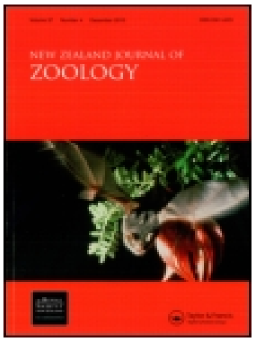

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Sympatric species diversity of New Zealand land snails

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Surveys for land snails of several bush patches on or near the Manukau Peninsula, southwest of Auckland, resulted in finding up to 60 species (only 3 introduced) in a single 4 ha patch of bush. Analysis of records from all bush patches suggests that an essentially sympatric community of about 72 native species is a probable reality, whereas in most areas of the world the sympatric existence of more than 15 land snail species is highly unusual. A first attempt at indicating the moisture, space, and foraging preferences of the 89 land snail species recorded from the Manukau Peninsula is presented, and an attempt is made to indicate broad categories of species association or habitat preference within this area. Many species occur throughout litter types (40–75% of all species in one bush patch would be in a 20×30 cm bag of litter from one spot), and it is hypothesised that the qualities of moisture retention and air space are more significant to the snails than the species of plant that provided the litter. This sympatric land snail diversity is normal from the central North Island up into Northland, but diversity levels drop sharply in the far north and southward from Mt Egmont/East Cape. Most of the South Island has 15–20 sympatric land snail species, with even greater reduction on Stewart Island and the subantarctic islands. It is hypothesised that the high sympatric diversity level reached in the Manukau area results from equability of the moisture regime. This diversity is based in accumulation of phyletically unrelated taxa, not localised speciation. The land snail population here has the aspect of a mature community. Even few-hectare patches of bush can hold near-maximum land snail communities, if they are protected against burning, clearing, and trampling of the litter by stock. The preservation of such patches is urged, for the conservation not only of the land snails but of the other soil micro-organisms that coexist.

Keywords: Gastropoda; land snails; species diversity; sympatry; native bush; relictual habitat; Manukau Peninsula; species lists; population structure

INTRODUCTION

Although the latest checklist of New Zealand molluscs (Powell 1976) lists 315 species of native land snails and slugs, approximately 520 species are currently represented in the collections of the National Museum of New Zealand (NMNZ). Nearly all of the increment (Table 1) is in the families Punctidae and Charopidae (in the sense of Solem, in press). Systematic revisions will be long-term undertakings (Climo, in prep.), and meaningful phyletic and biogeographic studies must await completion of the basic systematic reviews.

Many biogeographically interesting but remote areas of New Zealand have either been inadequately sampled for land molluscs or not yet sampled at all, so the total fauna will substantially exceed 520 species—provided that major extinction does not precede sampling.

A serious handicap to any attempt at assessing the patterns of local occurrence and ecology of New Zealand's land snails is the almost total lack of basic life history data. The only small land snail for which the life history has been published is *Austrosuccinea archeyi* (Powell), an extremely localised and rare annual species (Powell 1950). For the numerically dominant Punctidae and Charopidae we do not know feeding specialisations, length of life, breeding season, annual or seasonal fluctuations in numbers, activity cycle, difference (if any) in feeding and shelter niches, growth rate, causes of mortality, or mating

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behaviour for any New Zealand species. A world of studies awaits attention.

It has long been axiomatic among collectors of New Zealand land snails that a patch of bush from which less than 25 native species can be extracted is seriously disturbed, and 'good bush' routinely yields 35–40 species on a 'grab litter and run' visit. Single litter samples containing 60–70 species have been collected in the past few years from areas of a square metre or two. That so high a level of sympatric diversity is accepted as the norm astounds a malacologist experienced in most other areas of the world. Most areas in Australia, Africa, the New World, and the Pacific islands have 5–7 species sympatric, with 'good' areas yielding 10–12 species. Only in parts of Europe are levels of 12–18 sympatric species common, and a few special situations on Pacific islands, the Greater Antilles, and in temperate rain forests of northern New South Wales and Queensland have maximal diversity levels of 20–30 species (Solem, in prep.). No other area in the world even approaches the level of sympatric land snail diversity accepted as normal in New Zealand.

In planning a preliminary investigation of this phenomenon, Solem and Climo decided to try to establish a baseline level of sympatric land snail diversity by investigating an area of low topographic and floristic diversity containing a land snail fauna not obviously elevated in numbers by the packing effect of two or more formerly isolated faunas coming together since the last glaciation. The focus would be on both the number of species present and any data on niche specialisation that could be determined. For 17 years David Roscoe has been collecting land snails in many parts of New Zealand. Because of his excellent knowledge of their local ecology and the niches liable to yield live specimens, he was invited to participate in this project.

All three authors took part in the basic field survey (10–14 February 1981); supplementary field work and comparative collection near the Waitomo Caves were undertaken by the senior authors only (15–20 February 1981).

Selection of the Manukau Peninsula, south-west of Auckland and separated from it by the Manukau Straits*, as the primary study area was based on several factors. Geologically it consists of wind-blown sands of Pliocene to Holocene age with minor amounts of fluviatile Holocene sediment on the Waiuku River side of the peninsula (Schofield 1967).

Table 1. Taxonomic components of New Zealand's native land snail fauna

Family	Species listed by Powell (1976)	Species in NMNZ Collection
Hydrocenidae	1	1
Liareidae	28	32
Succineidae	1	1
Athoracophoridae	24	24
Achatinellidae	2	2
Charopidae	145	218
Punctidae	76	204
Paryphantidae	35	35
Bulimulidae	3	3
	315	**520**

The central area from Wattle Bay to Waipipi Creek is of old, consolidated, cross-bedded dune sands of the Wanganui Series, containing numerous thin, parallel bands of harder limonite. There are no rock exposures, and the high, consolidated dune faces provide refugia for patches of bush. South of the Waikato River, Mesozoic siltstones overlain by exposures of lime-rich sediment of Pliocene to Oligocene age provide a contrasting habitat of limestone crevices and shelves. To the east of Waiuku lies the rich market garden area around Pukekohe, extending to the Mesozoic rock area of the Bombay Hills. This agricultural basin is composed of early Pleistocene scoriaceous Franklin Basalts eroded into fertile soils.

It is not a geologically, topographically, nor floristically complex area. There is not a long and complex history of isolation and reunification of islands with the probability of allopatric speciation. Furthermore, most of the land snails to be expected in this region would have ranges extending well to the north and south of the Manukau. Specialised Northland elements would mostly be absent, and, without limestone exposures, the central North Island rock-associated snails would be absent. We could anticipate a generalised lowland assemblage of land snails comprising mostly species in the main—if not actual middle—portion of their range.

The climate of the peninsula is equably moist. Rainfall records from Manukau Heads, Waiuku, and Pukekohe cover from 17 to 98 years, and permit a few generalisations. Annual averages are 1119 mm at Manukau Heads, 1419 mm at Waiuku, and 1395 mm at Pukekohe. The April–September period is dependably wetter, with a 110–158 mm monthly average, but even the drier months are moist by most standards. At Waiuku and Pukekohe the October–March mean monthly rainfall always exceeds 90 mm except in January at Pukekohe, where it dips to 76 mm. Manukau Heads is distinctly less rained on, September–March averaging 74–85 mm and the

'Manukau Straits' and 'Manukau Peninsula' (Fig. 1) are not gazetted names, but are highly apposite to the needs of this paper. Note, though, that the late Cenozoic feature known as the Manukau Straits was much larger than the present seaway, which mirrors part of its course.

April–August wet season only 95–132 mm monthly.

A perhaps more important feature for the land snails is the occasional occurrence of stress periods—single months, or rarely two months in succession, during which very little rain is recorded. During such periods all except the wettest and most sheltered litter spots will dry out, producing mass snail mortality. The frequency of occurrence of such predictably unpredictable catastrophes will have significant effects on both species composition and population levels of individual species. As an arbitrary indicator of such stress periods we have chosen to tally all months in which the rainfall is less than 30 mm as a near disaster, and any consecutive two-month period in which total rainfall is less than 30 mm as a catastrophe.

At Manukau Heads, with 43 years of observations, 44 of 264 months (16.7%) between October and March had less than 30 mm. This happened most frequently in February (14 instances, 31.8%), but also in January (11, 25.6%), March (9, 20.5%), October (5, 11.4%), November (3, 6.8%) and December (2, 4.5%). Out-of-season shortfalls of less than 30 mm were recorded twice each in April, June, and September. Catastrophic two-month periods have been recorded five times: February–March in 1939 (26 mm); and January–February in 1954 (26 mm), 1957 (18 mm), 1964 (26 mm), and 1974 (26 mm). In January–March 1978 there was a total rainfall of only 62 mm, in monthly falls of 14, 31, and 17 mm. Thus, short drought periods would be a relatively normal experience for land snails in bush patches on the northern tip of the Manukau Peninsula.

The 98 years of records for Waiuku reveal more felicitous snail weather. Only 45 of 591 months (7.6%) in the October–March period show less than 30 mm rainfall. These are concentrated in February (19, 19.4%), January (8, 8.2%), March (7, 7.1%), December (5, 5.1%), and October (4, 4.0%). November (2, 2.0%) and a few out-of-season occurrences, two in September and one in April, complete the record. Catastrophes have been recorded only in January–February 1908 (8 mm) and February–March 1939 (25 mm). Although one in five Februaries can be unpleasantly dry, a snail's moisture supply is clearly more dependable at Waiuku than at Manukau Heads.

Pukekohe, in 18 years of records, shows only 6 of 111 months (5.4%) with under 30 mm, and no catastrophes.

The above are crude indicators of moisture stress periods for litter inhabitants, but are the only data available for the Manukau Peninsula. Many areas of New Zealand have more dependable and more extensive dry spells. We consider determination of such stress periods for a site to be a more useful indicator of its snail habitability than such variables as gross rainfall regime or exposed evaporation rate. Litter, almost by definition, accumulates in low-lying pockets and thus collects run-off water. Because of shade cover, evaporation will be relatively slow. The length of time between significant additions to the water running into litter is a critical indicator of stress periods.

TAXONOMY AND CLASSIFICATION

The enormous increase in number of collected land snail species documented in Table 1 has created a number of problems for contemporary workers. Monographic revisions are not yet available, but from work accomplished to date it is possible to recognise and delineate ranges for many unnamed species, and to know that many nominal genera are in reality 'form units' without phyletic coherence. Throughout this report we have had to deal with this situation. By using such terms as 'n.sp. aff.' to convey a sense of shell morphotype and 'n.sp. 6' to indicate an undescribed taxon of distinctive facies, we have attempted to convey maximum information short of describing new taxa, which is not a function of this study. Similarly, by citing a species as, for instance, *'Charopa' chrysaugeia*, we intend to convey that although currently placed in this genus it may or may not have definite phyletic affinity to *Charopa coma*, the genotype. Particularly for the punctids, the present genera are insufficient to present the actual phyletic diversity.

The species reported here from the Manukau Peninsula are readily distinguished in sympatry by shell morphology, and all are represented in areas quite distant from the Manukau. Although they lack formal names and any genealogical framework, they are recognisable units with substantial extralimital ranges, and thus 'act as good species'. For purposes of discussing sympatric diversity, we have adequate data from which to recognise species units. It would be preferable if their phyletic affinities were known, but the lack of such data constrains only the potential discussion of how this diversity originated.

For future reference, museum catalogue numbers for such new taxa are listed in Appendix 1 and 2. Reference to this study will be made when descriptions are published.

STUDY AREAS

The Manukau Peninsula, extending north from the Waikato River and Waiuku on the west side of the Waiuku River to the Manukau Straits west of Auckland, is composed of elevated, consolidated sand dunes. In the south the topography is moderately rolling, yet near the northern tip are steep-sided dunes of slightly over 275 m elevation, perhaps the

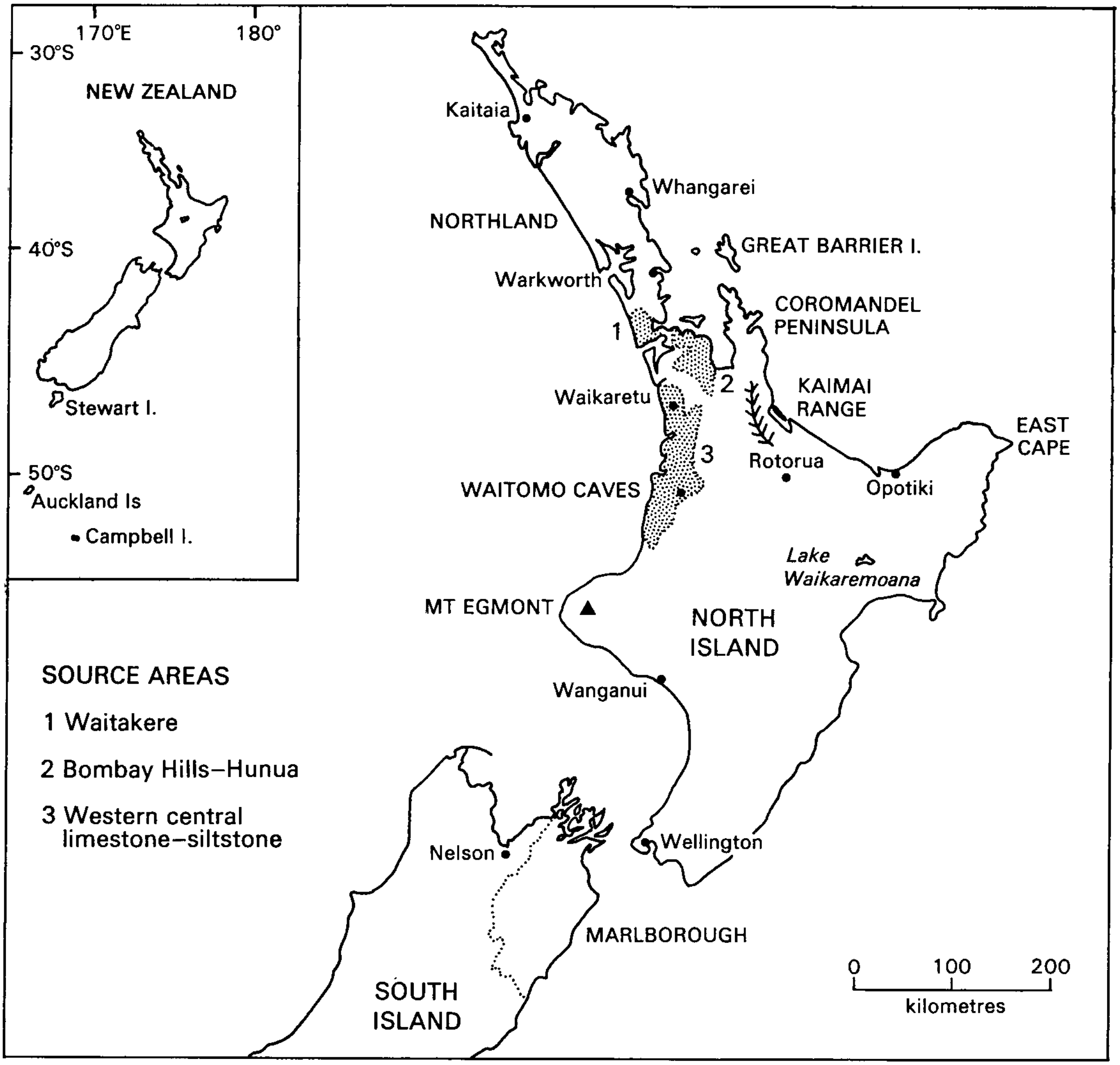
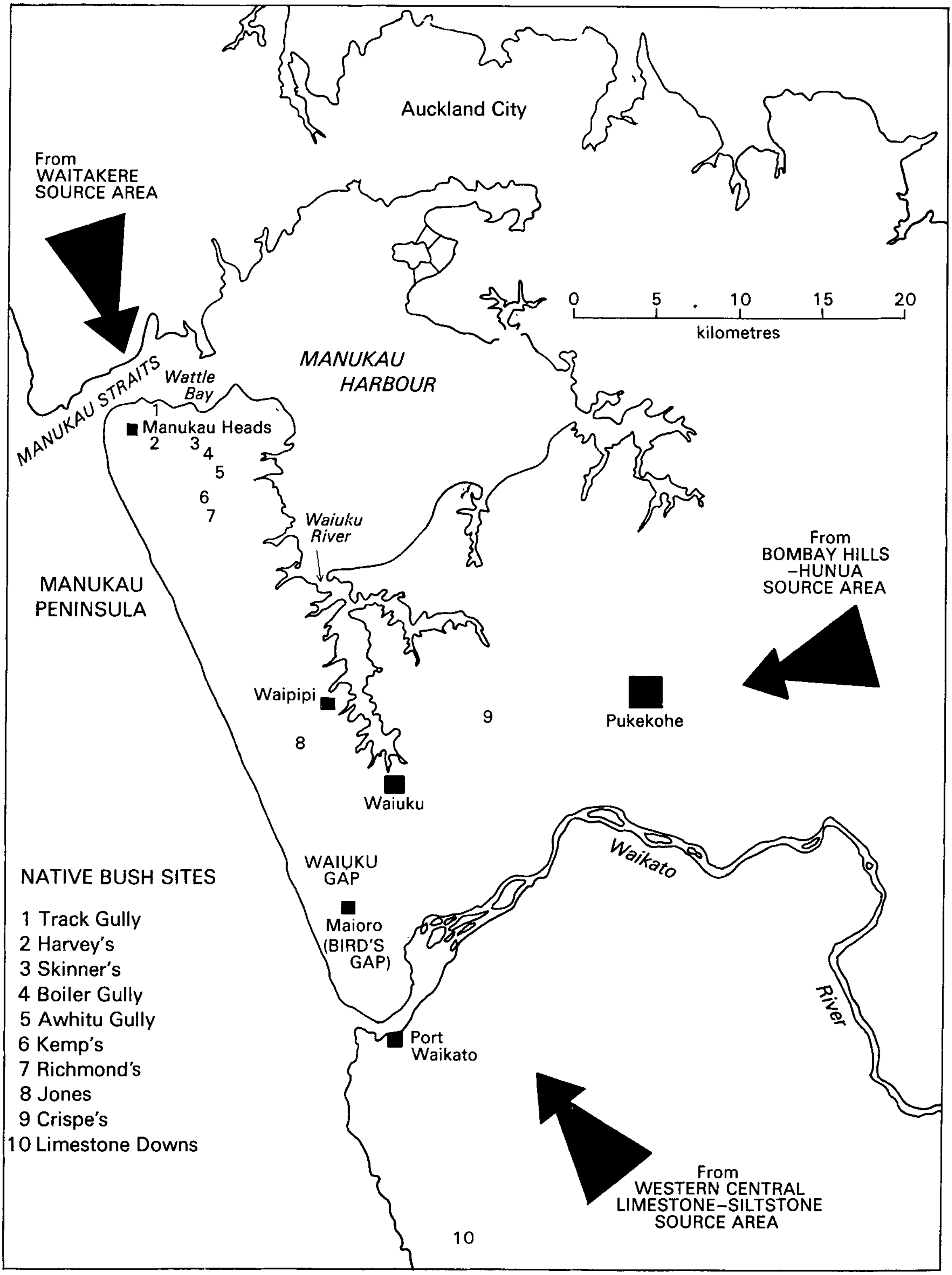


Fig. 1 *(includes opposite page).* Maps showing snail sampling localities and major features mentioned in text. Air distance between localities (km): Jones Bush – Harvey's Bush 18.9, Crispe's Bush 11.6, Waiuku 6.8, Limestone Downs 25.8; Waiuku – Harvey's Bush 26.6, Crispe's Bush 7.2, Limestone Downs 23.6; Limestone Downs – Crispe's Bush 28.5, Harvey's Bush 47.4.

highest in the world. There are no exposed rock formations. The native vegetation would have been unspecialised lowland bush associations and extensive stands of kauri (*Agathis australis* Salisb.), the former existing today as scattered remnants clinging to streamside slopes on the steepest and least economically useful topography. Most of the peninsula was long ago converted to pasture for sheep and cattle. A few patches of bush are adequately fenced against disturbance by stock, yet most of them attain marginal protection through sheer slopes or highly dissected contours that discourage visits by man or stock.

On a hurried faunistic survey collecting trip in 1977, David Roscoe and Bruce Hazelwood contacted a well known Waiuku naturalist, Mr Norman Douglas, who helped locate several bush patches and obtain permission to sample from them. One of these, Jones Bush (which became Waipipi Scenic Reserve in 1975), yielded 41 land snail species on


Auckland City
From
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0 5 10 15 20
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Waiuku
River
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BOMBAY HILLS
-HUNUA
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MANUKAU
PENINSULA
Waipipi
9
Pukekohe
8
Waiuku
WAIUKU
GAP
Waikato
Maioro
(BIRD'S
GAP)
River
Port
Waikato
NATIVE BUSH SITES
1 Track Gully
2 Harvey's
3 Skinner's
4 Boiler Gully
5 Awhitu Gully
6 Kemp's
7 Richmond's
8 Jones
9 Crispe's
10 Limestone Downs
From
WESTERN CENTRAL
LIMESTONE-SILTSTONE
SOURCE AREA
10

3 January 1977 from a lumped sample covering several types of litter. There was minimal sign of disturbance in the bush, and these preliminary results suggested that this area would provide a good example of snail diversity in 'normal lowland bush'. Jones Bush is far enough inland to avoid influences from xerophytic coastal vegetation, and lacks limestone outcrops, which tend to accumulate a specialised snail fauna.

Fig. 1 indicates the position of Jones Bush relative to several other bush patches from which we took samples for comparison; additional bush patches from which Norman Douglas has collected material cited in this study are also plotted.

The Manukau Peninsula is accretional land gradually built up from ocean sand deposits elevated into high dunes and then consolidated. It is not vicariated land with an intact fauna. Thus, it is important to consider the origins and dispersal routes of its land snail fauna. There are three sources from which the Manukau Peninsula can receive land snails: (1) across the Manukau Straits from the Waitakere Range to the north; (2) from the Bombay Hills and Hunua Range to the east through the Waiuku and Waikato river deltas; and (3) from the northern edge of the central limestone masses that lie just south of the Waikato River. In most of the Manukau Peninsula one would expect to find land snail species with excellent to good dispersal capabilities, representing a 'typical' lowland assemblage basically uncontaminated by relicts, superimposed major faunas, very slow dispersalists, and inhabitants of rock outcrops. Four-fifths of the 83 native land snail species recorded in this paper from the Manukau Peninsula have ranges that extend significantly north and south of the peninsula; one-twelfth are at or near their northern range limit; one-tenth are at or near the southern limit; and one species is at its western limit. Thus, questions as to the direction of colonisation have considerable signifiance.

Jones Bush (37°13'10"S, 174°39'50"E) sits mostly on the high north slope of Parakau Creek, a tributary of the Waiuku River, west-south-west of Waipipi. About half of its 4.22 ha comprises dense native bush. It has been at most lightly visited by stock, judging by vague traces of a few stock tracks forming narrow terraces on the upper fringe. At the western end are the concrete foundations of an old house, and garbage pits on the northern fringe indicate 19th century habitation. Comparatively few big native trees remain, mostly along the stream bank, but the entire Reserve is ringed by large *Pinus radiata*, an introduced North American tree. Both topography and prevailing winds favour continued wet conditions. Much of the bush has a 'rich snail habitat' appearance to the eyes of collectors. For most, if not all, of this century Jones Bush has been allowed to regenerate. It has long been considered the finest bit of bush in the area, and its purchase and designation as a Scenic Reserve by the Department of Lands and Survey showed excellent discernment.

The upper northern edges are relatively dry with thin broad-leaf* litter and relatively large numbers of saplings, but the slope soon descends abruptly into gullies and ravines. Heavy patches of mamaku (*Sphaeropteris medullaris* (Forst.f.) Bernk.) and king fern (*Marattia salicina* Smith) line the creek side and extend at least partly up the gullies. Puriri (*Vitex lucens* Kirk) is dominant in the uplands, and a few big rimu trees (*Dacrydium cupressinum* Lamb.) exist. Diversity of broadleaf plants increases up the slopes. The lack of extensive streamside shelves probably explains the relative paucity of nikau palms (*Rhopalostylis sapida* Wendl. et Drude). No stands of flax (*Phormium tenax* J.R. et G. Forst.) were noticed. The absence of big logs probably indicates that large trees were cut from the upper slope before 1900. Although no literature exists on the decomposition rate of fallen logs in New Zealand, anecdote suggests that there is a 50–75-year 'ground life' for most large trees, and that even large kauri trees are reduced to a shell in less than a century (M. Daniels, pers. comm.).

The implicit conclusion that floral diversity is low relative to many bush patches, and that regeneration is occurring on the outer fringes, is correct. However, in terms of snail habitat the basically south-facing (i.e., shaded) slopes, dissected topography, high moisture retention features, and relatively long period (for New Zealand bush) without stock grazing more than compensate for the floral poverty. The extensive king fern patches indicate that Jones Bush has not been burned out since European settlement. A burned puriri stump on the upper slope indicates fringe fires, but both the conditions and local memory attest to a long period of little disturbance.

For comparative purposes several other bush patches (Fig. 1) were selected with the guidance of Norman Douglas. They were an exposure of limestone 25 km to the south (Limestone Downs), a regenerating bush patch north-east of Waiuku (Crispe's Bush), and three patches (Harvey's Bush, Track Gully, and Awhitu Gully) at the northern end of the Manukau Peninsula.

The nearest lime-rich outliers of the western central North Island Cenozoic sequence are south of Port Waikato, on Puriri Station and Limestone

*We use the term 'broadleaf' as a convenient distinction from small-leaved native species such as the podocarps and southern beech (*Nothofagus* spp.).

Downs Station. They are basically of Pliocene to Oligocene age (Schofield 1967), and are a combination of mudstone, which contains few crevices, and bedded limestone that fractures and weathers open, providing luxury shelters for land snails. A projecting ridge on **Limestone Downs Station** (37°27'30"S, 174°44'30"E) in the drainage of Waikawau Stream was sampled on 13 February 1981. 'Snaily'-looking exposures on the north face had been so altered by burning and grazing that the observed land snail fauna consisted of the introduced species *Helix aspersa, Oxychilus cellarius, Cionella lubrica*, and *Vallonia pulchella* plus recently dead specimens of the native carnivorous species *Rhytida greenwoodi*. Up the slopes, scattered dead examples of a few native micro-snails were observed but not taken. At the top of a small saddle, a flat-topped limestone pinnacle about 2.5 m in diameter yielded litter containing dead examples of *Mocella eta* (1), *'M.'* n.sp. aff. *maculata* (9), *'M.'* aff. *manawatawhia* (4), *Charopa coma* (12), *Phenacohelix giveni* (21), *P. ponsonbyi* (1), *'Phrixgnathus' levis* (1), *'P.' moellendorffi* (1), *Paralaoma caputspinulae* (2), and *Oxychilus cellarius* (2). On the south side of this ridge, to the east, another ridge angles in to the main spur, forming first a narrow valley, and then a short ravine of massive, jumbled rock. The numbers of introduced snails drop dramatically as the terrain roughens, native plants increase, and the topography makes travel difficult even for goats. Near the head of the ravine snails were taken from black, loamy soil on slanting rock surfaces. Flatter areas of high moisture had been trampled by stock, and thus were unsuitable as snail habitat. Snail-inhabited litter was of medium moisture content; neither dry litter nor very wet litter niches were available for sampling. The area of semi-native bush was about 0.2 ha, clinging in isolated patches to the ravine sides and isolated among miles of pasture lands.

Crispe's Bush (37°12'30"S, 174°47'25"E) is north-east of Glenbrook and north of Sommerville Road. Samples were taken on 13 and 17 February 1981. It is now fenced against stock, and presents a spectacular approach across paddocks with a line of perhaps 100-year-old puriri and rimu interspersed with nikau palms. A few huge puriri stumps are on the upper slopes, and the stream side has young trees, ferns, nikau palms, and saplings in profusion. The largest puriri in the Waiuku area is at mid slope on the north bank. In comparison with Jones Bush the topography is gentler, the area more extensive, and the vegetation clearly in a regenerating phase. There are fewer big trees and no king ferns or mamaku. As at Jones Bush, the absence of the big log habitat undoubtedly has had an effect on the snail fauna.

Harvey's Bush (37°03'20"S, 174°33'30"E) is less than a kilometre inland from South Head and south-south-west of Te Pirau Point, just south of Hartner Road. Samples were taken there on 15 February 1981. The bush patch lies on the east-south-east face of a precipitous dune, and is open to stock grazing. Much of the bush is on 50–70° slopes, providing moderate protection from disturbance, and also making a meaningful estimate of area quite difficult. The ravine bottom is overhung by relictual patches of king fern, mamaku, and nikau. All but the upper fringe of the slope is in dry broadleaf forest of fair-sized trees, with an understorey of ferns. Ridge tops are in mixed rimu/broadleaf forest. Litter pockets are patchy because of topography and stock trampling. There is clear evidence of goat grazing on understorey plants, and some evidence of slope terracing by stock. It is an old-appearing patch with tree size limited by topography and thin soil, showing signs of incipient rapid degeneration because of inroads by stock. The combination of relatively dwarfed trees and extreme slopes probably means that Harvey's Bush has not been logged, so a good snail fauna could be expected, subject to local extinctions caused by recent disturbance.

A small, opportunistic litter sample was taken on the same day from the head of **Track Gully,** a north-facing slope on the Manukau Straits. The bush is a small patch of broadleaf and mamaku on a steep slope seepage area, and is located about 300 m north-west of the edge of Harvey's Bush. The sample came from a fenced-off pump station area.

Awhitu Gully (37°06'30"S, 174°35'18"E) lies a kilometre inland of Wattle Bay. The bush, visited on 15 February 1981, is on an undulating north-facing slope with kauri on the ridges and mixed broadleaf and tree ferns in the small, shallow gullies. It is of about the same area as Jones Bush. A swamp on the low side and a steep scarp at the top provide partial protection from grazing, and the vegetation shows few signs of disturbance. The kauri has not been milled in this century. Litter samples were taken from a broadleaf-clad gully and then from around the base of the largest kauri tree.

SAMPLING PROCEDURES

General sampling of bush patches in New Zealand for land snails traditionally involves bagging quantities of litter snatched from several micro-habitats, taking a maximum of partly decomposed material as opposed to intact surface leaves. This method is supplemented by hand-picking material from litter and from tree trunks and branches up to 2.5 m above the ground, and by beating ferns and small saplings into cloth sheets to obtain arboreal snails. Dead shells of arboreal species occur frequently in litter samples, such that 'snatch and run' tactics obtain a fair proportion of the species present.

Our sampling proposals for Jones Bush were altered in several respects. Use of quadrats had to be abandoned because of patchiness of litter pockets and topographic features. Not only does the dissected topography result in pockets of litter, but where deep litter is composed of mamaku or other fronds in a vast, tangled mass, with different degrees of decomposition interspersed from top to bottom, quadrat sampling is impossible.

A drought-breaking rain had just preceded our first visit to Jones Bush, and heavier rains occurred during the field period. Thus, a mixture of shelter and foraging sites were sampled at the same time, without our being able to segregate them. Much greater mphasis was given to hand-picking, which greatly increased the number and proportion of species ollected alive (Table 2). Hand-picking from the surface leaves on foot squares of broadleaf litter, from nikau boles by the stream, and from arborear strata was then supplemented by bagging litter from single vegetation types. Hand-picked materiar vas drowned overnight in water, fixed in 95% ethanol, and preserved in 70% ethanol.

Standard treatment of bagged litter is as follows. The contents of a bag are washed through sieves of 1.5 and 0.5 mm diagonal measure mesh. The fine-grained dirt is discarded, since shell protoconchs of 0.2–0.5 mm cannot be identified. The upper sieve fraction is placed a handful at a time in a large bucket nearly full of water, and the debris is stirred vigorously. Because a bubble of air is trapped inside, dead shells of recent demise float to the top together with large litter fragments. Live specimens and partly decayed or broken dead shells that lack an entrapped air bubble sink to the bottom. Floating material is scanned for shells, which are hand-extracted with fine forceps or a pen nib. The material is stirred, scanned, and stirred again until no more specimens are spotted for about a minute. The floating debris is then discarded, and the bottom dirt and litter is poured on to a plate and hand-sorted for live snails and slugs plus identifiable, although damaged, empty shells. The live material is drowned overnight, fixed in 95% ethanol, then preserved in 70% ethanol. (Formalin, even if buffered and used only as a short-term fixative, adversely changes many anatomical structures in the snail's body so that the material, even if stored in ethanol, becames almost useless for study within 2 or 3 years. Specimens kept in ethanol for more than half a century, in complete contrast, are readily dissected and illustrated.) Dead shells from both the float and bottom litter are air-dried, then stored in vials for further processing.

Table 2. Proportion of live-collected land snail species from six bush relicts sampled

Location	Total species	Live-collected species	% live-collected
Jones Bush	57	45	78.9
Crispe's Bush	49	18	37.0
Limestone Downs	36	12	33.3
Harvey's Bush	44	15	34.1
Awhitu Gully	32	10	31.3
Track Gully	25	5	20.0

The above method is effective and efficient in New Zealand for sampling wet litter. The small New Zealand land snails are extremely hydrophilic, following moisture down and not sealing to leaf or log surfaces except as a last resort when immediate desiccation threatens. Arboreal taxa such as *Serpho kivi, Lamellidea novoseelandica, Flammulina perdita,* and several *'Phrixgnathus'* species seal themselves to leaves or tree trunks, but the litter taxa seem to move to wetness. If placed in jars they will not seal to the sides, but sit and shrivel in their drying litter. The epiphragms—mucus sheets used to close the aperture of the shell and/or to seal the shell to a surface—are thin, uncalcified, and readily dissolve in water. If arboreal snails sealed to leaves or tree trunks dry out and die, the next rain can dissolve their epiphragms and produce a 'shower' of dead shells into the litter. Such accumulations of arboreal species in litter occur routinely, and are especially noticeable at the end of dry spells.

The persistence of dead shells in moist litter in New Zealand forests is unknown. We hypothesise that it would be fairly short during moister periods, weeks or a few months at most, but can offer no direct evidence. The general pattern in much of New Zealand is for moisture to be available in at least protected litter pockets throughout the year. At most a short summer pause in rainfall browns the grass, but leaves the deep litter piles in the bush moist. The characteristics of the New Zealand bush snails that permit this sampling method to be effective are probably due to continued presence of moist niches.

In Australia or the Northern Hemisphere, where the land snails must aestivate over a dependable and predictably much longer dry spell, epiphragms are multiple, strongly calcified, or both. The snail may burrow into the soil, lie free on the surface, or seal tightly to a rock, log, twig, rolled-up leaf, or another snail shell. At times the epiphragm seal is so strong that either the substrate or the shell will break before the epiphragm separates, when one tries to pull the snail off its attachment surface. The live snails can readily dissolve these seals, usually in only a few seconds, but water is ineffective. Thus, newly dead shells sealed to litter bits would be much less responsive to the flotation method of separation used in New Zealand with such success.

There is undoubtedly bias in hand-extraction from float and bottom debris. Shells that closely approximate in size and colour the decomposed litter grains (minute punctids in particular) will be discriminated against, but the bias would operate with near equality for most samples. Thus, an under-representation of minute punctids must be expected and accepted. Results from bagged litter should be considered comparable to the extent that the samples were taken in comparable fashion and amount, and that litter types were similar from place to place.

Comparison of the percentage of species collected alive among the bush patches sampled (Table 2) points out an obvious limitation of the bagged litter technique. In Jones Bush, where there was extra emphasis on hand-picking, 78.9% of the species found were taken alive; where only bagged litter samples were taken, only 20.0–37.0% of the species were taken alive.

Further comments are included in the discussion of results from each bush area.

ANALYSIS OF LITTER SAMPLES

Data on land snails extracted from the selected litter samples from our Manukau area bush patches are presented in Appendix 3. For convenience, results of hand-picking have been incorporated as a separate category.

Differences in the species lists from each patch of bush are discussed below ('Faunistic Summary'); the analysis here is of differences among samples as to species occurrence and proportion. Since the data from Jones Bush are the most comprehensive, these are discussed in most detail; data from the bush patches examined subsequently are compared with the Jones Bush results.

This is a qualitative rather than quantitative discussion. The samples are not equivalent in size or in area 'scratched up', and the low numbers of each species obtained make statistical tests of either occurrence or abundance an idle exercise. Drought-breaking rains preceded our sampling efforts. The awakened snails were in both shelter and foraging sites during our field work, which makes mathematical analysis of site variability of little value. We *can* show that many species range over several litter types, and suggest factors that may be influencing micro-distribution in New Zealand bush patches.

At **Jones Bush** we initially took eight different samples, and on 17 February 1981 in a follow-up hand-picking session we attempted to locate a few species that we considered to be almost certainly present, and to refine our concepts of habitat types and relative distributions. The initial samples, summarised in Appendix 3A, were as follows:

(1) hand-picking from leaves and trunks of broadleaf trees and saplings, 0.3–2.5 m above ground level, in an area of about 25 m² just above the steep-sided gully that yielded the mamaku sample;

(2) under a single big rimu, mid-terrace level, about 3 m outside the Reserve fence, open to stock, some introduced ground plants present (grasses), both hand-picking and bagged litter;

(3) pure stand of puriri, about 30 m into Reserve from upper boundary, several big trees, litter 3–20 cm deep, soil below loamy and spongy; bagged litter only;

(4) upper slope mixed dry broadleaf cover, same area as arboreal sample, live snails hand-picked from intact leaves in a square foot with very thin under-litter (tabulated as 'Live eye'), and bagged litter of partly decomposed to decomposed leaves in adjacent pockets of deeper litter;

(5) bagged litter from small hillocks in the dry broadleaf zone that had been colonised by young ferns, litter spongy, with light leaf cover;

(6) hand-picking from a few scattered fallen nikau boles beside the stream (no concentration of nikau palms sufficient to accumulate proper litter exists in Jones Bush);

(7) hand-picking and bagged litter from mamaku piles at the mid-slope base of a 5 m, mostly unvegetated cliff face just below the area for samples 4 and 5 (area is head of gully from which sample 8 was obtained), litter including some upper soil and soil/litter interface from three moderately deep piles within a 5-m-square area;

(8) hand-picking and bagged litter from a deep pile of mamaku at gully base beside stream, upper soil not included but interface area sampled.

In effect, samples 1, 4, 5, 7, and 8 form a partial transect of the Reserve. Sample 6 was about 20 m downstream from sample 8, and samples 2 and 3 were near the eastern edge.

On 17 February 1981, 2 days after heavy rains, an attempt was made to sample nikau leaf axils and check added dry areas. In the axils of two nikau palms beside the stream, two live and three dead '*Phrixgnathus*' n.sp. 59 were found, adding this species to the faunal list. A copulating pair of *Liarea hochstetteri carinella*, one live '*Thalassohelix*' *ziczac*, one live *Suteria ide*, two live *Phenacohelix giveni*, one live *Fectola mira*, and one live *Geminoropa cookiana* were taken under slimy, wet ground litter at the tree bases. Only the added species is included in Appendix 3A. The dry zone vegetation produced no further native species; *Helix aspersa* and *Oxy-*

chilus cellarius were seen there but not collected.

A litter sample taken on 3 January 1977 by David Roscoe and Bruce Hazelwood contained three additional species (*Laoma marina, Cavellia roseveari, 'Paralaoma'* n.sp. 40), so that 60 species of land snail are actually known from Jones Bush. However, this analysis deals only with the 57 species and 2168 specimens recorded from our 1981 samples. With the mixture of hand-picking and litter samples, live and dead specimens, there are 318 separate occurrence records of the species. Tables 3–5 summarise a few patterns.

Table 3 summarises gross numbers from the different habitats. The maximum number of species—38 of the potential 57—were found in the upper mamaku sample. Comparatively few of these (*Lamellidea novoseelandica, Flammulina perdita, 'Phrixgnathus' erigone*) are primarily arboreal species to be expected in ground litter as 'showered-down' dead shells. Since three live *'Phrixgnathus' erigone* were in the mamaku litter, the species was clearly inhabiting this space, at least temporarily. Thus, a potential 36 species were in this ground area, of which one sample produced 17 alive. The lower numbers of species and specimens under the 'Arboreal' and 'Nikau' headings reflect limited effort and habitat specialisation rather than major distinctions. The drier puriri litter, although yielding the largest number of specimens, had a reduced species list of 19. Rimu, dry broadleaf, and young fern areas each relinquished 24–28 species. The wetter lower mamaku sample yielded 32 species. A specialised ground sample hand-picked from a foot square of intact leaves (sample 4 'Live eye') produced 11 species and 27 live specimens, including two *'Phrixgnathus'* (*erigone* and *ariel*) that at least forage arboreally. The sample was a few metres from any tree or sapling base, so a significant movement potential is indicated. Yet another comparison can be made easily, since the arboreal, dry broadleaf, and young fern habitats were all contained within a 5-m-square area. Combined species diversity for these samples totalled 37, of which 32 species were taken alive. Ten of these are considered to be arboreal, but several of these tree-dwellers did occur alive in the litter.

It is evident that species occurrence levels of 42–49% of the total fauna are normal in spot litter samples from under rimu, dry broadleaf, and young ferns, and that levels are elevated to 56.1–66.7% in mamaku piles.

Table 4 indicates that there are differences within litter of the same type. The number of specimens from the upper mamaku heaps was 2.04 times the number extracted from the lower litter pile. Species whose representation was clearly disproportionate to this ratio are 20 in number, almost half the 42 species recorded from the combined samples (Appendix 3A). From the information in Fig. 2 it is clear that the native tramps (*Cavellia buccinella, Mocella eta, 'Paralaoma'* n.sp. 29), plus *Therasiella neozelanica,* have noticeably reduced numbers in the streamside litter, as do some taxa with a preference for well drained or moderately wet litter (*Cytora torquilla, Omphalorissa purchasi, 'Charopa' fuscosa, Allodiscus urquharti, 'Paralaoma'* n.sp. 38, *Cionella lubrica*). The reverse is seen for *Liarea hochstetteri carinella, Allodiscus* n.sp. aff. *granum, 'Phenacohelix'* n.sp. 1, *Therasiella celinde,* and *Laoma leimonias,* all of which are absent or in proportionately reduced numbers in the upper mamaku sample. This sample came from the head of a gully, and would be sub-

Table 3. Summary of land snail sample data, Jones Bush, to show species diversity observed in microhabitats

Habitat	NUMBER OF SPECIMENS Live	Dead		Total species*
Arboreal	51	—	**51**	14 (14)
Rimu	37	338	**375**	24 (9)
Puriri	83	589	**672**	19 (10)
Dry broadleaf	51	82	**133**	28 (19)
Young ferns	30	192	**222**	24 (11)
Nikau	32	—	**32**	8 (8)
Upper mamaku	64	394	**458**	38 (17)
Stream mamaku	60	165	**225**	32 (13)

*Exclusive of introduced slugs; in parenthesis, number taken as live specimens.

Table 4. Disparate records of land snail abundance from Jones Bush mamaku samples

Species	NUMBER OF SPECIMENS IN Upper edge	Stream edge
Omphalorissa purchasi	76	5
Liarea hochstetteri	11	17
Cytora torquilla	43	12
Delos coresia	33	11
Cavellia buccinella	19	1
Mocella eta	21	5
'Charopa' fuscosa	15	1
Huonodon pseudoleiodon	9	14
'Allodiscus' urquharti	8	—
A. n.sp. aff. *granum*	7	13
Geminoropa cookiana	8	5
'Phenocohelix n.sp. 1	2	6
Therasiella neozelanica	22	4
T. n.sp. aff. *neozelanica*	9	—
T. celinde	—	3
Laoma n.sp. aff. *marina* 1	4	—
L. leimonias	12	36
'Paralaoma' n.sp. 38	20	—
'P.' n.sp. 29	20	3
Cionella lubrica	12	1
EXPECTED RATIO:	2.04	1

Table 5. Most abundant land snail species in Jones Bush, as inferred from numbers recovered from all samples

Species	Number of specimens Live	Dead		n*
Omphalorissa purchasi	39	269	**308**	4
Laoma leimonias	59	195	**254**	5
'Mocella' n.sp. aff. *maculata*	37	111	**148**	5
Cavellia buccinella	15	121	**136**	5
'Paralaoma' n.sp. 29	10	90	**100**	4
Cionella lubrica	2	94	**96**	4
Therasiella neozelanica	8	85	**93**	5
Lamellidea novoseelandica	3	74	**77**	6
Delos coresia	5	66	**71**	6
Cytora torquilla	10	56	**66**	4
Flammulina perdita	5	60	**65**	4
Mocella eta	14	47	**61**	4
'Phrixgnathus' erigone	18	38	**56**	5
'Charopa' fuscosa	9	41	**50**	5
'Paralaoma' n.sp. 38	11	33	**44**	2
Laoma n.sp. aff. *marina* 1	4	36	**40**	4
	249	**1416**	**1665**	
% of entire samples:	61.3	80.5	77.1	

*Number of habitats in which species was recorded

ject to wash-down snail recruitment from the dry broadleaf/young fern assemblages on top of the terminal cliff. The lower mamaku pile was considerably wetter and better protected.

Table 5 reinforces the above observations. Of the 17 species represented by 40 or more individuals, only *'Paralaoma'* n.sp. 38 occurred in just two habitats. This is probably an artefact of collecting, since its preferred habitat (see Appendix 1) is on newly fallen leaves, and these are not normally part of the litter that is bagged for sorting. All the other species were taken in four to six habitats. This phenomenon is not restricted to the commoner species. Of those with 20–35 specimens collected, *Rhytida greenwoodi*, *Huonodon pseudoleiodon*, *'Phrixgnathus' ariel*, *'Paralaoma'* n.sp. 8, and *Paralaoma serratocostata* were recorded from four habitats each, and *Liarea hochstetteri carinella* plus *'Phrixgnathus' conella* from three habitats. Even the comparatively scarce *'Phenocohelix'* n.sp. 1 (11 specimens, 3 habitats) and *Phenacohelix giveni* (7 specimens, 4 habitats including hand-picking from nikau) show a wide range of litter occurrences.

Much less emphasis was given to hand-picking in the other bush patches, primarily because it takes a long time, so the proportion of live-collected species is significantly reduced (Table 2). The proportions of specimens collected alive were 18.8% in Jones Bush, 9.5% in Harvey's Bush, 8.5% in Crispe's Bush, 4.6% at Limestone Downs, and 2.7% at Track Gully, in direct relation to the time devoted to hand-picking.

In **Crispe's Bush** (Appendix 3B) six litter types were sampled:
(1) from the side of a large 'live log', a quite big puriri that has one trunk extending more than 10 m along the ground, mostly in contact with the soil surface;
(2) mixed nikau and fern litter on the upper slopes with canopy of rimu and puriri;
(3) scattered small pockets of broadleaf litter from mid to upper slope, bagged by David Roscoe during a heavy rain shower on 13 February 1981;
(4) litter alongside a large, rotten puriri log that angles downward from the upper (south) edge of the bush:
(5) broadleaf litter near the stream bank in the centre of the bush patch;
(6) fern debris by the stream.

Species counts were lowest (9 and 16) for the log litter samples, in the range 20–27 for the spot litter samples, and 36 (73.5% of the 49 recorded) in the scattered broadleaf sample. The spot sample records of 41.7–56.3% of total species compare well with the Jones Bush figures.

Both log habitats were near the bush fringe, and produced mainly tramp or generalist species plus the ridge-loving *Obanella rimutaka*. The rotten log did yield such characteristic log species as *Fectola infecta*, *Allodiscus tessellatus*, and *Therasiella celinde*. The broadleaf litter from beside the stream added *'Charopa' chrysaugeia* and *'Flammulina' feredayi* to the scattered broadleaf sample roster. Specimen numbers in most samples were so small that we attach no importance to variations in proportional species composition between samples.

Harvey's Bush (Appendix 3C) presented sampling difficulties because of the sheer topography. Three habitats were sampled:
(1) combined ponga*/broadleaf from south-facing mid-slope area about 50 m up from base;
(2) mixed broadleaf litter about 50 m upslope and then west of the first sample;
(3) mamaku/nikau litter near head of gully at ravine base on south slope.

Obtaining the first two samples required hunting out several small patches of litter because of stock disturbance, so they were accumulated from several square metres. The mamaku/nikau sample was taken from a much smaller area.

The mixed broadleaf contained 31 of the 44 species (70.5%), and the mamaku/nikau had 32 (72.7%). There was a reduction to 26 (59.1%) in the ponga/broadleaf mid-slope sample. Sixteen species were represented in all three samples, all by 10 or more

*A Maori name embracing a number of tree ferns other than mamaku, which suits the level of distinction we wish to make.

specimens. Four other species represented by 10 or more examples were each absent from one litter type—*Delos jeffreysiana* and *Phenacohelix giveni* from the ponga/broadleaf, *Huonodon pseudoleiodon* and *Suteria ide* from the mixed broadleaf. These are probably sampling artefacts, as are absences of species represented by nine or fewer specimens from litter types. The sheer slopes of Harvey's Bush undoubtedly contribute to the mixing of populations, at least on the mid and lower slopes, where water runoff carries snails down-slope. More extensive sampling should confirm near uniformity of the fauna throughout Harvey's Bush, however.

Awhitu Gully (Appendix 3D) contained a reduced fauna of 32 species, 28 taken from fern/nikau litter in a shallow gully between ridges of kauri forest. Only 15 species were in the latter under a big kauri tree. Four species in this sample (*'Charopa' ochra, Therasiella celinde, T. tamora,* and *'Phrixgnathus' pirongiaensis*) were not taken in the fern/nikau sample. *T. celinde* is common on the Manukau Peninsula, but *'C.' ochra* and *T. tamora* were very rare and *'Phrixgnathus' pirongiaensis* was not recorded elsewhere. With these limited data, the significance of the kauri occurrences must remain uncertain. Formerly kauri stands were quite extensive on higher slopes and ridges, but the easily accessible trees were milled decades ago.

Neither **Limestone Downs** nor **Track Gully,** where single samples were taken, provide significant habitat selection data. Species list peculiarities (Appendix 3E) are discussed in the 'Faunistic summary' (below).

Our conclusion from the above limited data is that type of litter *per se* seems to have no meaningful influence on species occurrence. Small quantities of litter, generally less than would fill a 20 × 30 cm plastic bag, routinely yield 40–75% of the total land snail species living in a particular patch of bush. Percentages at the high end of the range are from wetter, deeper litter in species-rich patches, or from any 'good litter' sample, with less regard for moisture level, in bush patches with reduced to depauperate faunas.

Abundance does seem to be correlated with depth and moistness of litter, and some vertical stratification of the litter habitat into both resting and foraging niches seems probable.

SPATIAL AND MOISTURE PREFERENCES OF LAND SNAILS IN JONES BUSH

On the basis of data from several sources summarised in Appendix 1, including our direct observations of snails in Jones Bush, it is possible to outline several categories of species association or similarity in habitat preference. Such assignments must be tentative, and it must be emphasised that these are usually preferences, not restrictions. Many species occur throughout the range of habitats, although most abundant under one set of conditions. Despite its limitations, this first approximation in defining habitat specialisation and space discrimination is a necessary prelude to any interpretation of the nature and apparent stability of the high diversity levels shown by land snails in New Zealand bush.

'Tramp species' have wide geographic ranges, often the entire North Island and warmer parts of the South Island; occur in a broad range of slightly drier or fringe habitats; and sporadically penetrate wetter, more favourable habitats, but are abundant only in the disturbed dry fringes. In New Zealand the introduced land snails *Helix aspersa, Cionella lubrica, Oxychilus cellarius,* and *Vallonia* spp. exemplify this type of distribution. Frequently they will be present in almost astronomical numbers in open, disturbed pasture or pasture/bush fringes, dwindling to rare status in wetter bush areas where native snails are present. Five native species form a common dry-litter assemblage on the bush fringes—*Cavellia buccinella, Mocella eta, 'Mocella'* n.sp. aff. *maculata, 'Paralaoma'* n.sp. 29, and *'Paralaoma' lateumbilicata.* They are common to abundant in dry bush fringes, and in poor bush patches may be the only native species present. When the litter becomes deeper in these drier zones, and is not disturbed, *Therasiella neozelanica* is added in small numbers, but regardless of litter depth it drops out in response to any disturbance by stock trampling. If bush is cut, and one isolated big tree is left standing, the first five species will persist so long as stock do not trample the litter. Evidently they have high dispersal capabilities, and are the first colonisers of regenerating bush after fire or clearing. In good bush, it must be emphasised, they will occur in wet litter. *Cavellia buccinella* was present, and both *Mocella eta* and *'M.'* n.sp. aff. *maculata* were common, in the Jones Bush mamaku piles. These species seem to be generalists, common in and tolerant of dry conditions.

Moderately damp to wet litter generalists are intolerant of forest clearance or trampling. They require pockets of moist litter for survival, but show no clear preferences as to litter type. If the litter is deep, wet but not slimy, stable, and sheltered they will survive and flourish. They are not present in the outer zone of dryness and disturbance. In the generally broadleaf litter of Jones Bush, where habitat spaces for crawling persist until the final stages of decay or compression, species are more globular than those in the relatively compact, smaller-leaved beech litter where flattened shells and small size have adaptive significance. We recognise 13 species in this category, with some spatial separation. *'Paralaoma'* n.sp. 38 is found at the top of the litter, under and on newly fallen leaves. *Laoma leimonias* and *Huonodon pseudoleiodon* generally prefer the middle litter areas with older but still undecomposed leaves. The latter species is found also on the underside of logs or, more rarely, stones. *'Phenacohelix'* n.sp. 1 has been picked from the darkest cavities in well moistened litter. *Laoma* n.sp. aff. *marina* 1, *'Phrixgnathus' conella, 'P.' poecilosticta,* and probably *'P.' moellendorffi* live in large lower cavities or on the ground surface. The distribution of *'P.' moellendorffi* is very patchy; no live material was obtained during this study, and we are not certain that it is correctly associated here. *'Paralaoma'* n.sp. 1 and 8, and probably n.sp. 40, are globular, and *'P.' serratocostata* is pyramidal; all occupy the area of fine grain decomposition near the litter base. *Laoma marina*, collected by Hazelwood and Roscoe in 1977 but not found in our survey of Jones Bush, is a ground surface dweller also. The occurrence of these 13 species is not linked, either ecologically or geographically, so far as we can detect from the limited records. Of the 11 species taken in the 1981 survey, all but the rare *'Phrixgnathus' moellendorffi* were found in the upper mamaku samples, 7 were found in the lower mamaku pile, 6 in puriri, and 5 in rimu litter. In the other bush patches (and including *Laoma marina* and *'Paralaoma'* n.sp. 40 in these proportions), Harvey's Bush had 10 of 13 species, Crispe's had 8, Limestone Downs and Awhitu Gully had 6, and even the less heavily sampled Track Gully fragment had 5 species. We could detect no pattern to the absences.

Moderate wetness is necessary for all the above, but the quality of the available air space rather than the botanic origin of the litter seems to be most important. Further study is needed to determine limiting factors and actual specialisations of these 13 inhabitants of moderately damp litter.

A more specialised group—*Cytora cytora, C. torquilla. Therasiella serrata,* and *T.* n.sp. aff. *neozelanica*—live in friable, broken-down litter that is deeper, well drained, and loamy. They are found most often next to the soil surface. In form they are pyramidal or tall-spired, and all have periostracal projections from the shell periphery. All four species are patchy in geographical and local distribution. All but *Therasiella serrata* were taken in the upper mamaku sample; only the *Therasiella* spp. were in the rimu.

Wet, but not permanently soaked, well drained situations are the preferred habitat of *Liarea hochstetteri carinella.* It is often patchily abundant in relatively thin litter, although it may also be plentiful in mamaku piles.

Slimy interfaces in the wettest litter are the moistest identified niche. *Fectola mira* is found between closely appressed slimy surfaces of, for example, nikau boles. *'Laoma' mariae* will be on the ground under slimy decomposed logs in small cavities. It seems to prefer one surface clear, one slimy, whereas *F. mira* 'wallows in slime'. *'Charopa'* n.sp. aff. *pseudanguicula* has been taken with *Fectola mira* in slime (one specimen in Jones Bush) and closely resembles it in size, colour, and sculpture prominence and contours, but was most abundant on tree trunks (nine specimens in Jones Bush). This serves to emphasise the nature of these niche categories as snail preferences, not exclusive habitats.

Three species with currently patchy geographic distributions appear to be highly sensitive to litter disturbance. *Omphalorissa purchasi* is occasionally superabundant, often arboreal, in neither the driest nor wettest litter, and its absence is a clear sign of disturbance during European habitation of New Zealand. *'Charopa' fuscosa,* near or at its southern range limit in Jones Bush, ranges northward to central Northland, but is quite patchy in distribution, is locally habitat restrictive or rare, and may be limited by disturbance. Its preferred habitat seems to be under compressed broadleaf litter. *'Allodiscus' urquharti* is in very deep, friable, particulate litter, and appears to be comparatively sporadic in occurrence and sensitive to disturbance. The reason for these three species being more sensitive to disturbance than members of the preceeding categories is unknown.

Life under logs or in deep, sticky mamaku piles offers another set of space, texture, and moisture retention parameters. Seven of the Jones Bush species seem to be associated with this habitat. *Therasiella celinde* and *Fectola infecta* rest attached to the undersurface of sticks and logs. *'Thalassohelix' ziczac* and *Suteria ide* are found in microcavities in the ground under logs or in jumbled branch or twig litter. *Allodiscus* n.sp. aff. *granum* lives in cavities near the base of large litter piles or logs. *Geminoropa cookiana* is in the basal grit and loam next to the ground. *Flammulina chiron,* in other areas, has been observed in such piles and on the undersurface of logs. Jones Bush is relatively poor in log-associated species, since this habitat is very rare. Other Manukau Peninsula species such as *'Charopa' ochra* (friable deep litter near logs), *Charopa coma* (large logs or rocks), *'Charopa' costulata* (new logs), *Allodiscus dimorphus* and *A. tessellatus* (logs), and *A. planulatus* (rotten logs) may be absent today from Jones Bush, or so rare as to escape our sampling, because of the absence of suitable niches.

Three relatively large carnivorous species show different space preferences. *Rhytida greenwoodi,* the largest native snail in Jones Bush, prefers well drained slopes in deep litter. Elsewhere it is commonly associated with litter-filled rock ledges. The comparatively small *Delos coresia* lives in the active decay zone of large mamaku fronds, or under the cover of 3-5-cm leaves. *Delos jeffreysiana* prefers larger (10 cm) leaves, logs, or nikau boles for shelter. All three will forage extensively from these preferred shelter sites.

The transition from ground to arboreal habitat is gradual. Species such as *Phenacohelix giveni* are found commonly on the tops of logs or on very young fern shoots low to the ground. This habit is more common elsewhere than in Jones Bush, where *P. giveni* was rare. *'Charopa' pilsbryi* and *'C.' pseudanguicula* shelter under the curled edges of bark on the trunks of trees such as live rimu or recently dead *Coprosma*, or under the edge of decay spots on any tree trunk. *'Charopa' chrysaugeia, Fectola unindentata, 'Phrixgnathus' ariel, 'Phrixgnathus' elaiodes, 'Charopa'* n.sp. aff. *pseudanguicula*, and *Flammulina perdita* are commonly found crawling on tree trunks, vines, and saplings. Their dry-period shelter sites are unknown.

Flammulina perdita has been taken on the surface of broad leaves. Small twigs and broad leaves are the main habitat in wet periods for *Lamellidea novoseelandica* and *'Phrixgnathus' erigone*. In drier periods they will retreat to litter layers, often on to browned but not yet decayed leaves. Both species are found on the underside of leaves on saplings, and on the underside of supplejack (*Ripogonum scandens* J.R. et G. Forst.) vines. *Serpho kivi* adults are collected almost exclusively on the undersurface of large leaves; juveniles can be found on tree trunks and branches. *Athoracophorus bitentaculatus* forages on leaf surfaces, but shelters in the slime-filled axils of monocots. Suspended litter in tree crotches or the base of leaf axils is the resting niche of *'Phrixgnathus'* n.sp. 59 and *Huonodon hectori*.

'Paralaoma' n.sp. aff. 33, represented by a single dead shell in the upper mamaku litter, has never been collected alive, and its niche is unknown. *Phenacohelix pilula*, represented by one dead shell in the rimu litter, is elsewhere associated with grasses and other monocots on drier banks or more open, dry forest areas. It is not a tramp species, and not disturbance-sensitive, but prefers more open bush and coastal exposures. It thus cannot be associated with the generalist species of moderately wet to wet litter.

A summary of these preferences is given in Fig. 2. No attempt has been made to indicate habitat *range*, only basic space and moisture preference. That range is quite different is shown by taxa such as *'Charopa' chrysaugeia, C.* n.sp. aff. *pseudanguicula*, and *'Laoma' mariae*, all of which were hand-picked from tree trunks and leaves 1–2 m above ground in broadleaf uplands and also found in nikau slime by the stream. *Suteria ide* was represented by a live arboreal juvenile and a live adult from the lower mamaku sample.

Such samples taken shortly after light rain will include a mixture of shelter and foraging spaces. Since habitat parameters are at present undefined for all species, this first approximation of space and moisture preferences is liable to substantial modification by future studies. Nevertheless, it does suggest that the land snails of Jones Bush, although capable of inhabiting a range of litter types, do show specialisation as regards the quality of space and moisture selected for their primary abode. They differ considerablv in tolerance of dryness and disturbance.

Vertical texture and space preferences within a litter pile will probably be shown to be critical to an understanding of species niches, i.e., the way in which species partition the pile. Currently we can offer not a bit of hard data on niche specialisation, only the preference estimates outlined above and summarised in Fig. 2. Complicating factors in any study will be the comparatively small number of specimens in any given sample and the difficulty of finding living specimens of most species. We consider it useless to comment now on the varying pattern of species numbers observed; data on seasonal abundance and reproductive cycle are first required for at least a few species.

Questions of size, shape, and sculpture differences relating to these habitats will be discussed elsewhere (Solem & Climo, in prep.).

FAUNISTIC SUMMARY

The 1981 samples reported on here, and the 1977 litter sample from Jones Bush, contained a total of 84 species of land snail. We record a further three species collected on the Manukau Peninsula by Norman Douglas but not found by us, and another two whose ranges suggest that they could occur on the Peninsula, but that have not yet been recorded there.

Of the 87 recorded species, *Cionella lubrica, Oxychilus cellarius, Helix aspersa*, and *Vallonia* spp. are accidental imports from Europe that are ubiquitous pests in New Zealand gardens. *Paryphanta busbyi* is native to Northland, and may have been introduced to the Manukau early in this century by the Rev. Webster, a pioneer conchologist and naturalist. Its nearest natural population is at Warkworth, 88 km north of the Manukau Straits. This

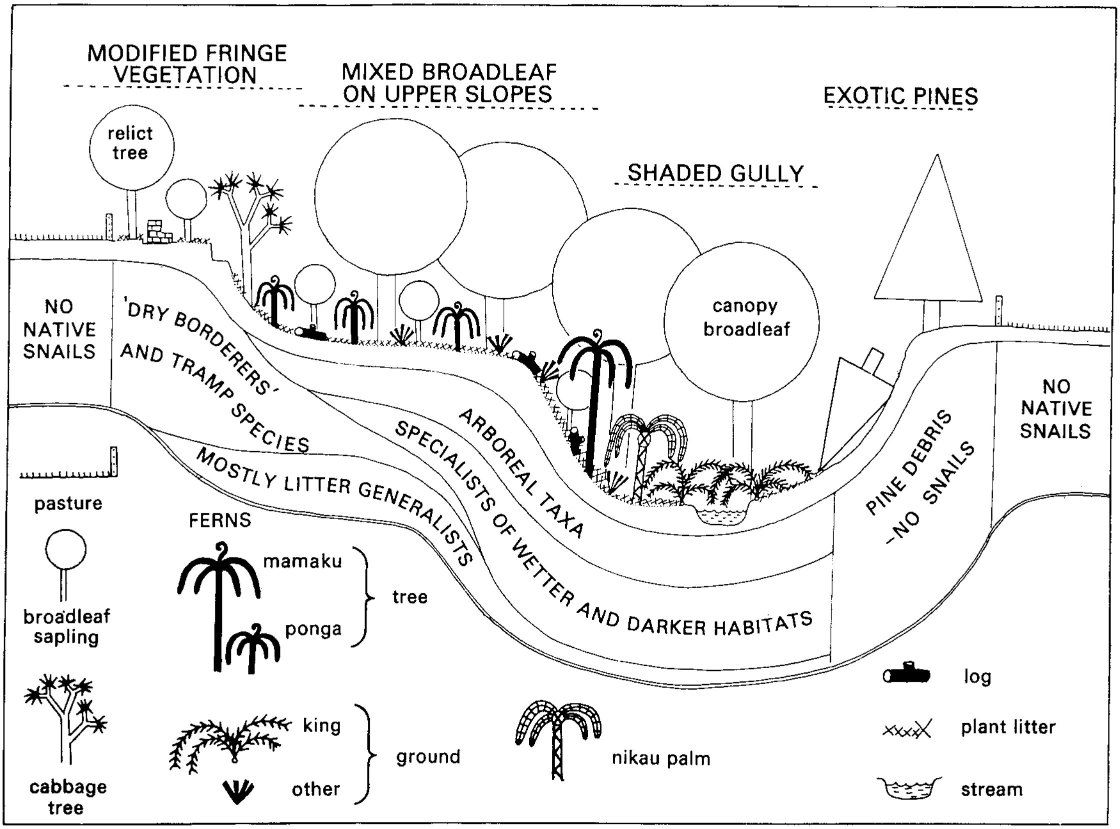

Fig. 2. Schematic representation of land snail space and moisture preferences in Jones Bush, Manukau Peninsula. Species components were identified as follows.

Fringe tramps. INTRODUCED – *Cionella lubrica, Oxychilus cellarius, Helix aspersa, Vallonia* sp. NATIVE – *Cavellia buccinella, Mocella eta, 'M.'* n.sp. aff. *maculata, 'Paralaoma'* n.sp. 29, *'P.' lateumbilicata, Therasiella neozelanica* (only if undisturbed).

Dry clearings. *Phenacohelix pilula.*

Medium to wet litter. GENERALISTS: in newly fallen leaves – *'Paralaoma'* n.sp. 38; in older fallen leaves – *Laoma leimonias, Huonodon pseudoleiodon*; in cavities in litter – *'Phrixgnathus'* n.sp., *'P.' conella, 'P.' poecilosticta, 'P.' moellendorffi, Laoma marina, L.* n.sp. aff. *marina* 1 (all in larger, lower cavities near ground surface or on it); in area of fine-grain decomposition near litter base – *'Paraloama'* n.sp. 1, *'P.'* n.sp. 8, *'P.'* n.sp. 40, *'P.' serratocostata*; in friable, broken-down litter, well drained conditions – *Cytora cytora, C. torquilla, Therasiella serrata, T.* n.sp. aff. *neozelanica, 'Allodiscus' urquharti, Omphalorissa purchasi* in undisturbed areas. WETTER, WELL DRAINED LITTER: *Liarea hochstetteri carinella.* UNDISTURBED COMPRESSED BROADLEAF: *'Charopa' fuscosa.* LOG-ASSOCIATED: undersurface of logs – *Fectola, Therasiella celinde, Flammulina chiron*; on ground under logs – *'Thalassohelix' ziczac, Suteria ide*; in heavy litter by logs or under logs – *Allodiscus* n.sp aff. *granum, Geminoropa cookiana* in loam and grit next to ground. SLIMY INTERFACES: both surfaces, *Fectola mira*; one surface clear, *'Laoma' mariae*; *'Charopa'* n.sp. aff. *pseudanguicula* (also arboreal).

Carnivores. Deep, well drained litter – *Rhytida greenwoodi*; decay zone of mamaku or medium-sized leaves – *Delos coresia*; logs, nikau, or large leaf decay zone – *D. jeffreysiana.*

Arboreal. Tree trunks, vines, saplings – *'Charopa' chrysaugeia, 'C.'* n.sp. aff. *pseudanguicula* (also slimy surfaces), *Fectola unidentata, 'Phrixgnathus' ariel, 'P.' elaiodes, Flammulina perdita* (also leaves), juveniles of *Serpho kivi*; on leaves – *Lamellidea novoseelandica, 'Phrixgnathus' erigone,* adults of *Serpho kivi, Flammulina perdita* (also trunks), *Athoracophorus bitentaculatus* forages here; 'suspended litter' in leaf axils, tree forks – *Huonodon hectori, 'Phrixgnathus'* n.sp. 59, *Athoracophorus bitentaculatus* shelters here; under bark curls on trunks or in decay spots on trunks – *'Charopa' pilsbryi, 'C.' pseudanguicula*; on log tops or young ferns – *Phenacohelix giveni.*

leaves 82 native species whose distributions seem to be the result of primarily natural causes.

Sixty-six (80.5%) of these have distributions that extend considerably north and south of the Manukau Peninsula. Their presence in any given patch of bush requires no gross distributional explanation; local habitat and disturbance criteria must be considered. Sixteen species (19.5%) reach a known limit of distribution within the area of our survey, in one of three different patterns. Eight species (9.8%) reach their known southern range limit. They are:

Cytora pallida
'Charopa' fuscosa
'Phenacohelix' n.sp. 1
Therasiella serrata
Laoma n.sp. aff. *marina* 1
Phrixgnathus' glabriusculus
'Paralaoma' francesci
Egestula egesta

Seven species (8.5%) reach their known northern range limit. They are:

'Charopa' ochra
Allodiscus n.sp. aff. *granum*
Geminoropa cookiana
Therasiella n.sp. aff. *neozelanica*
'Phrixgnathus' poecilosticta
'P.' levis
'P.' n.sp. 61

One species (1.2%), *Schizoglossa worthyae*, reaches its known western range limit at Crispe's Bush.

More detailed information on the distribution of those species that reach a known range limit in or near the area is given in Appendix 1, together with habitat preference notes for all 89 species, insofar as such data could be provided.

In our 1981 collecting (Appendix 3) we obtained 4502 specimens of 82 species plus 31 specimens of introduced slugs that are not considered further in this analysis. An additional five species were taken, either in the 1977 Jones Bush litter sample (*'Paralaoma'* n.sp. 40, *Cavellia roseveari*) or in earlier years by Norman Douglas (*Cavellia roseveari, Egestula egesta, Paryphanta busbyi, 'Phrixgnathus'* n.sp. 55), but not by us in 1981. All the Jones Bush material has been included in Appendix 3A.

Of the 82 species we collected, living examples were obtained of 64 (78.0%). For the 18 species not found living, 11 were taken at only a single station and are represented by 1-3 examples; 4 species were found at 2–4 stations, but only 1–5 specimens at each; 12 dead specimens of *Cytora pallida* were found at Harvey's Bush; *'Phrixgnatus' moellendorffi* was sparse (1–3 examples) at three stations but common (17 specimens) at Track Gully; and only *'Paralaoma' serratocostata* was abundant (7–25 dead specimens), at 3 stations. If our assumption of brief persistence for dead shells in moist litter is correct, then all the species should be alive on the Manukau Peninsula at the present time. Single live specimens were taken of only two species, the native slug *Athoracophorus bitentaculatus* and the log-dwelling charopid *Allodiscus dimorphus.*

Numbers of the most abundantly represented species, *Omphalorissa purchasi* and *Fectola unidentata,* were heavily skewed by chance sampling of local nodes of temporary abundance. That such local population increases occur occasionally is common knowledge among the snail-conscious, although not documented in the literature for New Zealand.

Since Jones Bush is the least undisturbed of the sampled patches, was most intensively studied, and lies furthest from all three hypothetical source areas, we use this patch as a potential standard of comparison. We record 60 species of land snail from Jones Bush (Appendix 3A). Of the 57 species collected in 1981, 45 (78.9%) were taken alive and 55 (96.5%) were represented by dead shells. Three of the 60 species—*Cionella lubrica, Oxychilus cellarius,* and *Helix aspersa*—are introductions from Europe. The remaining 57 species are New Zealand endemics, which is a remarkable number of land snail species to pack into one small patch of bush, considering that in most areas of the world 5–10 species is the typical diversity level.

We do not consider that 57 native species is the actual or potential maximum land snail diversity level for Jones Bush.

POTENTIAL ADDITIONS TO FAUNAL LIST

There are 29 land snail species that were not taken in Jones Bush but that are, or could be, recorded from the Manukau Peninsula. Six of these can be dismissed as potential current inhabitants of Jones Bush because of geographic factors. *Schizoglossa worthyae* reaches its western limit of distribution at Crispe's Bush; *Cytora pallida, 'Phrixgnathus' glabriusculus,* and *Egestula egesta* reach their current southern limit of distribution with their trans-Manukau Straits colonisation from the Waitakere Range to the northern tip of the Manukau Peninsula; and *'Phrixgnathus' levis* and *'Phrixgnathus'* n.sp. 61 reach their northern limit on the limestones just south of Port Waikato. The destruction of most lowland bush and establishment of extensive pastureland barriers among the remnants will probably prevent natural range extension by these species in the foreseeable future.

Liarea egea egea, Charopa coma, and *Otoconcha dimidiata* may be slow dispersalists that did not reach the area of Jones Bush, and now probably never will by natural means. *Liarea egea egea* is recorded here from Limestone Downs, places on the northern tip of Manukau Peninsula, and the Bombay Hills. Records of *L. egea* and *L. hochstetteri* in sympatry exist, so exclusion is not a likely explanation. The virtual absence of the very widespread and common *Charopa coma* from our sampling area is very surprising. The single specimen taken in Harvey's Bush is the first Manukau Peninsula record, and we interpret the absence of this species as the result of slow natural dispersal. *Otoconcha dimidiata* is conspicuous by its absence. It was common in the Waitakere Range, and still is in Titirangi Beach Reserve, on the northern side of Manukau Harbour; is quite common in the central North Island limestone areas; and has been reported as far north as Whangarei. Why the Manukau Peninsula remains a gap in its wide distribution is a mystery to us.

Lack of appropriate habitat is the most probable explanation for the absence of *'Mocella'* n.sp. aff. *manawatawhia* and *Paralaoma caputspinulae*, which prefer dry coastal slopes, and of *Obanella rimutaka*, which prefers limestone crags or exposed ridge areas. Neither habitat is represented in Jones Bush.

Paryphanta busbyi purportedly was introduced into two areas of the central Manukau Peninsula many years ago, but does not seem to have spread significantly, and so would not be expected in Jones Bush.

There are thus 16 additional species that we can identify as possible additions to the Jones Bush land snail fauna. Inevitably the introduced *Vallonia* spp. will be found on disturbed roadside or grassy fringes. We did not look for them.

Drier podocarp litter or more open areas could be expected to yield *Cytora hedleyi, Therasia decidua, Phenacohelix ponsonbyi, Pasmaditta jungermanniae, 'Phrixgnathus'* n.sp. 55, *'Paralaoma'* n.sp. 33, and possibly *'Paralaoma' francesci*. The type locality "Waiuku" for *'P.' francesci* may not be accurate. All NMNZ records of *'P.' francesci* are from Northland, except for the type series and the single specimen from Harvey's Bush recorded here. This could be another example of a species at its southern range limit on the tip of the Manukau Peninsula.

Both *'Flammulina' feredayi* and *Therasiella tamora* should be sought on the ground under deep, wet litter piles. The niche of *'Phrixgnathus' pirongiaensis* is unknown; from shell morphology we would expect to find it too in deep, wet litter, but probably living above ground level in decomposed materials.

This leaves another five charopid species that are associated with logs to varying degrees. *'Charopa' costulata* and *'Charopa' ochra* prefer powdery or friable deep litter near logs. *Allodiscus dimorphus, A. tessellatus*, and *A. planulatus* are commonly associated with rotten logs or the ground surface under them. The first two *Allodiscus* are recorded from bush patches on either side of Jones Bush, and thus clearly could be present. The other three species are not widely recorded in the Manukau area, but have wide general ranges, and thus cannot be recorded as probable inhabitants of Jones Bush with the same confidence. The rarity or absence of these species may be due to local extinction after milling of large trees before 1900 broke the cycle of windthrow and slow decay. Certainly the paucity to absence of the large-log habitat in the bush patches investigated makes survival of log-associated species less likely, unless they shift to alternative niches.

To summarise the above observations, 9 of the 29 species not taken in Jones Bush are probably absent for reasons of geography or hypothetical slow dispersal; 3 are absent because their habitat is lacking; and 1 is a limited introduction to another part of the Peninsula. Fringes or drier podocarp areas could shelter another 7 or 8 species; 3 should be looked for in wetter litter; and 5 log-associated species may be affected by the destruction of the large-log habitat on the Manukau Peninsula.

We would anticipate another 10 or 11 litter species and at least 2 of the 5 large-log species (*Allodiscus dimorphus* and *A. tessellatus*) to be actually or potentially present in Jones Bush. This would bring the total land snail fauna, exclusive of introduced slugs, to 72 and possibly even 76 species, of which only 4 are introduced exotics.

We can propose no reasons why these species could not coexist successfully with those already recorded from Jones Bush. Thus, a lowland bush 'climax community' of land snails in this area of New Zealand is postulated as consisting of up to 72 native species, without adding species of limited range, coastal habitat, or slow dispersal.

The comparatively small numbers of individuals found for many species, the presence of three additional 'low-incidence' species in the 1977 litter sample, and experience with other bush patches strongly suggest that several of these species are present in Jones Bush but have yet to be collected. Sampling in other seasons, particularly hand-picking during snail activity periods, could be expected to extend the fauna list over the 60 that we recorded.

Investigations of the other bush patches were less extensive, and signs of disturbance, either current or comparatively recent, were clear. The number of species recorded from each (Table 2) is smaller, and there are minor differences in species lists that relate to geographic, topographic, and disturbance factors. The following comments are comparative and analytic as to differences.

Crispe's Bush had 40 species (Appendix 3B) with the large carnivorous slug *Schizoglossa worthyae* the most obvious addition from the Bombay Hills – Hunua Range source area. Other added species are drier slope and podocarp litter taxa (*Cytora hedleyi*, *'Mocella'* n.sp. aff. *manawatawhia*, *Phenacohelix ponsonbyi*, *Pasmaditta jungermanniae*) reflecting the gentler topography and large rimu trees on the upper edges, a ridge-dwelling species (*Obanella rimutaka*), a deep litter dweller (*'Flammulina' feredayi*), and two log-associated snails (*Allodiscus tessellatus*, *A. planulatus*). Most of these could occur in Jones Bush, and indeed some 40 species were found in both patches. Twenty species found in Jones Bush were not taken in Crispe's Bush. Of these, 7 were collected only in Jones Bush; 8 occur mostly in very small numbers, and could easily have been missed by our sampling procedures; the appropriate niches for athoracophorid slugs in Crispe's Bush were not carefully checked; and the introduced species *Cionella lubrica* and *Helix aspersa* would be on the fringes. The only clearly significant deletions are *Omphalorissa purchasi*, a highly sensitive indicator of disturbed bush, and *Laoma leimonias*, a species that was abundant in the better bush patches (Jones, Harvey's, Awhitu Gully) but absent from the scruffy Track Gully and barely represented (one dead shell) in the Limestone Downs bush fragment. It may be that *L. leimonias* too can serve as an indicator of litter disturbance.

Crispe's Bush is regenerating quite well, and none of the absent species would seem to be incapable of current residence. The protection against trampling by stock, gentler topography with more extensive dry fringes, and potential large log recruits from the many upland rimu trees make Crispe's Bush a potentially highly significant reservoir for native land snail species.

Sampling in Harvey's Bush resulted in a list of 44 species (Table 2, Appendix 3C). Additional species not present in Jones Bush include the ridge species *Obanella rimutaka*, four over-water migrants from the Waitakere Range that have not gone further south (*Cytora pallida*, *Charopa coma*, *'Phrixgnathus' glabriusculus*, and possibly *'Paralaoma' francesci*), plus three species that should be found in Jones Bush (*Cytora hedleyi*, *'Charopa' ochra*, *Phenacohelix ponsonbyi*). In addition, *Liarea egea egea* is substituted for *L. hochstetteri carinella*. Other apparent changes in the snail fauna of Harvey's Bush seem to be topographically associated, either directly or as a sampling artefact. The sheer slope of Harvey's Bush means that there is practically no dry upper fringe. Thus, the absence of *Therasiella* n.sp. aff. *neozelanica* and the European imports plus the great reduction in abundance of *Cavellia buccinella* (two dead shells) is understandable. Decrease in numbers of arboreal shells in the samples may be artefact. The sheer slopes might result in dead shells of arboreal species being washed down into the stream rather than accumulating in litter as they do on shallower slopes. The absence or reduced abundance of log-associated and deep litter species may be attributable to the same factors. The near absence of the disturbance-sensitive *Omphalorissa purchasi* (two dead shells) is significant. Openness to stock and 'cliff face' contours together probably account for most of the changes. Harvey's Bush is a good snail refugium, but is showing signs of degeneration due to trampling by stock.

Awhitu Gully was sampled because of its kauri stands. The pure kauri litter proved to be depauperate (15 species) relative to the mixed forest gully litter (28 species) (Appendix 3D). The only additions in the kauri litter to those listed from Harvey's Bush are *Therasiella tamora* and *'Phrixgnathus' pirongiaensis*. Other species in mixed forest litter are the dry-zone species *'Mocella'* n.sp. aff. *manawatawhia* and *Therasiella* n.sp. aff. *neozelanica*; two deep-litter *'Paralaoma'* (n.sp. 1 and n.sp. 33); and the log-associated *Allodiscus dimorphus* and *A. tessellatus*. The change in topography from cliff to rolling country is ample explanation for these additions.

Track Gully is a degraded remnant, exposed to Manukau Harbour winds and direct insolation. Only 25 species were found. In comparison with Harvey's Bush, 300 m away, two species of dry, open areas (*Therasia decidua*, *Phenacohelix pilula*), three leaf axil-associated arboreal taxa (*Huonodon hectori*, *'Phrixgnathus'* n.sp. 59, *'Paralaoma'* n.sp. 38), and a tree trunk form (*Flammulina perdita*) were added. The other 19 species were shared with Harvey's Bush. Absences are obvious indicators of disturbance (*Omphalorissa purchasi*, *Laoma leimonias*), dryness, and the absence of deep, wet litter and log habitats (*'Charopa'*, *Allodiscus*, *'Laoma'*, most *'Paralaoma'*). The richness of the New Zealand land snail fauna is such that a list of only 25 species is considered depauperate.

Limestone Downs was visited in order to sample the fringe of the limestone fauna south of the Waikato River. The 36 species collected include 10 that were not taken at Jones Bush. The ranges of *Liarea egea egea*, *Charopa coma*, and *'Phrixgnathus' levis* do not extend to Jones Bush. The inhabitant of dry litter *Phenacohelix ponsonbyi* and the litter species *'Charopa' costulata* and *Therasiella tamora* are likely to occur there. *Vallonia* sp. lives on the fringes of Jones Bush. Lack of suitable habitat excludes the ridge-preferring *Obanella rimutaka* and the dry-zone or coastal species *Paralaoma caputspinulae* and *'Mocella'* n.sp. aff. *manawatawhia*. There are undoubtedly richer bush patches south of the area sampled, but this patch did serve to delineate some range limits and provide a modest contrast to Jones Bush.

In summary, the additional species at other localities relative to Jones Bush can be accounted for as follows: range limitation of more southern species; chance collection of rare species; and proportional increase in area of dry fringe habitat sampled. The absence of species that are found at Jones Bush and are not excluded because of range limitation is probably due to several factors, the most likely being destruction and disturbance of litter by stock, restricted extent or absence of certain habitats, and the different type of litter accumulation and packing on a steep slope relative to more gentle topography.

Each bush patch has its own proportional representation of the South Auckland snail fauna; the variations are indicative of local topography, recentness and degree of disturbance, and proximity to one of the three colonisation source areas. In terms of species composition, and ignoring range limit taxa, all these bush patches originally *represented* lowland bush of which the snail faunas had the potentional of approaching the species diversity documented for Jones Bush. The Track Gully patch is too degraded and exposed and the Limestone Downs one too small and pasture-bound to have much chance of reaching high levels of diversity. The Awhitu Gully patch should have had a larger species list than we obtained. Possibly the degree of disturbance early in this century was greater than we realise, and the snail fauna has not recovered from significant extinctions.

Harvey's Bush is an excellent patch that should be protected by fencing against degeneration caused by inroads of stock. Its maximum potential land snail fauna will remain below that of Jones Bush, because the steep slopes limit dry areas, deep litter, and log habitats. It represents a southern range limit for several taxa, and is thus a biogeographic landmark.

Crispe's Bush is well on its way to full regeneration. Its size and topography suggest a capability for eventually equalling, if not exceeding, Jones Bush in total land snail diversity. It should continue to receive protection. Natural tree falls should be allowed to occur, and the logs be permitted to decay.

Because these patches of bush are now effectively isolated by comparatively vast tracts of pasture and farmlands uninhabitable by native snails, natural recolonisation is far less probable than it would have been before European settlement. A carefully planned programme of selective restocking should be considered. For example, placing small numbers of *Omphalorissa purchasi* and *Laoma leimonias* in a single place in Crispe's Bush would simply restore a natural component to the fauna. At the same time this would permit the spread of each species through the bush to be easily monitored by a local naturalist, and provide valuable experience of the restocking potential of land snails.

SYMPATRIC DIVERSITY LEVELS ELSEWHERE IN NEW ZEALAND

An obvious and significant question is whether the 72 essentially sympatric species potentially present in Jones Bush represent an unusually high diversity by New Zealand standards. We lack strictly comparable data for most areas, and must rely on general impressions and partial data in presenting a hypothesis. We are doing so in hopes of stimulating the detailed local work that will be necessary to test it.

From Auckland northward there appears to be a gradual reduction in the number of land snail species, although we cannot state whether this is gradually clinal or with clear steps of diminishing diversity. While equally favourable bush patches just north of Auckland may have the potential for diversity equivalent to that seen in Jones Bush, the numbers would decrease by deletion, despite the entrance of some species belonging to a specialised Northland fauna, until a maximum of about 30–35 sympatric species is reached at the level of Kaitaia (L. Price, pers. comm.).

We have direct evidence of equivalent diversity in the central North Island. Appendix 3F lists the snails recovered from four bags of litter taken by us from limestone cliffs and a cave 8 km southwest of Waitomo Caves, at the Mahoe road junction. The samples were from:

(1) compacted yellow dry dirt 4 m inside a cave mouth that contained clearly subfossil to fossil material;

(2) under ground ferns and broadleaf litter in bush margin at right side of cave entrance;

(3) behind large rock at top of talus leading into the cave, from black dirt litter on cave side of rock;

(4) black loam in tree root crevices on top of the same rock, which was about 1 m high, with a tree growing out of it.

Samples 2–4 were taken from spots within an area of about 3×5 m. Since the dry sample came from about 4 m into the cave, less than 7 m separated the most distant samples.

Of the 65 species obtained (marked 'wa' in Appendix 1 and 2), 22 were not collected on the Manukau Peninsula. The other 43 (66.2%) were taken in the Manukau survey, and 35 of these were in Jones Bush itself. Despite the individual samples' close proximity, species counts ranged from 36 to 50. Most of the differences would be accounted for by relatively rare taxa; 22 species were represented by only 1–3 specimens in all.

A few species deserve special comment. *Allodiscus tullia* and *Suteria raricostata* have only been found dead in cave deposits in this area of New Zealand. They now seem to be alive only in forest situations of higher elevation, or further south. Their restriction to the cave material is probably an accurate indication that they were living there, but are now locally extinct. *'Geminoropa' moussoni* may be more recently extinct locally, as dead specimens occur in many litter samples, but its status is uncertain. There are a few obvious allopatric species pairs in the Manukau and Waitomo areas. Thus, *Schizoglossa worthyae*, *'Mocella'* n.sp. aff. *maculata*, *Allodiscus tessellatus*, and *Laoma* n.sp. aff. *marina* 1 on the Manukau are replaced by closely related, allopatric taxa at Waitomo.

A litter sample collected by Bruce Hazelwood from Stubb's Farm, Waitomo, that was taken within a few hundred metres of our station and contained 58 species (catalogued as NMNZ 61488–61545) provides an extensive list of species additions; taxa not taken in the Manukau are indicated by an asterisk:

Rhytida greenwoodi
*'*Charopa*' titirangiensis*
*'*Charopa*' montivaga*
**Cavellia anguicula*
'Thalassohelix' ziczac
Therasiella celinde
'Phrixgnathus' moellendorffi
'P.' n.sp. 59
Pasmaditta jungermanniae
*'*Paralaoma*'* n.sp. 5
'P.' lateumbilicata
P. caputspinulae
Cionella lubrica
Vallonia sp.

Combining these would result in a sympatric fauna of 80 species—4 introduced, 3 native but probably locally extinct, and 73 native and extant. The proportion of taxa represented in the Manukau Peninsula remains the same. Thus, the limestone area at least equals the Manukau Peninsula in land snail diversity, and probably surpasses it.

In the Wellington area Frank Climo has collected a total of 53 land snail species. These are indicated by 'wc' in Appendix 1 and 2. The maximum number taken sympatrically to date is 33, from a patch of bush near Days Bay. Expansion of sampling coverage eastward to other limestone areas would have increased the number of central North Island species slightly, but would not have changed the overall pattern that emerges.

Of the 53 species from Wellington, 23 (43.4%) were taken on the Manukau and 7 (13.2%) were found at Waitomo. Of the remaining 23 species, *Cavellia brouni*, *Ptychodon wairarapa*, and *Huonodon microundulata* are widely distributed in the southern North Island and South Island. The remaining 20 species are widely distributed southern North Island taxa. There are no endemic species near Wellington.

The late Pleistocene topography of the Wellington area was virtually an unstable talus of periglacial solifluction debris, with only the sea coast fringes heavily vegetated, so the fauna now present has had to disperse and accumulate mainly from the local coastal forest refugium in a period of perhaps 10 000 years. In addition rocky, elevated topography, greater frequency of dry spells, and probable high degree of bush disturbance combine to reduce the moisture and stability quality of snail habitat. The reduced diversity probably results from historical factors, periglaciation, poor water-retaining qualities of the thin soils overlying Mesozoic rocks, and disturbance by man.

The Nelson area is recognised as a refugium, and many of the land snail species are endemic, yet maximum known diversity is only 38 species in a bush patch in Aniseed Valley. We suspect that the hard rock substrate, rugged topography favouring run-off rather than water accumulation, periodic dry spells, and Pleistocene vegetation changes have had a cumulative effect. There is also evidence that southern beech may be a less favourable habitat for land snails than broadleaf forest. Beech leaves are small and hard, and they lie like shingles on a roof when piling into litter. In contrast, the softer broad leaves will curl or crinkle in the litter, providing crannies and crevices during much of the decomposition process. This additional air space for movement, as well as the greater moisture retention potential of curled broadleaf litter, could be a key difference in explaining the greater diversity of the North Island's broadleaf-associated snail fauna.

South of Nelson, the alpine barrier chain has a rain shadow effect. The drier eastern slopes and considerably drier Canterbury Plains with marked seasonality of rainfall, the very young age of the post-Pleistocene alluvial east coast plains, decreasing temperature, and the dominance of beech forest on the mountains combine to restrict areas of high land snail diversity to isolated geographic pockets. Even here, with marked pocket endemism, sympatric diversity of 15–20 species is rarely exceeded. This information is mainly from alpine pockets east of the Main Divide; the situation in the much wetter west coast habitats is unknown at present. What little we know derives from spot collecting, rather than litter sampling, and this in only comparatively few areas. The few available collections are not rich in species, and give an impression of a relatively acidic environment that is inhospitable to land snails.

Stewart Island has been better investigated, but the maximum sympatric species diversity recorded (at Halfmoon Bay) is only 15. Auckland Island, which still has a forest providing moisture retention, appears to have perhaps five sympatric species. Campbell Island, which is without forest, also has five sympatric species.

Southward from the central North Island, then, there is a clear and quite precipitous decline in sympatric land snail diversity which is much more marked than the decline from Auckland to North Cape. Determining this trend from published faunal lists is quite difficult, since few collections have been made in such a way as to reveal actual sympatry, and most reports on local faunas fail to indicate species associations. There is thus an urgent need for sampling of single bush patches over most areas of New Zealand, so that patterns of sympatry can be adequately documented.

We anticipate that there will be a clear correlation between sympatric diversity and the following simple dicta.

(1) Areas with periodic interruption of moisture replenishment to the litter will have reduced diversity relative to areas with a less stressful moisture regime.

(2) Patches in which the spatial quality of the litter is improved by leaves that curl and crinkle will exceed in diversity patches where the litter is composed of hard leaves with little intervening air space.

(3) Areas colonised from refugia in post-Pleistocene times will have less diverse faunas composed of quickly dispersing species.

(4) Exposed, wind-swept areas will have a reduced moisture-loving component, although they may pick up taxa more typical of coastal xerophytes.

(5) Areas of hard rock substrate and rough topography will have depressed faunal levels.

(6) Areas with very high rainfall and an acidic temperate rain forest environment will lack appropriate litter conditions and have a sparse fauna of a few species each at low levels of abundance.

These predictions derive from our collective diverse experiences in many parts of New Zealand and overseas, plus our growing confidence that the two most significant factors for New Zealand land snails are continuity of moisture and quality of space within litter piles.

It is premature to attempt to grade the above predictions in order of importance. After several hundred bush patches from all parts of New Zealand have been sampled, and the results tabulated, quantification should be possible in terms of both overall impact on New Zealand land snail diversity and local effects on particular bush patches. However, we venture to anticipate that the order adopted here will closely approximate the situation for New Zealand as a whole.

The cave area of the north-western central North Island up to Auckland has the highest level of sympatric land snail diversity known from New Zealand, and thus from the world. The fact that this area has been the prime collecting ground for New Zealanders has led to the presumption mentioned in the Introduction about norms of diversity. It is in reality a special area away from which diversity declines. How much of a decline, and in what fashion (cline or step cline), will be revealed by local sampling and comparison of bush patches throughout New Zealand. We invite others to help.

ORIGIN AND MAINTENANCE OF HIGH DENSITY

In the current absence of genealogical hypotheses concerning the species-dominant punctid and charopid radiations, it is not possible to state how closely related to each other are most of the taxa from the Manukau Peninsula. An obvious way in which local diversity can be increased is for isolation to produce allopatric species pairs that become sympatric upon removal of dispersal barriers (if you are a dispersalist biogeographer) or unification of separated areas (if you are a vicariance biogeographer).

For the 85 native species identified as actual or potential inhabitants of the Manukau, it is possible to identify only two such situations: *'Charopa' fuscosa* and *'C.' chrysaugeia* form a pair of closely related species, the former at its southern range limit in Jones Bush and the latter extending from central Northland to the northern fringe of the South Island. They are certainly congeneric and are probably an old allopatric pair. *Laoma marina, L.* n.sp. aff. *marina* 1 (the Northland representative), and *L.* n.sp. aff. *marina* 2 from the Waitomo Caves are a closely linked group with ranges that overlap in the Auckland area. This is probably a younger situation.

The other 81 native species on the Manukau Peninsula show no such one-to-one links. Nearest relationships would be traceable separately to extralimital taxa, and no two to the same immediate progenitor—nor even a clear common 'grandparent' that we can identify from existing knowledge. Some may be discovered in time, as monographs of the punctids (Climo, in prep.) and the charopids are completed, but the relationships will be comparatively remote.

Thus, the picture of high land snail diversity on the Manukau is quite different from classic island speciation explosions. The famous *Drosophila* radiation in Hawaii, that of cryptorhynchid weevils on Rapa (Zimmerman 1938), and the monophyletic radiation of endodontid land snails on Rapa (Solem

Table 6. Proportionate family representation of native land snail species in areas of New Zealand that have been intensively sampled

Bush patch or area (total species)	NUMBERS (AND PERCENT) OF Charopids	Punctids	Others
Jones Bush (57)	28 (49.1)	16 (28.1)	13 (22.8)
Crispe's Bush (48)	27 (56.3)	12 (25.0)	9 (18.7)
Harvey's Bush (44)	19 (43.2)	15 (34.1)	10 (22.7)
Awhitu Gully (32)	17 (53.1)	10 (31.2)	5 (15.7)
Track Gully (24)	12 (50.0)	9 (37.5)	4 (16.5)
Limestone Downs (32)	15 (46.9)	11 (34.4)	6 (18.7)
Near Waitomo (63)	36 (57.1)	22 (34.9)	5 (8.0)
Wellington area (53)	34 (64.2)	15 (28.3)	4 (7.5)
Days Bay, Wellington (33)	24 (72.7)	7 (21.2)	2 (6.1)
Aniseed Valley, Nelson (38)	23 (60.5)	12 (31.6)	3 (7.9)
Halfmoon Bay, Stewart I. (15)	6 (40.0)	8 (53.3)	1 (6.7)

1976) that produced 5 genera, 17 species, and 24 geographic races, with a maximum of 9 sympatric species, show many indications of phylogenetic adolescence. Linkages are clear, and species gaps are small—missing links just aren't missing.

In contrast, the Pacific Island Achatinellidae (Cooke & Kondo 1960, p. 40) show a ". . . lack of cohesion between the subfamilies . . . One is forced to the conclusion that the family is an ancient one, having lost a great many intermediate members in its evolution. Thus, no 'family tree' can possibly be constructed to show the relative positions of the subfamilies to each other." Subsequently, cladistic analysis techniques could challenge this conclusion, although determining polarity and direction of character change in this group seems next to impossible. Solem & Yochelson (1979) assign several Late Paleozoic fossil land snails to this family, providing paleontological evidence of true antiquity.

The assemblage of land snails on the Manukau can best be interpreted as a biologically mature radiation with casual coexistence of species the rule. We can identify no clear examples of competition or exclusion; we found only a few narrow niche specialists; we found very high levels of one-spot sympatry in a variety of moisture and litter types; and we found generally low population levels (excluding a few clear examples of 'blooms') of nearly all species. We propose that this adds up to a mature and balanced community that has gradually evolved interspecific compatibility through continuity of optimum conditions in the physical environment.

We lack the means of testing this hypothesis, for want of data on genealogical relationships. Many areas of New Zealand, particularly in the Northland to south-central North Island region, should have bush patches sampled for comparative purposes. Means of sampling larger numbers of live specimens, without severely damaging the habitat, must be devised in order to allow valid statistical analysis. Life history data, particularly in regard to annual and seasonal fluctuations in numbers, are urgently required for taxa in this area of high diversity. Studies on the decay rate of dead shells in leaf litter of different moisture levels (dry to sopping), as opposed to talus slope or cave mouth situations, will be of fundamental aid in interpreting litter samples and cave accumulations.

To propose that these species (a) accumulated gradually; (b) are now interacting little, if at all, because over a long period selection pressure was for avoidance of interaction; (c) became capable of living wherever space and moisture were good; and (d) share this space vertically with numerous other species, is unsatisfactory, but is the best explanation that we can offer.

The only test that we can apply at present is an essentially negative one: to look at the taxonomic composition of those groups that 'drop out' as diversity decreases in other parts of New Zealand.

Table 6 summarises changes in faunal composition, with the native snails lumped into three categories—punctids, charopids, and others (comprising the families Hydrocenidae, Liareidae, Achatinellidae, Rhytididae, and Athoracophoridae). It is evident from the data in the table that, except in the better bush patches (Jones, Crispe's, and Harvey's) the numbers of 'others' are drastically lowered. In the Manukau area charopids seem more sentive to disturbance than do the punctids; there is a greater numerical and proportional drop in charopid taxa. Only in the far south, on Stewart Island, Campbell Island, and the Auckland Islands, do punctid species outnumber charopids. It is not possible to discuss in more detail the charopid and punctid deletions until genealogies and detailed distribution maps are available.

The reduction of species numbers in other taxa most probably will be shown to have a simple climatic link. The land prosobranchs are, with very few exceptions, tropical and subtropical in distribution. The Achatinellidae also show a very strong tropical bias. Of the Rhytididae, *Delos* and *Schizoglossa* are absent from the South Island, *Rhytida* is reduced in diversity there, and *Wainuia* has a dislocated relictual distribution.

We believe that until adequate information is available on genealogy, life history, population fluctuations, and persistence in litter, and until many more bush patches are sampled, no adequate theory as to why there are so many sympatric land snails in New Zealand forests can be developed. We can point out that this is a real phenomenon; that spatial quality and moisture seem to be the factors of importance to individual species; that this high diversity is not composed of a few monophyletic species swarms; that it is a balanced situation characteristic of the central North Island through to Northland; and that diversity levels rapidly diminish both northward and southward from the core. We have proposed six criteria (p. 473) that may explain the differing patterns of diversity. We suspect that throughout the varied Miocene–Holocene shifts of climate and vegetation in this area of New Zealand, relictual pockets of wet gully vegetation persisted, supporting these land snails, which are thus an old assemblage. But we cannot prove it with present data.

DISCUSSION

An obvious comparison must be made with the classic report of Boycott (1934) on the basic ecology of British land molluscs. He was concerned with 83 species of land snail throughout the British Isles (almost exactly the number we found on the Manukau Peninsula) plus 19 species of slug. He had available the fruits of more than a century of observation by British naturalists on life history, feeding, shelter preferences, predation, and local habitat preferences, plus compilations of distributional records. He also had a reasonably mature classification to assist him in reaching his conclusions. The 186-item bibliography in his paper is an indication of the background data available.

Boycott concluded that shelter, lime, and moisture were key factors in understanding local occurrences, plus historical factors of climate and dispersal. He identified calciphiles and calciphobes, a significant fauna associated with human habitation, and a smaller relict fauna indicative of 'natural conditions'. (This natural fauna is relictual because man has modified the British countryside for several thousand years. His devastation of the New Zealand biota, in contrast, has been proceeding for perhaps a thousand years.) Boycott indicated the existence of a strong component of geographic restriction, probably resulting from climatic factors.

The directly comparable section of Boycott's report (p. 26) involved discussion of two patches of woodland with "an uncommonly rich fauna": Whitcombe Wood, by Birdlip in Gloucester, an "ancient beech–ash wood on oolite" with 9 species of slug and 28 of land snail; and Torc Woods, at Muckross in Kerry, "an acid wood predominantly oak and rather wet" with 5 species of slugs and 19 of land snail. Boycott suggested that 3 of the snails found at Torc would occur at Whitcombe, but that 11 of those at Whitcombe would have been excluded from Torc by geography, and another 4 by soil factors. For an "uncommonly rich fauna" such levels of sympatric diversity are considerably below what New Zealand bush areas can support.

It is frustrating that, although writing 47 years after the publication of Boycott's landmark study, we stand in near total ignorance of the biology of New Zealand's land snails. Decades of effort will be required to generate knowledge equal to that available to Boycott. It is even more frustrating to realise that the opportunity to obtain such data is fading rapidly as bush is opened to stock, milled, or burned. We stress that land snails do not require great areas in order to persist. Even small bush patches like Jones, Crispe's, and Harvey's on the Manukau Peninsula can hold very high numbers of land snail species. Preservation even of small bush patches should therefore be given due priority. Tax relief for the retention of bush reserves on otherwise productive farmland, encouragement of local pride in holding a special bit of New Zealand in trust for the future, and perhaps modest help with the cost of necessary fencing to avoid degeneration through grazing, could all have a major influence.

Land snails are indicators of bush quality, and are relatively easy to sample. The presence of certain species is potentially useful as a guide to native habitats that would also contain numerous soil arthropods, microfloral elements, and other native organisms of which we as yet know very little. By using samples of land snails to indicate residual areas of good bush, a major contribution to conservation effort can be made at the same time as materials are accumulating for the faunistic and phyletic studies of land snails needed to test the hypotheses we have advanced here.

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Appendix 1. Habitat preferences of species recorded from or potentially occurring on the Manukau Peninsula. Species also found at Waitomo (wa) or Wellington (we) are indicated. NMNZ registration numbers are given in parenthesis for voucher suites of new taxa mentioned.

The following notes summarise field observations by Frank Climo and David Roscoe over a combined total of 35 years of collecting land snails in various parts of New Zealand. All species that we collected during our Manukau survey are included in the primary list. Short supplementary lists cover taxa known from the Manukau Peninsula that we did not find in our samples, and a few taxa not yet recorded from the peninsula that might be recorded eventually.

A major difficulty in preparing this list is the chaotic state of classification and of species names, and we have had to adopt several conventions to maximise information (p. 455). In a few instances—such as *Huonodon pseudoleiodon* (Suter, 1890) and *Pasmaditta jungermanniae* (Petterd, 1879)—a new combination of generic and specific name is presented (*Huonodon*) or a trans-Tasman identification not yet confirmed by dissection is postulated (*Pasmaditta*). In the circumstances, no more precise set of names can be published.

The emphasis in the following list is on space, texture, and moisture selection by each species, pattern of occurrence, and sensitivity to disturbance. Geographical range data are included only when the Manukau Peninsula is at or near a limit; otherwise, the species are known from areas well to the north and south.

FAMILY HYDROCENIDAE

(wa,we) *Omphalorissa purchasi* (Pfeiffer, 1862) – wide range of litter habitats in moderately wet conditions, occasionally arboreal, frequently clustered in large numbers; highly sensitive to disturbance, very useful indicator of undisturbed bush.

FAMILY LIAREIDAE

(wa) *Liarea hochstetteri carinella* (Pfeiffer, 1861) – usually in well drained situations under leaves, avoids permanently soaked niches, likes well moistened areas on well drained slopes, colonial; locally may occur sympatrically with *L. egea*; range extends south of Waiuku to southern edge of western central North Island limestone area, replaced on eastern side of North Island south of Auckland and west to Bombay Hills by *L. egea*.

Liarea egea (Gray, 1850) – may prefer drier conditions than *L. hochstetteri carinella*, but they occur sympatrically on range fringes; widespread on northern tip of Manukau Peninsula, also from Limestone Downs and Bombay Hills.

Cytora cytora (Gray, 1850) – patchy distribution, low numbers under leaves in well drained situations.

Cytora hedleyi (Suter, 1894) – found mainly in podocarp litter, more common in east coast areas, also recorded from Kemp's Road Reserve by Norman Douglas.

Cytora pallida (Hutton, 1883) – no niche specialisation noted in comparison with other *Cytora*; a northern species just at its southern range limit, collected from Harvey's Bush 21 Jan 1968 by Norman Douglas.

Cytora torquilla (Suter, 1894) – locally abundant, clustered, in rich, finely granulated litter on slopes, much less common in muck or other very wet areas.

FAMILY ATHORACOPHORIDAE

Athoracophorus bitentaculatus (Quoy & Gaimard, 1832) – shelters in slimy leaf axils of monocots, forages on leaf surfaces, arboreal, one individual on young kohekohe (*Dysoxylon spectabile* (Forst.f.) Hook.f.) plants 1.6 m above ground.

FAMILY ACHATINELLIDAE

(we) *Lamellidea novoseelandica* (Pfeiffer, 1853) – arboreal on understorey angiosperms, often coastal, usually abundant.

FAMILY RHYTIDIDAE

(wa,we) *Delos coresia* (Gray, 1850) – under cover of leaves 3–5 cm in diameter or large mamaku fronds in zone of active decay, forages out from this, colonial, but well spaced within colonies.

(wa) *Delos jeffreysiana* (Pfeiffer, 1853) – under logs and 10+ cm leaves, nikau boles, rarely in mamaku piles; distribution patchy, more colonial tnan *D. coresia,* more sporadic in occurrence.

(wa) *Rhytida greenwoodi* (Gray, 1850) – well drained slopes, especially rock ledges with litter, but also under mamaku, deep wet litter, logs; scattered individuals.

Schizoglossa worthyae Powell, 1949 – under large heaps of wet debris or logs; Crispe's Bush is the known western limit of distribution, Patumahoe the southern, and Whangarei the northern.

FAMILY CHAROPIDAE

(wa,we) *Cavellia buccinella* (Reeve, 1852) – hardy, primarily bush fringe but low numbers present in wet litter, commoner in dry litter areas, rarely on logs; increase in number indicates rising disturbance of habitat, persists in grass clumps after bush cleared; ubiquitous.

(wa) *Cavellia roseveari* (Suter, 1896) – soil surface in medium litter, seems to be absent where punctids of equivalent habitat are present; taken at Harvey's Bush 5 Nov 1968 by Norman Douglas, and Jones Bush 3 Jan 1977 by Bruce Hazelwood, not found during this survey.

(wa,we) *Mocella eta* (Pfeiffer, 1853) – same conditions as *Cavellia buccinella,* but more often on logs.

(wa) *'Mocella'* n.sp. aff. *maculata* (Suter, 1891) (M69305) – extremely abundant in limestone litter, under logs, on slopes in medium litter, intermediate between *Mocella eta* and *Cavellia buccinella* in habitat and occurrences.

(we) *'Mocella'* n.sp. aff. *manawatawhia* (Powell, 1935) (M57388) – prefers coastal xerophytic forest in litter, not known from wet litter; also recorded between Blowholes, Manukau Heads, 30 Jan 1968 by Norman Douglas.

(wa,we) *'Charopa' pseudanguicula* Iredale, 1913 – under flaking bark on tree trunks or rotting logs, early in decay cycle.

(wa) *'Charopa' chrysaugeia* (Webster, 1904) – rare, arboreal or wet litter in undisturbed situations, preference unknown.

(wa) *'Charopa'* n.sp. aff. *pseudanguicula* Iredale, 1913 [No.] 1 (M63244) – wet, slimy surfaces of compressed litter, also on tree trunks.

'Charopa' fuscosa (Suter, 1894) – under compressed broadleaf litter, rare; Jones Bush is the known southern limit of distribution.

(wa) *'Charopa' pilsbryi* (Suter, 1894) – under loosened bark of fallen logs.

(wa,we) *Charopa coma* (Gray, 1843) – under well decomposed logs, under rocks, tolerates dry conditions.

'Charopa' costulata (Hutton, 1883) – in well decomposed, wet, powdery litter near logs; also taken at Waiuku Gap on 30 Aug 1970 by Norman Douglas.

(wa) *'Charopa' ochra* (Webster, 1904) – friable deep litter near logs in good forest; known northern range limits are Waitakere Range and Coromandel Peninsula.

(wa) *Fectola mira* (Webster, 1908) – wet, slimy surfaces of compressed litter; usually with *'Charopa'* n.sp. aff. *pseudanguicula* 1 but always more abundant.

Fectola unidentata Climo, 1978 – lower regions of tree trunks and rotten logs in early decay, in cracks on bark; small, scattered, relict distribution.

Fectola infecta (Reeve, 1852) – frequently on underside of logs, also in friable litter, often rock ledges, locally abundant on limestone, found in wet areas, but drier than preferred areas of other *Fectola.*

(wa,we) *Huonodon pseudoleiodon* (Suter, 1890) – wet (but not slimy) litter, sometimes underside of logs in any stage of decay; wide range of vegetation types, a generalist, not common in limestone areas.

(wa,we) *Huonodon hectori* (Suter, 1890) – litter in tree forks or leaf axils, rarely found alive on ground.

Allodiscus dimorphus (Pfeiffer, 1853) – usually under large very rotten logs, but drier sections ('sleeps cheap, eats well'); also recorded from Boiler Gully Road on 26 Dec 1969 and under flax at Bird's Gap, Maioro, on 28 Aug 1970 by Norman Douglas.

Allodiscus tessellatus Powell, 1941 – under logs or in wet litter; also recorded from Richmond's Bush by Norman Douglas.

'Allodiscus' urquharti Suter, 1894 – very damp, friable particulate litter, not in compacted leaf layers.

(wa,we) *Allodiscus* n.sp. aff. *granum* (Pfeiffer, 1857) (M51836) – upper, more open sections of mamaku heaps, moist areas in early decay; also in cavities in stable scree; known northern limits of range are Great Barrier Island in extreme east, Hunua Range centrally, and Manukau Peninsula in west.

(wa,we) *Allodiscus planulatus* (Hutton, 1883) – on ground surface under rotten logs.

(we) *Geminoropa cookiana* (Dell, 1952) – deep, friable litter; scattered disjunct distribution from coastal Nelson and Marlborough in the South Island to known northern range limit on Manukau Peninsula.

(wa) *Serpho kivi* (Gray, 1843) – on broad leaves, branches; rests on underside of leaves.

(wa,we) *Flammulina perdita* (Hutton, 1883) – on trunks of big trees, in crotches, bark crevices, epiphytes.

Flammulina chiron (Gray, 1850) – logs in deep, wet forest, ravines, tree and branch jumbles; distribution patchy over a wide area.

'Flammulina' feredayi (Suter, 1891 – deep, wet litter near ground level, but not in slime.

(wa) *'Thalassohelix' ziczac* (Gould, 1848) – deep litter on wet ground, not on logs; cavity size, not litter type, seems significant; area must be well shaded.

(we) *Therasia decidua* (Pfeiffer, 1857) – under monocots, bush clearings on banks, broadleaf canopy.

(wa,we) *Suteria ide* (Gray, 1850) – under logs and stones, leaf litter alongside.

(wa) *Phenacohelix giveni* Cumber, 1961 – loose litter on well drained slopes, occasionally in litter on top of logs or arboreal; undisturbed areas needed.

(wa) *Phenacohelix pilula* (Reeve, 1852) – drier banks, associated with grasses or other monocots; open forest areas or dry forest fringes.

'Phenacohelix' n.sp. 1 (M30321) – slopes littered with nikau, flax, or other monocotyledons; wet to medium dry; central Northland southward to Auckland, then along west coast to known southern limit at Limestone Downs.

Phenacohelix ponsonbyi (Suter, 1897) – may need a slightly wetter habitat than *Phenacohelix giveni*, with which it occurs frequently in limestone areas.

(wa,we) *Therasiella neozelanica* Cumber, 1967 – wet litter in lowest layers next to soil; slope or type of litter variable.

Therasiella serrata Cumber, 1967 – deep heaps of litter, generally wetter than for *T. neozelanica*, next to soil; known range central Northland southward to East Cape area, Rotorua, and Port Waikato area, i.e., near south-western limit.

Therasiella n.sp. aff. *neozelanica* Cumber, 1967 (M68186) – rare, usually with *Therasiella neozelanica*; known range from central North Island at level of Rotorua to Coromandel Peninsula in east and Manukau Peninsula in west.

(wa) *Therasiella celinde* (Gray, 1850) – in small cavities next to ground under small bits of wood or logs; common in Auckland area, rare south of Waiuku and Rotorua, but known down to Mt Egmont and Opotiki.

Therasiella tamora (Hutton, 1883) – same preference as *Therasiella serrata*; also recorded from Boiler Gulley Road on 29 Oct 1967 by Norman Douglas.

FAMILY PUNCTIDAE

(wa,we) *Obanella rimutaka* Dell, 1952 – most commonly on rock exposures 'with a view,' limestone pillars or crags, diverse topography.

'Laoma' mariae (Gray, 1843) – slimy, wet ground surface under broadleaf litter or between slimy layers as adults, juveniles higher in litter.

Laoma n.sp. aff. *marina* (Hutton, 1883) 1 (M58164) – similar in preference to *'Laoma' mariae*, but somewhat drier niches; central Northland to known southern range limit at Limestone Downs.

(wa,we) *Laoma marina* (Hutton, 1883) – on leaves and twigs in wet areas, similar to *'Phrixgnathus' glabriusculus* (Pfeiffer, 1853); recorded from Skinner's Bush on 29 Oct 1967 and Kemp's Road Reserve on 15 Feb 1970 by Norman Douglas.

(wa) *Laoma leimonias* (Gray, 1850) – in wet, undecomposed, broadleaf litter; known southern range limit at Waitomo Caves.

(wa) *'Phrixgnathus' erigone* (Gray, 1850) – found in encrusting materials on saplings and small tree trunks, forages on undersides of leaves; prefers very moist sections of bush; central Northland to known southern range limit in Waitomo area.

(wa,we) *'Phrixgnathus' ariel* (Hutton, 1883) – trunks and branches of larger trees with less encrusting matter; more tolerant of disturbance and drier aspects of bush.

'Phrixgnathus' elaiodes (Webster, 1904) – on trunks of trees, generally with bark that scales loose; all of Northland to known southern range limit at Great Barrier Island in the east and Waikaretu in the west.

(wa) *'Phrixgnathus' moellendorffi* Suter, 1896 – ground surface under drier litter; near southern edge of patchy distribution, which extends from central Northland to Great Barrier Island in the east and through Auckland to the Waitomo limestone country in the west.

(wa) *'Phrixgnathus' conella* (Pfeiffer, 1862) – ground surface under moist litter (knees of trousers get wet, not soaked, when kneeling); known southern range limit near Waitomo limestone country.

(wa) *'Phrixgnathus' poecilosticta* (Pfeiffer, 1852) – same preference as *'Phrixgnathus' conella*; known northern range limit is Auckland city area.

'Phrixgnathus' glabriusculus (Pfeiffer, 1853) – spaces in wet litter above ground level; at its known southern range limit, recorded from Wattle Bay, Manukau Heads, on 21 Jan 1968 by Norman Douglas.

(wa) *'Phrixgnathus' pirongiaensis* Suter, 1894 – wet deep litter.

'Phrixgnathus' levis (Suter, 1913) – under moist broadleaf litter, often associated with limestone ledges; known range Wanganui to Port Waikato (Manukau Peninsula to north of known range).

(wa) *'Phrixgnathus'* n.sp. 59 (M38399) – suspended litter in kiekie (*Freycinetia banksii* A. Cunn.) or nikau leaf axils, and slime-filled axils of flax.

(wa) *Pasmaditta jungermanniae* (Petterd, 1879) – records of dead shells in litter from patches of 'good bush' scattered through New Zealand; niche unknown; distribution trans-Tasman.

'Paralaoma' n.sp. 38 (M57846) – slimy interspaces between broad leaves in litter as juveniles, only observed on black fungus on a sapling as adults; scattered relict distribution.

(wa,we) *'Paralaoma'* n.sp. 29 (M47339) – slimy layers of broadleaf litter and wetter parts of other litter; ubiquitous.

(wa,we) *'Paralaoma' lateumbilicata* (Suter, 1890) – friable dry litter, lower layers, often in thin litter.

(wa,we) *'Paralaoma'* n.sp. 1 (M48062) – fine-grained, tightly packed, deep, well decomposed litter; known range southern Northland to northern South Island.

(wa,we) *'Paralaoma'* n.sp. 8 (M68455) – often sympatric with *'Paralaoma'* n.sp. 1; sometimes tolerates slightly more grainy litter.

'Paralaoma' serratocostata (Webster, 1906) – ground surface under any very wet litter.

(wa) *'Paralaoma'* n.sp. 40 (M12041) – in medium moist litter; sporadic distribution from Auckland to Waitomo and Lake Waikaremoana.

(wa,we) *Paralaoma caputspinulae* (Reeve, 1852) – dry, open country or coastal areas, very hardy; distribution trans-Tasman.

'Paralaoma' francesci (Webster, 1904) – dry, friable podocarp litter; known southern range limit is at Waiuku.

(wa) *'Paralaoma'* n.sp. 33 (M55771) – rare in litter samples, more often podocarp samples, not collected alive yet, preference unknown.

'Paralaoma' n.sp. aff. 33 (M63508) – known from a few dead specimens in litter from the Auckland area, preference and range unknown.

FAMILY CIONELLIDAE (introduced)

(wa) *Cionella lubrica* (Müller, 1774) – in large-grain loam or thin litter on dry slopes and disturbed bush margins, gardens, on limestone; extremely abundant in disturbed areas, usually rare in native bush.

FAMILY ZONITIDAE (introduced)

(wa,we) *Oxychilus cellarius* (Müller, 1774) – same basic conditions as *Cionella lubrica.*

FAMILY HELICIDAE (introduced)

(wa,we) *Helix aspersa* (Müller, 1774) – gardens, limestone areas, coastal disturbed bush, rare in native bush.

FAMILY VALLONIIDAE (introduced)

Vallonia sp. – paddocks, gardens, lawns, recently disturbed slopes under thin litter; also recorded from Wattle Bay on 21 Aug 1968 by Norman Douglas.

Species recorded from Manukau Peninsula but not taken in this survey

FAMILY RHYTIDIDAE

Paryphanta busbyi (Gray, 1840) – colonies in the central part of the peninsula purportedly were introduced by Rev. Webster early in this century.

FAMILY CHAROPIDAE

Egestula egesta (Gray, 1850) – in wet litter next to soil; at known range limit, recorded from Blow Holes, Manukau Heads, on 13 Nov 1966 by Norman Douglas.

FAMILY PUNCTIDAE

'Phrixgnathus' n.sp. 55 (M37499) – ground surface under dry litter; recorded from jetsam at Wattle Bay on 4 Oct 1970 by Norman Douglas.

Species not recorded from Manukau Peninsula but possibly present there

FAMILY CHAROPIDAE

(we) *Otoconcha dimidiata* (Pfeiffer, 1853) – under logs or nikau boles; distribution central North Island to Northland.

FAMILY PUNCTIDAE

(wa) *'Phrixgnathus'* n.sp. 61 (M61668) – in very damp litter; known northern range limits are Kaimai Range in the east and Port Waikato limestones in west.

Appendix 2. Species from Waitomo (wa) and Wellington (we) not included in the primary Manukau list (Appendix 1). Waitomo listings based on collections made during this study (Appendix 3F) and on collections made by B. F. Hazelwood from Stubbs's Farm (NMNZ M61488–61545); Wellington area listings based on NMNZ collections. NMNZ registration numbers are given in parenthesis for voucher suites of new taxa mentioned below that are not covered in Appendix 1.

(wa) *Schizoglossa novoseelandica* (Pfeiffer, 1862)
(we) *Wainuia urnula* (Pfeiffer, 1855)
(wa) *Cavellia colensoi* (Suter, 1890)
(wa,we) *C. anguicula* (Reeve, 1852)
(we) *C. irregularis* (Suter, 1890)
(we) *C. brouni* (Suter, 1891)
(we) *C. biconcava* (Pfeiffer, 1853)
(wa) *'Mocella' prestoni* (Sykes, 1895)
(wa) *'M.' accelerata* (Climo, 1970)
(wa) *'M.'* n.sp. aff. *segregata* (Suter, 1894) (M67975)
(wa) *'Charopa'* n.sp. aff. *pseudanguicula* Iredale, 1913 [No.] 2 (M56064)
(wa) *'Charopa' titirangiensis* (Suter, 1896)
(wa) *'Charopa' montivaga* Suter, 1894
(wa,we) *Fectola trilamellata* Climo, 1978
(wa) *Pulchridomus barbatulus* (Reeve, 1852)
(we) *Huonodon microundulata* (Suter, 1890)
(we) *Ptychodon wairarapa* (Suter, 1890)
(wa) *Thermia subincarnata* (Suter, 1894)
(wa,we) *Allodiscus* n.sp aff. *tessellatus* Powell, 1941 (M30525)
(wa) *A. tullia* (Gray, 1850)
(wa) *'Geminoropa' moussoni* (Suter, 1890)
(we) *'G.'* n.sp. aff. *moussoni* (Suter, 1890) (M68610)
(we) *'G.' subantialba* (Suter, 1890)
(wa) *'G.' vortex* (Murdoch, 1897)
(we) *Flammulina crebriflammis* (Pfeiffer, 1853)
(wa) *F.* n.sp. aff. *crebriflammis* (Pfeiffer, 1853) (M57323)
(we) *F. zebra* (Le Guillou, 1842)
(we) *F.* n.sp. 1 (M69527)
(we) *Flammoconcha compressivoluta* (Reeve, 1852)
(we) *Therasia traversi* (Smith, 1884)
(wa) *Suteria raricostata* Cumber, 1962
(we) *Pseudallodiscus ponderi* Climo, 1971
(we) *Phenacharopa novoseelandica* (Pfeiffer, 1853)
(we) *Phenacohelix rusticus* (Suter, 1894)
(we) *P. lucetta* (Hutton, 1884)
(wa) *Laoma* n.sp. aff. *marina* (Hutton, 1883) 2 (M55176)
(we) *'Phrixgnathus' phrynia* Hutton, 1883
(we) *'P.' celia* Hutton, 1883
(wa) *'P.'* n.sp. 61 (M61668)
(wa,we) *'P.' viridula* (Suter, 1909)
(we) *'Paralaoma'* n.sp. 11 (M25419)
(we) *'P.'* n.sp. aff. 2 (M25426)
(wa) *'P.'* n.sp. 5 (M51747)
(wa) *'P.'* n.sp. 32 M51937)
(we) *'P.'* n.sp. 7 (M69062)
(wa) *'P.'* n.sp. aff. 7 (M63509)
(wa) *'P.'* n.sp. 45 (M56425)
(wa) *'P.' miserabilis* (Iredale, 1913)
(we) *'P.'* n.sp. 30 (M61571)
(we) *'P.'* n.sp. 69 (M56626)

Appendix 3A. Results of 1977 and 1981 sampling in Jones Bush (L, live; D, dead; e, sampled by eye; f, sampled by flotation)

	ARBOREAL	RIMU				PURIRI		DRY BROADLEAF			YOUNG FERNS		NIKAU	UPPER MAMAKU				STREAM MAMAKU				Total	Total	Total
		Le	De	Lf	Df	Lf	Df	Le	Lf	Df	Lf	Df		Le	De	Lf	Df	Le	De	Lf	Df	live	dead	snails
Omphalorissa purchasi	—	—	—	—	—	17	159	1	—	1	2	47	—	—	1	19	56	—	—	—	5	39	269	308
Liarea hochstetteri carinella	—	—	—	—	—	—	—	—	2	1	—	—	6	2	—	—	3	6	3	1	7	17	14	31
Cytora cytora	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	1	—	—	—	2	2	3	5
Cytora torquilla	—	—	—	—	—	—	—	—	5	3	—	2	1	—	2	4	37	—	1	—	11	10	56	66
Athoracophorus bitentaculatus	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
Lamellidea novoseelandica	3	—	3	—	56	—	1	—	—	5	—	5	—	—	—	—	1	—	—	—	3	3	74	77
Delos coresia	—	1	—	—	1	—	13	—	1	3	1	6	1	—	14	—	19	—	4	1	6	5	66	71
D. jeffreysiana	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Rhytida greenwoodi	—	2	4	1	4	—	2	—	—	—	—	3	—	—	2	—	3	—	—	—	2	3	20	23
Cavellia buccinella	—	—	5	3	7	4	72	4	—	7	3	11	—	—	—	1	18	—	—	—	1	15	121	136

Mocella eta	—	—	—	—	—	1	12	—	—	3	9	10	—	1	1	1	18	1	1	1	2	14	47	61
'M.' n.sp. aff. *maculata*	—	—	2	—	2	22	49	1	—	3	1	1	—	—	2	1	31	11	18	1	3	37	111	148
'Charopa' pseudanguicula	5	—	—	—	1	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	5	3	8
'C.' chrysaugeia	1	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	4	—	4
'C.' n.sp. aff.																								
pseudanguicula 1	9	—	—	—	—	—	—	—	—	—	—	3	1	—	—	—	—	—	—	—	—	10	3	13
'C.' fuscosa	—	—	—	—	2	4	19	—	2	1	2	4	—	—	—	1	14	—	—	—	1	9	41	50
'C.' pilsbryi	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	3
Fectola mira	—	—	—	—	—	—	—	—	—	—	—	—	14	—	1	—	1	—	1	—	—	14	3	17
F. unidentata	4	—	—	—	—	—	—	—	—	1	—	3	—	—	—	—	—	—	—	—	—	4	4	8
F. infecta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	2	2
Huonodon pseudoleiodon	—	—	—	—	—	—	—	—	2	2	3	2	1	2	3	1	3	9	5	—	—	18	15	33
H. hectori	—	—	3	1	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	16	17
'Allodiscus' urquharti	—	—	—	—	—	—	—	—	—	5	—	2	—	—	—	3	5	—	—	—	—	3	12	15
A. n.sp. aff. *granum*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	3	1	9	1	2	2	18	20
Geminoropa cookiana	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	3	5	—	1	3	1	7	7	14
Serpho kivi	3	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	3	2	5
Flammulina perdita	4	1	28	—	11	—	—	—	—	—	—	17	—	—	3	—	—	—	—	—	1	5	60	65
F. chiron	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
'Thalassohelix' ziczac	—	—	—	—	—	—	—	—	—	3	—	—	—	—	7	—	3	1	12	—	1	1	26	27
Suteria ide	1	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	5	1	2	—	1	2	13	15
Phenacohelix giveni	1	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	2	—	—	—	—	2	3	5
'P.' pilula	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
'P.' n.sp. 1	—	—	—	—	—	—	1	1	—	1	—	—	—	—	1	1	—	2	3	—	1	4	7	11
Therasiella neozelanica	—	—	6	—	12	1	34	—	1	—	—	13	—	—	5	5	12	1	2	—	1	8	85	93
T. serrata	—	—	1	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	5
T. n.sp. aff. *neozelanica*	—	2	2	2	10	—	—	—	—	—	—	—	—	—	2	—	7	—	—	—	—	4	21	25
Therasiella celinde	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	2	3	5
'Laoma' mariae	1	—	—	—	—	—	—	1	—	—	—	1	—	—	2	—	—	—	1	—	—	2	4	6
L. n.sp. aff. *marina* 1	—	—	—	—	—	—	12	4	—	13	—	7	—	—	—	—	4	—	—	—	—	4	36	40
L. leimonias	—	7	15	15	65	4	61	8	5	14	1	11	—	—	3	1	8	18	10	—	8	59	195	254
'Phrixgnathus' erigone	8	—	—	—	5	—	—	4	—	3	—	—	3	—	3	3	15	—	3	—	9	18	38	56
'P.' ariel	8	—	—	—	—	—	—	1	—	—	1	22	—	—	—	—	—	—	—	—	2	10	24	34
'P.' elaiodes	2	—	10	—	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	17	19
'P.' moellendorffi	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	2	2
'P.' conella	—	1	16	—	13	—	—	1	—	2	—	—	—	—	—	—	2	—	—	—	—	2	33	35
'P.' n.sp. 59	—	—	—	—	—	—	—	—	—	—	—	—	2*	—	—	—	—	—	—	—	—	2*	—	2*
'P.' poecilosticta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	1	1	—	2	1	6	7
'Paralaoma' n.sp. 38	—	—	—	—	—	7	17	—	—	—	—	—	—	—	—	4	16	—	—	—	—	11	33	44
'P.' n.sp. 29	—	—	—	—	15	2	50	—	2	8	—	—	—	—	—	6	14	—	—	—	3	10	90	100
'P.' lateumbilicata	—	—	—	—	2	—	—	—	2	1	—	—	—	—	—	—	—	—	—	—	—	2	3	5
'P.' n.sp. 1	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	4	4
'P.' n.sp. 8	—	—	1	—	4	—	4	—	—	—	—	4	—	—	—	1	2	—	—	—	4	1	19	20
'P.' n.sp. aff. 33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1
'P.' serratocostata	—	—	—	—	—	—	15	—	—	2	—	1	—	—	—	—	4	—	—	—	3	—	25	25
Cionella lubrica	—	—	—	—	—	—	67	*	—	—	2	14	—	—	—	—	12	—	—	—	1	2*	94	96
Oxychilus cellarius	—	—	—	—	—	—	—	†	—	—	—	—	—	—	—	—	—	—	—	—	—	—	†	—
Slugs	—	—	—	—	—	19	—	—	1	—	4	—	—	—	—	4	—	—	—	—	—	4	—	28
Helix aspersa	—	—	—	—	—	—	—	†	—	—	—	—	—	—	—	—	—	—	—	—	—	—	†	—
TOTAL LIVE	51	15		22		83		27	24		30		32	5		59		52		8		408		
TOTAL DEAD			96		242		589			82		192			67		327		79		86		1760	2168
TOTAL SPECIES	10	7	13	5	23	10	18	11	10	21	11	24	8	3	21	16	33	11	19	6	28	45	52	
TOTAL SPECIES AT STATION		15			23		19			23		24		22			31		19		28		57	

*Recorded in subsequent hand-picking from leaf axils
†Seen, but not collected

Appendix 3B. Results of sampling in Crispe's Bush (conventions as for App. 3A)

	BIG LIVE LOG		NIKAU AND FERN, UPPER SLOPE		BROADLEAF, UPPER SLOPE		ROTTEN PURIRI LOG		BROAD-LEAF BY STREAM	FERN DEBRIS BY STREAM		Total	Total	Total
	Lf	Df	Lf	Df	Lf	Df	Le	Df	Df	Lf	Df	live	dead	snails
Liarea hochstetteri	—	—	2	9	3	11	—	—	4	1	5	6	29	35
Cytora cytora	—	—	—	2	—	5	—	—	6	—	1	—	14	14
C. torquilla	—	—	—	—	—	2	—	—	1	—	—	—	3	3
C. hedleyi	—	—	—	1	3	4	—	—	—	—	2	3	7	10
Lamellidea novoseelandica	—	6	—	—	3	5	—	—	1	—	—	3	12	15
Delos coresia	—	—	—	4	—	12	—	1	2	—	10	—	29	29
Rhytida greenwoodi	—	—	—	—	—	—	—	—	—	—	1	—	1	1
Schizoglossa worthyae	—	—	—	—	—	1	—	—	—	*	1	*	2	2
Cavellia buccinella	3	11	—	—	—	—	—	—	—	—	—	3	11	14
Mocella eta	1	8	—	3	3	2	—	—	3	1	6	5	22	27
'Mocella' n.sp. aff. *maculata*	—	—	—	1	—	—	—	1	—	—	—	—	2	2
'M.' n.sp. aff. *manawatawhia*	—	—	—	—	—	—	—	1	—	—	—	—	1	1
'Charopa' pseudanguicula	—	1	—	—	—	1	—	—	—	—	—	—	2	2
'C.' chrysaugeia	—	—	—	—	—	—	—	—	1	—	—	—	1	1
Fectola mira	—	—	—	—	—	1	—	—	—	—	—	—	1	1
F. infecta	—	—	—	3	—	4	2	1	1	—	1	2	10	12
Huonodon pseudoleiodon	—	—	—	3	1	3	—	1	2	1	—	2	9	11
H. hectori	—	—	—	1	—	2	—	—	—	—	1	—	4	4
'Allodiscus' urquharti	—	—	—	—	—	2	—	—	4	—	—	—	6	6
A. n.sp. aff. *granum*	—	—	—	—	—	—	—	—	—	—	2	—	2	2
Allodiscus tessellatus	—	—	—	2	—	10	1	2	9	3	2	4	25	29
A. planulatus	—	—	—	—	—	—	—	—	—	—	1	—	1	1
Geminoropa cookiana	—	—	—	—	—	—	—	—	—	—	1	—	1	1
Serpho kivi	—	—	—	3	—	1	—	—	—	—	—	—	4	4
Flammulina perdita	—	2	—	—	—	1	—	—	1	—	—	—	4	4
F. chiron	—	—	—	—	—	3	—	—	—	—	—	—	3	3
'F.' feredayi	—	—	—	—	—	—	—	—	1	—	—	—	1	1
'Thalassohelix' zigzac	—	—	—	—	—	5	—	—	—	—	—	—	5	5
Phenacohelix giveni	—	—	—	1	—	—	—	—	—	—	1	—	2	2
'P.' n.sp. 1	1	17	—	3	—	6	—	—	—	—	2	1	28	29
P. ponsonbyi	—	1	—	1	1	6	—	—	—	—	—	1	8	9
Therasiella neozelanica	—	4	—	9	—	5	—	2	12	—	10	—	42	42
T. serrata	—	—	—	—	—	1	—	—	—	—	—	—	1	1
T. n.sp. aff. *neozelanica*	—	—	—	—	—	4	—	—	5	—	3	—	12	12
T. celinde	—	—	—	—	—	2	1	8	—	—	2	1	12	13
Obanella rimutaka	—	1	—	—	—	—	—	—	—	—	—	—	1	1
'Laoma' mariae	—	—	—	—	1	1	—	—	4	—	1	1	6	7
L. n.sp. aff. *marina* 1	—	—	—	—	1	5	—	—	—	—	—	1	5	6
L. marina	1	—	1	9	1	17	—	1	12	—	10	3	49	52
'Phrixgnathus' erigone	—	1	—	3	—	11	—	—	—	1	5	1	20	21
'P.' ariel	—	2	—	4	—	10	—	—	7	—	4	—	27	27
'P.' conella	—	—	—	—	—	1	—	—	—	—	1	—	2	2
Pasmaditta jungermanniae	—	—	—	—	—	1	—	—	—	—	—	—	1	1
'Paralaoma' n.sp. 29	1	3	—	1	3	14	—	—	1	—	4	4	23	27
'P.' n.sp. 1	—	—	—	—	—	1	—	—	—	—	—	—	1	1
'P.' n.sp. 8	—	2	—	4	—	4	—	—	4	—	2	—	16	16
'P.' serratocostata	—	2	—	1	—	3	—	—	—	—	1	—	7	7
Oxychilus cellarius	—	1	—	—	—	—	—	—	—	—	—	—	1	1
Slugs	—	—	1	—	1	—	—	—	—	1	—	3	—	3
TOTAL LIVE	7		4		21		4			8		44		
TOTAL DEAD		62		68		167		18	81		80		476	520
TOTAL SPECIES	5	15	3	21	10	36	3	9	20	6	26	16	48	48
TOTAL SPECIES AT STATION	16		21		36		9		20	27				

N.B. *Serpho kivi* seen live, not taken

Appendix 3C. Results of sampling in Harvey's Bush (conventions as for App. 3A)

	MID SLOPE, BROADLEAF		HIGHER RIDGE, MIXED BROADLEAF		MAMAKU/NIKAU, HEAD OF GULLY AT BASE						
	Lf	Df	Lf	Df	Le	De	Lf	Df	Total live	Total dead	Total snails
Omphalorissa purchasi	—	1	—	1	—	—	—	—	—	2	2
Liarea egea	5	22	5	21	2	3	5	9	17	55	72
Cytora cytora	—	—	—	—	1	—	—	—	1	—	1
C. hedleyi	—	—	—	2	—	—	—	3	—	5	5
C. pallida	—	1	—	3	—	3	—	5	—	12	12
C. torquilla	—	—	—	—	—	—	—	3	—	3	3
Lamellidea novoseelandica	—	4	—	5	—	—	—	—	—	9	9
Delos coresia	1	5	1	12	—	—	2	6	4	23	27
D. jeffreysiana	—	—	1	—	1	2	3	5	5	7	12
Rhytida greenwoodi	—	—	—	2	—	2	—	—	—	4	4
Cavellia buccinella	—	1	—	1	—	—	—	—	—	2	2
Mocella eta	—	9	—	7	—	1	—	4	—	21	21
'*M.*' n.sp. aff. *maculata*	—	3	—	1	—	—	—	1	—	5	5
'*Charopa*' *pseudanguicula*	—	—	—	1	—	—	—	—	—	1	1
C. coma	—	1	—	—	—	—	—	—	—	1	1
'*C.*' *ochra*	—	2	—	—	—	—	—	—	—	2	2
'*C.*' *chrysaugeia*	—	—	—	—	—	—	—	3	—	3	3
Fectola mira	—	—	—	1	2	—	—	2	2	3	5
Huonodon pseudoleiodon	2	5	—	—	5	2	1	7	8	14	22
Serpho kivi	—	—	—	—	—	1	—	—	—	1	1
Flammulina chiron	—	2	—	1	—	—	—	—	—	3	3
'*Thalassohelix*' *ziczac*	1	10	1	16	2	5	2	4	6	35	41
Suteria ide	—	3	—	—	—	10	—	6	—	19	19
Phenacohelix giveni	—	—	—	2	—	7	—	2	—	11	11
P. ponsonbyi	—	—	—	1	—	—	—	—	—	1	1
'*P.*' n.sp. 1	—	10	1	12	2	11	—	6	3	39	42
Therasiella neozelanica	—	4	—	4	—	—	2	13	2	21	23
T. serrata	—	4	—	5	—	—	1	2	1	11	12
T. celinde	—	—	—	—	—	—	—	2	—	2	2
Obanella rimutaka	—	—	—	—	—	—	—	1	—	1	1
Laoma marina	2	18	—	38	3	4	2	20	7	80	87
L. n.sp. aff. *marina* 1	—	—	—	1	—	—	—	—	—	1	1
L. leimonias	—	14	2	43	—	—	—	1	2	58	60
'*Phrixgnathus*' *erigone*	—	5	—	4	—	2	—	14	—	25	25
'*P.*' *ariel*	—	—	—	1	—	—	—	—	—	1	1
'*P.*' *glabriusculus*	—	9	—	6	—	—	—	2	—	17	17
'*P.*' *moellendorffi*	—	—	—	—	—	—	—	3	—	3	3
'*P.*' *conella*	1	5	—	17	—	2	—	2	1	26	27
'*Phrixgnathus*' *poecilosticta*	—	10	—	6	2	6	2	28	4	50	54
'*Paralaoma*' n.sp. 29	—	4	—	7	—	—	—	3	—	14	14
'*P.*' *lateumbilicata*	—	—	—	6	—	—	—	—	—	6	6
'*P.*' n.sp. 8	—	—	—	—	—	—	1	4	1	4	5
'*P.*' *serratocostata*	—	2	—	2	—	—	—	6	—	10	10
'*P.*' *francesci*	—	1	—	—	—	—	—	—	—	1	1
TOTAL LIVE	12		11		20		21		64		
TOTAL DEAD		155		229		61		167		612	676
TOTAL SPECIES	6	26	6	30	9	15	10	29	15	43	44
TOTAL SPECIES AT STATION	26		31		17		29				

Appendix 3D. Results of sampling in Awhitu Gully (conventions as for App. 3A)

	FERN/NIKAU IN BROADLEAF, SHALLOW GULLY			UNDER LARGEST KAURI TREE		Total live	Total dead	Total snails
	Le	Lf	Df	Lf	Df			
Liarea egea	—	1	19	—	—	1	19	20
Cytora cytora	—	—	2	—	—	—	2	2
Lamellidea novoseelandica	—	—	1	—	—	—	1	1
Delos coresia	—	—	3	—	—	—	3	3
Rhytida greenwoodi	—	—	2	—	1	—	3	3
Cavellia buccinella	—	—	5	—	—	—	5	5
Mocella eta	—	4	23	—	—	4	23	27
'M.' n.sp. aff. *manawatawhia*	—	1	—	—	—	1	—	1
'Charopa' ochra	—	—	—	1	—	1	—	1
Allodiscus tessellatus	—	—	1	—	6	—	7	7
A. dimorphus	1	—	—	—	—	1	—	1
Serpho kivi	—	1	4	—	—	1	4	5
'Thalassohelix' ziczac	—	—	10	—	—	—	10	10
Phenacohelix giveni	1	—	—	—	—	1	—	1
'P.' n.sp. 1	—	—	5	—	—	—	5	5
Therasiella neozelanica	—	—	2	—	5	—	7	7
T. serrata	—	—	9	—	—	—	9	9
T. n.sp. aff. *neozelanica*	—	—	2	—	7	—	9	9
T. celinde	—	—	—	—	4	—	4	4
T. tamora	—	—	—	—	1	—	1	1
Laoma marina	1	—	—	—	1	1	1	2
L. leimonias	—	2	51	5	12	7	63	70
'Phrixgnathus' pirongiaensis	—	—	—	—	2	—	2	2
'P.' erigone	—	—	2	—	1	—	3	3
P.' glabriusculus	—	—	1	1	11	1	12	13
'P.' conella	—	—	3	—	1	—	4	4
'P.' poecilosticta	—	—	2	—	13	—	15	15
'Paralaoma' n.sp. 29	—	—	4	—	—	—	4	4
'P.' lateumbilicata	—	—	16	—	-	—	16	16
'P.' n.sp. 1	—	—	1	—	4	—	5	5
'P.' n.sp. 8	—	—	4	—	—	—	4	4
'P.' n.sp. 33	—	—	1	—	—	—	1	1
TOTAL LIVE	3	9		7		19		
TOTAL DEAD			173		69		242	261
TOTAL SPECIES	3	5	24	3	14	10	28	32
TOTAL SPECIES AT STATION		28		15				

Appendix 3E. Results of sampling at Track Gully and Limestone Downs (conventions as for App. 3A)

	TRACK GULLY		LIMESTONE DOWNS	
	L	D	L	D
Omphalorissa purchasi	—	—	—	9
Liarea hochstetteri carinella	—	—	—	4
L. egea egea	—	—	2	13
Cytora hedleyi	—	1	—	—
Lamellidea novoseelandica	—	8	—	25
Delos coresia	—	23	2	7
Rhytida greenwoodi	—	—	—	12
Cavellia buccinella	—	—	1	10
Mocella eta	1	40	2	25
'Mocella' n.sp. aff. *maculata*	—	—	5	71
'M.' n.sp. aff. *manawatawhia*	—	—	—	15
'Charopa' pseudanguicula	—	3	—	—
C. coma	—	—	—	2
'C.' costulata	—	—	—	2
Fectola unidentata	—	—	—	362
F. infecta	—	—	1	13
Huonodon pseudoleiodon	—	—	—	1
H. hectori	—	2	—	4
Flammulina perdita	—	4	—	3
F. chiron	—	3	—	—
'Thalassohelix' ziczac	1	17	—	—
Therasia decidua	1	3	—	—
Phenacohelix giveni	—	12	—	4
P. pilula	1	2	—	—
'P.' n.sp. 1	1	14	—	9
P. ponsonbyi	—	—	—	14
Therasiella neozelanica	—	2	—	—
T. celinde	—	2	—	—
T. tamora	—	—	—	1
Obanella rimutaka	—	2	—	5
Laoma mariae	—	—	5	11
L. n.sp. aff. *marina* 1	—	—	—	1
L. leimonias	—	—	—	1
'Phrixgnathus' erigone	—	15	—	—
'P. ariel	—	2	—	1
'P.' moellendorffi	—	17	—	1
'P.' conella	—	5	1	—
'P.' poecilosticta	—	1	—	—
'P.' levis	—	—	3	9
'P.' n.sp. 59	—	1	—	—
'Paralaoma' n.sp. 38	—	1	—	—
'P.' n.sp. 29	—	2	3	—
'P.' lateumbilicata	—	—	—	6
P. caputspinulae	—	—	—	1
Cionella lubrica	—	—	3	5
Oxychilus cellarius	—	—	5	27
Helix aspersa	—	1	†	†
Vallonia sp.	—	—	—	3
TOTAL LIVE	5		33	
TOTAL DEAD		183		677
TOTAL SPECIES	5	25	12	34
TOTAL SPECIES AT STATION	25		36	

† Seen but not collected

Appendix 3F. Results of sampling from near Waitomo Caves (dead shells); first column – occurrence at Manukau Peninsula (ma) and Wellington (we)

		Cave talus	Bush margin	Black loam	Rock top	Total snails
(ma,we)	*Omphalorissa purchasi*	46	22	25	20	113
(ma)	*Liarea hochstetteri carinella*	—	1	1	1	3
(ma,we)	*Delos coresia*	10	2	10	4	26
(ma)	*D. jeffreysiana*	4	1	—	—	5
	Schizoglossa novoseelandica	—	—	2	2	4
(ma,we)	*Cavellia buccinella*	3	1	1	2	7
(ma)	*C. roseveari*	—	1	—	—	1
(ma)	*C. colensoi*	39	3	12	1	55
(ma,we)	*Mocella eta*	11	8	12	29	60
(ma)	*'M.'* n.sp. aff. *maculata*	42	5	13	10	70
	'M.' prestoni	2	—	—	1	3
	'M.' accelerata	1	2	—	5	8
	'M.' n.sp. aff. *segregata*	1	—	—	—	1
(ma,we)	*'Charopa' pseudanguicula*	22	2	2	9	35
(ma)	*'C.'* n.sp. aff. *pseudanguicula* 1	2	2	1	—	5
	'C.' n.sp. aff. *pseudanguicula* 2	56	31	20	59	166
(ma)	*'C.' chrysaugeia*	2	1	1	—	4
(ma)	*'C.' pilsbryi*	2	—	—	—	2
(ma,we)	*Charopa coma*	1	1	4	1	7
(ma)	*'C.' ochra*	—	2	—	—	2
(ma)	*Fectola mira*	5	1	—	—	6
(we)	*F. trilamellata*	15	—	13	1	29
(ma)	*Pulchridomus barbatulus*	3	—	—	—	3
(ma,we)	*Huonodon pseudoleiodon*	2	—	—	—	2
(ma,we)	*H. hectori*	101	26	34	63	224
	Thermia subincarnata	1	—	—	—	1
(we)	*Allodiscus* n.sp. aff. *tessellatus*	3	1	2	—	6
(ma)	*A.* n.sp. aff. *granum*	4	2	—	1	7
(ma,we)	*A. planulatus*	—	—	1	7	8
	A. tullia	26	—	—	—	26
	'Geminoropa' moussoni	63	2	—	—	65

		Cave talus	Bush margin	Black loam	Rock top	Total snails
(ma)	*Serpho kivi*	—	—	—	2	2
(ma,we)	*Flammulina perdita*	—	—	1	—	1
	F. n.sp. aff. *crebriflammis*	2	—	1	—	3
(ma,we)	*Suteria ide*	5	7	9	4	25
	S. raricostata	3	—	—	—	3
(ma)	*Phenacohelix giveni*	26	24	12	23	85
(ma)	*P. pilula*	6	1	1	—	8
(ma)	*P. ponsonbyi*	30	6	12	17	65
(ma.we)	*Therasiella neozelanica*	2	1	6	2	11
(ma)	*T. tamora*	—	—	—	3	3
(ma,we)	*Obanella rimutaka*	44	8	2	5	59
(ma,we)	*'Laoma' mariae*	4	11	14	16	45
	L. n.sp. aff. marina 2	3	4	7	1	15
(ma.we)	*L. marina*	3	—	—	—	3
(ma)	*L. leimonias*	6	1	1	—	8
(ma)	*'Phrixgnathus' erigone*	35	36	20	53	144
(ma)	*'P.' ariel*	11	1	—	—	12
(ma)	*'P.' conella*	—	5	4	4	13
(ma)	*'P.' poecilosticta*	—	—	1	—	1
(ma)	*'P.' pirongiaensis*	2	—	1	—	3
	'P.' n.sp. 61	2	11	9	2	24
(we)	*'P.' viridula*	5	1	—	1	7
(ma,we)	*'Paralaoma'* n.sp. 29	56	14	35	66	171
(ma,we)	*'P.'* n.sp. 1	—	2	1	1	4
(ma,we)	*'P.'* n.sp. 8	5	—	5	—	10
(ma)	*'P.' serratocostata*	1	2	2	1	6
(ma)	*'P.'* n.sp. 40	—	—	1	—	1
	'P.' n.sp. 32	28	3	2	28	61
(ma)	*'P.'* n.sp. 33	—	—	—	3	3
	'P.' n.sp. aff. 7	1	—	—	—	1
	'Paralaoma' miserabilis	2	—	—	—	2
	'P.' n.sp. 45	24	10	4	12	50
(ma)	*Oxychilus cellarius*	—	1	—	—	1
(ma)	*Helix aspersa*	—	1	—	—	1
	TOTAL SHELLS	773	267	305	460	1805
	TOTAL SPECIES	50	42	40	36	65