

ACIDOPHILIC TERRESTRIAL GASTROPOD COMMUNITIES OF NORTH AMERICA

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(Received 10 September 2009; accepted 19 October 2009)

ABSTRACT

Habitats with soil pH < 4 and Ca < 100 ppm, such as pocosins, *Sphagnum* bogs and heathlands, would appear inimical to land-snail biodiversity. Nevertheless, a survey of 1,356 sites, c. 1/2 million individuals and over 240 species (c. 1/5 of the continental fauna) across North America shows that c. 10% of species appear to favour such highly or moderately acidic sites, spread from subtropical forests of the Gulf of Mexico coast to the arctic tundra. Nonmetric multidimensional scaling ordination of faunas from 292 sites that support at least five co-occurring species documents that the principal axis of compositional variation in highly and moderately acidic habitats is significantly ($P < 0.0005$) correlated with latitude, while the second axis is significantly ($P < 0.0005$) correlated with moisture level. Composition was found to vary continuously along both axes, implying that discrete acidophilic communities are not present. While highly and moderately acidic sites were shown to have significantly ($P < 0.000000005$) lower richness and abundance compared with neutral/calcareous habitats, even the most acidic sites still typically supported 5–10 species. Abundance distributions in highly acidic habitats were found to be more uneven than those of neutral/calcareous sites. The greater richness of the North American acidophilic land snail fauna compared with that in Europe has allowed communities to display replacement-driven compositional turnover. These results demonstrate that it is vitally important for biodiversity surveys of North American land snails not to ignore acidic habitats, because they harbour an important and surprisingly diverse fauna.

INTRODUCTION

It is well established that terrestrial gastropod communities in lime-rich habitats such as carbonate bedrock outcrops, fens, chalk grasslands and rich upland and lowland forests often support abundant and diverse land-snail communities (e.g. Boycott, 1934; Burch, 1962; Kerney & Cameron, 1979; Stanisci, 1997; Barker & Mayhill, 1999; Nekola, 1999; Schilthuisen, 2004; Horsák, 2005). In fact, one of the principle global trends identified in land-snail ecology is the strong positive correlation between individual abundance, species richness and the pH of the organic litter in which land-snail communities reside (Valovirta, 1968; Wäreborn, 1970; Waldén, 1981; Outeiro, Agüera & Parejo, 1993; Barker & Mayhill, 1999; Nekola & Smith, 1999; Hermida, Ondina & Rodreiguez, 2000; Pokryszko & Cameron, 2005; Horsák, 2006). This is not surprising given the high metabolic calcium demands of land snails not only for shell generation but also for egg production (Wäreborn, 1970; Gårdenfors, 1992). Across the entire north-western European fauna of about 300 species, only five (*Columella aspera*, *Vertigo ronneyensis*, *Vertigo lilljeborgi*, *Zonitoides excavatus* and *Zoogenetes harpa*) have been noted to favour acidic habitats (Boycott, 1934; Kerney & Cameron, 1979). Highly acidic habitats, such as *Sphagnum* bogs, heathlands and pine forest have thus generally been regarded as unfavourable for high land-snail biodiversity (Karlin, 1961; Kerney & Cameron, 1979; Horsák & Hájek, 2003).

No strongly acidophilic/calcareous land-snail fauna had previously been reported from North America (Pilsbry, 1948; Hubricht, 1985) when *Vertigo malleata* was described and shown to be limited to ombrotrophic peatlands of the Atlantic coastal plain (Coles & Nekola, 2007). These sites possess soils with organic litter pH ranging from 3.5 to 4.0 and Ca concentrations of only 25–100 ppm (Woodwell, 1958; Richardson, 1983). An additional 35 co-occurring species, representing

about one-fifth of the entire North American Atlantic coastal plain fauna, were noted from these and adjacent upland pine-flatwood sites, which have soil pH ranging from 3.5 to 4.5 and Ca ppm values of 20–500 (Binkley *et al.*, 1992). Some of the species observed in these habitats, such as *Triodopsis soelneri* and *Vertigo alabamensis*, are thought to be among the continent's rarest species (Hubricht, 1985; NatureServe, 2009).

Does this apparent acidophilic land-snail fauna from the Atlantic seaboard represent an idiosyncratic outlier, or do similar faunas occur across North America? How many species should be considered acidophilic/calcareous within the continental fauna? What major gradients in community composition can be identified, and with which environmental variables do these correlate? How does community richness and abundance vary between base-rich and base-poor habitats across the major land-snail habitat types? To provide a better understanding of the community ecology of acidophilic land-snail communities within North America these issues are addressed in the present paper.

MATERIAL AND METHODS

Study sites

Land-snail faunas were analysed from 1,356 sites ranging from the Alaskan North Slope and southern California coast eastwards to central Quebec, and the Atlantic seaboard from Maine to Georgia (Fig. 1). Matrix vegetation varies from tundra and taiga in the north, to tallgrass prairie in the Midwest, to mixed deciduous-conifer forest in the southwest and to mixed boreal-hardwood, deciduous and evergreen subtropical forest in the east and south (Barbour & Billings, 1988). Using the principal land-snail community types identified by Nekola (2003), this sample includes 377 rock outcrops,



Figure 1. Location of all 1,356 sampling sites. Black circles represent highly or moderately acidic habitats; open circles represent neutral/calcareous stations.

357 upland forests, 286 lowland forests, 114 upland grasslands and 222 lowland grasslands.

Field methods

Documentation of terrestrial gastropod faunas from representative 100–1,000 m² areas within sites was accomplished by hand collection of larger shells and litter sampling for smaller taxa. Particular focus was placed on the latter approach as it provides the most complete assessment of site faunas (Oggier, Zschokke & Baur, 1998; Cameron & Pokryszko, 2005). As suggested by Emberton, Pearce & Randalana (1996), collections were made at places of high micromollusc density such as loosely compacted leaf litter lying on top of highly compacted damp mineral soil or humus. Approximately 500 ml of sieved litter ranging from 0.425 to 9.5 mm in minimum particle size was retrieved from each site, either by field sieving or collection of *c.* 4 l of unsorted leaf litter. These unsorted bagged samples were slowly and completely dried with the *c.* 500 ml of sorted litter extracted from each sample in the laboratory by use of careful but vigorous water disaggregation. A half litre of sieved litter was set as the sample goal, as this volume typically captured 10 times the number of individuals as species, which is advocated by Cameron & Pokryszko (2005) for accurate documentation of land-snail community composition.

The latitude–longitude position of each site was determined using either USGS 7.5 min topographic maps or a hand-held GPS. Each site was scored in one of the five principal land-snail habitat categories identified by Nekola (2003). Sites were also scored along a moisture gradient from 1 (dry vertical rock outcrops and xeric uplands) to 5 (completely saturated vegetation mats). Scores of 2 represented dry-mesic uplands, 3 represented mesic sites and 4 lowland sites with nearly saturated soils.

The soil acidity of each site was assessed by observation of exposed bedrock, vascular plant and bryophyte cover. Bryophyte composition was particularly noted as this group serves as one of the best bio-indicators of soil-water solution acidity (Vitt & Chee, 1990). Sites were categorized as ‘highly

acidic’ when exposed bedrock consisted of silica sand, shale, quartzite, schist, gneiss or felsic igneous rock, when vascular plant cover was dominated by pines and/or oaks, the shrub layer was limited to various heaths, *Myrica* and/or *Ilex*, and when bryophytes were limited to acidophilic genera such as *Leucobryum*, *Polytrichum* and *Sphagnum* (Crum & Anderson, 1981). Sites were categorized as ‘moderately acidic’ when exposed bedrock consisted of CaCO₃-cemented sandstone or intermediate to intermediate-felsic igneous rock or when vascular plant and bryophyte cover included not only acidophilic taxa but also more base-demanding genera such as *Climacium*, *Hypnum*, *Mnium*, *Rhodobryum*, *Rhytididelphus* and *Thuidium* (Crum & Anderson, 1981). Sites were characterized as ‘neutral or calcareous’ when exposed bedrock consisted of carbonates or mafic/ultramafic igneous rock and/or when acidophilic vascular plants and bryophytes were absent.

Laboratory procedures

Retained leaf litter fractions were passed through a standard sieve series [ASTME 3/8" (9.5 mm), #10 (2.0 mm), #20 (0.85 mm) and #40 (0.425 mm) mesh screens], and then hand picked against a neutral-brown background. All shells and shell fragments were removed, and assigned to species (or subspecies) using the author’s reference collection. The total numbers of shells per species per site were recorded, as were the number of unassignable immature individuals and fragmentary shells. Nomenclature is based principally on Hubricht (1985), with updates by Turgeon *et al.* (1998), Nekola (2004) and Nekola & Coles (in press). Authors and dates for each species are given in Table 1.

Statistical procedures

Occurrences for all species encountered were analysed in terms of their presence/absence in highly acidic, moderately acidic, or neutral/calcareous soils. The species limited only to highly acidic and/or moderately acidic sites were identified, as well as those species limited to neutral/calcareous sites. Additionally, species found across the entire base-status spectrum were enumerated.

The impact of base-status on population size was documented by first recording the observed population sizes for each species across all sites. These abundances were then grouped by their soil acidity category, with statistical difference in abundances between these groups being calculated using the nonparametric Kruskal–Wallis test. To provide appropriate statistical power to mitigate potential type-II errors, tests were limited to the 128 species with at least 10 total occurrences and 30 total individuals. A Bonferroni correction was used to modify the significance threshold of these tests to 0.05/128 or 0.00039.

Gradients in composition of acidic habitat land-snail communities were identified via global nonmetric multidimensional scaling (NMDS) using DECODA (Minchin, 1990). NMDS was used as it makes no assumptions regarding the underlying nature of distributions of species along compositional gradients. As such, NMDS is the most robust form of ordination for detection of ecological patterns (Minchin, 1987). To ordinate sites, a matrix of dissimilarity coefficients was calculated between all pairwise combinations of highly or moderately acidic sites with five or more species, using the Czekanowski (Bray–Curtis) index (Faith, Minchin & Belbin, 1987) on species abundance data which had been doubly standardized, first to make all species maxima = 1, and then to equalize the total number of individuals per site. All species (including the most rarely encountered) were considered. NMDS in one through four dimensions was then performed, with 200

Table 1. Calcifuge/calcolic status of species, based on their presence or absence across the soil acidity spectrum.

Occurring only in highly acidic sites:

Daedalochila leporina (Gould, 1848)

Glyphyalinia n. sp.

Mesomphix perlaevis (Pilsbry, 1900)

Neohelix divesta (Gould, 1851)

Neohelix solemi Emberton, 1988

Triodopsis soelneri (J.B. Henderson, 1907)

Vertigo oralis Sterki, 1898

Occurring only in moderately acidic sites:

Lobosculum pustula (Férussac, 1822)

Pristiloma arcticum (Lehnert, 1884)

Occurring only in highly or moderately acidic sites:

Glyphyalinia luticola Hubricht, 1966

Paravitrea petrophila (Bland, 1883)

Triodopsis juxtidentis (Pilsbry, 1894)

Vertigo alabamensis Clapp, 1915

Vertigo malleata Coles & Nekola, 2007

Occurring in both acidic and neutral/calcareous habitats:

Anguispira alternata (Say, 1817)

Anguispira fergusonii (Bland, 1861)

Carychium exiguum (Say, 1822)

Carychium exile H.C. Lea, 1842

Carychium mexicanum Pilsbry, 1891

Catinella avara (Say, 1824)

Cepaea hortensis (Müller, 1774)

Cochlicopa lubrica (Müller, 1774)

Cochlicopa lubricella (Porro, 1838)

Cochlicopa morseana (Doherty, 1878)

Columella columella alticola (Ingersoll, 1875)

Columella simplex (Gould, 1841)

Daedalochila dorfeuilliana (I. Lea, 1838)

Deroceras leave (Müller, 1774)

Discus catskillensis (Pilsbry, 1898)

Discus cronkhitei (Newcomb, 1865)

Discus patulus (Deshayes, 1830)

Discus patulus edentulus (Pilsbry, 1948)

Discus shimaki (Pilsbry, 1890)

Euchemotrema fraternum (Say, 1824)

Euchemotrema leai leai (A. Binney, 1840)

Euconulus alderi (Gray, 1840)

Euconulus chersinus (Say, 1821)

Euconulus dentatus (Sterki, 1893)

Euconulus fulvus (Müller, 1774)

Euconulus fulvus alaskensis (Pilsbry, 1899)

Euconulus polygyratus (Pilsbry, 1899)

Euconulus trochulus (Reinhardt, 1883)

Gastrocopta contracta (Say, 1822)

Gastrocopta holzingeri (Sterki, 1889)

Gastrocopta pentodon (Say, 1821)

Gastrocopta riparia Pilsbry, 1948

Gastrocopta rupicola (Say, 1821)

Gastrocopta tappaniana (C.B. Adams, 1842)

Glyphyalinia indentata (Say, 1823)

Glyphyalinia rhoadsi (Pilsbry, 1899)

Glyphyalinia solida (H.B. Baker, 1930)

Continued

Table 1. Continued

Glyphyalinia wheatleyi (Bland, 1883)

Guppya sterkii (Dall, 1888)

Haplotrema concavum (Say, 1821)

Hawaiiia minuscula (A. Binney, 1840)

Helicodiscus inermis H.B. Baker, 1929

Helicodiscus notius Hubricht, 1962

Helicodiscus parallelus (Say, 1817)

Helicodiscus shimaki Hubricht, 1962

Hendersonia occulta (Say, 1831)

Inflectarius inflectus (Say, 1821)

Mesodon elevatus (Say, 1821)

Mesodon zaletus (A. Binney, 1837)

Mesomphix capnodes (W.G. Binney, 1857)

Mesomphix friabilis (W.G. Binney, 1857)

Mesomphix globosus (MacMillan, 1940)

Mesomphix subplanus (A. Binney, 1842)

Neohelix albolabris (Say, 1816)

Neohelix alleni (Wetherby in Sampson, 1883)

Nesovitrea binneyana (Morse, 1864)

Nesovitrea electrina (Gould, 1841)

Oxyloma retusa (I. Lea, 1834)

Paravitrea andrewsae (W.G. Binney, 1858)

Paravitrea lamellidens (Pilsbry, 1898)

Paravitrea multidentata (A. Binney, 1840)

Paravitrea significans (Bland, 1866)

Paravitrea simpsoni (Pilsbry, 1889)

Patera binneyanus (Pilsbry, 1899)

Patera perigraptus (Pilsbry, 1894)

Planogyra asteriscus (Morse, 1857)

Pomatiopsis lapidaria (Say, 1817)

Punctum blandianum Pilsbry, 1900

Punctum californicum Pilsbry, 1898

Punctum minutissimum (I. Lea, 1841)

Punctum n. sp.

Punctum randolphi (Dall, 1895)

Punctum vitreum H.B. Baker, 1930

Pupilla hebes (Ancy, 1881)

Pupilla muscorum (Linné, 1758)

Pupisoma dioscoricola (C.B. Adams, 1845)

Pupisoma macneilli (Clapp, 1918)

Stenotrema barbatum (Clapp, 1904)

Stenotrema labrosum (Bland, 1862)

Stenotrema stenotrema (Pfeiffer, 1819)

Stenotrema unciferum (Pilsbry, 1900)

Striatura exigua (Stimpson, 1847)

Striatura ferrea Morse, 1864

Striatura meridionalis (Pilsbry & Ferriss, 1906)

Striatura milium (Morse, 1859)

Strobilops aenea Pilsbry, 1926

Strobilops affinis Pilsbry, 1893

Strobilops labyrinthica (Say, 1817)

Strobilops texasiana Pilsbry & Ferriss, 1906

Succinea ovalis Say, 1817

Succinea strigata Pfeiffer, 1855

Trichia hispida (Linné, 1798)

Triodopsis hopetonensis (Shuttelworth, 1852)

Vallonia costata (Müller, 1774)

Continued

Table 1. *Continued*

Vallonia gracilicosta Reinhardt, 1883
Vallonia pulchella (Müller, 1774)
Ventridens brittsi Pilsbry, 1892
Ventridens cerinoideus (Anthony, 1865)
Ventridens intertextus (A. Binney, 1841)
Ventridens pilsbryi Hubricht, 1964
Vertigo AK 1
Vertigo AK 2
Vertigo AK 3
Vertigo AK 5
Vertigo arthuri (von Martens, 1884)
Vertigo bollesiana (Morse, 1865)
Vertigo coloradensis (Cockerell, 1891)
Vertigo columbiana Sterki, 1892
Vertigo cristata Sterki, 1919
Vertigo elatior Sterki, 1894
Vertigo aff. *genesii* (Gredler, 1865)
Vertigo gouldii (A. Binney, 1843)
Vertigo hannai Pilsbry, 1919
Vertigo hubrichti Pilsbry, 1934
Vertigo milium (Gould, 1840)
Vertigo modesta hoppii (Möller, 1842)
Vertigo modesta modesta (Say, 1824)
Vertigo modesta ultima Pilsbry, 1948
Vertigo nylanderi Sterki, 1909
Vertigo oscariana (Sterki, 1890)
Vertigo oughtoni Pilsbry, 1948
Vertigo ovata Say, 1822
Vertigo paradoxa Sterki, 1900
Vertigo perryi Sterki, 1905
Vertigo pygmaea (Draparnaud, 1801)
Vertigo rugosula Sterki, 1890
Vertigo ventricosa (Morse, 1865)
Vitrina alaskana Dall, 1905
Vitrina limpida Gould, 1850
Vitrinizonites latissimus (Lewis, 1875)
Zonitoides arboreus (Say, 1816)
Zonitoides nitidus (Müller, 1774)
Zoogenetes harpa (Say, 1824)

Occurring only in neutral/calcareous sites:
Allogona profunda (Say, 1821)
Anguispira kochi (Pfeiffer, 1845)
Anguispira strongylodes (Pfeiffer, 1854)
Anguispira jessica Kutchka, 1938
Appalachina sayana (Pilsbry, 1906)
Carychium clappi Hubricht, 1959
Carychium nannodes Clapp, 1905
Catinella exile (Leonard, 1927)
Catinella gelida (F.C. Baker, 1927)
Catinella vermeta (Say, 1829)
Catinella wandae (Webb, 1953)
Cepaea nemoralis (Linné, 1798)
Daedalochila bisontes Coles & Walsh, 2006
Daedalochila lithica (Hubricht, 1961)
Daedalochila peregrina (Rehder, 1932)
Discus macclintockii (F.C. Baker, 1928)

Continued

Table 1. *Continued*

Discus rotundatus (Müller, 1774)
Euchemotrema hubrichti (Pilsbry, 1940)
Euchemotrema leai aliciae (Pilsbry, 1893)
Gastrocopta abbreviata (Sterki, 1909)
Gastrocopta armifera (Say, 1821)
Gastrocopta corticaria (Say, 1816)
Gastrocopta cristata (Pilsbry & Vanatta, 1900)
Gastrocopta pellucida (Pfeiffer, 1841)
Gastrocopta procera (Gould, 1840)
Gastrocopta rogersensis Nekola & Coles, 2001
Gastrocopta similis (Sterki, 1909)
Gastrocopta sterkiiana Pilsbry, 1912
Glyphyalinia caroliniensis (Cockerell, 1890)
Glyphyalinia cumberlandiana (Clapp, 1919)
Hawaiiia n. sp.
Helicina orbiculata (Say, 1818)
Helicodiscus n. sp.
Helicodiscus roundyi (Morrison, 1935)
Helicodiscus singleyanus (Pilsbry, 1890)
Inflectarius edentatus (Sampson, 1889)
Inflectarius subpalliatius (Pilsbry, 1893)
Lamellaxis gracilis (Hutton, 1834)
Lobosculum pustuloides (Bland, 1851)
Mesodon clausus clausus (Say, 1821)
Mesodon normalis (Pilsbry, 1900)
Mesodon thyroidus (Say, 1816)
Mesomphix cupreus (Rafinesque, 1831)
Mesomphix inornatus (Say, 1821)
Mesomphix rugeli (W.G. Binney, 1879)
Microphysula cookei (Pilsbry, 1922)
Neohelix dentifera (A. Binney, 1837)
Neohelix major (A. Binney, 1837)
Oxychylus cellarius (Müller, 1774)
Oxychylus draparnaudi (Beck, 1837)
Oxyloma haydeni (W.G. Binney, 1858)
Oxyloma peoriensis (Wolf, in Walker, 1892)
Oxyloma verilli Bland, 1865
Paravitrea AR 1
Paravitrea tridens Pilsbry, 1946
Patera clenchi (Rehder, 1932)
Patera pennsylvanicus (Green, 1827)
Pilsbryna quadrilamellata Slapcinsky & Coles, 2002
Polygyra cereolus (Muhlfeld, 1818)
Polygyra septemvolva Say, 1818
Pomatiopsis cincinnatiensis (I. Lea, 1840)
Punctum conspectum (Bland, 1865)
Punctum smithi Morrison, 1935
Pupoides albilabris (C.B. Adams, 1821)
Rabdotus dealbatus (Say, 1821)
Stenotrema altispira (Pilsbry, 1894)
Stenotrema hirsutum (Say, 1817)
Stenotrema pilsbryi (Ferriss, 1900)
Succinea indiana Pilsbry, 1905
Succinea putris (Linné, 1798)
Trichia striolata (Pfeiffer, 1828)
Triodopsis cragini Call, 1886
Triodopsis discoidea (Pilsbry, 1904)

Continued

Table 1. *Continued*

<i>Triodopsis neglecta</i> (Pilsbry, 1899)
<i>Triodopsis obsoleta</i> (Pilsbry, 1894)
<i>Triodopsis tridentata</i> (Say, 1816)
<i>Triodopsis vulgata</i> (Pilsbry, 1948)
<i>Vallonia excentrica</i> Sterki, 1893
<i>Vallonia parvula</i> Sterki, 1892
<i>Vallonia perspectiva</i> Sterki, 1892
<i>Ventridens acerra</i> (Lewis, 1870)
<i>Ventridens ligera</i> (Say, 1821)
<i>Vertigo</i> AK 4
<i>Vertigo binneyana</i> Sterki, 1890
<i>Vertigo clappi</i> Brooks & Hunt, 1936
<i>Vertigo meramecensis</i> Van Devender, 1979
<i>Vertigo morsei</i> Sterki, 1894
<i>Vertigo parvula</i> Sterki, 1890
<i>Vertigo tridentata</i> Wolf, 1870
<i>Webbhelix multilineata</i> (Say, 1821)
<i>Xolotrema denotata</i> (Férussac, 1821)
<i>Xolotrema fosteri</i> (F.C. Baker, 1932)
<i>Zonitoides limatulus</i> (W.G. Binney, 1840)

maximum iterations, a stress ratio stopping value of 0.9999 and a small stress stopping value of 0.01. Output was scaled in half-change units, so that an interpoint distance of 1.0 will correspond, on average, to a 50% turnover in species composition.

Because a given NMDS run may locate a local (rather than the global) stress minimum, multiple NMDS runs were conducted on a given set of data from different initial random starting points to assess the stability of an individual solution (Minchin, 1987). In this analysis, DECODA used a total of 10 random starting configurations. Solutions in each of the four dimensions were compared using a Procrustes transformation to identify those that were statistically identical. The number of unique solutions, and number of runs which fell into each, was then calculated across each dimension. The modal solution out of 10 runs was identified, and was considered to be a global optimum when it was achieved in at least 50% of starts.

Compositional variation across the diagram was documented by dividing it into regions whose boundaries were either 0.5 standard deviation above or below the ordination centroid along all major axes of variation. Within each of these regions, all taxa found within at least 25% of included sites were identified.

Environmental correlations with this diagram were determined by calculating in DECODA the maximum correlation vector for site latitude and moisture level. The significance of each was estimated through Monte-Carlo simulations using 1,000 replications.

Full two-way ANOVAs were used to test for differences in the central tendency of richness and log-transformed abundance across the three acidity levels and five major terrestrial gastropod habitat types. ANOVA was performed as richness and log-transformed abundance were essentially normally distributed across all three categories of habitat acidity. Even though log-transformation greatly alters the appearance of the species abundance distribution within sites, this technique is appropriate when comparisons of identically transformed data are made between sites (Nekola *et al.*, 2008). The patterns among habitat types and acidity levels were visualized using box plots.

Abundance distribution variation between highly acidic, moderately acidic and neutral/calcareous categories within

each major habitat type was displayed using rank–frequency (dominance–diversity) plots. These were created by calculating the proportional abundance for each species within a given site. Abundances were then sorted from most to least abundant. The median proportional abundance for the most abundant species was then determined across all sites of a given base-status within that habitat type. This process was repeated for the second, third, fourth etc. to the least abundant species. These abundance values were plotted on a log-axis *vs* rank position. This process was repeated for all three base-status levels within a given habitat type.

RESULTS

Even though almost two-thirds of sites sampled in California and the Southwest occurred on highly felsic igneous outcrops, acidophilic vegetation was never noted, with vascular plants and bryophytes appearing essentially identical across the bedrock acidity spectrum. In addition, no differences were noted between the land-snail community compositions of these sites. This result is almost certainly due to the high rates of dryfall Ca inputs (Waring & Schlesinger, 1985) which have been estimated to range between 190 and 200 mg/m²/year in southern California (Ellis, Verfaillie & Kummerow, 1983). Because of low leaching rates, at least 98% of soil Ca in the Southwest originates from atmospheric deposition (Capo & Chadwick, 1999), allowing ample base to be present in all soils, no matter what the parent material. For this reason, all 162 sites sampled in Arizona, California, Colorado and New Mexico have been eliminated from further analysis, because none actually represents acidophilic conditions, regardless of the underlying bedrock type.

Calcifuge/calcirole status

Of the 1,194 analysed sites outside of the Southwestern USA, land snails were observed from 1,188. Of these, 391 were observed to be highly or moderately acidic: 91 rock outcrops, 67 upland forests, 124 lowland forests, 22 upland grasslands and 87 lowland grasslands. In total, 241 species (*c.* 40% of the eastern and northern North American fauna and *c.* 20% of the entire North American fauna) and 486,153 identified individuals were encountered across these sites. Essentially all wide-ranging eastern and northern taxa were observed, with most of the unencountered species representing regional endemics, principally in the Polygyridae and Zonitidae (Hubricht, 1985).

Seven species only occurred in highly acidic habitats, two only in moderately acidic habitats and a remaining five only in either moderately or highly acidic habitats (Table 1). While 93 species were restricted to neutral/calcareous habitats, the remaining 134 were found both in neutral/calcareous and moderately/highly acidic sites.

Kruskal–Wallis analysis of abundances between highly acidic, moderately acidic and neutral/calcareous sites for the 128 species with at least 10 occurrences and 30 individuals (Table 2) documented 10 species with abundances that were significantly ($P < 0.00039$) greater in highly acidic sites, and an additional seven that significantly ($P < 0.00039$) favoured moderately acidic sites. One species tended ($0.05 < P < 0.00039$) to favour moderately acidic sites. A total of 34 species was shown to display no significant ($P > 0.05$) changes in abundance across the acidity spectrum. Of these, 23 had only between 10 and 30 total occurrences, making it probable that some of these nonsignificant test scores represent type-II errors. This is particularly likely for *Discus macclintockii*, *Hawaiiia* n. sp. and *Oxyloma verrilli*, which had their twelve or fewer occurrences limited to neutral/calcareous habitats. Likewise, it seems

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Table 2. Base-status preferences based upon Kruskal–Wallis analysis of site abundance.

Species	P-value
Species significantly favouring highly acidic sites:	
<i>Euconulus chersinus</i>	0.00000039
<i>Glyphyalinia luticola</i>	0
<i>Glyphyalinia</i> n. sp.	0
<i>Glyphyalinia solida</i>	0
<i>Striatura meridionalis</i>	0.00000009
<i>Strobilops texasiana</i>	0
<i>Ventridens cerinoideus</i>	0.00000002
<i>Vertigo alabamensis</i>	0
<i>Vertigo malleata</i>	0
<i>Vertigo modesta hoppii</i>	0.00004532
Species significantly favouring moderately acidic sites:	
<i>Planogyra asteriscus</i>	0.00000001
<i>Striatura exigua</i>	0.00000002
<i>Striatura ferrea</i>	0.00002965
<i>Vertigo cristata</i>	0
<i>Vertigo perryi</i>	0
<i>Vertigo ventricosa</i>	0
<i>Zoogenetes harpa</i>	0
Species tending to favour moderately acidic sites	
<i>Vertigo nylanderi</i>	0.02831
Species demonstrating no preference in base status of habitat (≥ 30 occurrences):	
<i>Cochlicopa morseana</i>	0.1217
<i>Euconulus fulvus alaskensis</i>	0.9992
<i>Glyphyalinia rhoadsi</i>	0.2121
<i>Pupilla hebes</i>	0.08355
<i>Striatura milium</i>	0.06981
<i>Succinea strigata</i>	0.4538
<i>Vertigo AK 2</i>	0.906
<i>Vertigo coloradensis</i>	0.1796
<i>Vertigo hannai</i>	0.5831
<i>Vertigo modesta modesta</i>	0.1135
<i>Vertigo ovata</i>	0.3306
Species demonstrating no preference in base status of habitat (< 30 occurrences):	
<i>Discus macclintockii</i>	0.08603
<i>Euconulus dentatus</i>	0.404
<i>Euconulus trochulus</i>	0.7056
<i>Glyphyalinia wheatleyi</i>	0.0512
<i>Hawaiiia</i> n. sp.	0.08603
<i>Helicodiscus inermis</i>	0.0714
<i>Helicodiscus notius</i>	0.1385
<i>Inflectarius inflectus</i>	0.2089
<i>Neohelix albolabris</i>	0.0578
<i>Oxychylus cellarius</i>	0.08603
<i>Oxyloma verrilli</i>	0.05241
<i>Paravitrea significans</i>	0.1658
<i>Pomatiopsis lapidaria</i>	0.0666
<i>Punctum blandianum</i>	0.1177
<i>Pupilla muscorum</i>	0.3372
<i>Strobilops aenea</i>	0.508
<i>Ventridens brittsi</i>	0.9471
<i>Vertigo AK 1</i>	0.3169

Continued

Table 2. Continued

Species	P-value
<i>Vertigo AK 3</i>	0.1944
<i>Vertigo AK 5</i>	0.9488
<i>Vertigo genesii</i>	0.819
<i>Vertigo modesta ultima</i>	0.2797
<i>Vertigo oscariana</i>	0.2958
Species significantly favouring neutral/calcareous sites:	
<i>Allogona profunda</i>	0.00001154
<i>Anguispira alternata</i>	0
<i>Carychium exiguum</i>	0
<i>Carychium exile</i>	0
<i>Catinella avara</i>	0.00000003
<i>Cochlicopa lubrica</i>	0
<i>Cochlicopa lubricella</i>	0
<i>Columella simplex</i>	0
<i>Deroceras laeve</i>	0
<i>Discus catskillensis</i>	0.00000001
<i>Discus cronkhitei</i>	0.00000013
<i>Euchemotrema fraternum</i>	0
<i>Euchemotrema leai leai</i>	0
<i>Euconulus alderi</i>	0.0001001
<i>Euconulus fulvus</i>	0.00000592
<i>Euconulus polygyratus</i>	0
<i>Gastrocopta armifera</i>	0
<i>Gastrocopta contracta</i>	0
<i>Gastrocopta corticaria</i>	0
<i>Gastrocopta holzingeri</i>	0
<i>Gastrocopta pentodon</i>	0
<i>Gastrocopta similis</i>	0.00000013
<i>Vallonia perspectiva</i>	0
<i>Vallonia pulchella</i>	0.00000001
<i>Vertigo arthuri</i>	0.00000276
<i>Vertigo bollesiana</i>	0.00000102
<i>Vertigo elatior</i>	0
<i>Vertigo gouldi</i>	0
<i>Gastrocopta tappaniana</i>	0.00000005
<i>Glyphyalinia indentata</i>	0
<i>Guppya sterkii</i>	0.0001567
<i>Haplotrema concavum</i>	0.0001865
<i>Hawaiiia minuscula</i>	0
<i>Helicodiscus parallelus</i>	0
<i>Helicodiscus shimeki</i>	0.0001685
<i>Helicodiscus singleyanus</i>	0.0001555
<i>Hendersonia occulta</i>	0
<i>Nesovitrea binneyana</i>	0
<i>Nesovitrea electrina</i>	0
<i>Oxyloma retusa</i>	0.00000399
<i>Paravitrea multidentata</i>	0.00000049
<i>Punctum vitreum</i>	0
<i>Pupoides albilabris</i>	0.00000021
<i>Stenotrema barbatum</i>	0.0001403
<i>Strobilops affinis</i>	0.00008082
<i>Strobilops labyrinthica</i>	0
<i>Succinea ovalis</i>	0.00008805
<i>Vallonia costata</i>	0
<i>Vallonia gracilicosta</i>	0
<i>Vallonia parvula</i>	0.0000716

Continued

Table 2. *Continued*

Species	P-value
<i>Vertigo hubrichti</i>	0
<i>Vertigo milium</i>	0
<i>Vertigo paradoxa</i>	0.00000027
<i>Vertigo pygmaea</i>	0.0001343
<i>Vertigo tridentata</i>	0
<i>Zonitoides arboreus</i>	0
Species tending to favour neutral/calcareous sites:	
<i>Catinella exile</i>	0.0005619
<i>Catinella 'gelida'</i>	0.000435
<i>Catinella 'vermeta'</i>	0.03188
<i>Columella columella alticola</i>	0.04251
<i>Gastrocopta procera</i>	0.002008
<i>Gastrocopta rogersensis</i>	0.00552
<i>Mesodon clausus clausus</i>	0.0007254
<i>Mesodon thyroideus</i>	0.004289
<i>Neohelix alleni</i>	0.002879
<i>Oxyloma haydeni</i>	0.02484
<i>Punctum minutissimum</i>	0.00181
<i>Punctum n. sp.</i>	0.007416
<i>Triodopsis tridentata</i>	0.0071
<i>Webbhelix multilineata</i>	0.00552
<i>Vertigo meramecensis</i>	0.001558
<i>Vertigo morsei</i>	0.002587
<i>Vertigo oughtoni</i>	0.02095
<i>Vitrina limpida</i>	0.001014
<i>Xolotrema fosteri</i>	0.04088
<i>Zonitoides nitidus</i>	0.001456

The significance threshold has been modified to $P \leq 0.00039$ based on a Bonferroni correction.

probable that with additional observations *Punctum blandianum* will be found strongly to favour acidic sites, as its population sizes are more than five times greater on highly acidic as compared to neutral/calcareous sites. The remaining 76 taxa either significantly ($P < 0.00039$) favoured (56 species) or tended ($0.05 < P < 0.00039$) to favour (20 species) neutral/calcareous sites.

Compositional gradients

Visual observation of the optimal NMDS result (the two-dimensional solution) using all 305 highly or moderately acidic sites with at least five observed species indicated a group of 13 outliers along Axis 1 that represented tundra or near-tundra sites in Alaska and northern Manitoba. To assist gradient interpretation, these sites were assigned to a unique compositional group, and then removed from analysis. NMDS of the remaining 292 sites in one dimension generated a minimum stress configuration of 0.2603, which was achieved from nine of 10 random starting configurations. Procrustes analysis showed that these solutions fell into only a single group. NMDS along two dimensions generated a minimum stress configuration of 0.1934, which was achieved from all 10 random starting configurations. Procrustes analysis showed that these solutions fell into three unique categories, of which one was achieved in six different starts. NMDS along three dimensions generated a minimum stress configuration of 0.1489, which was achieved from six of the 10 random starting configurations. Procrustes analysis showed that these minimum stress solutions fell into

two unique groups, each achieved in three different starting configurations. NMDS along four dimensions generated a minimum stress configuration of 0.1220, which was achieved from nine of 10 random starting configurations. Procrustes analysis showed that each of these solutions was unique.

Based on these results the modal configuration from the two-dimensional NMDS was chosen as the most stable for depicting land-snail community composition trends (Fig. 2). Approximately two complete turnovers in species composition are indicated along the first axis, with a single complete turnover being noted along the second. Environmental biplot analysis (Fig. 3) demonstrates that the first axis strongly ($P < 0.0005$) correlates with site latitude, with a maximum observed correlation of $r = 0.8366$. The second axis strongly ($P < 0.0005$) correlates with water level, with a maximum observed correlation of $r = 0.6753$. Ordination region one is found in the upper left of the diagram, and principally represents low latitude wetlands such as pocosins and bay-head swamps. Twelve species were found to occur in at least 25% of these sites (Table 3). Ordination region two is found at the mid-left side of the diagram, and principally represents low latitude mesic sites such as pine forest, bay forest and heathlands. Nine species were found to occur in at least 25% of these sites. Ordination region three is found on the lower left side of the diagram, and principally represents low latitude xeric sites such as dry bedrock outcrops, talus slopes and heath balds. Nine species were found to occur in at least 25% of these sites. Ordination region four is in the upper-mid portion of the diagram, and principally represents mid-latitude wetlands such as sedge meadows, and swamps of tamarack, northern white cedar, willow, red maple and alder. Twenty-three species were found to occur in at least 25% of these sites. Ordination region five is found in the centre of the diagram, and principally represents mid-latitude mesic sites such as pine, hemlock and yellow birch forests as well as some mesic bedrock outcrops. Fourteen species were found to occur in at least 25% of these sites. Ordination region six is on the bottom margin of the diagram, and principally represents mid-latitude xeric sites such as exposed bedrock outcrops and dry upland forest. Fourteen species were found to occur in at least 25% of these sites. Ordination region seven is on the upper right of the diagram, and principally represents high-latitude wetlands such as cattail swamps, sedge meadows and *Sphagnum* bogs. Ten species were found to occur in at least 25% of these sites. Ordination region eight is on the right-centre margin of the diagram, and principally represents high-latitude mesic sites such as heathlands, spruce-fir forest and some mesic rock outcrops. Eleven species were found to occur in at least 25% of these sites. Ordination region nine is found on the lower right of the diagram, and principally represents high-latitude xeric sites such as exposed bedrock outcrops. Nine species were found in at least 25% of these sites. Lastly, ordination region 10 represents the outlier sites found along the middle of Axis 2 to the right of the ordination diagram. These sites represent tundra sites across the full extent of the moisture gradient, ranging from sedge meadows to exposed rock outcrops. Ten species were found in at least 25% of these sites.

Richness and abundance patterns

ANOVA of richness and abundance patterns between the three soil acidity classes within the five major land-snail habitat types demonstrate that soil acidity imposed a highly significant ($P < 0.000000005$) negative impact on both site richness and log-transformed abundance (Table 4). Median richness levels ranged from 4.5 to 10 species per site in highly acidic soils, increased to 7–15 in moderately acidic soils, and were 11.5–20 in neutral/calcareous sites (Fig. 4). Median total abundance

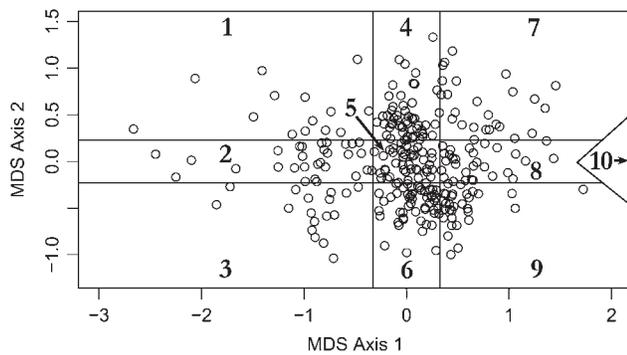


Figure 2. Optimum two-dimensional NMDS solution, showing locations of the 10 regions used to determine compositional changes.

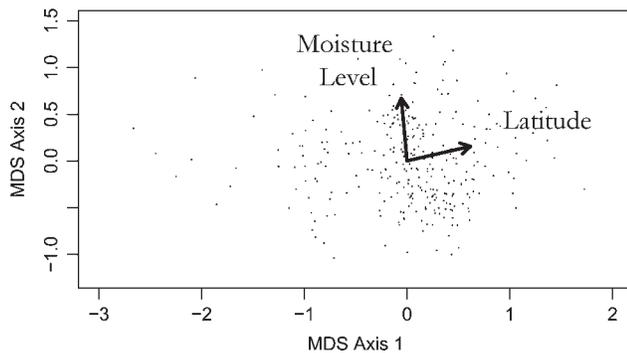


Figure 3. Environmental biplot diagram showing the vectors of maximum correlation for latitude and moisture levels.

ranged from 50.5 to 119.5 individuals in highly acidic soils to 57–292.5 in moderately acidic soils and 211–440 in neutral/calcareous sites (Fig. 4). Habitat type also had a highly significant ($P < 0.000000005$) impact on site richness, but only a marginally significant ($P = 0.04$) impact on log-transformed total abundance. Bedrock outcrop sites had the highest observed richness with a median score ranging from 10 to 20 species, followed by upland forests (8–15), lowland forests (6–15), lowland grasslands (5–12) and upland grasslands (4.5–11.5). While the interaction between habitat type and soil acidity significantly impacted site richness ($P = 0.001$), no effect on log-transformed abundance was noted ($P = 0.69$). The significant interaction appears due to the fact that richness of highly and moderately acidic bedrock outcrop sites was identical, as were the richness of moderately acidic and neutral/calcareous upland forests (Fig. 4).

Rank–abundance plots across all five habitat types demonstrate a clear tendency for highly acidic sites to have more uneven abundance distributions than for neutral/calcareous sites (Fig. 5), with the commonest species in highly acidic habitats tending to have a higher proportional median abundance and with scores rapidly decreasing to much smaller values for a given rank. In most cases, curves from moderately acidic sites were intermediate between highly acidic and neutral/calcareous sites. Exceptions to this were noted in lowland forest and upland grasslands, in which the curves for moderately acidic and neutral/calcareous sites were largely coincident.

DISCUSSION

The North American acidophilic land-snail fauna

These analyses clearly document that *Vertigo malleata* is not an idiosyncratic anomaly within the North American

land-snail fauna. Almost two-thirds of all analysed northern and eastern North American species were found to occur at least occasionally in highly to moderately acidic habitats. Of these, 16 (*Daedalochila leporina*, *Euconulus chersinus*, *Glyphyalinia laticola*, *Glyphyalinia* n. sp., *Glyphyalinia solida*, *Mesomphix perlaevis*, *Neohelix divesta*, *Neohelix solemi*, *Striatura meridionalis*, *Strobilops texasiana*, *Triodopsis soelneri*, *Ventridens cerinoideus*, *Vertigo alabamensis*, *V. malleata*, *Vertigo modesta hoppii* and *Vertigo oralis*) only occurred or had statistically higher abundance in highly acidic sites. An additional 10 (*Lobosculum pustula*, *Planogyra asteriscus*, *Pristiloma arcticum*, *Striatura exigua*, *Striatura ferrea*, *Vertigo cristata*, *Vertigo nylanderii*, *Vertigo perryi*, *Vertigo ventricosa* and *Zoogenetes harpa*) only occurred or had statistically higher abundance in moderately acidic sites. *Paravitrea petrophila* and *Triodopsis juxtidentis* were also only seen in moderately and highly acidic sites. Thus, about 12% of the sampled fauna exhibits clear signs of acidophilic/calcifugic affinities. Almost all of these taxa are wide-ranging, with only one (*Triodopsis solneri*) being a local endemic. While other presumed acidophiles (e.g. *Catinella oklahomarum*, *Inflectarius downeanus*, *Mesodon normalis*, *Neohelix dentifera*, *Praticolella bakeri*, *Praticolella jejuna*, *Praticolella lawae* and *Praticolella mobiliana*) have been reported previously (Hubricht, 1985), they have either not yet been encountered or have too few observed occurrences to draw firm conclusions regarding their preferred base status. The actual number of acidophilic/calcifugic land-snail species in North America is thus certainly higher than is reported here. It is therefore vitally important for North American land-snail biodiversity surveys not to ignore acidic habitats, because they harbour an important and surprisingly diverse fauna.

Acidophilic tendencies are not limited to a few closely related groups, with the taxa listed above representing at least eight families (Euconulidae, Gastrodontidae, Oxychilidae, Polygyridae, Pristolomatidae, Valloniidae and Vertiginidae of Bouchet *et al.*, 2005). With additional sampling, two more (Punctidae and Succineidae) will also likely be added to this list. Most of this fauna shares little phylogenetic overlap with the known European acid-tolerant fauna: only two of the above genera (*Vertigo* and *Zoogenetes*) possess acidophilic taxa in both the Old and New Worlds (Kerney & Cameron, 1979). Instead, most of the North American acidophilic fauna represents endemic families or genera, such as the Polygyridae (representing one-fifth of identified acidophilic species) and the gastrodontid genus *Striatura* (all species demonstrated acidophilic or generalist tendencies). Biogeographically, acidophilic species were found to range across the entire continent from semitropical forests of the Gulf Coast to arctic tundra on the Alaska North Slope. These factors all strongly suggest that the evolution of acidophilic traits has occurred *in situ* multiple times within North America.

A few clear analogues between the European and North American acidophilic faunas can be observed, however. For instance, *Vertigo ronneyensis* not only shares a very similar shell with *V. cristata*, but also an apparent preference for acidic taiga soils (Kerney & Cameron, 1979). Additionally, *Vertigo lilljeborgi* not only shares roughly similar shell characteristics with *V. perryi*, but similar affinities with tussock-side sedge litter accumulations in acidic wet meadows. The Holarctic *Zoogenetes harpa* also appears to demonstrate acidophilic tendencies across its range. It remains unknown how close the evolutionary relationships between these taxa and populations may be, given that at least some supposed Holarctic land-snail species can be shown to be members of only distantly related clades based on their mitochondrial DNA sequences (Nekola, Coles & Berghthorsson, in press).

Table 3. Ordered matrix of species frequency within each of the 10 identified NMDS ordination regions, with the reported number representing the per cent of sites within that region which supported populations of that given species.

Species	Region 1	Region 2	Region 3	Region 4	Region 5	Region 6	Region 7	Region 8	Region 9	Region 10
<i>Vertigo malleata</i>	64.3	41.4								
<i>Strobilops texasiana</i>	57.1	55.2								
<i>Punctum minutissimum</i>	57.1	82.8	35.3	86.5	88.4	65.4				
<i>Gastrocopta pentodon</i>	50.0	62.1	70.6		27.9					
<i>Vertigo milium</i>	35.7									
<i>Striatura milium</i>	35.7	34.5		78.9	95.4	84.6				
<i>Striatura meridionalis</i>	35.7	48.3	76.4							
<i>Euconulus chersinus</i>	35.7									
<i>Gastrocopta tappaniana</i>	35.7			80.8			36.0			
<i>Glyphyalinia solida</i>	35.7									
<i>Hawaiiia minuscula</i>	35.7									
<i>Gastrocopta contracta</i>	28.6									
<i>Zonitoides arboreus</i>		34.5	58.8	44.2	53.5	88.5		51.7	74.2	
<i>Vertigo alabamensis</i>		31.0								
<i>Glyphyalinia indentata</i>		27.6	47.1							
<i>Columella simplex</i>			29.4	80.8	72.1	36.5	28.0	51.7		
<i>Haplotrema concavum</i>			29.4							
<i>Helicodiscus parallelus</i>			29.4		27.9					
<i>Guppya sterkii</i>			29.4							
<i>Nesovitrea electrina</i>				92.3	32.6		80.0	58.6		
<i>Striatura exigua</i>				78.9	65.1	51.9		27.6	29.0	
<i>Carychium exiguum</i>				71.2						
<i>Strobilops labyrinthica</i>				67.3	81.4	42.3				
<i>Euconulus fulvus</i>				67.3	79.1	36.5	48.0	93.1	71.0	
<i>Euconulus alderi</i>				65.4			32.0			
<i>Vertigo cristata</i>				59.6	74.4	67.3		72.4	80.7	
<i>Vertigo nylanderi</i>				51.9						
<i>Vertigo ventricosa</i>				50.0			28.0			
<i>Nesovitrea binneyana</i>				50.0	79.1	71.2	32.0	55.2	74.2	
<i>Planogyra asteriscus</i>				46.2	32.6					
<i>Striatura ferrea</i>				34.6	41.9			27.6		
<i>Discus catskillensis</i>				32.7	65.1	76.9			74.2	
<i>Vertigo elatior</i>				32.7						
<i>Punctum n. sp.</i>				30.8						
<i>Succinea ovalis</i>				30.8						
<i>Helicodiscus shimaki</i>				30.8	39.5	36.5				
<i>Carychium exile</i>				26.9						
<i>Vertigo bollesiana</i>					34.9					
<i>Zoogenetes harpa</i>						44.2		48.3	38.7	
<i>Vertigo paradoxa</i>						38.5			38.7	
<i>Anguispira alternata</i>						26.9				
<i>Discus cronkhitei</i>							40.0	51.7	38.7	
<i>Vertigo perryi</i>							32.0			
<i>Vertigo modesta modesta</i>							28.0			69.2
<i>Vitrina limpida</i>								27.6		
<i>Euconulus fulvus alaskensis</i>										76.9
<i>Vertigo modesta hoppii</i>										76.9
<i>Vertigo AK 2</i>										61.5
<i>Vertigo hannai</i>										46.2
<i>Succinea strigata</i>										46.2
<i>Columella columella alticola</i>										38.5
<i>Pupilla hebes</i>										38.5
<i>Vertigo modesta ultima</i>										38.5
<i>Vertigo genesii</i>										30.8

Only species with a frequency of at least 25% within a region are listed.

Acidic land-snail habitats

Acidophilic land-snail faunas were observed in a number of habitat types across the continent. In the south, some of the most diverse assemblages occurred in ombrotrophic pocosin peatlands, bayhead seepage swamps, Atlantic white cedar forests, pine-wiregrass savanna, pine barrens, heath balds and upland oak woods. To the north, other important reservoirs for acidophilic land-snail diversity included *Sphagnum* bogs, swamps of base-poor cattail, sedge, northern white cedar, red maple, balsam fir and tamarack, wooded igneous rock outcrops and base-poor upland forests. Acidophilic land snails were also abundantly found across North America in base-poor taiga and acidic tundra over base-poor rock such as sandstone, quartzite and gneiss.

It is astonishing not only that land-snail communities exist on such sites, but also that many of the included species possess large populations (up to 2,000/m²; Coles & Nekola, 2007) and strongly calcified shells (e.g. *S. texasiana*, *V. alabamensis*). Because of the very small Ca pools in such habitats (Binkley *et al.*, 1992), it is clear that these populations must be successfully capturing Ca that is fluxing rapidly through the environment. Ca sources in these sites are undoubtedly various organically derived Ca salts, including Ca citrate and Ca oxalate (Wäreborn, 1970), which are leached from various tree and shrub species such as

aspen, dogwood or cedar (Karlin, 1961; Nation, 2007). Because of the high densities of individuals observed in their litter accumulations, it appears that heaths such as *Chamaedaphne*, *Gaylussacia*, *Lyonia*, *Kalmia*, *Vaccinium* and *Zenobia*, and other shrubs such as *Ilex*, *Gordonia*, *Magnolia* and *Myrica*, must also be important Ca sources. No matter the source, all acidophilic land snails must have evolved highly efficient Ca-pumps that are able to move ions counter to very strong osmotic gradients. If these pumps require low Ca concentrations or pH for proper functioning, it might provide a metabolic explanation for the calcifugic behaviour of some species.

Because of the very high soil acidity at many of these sites (e.g. pH < 4; Woodwell, 1958; Binkley *et al.*, 1992), the shells of many acidophilic snails are being actively dissolved even on living individuals. For instance, it is difficult to find living *V. malleata* or *V. alabamensis* individuals that do not possess at least one shell ulceration. Incipient ulcers can be seen in the individuals figured by Coles & Nekola (2007) as opaque white patches on otherwise translucent shells. Shell erosion is so rapid in these habitats that no adult shells of the seasonally active *V. alabamensis* could be found during autumn sampling, even on sites that supported colonies of >200 individuals/m² in spring (Nekola & Coles, in press).

Acidophilic land-snail community composition gradients

The dispersion of sites across the optimal two-dimensional NMDS ordination diagram is continuous along both axes, implying that there are no hard compositional breaks within the fauna. This can be readily seen in the continuous variation exhibited in pineland and ombrotrophic bog faunas along the Atlantic seaboard, with sites in the New Jersey Pine Barrens being intermediate between eastern Maine raised bogs and Carolina pocosins (Coles & Nekola, 2007). Similar transitions can be found between Atlantic coastal plain and mixed-deciduous forest faunas in central Massachusetts and southern Maine, between mixed-deciduous and taiga faunas along the Cote Nord in eastern Quebec and the western shore of Lake Superior, and between taiga and tundra faunas in the Alaskan interior, at Churchill, Manitoba, and in central Quebec.

Analysis of environmental covariates identifies essentially the same organizing factors as have been previously shown in calcareous sites in the Great Lakes region (Nekola, 2003):

Table 4. Summary statistics for ANOVA on the impacts of soil acidity and habitat type on community richness and log-transformed individual abundance.

Predictor variable	df	Sum-of-squares	Mean squares	F-value	P
A. Site richness					
Habitat type	4	10,181	2,545	86.459	<0.000000005
Soil acidity	2	11,602	5,801	197.064	<0.000000005
Habitat type * soil acidity	1	302	302	10.260	0.001396
B. Log-transformed total abundance					
Habitat type	4	17.97	4.5	2.5178	0.03981
Soil acidity	2	451.26	225.6	126.4315	<0.000000005
Habitat type * soil acidity		0.28	0.3	0.1596	0.68959

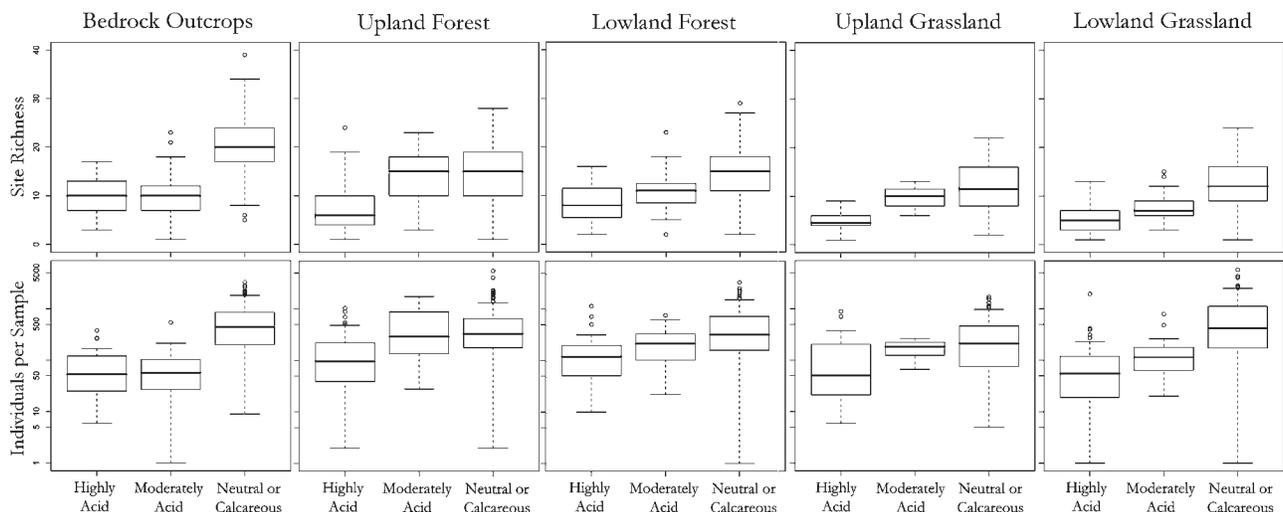


Figure 4. Box-plot diagrams demonstrating the impact of habitat type and soil acidity on site richness (top) and log-transformed site abundance (bottom).

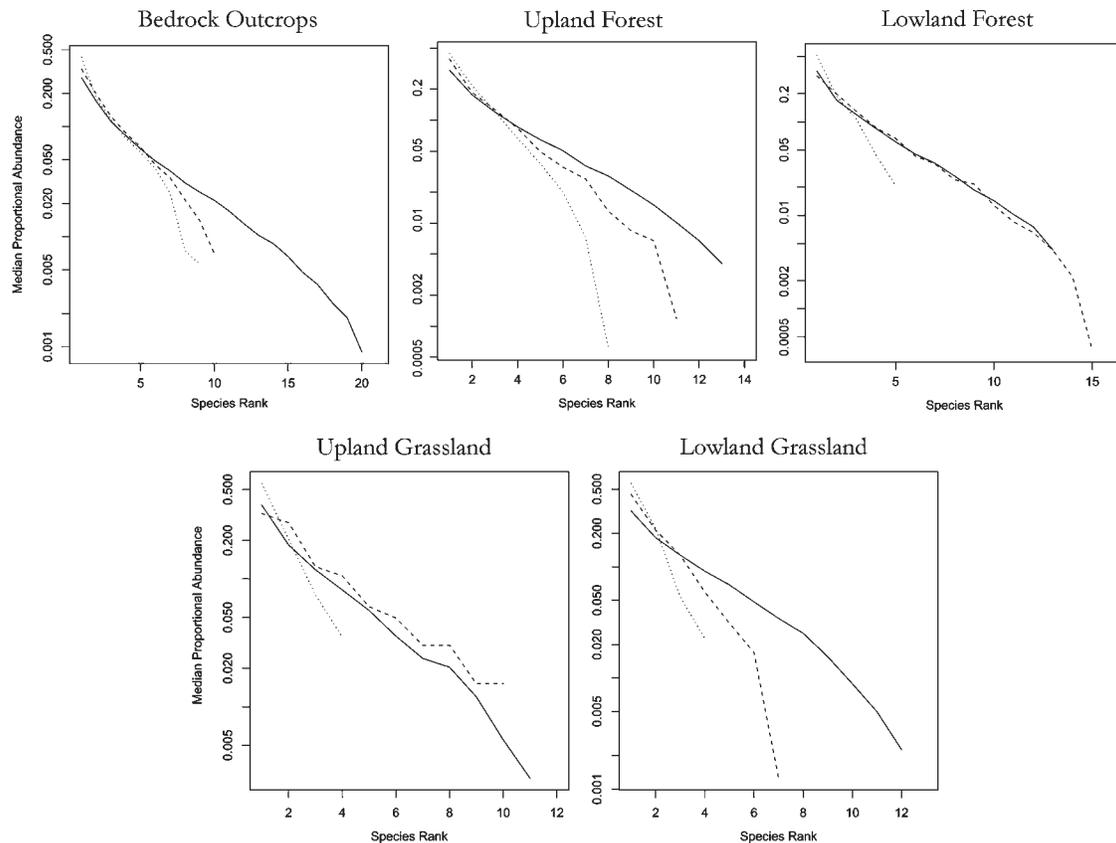


Figure 5. Rank–abundance (a.k.a. dominance–diversity) plots for median proportional abundance across all highly acidic (dotted line), moderately acidic (dashed line) and neutral/calcareous (solid line) sites within a given major habitat type.

latitude was most strongly correlated with the first axis, while water level was strongly related to the second. As a result, it appears that at a continental scale acidophilic faunas respond in similar ways to the same environmental variables as do calciphilic faunas. Although found to be very important in base-rich communities, the impact of soil surface architecture was not documented in the current analysis, because thick organic litter accumulations (e.g. ‘duff soils’) were present on essentially all sites. However, acidic soils did tend towards turf-style architecture with increasing water levels.

Diversity patterns

While faunas of acidic habitats were both more depauperate in species and individuals than those of neutral/calcareous sites, median richness fell by no more than half, while abundance fell by no more than an order of magnitude. Median richness of even the most acidic sites ranged up to 10 species. This contrasts with patterns observed in Europe, where moderately acidic sites may often harbour as many species as typical base-rich sites (Bishop, 1977, 1980; Tattersfield, 1990; Cameron & Greenwood, 1991), and the most acidic sites typically have maximum diversity levels of <10 (Kerney & Cameron, 1979).

As in Europe (Cameron & Pokryszko, 2005), faunas were found to become increasingly uneven in their abundance distributions with increasing soil acidity. Acidic site faunas thus tend to be dominated by a relatively few common species, with the remainder being rare. This pattern is common among a large number of high-stress communities (Whittaker, 1975). The steepness of the rank–abundance curve on acidic sites also

indicates that adequate documentation of site faunas may require extra field collection effort as compared to sites with higher base status (Cameron & Pokryszko, 2005).

Acidophilic land-snail communities in a global perspective

This documentation of acidophilic land-snail faunas is not without precedent. Bishop (1977), Tattersfield (1990) and Cameron & Greenwood (1991) have reported on land-snail community patterns from acidic sites in southwestern Ireland, the English Pennines and Scottish Highlands, respectively. Valovirta (1968), Wäreborn (1970), Waldén (1981), Gärdenfors (1992) and Mänd, Ehlvest & Kristaja (2001) have documented acidophilic land-snail faunas in Scandinavia and the Baltic Republics. Agócsy (1968) and Štamol (1991) have documented acidophilic land-snail faunas from eastern Europe, while Bishop (1980) also demonstrated the existence of such faunas in Italy. The existence of a low-elevation acidophilic fauna from the North Island of New Zealand is also suggested by the work of Barker & Mayhill (1999). The species found on these sites can make up a not-inconsequential fraction of their respective regional faunas: Boycott (1934) reported roughly half of the British land-snail fauna to be ‘indifferent to lime’, occurring freely in both acidic and calcareous sites, while Bishop (1977) reported that about 40% of all Irish land snails occur in acidic woodlands.

What makes the North American fauna outstanding, however, is the presence of so many clearly acidophilic/calcifugic species. While these make up an estimated 10% of the sampled northern and eastern North American fauna, Boycott (1934) could only identify one such species from Britain. Even with updating by Kerney & Cameron (1979), it is clear that

perhaps 1% or less of the northwestern European land-snail fauna can be considered acidophilic. This has profound implications in terms of composition gradients. First, the lack of acid-preferring species allows for considerable stochastic compositional variation between adjacent European acidic sites (Cameron & Pokryszko, 2005). In North America, however, the presence of acidophilic species allows for much greater consistency in site composition: the standard deviations of Axis 1 and Axis 2 scores for Carolina pocosins were only 0.36 and 0.25, respectively (implying *c.* 82–87% similarity), 0.26 along both Axis 1 and 2 for New England conifer swamps (*c.* 87% similarity), and 0.20 and 0.19 (*c.* 90% similarity) for western Lake Superior igneous outcrop sites.

Acidic-habitat faunas throughout Europe also tend to be characterized by a suite of ubiquitous species which occur across the entire base-status gradient. The major compositional change with increasing base-status is the continuous addition of increasingly calciphilic species (Valovirta, 1968; Waldén, 1981; Cameron & Greenwood, 1991; Horsák & Hájek, 2003) until a few taxa drop out at the sites of highest base-status (Horsák, 2006). Among European studies, only Agócsy (1968) did not recognize this pattern, instead noting that about 60% of acidic-habitat snails were restricted to these sites, whereas there was only 20% similarity between the faunas of adjacent acidic and calcareous habitats. European land-snail community compositions can thus be generally characterized as being nested along a base-status axis. Although also suggested from coastal British Columbia forests by Cameron (1986), this pattern appears not to be typical for the rest of North America. Rather, acidophilic faunas are made not only of species 'indifferent' to lime, but also a group of species (*c.* 20% of site faunas) that actually favour highly or moderately acidic sites. As a result, replacement-driven turnover in species occurrence can be seen along the base-status axis across much of North America.

An important question that remains unanswered, however, is why North America and Europe differ so much in their frequency of acidophilic land-snail species. Given the apparently frequent presence of acidophiles in land-snail faunas of West Africa (De Winter & Gittenberger, 1998) and Borneo (Schilthuizen & Rutjes, 2001), it seems possible that a productive line of inquiry may be directed at determining why Europe has an unusually depauperate fauna, as opposed to concentrating on why that of North America appears strangely enriched.

ACKNOWLEDGEMENTS

Major funding for this project was provided by the National Science Foundation (EAR-0614963), the Maine Department of Inland Fisheries and Wildlife, Wildlife Resource Assessment Section, the Massachusetts Natural Heritage and Endangered Species Program, and the Minnesota Nongame Wildlife Tax Checkoff and Minnesota State Park Nature Store Sales through the Minnesota Department of Natural Resources Natural Heritage and Nongame Research Program. Brian Coles provided innumerable insights regarding field sampling and microhabitat preferences for many of these species, as well as thoughts regarding potentially analogous species in Europe and North America. Invaluable suggestions on earlier drafts were provided by Linda Fey, Robert Cameron and two anonymous reviewers.

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