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AN AREA OF EXCEPTIONAL LAND SNAIL DIVERSITY: THE MACLEAY VALLEY, NORTH-EASTERN NEW SOUTH WALES

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Abstract

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In the Macleay Valley region, north-eastern New South Wales, the combination of rainforest and limestone has provided a unique environment for the evolution of a quite remarkable land snail fauna. 108 native species have been recorded in an area approximately bounded by the Nambucca River in the north, the Hastings River in the south and the eastern escarpment of the Great Dividing Range in the west. Much of this diversity is centred on a series of limestone exposures which outcrop in an east-west direction from just west of Kempsey to the ranges of the Werrikimbe National Park. Diversity levels on the limestones are high with 39 species of land snails recorded at an outcrop near Yessabah. In contrast rainforest sites have smaller numbers of species. Comparatively few species inhabit the sclerophyll forests. A number of species are endemic to the limestones and some of these exhibit specialised microhabitat preferences. This study examines the distribution of these species within the Macleay Valley region and elsewhere, and attempts to explain the development of this fauna in terms of past climate-induced changes in vegetation communities within the region. The implications of these findings for land snail conservation are discussed.

Introduction

The Macleay Valley in north-eastern New South Wales is an area of exceptional land snail diversity. Stanisic (1994) briefly discussed the significance of this region in an overview of land snail distribution in eastern Australia. Reasons for this concentration of terrestrial molluscs fauna in such a comparatively small area were linked to the co-occurrence of two significant land snail habitats — rainforest and limestone. Rainforest in the region is a complex mixture of a variety of structural types, and the limestone, as a series of isolated outcrops, is extensive and geographically unusual. In New South Wales, limestone outcrops occur mainly along the central and western parts of the Great Dividing Range from the Queensland to Victorian borders. The limestone outcrops of the Macleay Valley are unique in that they occur east of the Great Divide.

Moisture is critical for the survival of land snails. Because areas of rainforest are indicative of long term moisture stability it is not surprising that significant snail communities live in the rainforests of eastern Australia (Bishop, 1981; Smith, 1984; Stanisic, 1994). However the influence of limestone on the distribution of land snails in eastern Australia is largely undocumented. Stanisic (1990) described new Charopidae from outcrops in the Macleay Valley and discussed the refugial nature of limestone habitats.

This study focusses on the land snails of the Macleay Valley region and specifically examines the significance of both rainforest and limestone outcrops in relation to their distribution within this area.

Study area

The Macleay Valley is situated west of the township of Kempsey, NSW. The study area is approximately bounded by the Nambucca and Hastings Rivers (in the north and south respectively) and the coastline and the Great Escarpment (in the east and west respectively). Collecting sites are confined within 30°30′–31°30′S and 152°00′–153°00′E (Fig. 1).

Rainfall in the region is generally non-seasonal (Nix, 1981) but highly variable. Mean annual rainfall is 1000–2000 mm but may exceed 3500 mm on some of the highest peaks where cool temperate rainforest occurs. In the lowlands and foothills, areas of dry rainforest receive 630–1100 mm and are characterised by a markedly seasonal climate.

The region supports a diverse array of vegetation communities including several distinct rainforest structural types (Fig. 2). On the coast, littoral rainforest, sometimes mingled with sub-

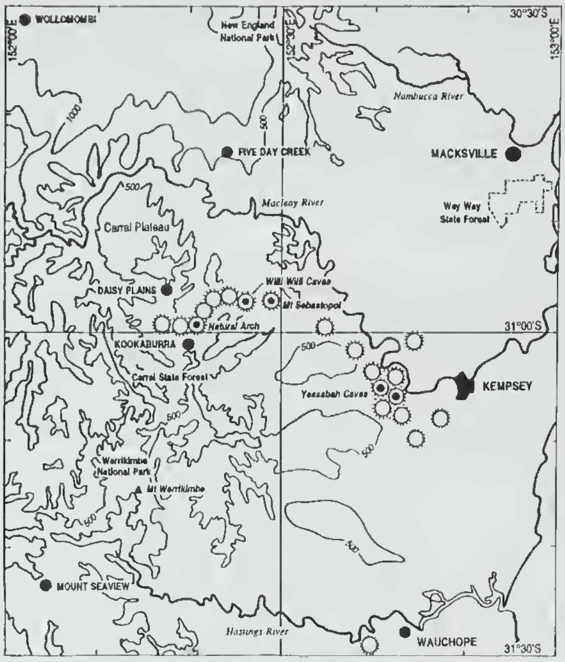

Figure 1. Study area. Limestone outcrops represented by spiked circles.

tropical rainforest, e.g. Sea Acres Nature Reserve (31°27'S, 152°55'E), occurs among drier sclerophyllous communities. Open woodland communities, often largely cleared for farming dominate the less populated lowlands. In lowland areas where rainfall is high due to local topographic effects, subtropical rainforest flourishes e.g. Way Way State Forest (30°47'S, 152°56'E) and Wilson River Primitive Reserve (Fig. 2A. 31°12'S, 152°28'E). Along water courses, e.g., Maria River (31°08'S, 152°49'E), riverine rainforest provides important corridor habitat. On wetter slopes of the foothills of the Great Divide, wet sclerophyll forest alternates with dry sclerophyll and dry rainforest. The latter forest type is characterised a number of deciduous and semi-deciduous tree species and is a feature of the region (Floyd, 1983). In spite of the fact that these forests are comparatively depauperate floristically, their presence indicates a higher and more stable moisture regime than that available to nearby sclerophyll forest communities. Often this rainforest type is found growing on rock outcrops (limestone and volcanic) which not only act as sinks for available moisture but also as local fire shadows. There is an ample litter layer to provide considerable living spaces for land snails. Large stands of dry rainforest are located on the mid-slopes of Mt Seaview (Fig. 2D. 31'24°S, 152'15°E), west of Wauchope (Floyd, 1980), and in the upper Macleay River valley on the Bellbrook-Wollomombi Rd (30°45'S, 152°22'E). Most of the limestone outcrops in the region are covered in this type of vegetation. On the upper slopes and plateaux of the western ranges, warm temperate rainforest dominates. Much of this has been logged in the past (Adam, 1987) but reasonable stands are still present in such places as the Carrai Plateau (30°55'S, 152°17'E), Fenwicks Flora Reserve (Fig. 2B. 31°17'S, 152°08'E) and Werrikimbe National Park (31°14'S, 152°17'E). On the very tops of the highest peaks e.g. Banda Banda Flora Reserve (31°09'S, 152°25'E), small stands of cool temperate rainforest, dominated by *Nothofagus moorei*, occur. The limestones of the Macleay Valley (Fig. 1) occur as an archipelago of outcrops from near Sherwood, just west of Kempsey, in a west-northwest direction to Stockyard Creek in the Werrikimbe National Park (Lishmund et al., 1986). Those in the lower Macleay River valley, e.g., Yessabah (31°05'S, 152°41'E), Sherwood (31°03'S, 152°41'E), are situated amidst dry woodland and support islands of dry rainforest. The limestone rock traps moisture and allows rainforest species to persist in otherwise inhospitable countryside. In contrast some of the more westerly outcrops are located among stands of dense rainforest, e.g., The Castles (Fig. 2C. 30°59'S, 152°19'E). Some of the outcrops are only very low exposures but the majority are substantial karst towers. In all cases their occurrence signals a dramatic change in vegetation and land snail fauna to that of the surrounding forests, especially when they occur in the drier woodland landscape.

In both of these main habitat types, i.e., rainforest and rainforest with limestone, land snails are favoured by a number of environmental factors which are not part of the sclerophyllous forest habitat profile. The ecologic factors which favour rainforest e.g. moisture and eutrophic soils are also those which favour the success of terrestrial molluscs. In addition rainforest provides ample food and shelter for snails (Bishop, 1981). Of particular importance to the snails is the accumulated litter and debris which characterise the forest floor of rainforests and provides a wide array of living spaces. Limestone outcrops, with their vegetative cloak of rainforest, are able to provide similar benefits for land snails with the added bonus of a ready supply of calcium for shell production. The complex array of cracks and holes which are a feature of limestone outcrops (Fig. 2E) enhance the matrix of

Figure 2. Land snail habitats in the study area. A, subtropical rainforest, Wilsons River Primitive Reserve; B, warm temperate rainforest, Fenwicks Flora Reserve; C, The Castles; D, dry rainforest, Mt Seaview Nature Reserve; E, microtopography of limestone habitat at Yessabah.

microhabitat types available for exploitation as living space.

Sampling methodology

Preliminary sampling of the area by the author began in 1987 but intensified in 1992 as part of a wider study to examine the charopid land snail fauna of limestone outcrops in eastern New South Wales. Eighty-five sites are included in the data set of localities used in this study. Each site is uniquely defined by a combination of latitude, longitude, altitude and a habitat descriptor which is vegetation-based. Of these, thirteen represent casual collecting, largely by non-specialist personnel. The majority (72) have involved the author and were sampled according to a systematic protocol. Many sites within the study area have been visited on more than one occasion.

Snails were hand collected and a quantity of leaf litter was taken from each site for sorting by microscope. Because snails lend themselves to 'post-mortem' sampling, litter sorting is an effective method for determining the presence or absence of species. This is particularly critical in a study such as this in which small snails ($<$ 5 mm shell diameter or height) form the greater proportion of species present. All specimens were identified to species using both shell and animal characters by the author.

Results

The data set of examined material consists of 10 285 specimens belonging to 111 species. Of these, three species are introductions and are not included in the analyses. The remaining 108 species (69 undescribed) belong to 14 families. Species diversity is not evenly spread across families (Fig. 3). The largely litter-dwelling, tiny-shelled Charopidae is by far the most speciose with 53 species. Preliminary taxonomic studies show that this charopid diversity is only partially due to local radiations. There is however evidence of vicariant species. The charopid *Letomola contortus* (Hedley, 1924), from the Yessabah-Sherwood limestones, has an undescribed sister species in the more westerly Mt Sebastopol-Castles limestone blocks. Similarly the charopid *Coenocharopa yessabahensis* (Stanisic, 1990), from Yessabah has a sister species in the dry rainforests of the Mt Seaview area. The larger-shelled Camaenidae are next most diverse with 17 species represented including a significant local radiation of 'chloritids' (Fig. 6C) which show parapatric ditributions in the dry rainforest-sclerophyll forest complex. A number of new species of helicarionid semislug (Fig. 6E) including the large *Parmavitrina planilabris* (Cox, 1866) (Fig. 6D) are features of the snail fauna. Some carnivorous rhytidids (Fig. 6F) are also endemic to the region.

Numbers of species per site (Fig. 4) varied markedly. Sites which included limestone recorded the highest numbers of species. The large outcrops at Yessabah (39 species), Natural Arch (34 species) and Mt Sebastopol (32 species) yielded the most species per site. However, even the smaller outcrops yielded relatively high numbers of species e.g. West of Sherwood (23) and south of the Willi Willi Rd (23). In comparison the best rainforest sites were in subtropical rainforest at the Pines rest area, Way Way State Forest and dry rainforest on the Wollomombi Rd in the upper Macleay River valley where 20 species were recorded. Other notable rainforest sites were the Mt Seaview Nature Reserve (18 species) and Fenwicks Flora Reserve (16 species). Cool temperate rainforest sites were comparatively impoverished (7–10 species). In contrast the sclerophyll sites all registered less than 10 species with many sites recording less than 5 species. These figures are not absolute and should be regarded only as indicators of site richness. The patchy nature of snail distribution in the natural environment (Stanisic, pers. obs.) makes it highly likely that additional species will be discovered in the region.

Examination of species distributions within broad habitat types shows that the limestone/rainforest biotope (10 sites) supports 67 species throughout the study region. Sites with rainforest alone (47) account for 85 of the species. Sites classified as dry and wet sclerophyll forest and including partially cleared woodland (28) were comparatively depauperate with only 31 species represented. If the rainforest/limestone biotope is considered as part of the rainforest habitat then 105 of 108 species are living in closed forests. Dry rainforest sites, including those with limestone support 71 species.

The insular nature of the region's land snail fauna is evident in the analysis of the species distribution profiles (Fig. 5). Forty-eight species occur only within the study area. Most of these belong to the Charopidae (32 species) which are very small and presumably less able to disperse. However, somewhat surprisingly, there are also a significant number of larger Camaenidae (9 species) endemic to the region. In the case of the

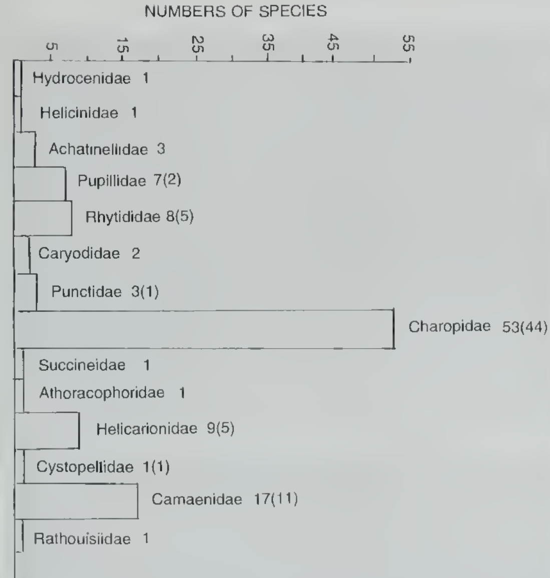

Figure 3. Distribution of Macleay Valley land snails among families. Numbers in brackets indicate undescribed species.

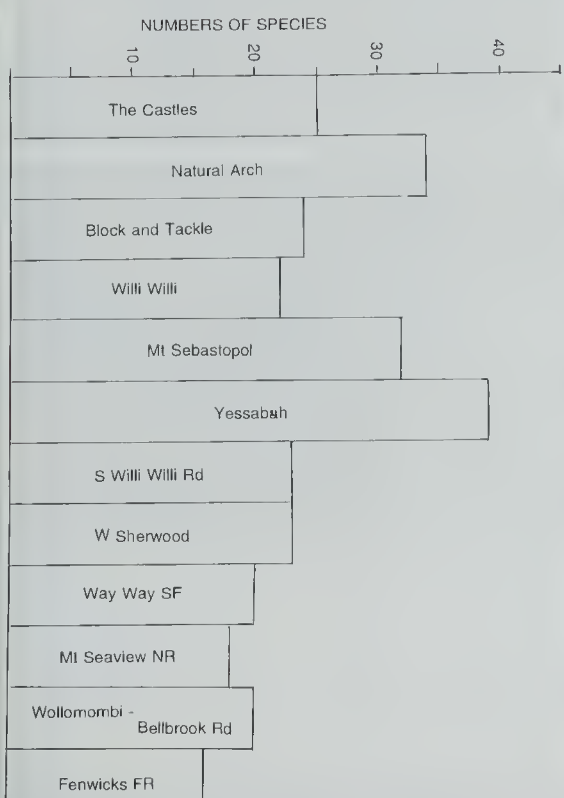

Figure 4. Numbers of species from selected limestone and rainforest sites. First eight localities on left are limestone sites.

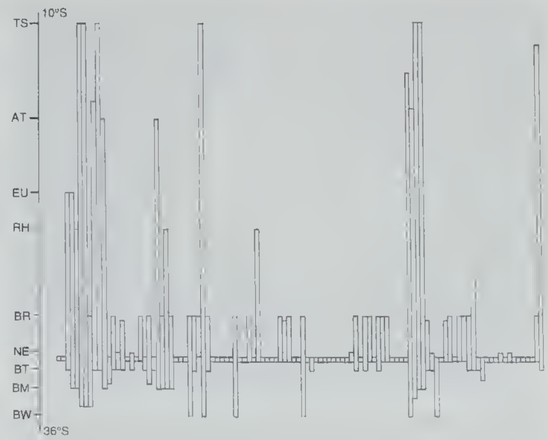

Figure 5. Distribution profiles (north-south) of Macleay Valley land snails along the east coast of Australia. BW = Braidwood; BM = Blue Mountains; BT = Barrington Tops; NE = New England at Armidale; BR = Border Ranges of Queensland/New South Wales; RH = Rockhampton; EU = Eungella west of Mackay; AT = Atherton Tableland; TS = Torres Strait. Study area located between BT and NE. Note the high number of study-area endemics represented by the interrupted line of squares.

Charopidae the endemism is centered on the limestone outcrops and high altitude rainforest areas such as the Carrai Plateau and Fenwicks Flora Reserve. In contrast the camaenid endemics are largely confined to the drier lowland and foothill environments. A significant proportion of species belong to the land snail faunal subregion which extends from the Border Ranges of southeastern Queensland to Barrington Tops in central New South Wales (Stanisic, 1994: Fig. 2, subfaunal unit G). However, there are also a considerable number of wider ranging species which complement the faunal make-up. The study area is the southern limit for a number of northern subtropical elements including *Papuexul bidwilli* (Reeve, 1853) (Fig. 6B) and the mainly calciphilic Hydrocenidae represented by *Georissa laseroni* (Iredale, 1937) (Fig. 6A).

Within the study area 26 species occurred only within the rainforest biotope including 15 (14 charopids) which are endemic to the study region. Most of these local rainforest endemics (10) were restricted to the warm temperate and cool temperate forests above 800 metres. Of particular note was the subtropical rainforest at Way Way State Forest where 4 endemic species were recorded. Sixteen species occurred only on

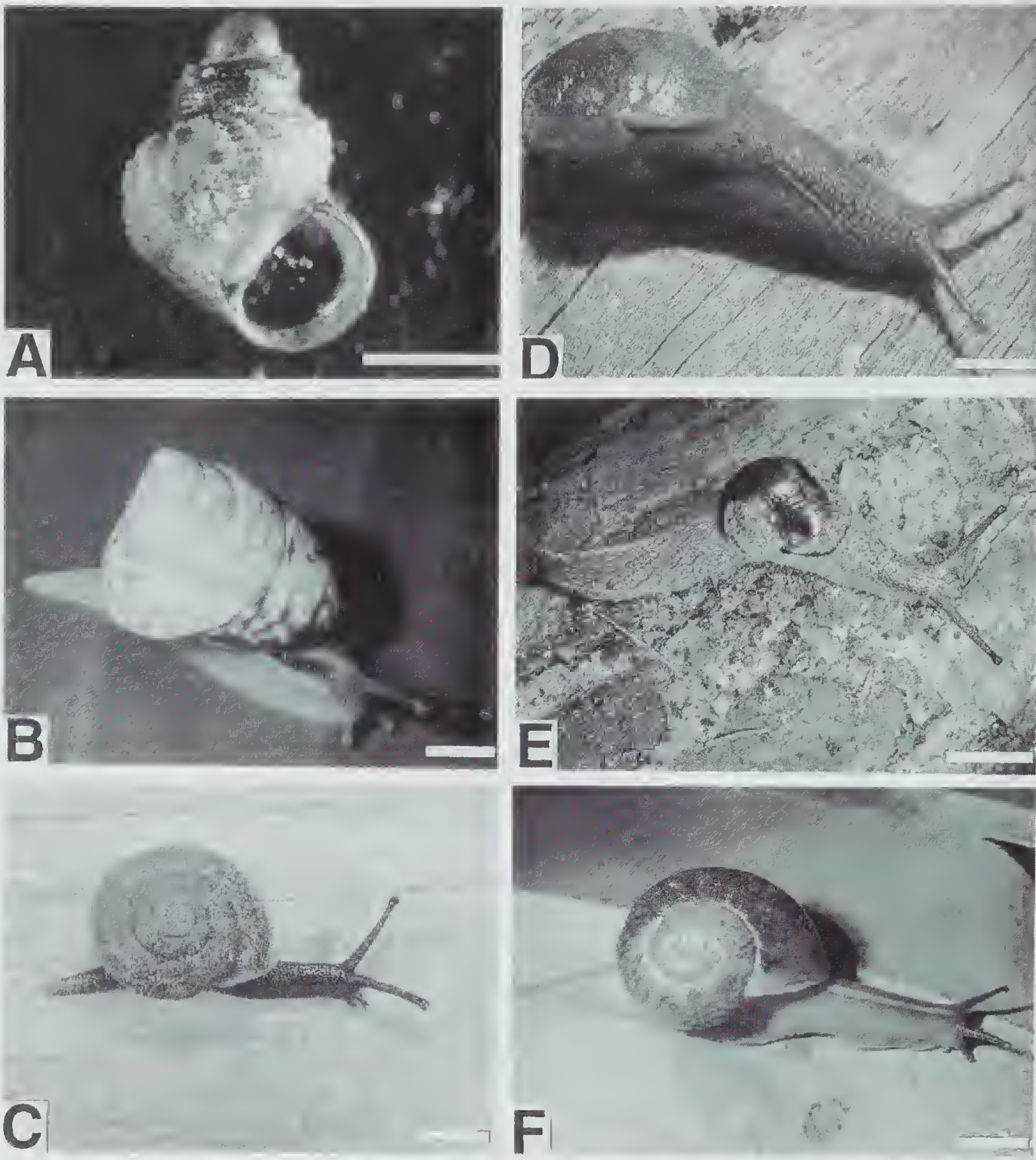

Figure 6. Land snails of the Macleay Valley region. A, *Georissa laseroni*; B, *Papuexul bidwilli*; C, a new species of camaenid from Kippara State Forest; D, *Parmavitrina planilabris*; E, a new semislug from dry habitat near Temagog; D, a new species of carnivorous snail (Rhytididae) from Thumb Creek State Forest. Scale lines: A = 1 mm; B, C = 5 mm; D, E, F = 10 mm.

the limestone outcrops and in no other habitat type. This group of habitat-restricted species included 11 (10 charopids) which are endemic to the region. The more easterly outcrops had the higher levels of endemism. A number of these limestone-restricted species lived on the surface of the karst. These include the charopids *Letomola contortus*, *Coenocharopa yessabahensis* and *Rhophodon kempseyensis* (Stanisic, 1990) as well as *Georissa laseroni*. In absolute contrast the sclerophyllous component of the vegetation mosaic included only 3 species not found in the other habitat types. Not suprisingly the limestone sites showed most affinity with the pure rainforest sites (49 species in common) and very reduced affinity with the sclerophyllous sites (16 species in common).

Discussion

The land snail fauna of the Macleay Valley region in north-eastern NSW is remarkably diverse. Numbers of species per individual site are among the highest in eastern Australia (Stanisic, 1994). The total number of species compares favourably with that of the Wet Tropics biogeographic region (Stanisic et al., 1994). This region (approximately 15–19°S, 145–146°30′E) is considerably larger than the Macleay Valley yet supports only 222 species (185 endemic) on current estimates. In spite of extensive and widespread collecting I do not know of any other area of comparable size in eastern Australia which supports more than 100 species including such a large endemic component.

Land snails are slow moving and particularly prone to desiccation. Both these factors would make them peculiarly sensitive to past events of climatic drying which have reduced rainforests (= closed forests) on the Australian continent to isolated fragments (Adam, 1992). This change to drier conditions has been gradual but presumably involved many episodes of contraction and expansion (Kershaw, 1981) during which time the sclerophyllous forest types came to dominate the landscape. Land snails appear to have retained a high profile in the rainforests with relatively little radiation into surrounding drier forests. This pattern is strongly evident in the Macleay Valley region where 105 (37 endemics) species live in closed forest environments and highlights the importance of rainforest refugia as providers of long term moisture stability. However, the history of environmental change in the Macleay Valley region has been complicated by the presence of limestone outcrops which have enabled the closed forest habitats to persist in otherwise dry areas. By acting as moisture reservoirs and fire shadows they have provided an important secondary habitat for the land snails. The presence of limestone endemics which exploit the limestone surface as living space and show possible feeding apparatus specialisation (Stanisic, 1990), demonstrates their significance as epicentres of evolution. In sclerophyllous countryside e.g. Yessabah, they provide a stark contrast in species numbers between adjacent habitat types. The Yessabah outcrop supports 39 species yet any surrounding sclerophyll site has less than 10 species. A similar though less remarkable contrast is seen between limestone sites and rainforest sites.

The derivation of this rather unique and diverse regional community of land snails would appear to be intimately tied to the presence of two important snail refugia — limestone and rainforest. In the context of past climatic changes they would have provided 'safe havens' for wider spread species and important centres of evolution as mesic communiies were isolated in moist refugia (Galloway and Kemp, 1981). The presence of numerous endemics in the upland rainforests, on limestone karsts, and in isolated refugia such as Way Way State Forest are probable testimony to these past events. Patterns of past connections and subsequent isolation are supported by the presence of disjunctly distributed sister species. The intensity of these historical changes is particularly evident at the dry rainforest-sclerophyll ecotone where a significant radiation of closely related camaenids has occurred. Their distribution patterns suggest a complex history of environmental sifting. In this habitat type, the modern-day influence of annual burning to reduce fuel build-up would also play an important part in the survival of snail populations and species.

Conservation

From a conservation viewpoint the above findings have wide-ranging implications. Limestone habitats are important refugia for land snails. Invertebrates in these habitats often receive indirect protection because of the tourist and recreational potential of limestone caves. However, a large number of outcrops do not contain caves (Lishmund et al., 1986) yet still support significant invertebrate communities, particularly land snails. Some of these species are restricted endemics. From a land snail perspective all limestones should be included in the National Estate.

There has been a tendency to focus on humid and moist rainforest types in the conservation debate to the detriment of the dry rainforest communities which are widespread in eastern Australia (Gillison, 1987). Their visually unattractive appearance and limited tourist potential has, in some cases, resulted in their large scale and largely uncontested removal e.g. brigalow. Their representation in the National Estate, particularly in north-eastern New South Wales (Floyd, 1987), is poor. This study shows that they are important habitats for land snails and deserve greater consideration in listing proposals.

Finally, it is difficult to see how the outcomes of this study could have been achieved without significant taxonomic input. Much of the invertebrate consevation debate is being reduced to rapid biodiversity assessment which involves limited systematic involvement. Knowledge of species ecology, their degree of endemism and relationships to each other-all essential components of the systematist's craft-have been central to identifying the key conservation issues of this study.

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