

TERRESTRIAL GASTROPOD RICHNESS PATTERNS IN WISCONSIN CARBONATE CLIFF COMMUNITIES

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ABSTRACT

The patterns of terrestrial gastropod richness within two species-rich carbonate cliff habitats in eastern Wisconsin were analyzed at two differing sample scales. Up to 23 taxa were found in 1 m² quadrats, and 21 taxa in 0.04 m² quadrats. These observations are among the highest reported globally for 1 ha or smaller samples. At the 1 m² scale, samples collected within 5 m of bedrock outcrops had higher richness than more distant sites. At this scale, only soil pH (not Ca, Mg, N, P, K, percent organic matter, vascular plant species richness, or surface and 20 cm depth soil temperatures) was found to significantly correlate with species richness. At the 0.04 m² scale, the richest sites were restricted to areas within 0.5 m of cliff bases. Comparison of maximum richness levels across varying spatial scales demonstrate that up to a third of the total fauna may co-exist in <0.04 m² regions (alpha diversity), up to half of the fauna may coexist in <100 m² regions (beta diversity), while the remainder of the taxa (gamma diversity) occurs between regions separated by at least 10 km.

Key words: terrestrial gastropods, species richness, diversity patterns, conservation, North America, Niagaran Escarpment.

INTRODUCTION

While a number of studies have documented richness in terrestrial gastropod communities at relatively large (> 100 m²) sample scales (e.g., Paul, 1975; Solem et al., 1981; Waldén, 1981; Cameron, 1986; Nilsson et al., 1988; Emberton, 1995; Tattersfield, 1996; Emberton et al., 1997), fewer have analyzed terrestrial gastropod community structure at smaller scales within sites. The research that has been conducted at this scale has demonstrated terrestrial gastropod community structure can change markedly over limited (e.g., <100 m) spatial extents. For instance, Berry (1966) demonstrated significant changes in faunal composition between moss-covered and moss-free segments on a single limestone cliff. Agócsy (1968) reported substantial differences in species composition and abundance between adjacent limestone and sandstone outcrops. Cameron (1978) reported significant shifts in the faunas found on adjacent vertical and horizontal surfaces. Kralka (1986) demonstrated that over 60% of terrestrial gastropod species clustered significantly within individual boreal forest stands. Small-scale patterns in terrestrial gastropod distribution are also suggested by the control

of soil chemistry on community structure (Outeiro et al., 1993; Hermida et al., 1995), as soil chemistry is known to be highly variable over 1–2 cm distances (Burrough, 1986).

Unfortunately, little is known about small-scale community composition and diversity patterns within the richest known global sites. At the Waipipi Scenic Reserve in New Zealand, Solem et al. (1981) did not quantitatively subsample the fauna, but rather documented total gastropod diversity over the entire 4.2 ha reserve. Emberton (1995) documented total species richness within a 4-hectare region near Manombo, Madagascar without measuring diversity from subsamples within this site. Similarly, Emberton et al. (1997) only documented total richness from entire 4-hectare regions in eastern Tanzania. Diversity gradients at Pine Mountain, Kentucky, the richest North American terrestrial gastropod site, have not been documented (Emberton 1995). The smallest quadrats sampled by Tattersfield (1996) from the Kakamega Forest Reserve in Kenya were 40 × 40 meters in size, while the minimum quadrat size sampled by deWinter & Gittenberger (1998) in southwestern Cameroon was 20 × 20 meters. While Schmid (1966) did measure terrestrial gastropod richness from individual 1 m²

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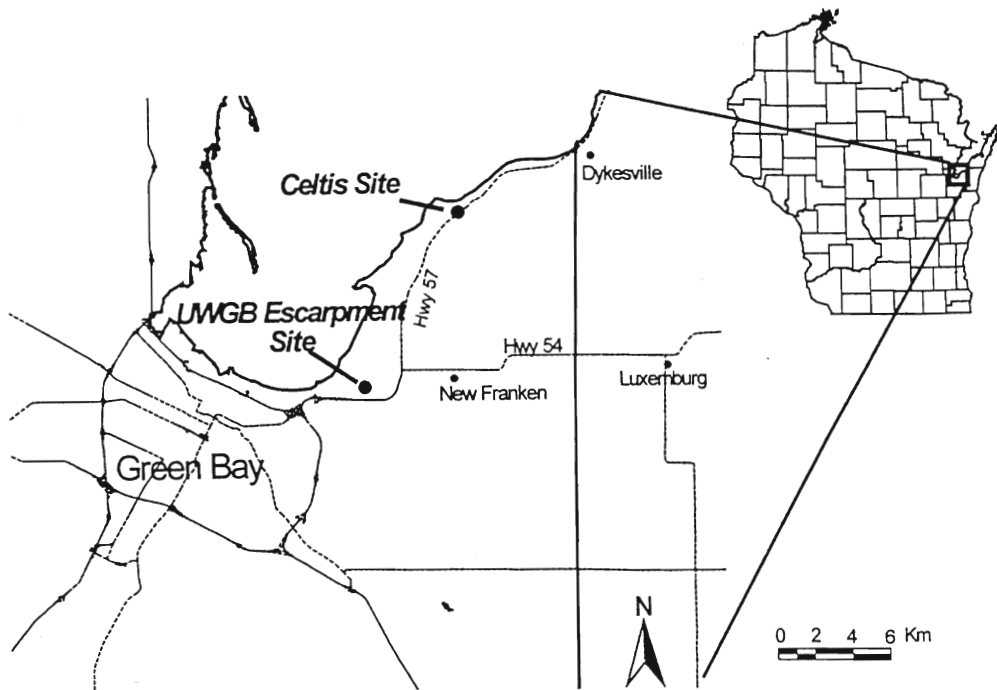


FIG. 1. Location of the Celtis and UWGB Escarpment sites in northeastern Brown County, Wisconsin, USA.

quadrats near Tübingen, Germany, these were not part of a larger, systematic sampling regime and were not used to document diversity gradients within habitats.

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 Previous analyses (Nekola, ~~in press A~~) have shown that carbonate cliffs from the Great Lakes region in North America are among the richest terrestrial gastropod communities reported from less than 1 ha scales. However, like other high diversity communities, nothing was known of: (1) diversity gradients within these sites; (2) the environmental factors within sites that correlate with high richness microsites, and (3) the scales of organization for faunal diversity within and between sites. This paper attempts to address these questions by analyzing terrestrial gastropod diversity patterns at two sampling scales (1 m² and 0.04 m²) within two high-richness carbonate cliff sites in northeastern Wisconsin, U.S.A.

MATERIALS AND METHODS

Study Sites

Two wooded carbonate cliffs in Brown County, Wisconsin, with high levels of terres-

trial gastropod species richness were chosen for study (Fig. 1). Both occur along the Niagaran Escarpment, a 1,300 km band of outcropping Silurian-age limestones and dolomites that can be roughly divided into five 200–300 km long regions (northeastern Iowa; eastern Wisconsin through the Garden Peninsula of Michigan; eastern Upper Peninsula of Michigan though Manitoulin Island; Bruce Peninsula though south-central Ontario; and southeastern Ontario to western New York State) which are separated by low areas with little or no bedrock exposure. Within the eastern Wisconsin region, the Niagaran Escarpment is naturally divided into 31 isolated 2–8 km sections of exposed bedrock that emerge above Pleistocene tills and alluvium.

The Celtis site (87°50'52"W, 44°36'35"N) is situated within a 7 km-long Niagaran Escarpment section near the settlement of Benderville. Its canopy is dominated by old-growth sugar maple (*Acer saccharum* Marsh.), white cedar (*Thuja occidentalis* L.), paper birch (*Betula papyrifera* Marsh.) and hackberry (*Celtis occidentalis* L.). The bedrock outcrop at the Celtis site is divided into a 3–6 m primary upland cliff and a 2–5 m secondary cliff associated with a large bedrock block displaced downslope approximately 10 m (Fig. 2). Cool

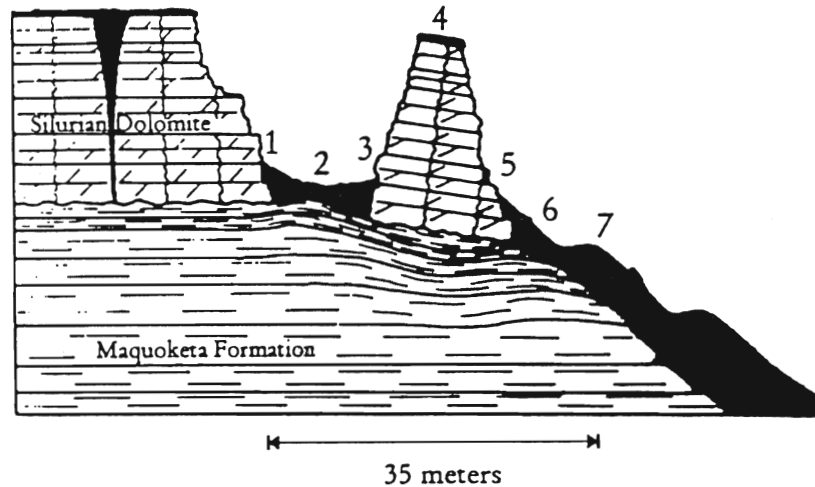


FIG. 2. Schematic profile of the bedrock outcrop at the Celtis site, with location of 1 m² quadrats along each transect. Vertical exaggeration is approximately 4x the linear extent.

air seepage from bedrock fissures and talus occurs throughout the growing season. The presence of large displaced talus blocks, expanded bedrock joints, and an extensive subtending talus indicate that this area was subjected to intense periglacial erosion during the late Pleistocene (Stieglitz et al., 1980). This location harbors the single most diverse terrestrial gastropod assemblage known from the Great Lakes region, with 34 taxa (Nekola, ~~in press~~ A). Included in this fauna are the glacial relicts *Catinella gelida* (F. C. Baker, 1927), *Hendersonia occulta* (Say, 1831), *Vallonia gracilicosta albula* (Sterki, 1893), and *Vertigo hubrichti* Pilsbry, 1934 (Nekola et al., 1996)

The University of Wisconsin—Green Bay (UWGB) Escarpment site (87°54'21"W, 44°31'48"N) is located within a 4-km Niagaran Escarpment section located near the Bay Settlement community. This site consists of a single 2–5 m tall upland cliff within a white cedar and box elder (*Acer negundo* L.) canopy. Large displaced talus blocks are absent. This site was extensively modified by small-scale quarrying for lime and building material approximately a century ago (Stieglitz et al., 1980). As these activities were carried out with hand tools and were spatially limited, this site consists of a mixture of modified and unmodified cliff segments. Unmodified segments appear essentially identical to the upland outcrop at the Celtis site. A total of 25 terrestrial gastropod taxa have been located here, including the glacial relicts *Vallonia gra-*

cilicosta albula, *Vertigo hubrichti*, and *Vertigo* n. sp. ("*V. iowaensis*" of Frest, 1991).

Data Sets

A representative and relatively undisturbed section of exposed cliff was identified at each site. From a random starting point within these sections, five transects were laid out perpendicular to the cliff face at 5-m intervals. Along each transect both 1 m² and 0.04 m² samples were sampled:

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1 m² Quadrats: At the Celtis Site, seven quadrats, each separated by 5-m distances, were collected along each transect (Fig. 2) for a total of 35. At the UWGB Escarpment, three quadrats, separated by 5 m distances, were collected from each transect for a total of 15. Only three samples per transect were gathered from the UWGB Escarpment site to avoid highly disturbed forest and recreational trails occurring at greater distances from the cliff base.

The vascular plants growing on or over each quadrat were recorded and their species richness calculated. Soil temperatures at the ground surface and at 20 cm depth were measured using a thermocouple thermometer. A 100 gm dry weight soil sample was collected by subsampling the corners and center of each quadrat. These samples were sent to the Wisconsin State Soils Lab at the University of Wisconsin—Madison for analysis of

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percent organic matter, N, P, K, S, Ca, Mg, and pH, using methods outlined in Dahnke (1988).

Terrestrial gastropod assemblages were determined by collecting a total of 4–5 deciliters of soil litter from the corners and center of each quadrat. Samples were slowly and completely dried in either a low-temperature soil oven (approx. 80–95°C) or in full sun in a greenhouse. Dried samples were then soaked in water for 3–24 h, and subjected to careful but vigorous washing through a standard sieve series (ASTME 3/8" (9.5 mm), 10 (2.0 mm), 20 (0.85), and 40 (0.425 mm) mesh screens). The washed fractions were re-dried and then re-sifted through the original sieve series. The dry, resorted fractions were hand picked against a neutral-brown background using a small sable brush. All shells and shell fragments were removed.

Recovered, identifiable shells were assigned to species (or subspecies) using the author's reference collection and the Hubricht Collection at the Field Museum of Natural History. From this, species composition and richness per quadrat was calculated. All specimens are housed in collections maintained at the University of Wisconsin-Green Bay.

0.04 m² Quadrats: 20 × 20 cm quadrats were collected adjacent to 1 m² quadrats along each of the five established transect lines. Quadrats were sampled at distances of 0, 0.5, 1.0, 1.5, and 2.0 meters from cliff bases. The primary and secondary cliffs at the Celtis site (located at positions 1 and 5, respectively, on Fig. 2), and the primary cliff at the UWGB Escarpment were analyzed in this fashion for a total of 75 observations. For each quadrat, transect position and distance from the cliff base were recorded, and a 2–3 deciliter soil litter sample collected. These litter samples were subjected to the same laboratory procedures described for the 1 m² samples to determine terrestrial gastropod composition and richness.

Comparison of Maximum Richness Levels: The maximum richness of 0.04 m² and 1 m² samples from each site were compared with known richness values from a series of nested samples of increasing sample grain. These grains include each site (observed from a 100 m² quadrat), escarpment section, escarpment region, Brown County, and the state of Wisconsin. Richness values at these increasing scales of observation are based upon species lists from other sites (summarized in Nekola, in

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~~press-A~~), augmented by other published records (Levi & Levi, 1950; Teskey, 1954; Jass, 1986). Richness estimations were limited to carbonate cliff habitats for Escarpment sections and regions, while those for Brown County and the state of Wisconsin included all habitat types.

To compare the maximum richness values from this study with other reported maximum richness values, a survey was made of the published literature to identify other datasets in which both terrestrial gastropod richness and sample grain were reported. If multiple examples of such data were found from a single paper, only the richest were entered for a given sample size. Through this process, a total of 35 records from four continents (Africa, Australia, Eurasia, and North America) were recorded (Burch, 1956; Schmid, 1966; Agócsy, 1968; Mason, 1970; Berry, 1973; Paul, 1975; Uminski & Focht, 1979; Bishop, 1980; Solem et al., 1981; Van Es & Boag, 1981; Waldén, 1981; Nilsson et al., 1988; Cameron & Greenwood 1991; Young & Evans, 1991; Cameron, 1992; Outeiro et al., 1993; Getz & Uetz, 1994; Cowie et al., 1995; Emberton, 1995; Wardhaugh, 1995; Tattersfield, 1996; Emberton et al., 1997; de Winter & Gittenberger, 1998).

Statistical Analyses

1 m² Quadrats: Analysis of the effect of quadrat position and site on richness was conducted via ANOVA. These data were graphically represented using box plots (Velleman & Hoaglin, 1981). In box plots, the central line represents the median of the sample, the margins of the box represent the interquartile distances, and the fences represent 1.5 times the interquartile distances. For data having a Gaussian distribution, approximately 99.3% of the data will fall inside of the fences. Outliers falling outside of the fences are shown with asterisks. Identification of the environmental variables that best predict observed richness was accomplished through multiple linear regression using a backwards stepwise selection procedure. Beginning with the most non-significant, variables were removed from the model until all remaining p-values fell below the 0.05 level. Analysis of residuals and individual variable distributions indicated that data transformations were not necessary.

0.04 m² Quadrats: Analysis of the effect of quadrat position, cliff position, and site location on richness was conducted via

ANOVA. These data were graphically represented for each of the three sampled cliffs (Celtis Site primary and secondary, and UWGB Escarpment primary) using box plots. A full ANOVA with all interaction terms was not conducted as a secondary cliff was not present at the UWGB Escarpment site.

Comparison of Maximum Richness Levels: The percent of total richness from the five nested larger sample areas overlying each maximally-rich 0.04 m² (and 1 m²) quadrat was calculated for each site. The richness of these different sample areas was natural-log transformed and regressed against natural log-transformed estimates of habitat area. Habitat size estimates for Niagara Escarpment sections and regions were generated by multiplying average cliff-base habitat width (approx. 5 m) by habitat length. The natural log of maximum richness vs. the natural log of sample size was also plotted for the 35 literature richness records and for the maximum richness 0.04, 1, and 100 m² quadrats from the Celtis and UWGB Escarpment sites. While the limited number of samples prevented use of inferential statistics to test for significant differences between the maximum species area curves for carbonate cliffs ($n = 3$ for each site) and other habitats, a qualitative assessment was made.

RESULTS

1 m² Quadrats

Richness of terrestrial gastropods at the two sites ranged between 0 and 23 taxa (Tables 1, 2), with a mean of 6.6 taxa/ quadrat. Across both sites, mean richness was 9.9 from quadrats collected at transect position 1, 7.1 at position 2, 7.2 at position 3, 6.8 at position 4, 5.8 at position 5, 2.4 at both positions 6 and 7 (Fig. 3). ANOVA of these data demonstrated that this variation was weakly significant ($p = 0.04$; Table 3). Further ANOVA tests demonstrated that no significant differences were present between the mean richness of transect positions 1–5 ($p = 0.326$), or between the Celtis and UWGB Escarpment sites ($p = 0.646$). No interaction between transect position and site on richness was observed ($p = 0.947$). Backwards stepwise linear regression of ten environmental variables on richness demonstrated that only pH ($p < 0.0005$) and P ($p = 0.04$) were significant predictors (Table

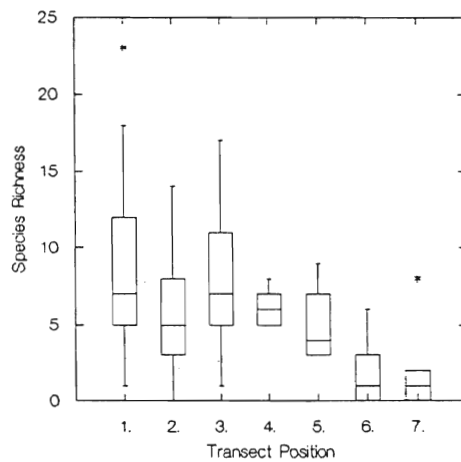


FIG. 3. Box-plot diagram of terrestrial gastropod richness at 1 m² scales with increasing distance from the primary upland cliff.

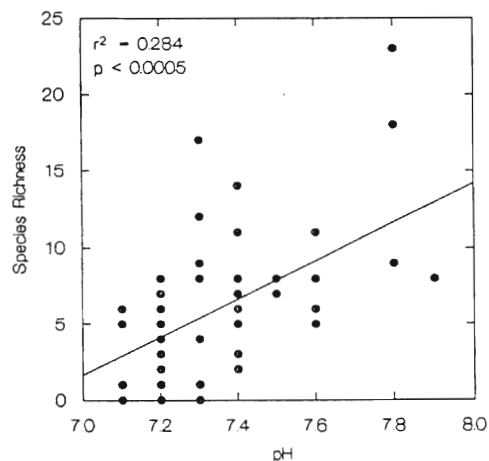


FIG. 4. Scatterplot of terrestrial gastropod richness in 1 m² quadrats vs. soil pH, with best-fit line. Twelve of the data points are not apparent in this graph as they overlap previously plotted values.

4), accounting for almost 30% of observed richness variation. However, this level of significance of P appears to be based upon a single outlier. When this observation was removed from analysis, the p value for P in a multiple linear regression of pH and P on richness dropped to 0.266. The amount of variation in richness accounted for by pH alone was found to exceed 28% (Fig. 4).

TABLE 2. Abundance and richness of terrestrial molluscs in 15 1 × 1 m² quadrats at the UWGB Escarpment site

Transect	A	A	A	B	B	B	C	C	C	D	D	D	E	E	E	
Quadrat	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	
<i>Auguispira alternata</i> (Say, 1817)	2			6			1						3	1	3	2
<i>Carychium exile</i> H. C. Lea, 1842	12	6	11	8	15	8	18	10	3	2			6	2	6	5
<i>Catinella avara</i> (Say, 1824)								1								
<i>Cochlicopa lubrica</i> (Müller, 1774)		2	1	3	8	7	5	5	4	3	11	1	2	3		
<i>Cochlicopa lubricella</i> (Porro, 1838)				1											1	
<i>Discus cronkhitei</i> (Newcomb, 1865)	1	1		1	3	1			3		3	1				
<i>Gastrocopta armifera</i> (Say, 1821)				1												1
<i>Gastrocopta holzingeri</i> (Sterki, 1889)										3				1	1	1
<i>Hawaiiia miniscula</i> (A. Binney, 1840)			2	1								4	1	1		2
<i>Helicodiscus shimaki</i> Hubricht, 1962								1	1							
<i>Strobilops labyrinthica</i> (Say, 1817)				1	1			1						1	1	
<i>Succinea ovalis</i> Say, 1817	2		4	8	2				3	2	2	1			1	2
<i>Triodopsis multilineata</i> (Say, 1821)									1							
<i>Vallonia costata</i> (Müller, 1774)			1		6	19	14	5	16	7	8	30	10	20	2	
<i>Vallonia gracilicosta</i> Reinhardt, 1883											3			1		
<i>Vallonia pulchella</i> (Müller, 1774)						1			1							
<i>Vertigo gouldi</i> (A. Binney, 1843)					1							1		2		
<i>Vertigo hubrichti</i> (Pilsbry, 1934)															5	
<i>Vertigo iowaensis</i>													1			
<i>Vertigo pygmaea</i> (Draparnaud, 1801)	4		2	2	1	3	2	9	1	1	4	1	1	7		
Immature Individuals	1	2		4	2	3	5	3		2		2	13	3		
Total Individuals	22	12	21	42	52	36	37	45	23	25	55	26	57	22	12	
Richness	5	4	6	11	8	5	6	6	8	8	7	8	12	9	5	

TABLE 3. Summary statistics for ANOVA of terrestrial gastropod species richness in 1 m² quadrats vs. quadrat distance from base of primary cliff at both the Celtis and UWGB Escarpment sites.

Source	Sum-of-Squares	df	F-Ratio	p
Distance from base	313.48	6	2.688	0.026
Error	835.90	43		
Squared multiple r:	0.273			

TABLE 4. Results of backwards stepwise linear regression of 10 environmental variables on terrestrial gastropod species richness at 1 m² grains. Variables are listed in the order in which they were removed from the model. The p-values reported are those immediately prior to removal of that variable from the model.

Variable	p-value
Mg	0.968
Percent Organic Matter	0.783
Soil Temperature at 20 cm Depth	0.406
K	0.314
Vascular Plant Species Richness	0.293
Ca	0.283
N	0.167
Surface Soil Temperature	0.121
P	0.040
pH	< 0.0005

0.04 m² Quadrats

Terrestrial gastropod richness varied from 0 to 21 taxa on all three sampled cliffs (Tables 5–7). At the primary upland cliff at the Celtis site, average species richness was 16.8 at the cliff base, 9.4 at 0.5 m, 3.2 at 1 m, 2.8 at 1.5 m, and 2.2 at 2 m distances from the cliff. At the secondary cliff at the Celtis site, average species richness was 14.4 at the cliff base, 11.2 at 0.5 m, 5.2 at 1 m, 2.8 at 1.5 m, and 2.8 at 2 m distances from the cliff. At the UWGB Escarpment site, average species richness was 8.0 at the cliff base, 8.0 at 0.5 m, 6.0 at 1 m, 5.8 at 1.5 m, and 6.4 at 2 m distances from the cliff (Fig. 5). ANOVA of these data (Table 8) demonstrated that distance from the cliff base and the interaction between this variable

TABLE 5. Abundance and richness of terrestrial molluscs in 25 20 x 20 cm² quadrats at the Celtis site primary cliff

Transect	Quadrat																													
	A 1	A 2	A 3	A 4	A 5	A 6	A 7	A 8	A 9	A 10	A 11	A 12	A 13	A 14	A 15	A 16	A 17	A 18	A 19	A 20	A 21	A 22	A 23	A 24	A 25					
<i>Anguispira alternata</i> (Say, 1817)	36	9	2							12	2	2	1	9	1	9	1	1	35	3						15	1	1		
<i>Carychium exile</i> H. C. Lea, 1842	2	1								7									13	1						39	40			
<i>Catinella gelida</i> (F. C. Baker, 1927)																														
<i>Cochlicopa lubrica</i> (Müller, 1774)	1				1																									
<i>Cochlicopa lubricella</i> (Porro, 1838)	2					2																				2				
<i>Columella simplex</i> (Gould, 1841)																														
<i>Deroceras laeve</i> (Müller, 1774)	1					4	1																							
<i>Discus caeskillensis</i> (Pilsbry, 1898)	1	1				5																								
<i>Gastrocopta armifera</i> (Say, 1821)	1					2																								
<i>Gastrocopta contracta</i> (Say, 1822)	2	4	1																											
<i>Gastrocopta corticaria</i> (Say, 1816)	5	1				1																								
<i>Gastrocopta holzingeri</i> (Sterki, 1889)	5	1			1																									
<i>Gastrocopta pentodon</i> (Say, 1821)	5	1	1			1																								
<i>Glyphyalinia indentata</i> (Say, 1823)																														
<i>Hawaii miniscula</i> (A. Binney, 1840)	1	1	2																											
<i>Helicodiscus parallelus</i> (Say, 1817)																														
<i>Helicodiscus shimeki</i> Hubricht, 1962	4	1																												
<i>Hendersonia occulta</i> (Say, 1831)	1	2																												
<i>Paravitrea multidentata</i> (A. Binney, 1840)	2					1																								
<i>Punctum vitreum</i> H. B. Baker, 1930	2																													
<i>Sirobilops labyrinthica</i> (Say, 1817)	1	1																												
<i>Vallonia costata</i> (Müller, 1774)																														
<i>Vallonia gracilicosta</i> Reinhardt, 1883																														
<i>Vertigo gouldi</i> (A. Binney, 1843)	34	8	6			10																								
<i>Vertigo hubrichti</i> (Pilsbry, 1934)	2					1																								
<i>Vertigo pygmaea</i> (Draparnaud, 1801)	18	2	2	1																										
<i>Zonitoides arboreus</i> (Say, 1816)	17	4		1		1																								
Immature	16	6	5	1		4	3	1																						
Total	154	47	20	5	1	52	7	6	2	6	57	12	1	5	1	108	23	2	2	2	2	2	2	2	2	330	138	5	4	2
Richness	19	15	7	4	1	13	3	2	2	5	13	7	1	3	1	16	7	2	2	1	2	1	2	1	2	21	16	4	3	2

TABLE 6. Abundance and richness of terrestrial molluscs in 25 20 x 20 cm² quadrats at the Celtis site secondary cliff

Transect	A					B					C					D					E				
Quadrat	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
<i>Anguispira alternata</i> (Say, 1817)	10	20	1			8	2				6					24	4	1	2		23	6	1	2	3
<i>Carychium exile</i> H. C. Lea, 1842	2	4	2			2					10					30	6				67	23			3
<i>Catinella gelida</i> (F. C. Baker, 1927)							1	2								1	2				3	3			2
<i>Cochlicopa lubrica</i> (Müller, 1774)	1	1	1			1					2	1				1	1				3				1
<i>Deroceras laeve</i> (Müller, 1774)	1	1	1			1					2					1									
<i>Discus catskillensis</i> (Pilsbry, 1898)	4					1	1				4					3					1				
<i>Euconulus fulvus</i> (Müller, 1774)						1																			
<i>Euconulus polygyratus</i> (Pilsbry, 1899)	4					1										2	1				3				
<i>Gastrocopta armifera</i> (Say, 1821)											11														
<i>Gastrocopta contracta</i> (Say, 1822)	4	2														2					14	8	1	1	
<i>Gastrocopta corticaria</i> (Say, 1816)	5	2	1	1							4					3	1				1				
<i>Gastrocopta holzingeri</i> (Sterki, 1889)	1	2				3					8	6				40	21	1	1		58	33	12	10	5
<i>Gastrocopta pentodon</i> (Say, 1821)	5	1	1			1										4									
<i>Glyphyalinia indentata</i> (Say, 1823)																1					1				
<i>Glyphyalinia rhoadsi</i> (Pilsbry, 1899)																1					1				
<i>Guppya sterkii</i> (Dall, 1888)																									
<i>Hawailia miniscula</i> (A. Binney, 1840)	1	1	4													1					3	16	9	1	1
<i>Helicodiscus parallelus</i> (Say, 1817)																1									
<i>Helicodiscus shimiki</i> Hubricht, 1962	19	5	3			2										3					11	3			
<i>Hendersonia occulta</i> (Say, 1831)	2	8	1	3	1	8	1	8			2	1	1			2	5	1	1		2	1			
<i>Nesovitrea binneyana</i> (Morse, 1864)	1															1									
<i>Paravitrea multidentata</i> (A. Binney, 1840)	4	1				1					1					1									
<i>Punctum vitreum</i> H. B. Baker, 1930	1	1	1			1					1					4	1				6	5			1
<i>Strobilops labyrinthica</i> (Say, 1817)	2	1	1			1					2					1	1				5	1			
<i>Vertigo gouldi</i> (A. Binney, 1843)	1	3	1	1		1	1				23	3				1	13	5	2		2	29	35	4	4
<i>Vertigo Hubrichti</i> (Pilsbry, 1934)																									
<i>Vertigo pygmaea</i> (Draparnaud, 1801)	24	6				3					1					6					5				
<i>Zonitoides arboreus</i> (Say, 1816)	1	6									17	2				5	4				34	20	4	3	4
Immature	91	58	25	3	3	18	25	2	1	6	81	13	1	0	3	151	52	6	4	2	280	148	26	21	22
Total	18	15	12	3	1	8	11	1	1	3	12	4	1	0	2	20	13	5	3	1	15	12	8	5	8
Richness																									

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TABLE 7. Abundance and richness of terrestrial molluscs in 25 20 x 20 cm² quadrats at the UWGB Escarpment cliff

Transect	A	A	A	A	A	A	B	B	B	B	B	C	C	C	C	C	C	D	D	D	D	D	D	E	E	E	E	E		
Quadrat	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
<i>Anguispira alternata</i> (Say, 1817)	3	1				1	1	1	1	2	1	1	2			2		1			3									
<i>Carychium exile</i> H. C. Lea, 1842	4	5	13	10	9	16	24	12	29	11	93	23	13	18		1	7	9	8	1	18	49	29	36						
<i>Catinella avara</i> (Say, 1824)										1																				
<i>Cochlicopa lubrica</i> (Müller, 1774)	1	2	3	1	1	1			1	3	2				9	7	1	2	3	2	4	4	2	5						
<i>Cochlicopa lubricella</i> (Porro, 1838)												2	2			2														
<i>Discus cronkhitei</i> (Newcomb, 1865)						1			1		1	1			1	5					2	1								
<i>Gastrocopta armifera</i> (Say, 1821)						1			1		1	1			1	1		2												
<i>Gastrocopta contracta</i> (Say, 1822)																														
<i>Gastrocopta holzingeri</i> (Sterki, 1889)																1	1	1												
<i>Hawaiiia miniscula</i> (A. Binney, 1840)																1		1												
<i>Helicodiscus shimiki</i> Hubricht, 1962																														
<i>Strobilops labyrinthica</i> (Say, 1817)	1	3	1	2	1	2			2	2	1	2	1			1	2	2	1	1										
<i>Succinea ovalis</i> Say, 1817																														
<i>Triodopsis multilinata</i> (Say, 1821)																														
<i>Vallonia costata</i> (Müller, 1774)	3	3	2	1	5	5	2	2	2	3	2	1				8	20	7	3	2	7	9	1	2						
<i>Vallonia gracilicosta</i> Reinhardt, 1883																														
<i>Vallonia pulchella</i> (Müller, 1774)	1					1																								
<i>Vertigo gouldi</i> (A. Binney, 1843)																														
<i>Vertigo hubrichti</i> (Pilsbry, 1934)																														
<i>Vertigo iowaensis</i>																														
<i>Vertigo milium</i> (Gould, 1840)	1					1				1																				
<i>Vertigo pygmaea</i> (Draparnaud, 1801)	5	3	2	1	1	5	2	2	2	5	2	4	1		6	6	2	5	7	4	4	5	6	2						
Immature	4	3		5	6	5	1	10	7	1	7	9		4	25	18	18	26	10	12	18	9	21							
Total	23	22	22	22	25	19	26	39	26	38	29	107	41	17	26	56	65	38	49	32	31	68	74	63	58					
Richness	8	8	6	7	7	6	6	4	5	6	10	5	6	4	5	10	10	6	7	6	6	12	8	6	8					

TABLE 8. Summary statistics for ANOVA of terrestrial gastropod species richness in 0.04 m² quadrats vs. quadrat distance from cliff base, cliff position, and site location.

Source	Sum-of-Squares	df	F-Ratio	<i>p</i>
Site	0.08	1	0.008	0.928
Cliff position	2.88	1	0.296	0.589
Distance from base	406.08	4	10.423	< 0.0005
Distance * Site	271.72	4	6.974	< 0.0005
Distance * Cliff	25.12	4	0.645	0.633
Error	584.04	60		

Squared multiple *r*: 0.699

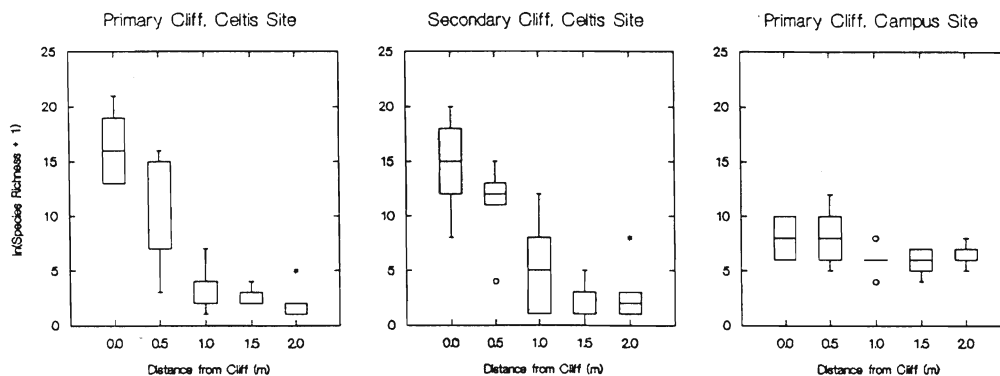


FIG. 5. Box-plot diagram of terrestrial gastropod richness from 0.04 m² scales at increasing distances from three cliff exposures at the Celtis and UWGB Escarpment sites.

and site were both highly significant ($p < 0.0005$). In all, distance from cliff base and site accounted for 70% of the observed variation in richness. Mean richness was not affected by cliff type (primary or secondary; $p = 0.649$) and cliff type did not interact with the rate of richness decrease from the cliff base ($p = 0.518$).

Comparison of Maximum Richness Levels

At the UWGB Escarpment, a maximum of 12 taxa were observed from single 0.04 and 1 m² quadrats. As this site represents the lone surviving carbonate cliff community within the 6 km Bay Settlement section, the total richness of this Escarpment section equals site richness (25 taxa). For the Celtis site, all small-scale richness values were higher, with a maximum richness of 21 taxa occurring in a single 0.04 m² sample, and 23 taxa in a single 1 m² sample. Carbonate outcrops along the 8 km Benderville Escarpment Section (within which the Celtis site occurs) support 38 taxa. All carbonate cliffs along the 350 km Eastern Wisconsin-Garden Peninsula Escarpment Re-

gion support 62 taxa. The total richness of Brown County terrestrial gastropods, across all habitat types, is 65 taxa, while a total of 95 taxa have been documented across all habitats in the state of Wisconsin (Table 9).

The faunas of maximum richness 0.04 m² quadrats at the Celtis site thus account for up to 91% of maximum 1 m² richness, 62% of site richness, 55% of Escarpment section richness, and 34% of Escarpment region richness. Individual 0.04 m² quadrats also harbored up to 32% of the entire county fauna, and 22% of the entire state fauna. Given their similar maximum richness, almost identical results are present for maximum richness 1 m² quadrats, which can harbor up to 68% of the entire site fauna, 61% of the Escarpment section fauna, and 37% of the entire Escarpment region fauna. Individual 1 m² quadrats can also harbor up to 35% of the entire county fauna, and 24% of the entire state fauna. Because of the lower richness levels at the UWGB Escarpment Site, these numbers tended to be lower by almost 30–50% from Celtis site levels. Regression analysis demonstrates that a high correlation ($p < 0.0005$; $r^2 =$

TABLE 9. Percent of site, escarpment section, escarpment region, county, and state terrestrial gastropod faunas contained within maximum diversity 0.04 and 1 m² quadrats.

UWGB Escarpment Site			
Sample Grain	Richness	Percent Overlap	
		0.04 m ²	1 m ²
0.04 m ²	12		
1 m ²	12	100	
Site (100 m ²)	25	48	48
Niagara Escarpment			
Bay Settlement Section	25	48	48
Eastern Wisconsin Region	62	19	19
Brown County	65	18	18
Wisconsin	95	13	13

Celtis Site			
Sample Grain	Richness	Percent Overlap	
		0.04 m ²	1 m ²
0.04 m ²	21		
1 m ²	23	91	
Site (100 m ²)	34	62	68
Niagara Escarpment			
Benderville Section	38	55	61
Eastern Wisconsin Region	62	34	37
Brown County	65	32	35
Wisconsin	95	22	24

0.839) exists between natural log-transformed richness and sample area, with the best-fit line having an intercept of 2.93 and a slope of 0.063 (Fig. 6). This translates to an average richness of 18.7 taxa per 1 m² and 33.4 taxa per hectare.

Comparison of maximum richness from 0.04 and 1 m² quadrats to other reported maximum richness values demonstrates the Celtis site site is among the richest reported globally from small observational scales (Fig. 7). Maximum richness levels at the Celtis site compare favorably with the richest reported 1–400 m² samples in Germany, Sweden, and Scotland (Schmid, 1966; Waldén, 1981; Cameron & Greenwood 1991). The richest global terrestrial gastropod faunas, collected over larger areas (400–40,000 m²) in New Zealand, Madagascar, Tanzania, and Cameroon appear to fall along the same maximum species-area curve defined from the Celtis Site. While maximum richness at the UWGB Escarpment is lower, these observations still lie within the upper half of previously reported maximum richness levels for the given range of sample scales.

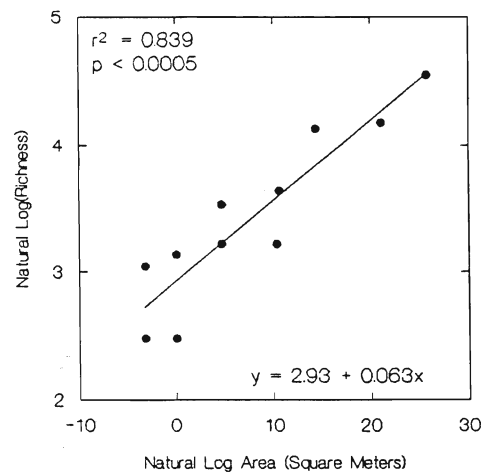


FIG. 6. Scatterplot of natural log-transformed terrestrial gastropod richness vs. natural log-transformed sample area for Wisconsin carbonate cliff land snail faunas. The scales of observation include: maximum-richness 0.04, 1, and 100 m² quadrats from the Celtis and UWGB Escarpment sites; the respective escarpment sections for each; escarpment region; county; and state.

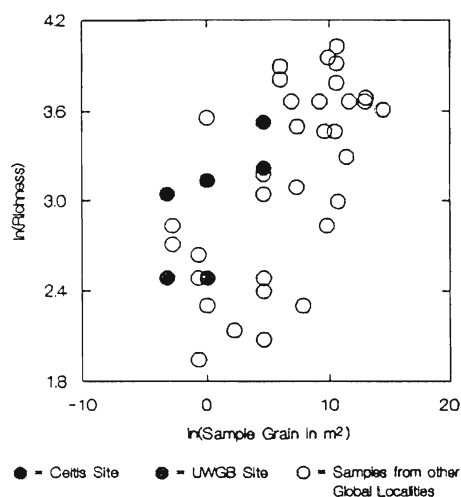


FIG. 7. Species-area plot of maximum-richness 0.04, 1 and 100 m² quadrats from the Celtis and UWGB Escarpment sites compared to other maximum richness levels reported from other global sites.

DISCUSSION

Diversity Patterns Within Carbonate Cliff Communities

The high richness of terrestrial gastropods within carbonate cliff habitats occurs down to very limited spatial scales, with up to 62% of site richness (and up to 22% of total state richness) being found within single 0.04 m² areas along cliff bases. The limitation of high-diversity assemblages to the immediate vicinity of vertical bedrock outcrops is striking, with richness decreasing by almost six-fold from 0 to 1 m from cliff bases. This rapid and drastic reduction in richness helps explain why, on average, 0.04 m² quadrats at cliff bases harbor more species than adjacent 1 m² quadrats. As the 1 m² samples consisted of pooled subsamples taken from the corners and center of each quadrat, only two subsamples per quadrat were thus collected from mollusc-rich microsites. This had the unintended effect of diluting snail density and richness. However, the 0.04 m² cliff-base quadrats, which consisted to a similar total volume of soil litter, were collected entirely from the richest microsites, so that no dilution in snail density or richness occurred.

While diversity at the 0.04 m² scale was markedly higher adjacent to cliffs at the undis-

turbed Celtis site, such spatial limitation of richness was not observed at the UWGB Escarpment. In addition, maximum (but not mean) richness at both 0.04 and 1 m² scales at the UWGB Escarpment site was roughly one-half that recorded at the Celtis Site. It is probable that these lower maximum diversity levels, and lack of strong micro-scale diversity gradients, are related to this site's past quarrying history, which may have simplified the range of microhabitats present along the cliff base.

The exact mechanisms that lead to high levels of terrestrial gastropod richness at micro-scales within these carbonate cliff sites have not been documented. First, it is not known how many of these shells originate from individuals living in the quadrat versus shells that have been deposited from nearby areas, such as adjacent vertical rock faces. If this latter process is important, levels of micro-scale sympatry could be substantially lower than the observed shell richness suggests. However, preliminary observations of living individuals on cliff bases and adjacent vertical faces suggest that the majority of shells originate from within quadrats. Additionally, most species observed from cliff-base quadrats are represented by at least one living snail or recently dead shell, while species reported from more distant quadrats are almost always represented by long-dead shell fragments.

Second, even if shells from high-richness microsites are locally derived, observed richness may be exaggerated if shells persist in the soil for long periods. In this case, species lists will represent an integration over the persistence-time of shells. This could lead to an overestimate of microsympatry if local faunas are in a state of constant flux. Use of radioisotope dating on shells could provide a possible test for shell half-life, which would help set the temporal scales of integration for such shell-banks in carbonate cliff soils. However, the fact that most taxa are represented in samples by at least one live or recently dead shell suggests that high levels of sympatry are likely maintained at both limited temporal and spatial extents.

The existence of diverse terrestrial gastropod assemblages at very small scales on or adjacent to carbonate outcrops is also likely not unique to the two sites chosen for analysis. Qualitative observations of other carbonate cliffs in Illinois, Iowa, New York, Ontario, Wisconsin, and southwestern England sug-

gest that the co-occurrence of 20 or more taxa at 1 m² or smaller grains may be typical in undisturbed sites.

The limitation of high richness terrestrial gastropod assemblages to the immediate proximity of cliffs also indicates that these microhabitats must be afforded special protection if their biodiversity is to be protected. Unfortunately, planned and spontaneous recreational trails in reserves are often routed through these exact areas as they are aesthetically pleasing and provide access to charismatic natural features such as caves, fissures, and rock walls. Such trails may place any high-richness terrestrial gastropod assemblages in serious jeopardy. For instance, the cliff base at Bayshore County Park, 6 km north of the Celtis Site, has been turned into a graveled trail which now lacks a terrestrial gastropod fauna (Nekola, unpublished data).

Environmental Controls on Small Scale Richness Patterns

The literature regarding the environmental controls of terrestrial gastropod richness and abundance is very conflicting. Burch (1955) suggested that in eastern Virginia snail abundance (and presumably diversity) was related to soil organic matter, Ca, Mg, and K, but not pH. Lack of correspondence between terrestrial gastropod distribution and pH has also been demonstrated in southwestern Ireland (Bishop, 1977) and the Italian Alps (Bishop, 1980). However, Gleich & Gilbert (1976), stated that in central Maine soil moisture, but not soil Ca, was the most important determinant of snail abundance. Outeiro et al. (1993) demonstrated that soil texture and pH were the most important factors effecting terrestrial gastropod distribution in central Spain. Soil pH was also identified as an important determinant of terrestrial gastropod density and diversity by Waldén (1981) and Gärdenfors (1992) in southern Sweden, and by Bishop (1976) in Somerset, England. Getz (1974) and Getz & Uetz (1994) identified soil moisture, tree diversity, and leaf litter diversity as major determinants of diversity in the Great Smoky Mountains. However, Locasciulli & Boag (1987) demonstrated in Alberta forests that terrestrial gastropod abundance was not related to vegetation.

Within eastern Wisconsin carbonate cliff habitats, only soil pH (and not soil Ca, Mg, N, P, K, percent organic matter, soil temperature, or vascular plant richness) was found to cor-

relate significantly with terrestrial gastropod richness at the 1 m² scale. This result is consistent with the analysis of Bishop (1980), who states that soil pH will only be an important environmental correlate of terrestrial gastropod assemblages when soil Ca levels are high. Interactions between environmental variables may explain why such a diversity of factors exist that have (and have not) been shown to influence terrestrial gastropod richness across various habitats and regions. Thus, extrapolation of these results to other habitats or regions may be risky. These results do, however, provide insight into the environmental correlates of terrestrial gastropod richness within Ca-rich carbonate cliffs.

Spatial Scales of Terrestrial Gastropod Coexistence

A complete assessment of the scales over which terrestrial gastropod coexistence is mediated is not possible because the current data are restricted to five discrete spatial scales (0.04 m², 1 m², 100 m², approx. 3.5 ha, and approx. 1750 ha). However, given the wide total range covered, some preliminary insights into this issue can be made.

Three of the measured scales appear to harbor the bulk of terrestrial gastropods. Up to one-third of the total regional fauna may occur within individual 0.04 m² regions. Over 50% of the total regional fauna may occur within 100 m² regions on individual sites. The remainder of the fauna (almost 50% of the regional total) is largely found between sites on different Escarpment Sections (e.g., sites 10 km or more apart, corresponding to 3.5 + ha of cliff base habitat). However, little increase in richness was observed between 0.04 m² and 1 m² extents within sites, and between sites within the same Escarpment Section (100 m²–3.5 km of cliff base habitat).

One tentative conclusion that can be drawn from these results is that alpha diversity (*sensu* Whitaker, 1975) in these sites is best measured at scales no larger than 0.04 m², beta diversity (*sensu* Whitaker, 1975) is best measured at scales no larger than 100 m², and gamma diversity (*sensu* Cody, 1986) is best measured between sites at least 10 km distant from one another. Although Emberton (1995) states that distinctions between alpha, beta, and gamma diversity are hazy for terrestrial gastropod communities, these data suggest that such problems in resolution may be due to poorly chosen observational scales.

For instance, if the Celtis and UWGB Escarpment sites had been sampled at typical malacological sampling scales of 0.1 ha or larger, distinctions between alpha and beta diversity would be impossible to make, as sample resolution would be at least 1000 times greater than the scale at which alpha diversity likely exists.

Additional research will be necessary to document the mechanisms that allow for species coexistence at these differing scales. Ecological theory suggests that alpha diversity levels may be related to levels of niche partitioning between species (Auerbach & Shmida, 1987). However, competition and predation have only rarely been shown to influence terrestrial gastropod distribution and abundance (Cain, 1983; Cowie & Jones, 1987; Smallridge & Kirby, 1988). The high density of shells (up to 330 per 0.04 m² quadrat) further suggests that resource levels are also high, cautioning against use of resource-ratio models (e.g., Tilman, 1988). Identification of the small-scale coexistence mechanisms in these habitats may be of broad ecological importance, as it is rare for alpha diversity to constitute such a high proportion of regional diversity, and thus for the rate of species accumulation with increasing sample size to be so low (Rosenzweig, 1995).

At larger scales of observation, habitat heterogeneity may be important in determining levels of species richness (Auerbach & Shmida, 1987; Rosenzweig 1995). The few additional species added between site and escarpment section scales suggests that the universe of microenvironments found within a given carbonate cliff site may be very similar to those present within an entire Escarpment section. At the largest scales, coexistence of terrestrial gastropods will likely be mediated by large environmental gradients (including climate), differential colonization histories of habitats (Ricklefs & Schluter, 1993; Nekola, in press), and the incomplete dispersal of species between sites (Auerbach & Shmida, 1987).

It is important to note that the spatial scales of coexistence for terrestrial gastropod communities, and hence the optimal scales of observation, may differ between systems and landscapes. For instance, it is not clear that alpha diversity will always be confined to such small scales in habitats that support substantially lower densities of individuals and taxa. Gamma diversity will also likely vary between landscapes, as preliminary analyses have

documented for Niagaran Escarpment carbonate cliffs in which rates of community turnover may vary by an order-of-magnitude (Nekola, unpublished data). Such observations suggest that additional research will be necessary within and between a diversity of habitats and landscapes to determine if any general rules exist to guide the ecological sampling of terrestrial gastropod communities.

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LITERATURE CITED

- AGÓCSY, P., 1968, Data to quantitative conditions in the mollusk faunas of two different substrates in central Hungary. *Acta Zoologica Academiae Scientiarum Hungaricae*, 14: 1–6
- AUERBACH, M. & A. SHMIDA, 1987, Spatial scale and the determinants of plant species richness. *Trends in Ecology and Evolution*, 2: 238–242.
- BERRY, A. J., 1966, Population structure and fluctuations in the snail fauna of a Malayan limestone hill. *Journal of Zoology, London*, 150: 11–27.
- BERRY, F. G., 1973, Patterns of snail distribution at Ham Street Woods National Nature Reserve, East Kent. *Journal of Conchology*, 28: 23–35.
- BISHOP, M. J., 1976, Woodland mollusca around Nettlecombe, Somerset. *Field Studies*, 4: 457–464.
- BISHOP, M. J., 1977, The mollusca of acid woodland in West Cork and Kerry. *Proceedings of the Royal Irish Academy*, 77B: 227–244.
- BISHOP, M. J., 1980, The mollusca of acid woodland in the Italian province of Novara. *Journal of Conchology*, 30: 181–188.
- BURCH, J. B., 1955, Some ecological factors of the soil affecting the distribution and abundance

- of terrestrial gastropods in eastern Virginia. *The Nautilus*, 69: 62–69.
- BURCH, J. B., 1956, Distribution of terrestrial gastropods in plant associations in eastern Virginia. *The Nautilus*, 70: 60–64.
- BURROUGH, P. A., 1986, *Principles of geographical information systems for land resources assessment*. Oxford University Press, New York.
- CAIN, A. J., 1983, Ecology and ecogenetics of terrestrial molluscan populations. Pp. 597–647, In: W. D. RUSSELL-HUNTER, ed., *The Mollusca*. Vol. 6. *Ecology*. Academic Press, London.
- CAMERON, R. A. D., 1978, Differences in the sites of activity of coexisting species of land mollusc. *Journal of Conchology*, 29: 273–278.
- CAMERON, R. A. D., 1986, Environment and diversities of forest snail faunas from coastal British Columbia. *Malacologia*, 27: 341–355.
- CAMERON, R. A. D., 1992, Land snail faunas of the Napier and Oscar Ranges, Western Australia; diversity, distribution and speciation. *Biological Journal of the Linnean Society*, 45: 271–286.
- CAMERON, R. A. D. & J. J. D. GREENWOOD, 1991, Some montane and forest molluscan fauna from eastern Scotland: effects of altitude, disturbance, and isolation. *Proceedings of the Tenth International Malacological Congress* (Tübingen 1989), 437–442.
- CODY, M. L., 1986, Diversity, rarity, and conservation in Mediterranean-climate regions. Pp. 122–152, In: M. E. SOULE, ed., *Conservation Biology*. Sinauer Associates, Sunderland, Massachusetts.
- COWIE, R. H. & J. S. JONES, 1987, Ecological interactions between *Cepaea nemoralis* and *Cepaea hortensis*: competition, invasion, but no niche displacement. *Functional Ecology*, 1: 91–97.
- COWIE, R. H., G. M. NISHIDA, Y. BASSET & S. M. GON, III, 1995, Patterns of terrestrial gastropod distribution in a montane habitat on the island of Hawaii. *Malacologia*, 36: 155–169.
- DAHNIKE, W. C., 1988, Recommended chemical soil test procedures for the north-central region. *North Dakota Agricultural Experiment Station Bulletin*, 499, North Dakota State University, Fargo.
- DE WINTER, A. J. & E. GITTEBERGER, 1998, The terrestrial gastropod fauna of a square kilometer patch of rainforest in southwestern Cameroon: high species richness, low abundance, and seasonal fluctuations. *Malacologia*, 40: 231–250.
- EMBERTON, K. C., 1995, Land-snail community morphologies of the highest-diversity sites of Madagascar, North America, and New Zealand, with recommended alternatives to height-diameter plots. *Malacologia*, 36: 43–66.
- EMBERTON, K. C., T. A. PEARCE, P. F. KASIGWA, P. TATTERSFIELD & Z. HABIBU, 1997, High diversity and regional endemism in terrestrial gastropods of eastern Tanzania. *Biodiversity and Conservation*, 6: 1123–1136.
- FREST, T. J., 1991, *Summary status reports on eight species of candidate terrestrial gastropods from the Driftless Area (Paleozoic Plateau), upper Midwest*. Final Report, Contract #301-01366, USFWS Region 3, Ft. Snelling, Minnesota.
- GÄRDENFORS, U., 1992, Effects of artificial liming on terrestrial gastropod populations. *Journal of Applied Ecology*, 29: 50–54.
- GETZ, L. L., 1974, Species diversity of terrestrial snails in the Great Smoky Mountains. *The Nautilus*, 88: 6–9.
- GETZ, L. L. & G. W. UETZ, 1994, Species diversity of terrestrial snails in the southern Appalachian mountains, U.S.A. *Malacological Review*, 27: 61–74.
- GLEICH, J. G. & F. F. GILBERT, 1976, A survey of terrestrial gastropods from central Maine. *Canadian Journal of Zoology*, 54: 620–627.
- HERMIDA, J., P. ONDINA & A. OUTEIRO, 1995, Influence of soil characteristics on the distribution of terrestrial gastropods in northwest Spain. *European Journal of Soil Biology*, 31: 29–38.
- JASS, J. P., 1986, Supplemental distribution records for Wisconsin terrestrial gastropods. *Transactions of the Wisconsin Academy of Science, Arts, and Letters*, 74: 105–107.
- KRALKA, R. A., 1986, Population characteristics of terrestrial gastropods in boreal forest habitats. *American Midland Naturalist*, 115: 156–164.
- LEVI, L. R. & H. W. LEVI, 1950, New records of terrestrial gastropods from Wisconsin. *The Nautilus*, 63: 131–138.
- LOCASCIULLI, O. & D. A. BOAG, 1987, Microdistribution of terrestrial snails (Stylommatophora) in forest litter. *Canadian Field Naturalist*, 101: 76–81.
- MASON, C. F., 1970, Snail populations, beech litter production, and the role of snails in litter decomposition. *Oecologia*, 5: 215–239.
- NEKOLA, J. C., ~~in press A~~, 1999, Terrestrial gastropod richness of carbonate cliff and associated habitats in the Great Lakes region of North America. *Malacologia*, 41: 231–252. * 1999 *
- NEKOLA, J. C., ~~in press B~~, Paleoreugia and neoreugia: the influence of colonization history on ecological pattern. *Ecology*. *
- NEKOLA, J. C., T. A. SMITH & T. J. FREST, 1996, *Terrestrial gastropod faunas of Door Peninsula natural areas*. Report to Wisconsin Chapter, The Nature Conservancy, Madison.
- NILSSON, S. G., J. BENGTTSSON & S. ÅS, 1988, Habitat diversity or area per se? Species richness of woody plants, carabid beetles and terrestrial gastropods on islands. *Journal of Animal Ecology*, 57: 685–704.
- OUTEIRO, A., D. AGÜERA & C. PAREJO, 1993, Use of ecological profiles and canonical correspondence analysis in a study of the relationship of terrestrial gastropods and environmental factors. *Journal of Conchology*, 34: 365–375.
- PAUL, C. R. C., 1975, The ecology of mollusca in ancient woodland. I. The fauna of Hayley Wood, Cambridgeshire. *Journal of Conchology*, 28: 301–327.
- RICKLEFS, R. E. & D. SCHLUTER, 1993, Species

- diversity: regional and historical influences. Pp. 350–363, in R. E. RICKLEFS & D. SCHLUTER, eds., *Species diversity in ecological communities*. University of Chicago Press, Chicago.
- ROSENZWEIG, M. L., 1995, *Species diversity in space and time*. Cambridge University Press, New York.
- SCHMID, G., 1966, Die mollusken des Spitzbergs. *Der Spitzberg bei Tübingen, Natur und Landschaftsschutzgebiete, Baden-Württemberg*, 3: 596–701.
- SMALLRIDGE, M. A. & G. C. KIRBY, 1988, Competitive interactions between the terrestrial gastropods *Thebia pisana* (Müller) and *Ceriuella virgata* (DaCosta) from South Australia. *Journal of Molluscan Studies*, 54: 251–258.
- SOLEM, A., F. M. CLIMO & D. J. ROSCOE, 1981, Sympatric species diversity of New Zealand terrestrial gastropods. *New Zealand Journal of Zoology*, 8: 453–485.
- STEIGLITZ, R. D., J. M. MORAN & J. D. HARRIS, 1980, A relict geomorphological feature adjacent to the Silurian escarpment in northeastern Wisconsin. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters*, 68: 202–207.
- TATTERSFIELD, P., 1996, Local patterns of terrestrial gastropod diversity in a Kenyan rain forest. *Malacologia*, 38: 161–180.
- TESKEY, M. C., 1954, The mollusks of Brown County, Wisconsin. *The Nautilus*, 68: 24–28.
- TILMAN, D., 1988, *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton.
- UMINSKY, T. & U. FOCHT, 1979, Population dynamics of some land gastropods in a forest habitat in Poland. *Malacologia*, 18: 181–184.
- VAN ES, J. & D. A. BOAG, 1981, Terrestrial molluscs of central Alberta. *Canadian Field-Naturalist*, 95: 76–79.
- VELLEMAN, P. F. & D. C. HOAGLIN, 1981, *Applications, basics, and computing of exploratory data analysis*. Addison-Wesley Press, Reading, Massachusetts.
- WALDEN, H. W., 1981, Communities and diversity of land molluscs in Scandinavian woodlands. I. High diversity communities in taluses and boulder slopes in SW Sweden. *Journal of Conchology*, 30: 351–372.
- WALDHAUGH, A. A., 1995, The terrestrial molluscan fauna of some woodlands in northeast Yorkshire, England. *Journal of Conchology*, 35: 313–327.
- WHITTAKER, R. H., 1975, *Communities and ecosystems*. MacMillan Publishing, New York.
- YOUNG, M. S. & J. G. EVANS, 1991, Modern land mollusc communities from Flat Holm, South Glamorgan. *Journal of Conchology*, 34: 63–70.

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