Patterns of diversity and habitat relationships in terrestrial mollusc communities of the Pukeamaru Ecological District, northeastern New Zealand

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Abstract

Aim The New Zealand terrestrial mollusc fauna is among the most speciose in the world, with often remarkably high richness at lowland forest sites. We sought to elucidate general explanations for patterns of richness in terrestrial mollusc communities by analysis of species coexistence and habitat relationships within a New Zealand district fauna.

Location Pukeamaru Ecological District, eastern North Island, New Zealand.

Methods We sampled molluscs using qualitative methods at twenty-three sites and quantitatively by frame sampling of scrubland-forest floor litter at sixteen of these sites and analysed patterns of species richness and turnover in relation to regional species pools and local habitat attributes. We then tested for nonrandom assemblage of taxa along diversity and habitat gradients.

Results Ninety-four indigenous mollusc species were recorded from a district fauna estimated at 102 indigenous species: only two species were endemic. From the presumptive geological history of the district, the low endemism, and Brooks parsimony and indicator species analyses of faunal relationships, the communities were indicated to have resulted by accumulation of colonists from other New Zealand districts since the Miocene. Richness ranged from two or three indigenous species in dune habitats to fifty-nine species in a floristically rich forest. Beta diversity was high and site occupancy per species was low, indicating communities structured by successive replacement of ecological equivalents. Sites differing in vegetation had characteristic species assemblages, indicating a degree of habitat specialization. Canonical correspondence analysis indicated that canopy tree species, canopy height, floristic diversity, altitude, litter mass, and litter pH were important determinants of species assemblage in scrubland and forest. Richness was strongly associated with site floristic diversity and, for litter-dwelling species, the pH of litter substrate. High richness occurred at those sites supporting molluscs in high abundance. Shell-shape distributions were essentially Cainian unimodal, with communities dominated by snail species with subglobose to discoidal shells. Mean and variance of shell size increased with mollusc species richness and floristic diversity at sites, indicating dominance of communities by small-shelled species at early successional or floristically poor sites, and increased richness resulting from addition of larger snails into vacant niches. Shifts in shell form were associated with sympatry in several congeneric taxa.

Main conclusions The underdispersion of shell shape, relative to faunas elsewhere in the world, indicates that community structure in New Zealand land snail faunas has been constrained by limited phylogenetic diversity and/or by convergence upon successful adaptations. The remarkably high richness that characterizes these communities indicates special conditions allow coexistence of numerous species. The relationship between floristic diversity at sites and the richness, diversity, and shell-size distributions of the molluscs suggests assemblages structured around niche partitioning among competing species. While there is an element of congruence between vegetation and mollusc pattern, this study
INTRODUCTION

One of the central problems in ecology is to explain species diversity in communities, and a considerable number of hypotheses have been formulated. Zobel (1992) has formulated a general explanation of (plant) species coexistence utilising an idealized concept of the null community, defined as an undisturbed community within stable zonal vegetation including the whole pool of potential species. The number of potential species will then be dependent mainly on evolutionary factors such as speciation and extinction rates, and species traits. Zobel takes the view that there are no special ecological mechanisms for the maintenance of species richness (diversity, abundance) but only ecological mechanisms reducing richness or creating limited membership. This is consistent with the conclusion of Whittaker (1975) that there is not much evidence, either theoretical or empirical, for species diversity equilibrium. Thus, the majority of real communities always have a smaller species pool than the corresponding idealized null communities. The lack of a species in some local species pool can be explained by evolutionary traits (which may make species presence impossible under particular environmental conditions) and historical processes operating on a biogeographic scale (Whittaker, 1975). Within the local species pool, asymmetric interspecific interaction — such as competition and predation (Roughgarden & Diamond, 1986) — is postulated by Zobel as the main force reducing species richness. Such interactions take place on an ecological level, but their outcome is governed by evolutionally determined traits of individuals.

Terrestrialism in molluscs is ancient. The earliest fossils of terrestrial forms date from the mid Palaeozoic, and the adaptive radiation into the higher taxa that characterize extant faunas occurred in the Lower Cretaceous (Solem & Yochelson, 1979; Tillett et al., 1996). Their ancient origin and slow evolution at higher taxonomic levels, combined with often low vagility and high rates of allopatric speciation (Solem, 1984, 1990), make terrestrial molluscs superb biogeographic models. Plesiomorphically, terrestrial molluscs possess a coiled shell within which the visceral organs are contained and into which the cephalic structures can be fully withdrawn for protection. While shell loss has occurred independently in a number of lineages, giving rise to the slug body form, in most regions the extant terrestrial mollusc faunas are dominated by animals that retain the external shell (snails). The shell is particularly useful in investigations of evolution and ecology, in being species-specific yet malleable in both form and size by environment (e.g. Goodfriend, 1986; Emberton, 1994; 1995a; Chiba, 1996) within measurable developmental constraints (e.g. Gould, 1992), and with the individuals’ entire ontogeny conserved and on display in the shell of the mature animal.

Cain (1977, 1978a,b, 1981) has shown that in most snail faunas shell form is not randomly distributed, but rather there is a bimodal pattern of scatter when shell height (h) is plotted against shell diameter (d). Cain presented evidence that within a fauna families tend to combine to fill the h/d morphological space, but with little overlap. Most land snail families are confined to one or other of the two h/d modes. However, the presumed adaptive trough between the two modes has been crossed by a number of families (Cain, 1977; Cowie, 1995), indicating that ecology, not phylogenetics, underlies the bimodality of shell morphologies in faunas. Furthermore, in some faunas — such as those of Hawaii — families overlap broadly in both h < d and h > d modes (Cowie, 1995). Although many factors no doubt play a role, the generally bimodal distribution of shell shape begs a simple and general explanation. Cain suggested that ecological explanations might account for the bimodality, with shell shape tied evolutionally to niche characteristics. These niche characteristics remain unknown, although a few studies have tentatively confirmed Cain’s idea that shell shape may be related to the preferred angles of inclination on which the snails are active and the mechanics of carrying a shell of a certain shape (Cain & Cowie, 1978; Heller, 1987; Cameron & Cook, 1989; and references therein).

The New Zealand terrestrial mollusc fauna is characterized by hyperdiversity at two levels. First, extensive specific radiation has occurred in the families Liareidae, Rhytidiidae, Athoracophoridae and, in particular, the Punctidae and Charopidae (Solem et al., 1981). The result is a fauna among the most speciose in the world for its geographical extent, with about 1400 species. The second level of hyperdiversity is that of species richness at forest sites, where species number is often an order of magnitude higher than in communities typical of continental areas (Solem et al., 1981; Solem, 1984; Emberton, 1995b). In earlier analyses of land snail communities in the South Auckland province of New Zealand (Solem & Climo, 1985; Emberton, 1995b), the essentially unimodal pattern of shell shape (h < d), with overlap of the two numerically dominant families Charopidae and Punctidae, was highlighted. The underdispersion of shell shape, relative to faunas elsewhere in the world, indicates that community structure in New Zealand land snails was constrained by limited feature diversity through some accident of area history and/or by convergence upon successful adaptations, while the remarkably high alpha diversity indicates that special conditions allow coexistence of numerous species. A clear understanding of the factors

Keywords
Biogeographic patterns, community structure, habitat relationships, terrestrial molluscs.

mediating patterns of species coexistence under New Zealand conditions of high diversity may well be informative about constraints on species coexistence that operate in the relatively species-poor communities that characterize most continental areas.

The Raukumara Peninsula of the eastern North Island has long been recognized as having a peculiar biogeographic significance in New Zealand, with the flora characterized by low levels of species endemism and a remarkable mixture of plants that have their northern or southern limits on the peninsula (Kirk, 1897; Heginbotham & Esler, 1985; B.D. Clarkson, pers. comm.). These patterns of endemism and disjunct plant distributions have been related to the large-scale modification of the New Zealand region as a result of active tectonism and climate oscillations since the Oligocene (e.g. McGlone, 1985; Heads, 1989). This paper provides analyses of patterns in the diversity and community assemblages of terrestrial molluscs in lowland habitats of the Pukeamaru Ecological District, at the northern extremity of the Raukumara Peninsula. We determined the species composition for terrestrial molluscs at a range of sites and then analysed patterns of species richness and turnover in relation to regional species pools and local habitat attributes. We then attempted to test for nonrandom assemblage of taxa along diversity and habitat gradients, using shell morphology (b/d) as being indicative of possible niche requirements. In undertaking this research we sought to elucidate general explanations for patterns of richness of terrestrial mollusc communities.

MATERIALS AND METHODS

Study area

The Pukeamaru Ecological District (Simpson, 1982; McEwen, 1987) covers ≈98,000 ha at the northern extremity of the Raukumara Peninsula, in the eastern North Island of New Zealand, at 37°40′ latitude (Fig. 1).

The dominant geological features of the District are a Miocene sandstone-dominated sedimentary sequence, overlain by an allochthonous suite which incorporates Cretaceous-early Tertiary sedimentary rock units and a Matakaoa basaltic ophiolite suite (Moore, 1985; Gibson, 1987; Cooper, 1989). The allochthon has been interpreted as a subduction-accretion complex that was emplaced in the early Miocene. It is thought to have had a predominantly marine origin at no great distance to the NE of the present New Zealand region (Brook et al., 1987; Sporli, 1987). The Matakaoa ophiolite suite appears to be, at least in part, of oceanic origin and may have come from considerable distance before emplacement in the Miocene (Pirajno, 1979; Sporli & Balance, 1985; Brook et al., 1987; Sporli, 1987; Cooper, 1989). These suites overlie older (late Jurassic to early Cretaceous) sedimentary rocks of the Younger Torlesse/Mata River terrane, which are emergent south of the Pukeamaru Ecological District. Because of its presumptive marine origins, the allochthon is unlikely to have carried a terrestrial biota into the region (Cooper, 1989). Emergent land is thought to have occurred in the region during the early Miocene, but only as small, transient islands. More extensive land surfaces did not develop until the Pliocene, in association with formation of the Raukumara Range (Stevens, 1980).

The current relief of the district is dominated by steeply dissected hills, reaching 130–990 m in the Matakaoa basaltic ranges and 100–480 m in the sandstone-dominated sedimentary ranges. Extensive plateaux to weakly dissected uplifted marine terraces occur along the coastal zone at 20–300 m. Holocenic alluviums occupy the valley systems, while Holocenic gravel and sand dunes systems occur along sections of the coast.

The contemporary ecological character of the Pukeamaru Ecological District was documented during a 1984–85 survey for the Protected Natural Areas Programme (PNAP) (Regnier et al., 1988). As a consequence of this PNAP survey and earlier botanical investigations (e.g. Kirk, 1897; Cresswell, 1966; Druce, 1972; Heginbotham, 1979; Heginbotham & Esler, 1985) the flora of the District is well known. Regnier et al. (1988) recognized four broad bioclimatic zones, each with characteristic vegetation. The Coastal Zone includes all coastal hillslopes and extends up to 3 km inland along broad river valleys. Associations of Carpodetus serratus Fors. & Fors. (Escallionceae) – Pseudopanax lessonii (DC.) Koch (Araliaceae) and Vitex lucens Kirk (Verbenaceae) – Beilschmiedia tawa (Cunn.) Kirk (Lauraceae), which may occur together, are typical of the coastal zone. The Lowland Zone comprises the area beyond the coastal zone and inland to an altitude of ≈600 m, above which B. tawa ceases to be the dominant canopy species. The vegetation of this zone comprises a mixture of B. tawa-dominant broadleaf-podocarp and Nothofagus solandri (Hook. f.) or N. truncata (Colenso) (Fagaceae)-dominant broadleaf-podocarp forest types. Between ≈600 and 700 m Weinmannia racemosa L. f. (Cunoniaceae) and Ixerba brexioides Cunn. (Escallionceae), with Quintinia serrata Cunn. (Escallionceae), comprise the dominant canopy trees of the Lower Montane Zone. Above 700 m occur Upper Montane Zone forests characterized by Nothofagus menziesii (Hook. f.) Oersted. While not as extensive as in many other North Island lowland districts, habitat fragmentation as a result of deforestation for human settlement and pastoral agriculture has impacted significantly on the landscape, with many formerly extensive vegetation types now present as remnants. Deforestation for agriculture has virtually ceased, and some former pasture land is regenerating to forest through Leptospermum scoparium Fors. & Fors. f. or Kunzea ericoides (Rich.) Thompson (Myrtaceae)-dominant broadleaf scrublands.

The location of the sampling sites within the Pukeamaru Ecological District is illustrated in Fig. 1. A total of twenty-three sites were sampled for molluscs, comprising two dune, one swamp, and twenty scrubland-forest sites, spanning the range from Coastal to Lower Montane zones. For purposes of sampling, a site was defined as a area of ≈0.25 ha in extent and of uniform topography and vegetation, representative of the predominant ‘natural areas’ in the Ecological District identified by Regnier et al. (1988). The character of these sites is summarized in Table 1.

Sampling methods

During September 1992 and March 1993 a general survey of the mollusc fauna at each site was carried out by an assortment
of qualitative sampling techniques. Generalist ground dwellers were sampled by bagging quantities of litter taken from several microhabitats and spooning humus and litter material from microsites, which experience indicated, were liable to yield high numbers of species. The collected litter and humus material was air or oven dried (50 °C) and searched under a stereomicroscope for snails. This method was supplemented by hand-picking snails and slugs from specific habitats such as boles of *Rhopalostylis sapida* Wendl. & Drude, leaf axils of monocotyledons such as *Astelia* spp., *Carex* spp., *Phormium tenax* Forst., *P. cookianum* Le Jolis, *Cordyline banksii* Hook. f., *Freycinetia banksii* Cunn., *Collospermum hastatum* (Col.) Skottsb., and *R. sapida*, the underside and interior of rotted logs, from under lifting bark, from suspended litter, and from tree trunks and branches up to 2 m above the ground. Empty shells were air dried before curation, while live animals were drowned in water overnight, fixed in 95% ethanol, and preserved in 70% ethanol.

During the September 1992 visit, GMB undertook quantitative sampling of the forest floor community at sixteen of the scrubland-forest sites by collection of leaf litter from eight circular 0.086 m² frames randomly placed on the forest floor. On return to the laboratory, the litter was oven dried at 50 °C and sieved. All litter retained by a 5-mm mesh sieve was searched by eye for larger shells, and the material passing through the 5 mm mesh was searched under a stereomicroscope. Recovered shells were identified to species and tallied. The presence of dried soft tissue in the shells was taken as indicative of the animal having been alive at the time of sample collection, and this was recorded.

Diameter and height were measured for all shells in each sample with a calibrated ocular micrometer.

**Site characterization**

During the field work the character of the vegetation at each site was recorded by visual assessment: (i) the tree species which constituted 20% or more of the canopy – i.e. whose crowns were 50% or more exposed to the sky – were noted; (ii) the height of the canopy tier was estimated on a scale of 1–25 (approximating 0.5 m height intervals); and (iii) an index of floristic diversity was calculated from the sum product of species number × cover values for each tier. The tier classes recognized were (a) canopy (b) subcanopy > 2 m in height (c) subcanopy 0.3–2 m in height (d) ground cover < 0.3 m in height, and (e) epiphytes.
Table 1 Sites in the Pukeamaru Ecological District sampled for terrestrial molluscs.

<table>
<thead>
<tr>
<th>Site</th>
<th>Vegetation ¹</th>
<th>Geology</th>
<th>Altitude (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Whangaparaoa</td>
<td>Spinifex grassland</td>
<td>Holocene gravel and sandy dunes</td>
<td>0–10</td>
</tr>
<tr>
<td>2 Papatea</td>
<td>Beilschmiedea-Vitis-Broadleaf forest</td>
<td>Jurassic to Cretaceous sandstone and mudstone</td>
<td>50–150</td>
</tr>
<tr>
<td>3 Te Puia</td>
<td>Beilschmiedea-Dacrydium forest</td>
<td>Miocene calcareous mudstone and sandstone</td>
<td>340</td>
</tr>
<tr>
<td>4 Waenga</td>
<td>Beilschmiedea-Vitis to Beilschmiedea-Broadleaf forest</td>
<td>Cretaceous to Tertiary Matakoan volcanics</td>
<td>100–180</td>
</tr>
<tr>
<td>5 Rereaurua</td>
<td>Nothofagus forest</td>
<td>Cretaceous to Tertiary Matakoan volcanics</td>
<td>20–100</td>
</tr>
<tr>
<td>6 Rereaurua swamp</td>
<td>Typha-Broadleaf-Leptospermum-Phormium reed-shrubland</td>
<td>Holocene alluvium</td>
<td>15–20</td>
</tr>
<tr>
<td>7 Waiaroho</td>
<td>Dacrycarpus-Beilschmiedea-Prunus pumila forest</td>
<td>Cretaceous sandstone and mudstone</td>
<td>80–95</td>
</tr>
<tr>
<td>8 Hicks Bay</td>
<td>Broadleaf forest</td>
<td>Cretaceous to Tertiary Matakoan volcanics</td>
<td>20–100</td>
</tr>
<tr>
<td>9 East Cape</td>
<td>Beilschmiedea-Vitis-Planchnonea forest</td>
<td>Miocene calcareous silstone and sandstone</td>
<td>60–120</td>
</tr>
<tr>
<td>10 East Cape scrubland</td>
<td>Phormium-Pittosporum-Leptospermum shrub-flaxland</td>
<td>Miocene calcareous silstone and sandstone</td>
<td>80–120</td>
</tr>
<tr>
<td>11 Rangita</td>
<td>Dysoxylum-Vitex-Beilschmiedea-Planchnonea forest</td>
<td>Miocene calcareous silstone and sandstone</td>
<td>40–120</td>
</tr>
<tr>
<td>12 Taikawakawa</td>
<td>Beilschmiedea-Broadleaf forest</td>
<td>Miocene calcareous silstone and sandstone</td>
<td>200–280</td>
</tr>
<tr>
<td>13 Te Araroa</td>
<td>Leptospermum-Leucopogon scrub, Introduced grass-Muehlenbeckia grassland, and Typha-Phormium-Leptospermum reed-shrubland</td>
<td>Holocene shingle dune</td>
<td>0–10</td>
</tr>
<tr>
<td>14 Kakanui</td>
<td>Nothofagus-Wennmannia forest</td>
<td>Miocene sedimentary gravel and sand</td>
<td>300</td>
</tr>
<tr>
<td>15 Kakanui scrubland</td>
<td>Leptospermum tall scrub</td>
<td>Miocene sedimentary gravel and sand</td>
<td>250</td>
</tr>
<tr>
<td>16 Te Koau</td>
<td>Beilschmiedea-Vitis forest</td>
<td>Cretaceous to Tertiary Matakoan volcanics</td>
<td>160–200</td>
</tr>
<tr>
<td></td>
<td></td>
<td>overlain by Miocene calcareous mudstone</td>
<td></td>
</tr>
<tr>
<td>17 Te Koau Wemmannia</td>
<td>Wennmannia-Knightia-Broadleaf forest</td>
<td>Cretaceous to Tertiary Matakoan volcanics</td>
<td>200</td>
</tr>
<tr>
<td>18 Te Koau broadleaf</td>
<td>Broadleaf scrub and forest</td>
<td>Miocene calcareous silstone and sandstone</td>
<td>350–500</td>
</tr>
<tr>
<td>19 Rangita Planchnonea</td>
<td>Planchonella-Beilschmiedea-Dysoxylum-Vitex forest</td>
<td>Miocene calcareous silstone and sandstone</td>
<td>60–70</td>
</tr>
<tr>
<td>20 Oruaiti</td>
<td>Beilschmiedea-Broadleaf forest</td>
<td>Miocene calcareous mudstone and sandstone</td>
<td>40</td>
</tr>
<tr>
<td>21 Owha</td>
<td>Leptospermum-Broadleaf scrubland and forest</td>
<td>Miocene calcareous silstone and sandstone</td>
<td>40</td>
</tr>
<tr>
<td>22 Otanga</td>
<td>Beilschmiedea-Vitis-Litsea forest</td>
<td>Cretaceous to Tertiary Matakoan volcanics</td>
<td>60</td>
</tr>
<tr>
<td>23 Paoncone</td>
<td>Kunzea forest</td>
<td>Miocene sedimentary gravel and sand</td>
<td>60</td>
</tr>
</tbody>
</table>

¹ Vegetation type designations follow that of Regnier et al. (1988)

The altitude of the sampling sites was taken from NZMS topographic maps. The underlying geological strata were identified from various sources, including Kingma (1965), Chapman-Smith & Grant-Mackie (1971), Moore (1985), Gibson (1987), and Riddolls (1987).

After extraction of shells, the sieved portions of the litter samples were recombined, weighed, and then finely ground for determination of pH and elemental content using the methodologies of Blackmore et al. (1987).

Data analysis

Patterns of abundance, richness, and species turnover

The total number of individuals recovered per site is used as an estimate of abundance, and regressed on total species number (species richness) to determine whether sites supporting high populations also support high richness. These analyses were performed on data from combined sampling methods and for quantitative litter samples.

Patterns of diversity were examined using three direct measures: the total number of species recorded in the District (T), species richness per site, and the mean number of sites per species. Data on rates of site occupancy per species were subjected to analysis of variance using SYSTAT (Wilkinson, 1992) to examine differences among taxon groups. From the ratio of District total species to mean number of species per site, Whittaker's index (Whittaker, 1975) was calculated as an estimate of between-site (beta) diversity. A value of unity indicates perfect correspondence of faunas between sites, and increasing values indicate increasing differentiation. The reciprocal of Whittaker's index provides an estimate of geographical patterning in species distributions. Variance is minimal where there is a high level of successive geographical replacement, while variance is maximal when there is a mixture of a few very frequent and some very rare species (Cody, 1986; Cameron, 1992). Actual variances of sites per species were expressed as a proportion of the maximum possible for the observed values of total District species number and species per site (Cameron, 1992). The true total number of species in the District was estimated by least squares regression procedures for cumulative species totals plotted on sites ranked for observed richness.

Tests of nonrandom species concurrences

Whether or not positive or negative associations occur among taxa in the Pukeamaru fauna was examined by chi-square analysis of frequency tables constructed for all possible pairs.
of species. Two models were used to examine the concurrences of species pairs. In model A the probability that a species occurred at a given site was assumed to be the same for all sites, and the probability that two species occurred together at a given site was consequently the product of the probabilities for each of the two species. This is the usual model for independence. It is reasonable to expect, however, that concurrences may depart from independence owing to factors such as prevalence of the species and favourability of the site as habitat. Therefore, in model B the expected value of the probability of occurrence of a given species was predicted by fitting the logit-linear model logit \( P_i = a + bn_i + cs_j \) where \( n_i \) is the number of sites at which species \( i \) occurred, and \( s_j \) is the number of species found at site \( p \). If it is again assumed that the probability that two species occurred together at a site was just the product of the probabilities for each of the two species, model B provides for detection of any dependence (positive or negative) over and above the ‘average’ association. In both models the likelihood ratio statistic (LR) of the association between paired species was measured, in a frequency table of occurrences, as the square root of the product of the expected order of first occurrence

\[
LR = \left( (F_{ia}F_{ib}) - (F_{ia}F_{ib})^{0.5} \right)
\]

where \( F_a \) and \( F_b \) are, respectively, the frequencies of species \( a \) and \( b \) occurring at sites in the absence of the other, \( F_{ia} \) is the frequency of species \( a \) and \( b \) occurring at the same site, and \( F_{ib} \) is the frequency at which both species were absent. When the observed association was greater than expected (more concurrences) LR was made positive and when there were fewer concurrences than expected LR was made negative. Because the LR statistic has an approximate chi-squared distribution with 1 degree of freedom when the null hypothesis of independence is true, the statistic will have an approximate standard normal distribution. Therefore, the LR statistics calculated for all possible species pairs were ranked from highest to lowest and examined for departure from independence when graphed against their expected values (the expected order statistics from the normal distribution).

**Within-community dispersion of shell form and size as indicators of niche partitioning**

Snail community morphologies were examined from shell measurement data. Heights were plotted against diameters (Cain, 1977, 1981) for analysis of shell-shape distributions in the Pukeamaru fauna as a whole, or the range of taxa at individual sites, and for individual species at sites with and without sympatric congeners. Distributions of shell diameter, as an index of shell size (Emberton, 1995b), were examined in relation to species turnover and habitat gradients.

**Ordination of Pukeamaru communities in relation to environment**

Similarities in mollusc assemblages among the sampled sites were examined by simultaneous classification of plots and species using the polythetic divisive technique of indicator species analysis (ISA) (Hill et al., 1975), as implemented in the Cornell ecology program TWINSPAN (Hill, 1979).

Detrended canonical correspondence analysis (DCCA) was used to examine broad-scale relationships between mollusc and environmental factors using the Canonical Community Ordination CANOCO program (ter Braak, 1992). DCCA extracts the dominant gradients, with the constraint that they must be orthogonal linear combinations of supplied environmental variables (ter Braak, 1986, 1992). It also provides an assessment of the species most closely associated with each environmental variable. For DCCA, six dominant canopy species and the geological strata were imputed as nominal variables, while the canopy height index, the floristic diversity index, altitude, litter pH, and litter nitrogen, phosphorus, magnesium, sodium, sulphur and potassium were input as continuous quantitative variables. Nominal variables were identified as centroids and the quantitative variables as gradient vectors in the CANOCO output.

DCCA was restricted to the scrubland and forest sites proper; thus, the dune Sites 1 and 13 and the Rereauria swamp Site 6 were excluded, as were the less intensively sampled scrublands/forests at Sites 20–23 (no quantitative litter samples taken). Rare species can distort the ordination (ter Braak, 1987). Ordinations with and without downweighting of rare species gave almost exactly the same results, so downweighting was not performed. CANOCO’s Monte Carlo permutation routines were used for significance testing of relationships between mollusc assemblages and environmental variables. These routines produce permutations of the ordination being tested which are randomized with respect to the relationship requested for a particular analysis. In each instance ninety-nine permutations were performed, allowing a \( P = 0.01 \) resolution.

Abundance, diversity, and evenness were calculated for each site from the species abundance data and regressed against environmental factors identified as being significant in the DCCA ordination. Diversity was estimated from the Shannon-Weaver information statistic (Shannon & Weaver, 1949), referred to here as the Shannon-Weaver Index of Diversity,

\[
H' = - \sum_{i=1}^{s} (p_i \ln p_i)
\]

where \( s \) is the number of species recorded and \( p_i \) is the proportion of the sample in the \( i \)-th species, while evenness was estimated from the inverse of Simpson’s Index (Simpson, 1949),

\[
E = 1 \left( \sum_{i=1}^{s} p_i^2 \right)
\]

where \( p_i \) is as above.

**Faunal relationships of the Pukeamaru communities**

The historical or phylogenetic constraints to contemporary terrestrial mollusc assemblages at sites in the Pukeamaru Ecological District were examined by Brooks Parsimony...
Analysis (BPA). The implicit assumptions of BPA are that the geographical range of a descendant provides a partial estimate of the range of its immediate ancestral species and, collectively, the most parsimonious taxon distribution is the best estimate of geographical area relationships. Operationally, BPA examines an area/taxon matrix problem, areas being treated as independent variables and entire trees of taxa being encoded as dependent variables. In such matrices, terminal extant species are coded as apomorphies for the areas in which they occur, while ancestral species (estimated from cladograms of phylogenetic relationship) are coded as synapomorphies uniting areas (Brooks, 1981, 1988, 1990; Wiley, 1988). A cladogram of relationships among New Zealand gastropods (Barker, 1999) was used to code for apomorphies and synapomorphies.

From this cladogram, a site/taxon (including ancestral synapomorphies) matrix was compiled from each sampled Pukeamaru community (Sites 1–23, this study) and for communities sampled in the following districts (informal grouping of sites) elsewhere in New Zealand: Site 24 Three Kings Islands; Site 25 North Cape, Northland; Site 26 Poor Knights Islands; Site 27 Hunua Ranges, South Auckland; Site 28 Manukau Peninsula, South Auckland; Site 29 Maungakawa, Central Waikato; Site 30 Waitomo, South Waikato; Site 31 Pureora Ecological Area, South Waikato; Site 32 Tongariro National Park, Taupo; Site 33 Wellington; Site 34 Chatham Islands; Site 35 Catlins Ranges, Otago; Site 36 Fiordland National Park, Fiordland; Site 37 Waitutu, Southland; Site 38 Auckland Islands (Powell, 1948; Climo, 1971, 1973, 1991; Gardner & Goulstone, 1977; Mayhill, 1981, 1985; Solem et al., 1981; Goulstone, 1982, 1984, 1990; Mayhill & Broomfield, 1982; Mayhill & Goulstone, 1984, 1986; Mason, 1988; Roscoe, 1992; Goulstone et al., 1993; F.M. Climo, P.C. Mayhill, and J.F. Goulstone, pers. comm.; G.M. Barker, unpublished). Relationships of the areas were then explored by Wagner criterion of maximum parsimony (minimization of homoplasy) using PAUP (Swofford, 1985). Because of the large data set (thirty-eight sites, 463 taxa) searches were made by heuristic methods, using several optimization procedures. The trees were rooted in the analyses by introducing an ancestral vector of zero values.

A truncated matrix that included only extant species-level taxa was examined by ISA as implemented by TWINSPAN.

RESULTS

Patterns of diversity and habitat relationships of the Pukeamaru mollusc communities

A total of 105 terrestrial mollusc species was recorded during the study (Tables 2, 3; Appendix 1). Eleven naturalized species, representing eight families, were recorded from the District. The ninety-four indigenous species recorded represent seven families, namely Hydrocemeidae, Liareidae, Athoracophoridae, Achatinellidae, Charopidae, Punctidae, and Rhytididae. Cumulative indigenous species numbers plotted against sites ranked for ascending richness indicated that the asymptote was approached with our sample of twenty-three sites. Regression analysis estimated a District total of 102 indigenous species, and that a sample size of about twenty-six sites was needed to ensure that all taxa were represented. Species known from lowland forest in the District but not collected during the present investigation are the punctids Pasinellidae pungermanniiæ (Petterd) and Taguahelix campbellëca (Filhol) and the charopids Flammulina parva Suter, Cavellia reflationis (Suter), C. rosevarii (Suter), Geminoropa vortex (Murdock), and Mocella prestonii (Sykes).

The numbers of specimens collected at individual sites ranged from twenty-four to 810, and species numbers ranged from five to sixty-six (Table 2). There was a highly significant relationship between the total number of molluscs collected by the combined sampling methods at a site and the number of species recorded at that site:

\[
\text{Total species} = 13.7 + 0.0564 \times \text{Total molluscs collected}
\]

\[
R^2 = 0.656, P < 0.001
\]

Indigenous species = 12.0 + 0.0535 \times \text{Total molluscs collected}

\[
R^2 = 0.623, P < 0.001
\]

Given that approximately equal sampling effort was expended at each site, these relationships would suggest that high alpha diversity occurred at those sites supporting molluscs in high abundance.

At most sites the communities were dominated by indigenous species, but there were only five sites at which no naturalized molluscs were recorded, namely Sites 3, 5, 12, 14, and 17. While of varied forest type and subject to some disturbance by feral mammals, these sites were characterized by being buffered from deforestation and agriculture by tracts of indigenous vegetation. The sites occupied by naturalized molluscs were primarily characterized as having been subjected to heavy browsing by feral and domestic mammals or were forest communities regenerating from earlier deforestation. An exception were the Te Koau forest sites 16 and 18, where the grassland mollusc Vallonia excentrica Sterki (Valloniidae) occurred in low abundance in areas of broken canopy adjacent to walking tracks. The two dune communities (Sites 1 and 13) were characterized by a high proportion of naturalized species of European origin (Table 2).

Few mollusc shell specimens in the frame litter samples were without remains of soft tissue, indicating that the majority of snails were alive at the time of sample collection. Furthermore, strictly arboreal species were poorly represented in these quantitative litter samples. Therefore, no correction was made before analysis for empty shells or for shells of arboreal taxa in the litter samples.

Mollusc abundance in the eight-frame litter samples was particularly poor in the dune and swamp sites (Sites 1, 6, and 13), ranging from three to ten specimens, or 4.3–14.5/m². Species diversity in the litter was similarly restricted at these sites (Table 3). Mollusc abundance in the eight-frame litter samples from the remaining sixteen scrubland-forest sites ranged from fourteen to 554, equivalent to 20–805/m². The corresponding range in number of species recovered from these litter samples was four to thirty-nine. Over all nineteen sites sampled by the quantitative frame sampling method there was an asymptotic relationship between total mollusc abundance and species richness:
Table 2 Summary of the number of specimens, and richness and diversity at various taxon levels, in mollusc assemblages estimated by combined sampling methods at twenty-three sites in the Pukeamaru Ecological District

| Sites: | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
| Specimens collected | 70 | 539 | 75 | 810 | 194 | 34 | 674 | 345 | 683 | 181 | 241 | 214 | 48 | 246 | 68 | 773 | 60 | 127 | 267 | 95 | 70 | 143 | 24 |
| Total number of species | 9 | 53 | 32 | 64 | 39 | 6 | 54 | 45 | 30 | 19 | 32 | 29 | 8 | 33 | 8 | 51 | 14 | 30 | 11 | 22 | 22 | 6 | 5 |
| Number of indigenous species | 3 | 43 | 32 | 59 | 39 | 4 | 50 | 41 | 28 | 18 | 29 | 2 | 35 | 7 | 50 | 14 | 29 | 10 | 18 | 18 | 26 | 5 |
| Number of indigenous families | 3 | 5 | 6 | 5 | 3 | 6 | 6 | 5 | 4 | 6 | 4 | 2 | 5 | 3 | 4 | 4 | 4 | 3 | 4 | 3 | 3 | 0 |
| Number of naturalized species | 6 | 10 | 0 | 5 | 0 | 2 | 4 | 4 | 2 | 1 | 3 | 0 | 6 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 0 |
| Number of naturalized families | 4 | 7 | 0 | 3 | 0 | 2 | 4 | 4 | 2 | 1 | 3 | 0 | 5 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 0 |
| Shannon-Weaver Index of Diversity | 2.76 | 4.35 | 4.34 | 4.70 | 4.77 | 2.07 | 4.56 | 4.37 | 3.70 | 3.23 | 4.00 | 4.17 | 2.78 | 4.33 | 2.42 | 4.48 | 2.90 | 4.30 | 1.86 | 3.70 | 4.00 | 1.55 |

Table 3 Summary of the abundance, richness and diversity at various taxon levels, in litter-dwelling mollusc assemblages estimated by quantitative frame sampling at nineteen sites in the Pukeamaru Ecological District

| Sites: | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
| Specimens collected | 10 | 134 | 34 | 139 | 69 | 3 | 294 | 117 | 554 | 150 | 153 | 184 | 8 | 73 | 14 | 430 | 50 | 63 | 277 |
| Total number of species | 2 | 15 | 11 | 38 | 16 | 2 | 22 | 25 | 20 | 18 | 20 | 22 | 1 | 11 | 3 | 34 | 12 | 17 | 10 |
| Number of indigenous species | 1 | 5 | 11 | 38 | 16 | 2 | 22 | 25 | 20 | 18 | 20 | 22 | 1 | 11 | 3 | 34 | 12 | 17 | 10 |
| Number of indigenous families | 1 | 2 | 3 | 4 | 4 | 2 | 4 | 4 | 3 | 3 | 3 | 1 | 2 | 2 | 3 | 3 | 3 | 3 |
| Number of naturalized species | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Number of exotic families | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Shannon-Weaver Index of Diversity | 1.00 | 2.93 | 2.81 | 4.55 | 3.58 | 0.92 | 3.26 | 3.84 | 3.44 | 3.04 | 1.86 | 3.94 | 4.00 | 1.55 |
| Simpson Index of Evenness | 0.50 | 4.88 | 5.07 | 14.13 | 9.88 | 1.80 | 6.75 | 9.45 | 8.88 | 5.71 | 7.24 | 10.76 | 1.00 | 6.86 | 2.65 | 7.90 | 5.00 | 8.70 | 2.70 |

Note: Sites 1, 6, and 13 excluded from analyses of scrubland-forest litter-dwelling mollusc communities.

Table 4 Various measures of between-site diversity of indigenous molluscs in the Pukeamaru Ecological District, estimated by combined sampling methods

<table>
<thead>
<tr>
<th>Sites per species</th>
<th>Total no. of species</th>
<th>Mean species per site ± SE</th>
<th>Whittaker’s Mean ± SE</th>
<th>Maximum variance</th>
<th>Achieved variance</th>
<th>% achieved variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>All sites (n=23)</td>
<td>94</td>
<td>25.96 ± 3.49</td>
<td>3.54</td>
<td>6.39 ± 1.01</td>
<td>89.21</td>
<td>23.70</td>
</tr>
<tr>
<td>Charopidae</td>
<td>56</td>
<td>14.0 ± 2.19</td>
<td>3.86</td>
<td>5.96 ± 0.96</td>
<td>84.79</td>
<td>21.34</td>
</tr>
<tr>
<td>Punctidae</td>
<td>31</td>
<td>8.96 ± 1.08</td>
<td>3.46</td>
<td>6.40 ± 1.04</td>
<td>94.70</td>
<td>23.80</td>
</tr>
<tr>
<td>Other pulmonate families</td>
<td>2.61 ± 0.28</td>
<td>1.92</td>
<td>10.20 ± 1.31</td>
<td>137.20</td>
<td>39.69</td>
<td>28.93</td>
</tr>
<tr>
<td>Scrubland – forest sites (n=16)</td>
<td>91</td>
<td>31.88 ± 7.97</td>
<td>2.85</td>
<td>5.67 ± 1.00</td>
<td>47.25</td>
<td>15.84</td>
</tr>
<tr>
<td>Charopidae</td>
<td>54</td>
<td>17.62 ± 2.50</td>
<td>3.06</td>
<td>5.22 ± 0.94</td>
<td>45.68</td>
<td>14.06</td>
</tr>
<tr>
<td>Punctidae</td>
<td>30</td>
<td>11.12 ± 1.06</td>
<td>2.70</td>
<td>5.93 ± 1.06</td>
<td>50.48</td>
<td>17.81</td>
</tr>
<tr>
<td>Other pulmonate families</td>
<td>5</td>
<td>2.69 ± 0.25</td>
<td>1.86</td>
<td>8.60 ± 1.22</td>
<td>112.80</td>
<td>35.94</td>
</tr>
</tbody>
</table>

Total species = 8.478 ± 0.097 Total mollusc abundance R² = 47.0 P = 0.002.

Various measures of between-site or beta diversity are presented in Table 4. The species richness of indigenous taxa at individual sites was substantially lower than the total species pool for the District as a whole. For the Charopidae, the most speciose family in the Pukeamaru fauna, a total of fifty-six species-level taxa were recorded, but the maximum richness at an individual site was thirty-six species, an apparent 0.64
representation from the regional pool (the inverse of the Whittaker Index indicates a 0.25 saturation). Similarly, for the Punctidae thirty-one species were recorded as a District total but the maximum site total was nineteen species, or 0.61 of the possible maximum (0.29 saturation). The remaining three pulmonate families – Achatinellidae, Athoracophoridae, Rhytididae – were collectively represented by five species, of which a maximum of four were present at an individual site. The mean number of sites occupied per charopid or punctid species was significantly lower than for representatives of the other pulmonate families, when estimated from combined \( P < 0.01 \) and quantitative frame \( P < 0.05 \) sampling methods. This lower site occupancy reflects the high proportion of charoids and punctids that could be regarded as rare, in that each species occurred at less than 10% of the sites. While rare species occurred across the full range of site species richness, there was a significant correlation between total number of species and the number of rare species at a site:

Number of rare species = \(-0.554 + 0.067 \times \text{Total species} \)

\( R^2 = 0.297 \quad P < 0.0001 \).

Table 4 also shows the variance of sites per species relative to the maximum possible variance. The rather low relative variance indicates that successive replacements contribute to the observed species dispersion patterns across sites.

With ninety-four indigenous species in the Pukeamaru Ecological District there were 4278 possible pairs of species concurrences. If all pairs are individually tested for independence there is a very high likelihood of getting spurious significant results. Therefore, all pairs were examined simultaneously by looking for departures of ranked likelihood ratio statistics from their expected values, assuming independence (model A) and from a logit-linear model that takes into account the number of sites at which species occur and the species richness of each site (model B) (Fig. 2).

For model A, 2994 of the 4278 species pairs (70%) were indicated as having a positive association. Of these, 781 were significantly associated at \( P < 0.05 \). Only four pairs were indicated to be negatively associated at \( P < 0.05 \). But, as noted above, the chances of getting spurious significant results are very high. If there were 4278 independent tests, the likelihood of spurious results could be reduced by using the Bonferroni adjustment (Miller, 1981). Even though the 4278 tests performed here are clearly not all independent, the Bonferroni adjustment was applied. This reduced the number of significant results to just three positive associations, namely *Mocella eta* (Pfeiffer) with *Paralaoma lateumbilicata* (Suter), *Allodiscus urquharti* (Suter) with *Phrixgnathus ariel* Hutton, and *Pseudegestula montivaga* (Suter) with *Delos coresia* (Gray). The plot of the LR values (Fig. 2) also indicates a small number of positive associations standing out.

For model B the expected LR values line up with the observed values, the proportion of positive values being 45.6 ± 0.8 percentage (Fig. 2). The most notable departures from the expected values are the five highest-ranked LR statistics, which correspond to the species pairs *Mocella eta* with *Paralaoma lateumbilicata*, *Allodiscus urquharti* with *Phrixgnathus ariel*, *Phenacohelix ponsonbyi* (Suter) with *Chaureopa roscoei* Climo, *Pseudegestula montivaga* with *Delos coresia*, and *Allodiscus planulatus* (Hutton) with *Phrixgnathus* sp.2. These five (a-e, below) all show higher-than-expected concurrences:

<table>
<thead>
<tr>
<th></th>
<th><em>Mocella eta</em></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Paralaoma lateumbilicata</em></td>
<td>Absent</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th><em>Allodiscus urquharti</em></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phrixgnathus ariel</em></td>
<td>Absent</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th><em>Phenacohelix ponsonbyi</em></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chaureopa roscoei</em></td>
<td>Absent</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th><em>Pseudegestula montivaga</em></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Delos coresia</em></td>
<td>Absent</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th><em>Allodiscus planulatus</em></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phrixgnathus</em> sp.2</td>
<td>Absent</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th><em>Flammulina chiron</em></th>
<th></th>
</tr>
</thead>
</table>

The corresponding LR statistics are 4.39 ($P = 0.00001$), 3.65 ($P = 0.00026$), 3.42 ($P = 0.00062$), 3.31 ($P = 0.00094$), and 3.28 ($P = 0.00103$). Only the first is significant at $P = 0.05$ when the Bonferroni adjustment is made.

All concurrences of *M. etai* with *P. lateumbilicata*, *A. urquharti* with *P. ariel*, and *P. montivaga* with *D. coresia* were in mature, relatively undisturbed forests with floristic diversity index values $<5$. The one site at which *A. urquharti* occurred in the absence of *P. ariel* was also in floristically rich forest, while the two sites at which *D. coresia* occurred in the absence of *P. montivaga* were in moderately disturbed forests with intrusion of shrubland plant species.

The species *P. ponsonbyi*, *C. roscoei*, *A. planulatus* and *Phrixognathus* sp.2 were relatively rare in the District, in terms of both abundance and site occupancy. All concurrences of *P. ponsonbyi* with *C. roscoei* and of *A. planulatus* with *Phrixognathus* sp.2 were in mature, floristically rich forests (floristic diversity 5–10). The one site at which *Phrixognathus* sp.2 occurred in the absence of *A. planulatus* was also a floristically rich forest.

Only one species pair, *Flammulina chiron* (Gray) with *Paralaoma capitispinulae* (Reeve), has a lower-than-expected concurrence, with an LR statistic of $-3.41 (P = 0.00064)$ (see f, above).

A range of scrubland and forest habitats over a wide gradient of floristic diversity (1–9) were occupied by *Caputspinula*, while *F. chiron* was confined to mature, floristically rich forests (floristic diversity 5–10).

The Cainian shell-height-diameter (*h/d*) plot for pooled sites (Fig. 3) indicates an essentially unimodal shell-shape distribution pattern among snails in the Pukeamaru Ecological District: the fauna is strongly dominated by snails with rather flat shells (*b < d*). Using nontransformed data, the regression of *h* on *d* indicates a regression coefficient of 0.580 ± 0.02 SD, which is significantly less than unity where *b* equals *d*. The flat shell shape predominates in the Pukeamaru Charopidae, Punctidae, and Rhytididae; indeed, only the punctid *Laoma cicata* Suter has a shell in which height exceeds the diameter. In the Cainian shell *h/d* plot, the regression coefficient for the Charopidae (0.745 ± 0.026) is significantly higher (*P < 0.001*) than that for the Punctidae (0.550 ± 0.044), indicating a trend towards more globose shell shape in the former taxon. The single hydrocennid, *Georessa purhica* (Pfeiffer), and the two achatinellids – *Tornatellina novoseelandica* (Pfeiffer) and *Tornatellinops subperforata* (Suter) – have tall-spired shells *h > d*, whereas the sole liareid, *Cyrtora cytora* (Gray), is globose. Figure 3 also indicates that the majority of snails in the Pukeamaru fauna are small to minute, with a shell diameter less than 5 mm.

The two indigenous snail species – *T. novoseelandica*, *P. capitispinulae* – in the Whangaparaoa dune community (Site 1) are minute, with a mean shell diameter of 1.90 mm (2.33 mm when weighted by abundance). The single indigenous snail (*Tagaubelix sp.2*) in the Te Araroa dune community, Site 13, was similarly minute, with a shell diameter of 2.50 mm. Three indigenous snail species (*Phenacohelix perplexa* (Murdoch), *Serpho kivi* (Gray), *Iotula sp.9*) were recorded for the Rereauria swamp, Site 6; their mean shell diameter was 7.57 mm (weighted mean 4.09 mm). For the remaining sites, representing scrublands and forests, mean shell diameter for snails varied from 2.16 mm to 4.37 mm (weighted means 2.22–4.32 mm).

For the sixteen intensively sampled scrubland and forest sites there was a positive linear relationship between the mean shell diameter across all snail species resident at a site and both mollusc species richness and floristic diversity. Furthermore, the coefficient of variation of shell diameter increased with site mollusc diversity and floristic diversity. These relationships applied to shelled taxa estimated by quantitative frame sampling of the litter (Figs 4 and 5), and by combined sampling methods. Regression analysis failed to detect any intraspecific shift in shell size that could be related to mollusc or floristic diversity gradients.

Congeneric pairs or groups of species were represented in the District, often in sympatry at a number of sites. Only three species were sufficiently represented in samples and appropriately distributed across sites to permit examination of intraspecific shifts in shell size or form associated with sympathy.

*Huonodon hectori* (Suter) occurred at fifteen sites. Its shell was generally smaller and more strongly depressed or discoidal when in sympatry with *H. microrandulata* (Suter) and/or *H. pseudoleioda* (Suter), at 11 sites, than when allopatric at the remaining four sites (Fig. 6A). *Phenacohelix perplexa* was recovered at sixteen sites. Its shell possessed a more strongly raised spire (but not greater diameter) in allopatry than when sympatric with the congeners *P. ponsonbyi*, *P. pilula* (Reeve), and *P. gweni* Cumber (Fig. 6B). *Pseudegestula montivaga* was recovered at twelve sites, and half of them in sympathy with the congenic *P. brookesi* (Dell) and/or *Pseudegestula sp.1*. Regression analysis of shell height on shell diameter indicated no difference in *P. montivaga* shell size or form between allopatric and sympatric populations (Fig. 6C).

On the basis of species presence from combined sampling methods, the results of the ISA classification indicated that sites could be divided into three major groups representing different snail communities (indigenous and naturalized), namely (i) dunes and swamp (ii) scrubland to broadleaf forest of varied canopy height and intrusion of shrubby (early

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**Figure 3** Variation in shell shape and size among ninety-four shelled indigenous terrestrial mollusc taxa in the Pukeamaru Ecological District (single large species, *Rhytida greenwoodi* (Gray), of 14 mm height and 26 mm diameter, excluded). The line height $=$ diameter indicates the predominance of taxa possessing rather flat shells.
successional) species, and (iii) forest of high and largely closed canopy. Within groups (ii) and (iii), there is a clear trend for ISA to separate sites in order of increasing floristic diversity. The relationships between these groups are shown in Fig. 7.

Sites were classified into six groups in the ISA of species abundance in the frame litter samples (Fig. 8): (i) Leptospermum tall scrubland (Site 15); (ii) Weinmannia-Knightia broadleaf ridge-forest (Site 17); (iii) Beilschmiedia-Weinmannia-Dacrydium, Nothofagus, Beilschmiedia broadleaf forests and broadleaf scrubland-forest (Sites 3, 5, 12, 18); (iv) Beilschmiedia-Vitex broadleaf and Dacrycarpus-Beilschmiedia-Prumnopitys forests (Sites 2, 4, 7, 8, 11, 16); (v) Nothofagus-Weinmannia forest (Site 14); and (vi) East Cape Beilschmiedia-Vitex-Planchonella and Planchonella-Beilschmiedia-Dysoxylum-Vitex forests and Phoromium-Pittosporum-Leptospermum shrub-flaxland (Sites 9, 10, 19).

The results of the DCCA for scrubland-forest mollusc communities estimated by combined sampling of litter is presented as ordination diagrams in Fig. 9. Because of the varied sampling methods used to determine the species composition of the communities, and the varying abundance of specimens collected from the sites, the mollusc data were normalized before analysis by expressing each species as a proportion of the total collected at each site. The species and site points jointly represent the dominant patterns in community composition insofar as these can be explained by the environmental variables, and the species points and the vectors/centroids of the environmental variables jointly reflect the species’ distributions along each of the environmental gradients.

The environmental variables in this ordination, in conjunction with the species points, account for 45% of the variance in the weighted averages of the 105 molluscs (naturalized and indigenous) with respect to the ten environmental variables, the sum of all eigenvalues being 0.81.

For the communities examined here, there were correlations among the environmental variables used in the DCCA. Floristic diversity was associated positively with the Matakaoa volcanics and tended to be negatively associated with the Jurassic-Miocene sediments (Table 5). Floristic diversity was also

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**Figure 4** Community mean (A) and coefficient of variation (B) in shell diameter among shelled terrestrial mollusc taxa in the Pukeamaru Ecological District, estimated from quantitative frame sampling of litter, plotted against mollusc species richness at sixteen scrubland-forest sites.

**Figure 5** Community mean (A) and coefficient of variation (B) in shell diameter among shelled terrestrial mollusc taxa in the Pukeamaru Ecological District, estimated from quantitative frame sampling of litter, plotted against site floristic diversity at sixteen scrubland-forest sites.
Consequently, interpretation of the ordination axes was based on the interset correlation coefficients rather than the canonical coefficients.

The geological strata did not contribute significantly to the DCCA ordination of mollusc communities, and were excluded as environmental variables from the analyses as presented here. By reference to the interset correlation coefficients (Table 7) and the ordination diagram (Fig. 9), it is evident that axis 1 is strongly correlated with canopy height, floristic diversity, altitude, litter pH, litter nitrogen, and litter phosphorus gradients. The alignment of the species in the ordination suggests that in axis 1 the most important gradients influencing the mollusc community are floristic diversity and litter pH and/or altitude. In axis 2 the most significant gradient correlations are litter phosphorus, litter calcium, litter pH, litter nitrogen and litter mass. Vitex, Leptospermum/Kunzea, and podocarp centroids are significantly correlated with axis 1, and Beilschmiedia, Leptospermum/Kunzea and Nothofagus centroids correlate significantly with axis 2. With the exception of Nothofagus, these centroids are not informative owing to clustering about the ordination origin.

Because each site point lies at the centroid of the species points relevant to that site, one may infer from the ordination diagram which species are likely to be present at a particular site. Also, insofar as canonical correspondence analysis is a good approximation to the fitting of Gaussian response surfaces, the species points are approximately the optima of these surfaces, and hence the abundance or probability of occurrence of a species decreases with distance from its location in the diagram. Thus, among the indigenous species Sinployea sp.1, Pasmaditta miserablis (Iredale), Phenacohelix guveni, Alloiscus dimorphus (Pfeiffer), Suteria ide (Gray), Chaureopa rosoei, Pseudegestula brooksi, Phrixynathus sp.1, and Phrixynathus conicula (Suter) are aligned positively with the floristic diversity/canopy height gradient and Phrixynathus transitans (Suter), Iotula sp.4, and Phrixynathus conella (Pfeiffer) are aligned negatively. Likewise, Chaureopa subdepressa Climo, Iotula sp.3, Flammocharopa costulata (Hutton), and Iotula microreticulata (Suter) are strongly associated with the gradient of increasing altitude or presence of Nothofagus.

Litter-dwelling mollusc assemblage data was subjected to DCCA using estimates of species abundance from the frame samples. The ordination diagrams are presented in Fig. 10. Geological strata were again identified as not significant in the DCCA, and were suppressed in the analysis presented. The interset correlation coefficients (Table 7) indicate that axis 1 in the ordination is strongly correlated with canopy height, floristic diversity, altitude, litter pH, litter nitrogen, and litter phosphorus gradients. The alignment of the species in the ordination suggest that in axis 1 the most important gradients influencing the mollusc community are floristic diversity and litter pH and/or altitude. In axis 2 the most significant gradient correlations are litter phosphorus, litter calcium, litter pH, litter nitrogen, and litter mass. Vitex, Leptospermum/Kunzea, and podocarp centroids are significantly correlated with axis 1, and Beilschmiedia, Leptospermum/Kunzea and Nothofagus centroids correlate significantly with axis 2.

Figure 6 Variation in shell shape and size in three terrestrial mollusc species in the Pukeamaru Ecological District when allopatric (+) and when sympatric with congeneric species (O): A, Huonodon hectori (Suter); B, Phenacohelix perplexa (Murdoch); C, Pseudegestula montivaga (Suter).

Correlated with altitude and with litter mass on the forest floor. Litter mass was positively associated with Beilschmiedia, Vitex, and podocarps and negatively with Leptospermum/Kunzea, Nothofagus, and Weinmannia as major components of the canopy. Nothofagus, Weinmannia, and podocarps tended to be associated with the higher-altitude sites (Table 5). The pH and mineral content of the forest litter was found to be significantly correlated with the dominant forest canopy species, canopy height index, floristic diversity index, underlying geology, litter mass, and altitude (Table 6). Further, pH of the litter was correlated with its calcium content ($R^2=0.356$, $P<0.05$). Therefore, interpretation of the ordination axes was based on the interset correlation coefficients rather than the canonical coefficients.

Figure 7 Dendrogram from ISA classification of twenty-three sites in the Pukeamaru Ecological District, based on assemblages of indigenous and exotic terrestrial mollusc species estimated from combined sampling methods. Species were classed as present or absent for the analysis. Indicator species are given at each division level.

Mollusc species richness, diversity (expressed as the Shannon-Weaver function), and evenness (Simpson's Index) in the frame litter samples were positively correlated with floristic diversity (Figs 11, 12) and pH of the litter (Fig. 13). Mollusc abundance in the frame litter samples was not related to floristic diversity (P = 0.191) but was correlated with altitude and litter pH (Fig. 14).

Relationships of Pukeamaru mollusc communities

Indicator Species Analysis of the site/species presence matrix indicated that, while being divisible into three community groups associated with dunes, scrublands, and forests, the Pukeamaru mollusc fauna could be recognized as an entity distinct from any in other regions of New Zealand (Fig. 15). The ISA indicated the Pukeamaru communities to be most similar to communities in the Chatham Islands, the central and southern regions of the North Island, and the South Auckland-Waikato region of the North Island.

Alternative interpretations of relationships of the Pukeamaru sites to others in the New Zealand region were indicated by BPA. First, treating each Pukeamaru site as a distinct entity, BPA produced three equally parsimonious trees (length 1118, CI 0.637) when characters were encoded irreversible. A consensus tree (50% majority rule; Swofford, 1985) derived from this analysis (Fig. 16) indicated that the Pukeamaru dune communities, Site 1 and Site 13, had a history somewhat removed from the other Pukeamaru communities. Similar
Figure 9 Canonical correspondence analysis of indigenous and exotic terrestrial molluscs in scrubland-forest communities of the Pukeamaru Ecological District, estimated by combined sampling methods at sixteen sites. (A) Biplot of environmental factors and site ordination. Vector arrows indicating gradients of continuous variables and the centroids of categorical variables. Gradients of axes 1 and 2 are significant (P<0.05) according to a Monte Carlo permutation test (site numbering as in Table 1). (B) Species ordination (species numbering as in Appendix 1).

ecological conditions of these sites may have drawn similar species from the extralimital species pool. The remaining Pukeamaru sites were placed in two monophyletic groups; one including sites 3, 5, 14, 17, and 20 and the other the sixteen sites not yet enumerated. The former group of five sites was indicated to have close relationships to the faunas of the Poor Knights and Three Kings island groups in northern New Zealand, despite the very different current ecological conditions.

Second, pooling the Pukeamaru sites and treating them as
Table 5 Correlation matrix (Pearson’s correlation coefficients) of geological strata, litter mass, and altitude with floristic characteristics of the scrubland-forest sites sampled for molluscs in the Pukeamaru Ecological District.

<table>
<thead>
<tr>
<th>Geological Strata</th>
<th>Beilschmiedia</th>
<th>Vitex</th>
<th>Leptospermum &amp; Kunzea</th>
<th>Nothofagus</th>
<th>Weinmannia</th>
<th>Podocars</th>
<th>Canopy height index</th>
<th>Floristic diversity index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jurassic-Miocene sandstones/mudstones</td>
<td>0.140</td>
<td>0.052</td>
<td>-0.240</td>
<td>-0.364</td>
<td>-0.096</td>
<td>0.042</td>
<td>0.197</td>
<td>-0.193</td>
</tr>
<tr>
<td>Cretaceous-Tertiary basaltic Matakaoa volcanics</td>
<td>0.216</td>
<td>0.204</td>
<td>-0.444</td>
<td>0.193</td>
<td>0.329</td>
<td>0.304</td>
<td>0.087</td>
<td>0.554</td>
</tr>
<tr>
<td>Litter mass</td>
<td>0.737</td>
<td>0.387</td>
<td>-0.404</td>
<td>-0.311</td>
<td>-0.315</td>
<td>0.350</td>
<td>0.510</td>
<td>0.488</td>
</tr>
<tr>
<td>Altitude</td>
<td>-0.141</td>
<td>-0.036</td>
<td>-0.248</td>
<td>0.453</td>
<td>0.393</td>
<td>0.402</td>
<td>-0.078</td>
<td>0.510</td>
</tr>
</tbody>
</table>

Bold type in the body of the table indicates correlations significant at $P<0.05$.

Table 6 Correlation matrix (Pearson’s correlation coefficients) of floristic indices, geological strata, litter mass, and altitude with pH and mineral content of litter collected from scrubland-forest sites in the Pukeamaru Ecological District.

<table>
<thead>
<tr>
<th>pH</th>
<th>Nitrogen</th>
<th>Phosphorus</th>
<th>Sulphur</th>
<th>Magnesium</th>
<th>Calcium</th>
<th>Sodium</th>
<th>Potassium</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beilschmiedia</td>
<td>0.423</td>
<td>0.394</td>
<td>0.375</td>
<td>0.316</td>
<td>0.116</td>
<td>0.387</td>
<td>0.006</td>
</tr>
<tr>
<td>Vitex</td>
<td>0.775</td>
<td>0.200</td>
<td>0.632</td>
<td>0.313</td>
<td>0.632</td>
<td>0.045</td>
<td>0.465</td>
</tr>
<tr>
<td>Leptospermum &amp; Kunzea</td>
<td>-0.133</td>
<td>-0.597</td>
<td>-0.416</td>
<td>-0.230</td>
<td>0.076</td>
<td>-0.177</td>
<td>0.421</td>
</tr>
<tr>
<td>Nothofagus</td>
<td>-0.497</td>
<td>0.065</td>
<td>-0.318</td>
<td>-0.102</td>
<td>-0.318</td>
<td>-0.151</td>
<td>-0.288</td>
</tr>
<tr>
<td>Weinmannia</td>
<td>-0.005</td>
<td>0.606</td>
<td>0.328</td>
<td>0.572</td>
<td>0.059</td>
<td>-0.145</td>
<td>-0.217</td>
</tr>
<tr>
<td>Podocars</td>
<td>-0.253</td>
<td>0.567</td>
<td>-0.046</td>
<td>0.127</td>
<td>-0.561</td>
<td>0.306</td>
<td>-0.769</td>
</tr>
<tr>
<td>Canopy height index</td>
<td>-0.089</td>
<td>0.299</td>
<td>0.016</td>
<td>0.008</td>
<td>-0.418</td>
<td>0.592</td>
<td>-0.457</td>
</tr>
<tr>
<td>Floristic diversity index</td>
<td>0.008</td>
<td>0.542</td>
<td>0.004</td>
<td>0.091</td>
<td>-0.030</td>
<td>-0.073</td>
<td>0.476</td>
</tr>
<tr>
<td>Jurassic-Miocene sandstones/mudstones</td>
<td>0.260</td>
<td>-0.202</td>
<td>0.220</td>
<td>-0.009</td>
<td>-0.050</td>
<td>-0.070</td>
<td>0.132</td>
</tr>
<tr>
<td>Cretaceous-Tertiary basaltic Matakaoa volcanics</td>
<td>-0.104</td>
<td>0.608</td>
<td>0.012</td>
<td>0.194</td>
<td>0.083</td>
<td>0.025</td>
<td>-0.334</td>
</tr>
<tr>
<td>Litter mass</td>
<td>0.397</td>
<td>0.438</td>
<td>0.308</td>
<td>0.214</td>
<td>-0.008</td>
<td>0.216</td>
<td>-0.117</td>
</tr>
<tr>
<td>Altitude</td>
<td>-0.406</td>
<td>0.422</td>
<td>-0.171</td>
<td>0.071</td>
<td>-0.213</td>
<td>-0.269</td>
<td>-0.411</td>
</tr>
</tbody>
</table>

Scrubland-Forest sites only. Bold type in body of table indicates correlations significant at $P<0.05$.

One regional fauna, BPA produced a single most parsimonious tree (length 805, CI 0.537) (Fig. 17), indicating the Pukeamaru fauna to be most closely related to those of the central North Island and originating somewhat distant from the root of the tree. This tree is of quite different topology to that produced with the Pukeamaru sites analysed as separate entities.

**Discussion**

The highest number of indigenous terrestrial mollusc species recorded at a single site in the Pukeamaru Ecological District was fifty-nine. This is similar to richness recorded from forest remnants of Waipipi Reserve, South Auckland, New Zealand, and Manombo Reserve, Madagascar, which have been regarded as the most species-rich sites in the world (Solem et al., 1981; Solem, 1984; Solem & Climo, 1985; Emberton, 1995b). However, the analyses presented here indicate that, even in the most species-rich sites, the Pukeamaru communities are well below saturation with respect to the available regional pool of species, and therefore do not closely approach a hypothetical null community (sensu Zobel, 1992). While several species were widespread in the District, the communities are characterized by a rather low mean site occupancy per species. A high proportion of the species can be considered rare, in that they occurred at less than 10% of sites (one or two of the twenty-three sites sampled).

On present knowledge, only Taguahelix sp.2 and Climocella isolata Goulstone can be considered endemic to the Pukeamaru Ecological District. Taken collectively, the phenetic (ISA) and phylogenetic (BPA) treatments of the data suggest that, while there are similarities to other regions, the Pukeamaru communities have distinctive blends of taxa. The evidence that the Pukeamaru communities represent nested subsets of either a larger New Zealand fauna or of an East Cape fauna is weak. On the contrary, BPA suggests that Pukeamaru communities of high diversity were derived from communities of low diversity by addition of taxa, through either dispersal or speciation. The very low incidence of endemic species, and the geological history of the area, supports the view that the Pukeamaru communities developed from species immigrant from extralimital source communities to the north-west and south-west. BPA indicated closest relationships with the central North Island communities, which occupy broadly similar habitats. However, the low level of endemism in both...
Pukeamaru and the central North Island communities, and the very widespread distributions of many of the taxa involved, may indicate that these regions were drawing independently from the larger regional pool, rather than the Pukeamaru communities being derived from the central North Island. The extremely low endemism among molluscs in the Pukeamaru Ecological District mirrors that of terrestrial plants.

In the Pukeamaru District, mollusc species diversity and abundance at sites increase with floristic diversity. There have been few published studies on the relationship between diversity of the vegetation and that of the associated mollusc communities, although it has been recognized that mollusc communities can differ between vegetation community types (e.g. Körnig, 1966; Ant, 1969; André, 1981; Waldén, 1981; Nikolic & Stamol, 1990; Stamol, 1991, 1992, 1993). Mollusc species diversity and abundance may be regulated by niche availability, and thus species richness in the fauna may be correlated with increasing floral richness via site successional development. Sites of high floristic diversity can be presumed to have higher fractal complexity and more varied inhabitable substrate (microhabitat differentiation) than sites of low floristic diversity. Getz & Uetz (1994) found that in southern Appalachian land snail communities richness was influenced primarily by the diversity of plant species making up the forest floor litter. Species assemblage in these Appalachian communities was not associated with forest type.

Data from European woodlands indicate that terrestrial mollusc species with similar ecology tend to accumulate, rather than replace each other, when conditions become optimal (Waldén, 1981). While Boycott (1934) came to the conclusion that competition is not a limiting factor for British terrestrial molluscs, it is likely that subtle patterns of niche specialization (e.g. Cameron, 1978; Jennings & Barkham, 1979) and temporal differences in activity (e.g. Asami, 1993) exist among species. Cameron (1992) could find no evidence of competitive replacement in an analysis of site occupancy in three Northern Hemisphere woodland faunas. Geographic replacement was evident for camaenids in Western Australia (Solem, 1985; Cameron, 1992), but the relative contribution of competitive exclusion and vicariance has not been resolved. As indicated in the introduction to this paper, Cain (1977 & subseq.) and others have shown that in most terrestrial snail faunas there is a bimodal pattern of scatter when maximum shell height ($h$) is plotted against maximum shell diameter ($d$), the upper scatter ($h > d$) corresponding to tall-spired shells and the lower ($h < d$) to globose or discoidal shells. Observations at the faunal level on the deployment of shell shape in relation to preferred sites of activity (e.g. Cain & Cowie, 1978; Heller, 1987; Cameron & Cook, 1989) suggest an ecological explanation for the very common occurrence of the bimodal distribution of shell shape in land snails, tied at least in part to niche occupancy. However, in an analysis forest-dwelling land snail communities of Manombo (Madagascar), South Auckland (New Zealand), and Kentucky (U.S.A.), Emberton (1995b) identified both natural selection and phylogenetic constraints as contributing to the observed distribution of shell morphologies.

Eighty-two indigenous molluscs were recorded in the fauna of South Auckland examined by Solem et al. (1981) and Solem & Climo (1985), of which seventy-two are hypothesized to be microsympatric within lowland patches of relict forest. Solem (1984) suggested that ‘this situation is not the result of a few species blooms’, radiation of single lineages into many species, but appears to have evolved by gradual accumulation of taxa from all taxonomic parts of the New Zealand land snail fauna since the Miocene’. Solem (1984) postulated that one mechanism for development of high sympatric diversity was small-scale change in vegetation patch size, during Pleistocene and Holocene climate fluctuations, that permitted allopatric speciation and then character displacement to permit cohabitation when sympathy was re-established. In contrast to those faunas reported by Cain, the shell $h/d$ scatter plot for the South Auckland fauna (Solem & Climo, 1985) is unimodal, with overlap of the two numerically dominant families Charopidae and Punctidae. This was confirmed by Emberton’s (1995b) analysis of the community at one South Auckland site. Furthermore, in their analysis Solem & Climo (1985) could not demonstrate any correlations of shell feature with niche occupancy in the South Auckland snails. This suggests that competitive interaction between members of these two families is slight. However, Solem & Climo (1985) noted that, in the South Auckland mollusc communities, snail species with the

<table>
<thead>
<tr>
<th>Combined sampling methods:</th>
<th>Pearson's correlation coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><strong>Axis 1</strong></td>
</tr>
<tr>
<td>Beilschmiedia</td>
<td>-0.128</td>
</tr>
<tr>
<td>Vitex</td>
<td>0.217</td>
</tr>
<tr>
<td>Leptospermum &amp; Kunzea</td>
<td>0.317</td>
</tr>
<tr>
<td>Nothofagus</td>
<td>-0.260</td>
</tr>
<tr>
<td>Weinmannia</td>
<td>-0.154</td>
</tr>
<tr>
<td>Podocarps</td>
<td>-0.731</td>
</tr>
<tr>
<td>Canopy height index</td>
<td>-0.510</td>
</tr>
<tr>
<td>Floristic diversity index</td>
<td>-0.548</td>
</tr>
<tr>
<td>Altitude</td>
<td>-0.340</td>
</tr>
<tr>
<td>Litter mass</td>
<td>-0.217</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Quantitative frame sampling of litter:</th>
<th>Pearson's correlation coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beilschmiedia</td>
<td>-0.074</td>
</tr>
<tr>
<td>Vitex</td>
<td>0.399</td>
</tr>
<tr>
<td>Leptospermum &amp; Kunzea</td>
<td>0.433</td>
</tr>
<tr>
<td>Nothofagus</td>
<td>-0.293</td>
</tr>
<tr>
<td>Weinmannia</td>
<td>-0.223</td>
</tr>
<tr>
<td>Podocarps</td>
<td>-0.783</td>
</tr>
<tr>
<td>Canopy height index</td>
<td>-0.563</td>
</tr>
<tr>
<td>Floristic diversity index</td>
<td>-0.585</td>
</tr>
<tr>
<td>Altitude</td>
<td>-0.491</td>
</tr>
<tr>
<td>Litter mass</td>
<td>-0.148</td>
</tr>
<tr>
<td>Litter pH</td>
<td>0.602</td>
</tr>
<tr>
<td>Litter Nitrogen</td>
<td>-0.433</td>
</tr>
<tr>
<td>Litter Phosphorus</td>
<td>0.368</td>
</tr>
<tr>
<td>Litter Calcium</td>
<td>0.276</td>
</tr>
</tbody>
</table>
same shelter site preference differed by at least 40% in shell volume, suggesting niche partitioning among community members.

The analyses of the Pukeamaru communities reported here confirm the essentially unimodal pattern of shell shape in the Cainian plot of shell height on shell diameter reported previously for New Zealand communities (Solem & Climo, 1985; Emberton, 1995b). The strong predominance of depressed
Figure 11 Species richness in indigenous terrestrial mollusc communities at sixteen scrubland-forest sites in the Pukeamaru Ecological District, estimated by quantitative frame sampling of litter, in relation to floristic diversity of the habitat.

Figure 12 Species diversity and evenness in indigenous terrestrial mollusc communities, estimated by quantitative frame sampling of litter, in relation to floristic diversity of the habitat at sixteen scrubland-forest sites in the Pukeamaru Ecological District. (A) Shannon-Weaver Index. (B) Simpson’s Index.

Figure 13 Species richness in indigenous terrestrial mollusc communities, estimated by quantitative frame sampling of litter, in relation to pH of the litter at sixteen scrubland-forest sites in the Pukeamaru Ecological District.
1986) was not evident in our analysis of the communities in Pukeamaru scrublands and forests. Indeed, there is a clear trend for abundance to increase with species richness at these sites.

These facts suggest that the Pukeamaru communities are structured by resource partitioning to avoid competition. Colonising species apparently gain membership to the communities only if they are able to utilize niches not already occupied (Grant, 1972; Connell, 1980). Only in the case of sympatric congeneric species was there evidence that niches may diverge over time through competition, resulting in the snails becoming more different in shell morphology in the one location.

While both the South Auckland and Pukeamaru communities are characterized by high sympatric diversity, they also display extremely low levels of species endemism and low occurrence of sister species. Additional studies in areas of high endemism and high sympatric diversity, such as the Northland and Nelson regions of New Zealand, are now required if we are to understand the role of species interactions and saturation in the evolution of rich mollusc communities.

More detailed, quantitative biological data are needed to fully understand the ecology of spatial pattern of shell size among snails. Our analysis indicates that, on the forest floor, species that may be classed as detritivores or mycophages account for about 98% of the species and over 99% of individuals. Observations in the Pukeamaru Ecological District and elsewhere in New Zealand suggest that, while microsympatric species diversity can be high, the species assemblage at any one location on the forest floor varies greatly. Further, these species appear to have preferred niches within the litter profile, but quantitative information on this is not available. During this study, the litter from the eight frames was pooled before extraction of the snails, so information on spatial variability was lost. Predatory molluscs, represented by the rhytidid species *Rhytida greenwoodi* (Gray) and *Delos coreoa*, accounted for 1–2% of the species in the litter-dwelling communities. A small guild of detritivores was associated with logs and bark, exemplified by the charopids *Charopa coma*.

Figure 14 Abundance in indigenous terrestrial mollusc communities at sixteen scrubland-forest sites in the Pukeamaru Ecological District, estimated by quantitative frame sampling of litter, in relation to (A) altitude and (B) pH of the litter.

Figure 15 Dendrogram from ISA classification of twenty-three Pukeamaru sites (Box A, dune sites; Box B, scrubland sites; Box C, forest sites) and fifteen other New Zealand districts (24 Three Kings Islands; 25 North Cape; 26 Poor Knights Islands; 27 Huria Ranges; 28 Manukau Peninsula; 29 Maungakawa; 30 Waitomo; 31 Pureoroa; 32 Tongariro; 33 Wellington; 34 Chatham Islands; 35 Catlins; 36 Fiordland; 37 Waitutu; 38 Auckland Islands). Species classed as present or absent for the analysis.
Figure 16 Cladogram of relationships of twenty-three sites in the Pukeamaru Ecological District to fifteen other New Zealand district sites, based on BPA of 463 extant terrestrial mollusc species. Analysis performed by branch swapping, heuristic search mode in PAUP, using species presence as apomorphies of the sites and ancestral taxa, estimated from cladograms of phylogenetic relationships, as synapomorphies uniting sites. Taxon characters were treated as ordered. Pukeamaru sites 1–23, Extralimital sites 24–38 as in Figure 15.

Figure 17 Cladogram of relationships of the Pukeamaru Ecological District to fifteen other New Zealand district sites, based on BPA of 463 extant terrestrial mollusc species. Analysis performed by branch swapping, heuristic search mode in PAUP, using species presence as apomorphies of the sites and ancestral taxa, estimated from cladograms of phylogenetic relationships, as synapomorphies uniting sites. Taxon characters were treated as ordered. Pukeamaru sites 1–23 (treated collectively), Extralimital sites 24–38 as in Figure 15.
that assembly rules will be defined, and spatial pattern predicted, only through a better understanding of the linkage between regional species pool, organism traits, environment, and local community assembly. A crucial next step to understanding the remarkable diversity in New Zealand land snails is to determine patterns of diversity and habitat relationships in areas of high in situ speciation, and thus local endemism. The greater majority of New Zealand snails are confined to the leaf litter on the forest floor, which is probably the primal habitat of terrestrial molluscs. Litter is a highly complex, three-dimensional, horizontally stratified habitat which from the snail’s viewpoint is probably subdivided into many subunits: newly fallen leaves at the top of the litter; fragmented leaves, twigs, and decomposed litter further down; and wet litter and finely particulate humus above ground level. To these subunits can be added the interstices in bark and logs. Elucidation of the behavioural and functional attributes of the snails that allow niche partitioning in this rich assemblage of litter microhabitats will be essential to understanding local processes that promote high diversity in these animals.

ACKNOWLEDGMENTS

We thank Landcare Research for the invitation to participate in the ecological survey of the Pukeamaru Ecological District, and to the Department of Conservation and the Whanau-a-Apanui and Ngati Porou runanga for allowing us access to the sampling sites. John Dugdale, Rosa Henderson, and Grace Hall provided logistic support and companionship during the field trips. We are also indebted to Dr Neil Cox for advice on statistical analyses, and to Dr Frank M. Climo for advice on the systematics of Punctidae and Charopidae. Preparation of this article benefited greatly from comments on a early draft by C. Tymone Duval and Drs Fred Brook, Greg Sherley, and Robert H. Cowie.

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APPENDIX 1. Terrestrial Mollusca recorded from twenty-three sample sites in the Pukeamaru Ecological District

INDIGENOUS TAXA

**Gastropoda**

Superfamily Neritoidae

1. Georissa purchasi (Pfeiffer 1862)

Superfamily Hydrocenidae

2. Cytoza cytora (Gray 1850)

Superfamily Succineoida

Family Liaridae

1. Georissa purchasi (Pfeiffer 1862)

Family Charopidae

1. Georissa purchasi (Pfeiffer 1862)

Family Arionoidea

1. Tornatellides subperforata (Suter 1894)

Superfamily Arionoidea

1. Tornatellides subperforata (Suter 1894)

Family Charopidae

1. Tornatellides subperforata (Suter 1894)

1. Tornatellides subperforata (Suter 1894)

Family Arionoidea

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1. Tornatellides subperforata (Suter 1894)

Family Charopidae

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11. *Fectola infecta* (Reeve 1852)
12. *Fectula mira* (Webster 1908)
13. *Huonodon hectori* (Suter 1890)
14. *Huonodon microundulata* (Suter 1890)
15. *Huonodon pseudoleioda* (Suter 1890)
16. *Paracharopa chrysographa* (Webster 1904)
17. *Paracharopa bianca* (Hutton 1883)
18. *Paracharopa goulstonei* (Climo 1983)
19. *Allodiscus dimorphus* (Pfeiffer 1853)
20. *Allodiscus planulatus* (Hutton 1883)
21. *Allodiscus urquharti* (Suter 1894)
22. *Allodiscus granum* (Pfeiffer 1857)
23. *Huonodon microundulata* (Suter 1890)
24. *Phrixognathus conella* (Pfeiffer 1862)
25. *Phrixognathus serratocostata* Webster 1906
26. *Huonodon pseudoleioda* (Suter 1890)
27. *Phrixognathus sp.*
28. *Huonodon microundulata* (Suter 1890)
29. *Phrixognathus sp.*
30. *Huonodon microundulata* (Suter 1890)
31. *Mocella eta* (Pfeiffer 1853)
32. *Climocella akarana* Goulstone 1995
33. *Climocella barkeri* Goulstone 1996
34. *Climocella intermedia* (Climo 1986)
35. *Climocella isolata* Goulstone 1996
36. *Climocella sp.*
37. *Chaureopa depressa* Climo 1985
38. *Chaureopa roscoei* Climo 1985
39. *Chaureopa microumbilicata* Climo 1985
40. *Chaureopa subdepressa* Climo 1985
41. *Chaureopa titrangensia* (Suter 1896)
42. *Cochlicopa lubrica* (MuÈller 1774)
43. *Serpho kivi* (Gray 1843)
44. *Therasiella celinde* (Gray 1850)
45. *Therasiella sp.*
46. *Therasiella neozelandica* Cumber 1967
47. *Therasiella sp.*
48. *Therasiella serrata* Cumber 1967
49. *Therasiella tamora* (Hutton 1883)
50. *Thalassohelix zelandiae* Gray 1843
51. *Flammulina zebra* (Le Guillou 1842)
52. *Flammulina chiron* (Gray 1850)
53. *Flammulina crebriflammis* (Pfeiffer 1853)
54. *Flammulina perdita* (Hutton 1883)
55. *Flammulina feredayi* (Suter 1891)
56. *Flammulina sp.*
57. *Flammulina sp.*
58. *Flammulina sp.*
59. *Flammulina sp.*
60. *Flammulina sp.*
61. *Flammulina sp.*
62. *Flammulina sp.*
63. *Flammulina sp.*
64. *Flammulina sp.*
65. *Flammulina sp.*
66. *Flammulina sp.*
67. *Phrixognathus conella* (Pfeiffer 1862)
68. *Phrixognathus serratocostata* Webster 1906
69. *Phrixognathus sp.*
70. *Phrixognathus sp.*
71. *Taguahelix viridula* (Suter 1909)
72. *Taguahelix sp.*
73. *Taguahelix sp.*
74. *Pasmaditta miscerabilis* (Iredale)
75. *Iotula microreticulata* (Suter 1890)
76. *Iotula sp.*
77. *Iotula sp.*
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