6.58	11.82	0.74	2.39	2.27	8.87
Euconulidae	1.80	6.83	2.03	6.73	3.05	5.36	3.21	6.95	3.85	5.42	9.09	14.27	1.07	8.63	2.63	6.68	0.74	4.20	0.65	6.95
Ellobiidae	2.16	4.24	2.44	4.65	2.29	1.08	1.28	0.25	0.77	0.57			1.60	0.83			0.37	0.33	0.33	0.04
Punctidae	1.44	8.46	1.63	7.77	3.05	6.14	1.28	2.43	0.77	0.24	6.06	0.88	1.60	11.54	1.32	4.97	2.21	20.87	0.97	2.87
Humboldtianidae																			3.25	0.04
Helicinidae	0.72	–	0.41	0.52			0.64	–	2.31	4.77										
Binneyidae													4.28	–			0.37	–		
Subulinidae			0.41	–	1.53	0.29	1.28	–	6.15	7.17							0.37	–	0.33	–
Helicidae			1.63	0.44	1.53	–	2.56	–	1.54	–			1.60	–	1.32	–	2.58	0.48	0.65	–
Hygromiidae					2.29	–	0.64	–	0.77	–							0.37	–		
Megomphicidae													1.60	0.35			1.85	–		
Veronicellidae									6.15	–										
Agriolimacidae	0.72	–	0.81	1.31	1.53	0.91	0.64	0.34	0.77	0.13	3.03	1.34	2.67	0.31	2.63	1.09	1.11	1.22	0.97	0.31
Strobilopsidae	1.08	–	1.63	3.19	2.29	9.09	2.56	5.61	2.31	2.86										
Thysanophoridae									1.54	4.31			1.07	6.19	1.32	4.68			0.65	4.78
Truncatellidae									2.31	3.40							0.74	–		
Limacidae	0.72	–	1.63	–	1.53	–	1.92	–					2.14	–	1.32	–	1.48	–	0.65	–
Spiraxidae					0.76	–	0.64	0.34	0.77	3.04										
Pleurodontidae									3.08	1.62										
Cochlicopidae	1.08	0.95	0.81	1.28	0.76	0.42					3.03	0.13	1.07	0.12	1.32	0.20	0.37	–	0.33	2.41
Vitrinidae			0.41	–							3.03	0.39	0.54	1.15	1.32	13.65	0.37	2.81	0.33	3.99
Pomatiidae									1.54	3.34										
Pomatiopsidae	0.72	–	0.81	0.85	0.76	–	0.64	–												
Ferrussaciidae			0.41	–					1.54	0.07										
Charopidae													0.54	1.20	1.32	0.26			0.33	0.45
Sagdidae									0.77	1.77										
Oleacinidae									0.77	1.93										
Bradybaenidae									0.77	0.69										
Streptaxidae							0.64	–	0.77	0.62										
Helicarionidae									0.77	0.33										
Cepolidae									0.77	0.07										
Cochlicellidae					0.76	–											0.37	–		
Milacidae			0.41	–									0.54	–			0.37	–	0.33	–
Testacellidae													0.54	–			0.37	–		

R%, the percentage of species in the continental/regional fauna occurring within that family. S%, the percentage representation of that family within an average site within that region. Dashes indicate families that are present in the respective fauna but have not yet been encountered within sites.

Table 3. Comparison of family representation at regional *vs* site scales for terrestrial gastropods in North America.

A. 10 or more regions

Family	R > S	S > R	*P*-value
Agriolimacidae	14	5	0.063568
Cochlicopidae	11	5	0.210114
Discidae	6	12	0.237885
Ellobiidae	11	8	1.0
Euconulidae	**1**	**20**	**0.000021**
Gastrodontidae	*3*	*16*	*0.004425*
Haplotrematidae	3	7	0.343750
Helicodiscidae	7	9	0.803619
Oxychilidae	*5*	*15*	*0.041389*
Polygyridae	**16**	**0**	**0.000031**
Pristilomatidae	7	9	0.803619
Punctidae	**2**	**18**	**0.000402**
Pupillidae	10	7	0.629059
Strobilopsidae	*1*	*12*	*0.003418*
Succineidae	**17**	**2**	**0.000729**
Valloniidae	12	7	0.359283
Vertiginidae	**3**	**18**	**0.001490**
Vitrinidae	6	7	1.0

B. <10 regions

Family	R > S	S > R
Bradybaenidae	1	0
Cepolidae	1	0
Charopidae	1	2
Ferrussaciidae	1	0
Helicarionidae	1	0
Helicidae	5	0
Helicinidae	3	5
Helminthoglyptidae	2	0
Humboldtianidae	1	0
Hygromiidae	2	0
Megomphicidae	1	0
Monadeniidae	2	0
Oleacinidae	0	1
Oreohelicidae	3	0
Orthalicidae	3	1
Pleurodontidae	1	0
Pomatiidae	0	1
Pomatiopsidae	3	2
Sagdidae	0	1
Spiraxidae	2	1
Streptaxidae	1	0
Subulinidae	2	1
Thysanophoridae	0	4
Truncatellidae	0	1
Urocoptidae	1	1

R > S represents the number of regions in which family representation in the regional pool exceeded the representation on an average site. S > R represents the number of regions in which family representation within an average site exceeded the representation in the regional pool. Assuming the null of R > S = S > R, *P*-values for families present in at least ten regions are based on the bionomial sign test. Families with $P < 0.0028$ have been highlighted in bold font; families with $0.05 < P < 0.0028$ have been highlighted in *italic* font.

typical site faunas are dominated by families with small-sized individuals like the Vertiginidae and Gastrodontidae. Likewise, while the continental fauna demonstrates a left-skewed body-size spectrum dominated by species with biovolumes >90.5 mm^3, average site faunas are right-skewed and dominated by species with biovolumes <5.7 mm^3. Random draws representing the same number of individuals from the entire continental dataset contained on average at least seven times more species than the actual number observed at that site.

These discrepancies were generally also observed between sites and their respective biogeographic regions. Typically, families with small-sized individuals (Euconulidae, Gastrodontidae, Oxychilidae, Punctidae, Strobilopsidae, Thysanophoridae and Vertiginidae) were overrepresented in typical site faunas as compared to their respective regional species pool, while families with large-sized individuals (Helminthoglypidae, Monadeniidae, Oreohelicidae, Polygyridae and Succineidae) were underrepresented. This bias is demonstrated across most regions (e.g. Pacific Northwest, Great Basin, Southern Rockies, New England and Carolinas). However, both arctic regions tended to show little discrepancy between typical site body-size spectra and the regional pool. Site richness also generally ranged from two to six times smaller than would be expected from random draws from the respective regional individual pool. Even in the case of the Southern Appalachians, where the eight sampled sites were only collected across a 20-km extent and only 42 total species were encountered (15% of the entire regional fauna) the majority of sites were still found to have fewer species than would be expected from a random draw of all encountered individuals. As more samples are made across a larger extent within this region and more of this regional fauna is encountered, the distribution of observed to random ratio scores will be lowered and made to fall in line with other regions.

These analyses indicate that site faunas are not a simple random sample drawn from the continental or regional pool. Rather, important biases are present. The most important of these are not only the predictable filtering of species along environmental gradients (principally soil architecture, moisture and acidity; Nekola, 2003, 2010) but also purely geographic filtering caused by dispersal limitation and other forms of spatial constraint (Nekola & White, 1999; Hubbell, 2001).

As a result, it is not possible to extrapolate accurately these macroecological metrics across scales for North American terrestrial gastropods. Rather, the fauna looks considerably different depending upon whether one is looking down from continental scales, or up from site scales. From the continental-scale perspective, the fauna is generally dominated by families with large-sized individuals. However, from the site scale the fauna is dominated by a series of families with small body-sized individuals. Documenting the faunas of a few individual sites will thus not allow for an accurate portrayal of the continental fauna and knowledge of the continental fauna informs little about what one would expect within individual sites.

The lack of self-similarity within the North American terrestrial gastropod fauna appears to be principally caused by a strong inverse correlation between body and range size. In this fauna, many small species (especially within the Euconulidae, Gastrodotidae, Oxychilidae, Punctidae, Strobilopsidae and

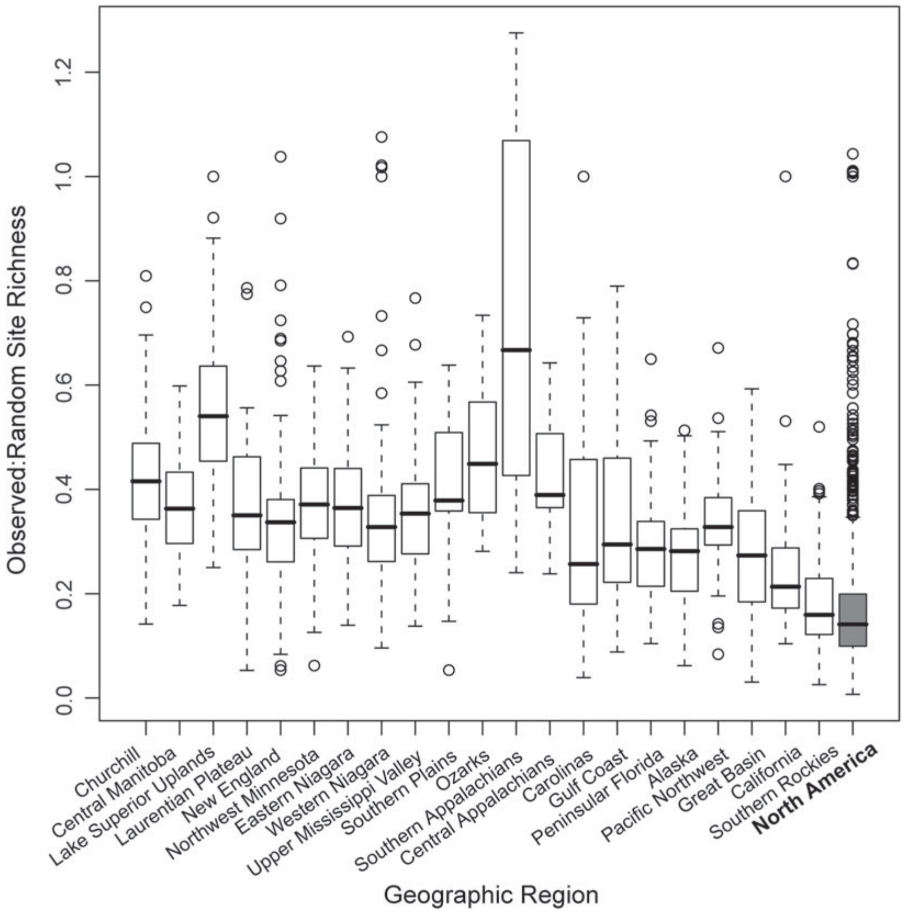

Figure 2. Box plot showing distribution of observed site richness *vs* randomized expectations from the regional/continental individual pool of terrestrial gastropods in North America. The site *vs* continental-scale comparison is identified by grey fill.

Vertiginidae) tend to have component species harboring extensive ranges. Examples include *Euconulus fulvus* (Müller, 1774), *E. alderi* Gray, 1840, *Punctum minutissumum* (I. Lea, 1841) and *Vertigo arthuri* von Martens, 1884, which range across the entire continent north of 38°N, while also extending south along the crest of the Rockies to the Mexican border. *Gastrocopta pellucida* (Pfeiffer, 1841), *Glyphyalinia umbilicata* (Singley, in Cockerell, 1893), *Hawaiia miniscula* (A. Binney, 1840) and *Straitura meridionalis* (Pilsbry & Ferriss, 1906) likewise extend across much of North America south of 35°N. And, both *Strobilops labyrinthica* (Say, 1817) and *Strobilops aenea* Pilsbry, 1926 range across most of the southeastern quarter of the continent. A number of genera with large body-sized species, however, demonstrate significant levels of allopatric replacement and local endemism. These are especially pronounced within the Polygyridae (e.g. *Ashmunella*, *Daedalochila*, *Stenotrema*, *Inflectarius*, *Patera*, *Triodopsis*, *Trilobopsis* and *Vespericola*), Helminthoglyptidae (e.g. *Helminthoglypta*, *Micrarionta* and *Sonorella*), Oreohelicidae (e.g. *Oreohelix* and *Radiocentrum*), Urocoptidae (e.g. *Holospira* and *Coelostemma*), Monadeniidae (*Monadena*) and Humboldtianidae (*Humboldtiana*), with it being uncommon for species within these genera to be sympatric at the site scale.

It seems likely that the combined effects of body size on passive dispersal and uniparental reproduction rates help explain this counter-intuitive pattern. Because terrestrial gastropods are among the poorest active dispersers known among terrestrial animals, with individuals moving perhaps no more than 1–10 m over their lifetime (Schilthuizen & Lombaerts, 1994) and populations being unable actively to cross barriers of only 100–1,000 m (Baur, 1988; Schilthuizen & Lombaerts, 1994),

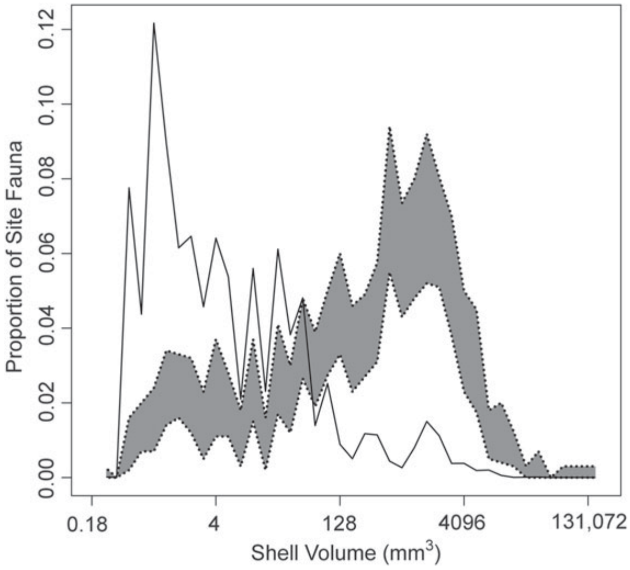

Figure 3. Site *vs* continental body-size spectra for terrestrial gastropods of North America as represented by 41 $\log_2$ body-size classes. The solid line represents the observed average for individual sites. The upper and lower dashed lines represent the maximum and minimum mean scores (respectively) observed for that size class across 1,000 random samples drawn per site from the continental pool. The range between these extremes has been filled with grey.

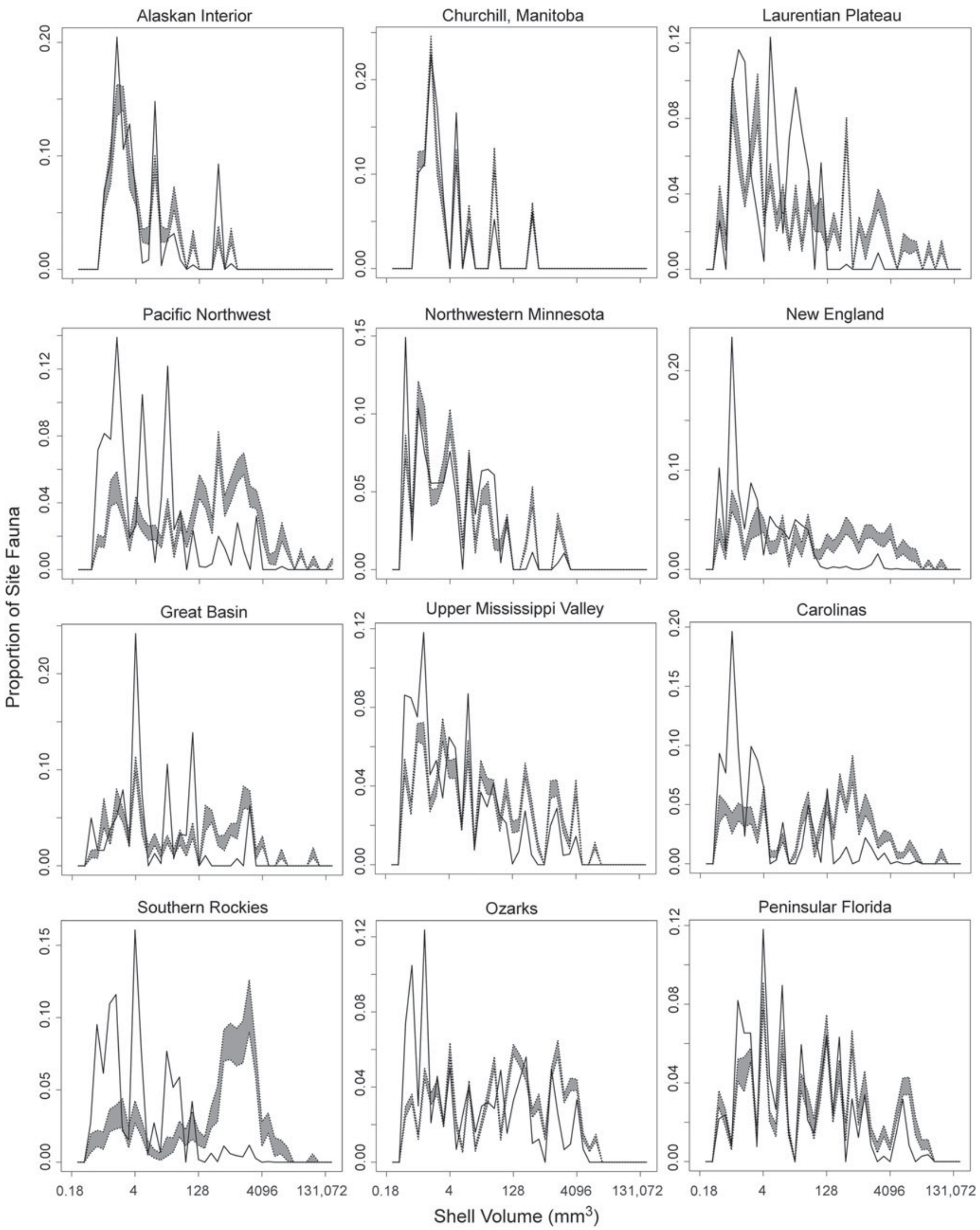

Figure 4. Site *vs* regional body-size spectra of terrestrial gastropods in North America, as represented by 41 $\log_2$ body-size classes across twelve selected biogeographic regions. Panels are arranged in three columns (western, central and eastern North America) from most northern (top) to most southern (bottom). In each panel, the solid line represents the observed average for individual sites in that region. The upper and lower dashed lines represent the maximum and minimum mean scores (respectively) observed for that size class across 1,000 random samples drawn per site from the respective regional pool. The range between these extremes has been filled with grey.

passive dispersal takes precedence in determining population movement and species range size. Small snails/slugs are much more easily moved via passive vectors than larger ones, because small-sized individuals are less likely to be pulled off by gravity or fluid mechanics during movement. Additionally, a number of North American genera with species of small body-size contain some that are capable of uniparental reproduction (Pokryszko, 1987; Bulman, 1990). For these, movement of only a single unmated individual is required to found a new population, greatly increasing the effectiveness of long-range dispersal events in causing range expansion. DNA sequence data illustrate, for instance, that members of the genus *Balea* have been repeatedly carried across 9,000 km of open sea in the eastern Atlantic Ocean by migrating birds (Gittenberger *et al.*, 2006). Species within the *Vertigo gouldii* group in North America may possess ranges exceeding 5,000 km in extent even though their modern ranges were covered by continental ice as recently as 12,000 yr BP (Nekola, Coles & Bergthorsson, 2009). This is not a universal pattern, however, with many Pristilomatidae and Helicodiscidae exhibiting local endemism in the eastern USA (e.g. *Helicodiscus*, *Paravitrea*, *Pilsbryna* and *Polygyriscus*). Comparison of the breeding systems and ecology between large-range *vs* small-range small body-sized species will undoubtedly document important differences. For instance, many locally endemic *Helicodiscus*, *Paravitrea* and *Polygyriscus* species tend to be restricted to highly insular rock talus habitats, perhaps making it easier for their populations to become isolated and speciate.

Because similar analyses have not yet been performed in other regions, it cannot be conclusively stated whether strong scale-dependence is a general phenomenon or is unique to North America terrestrial gastropods. Because a strong inverse correlation between body and range size (Pokryszko & Cameron, 2005; Cameron, Pokryszko & Horsák, 2010, 2012) in combination with an overabundance of small individuals and large species (Nekola *et al*., 2013) exists in the European fauna, it seems likely that scale-dependence also occurs there. Preliminary investigations of the New Zealand fauna (Nekola *et al*., 2013), however, show apparent strong coupling in species richness and individual abundance across the body-size spectrum. Given that this fauna, as well as that of eastern Australia (Stanisic *et al*., 2007, 2010), also harbours many narrow-range endemics of small body size (especially in the Charopidae and Punctidae), self-similarity within these faunas is possible. Yet, the commonness in western Australia of large body-size camaenids demonstrating strong alloptaric replacement with smaller species demonstrating extensive ranges (Solem, 1988; Cameron, 1992) suggests that at least parts of this continental fauna may behave in a fashion similar to that in North America.

Lastly, it is important to point out that at least some of the 'self-similar' patterns reported by Finlay *et al*. (2006) are almost certainly not rooted in ecological mechanisms. For instance, S-shaped species-abundance distributions along a rank-abundance axis and power-law species-area relationships have both been shown to be common expectations across a wide variety of complex systems spanning not only the physical, biological and social sciences but also the arts (Nekola & Brown, 2007). As a result, the similarity of these patterns across scales only means that these systems have remained complex across these scales—and no more. Given that complex systems typically demonstrate nesting, with a given system being made up of complex parts, while at the same time being a component of even larger-scale complex systems (Brown, 1994; West, 2006), these findings are to be expected and are likely mathematically trivial.

Because of scale-dependence, no easy mathematical short-cut exists for documenting the North American terrestrial gastropod fauna. It is not only impossible to look at a few sites and be able accurately to assemble continental or most regional scale biodiversity patterns, but it is also equally impossible to deduce the makeup of site faunas given knowledge of the continental or regional pool. This fauna can only be accurately known by looking at many sites spread across all biogeographic regions and then summarizing these data to allow for expression of emergent properties. The only way this can be accurately accomplished is thus through extensive, time consuming and expensive fieldwork.

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