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BIODIVERSITY RESEARCH

Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America

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Abstract: Previous ordination studies of land snail community composition have been limited to four or fewer habitat types from sites separated by no more than 300 km. To investigate the nature of large-scale patterns, North American land snail assemblages at 421 sites, representing 26 habitat types and covering a 1400 × 800 km area, were ordinated using global, nonmetric multi-dimensional scaling (NMDS). These data were then subjected to model-based cluster analysis and kmeans clustering to identify the main compositional groups and most important environmental covariables. Six primary compositional groups were identified. Three of these largely represent upland forest and rock outcrop sites, while the remaining largely represent either lowland forest, lowland grassland or upland grassland habitats. The geographical location and moisture level of sites also influences community composition. A strong compositional difference exists between sites having duff vs. turf soil surface layers. Only 8% of sites were improperly classified when soil surface architecture was used as the sole predictor variable. Fully 43% of taxa exhibited significant preferences towards one of these surface types, while only 15% of relatively common (10 + occurrence) taxa showed no preferences. Twelve groups of closely related taxa within the same genus had members that favoured different surface types, indicating that differential selection pressures have existed over evolutionary time scales. While turf faunas appeared unaffected by anthropogenic disturbance, duff faunas were strongly impacted, suggesting that their conservation will require protection of soil surface architecture.

Key words. Cluster analysis, community ecology, conservation biology, landscape pattern, multidimensional scaling, North America, soil architecture, terrestrial gastropods.

INTRODUCTION

Land snails are regarded typically as generalist herbivores, fungivores and detritivores (Burch & Pearce, 1990) that exhibit weak levels of intraspecific competition (Cain, 1983; Cowie & Jones, 1987; Smallridge & Kirby, 1988; Barker & Mayhill, 1999). As land snail communities can consume less than 0.5% of annual litter input per year (Mason, 1970), some speculate that few resources, beyond $CaCO_3$ (Boycott, 1934) and appropriate resting site availability (Pearce, 1997), will limit distribution. This concept is supported by high levels of microsympatry in land snail communities, where 13–35 (representing up to 50% of the regional fauna) co-occurring taxa can be found at < 1 m^2 grains (Schmid, 1966; Cameron & Morgan-Huws, 1975; Nekola & Smith, 1999; Cameron, 2002).

However, at landscape scales, land snail population size and faunistic composition has been suggested to vary with habitat and vegetation types (e.g. Burch, 1956; Wäreborn, 1970; Van Es & Boag, 1981; Young & Evans, 1991; Stamol, 1991; Stamol, 1993; Ports, 1996; Theler, 1997; Nekola, 2002). Habitat preferences for individual species have also been discussed (without supporting empirical data) at subcontinental scales

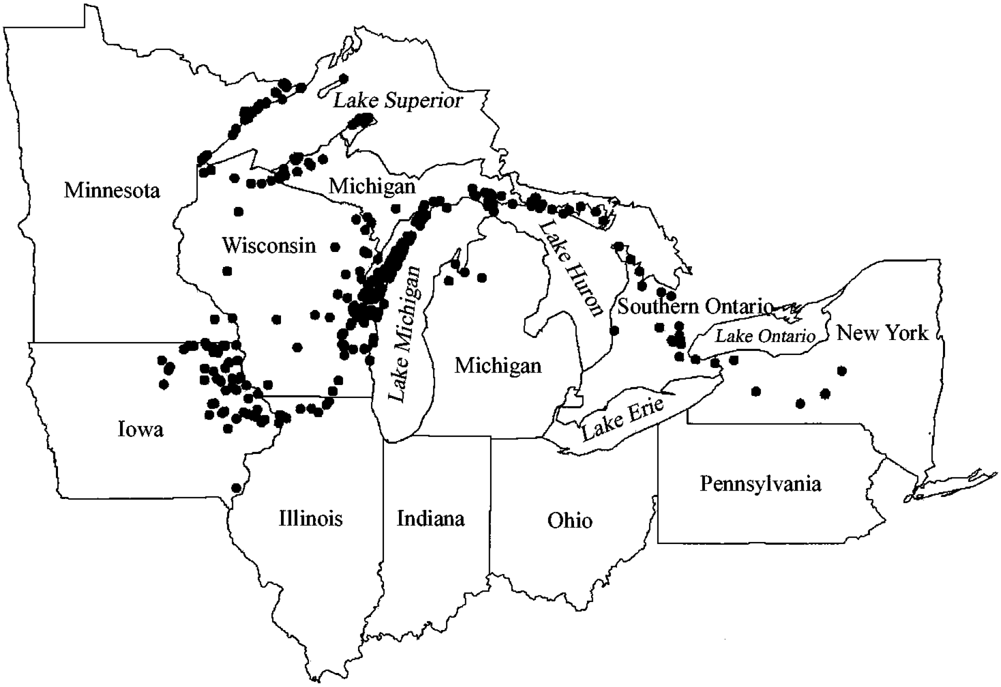

Fig. 1 Map of the study region showing the location of the 443 sample sites.

in both western Europe (Kerney & Cameron, 1979) and eastern North America (Hubricht, 1985).

Ordination techniques have documented significant species turnover along local environmental gradients in western Europe (e.g. Tattersfield, 1990; Magnin *et al.*, 1995; Hermida *et al.*, 2000; Ondina & Mato, 2001) and Pacific Island (e.g. Cowie *et al.*, 1995; Barker & Mayhill, 1999) faunas. Unfortunately, these (and all other published snail ordination) studies have been conducted only at limited ecological (< four sampled habitat types) and geographical (maximum separation of no more than 300 km) scales.

The following study addresses these concerns by using global nonmetric multi-dimensional scaling (NMDS) ordination and model-based cluster analysis to analyse land snail composition patterns within 26 habitat types across a 1400-km extent of central North America. These data will be used to address: (1) if land snail community composition predictably varies across this sub-continental region; and (2) what environmental and geographical factors underlie any such patterns. This study represents not only the first use of NMDS in the analysis of land snail communities, but also represents the first time North American faunas have been subjected to ordination.

METHODS

Study region

Land snail faunas were sampled across a 1400 × 800 km area centred on the western portion of the Great Lakes basin in eastern and central North America (Fig. 1). This area covers a wide range of bedrock, climate and vegetation types. Both Palaeozoic sedimentary and Precambrian igneous bedrock outcrops in the region. One of the more prominent sedimentary exposures is the Niagaran Escarpment, a band of Silurian limestones and dolomites extending from western New York state to north-eastern Iowa. Outcrops along the western Lake Superior shore typically represent late-Precambrian mafic igneous rocks associated with the Keewenawan mid-continental rift system (Anderson, 1983). Average

Table 1 Distribution of samples among surveyed habitat types. Habitat descriptions can be found in Nekola (1999)

Group	Habitat type	Sites sampled	Geographic range
Rock outcrop	Carbonate cliff	129	Illinois, Iowa, Minnesota, Michigan, Ontario, New York, Wisconsin
	Lakeshore carbonate ledge	23	Michigan, Ontario, Wisconsin
	Algific talus slope	27	Illinois, Iowa
	Igneous cliff	72	Michigan, Minnesota
	Sandstone/quartzite cliff	5	Wisconsin
	Shale cliff	3	New York
Upland forest	Oak–hickory forest	2	Wisconsin
	Maple–basswood forest	3	Wisconsin
	Hemlock–birch forest	1	Wisconsin
	Lakeshore forest	16	Michigan, Wisconsin
	Rocky woodland	26	Iowa, Michigan, Ontario, Wisconsin
Lowland forest	Floodplain forest	2	Wisconsin
	Black ash swamp	6	Wisconsin
	Tamarack swamp	33	Minnesota, Michigan, Ontario, Wisconsin
	White cedar swamp	16	Michigan, Ontario, Wisconsin
	Shrub-carr	2	Wisconsin
Upland grassland	Tallgrass prairie	1	Iowa
	Sand dune	1	Wisconsin
	Bedrock glade	13	Iowa
	Alvar	6	Michigan, Wisconsin
	Igneous shoreline	4	Michigan
	Successional old field	4	Wisconsin
Lowland grassland	Sedge meadow	5	Michigan, Wisconsin
	Fen	29	Iowa, Michigan, New York, Wisconsin
	Calcareous meadow	7	Michigan, Wisconsin
	Cobble beach	7	Michigan, Wisconsin

minimum winter temperatures range from –25 °C in northern Minnesota to –10 °C in western New York State. Average maximum summer temperatures range from 25 °C along the western Lake Superior shore to 30 °C in south-eastern Iowa. The average length of the 0 °C growing season varies from 100 to 110 days in northern Minnesota and Michigan to 180–190 days in southern Iowa, southern Ontario, and western New York state. In areas adjacent to or downwind from (east of) the Great Lakes (especially the Lower Peninsula of Michigan, southern Ontario, and western New York State), the climate tends to be buffered over that normally experienced in the continental interior, being warmer in the winter, cooler in the summer and having a longer growing season with more constant precipitation (Eichenlaub, 1979). Matrix vegetation varies from tallgrass prairie in the west to deciduous forest in the east to mixed boreal–hardwood forest in the north (Barbour & Billings, 1988).

Study sites

Four hundred and forty-three sites (Fig. 1) were surveyed across the range of habitats known to support diverse land snail assemblages (Nekola, 1999). The 26 habitats surveyed were broadly grouped into five major categories: rock outcrops, upland forests, lowland forests, upland grasslands and lowland grasslands (Table 1). While sites generally represent undisturbed examples of their respective habitats, an effort was also made to sample some (25 rock outcrop, 12 upland forest, nine lowland forest, four upland grassland and eight lowland grassland) that had been disturbed anthropogenically by grazing, logging, recreational/urban development or bedrock/soil removal. Examples of such sites include field-edge stone piles, abandoned agricultural fields, abandoned building foundations, old quarries, pastures, road verges and exploited forests.

Field methods

Documentation of terrestrial gastropods from each site was accomplished by hand collection of larger shells and litter sampling for smaller taxa from representative 100–1000 m^2 areas. Soil litter sampling was primarily used as it provides the most complete assessment of site faunas (Oggier *et al*., 1998). As suggested by Emberton *et al.* (1996), collections were made at places of high micromollusc density, with a constant volume of soil litter (approximately 4 L) being gathered from each site. For woodland sites, sampling was concentrated: (1) along the base of rocks or trees; (2) on soil covered bedrock ledges; and/or (3) at other places found to have an abundance of shells. For grassland sites, samples consisted of: (1) small blocks (*c*. 125 cm^3) of turf; (2) loose soil and leaf litter accumulations under or adjacent to shrubs, cobbles, boulders and/or hummocks; and (3) other locations observed to have an abundance of shells.

The latitude–longitude location of each sample was determined using either USGS 7.5 minute topographic maps or a hand-held GPS. To minimize bias from use of polar-coordinates, these locations were converted subsequently to Cartesian UTM Zone 16 coordinates using ARCINFO.

The presence or absence of anthropogenic disturbance and soil surface architecture (duff vs. turf) was also recorded from each site. For purposes of this study 'duff' soils represent sites where the organic horizon was deep (> 4 cm) and subtended by a friable upper A horizon consisting largely of humus and mineral soil. 'Turf' soils represent sites where the organic horizon is thin (< 4 cm) and immediately subtended by an upper A horizon firmly bound together by living plant roots. While many habitats only supported a single soil architecture type (e.g. all carbonate cliffs were duff, and all bedrock glades were turf), some (such as white cedar swamps) could possess either turf or duff surface layers, depending upon individual site conditions. Thus, habitat type could not be used as a surrogate for soil surface architecture.

Laboratory procedures

Samples were dried slowly and completely in either a low-temperature soil oven (*c*. 80–95 °C) or in a greenhouse. Dried samples were then soaked in water for 3–24 h, and subjected to careful but vigorous water disaggregation 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). These fractions were then dried and passed again through the same sieve series, and hand-picked against a neutral-brown background. All shells and shell fragments were removed.

All identifiable shells from each site were assigned to species (or subspecies) using the author's reference collection and the Hubricht Collection at the Field Museum of Natural History (FMNH). Identification of some additional specimens representing Holarctic taxa more common in western Europe were verified by Robert Cameron of the University of Sheffield, UK. All specimens have been catalogued and are housed in the author's reference collection at the University of Wisconsin — Green Bay. Nomenclature generally follows that of Hubricht (1985), with updates and corrections by Frest (1990, 1991) and Nekola (2002).

Statistical procedures

Ordination

Species lists were determined for each sample. Sites with four or fewer taxa were excluded from further analysis, as such samples can bias results and obscure compositional trends. The remaining sites were subjected to global nonmetric multidimensional scaling (NMDS) using DECODA (Minchin, 1990). NMDS was used as it makes no assumptions regarding the underlying nature of species distributions 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 sites using the Czekanowski (Bray–Curtis) index (Faith *et al.*, 1987). All species (including the most rarely encountered) were considered. NMDS in one to four dimensions was then performed, with 200 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 must be conducted on a given set of data from different initial random starting points to assess the stability of an individual solution (Minchin, 1987). For this ordination, DECODA used a total of 20 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 of the four dimensions (Minchin, 1990). The modal solution of 20 runs was identified, and was considered a global optimum when it was achieved in at least 50% of starts.

Identification of compositional groups

The chosen optimal NMDS solution was then subjected to model-based cluster analysis (Banfield & Raftery, 1992) to identify the number of compositional groups most supported by the data. Clustering was performed on the selected ordination output, rather than raw data, as ordination results are more robust and less susceptible to sampling or other inadvertent errors (Equihua, 1990). A sum-of-squares model was chosen, as it assumes that clusters will be spherical in ordination space, making them maximally compact and similar in composition. The approximate weight of evidence for k clusters (AWE_k) was calculated via the S + MCLUST algorithm (Statistical Sciences, 1995) for $k = 1$ to $n - 1$ clusters (where n = the total number of ordinated sites). The larger the AWE_k, the more evidence exists for that number of clusters. After the optimum number of clusters was determined, kmeans iterative relocation (Hartigan, 1975) was used to assign each site to a cluster. Kmeans clustering was chosen as it operates under the same sum-of-squares criteria used for AWE_k calculation.

Ordination interpretation

The number of occurrences (and frequency) of each species within each kmeans cluster was calculated. Species frequencies between clusters were compared using a Spearman's rank correlation. The 10 most frequent taxa, taxa reaching modal frequency and species richness for each cluster were calculated.

The frequency of the five major habitat groups between the compositional clusters was analysed using a contingency table. As predicted values were sparse (< 5) in more than one-fifth of cells, log-linear modelling was used to estimate significance (Zar, 1984).

The maximum correlation vectors for the four recorded environmental variables (UTM E coordinate, UTM N coordinate, soil surface type, presence of anthropogenic disturbance) was calculated by DECODA. The significance of each was estimated through Monte-Carlo simulations using 1000 replications.

Discriminant analysis was used to help further describe the impact of soil surface type and anthropogenic disturbance on site position in ordination space. Three tests were conducted: (1) effect of soil surface architecture (duff vs. turf) and the effect of anthropogenic disturbance separately for (2) duff and (3) turf soils.

Lastly, the number of duff and turf sites containing and lacking each species was calculated. The significance of observed differences in these ratios between duff and turf sites was estimated using log-linear modelling. As this test was repeated for each species, a Bonferroni correction was used to adjust the significance threshold. This conservative adjustment was used so that only the most robust deviations would be used for data interpretation.

RESULTS

Site ordination

One hundred and eight terrestrial gastropod taxa were identified from the 443 inventoried sites (Appendix I). Twenty-two sites were species poor (four or fewer taxa) and removed from further analysis. These included eight igneous cliffs, three lakeshore forests, three tamarack wetlands and single shale cliff, oak–hickory forest, maple–basswood forest, floodplain forest, sand dune, old field, sedge meadow and cobble beach sites.

Table 2 NMDS summary statistics from an ordination of 421 sites with five or more taxa

Dimensions	Stress level	Runs achieving minimum stress	Unique solutions	Number of runs in modal solution
1	0.339103	20	11	5
2	0.197412	20	6	10
3	0.147405	18	16	3
4	0.116912	18	18	1

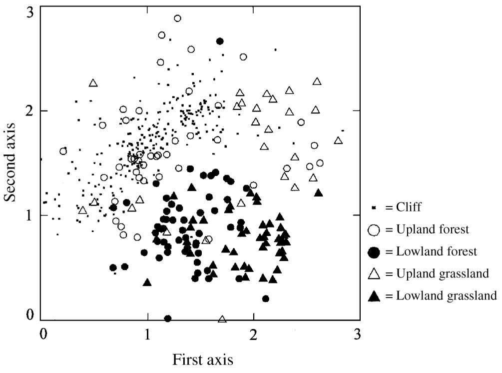

Fig. 2 NMDS ordination of 421 sites with land snail richness of 5 or more, showing distribution of the five main habitat groups. Units are scales in half-change units, such that a distance of 1 represents a 50% turnover in fauna composition.

Table 3 Approximate weight of evidence for k clusters (AWE_k) in land snail ordination based on a sum-of-squares model

No. of clusters	AWE_k	% Change from AWE_k to AWE_{k-1}
1	0	—
2	298.3	—
3	767.8	157.4
4	919.4	19.7
5	1097.8	19.4
6	1244.0	13.3
7	1335.2	7.3
8	1411.4	5.7
9	1456.7	3.2
10	1508.9	3.6
53	2131.5	—

NMDS of the remaining 421 sites demonstrated that the only stable solution occurred along two axes of variation, where one was achieved in 50% of starts. The minimum stress configuration of this solution was 0.197412. In other dimensions, the most stable solution(s) were achieved in five (one dimension), three (three dimensions) and one (four dimensions) runs (Table 2).

Identification and description of compositional clusters

Visual observation of the chosen NMDS ordination solution demonstrated apparent natural clustering in faunal composition, with at least one well-defined group existing in the lower-centre of the diagram (Fig. 2). AWE_k analysis demonstrated that the maximum score (2131.5) was achieved at the 53rd cluster. As this result provides too many groups to be useful for generalization of faunistic trends, AWE_k scores from $k = 1–10$ were calculated, along with the percentage increase in AWE_k from k to $k + 1$ clusters (Table 3). These data demonstrate that over 50% of maximum AWE_k was achieved by the 6th cluster. The percentage increase in AWE_k fell by almost 50% for cluster 7 (7.3%), and decreased steadily to the 3.4% range by cluster 10. Based on this, the optimal number of clusters was set at six (Fig. 3), even though it does not represent maximum AWE_k.

Contingency table analysis (Table 4) demonstrates that habitat representation significantly ($P < 0.00005$) varies between the six nonoverlapping kmeans clusters. Clusters A–C were equally ($P = 0.3778$) represented by rock outcrop and upland forest sites, while cluster D was dominated by lowland forests, cluster E by lowland grasslands and cluster F by upland grasslands. The 10 most frequent taxa also varied greatly,

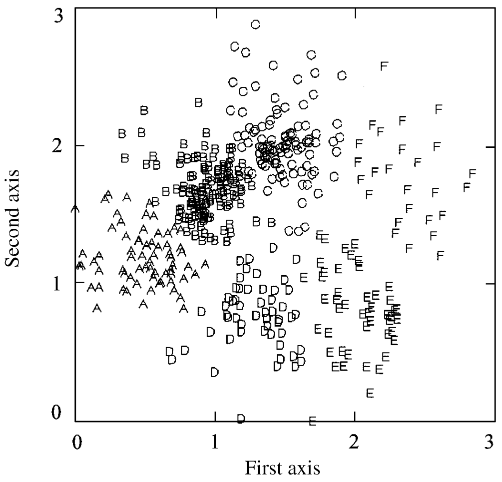

Fig. 3 NMDS ordination of 421 sites with land snail richness of five or more. Letters represent each of the six compositional clusters assigned via Kmeans Clustering.

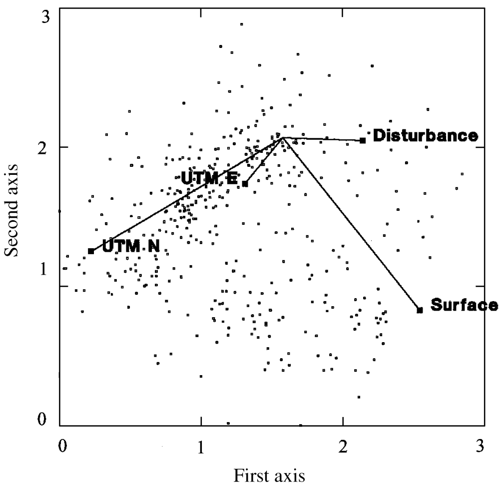

Fig. 4 Environmental biplot for NMDS ordination. The direction of each vector represents the angle of maximum correlation, while the length represents the strength of the correlation.

with approximately 50% turnover occurring between even the most similar groups (Table 5). Spearman's rank correlations of species occurrence frequencies indicated that clusters D and E were most similar (0.831), while clusters A and F were the most different (0.316). Six species possessed modal occurrence frequencies in cluster A, 25 in cluster B, 32 in cluster C, five in cluster D, 20 in cluster E and 20 in cluster F (Table 6). Forty-one total taxa were encountered in cluster A, 78 in cluster B, 87 in cluster C, 58 in cluster D, 60 in cluster E and 60 in cluster F (Appendix I).

Analysis of environmental co-variables

Monte Carlo testing of the maximum correlation vectors for the four recorded environmental variables (Fig. 4) demonstrated that all were highly significant ($P < 0.0005$), having maximum r-

Table 4 Contingency table analysis of main habitat groups vs. compositional clusters, with species richness within each cluster

Compositional cluster	Habitat group 1	2	3	4	5	Total sites	Species richness
A	57	6	2	4	0	69	41
B	100	20	2	1	0	123	78
C	86	9	4	3	0	102	87
D	2	2	37	2	11	54	58
E	0	1	10	2	34	47	60
F	5	5	0	15	1	26	60
Comparison	*Log-likelihood ratio statistic*					*d.f.*	*P*
Entire table	451.898					20	< 0.00005
Clusters A,B,C	8.593					8	0.3778
Clusters D,E,F	112.053					8	< 0.00005

Table 5 Ten most frequent taxa in each of the six compositional clusters

Rank order	Cluster A	Cluster B	Cluster C	Cluster D	Cluster E	Cluster F
1	*Discus catskillensis* (82.61%)	*Discus catskillensis* (93.50%)	*Punctum vitreum* (89.22%)	*Carychium exiguum* (88.89%)	*Gastrocopta tappaniana* (93.62%)	*Hawaiia minuscula* (57.69%)
2	*Nesovitrea binneyana* (82.61%)	*Punctum minutissimum* (91.06%)	*Gastrocopta contracta* (88.24%)	*Striatura milium* (83.33%)	*Carychium exiguum* (85.11%)	*Vallonia costata* (46.15%)
3	*Zonitoides arboreus* (82.61%)	*Zonitoides arboreus* (90.24%)	*Carychium exile* (88.24%)	*Nesovitrea electrina* (81.48%)	*Nesovitrea electrina* (85.11%)	*Cochlicopa lubrica* (46.15%)
4	*Vertigo cristata* (72.46%)	*Strobilops labyrinthica* (87.80%)	*Vertigo gouldi* (87.25%)	*Strobilops labyrinthica* (72.22%)	*Vertigo elatior* (74.47%)	*Helicodiscus parallelus* (46.15%)
5	*Striatura milium* (71.01%)	*Anguispira alternata* (84.55%)	*Anguispira alternata* (85.29%)	*Striatura exigua* (72.22%)	*Euconulus alderi* (70.21%)	*Gastrocopta contracta* (42.31%)
6	*Punctum minutissimum* (62.32%)	*Vertigo gouldi* (83.74%)	*Strobilops labyrinthica* (79.41%)	*Zonitoides arboreus* (68.52%)	*Hawaiia minuscula* (59.57%)	*Gastrocopta similis* (42.31%)
7	*Zoogenetes harpa* (53.62%)	*Columella simplex* (83.74%)	*Gastrocopta holzingeri* (78.43%)	*Vertigo elatior* (59.26%)	*Gastrocopta contracta* (57.45%)	*Punctum vitreum* (42.31%)
8	*Euconulus fulvus* (49.28%)	*Striatura milium* (73.98%)	*Hawaiia minuscula* (78.43%)	*Punctum minutissimum* (59.26%)	*Oxylama retusa* (55.32%)	*Gastrocopta holzingeri* (38.46%)
9	*Vertigo paradoxa* (49.28%)	*Helicodiscus shimeki* (66.67%)	*Gastrocopta pentodon* (74.51%)	*Gastrocopta tappaniana* (53.70%)	*Stenotrema leai* (55.32%)	*Vallonia pulchella* (38.46%)
10	*Striatura exigua* (46.38%)	*Euconulus fulvus* (65.85%)	*Zonitoides arboreus* (74.51%)	*Euconulus alderi* (48.15%)	*Deroceras* spp. (55.32%)	*Vertigo pygmaea* (38.46%)

Table 6 Taxa reaching modal frequencies in each compositional cluster

Cluster A	Cluster B	Cluster C	Cluster D	Cluster E	Cluster F
Nesovitrea binneyana	*Carychium nannodes*	*Allogona profunda*	*Carychium exiguum*	*Catinella avara*	*Catinella 'vermeta'*
Vertigo cristata	*Cochlicopa morseana*	*Anguispira alternata*	*Planogyra asteriscus*	*Catinella exile*	*Cepaea nemoralis*
Vertigo modesta modesta	*Columella simplex*	*Carychium exile*	*Striatura exigua*	*Cochlicopa lubricella*	*Cochlicopa lubrica*
Vertigo modesta parietalis	*Discus catskillensis*	*Catinella 'gelida'*	*Striatura milium*	*Discus cronkhitei*	*Gastrocopta armifera*
Vertigo paradoxa	*Discus patulus*	*Deroceras* spp.	*Vertigo nylanderi*	*Euconulus alderi*	*Gastrocopta procera*
Zoogenetes harpa	*Euconulus fulvus*	*Discus macclintockii*		*Gastrocopta tappaniana*	*Gastrocopta rogersensis*
	Euconulus polygyratus	*Gastrocopta contracta*		*Hawaiia* n.sp.	*Gastrocopta similis*
	Glyphyalinia rhoadsi	*Gastrocopta corticaria*		*Helicodiscus* n.sp.	*Glyphyalinia wheatleyi*
	Helicodiscus shimeki	*Gastrocopta holzingeri*		*Nesovitrea electrina*	*Helicodiscus inermis*
	Mesomphix cupreus	*Gastrocopta pentodon*		*Oxyloma peoriensis*	*Helicodiscus parallelus*
	Mesomphix inornatus	*Glyphyalinia indentata*		*Oxyloma retusa*	*Helicodiscus singleyanus*
	Oxychylus draparnaudi	*Guppya sterkii*		*Pomatiopsis lapidaria*	*Pupilla muscorum*
	Paravitrea multidentata	*Haplotrema concavum*		*Punctum* n.sp.	*Pupoides albilabris*
	Punctum minutissimum	*Hawaiia minuscula*		*Stenotrema leai*	*Succinea indiana*
	Striatura ferrea	*Hendersonia occulta*		*Strobilops affinis*	*Vallonia costata*
	Strobilops labyrinthica	*Mesodon clausus*		*Triodopsis multilineata*	*Vallonia excentrica*
	Triodopsis albolabris	*Mesodon pennsylvanicus*		*Vertigo elatior*	*Vallonia parvula*
	Triodopsis denotata	*Mesodon thyroidus*		*Vertigo milium*	*Vallonia pulchella*
	Triodopsis tridentata	*Oxychylus cellarius*		*Vertigo morsei*	*Vertigo pygmaea*
	Vallonia gracilicosta	*Punctum vitreum*		*Vertigo ovata*	*Zonitoides nitidus*
	Vertigo n.sp.	*Stenotrema barbatum*			
	Vertigo bollesiana	*Stenotrema fraternum*			
	Vertigo hubrichti	*Strobilops aenea*			
	Vitrina limpida	*Succinea ovalis*			
	Zonitoides arboreus	*Trichia striolata*			
		Triodopsis alleni			
		Triodopsis fosteri			
		Vallonia perspectiva			
		Vertigo gouldi			
		Vertigo meramecensis			
		Vertigo tridentata			
		Zonitoides limatulus			

Table 7 Two-dimensional correlation statistics for environmental variables in land snail ordination space

Variable	Maximum *r*	Angle to first axis	*P*
Entire ordination			
UTM E-W coordinate	0.2111	129.4	< 0.0005
UTM N-S coordinate	0.7909	148.9	< 0.0005
Soil surface type	0.7843	52.1	< 0.0005
Disturbance presence	0.2829	1.7	< 0.0005
Duff soil sites only			
UTM E-W coordinate	0.1020	100.4	0.190
UTM N-S coordinate	0.8409	134.7	< 0.0005
Disturbance presence			
Turf soil sites only	0.4812	31.9	< 0.0005
UTM E-W coordinate	0.5067	150.4	< 0.0005
UTM N-S coordinate	0.6690	162.0	< 0.0005
Disturbance presence	0.0671	1.3	0.820

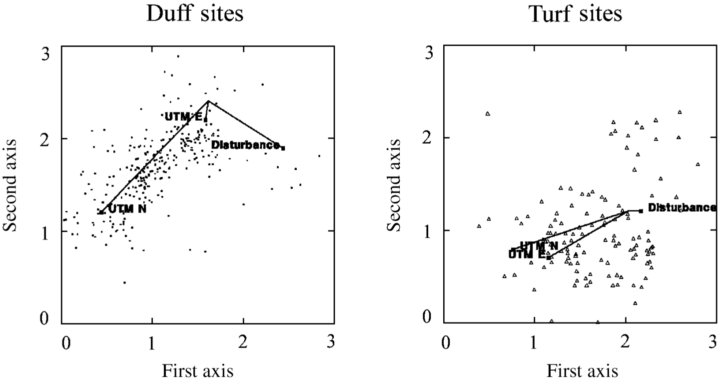

Fig. 5 Environmental biplots for duff and turf sites. The direction of each vector represents the angle of maximum correlation, while the length represents the strength of the correlation.

values ranging from 0.2111 to 0.7909 (Table 7). In duff sites, only UTM N coordinate and anthropogenic disturbance were found to correlate significantly ($P < 0.0005$) with the ordination diagram (Table 7). Northern sites tended to occur in the lower left of this group (maximum r = 0.8409), while disturbed sites tended to occur further to the right (maximum $r = 0.4812$; Fig. 5). In turf sites, only UTM N and E coordinates were found to correlate significantly ($P < 0.0005$) with the ordination diagram (Table 7). In this group, more northern (maximum r = 0.6690) and eastern (maximum r = 0.5067) sites tended to occur to the lower left (Fig. 5).

Discriminant analysis demonstrated that the location of duff and turf sites in ordination space differs significantly ($P < 0.0005$) (Table 8), with duff sites being essentially limited to the upper left half of the diagram, and turf sites being found largely in the lower right (Fig. 6). The classification summary for this analysis indicates that only 33 of the 421 sites (7.8%) were classified improperly when soil surface type was used as the sole predictor variable.

Discriminant analyses conducted separately on duff and turf sites demonstrated that disturbed duff sites were significantly ($P < 0.0005$) shifted to the right of undisturbed ones (Fig. 7). The

Table 8 Summary statistics for discriminant analysis of substrate and disturbance comparisons in land snail community ordination

Factor	Comparison Duff vs. turf (all sites)	 Disturbed vs. pristine (duff sites only)	 Disturbed vs. pristine (turf sites only)
Canonical correlation	0.784	0.482	0.067
Eigenvalue	1.596	0.302	0.005
Likelihood ratio	0.385	0.768	0.996
Approximate *F*	322.74	43.915	0.278
Number d.f.	2	2	2
Density d.f.	417	291	123
P	< 0.0005	< 0.0005	0.758

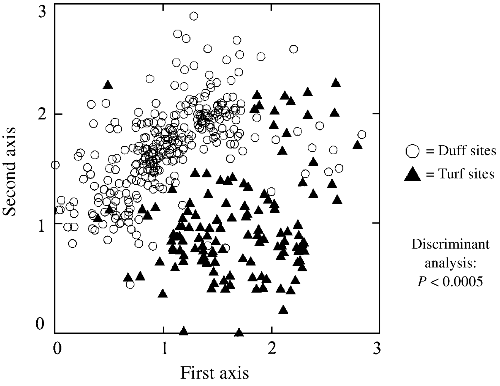

Fig. 6 Location of duff and turf sites within the ordination diagram.

classification summary for this analysis indicates that only 50 of the 295 duff sites (16.9%) were improperly classified when anthropogenic disturbance was used as the sole predictor variable. However, no significant differences ($P = 0.758$) were noted in the location of disturbed vs. undisturbed turf sites (Table 8).

Faunistic turnover between duff and turf soils

As differences in occurrence frequency between duff and turf sites were analysed for all 108 species, the significance threshold was lowered using a Bonferroni correction to $P = 0.000463$. Species with P-values ranging from 0.05 to 0.000463 were considered to possess statistically nonsignificant trends in their response to soil surface architecture. Species with P-values exceeding 0.05 were considered generalists.

Thirty-six species demonstrated no significant differences in their occurrence frequencies between duff and turf soils (Appendix I). Sixteen of these (*Cochlicopa lubricella*, *Deroceras* spp., *Discus cronkhitei*, *Gastrocopta armifera*, *Gastrocopta contracta*, *Haplotrema concavum*, *Hawaiia*

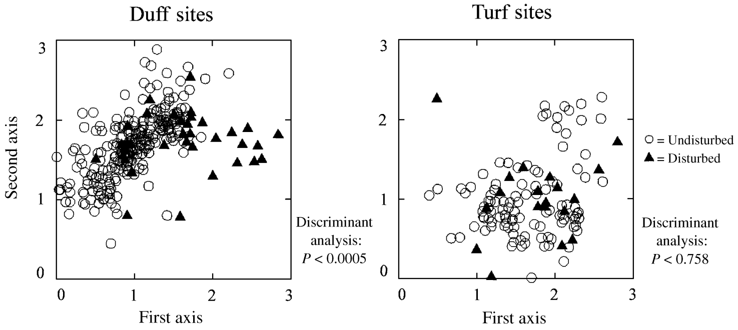

Fig. 7 Location of disturbed and undisturbed sites in the ordination diagram for duff and turf sites.

minuscula, *Helicodiscus parallelus*, *Helicodiscus singleyanus*, *Planogyra asteriscus*, *Striatura ferrea*, *Striatura milium*, *Triodopsis multilineata*, *Vallonia costata*, *Vertigo pygmaea*, *Vitrina limpida*) were found in 10 or more sites, and clearly represent generalists. However, the remaining 20 (*Carychium nannodes*, *Cepaea nemoralis*, *Discus patulus*, *Glyphyalinia wheatleyi*, *Helicodiscus inermis*, *Mesodon pennsylvanicus*, *Mesomphix cupreus*, *Mesomphix inornatus*, *Oxychylus cellarius*, *Oxychylus draparnaudi*, *Oxyloma peoriensis*, *Pomatiopsis lapidaria*, *Pupilla muscorum*, *Succinea indiana*, *Trichia striolata*, *Triodopsis denotata*, *Triodopsis fosteri*, *Vallonia excentrica*, *Vertigo modesta parietalis*, *Zonitoides limatulus*) are known from fewer locations, making Type 2 errors a significant concern. Additional data will be needed to adequately assess the response of these species to duff vs. turf soils.

Eighteen species (*Cochlicopa lubrica*, *Cochlicopa morseana*, *Discus macclintockii*, *Mesodon clausus clausus*, *Mesodon thyroidus*, *Punctum minutissimum*, *Punctum vitreum*, *Stenotrema barbatum*, *Strobilops aenea*, *Strobilops labyrinthica*, *Succinea ovalis*, *Triodopsis albolabris*, *Triodopsis alleni*, *Triodopsis tridentata*, *Vallonia perspectiva*, *Vertigo meramecensis*, *Vertigo modesta modesta*, *Vertigo tridentata*) nonsignificantly favoured duff sites. Another eight (*Gastrocopta procera*, *Gastrocopta rogersensis*, *Gastrocopta similis*, *Hawaiia* n.sp., *Helicodiscus* n.sp., *Striatura exigua*, *Vallonia pulchella*, *Zonitoides nitidus*) nonsignificantly favoured turf sites. While a number of these (e.g. *Discus macclintockii*, *Gastrocopta procera*, *Gastrocopta rogersensis*, *Vertigo meramecensis*) demonstrated very strong absolute preferences, their few total occurrences in combination with the conservative Bonferroni correction prevented them from exhibiting significant responses.

The remaining 46 species demonstrated clear and significant soil surface preferences. Twenty-eight species (*Allogona profunda*, *Anguispira alternata*, *Carychium exile*, *Catinella 'gelida'*, *Columella simplex*, *Discus catskillensis*, *Euconulus fulvus*, *Euconulus polygyratus*, *Gastrocopta corticaria*, *Gastrocopta holzingeri*, *Gastrocopta pentodon*, *Glyphyalinia indentata*, *Glyphyalinia rhoadsi*, *Guppya sterkii*, *Helicodiscus shimeki*, *Hendersonia occulta*, *Nesovitrea binneyana*, *Paravitrea multidentata*, *Stenotrema fraternum*, *Vallonia gracilicosta*, *Vertigo bollesiana*, *Vertigo cristata*, *Vertigo gouldi*, *Vertigo hubrichti*, *Vertigo* n.sp., *Vertigo paradoxa*, *Zonitoides arboreus*, *Zoogenetes harpa*) favoured duff soils, while another 18 (*Carychium exiguum*, *Catinella avara*, *Catinella exile*, *Catinella 'vermeta'*, *Euconulus alderi*, *Gastrocopta tappaniana*, *Nesovitrea electrina*, *Oxyloma retusa*, *Punctum* n.sp., *Pupoides albilabris*, *Stenotrema leai leai*, *Strobilops affinis*, *Vallonia parvula*, *Vertigo elatior*, *Vertigo milium*, *Vertigo morsei*, *Vertigo nylanderi*, *Vertigo ovata*) favoured turf soils.

DISCUSSION

These data demonstrate clearly that at large environmental and spatial scales most land snail species possess pronounced ecological preferences. They thus represent a paradox, being generalists at small scales, yet responding to specific environmental factors at larger ones. At large scales, species tend to congregate into six major compositional clusters related to habitat type, soil surface architecture, geography, moisture levels and presence of anthropogenic disturbance.

Habitat type

The six compositional clusters significantly differ in their habitat representations. Clusters A–D generally consist of forested sites while clusters E–F generally consist of grasslands. These results are in agreement with previous studies from other regions, including north-western Spain (Ondina & Mato, 2001), southern France (Magnin *et al.*, 1995), western Switzerland (Baur *et al.*, 1996), Croatia (Stamol, 1991, 1993), Hungary (Bába, 1989) and north-eastern Nevada (Ports, 1996). The contrast between open-ground and forest faunas is not limited to terrestrial gastropods. Other soil invertebrate groups that demonstrate this pattern include fungus-eating microarthropods (Branquart *et al.*, 1995), carabid beetles (McCracken, 1994), terrestrial amphipods (Taylor *et al.*, 1995) and collembola (Greenslade, 1997). In an ordination of global earthworm communities, Lavelle *et al.* (1995) demonstrated that open-ground and forest assemblages were distinct from the warm-tropics to the arctic. The distinction between forest and grassland faunas thus appears to be a general driving factor in soil biota community composition.

Soil surface architecture

The greater similarity of most lowland forest faunas to lowland grasslands, as opposed to upland forests and rock outcrops (Fig. 2), suggests additional factors underlie observed land snail composition patterns. The potential importance of soil surface architecture is implied as many lowland forest sites (e.g. tamarack, white cedar and most black ash swamp forests), and all lowland grasslands, possess turf soils. Only 8% of sites were improperly classified when soil surface type was used as the sole predictor variable (Table 7). Even this rate may be exaggerated, as most misclassifications were limited to two specific instances. First, even though having turf soils, igneous shoreline habitats had faunas almost identical to surrounding rock outcrop sites. Snails in this habitat, however, were largely restricted to friable accumulations of organic matter under stunted white cedar trees. Secondly, almost all duff sites with faunas similar to upland grasslands had experienced severe levels of anthropogenic disturbance.

Striking differences exist between the species of duff and turf sites: 43% of taxa significantly favoured one soil surface type over the other (even with use of a conservative Bonferroni-corrected significance threshold), while only 15% of frequent taxa (10 + occurrences) showed no preference. Inspection of these data indicate that for eight groups of closely related taxa within the same genus (24 total), one or more significantly favour duff soils, while the other(s) significantly favour turf (Table 9). In another four groups (10 additional taxa), one or more taxa significantly favour one of these soil types, while the other(s) exhibit a nonsignificant preference (Table 9). These 12 groups represent a wide variety of phylogenetic stocks (representing nine families: Carychiidae, Helicarionidae, Polygyridae, Punctidae, Pupillidae, Strobilopsidae, Succineidae, Valloniidae, Zonitidae), shell shapes (five wider than tall, five taller than wide and two equally tall as wide), and maximum shell dimensions (0.8 mm–12 mm). The presence of so many pairs of closely related duff- and turf-specialist taxa across such a wide range of phylogenies, shell shapes and dimensions suggests that very strong selective pressures between these soil surface types have extended over evolutionary time scales.

Table 9 Closely related intergeneric species pairs that demonstrate significant differences and/or nonsignificant trends in their soil surface preferences. A significance level of ** represents those species which possess $P < 0.000463$; * represent those species where $0.000463 < P < 0.05$

Duff-specialist	Sign. level	Turf-specialist	Sign. level	Family	Shell shape	Shell size (mm)
Carychium exile	**	*Carychium exiguum*	**	Carychiidae	Tall	1.5–2
Catinella 'gelida'	**	*Catinella avara*, *C. exile*, *C. 'vermeta'*	**	Succineidae	Tall	4–6
Euconulus fulvus	**	*Euconulus alderi*	**	Helicarionidae	Equal	3–4
Gastrocopta pentodon	**	*Gastrocopta tappaniana*	**	Pupillidae	Tall	2
Nesovitrea binneyana	**	*Nesovitrea electrina*	**	Zonitidae	Wide	4–7
Punctum minutissimum, *P. vitreum*	*	*Punctum* n.sp.	**	Punctidae	Wide	0.8–1.5
Stenotrema fraternum	**	*Stenotrema leai*	**	Polygyridae	Wide	8–12
Strobilops labyrinthica	*	*Strobilops affinis*	**	Strobilopsidae	Equal	2–3
Vallonia perspectiva	*	*Vallonia parvula*	**	Valloniidae	Wide	2
Vertigo gouldi 'group' (*V. bollesiana*, *V. cristata*, *V. gouldi*)	**	*Vertigo ovata 'group'* (*V. elatior*, *V. morsei*, *V. ovata*)	**	Pupillidae	Tall	1.5–3
Vertigo hubrichti, *V. paradoxa*, *V.* n.sp.	**	*Vertigo nylanderi*	**	Pupillidae	Tall	1.5–2
Zonitoides arboreus	**	*Zonitoides nitidus*	*	Zonitidae	Wide	4–6

It is not possible via the current analyses to definitively identify what such factors might be. They must be limited to the detritusphere (Coleman & Crossley, 1996), as almost 90% of snails live within 5 cm of the soil surface (Hawkins *et al*., 1998). One possible mechanism is increased competition with living plant roots in turf soils for inorganic nutrients (Lavelle *et al*., 1995). Another may be the greater organic litter thickness in duff soils, as the abundance (Berry, 1973), diversity (Cain, 1983; Locasciulli & Boag, 1987) and composition (Cameron & Morgan-Huws, 1975; Baur *et al*., 1996; Barker & Mayhill, 1999) of land snail communities often correlates positively with litter depth. The architecture of organic litter (Burch, 1956; Cameron, 1986; Young & Evans, 1991; Alvarez & Willig, 1993), and the underlying soil (Cameron, 1982; Hermida *et al*., 2000) may also have strong impacts on land snail community structure.

Similarly, the composition and abundance of other soil taxa communities can be influenced by organic litter depth and architecture, including amphipods (Taylor *et al*., 1995), microarthropods (Borcard & Matthey, 1995; Branquart *et al*., 1995; Kay *et al*., 1999; Whitford & Sobhy, 1999), collembola (Kovac & Miklisova, 1997) and ground beetles (McCracken, 1994). Thus, like habitat type, upper soil layer architecture appears to be another vital factor driving soil biota composition.

Geography

The geographical location of sites also influences community composition, particularly in duff soils (Fig. 5). Each of the three duff clusters have an unique geographical affiliation, with cluster A being largely restricted to the most northern sites, cluster B to sites in the northern half of the Lake Michigan–Huron basin, and cluster C to sites in Iowa, Illinois, and southern Wisconsin.

While a significant correlation with both latitude and longitude was also observed in turf sites, this result is almost certainly an artefact of the limitation of upland grassland sites to the south-west of the study region. Fens and lowland forests, found throughout, exhibited little geographical trends inside of the ordination diagram. Geographical location was presumably less important for these sites due to the overriding importance of habitat type and soil moisture.

Soil moisture and temperature

Soil moisture and sunlight levels also appear to influence land snail community composition in turf sites, with the driest and sunniest habitats (upland grasslands) being most different in composition from wet, shaded lowland forests. However, temperature and relative humidity, not sunlight, are probably the important driving factors (Suominen, 1999), as in both duff and turf sites the coolest and wettest habitats (northern cliff, upland forest and lowland forest) were most different in composition from the hottest and driest sites (southern cliff, upland forest and upland grassland).

Disturbance and conservation

Anthropogenic disturbance influences snail composition differentially between duff and turf sites. While turf faunas were not impacted, the most disturbed duff sites had faunas more characteristic of upland grasslands. Typical species found on such disturbed sites include *Cochlicopa lubrica*, *Pupilla muscorum*, *Vallonia costata*, *Vallonia excentrica*, *Vallonia pulchella* and *Vertigo pygmaea*. These faunistic differences may be related to differential changes in soil surface architecture with disturbance. Because undisturbed turf soils usually have thinner and less structurally complex organic litter layers, they may be less susceptible to soil compaction (and changes in composition) as compared to duff sites.

As anthropogenic soil compaction negatively impacts soil invertebrates more severely than plants in the same communities (Duffey, 1975), conservation of duff-specialist land snails will likely require protection of the soil litter layer architecture, perhaps by limiting forestry and recreation activities in duff soil sites of conservation importance. While turf sites appear to be more tolerant of human disturbance, this should not indicate that their land snail communities are immune to human activity. For instance, heavy grazing can negatively impact grassland snails (Cameron & Morgan-Huws, 1975), while the use of fire-management can lead to significant reductions in both species richness and abundance (Nekola, 2002b).

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/DDI/DDI165/DDI165sm.htm

Appendix 1

Table S1 Species occurrences and frequencies within the six main ordination clusters, and within sites with duff or turf organic horizons.

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Appendix I *continued.*

APPENDIX I

Species occurrences and frequencies within the six main ordination clusters, and within sites with duff or turf organic horizons

	Number of occurrences/frequency in cluster						Duff vs. turf		
Species	A	B	C	D	E	F	Duff	Turf	*P*-value
Allogona profunda (Say, 1821)	0	8	32	0	0	0	40	0	
	0.00	6.50	31.37	0.00	0.00	0.00	13.61	0.00	0.0000000
Anguispira alternata (Say, 1817)	19	104	87	0	3	3	212	4	
	27.54	84.55	85.29	0.00	6.38	11.54	71.86	3.17	0.0000000
Carychium exiguum (Say, 1822)	1	5	9	48	40	2	12	93	
	1.45	4.07	8.82	88.89	85.11	7.69	4.07	73.81	0.0000000
Carychium exile (H.C. Lea, 1842)	12	60	90	17	5	3	158	29	
	17.39	48.78	88.24	31.48	10.64	11.54	53.56	23.02	0.0000000
Carychium nannodes (Clapp, 1905)	0	1	0	0	0	0	1	0	
	0.00	0.81	0.00	0.00	0.00	0.00	0.34	0.00	0.3986709
Catinella avara (Say, 1824)	0	0	3	3	15	1	3	19	
	0.00	0.00	2.94	5.56	31.91	3.85	1.02	15.08	0.0000000
Catinella exile (Leonard, 1972)	0	0	0	2	14	0	0	16	
	0.00	0.00	0.00	3.70	29.79	0.00	0.00	12.70	0.0000000
Catinella ‘gelida’ (F.C. Baker, 1927)	0	1	26	0	0	0	27	0	
	0.00	0.81	25.49	0.00	0.00	0.00	9.15	0.00	0.0000078
Catinella ‘vermeta’	0	0	3	0	0	3	0	6	
	0.00	0.00	2.94	0.00	0.00	11.54	0.00	4.76	0.0001273
Cepaea nemoralis (Linné, 1798)	0	0	0	1	0	1	1	1	
	0.00	0.00	0.00	1.85	0.00	3.85	0.34	0.79	0.5522717
Cochlicopa lubrica (Müller, 1774)	7	23	34	7	9	12	72	20	
	10.14	18.70	33.33	12.96	19.15	46.15	24.41	15.87	0.0471465
Cochlicopa lubricella (Porro, 1838)	4	13	17	1	10	4	37	12	
	5.80	10.57	16.67	1.85	21.28	15.38	12.54	9.52	0.3684043
Cochlicopa morseana (Doherty, 1878)	3	23	9	2	1	0	35	3	
	4.35	18.70	8.82	3.70	2.13	0.00	11.86	2.38	0.0005306
Columella simplex (Gould, 1841)	25	103	67	26	5	2	187	41	
	36.23	83.74	65.69	48.15	10.64	7.69	63.39	32.54	0.0000000
Deroceras spp.	1	28	67	12	26	8	95	47	
	1.45	22.76	65.69	22.22	55.32	30.77	32.20	37.30	0.3131198

Appendix 1 *continued.*

	Number of occurrences/frequency in cluster						Duff vs. turf		
Species	A	B	C	D	E	F	Duff	Turf	*P*-value
Discus catskillensis (Pilsbry, 1898)	57	115	37	13	1	1	204	20	
	82.61	93.50	36.27	24.07	2.13	3.85	69.15	15.87	0.0000000
Discus cronkhitei (Newcomb, 1865)	13	15	15	4	20	6	47	26	
	18.84	2.20	14.71	7.41	42.55	23.08	15.93	20.63	0.2491709
Discus macclintockii (F.C. Baker, 1928)	0	1	9	0	0	0	10	0	
	0.00	0.81	8.82	0.00	0.00	0.00	3.39	0.00	0.0072231
Discus patulus (Deshayes, 1830)	0	1	0	0	0	0	1	0	
	0.00	0.81	0.00	0.00	0.00	0.00	0.34	0.00	0.3986709
Euconulus alderi (Gray, 1840)	0	1	1	26	33	0	1	60	
	0.00	0.81	0.98	48.15	70.21	0.00	0.34	47.62	0.0000000
Euconulus fulvus (Müller, 1774)	34	81	47	8	7	6	156	27	
	49.28	65.85	46.08	14.81	14.89	23.08	52.88	21.43	0.0000000
Euconulus polygyratus (Pilsbry, 1899)	2	58	42	3	2	0	98	9	
	2.90	47.15	41.18	5.56	4.26	0.00	33.22	7.14	0.0000000
Gastrocopta armifera (Say, 1821)	0	0	25	0	0	7	24	8	
	0.00	0.00	24.51	0.00	0.00	26.92	8.14	6.35	0.5198906
Gastrocopta contracta (Say, 1822)	0	46	90	7	27	11	133	48	
	0.00	37.40	88.24	12.96	57.45	42.31	45.08	38.10	0.1831730
Gastrocopta corticaria (Say, 1816)	0	9	58	0	0	2	65	4	
	0.00	7.32	56.86	0.00	0.00	7.69	22.03	3.17	0.0000001
Gastrocopta holzingeri (Sterki, 1889)	0	13	80	1	1	10	89	16	
	0.00	10.57	78.43	1.85	2.13	38.46	30.17	12.70	0.0000716
Gastrocopta pentodon (Say, 1821)	3	70	76	10	5	9	141	32	
	4.35	56.91	74.51	18.52	10.64	34.62	47.80	25.40	0.0000130
Gastrocopta procera (Gould, 1840)	0	0	2	0	0	2	0	4	
	0.00	0.00	1.96	0.00	0.00	7.69	0.00	3.17	0.0018020
Gastrocopta rogersensis (Nekola & Coles, 2001)	0	0	1	0	0	3	0	4	
	0.00	0.00	0.98	0.00	0.00	11.54	0.00	3.17	0.0018020
Gastrocopta similis (Sterki, 1909)	0	0	15	0	1	11	13	14	
	0.00	0.00	14.71	0.00	2.13	42.31	4.41	11.11	0.0138256
Gastrocopta tappaniana (C.B. Adams, 1842)	0	1	9	29	44	5	12	76	
	0.00	0.81	8.82	53.70	93.62	19.23	4.07	60.32	0.0000000

Appendix 1 *continued.*

	Number of occurrences/frequency in cluster						Duff vs. turf		
Species	A	B	C	D	E	F	Duff	Turf	*P*-value
Glyphyalinia indentata (Say, 1823)	2	48	46	4	6	7	94	19	
	2.90	39.02	45.10	7.41	12.77	26.92	31.86	15.08	0.0002203
Glyphyalinia rhoadsi (Pilsbry, 1899)	0	21	3	0	0	0	24	0	
	0.00	17.07	2.94	0.00	0.00	0.00	8.14	0.00	0.0000261
Glyphyalinia wheatleyi (Bland, 1883)	0	1	0	1	0	1	3	0	
	0.00	0.81	0.00	1.85	0.00	3.85	1.02	0.00	0.1423208
Guppya sterkii (Dall, 1888)	0	5	19	0	0	0	24	0	
	0.00	4.07	18.63	0.00	0.00	0.00	8.14	0.00	0.0000261
Haplotrema concavum (Say, 1821)	0	6	23	1	2	0	27	5	
	0.00	4.88	22.55	1.85	4.26	0.00	9.15	3.97	0.0516709
Hawaiia minuscula (A. Binney, 1840)	0	12	80	1	28	15	91	45	
	0.00	9.76	78.43	1.85	59.57	57.69	30.85	35.71	0.3304475
Hawaiia n.sp.	0	0	1	0	6	0	1	6	
	0.00	0.00	0.98	0.00	12.77	0.00	0.34	4.76	0.0019219
Helicodiscus inermis (H.B. Baker, 1929)	0	0	6	0	0	2	4	4	
	0.00	0.00	5.88	0.00	0.00	7.69	1.36	3.17	0.2308550
Helicodiscus n.sp.	0	0	0	0	5	0	0	5	
	0.00	0.00	0.00	0.00	10.64	0.00	0.00	3.97	0.0004766
Helicodiscus parallelus (Say, 1817)	9	30	46	16	10	12	85	38	
	13.04	24.39	45.10	29.63	21.28	46.15	28.81	30.16	0.7814013
Helicodiscus shimeki (Hubricht, 1962)	15	82	68	11	6	2	162	22	
	21.74	66.67	66.67	20.37	12.77	7.69	54.92	17.46	0.0000000
Helicodiscus singleyanus (Pilsbry, 1890)	0	0	9	0	0	3	8	4	
	0.00	0.00	8.82	0.00	0.00	11.54	2.71	3.17	0.7959002
Hendersonia occulta (Say, 1831)	0	25	50	0	3	3	75	6	
	0.00	20.33	49.02	0.00	6.38	11.54	25.42	4.76	0.0000001
Mesodon clausus clausus (Say, 1821)	0	1	16	0	0	0	16	1	
	0.00	0.81	15.69	0.00	0.00	0.00	5.42	0.79	0.0115199
Mesodon pennsylvanicus (Green, 1827)	0	0	1	0	0	0	1	0	
	0.00	0.00	0.98	0.00	0.00	0.00	0.34	0.00	0.3986709
Mesodon thyroidus (Say, 1816)	0	4	8	0	0	0	12	0	
	0.00	3.25	7.84	0.00	0.00	0.00	4.07	0.00	0.0032079

Appendix I *continued.*

	Number of occurrences/frequency in cluster						Duff vs. turf		
Species	A	B	C	D	E	F	Duff	Turf	*P*-value
Mesomphix cupreus (Rafinesque, 1831)	0	3	1	0	0	0	4	0	
	0.00	2.44	0.98	0.00	0.00	0.00	1.36	0.00	0.0907153
Mesomphix inornatus (Say, 1821)	0	5	0	0	0	0	5	0	
	0.00	4.07	0.00	0.00	0.00	0.00	1.69	0.00	0.0584018
Nesovitrea binneyana (Morse, 1864)	57	56	20	6	1	0	128	12	
	82.61	45.53	19.61	11.11	2.13	0.00	43.39	9.52	0.0000000
Nesovitrea electrina (Gould, 1841)	10	10	5	44	40	7	23	93	
	14.49	8.13	4.90	81.48	85.11	26.92	7.80	73.81	0.0000000
Oxychylus cellarius (Müller, 1774)	0	1	2	0	0	0	3	0	
	0.00	0.81	1.96	0.00	0.00	0.00	1.02	0.00	0.1423208
Oxychylus draparnaudi (Beck, 1837)	0	1	0	0	0	0	1	0	
	0.00	0.81	0.00	0.00	0.00	0.00	0.34	0.00	0.3986709
Oxyloma peoriensis (Wolf in Walker, 1892)	0	0	0	0	1	0	0	1	
	0.00	0.00	0.00	0.00	2.13	0.00	0.00	0.79	0.1199264
Oxyloma retusa (I. Lea, 1834)	0	0	5	2	26	1	4	30	
	0.00	0.00	4.90	3.70	55.32	3.85	1.36	23.81	0.0000000
Paravitrea multidentata (A. Binney, 1840)	4	72	12	0	0	1	89	0	
	5.80	58.54	11.76	0.00	0.00	3.85	30.17	0.00	0.0000000
Planogyra asteriscus (Morse, 1857)	7	4	0	7	0	0	9	9	
	10.14	3.25	0.00	12.96	0.00	0.00	3.05	7.14	0.0685170
Pomatiopsis lapidaria (Say, 1817)	0	0	3	1	3	1	3	5	
	0.00	0.00	2.94	1.85	6.38	3.85	1.02	3.97	0.0547007
Punctum minutissimum (I. Lea, 1841)	43	112	6	32	9	2	157	47	
	63.32	91.06	5.88	59.26	19.15	7.69	53.22	37.30	0.0026417
Punctum n.sp.	0	0	0	2	18	1	0	21	
	0.00	0.00	0.00	3.70	38.30	3.85	0.00	16.67	0.0000000
Punctum vitreum (H.B. Baker, 1930)	0	5	91	1	7	11	93	22	
	0.00	4.07	89.22	1.85	14.89	42.31	31.53	17.46	0.0022757
Pupilla muscorum (Linné, 1758)	0	3	0	2	0	1	4	2	
	0.00	2.44	0.00	3.70	0.00	3.85	1.36	1.59	0.8558760
Pupoides albilabris (C.B. Adams, 1821)	0	0	6	0	1	9	3	13	
	0.00	0.00	5.88	0.00	2.13	34.62	1.02	10.32	0.0000141

Appendix 1 *continued.*

	Number of occurrences/frequency in cluster						Duff vs. turf		
Species	A	B	C	D	E	F	Duff	Turf	*P*-value
Stenotrema barbatum (Clapp, 1904)	0	1	21	1	2	0	22	3	
	0.00	0.81	20.59	1.85	4.26	0.00	7.46	2.38	0.0287753
Stenotrema fraternum fraternum (Say, 1824)	2	47	42	0	0	0	90	1	
	2.90	38.21	41.18	0.00	0.00	0.00	30.51	0.79	0.0000000
Stenotrema leai leai (A. Binney)	0	0	2	6	26	6	2	38	
	0.00	0.00	1.96	11.11	55.32	23.08	0.68	30.16	0.0000000
Striatura exigua (Stimpson, 1847)	32	45	2	39	4	0	76	46	
	46.38	36.59	1.96	72.22	8.51	0.00	25.76	36.51	0.0278698
S*triatura ferrea* (Morse, 1864)	4	35	1	13	3	0	38	18	
	5.80	28.46	0.98	24.07	6.38	0.00	12.88	14.29	0.6992505
Striatura milium (Morse, 1859)	49	91	32	45	10	0	165	62	
	71.01	73.98	31.37	83.33	21.28	0.00	55.93	49.21	0.2052325
Strobilops aenea (Pilsbry, 1926)	0	1	5	0	0	0	6	0	
	0.00	0.81	4.90	0.00	0.00	0.00	2.03	0.00	0.0380037
Strobilops affinis (Pilsbry, 1893)	0	0	1	5	23	0	1	28	
	0.00	0.00	0.98	9.26	48.94	0.00	0.34	22.22	0.0000000
Strobilops labyrinthica (Say, 1817)	24	108	81	39	16	3	203	68	
	34.78	87.80	79.41	72.22	34.04	11.54	68.81	53.97	0.0038899
Succinea indiana (Pilsbry, 1905)	0	0	0	0	0	1	0	1	
	0.00	0.00	0.00	0.00	0.00	3.85	0.00	0.79	0.1199264
Succinea ovalis (Say, 1817)	9	26	24	4	9	2	60	14	
	13.04	21.14	23.53	7.41	19.15	7.69	20.34	11.11	0.0182788
Trichia striolata (Pfeiffer)	0	0	1	0	0	0	1	0	
	0.00	0.00	0.98	0.00	0.00	0.00	0.34	0.00	0.3986709
Triodopsis albolabris (Say, 1816)	0	14	1	0	0	0	15	0	
	0.00	11.38	0.98	0.00	0.00	0.00	5.08	0.00	0.0009592
Triodopsis alleni (Wetherby in Sampson, 1883)	0	1	14	0	0	0	14	1	
	0.00	0.81	13.73	0.00	0.00	0.00	4.75	0.79	0.0230409
Triodopsis denotata (Férussac, 1821)	0	2	1	0	0	0	3	0	
	0.00	1.63	0.98	0.00	0.00	0.00	1.02	0.00	0.1432081
Triodopsis fosteri (F.C. Baker, 1932)	0	0	1	0	0	0	1	0	
	0.00	0.00	0.98	0.00	0.00	0.00	0.34	0.00	0.3986709

Appendix 1 *continued.*

	Number of occurrences/frequency in cluster						Duff vs. turf		
Species	A	B	C	D	E	F	Duff	Turf	*P*-value
Triodopsis multilineata (Say, 1821)	0	0	8	1	6	0	8	7	
	0.00	0.00	7.84	1.85	12.77	0.00	2.71	5.56	0.1651915
Triodopsis tridentata (Say, 1816)	0	11	1	0	0	1	13	0	
	0.00	8.94	0.98	0.00	0.00	3.85	4.41	0.00	0.0021429
Vallonia costata (Müller, 1774)	1	10	21	2	8	12	38	16	
	1.45	8.13	20.59	3.70	17.02	46.15	12.88	12.70	0.9590560
Vallonia excentrica (Sterki, 1893)	0	0	1	0	0	3	2	2	
	0.00	0.00	0.98	0.00	0.00	11.54	0.68	1.59	0.3993604
Vallonia gracilicosta (Reinhardt, 1883)	1	28	19	0	0	1	48	1	
	1.45	22.76	18.63	0.00	0.00	3.85	16.27	0.79	0.0000001
Vallonia parvula (Sterki, 1892)	0	1	4	0	0	9	3	11	
	0.00	0.81	3.92	0.00	0.00	34.62	1.02	8.73	0.0001277
Vallonia perspectiva (Sterki, 1892)	0	0	41	0	0	3	39	5	
	0.00	0.00	40.20	0.00	0.00	11.54	13.22	3.97	0.0020759
Vallonia pulchella (Müller, 1774)	0	2	13	3	17	10	21	24	
	0.00	1.63	12.75	5.56	36.17	38.46	7.12	19.05	0.0005061
Vertigo bollesiana (Morse, 1865)	5	76	28	3	2	0	108	6	
	7.25	61.79	27.45	5.56	4.26	0.00	36.61	4.76	0.0000000
Vertigo cristata (Sterki, 1919)	50	25	0	3	0	0	72	6	
	72.46	20.33	0.00	5.56	0.00	0.00	24.41	4.76	0.0000002
Vertigo elatior (Sterki, 1894)	1	2	4	32	35	1	4	71	
	1.45	1.63	3.92	59.26	74.47	3.85	1.36	56.35	0.0000000
Vertigo gouldi (A. Binney, 1843)	4	103	89	0	1	1	192	6	
	5.80	83.74	87.25	0.00	2.13	3.85	65.08	4.76	0.0000000
Vertigo hubrichti (Pilsbry, 1934)	2	52	31	0	1	1	86	1	
	2.90	42.28	30.39	0.00	2.13	3.85	29.15	0.79	0.0000000
Vertigo meramecensis (Van Devender, 1979)	0	0	16	0	0	0	16	0	
	0.00	0.00	15.69	0.00	0.00	0.00	5.42	0.00	0.0006424

Appendix 1 *continued.*

	Number of occurrences/frequency in cluster						Duff vs. turf		
Species	A	B	C	D	E	F	Duff	Turf	*P*-value
Vertigo milium (Gould, 1840)	0	4	26	5	23	1	28	31	
	0.00	3.25	25.49	9.26	48.94	3.85	9.49	24.60	0.0000835
Vertigo modesta modesta (Say, 1824)	6	2	0	0	0	0	8	0	
	8.70	1.63	0.00	0.00	0.00	0.00	2.71	0.00	0.0164278
Vertigo modesta parietalis (Ancey)	3	1	0	0	0	0	4	0	
	4.35	0.81	0.00	0.00	0.00	0.00	1.36	0.00	0.0907153
Vertigo morsei (Sterki, 1894)	0	0	0	2	4	0	0	6	
	0.00	0.00	0.00	3.70	8.51	0.00	0.00	4.76	0.0001273
Vertigo n.sp. *sensu* (Frest, 1991)	1	26	17	0	0	1	45	0	
	1.45	21.14	16.67	0.00	0.00	3.85	15.25	0.00	0.0000000
Vertigo nylanderi (Sterki, 1909)	0	3	0	10	4	0	1	16	
	0.00	2.44	0.00	18.52	8.51	0.00	0.34	12.70	0.0000000
Vertigo ovata (Say, 1822)	0	0	1	4	23	0	2	26	
	0.00	0.00	0.98	7.41	48.94	0.00	0.68	20.63	0.0000000
Vertigo paradoxa (Sterki, 1900)	34	28	0	3	0	0	60	5	
	49.28	22.76	0.00	5.56	0.00	0.00	20.34	3.97	0.0000024
Vertigo pygmaea (Draparnaud, 1801)	0	1	19	2	9	10	26	15	
	0.00	0.81	18.63	3.70	19.15	38.46	8.81	11.90	0.3353210
Vertigo tridentata (Wolf, 1870)	0	1	32	0	0	4	32	5	
	0.00	0.81	31.37	0.00	0.00	15.38	10.85	3.97	0.0145287
Vitrina limpida (Gould, 1850)	7	17	0	3	4	2	22	11	
	10.14	13.82	0.00	5.56	8.51	7.69	7.46	8.73	0.6594118
Zonitoides arboreus (Say, 1816)	57	111	76	37	19	8	240	68	
	82.61	90.24	74.51	68.52	40.43	30.77	81.36	53.97	0.0000000
Zonitoides limatulus (W.G. Binney, 1840)	0	0	1	0	0	0	1	0	
	0.00	0.00	0.98	0.00	0.00	0.00	0.34	0.00	0.3986709
Zonitoides nitidus (Müller, 1774)	0	3	10	6	10	10	21	18	
	0.00	2.44	9.80	11.11	21.28	38.46	7.12	14.29	0.0248105
Zoogenetes harpa (Say, 1824)	37	11	0	2	0	0	46	4	
	53.62	8.94	0.00	3.70	0.00	0.00	15.59	3.17	0.0000629