

SNAIL FAUNAS IN SOUTHERN ENGLISH CALCAREOUS WOODLANDS: RICH AND UNIFORM, BUT GEOGRAPHICALLY DIFFERENTIATED

R.A.D. CAMERON¹, B.M. POKRYSZKO² & D.C. LONG³

¹Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK, and Department of Zoology, The Natural History Museum, London SW7 5BD, UK.

²Museum of Natural History, Wrocław University, Sienkiewicza 21, 50-335 Wrocław, Poland.

³83 Moorend Road, Leckhampton, Cheltenham GL53 0HB, UK.

Abstract The snail faunas of 30 400m² woodland sites distributed among the Chilterns, the western South Downs, the Cotswolds and the Wye Valley were sampled in a standardized way. Evidence shows that species inventories are nearly complete. All faunas show a high level of similarity to each other, on both presence and absence data, and on measures taking account of relative abundance. Sites from the same area cluster together in these analyses; this generally reflects differences in environmental conditions and history, which influence the occurrence and abundance of only a few species, rather than absolute geographical limitations on species. The Cotswolds have the richest faunas, due mainly to the wetland element at some sites. The Chilterns have the poorest; woodlands there are dry and mainly secondary. Nevertheless, the Chilterns hold three-quarters of all species found. Some of these sites are amongst the richest in N. Europe, and contain nearly all the regionally available fauna. These results are discussed in relation to earlier surveys in some of the same areas. Less intensive versions of the same sampling technique underestimate site richness and overestimate local heterogeneity. More extensive and repeated qualitative studies are far more effective for slugs, and provide good estimates of richness for areas of 25 ha or more. The results are also discussed in relation to the patterns seen in N. Europe and elsewhere.

Key words Land snails, woodlands, species richness and composition

INTRODUCTION

The land mollusc fauna of Britain, as of northern Europe as a whole, is very well known in general terms. Most native species have woodland or wetland affinities, reflecting the predominant vegetation before the development of agriculture (Boycott, 1934; Kerney, 1999). Although this fauna is regionally species poor relative to those of regions at lower latitudes, records from individual forest sites from a number of north European countries indicate that local faunas can be rich, even by global standards (Waldén, 1981; Solem, 1984; Cameron and Pokryszko, 2004; Pokryszko and Cameron 2005).

Two of us set out to examine such faunas, and to explore variation in richness and composition of forest faunas across that part of Europe from which all forests were absent during the last glaciation. In two recent papers (Cameron and Pokryszko, 2004; Pokryszko and Cameron, 2005) we used published reports of local forest faunas from across the region in addition to data from many sites sampled by us. Two important analytical problems emerged. First, the areas involved varied considerably, reflecting a variety of aims in the studies. Second, and most importantly, it was apparent that studies varied in the efficiency

with which they inventoried the faunas of their chosen areas. Efficiency varies with methods, but getting complete inventories of sites where abundance of individuals is generally low is extremely difficult in any case (Cameron and Pokryszko, 2005).

Included in the data we used in our studies were our own samples from calcareous woodland in southern England. In order to overcome, as much as possible, the effects of sampling error, and to get data compatible with others, analysis concentrated on groups of adjacent sites, considering the aggregate faunas. Within Britain, such aggregate faunas appeared to be very uniform in composition over distances within which faunas in some other parts of northern Europe show marked differences (Pokryszko and Cameron, 2005).

Here, we consider these samples in more detail. We show that they can be regarded as sufficiently complete, as inventories, to sustain detailed quantitative analysis. We use such analyses to expose geographical and ecological patterns, and to make comparisons with other studies, both for methodological and biological purposes. In particular, we use earlier, detailed studies of some of the sites made independently by one of us, D.C. Long. Where work has been done by authors independently, they are referred to by their initials: RADC; BMP; DCL.

SAMPLING AREAS AND SITES

Four areas were chosen for study. Two of these have been the subject of long term and ongoing study by DCL: the Wye Valley, with woodlands on Carboniferous Limestone and Devonian Old Red Sandstone, and, in much more detail, the Cotswolds, on Jurassic limestone. The other two, the western South Downs, and a part of the Chiltern Hills, are both on Cretaceous chalk; the former was a part of the area surveyed by Cameron (1973). Within each area, c. 400 m² sites were chosen by RADC and BMP that had full tree cover, that were not on habitat edges, and that appeared to contain appropriate microhabitats such as fallen and rotting timber and patches of deep litter. Eight sites were sampled on the South Downs and on the Cotswolds, and seven on the Chilterns and in the Wye valley. Most sites were roughly square (20 × 20m), but some were rectangular to ensure inclusion of appropriate microhabitats.

Appendix 1 lists the sites, and gives details of their locations and vegetation. In the Wye valley, the South Downs and the Chilterns, all sample sites were within 10 km of each other. In the Cotswolds, all but one site were within 12 km of each other, the exception being Midger Wood, 19 km from the nearest other site. All sampling was carried out in late April and early May 2003.

In the two areas on limestone, the woodlands sampled are all believed to be ancient, though subject to management. Five sites in the Wye valley, and four in the Cotswolds were located in National Nature Reserves, and the remaining sites in the Cotswolds are all in Gloucestershire Wildlife Trust Reserves. Beech *Fagus sylvatica* was present in all but one site (Midger Wood, Cotswolds, which has beech elsewhere in the wood), and was frequently the dominant tree. Coppicing (mostly of hazel *Corylus avellana*) had clearly taken place in many sites. In the Cotswolds, Siccaridge 3 and both Workman's Wood sites contained small areas of wooded wetland, with alder *Alnus glutinosa* or opposite-leaved saxifrage *Chrysosplenium oppositifolium*. The same was true for Lady Park Wood 3 and Symonds Yat 2 in the Wye valley. Symonds Yat 1 was on Devonian Sandstone rather than Carboniferous Limestone, but its vegetation and soil pH (7.0, colourimetrically determined) indicated a high level of available calcium.

The status of woodlands in the two areas on

chalk is harder to determine. On the western South Downs, the dominance of beech is largely the result of plantation (Cameron, 1973), but the ground vegetation suggests that at least patches of woodland along the scarp are ancient. The area of Rook Clift includes the remnants of coppicing, and a mixed canopy including large leaved lime *Tilia platyphyllos* (Mabey, 1996). Conversely, Cameron (1973) found ancient or subfossil shells of typical grassland snails, for example *Helicella itala*, at a number of sites then covered in mature woodland. Only Rook Clift 2 held *Chrysosplenium*; chalk soils are generally well drained, and sites were on the steep scarp slope. Evidence from successive editions of Ordnance Survey maps, and from the comparison of habitat notes taken in the 1970s and in 2003 show that woodland has expanded slightly by natural succession over the 20th century, and that the intensity of economic management has declined.

The scarp woodlands sampled on the Chilterns are similar, but with less evidence of the survival of ancient patches. One site, Chinnor 1, is shown unwooded in the 6th edition Ordnance Survey map (last full revision, 1930), and Chinnor 4 is shown as woodland edge. Non-native trees such as horse chestnut *Aesculus hippocastanum*, sycamore *Acer pseudoplatanus* and Norway maple *Acer platanoides* occur frequently, as does ivy *Hedera helix*, a species associated with disturbance. Far more old/subfossil shells of grassland snail species were found in the Chilterns than elsewhere (see below, results); only Chinnor 3 yielded none. All sites were on steep or moderate slopes, well drained and lacking any indications of wetland.

METHODS AND ANALYSIS

SAMPLING

Within each site, two people (RADC and BMP) searched by eye for one hour. All live specimens and fresh empty shells were collected, or, in the case of some large, or rare, species easily identified, were counted, noted, and left in situ. In addition, c. 10 litres of litter were collected from many spots within the site. The material was coarse-sieved in the field. Material held by a 10 mm mesh was inspected; slugs and snails were removed, and the remaining litter discarded. Finer fractions were bagged, allowed to dry, and then passed through graded sieves down to 0.5

mm mesh indoors. Material passing through 0.5 mm mesh was discarded. The remainder was searched for molluscs under good lighting, using a binocular microscope for the finest fraction. Material from three sites was retained and re-examined. In each case only a few shells were found on the second examination, and no species not already detected. These additional individuals are excluded from the analyses. Snail specimens were identified and counted. Only live animals (at the time of sampling) and fresh empty shells were included, but the occurrence of species represented only by very old shells, potentially subfossil, was noted.

Most slugs were identified in the field and released. Because bagged samples were dried, and because this method of sampling is not adequate for slugs (Cameron and Pokryszko, 2005), no counts were made by species; presence only was recorded. No dissections were carried out, and some specimens are therefore referred to species aggregates. Slugs are excluded from most analyses. Nomenclature follows Kerney (1999), except for *Zenobiella*, rather than *Perforatella subrufescens*.

ANALYSIS

The first stage in analysis was to check the completeness of the inventories for areas and sites by considering the relationship between number of species and number of individuals collected, by constructing rank/frequency diagrams, and by use of the Chao estimators of the number of species missed in any particular array (Southwood and Henderson, 2000; Cameron and Pokryszko, 2005). The Chao estimator shows the number of species that may be missing from a sample or set of samples; the number of missing species is given by the equation:

$$\text{Number of species missing} = \frac{(\text{number of singletons})^2}{2 \times \text{number of doubletons}}$$

For single samples, singletons are species represented by one individual, and doubletons those represented by two individuals. Where several samples are involved, the same measure can be used, adding all samples together, but it is also possible to use frequency of occurrence; this assumes that the samples come from the same community.

The degree of differentiation between sites was examined by Whittaker's Index ($I = \text{number of species in the area} / \text{mean number of species per site}$) and its variant $I_{\max} = \text{number of species in the area} / \text{number of species in the richest site}$). Then the similarities between all possible pairs of sites and areas were examined, using presence and absence data, with the Nei index, $I_N = \text{number of species in common} / \text{geometric mean of the number of species present at each site}$ (Pokryszko and Cameron, 2005). Differences in frequency of occurrence (proportion of sites occupied) between areas are considered briefly. Numbers of some species were also compared between areas. Given the variability in numbers among sites within areas, and the difficulties involved in interpreting a large number of statistical tests carried out on similar data, we have looked at differences in the rank order of abundances between areas, considering only large differences in ranks as meaningful.

The numbers retrieved were also used to order the sites using Correspondence Analysis (CA). Statistical analyses were performed with the software packages CANOCO for Windows 4.0 (ter Braak & Smilauer, 1998). Species abundance data were logarithmically transformed ($\log(X+1)$) in order to reduce the importance of the most abundant species and to make their distribution correspond to a normal law (Legendre & Legendre, 1984; Labaune & Magnin, 2001). Also, rare species abundance was down-weighted using an algorithm available in CANOCO.

Comparisons were then made between the results obtained in this study and those reported by Cameron (1973) for the South Downs, and those obtained by Long (1969, 1980 and unpublished) for the Cotswolds. The former were obtained from sites searched for one person-hour, with 1.5 litres of litter collected and sorted. No complete record of numbers was kept. The latter, mainly but not exclusively based on repeated visual searches, include intensive surveys of some woods, in which the faunas of particular sites or sections within each can be distinguished.

RESULTS

Appendix 2 shows the numbers of each species

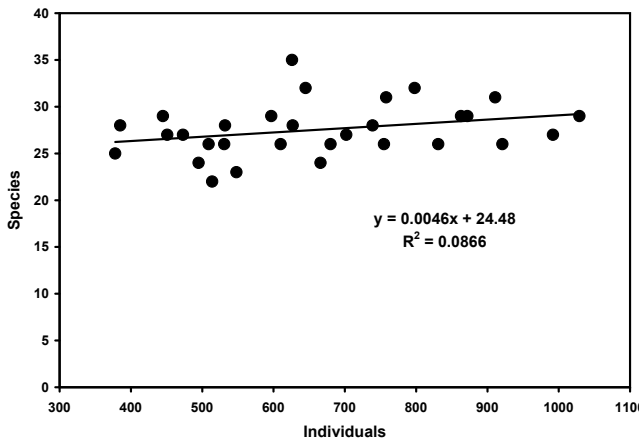


Figure 1 The regression of number of species on number of individuals for all sites used in the study.

of snail found alive or as fresh shells in each site. Appendix 3 shows the occurrence of slugs, and of snail species found only as ancient or subfossil shells. Overall, the array contains 43 species of snail found alive or fresh, and at least 14 species of slug; two of the latter are aggregates (*Arion ater* and *Arion hortensis*).

RELIABILITY OF SAMPLING

All sites sampled by RADC and BMP contain more than ten times as many individuals as species, the minimum ratio recommended by Cameron and Pokryszko (2005). None of the regressions of number of species on number of individuals for sites in each area approach significance. Since the number of sites, and therefore degrees of freedom in each is small, and differences between areas slight, an overall regression has also been calculated (Figure 1). Again, there is no significant relationship. Figure 2 shows the rank/ log % frequency of snail species in each area overall. It can be seen that there is, in each case, a marked steepening of the curve as the rarest species are reached. This indicates that any further species will be very rare, such that they can scarcely be considered as normal members of the fauna (Cameron and Pokryszko, 2005).

Table 1 shows the results of applying the Chao estimator to each site fauna. When, as here, the numbers of singletons and doubletons involved are small, the standard errors of these estimates are very large. As the site samples are similar in species richness and number of individuals, the mean value of the estimator is a useful indicator: 0.74 ± 0.19 . Overall, the samples appear to be complete, missing at most one or two species.

When frequency of occurrence in the whole array of 30 sites is considered, the singletons and doubletons are all species with optimum habitats outside woodland (Table 2). *Succinea putris* and *Vertigo substriata* are typically wetland species, *Abida secale* and *Monacha cantiana* are typical of more open habitats, and *Oxychilus draparnaudi* is usually anthropochorous.

Although the results of these tests do not guarantee the completeness of inventories (see discussion, below p. 24), we have analysed the data as they stand, taking no account of possible sampling error.

FAUNAL SIMILARITIES AND DIFFERENCES

Table 2 shows the frequency of occurrence of all 43 species of snail found in the study, by area and overall. 27 species (63%) were found in all four areas, and 16 (37%) were found in 90% or more of all sites. Table 3 shows the degree of differen-

Table 1 Species represented by single (S), and two (D) specimens at each sample site, and the resulting Chao estimator of missing species (see text). Sites are identified by the first letter of their names (Appendix 1). No realistic estimate can be made for Symonds Yat 2.

Chilterns				South Downs			
	S	D	Chao		S	D	Chao
A1	0	2	0	B1	3	2	2.25
A2	1	1	0.50	B2	1	1	0.50
C1	2	3	0.67	B3	1	4	0.12
C2	2	4	0.50	H1	4	3	2.70
C3	1	2	0.25	H2	0	1	0
C4	0	2	0	R1	0	2	0
C5	0	2	0	R2	2	3	0.67
				R3	4	2	4.0
Cotswolds				Wye valley			
	S	D	Chao		S	D	Chao
S1	3	4	1.12	L1	1	4	0.12
S2	1	2	0.25	L2	2	1	2.0
S3	3	2	2.25	L3	1	7	0.07
W1	0	2	0	H1	2	1	2.0
W2	1	3	0.17	H2	1	3	0.17
P	1	3	0.17	S1	2	2	1.0
R	1	8	0.06	S2	1	0	na
M	1	3	0.17				

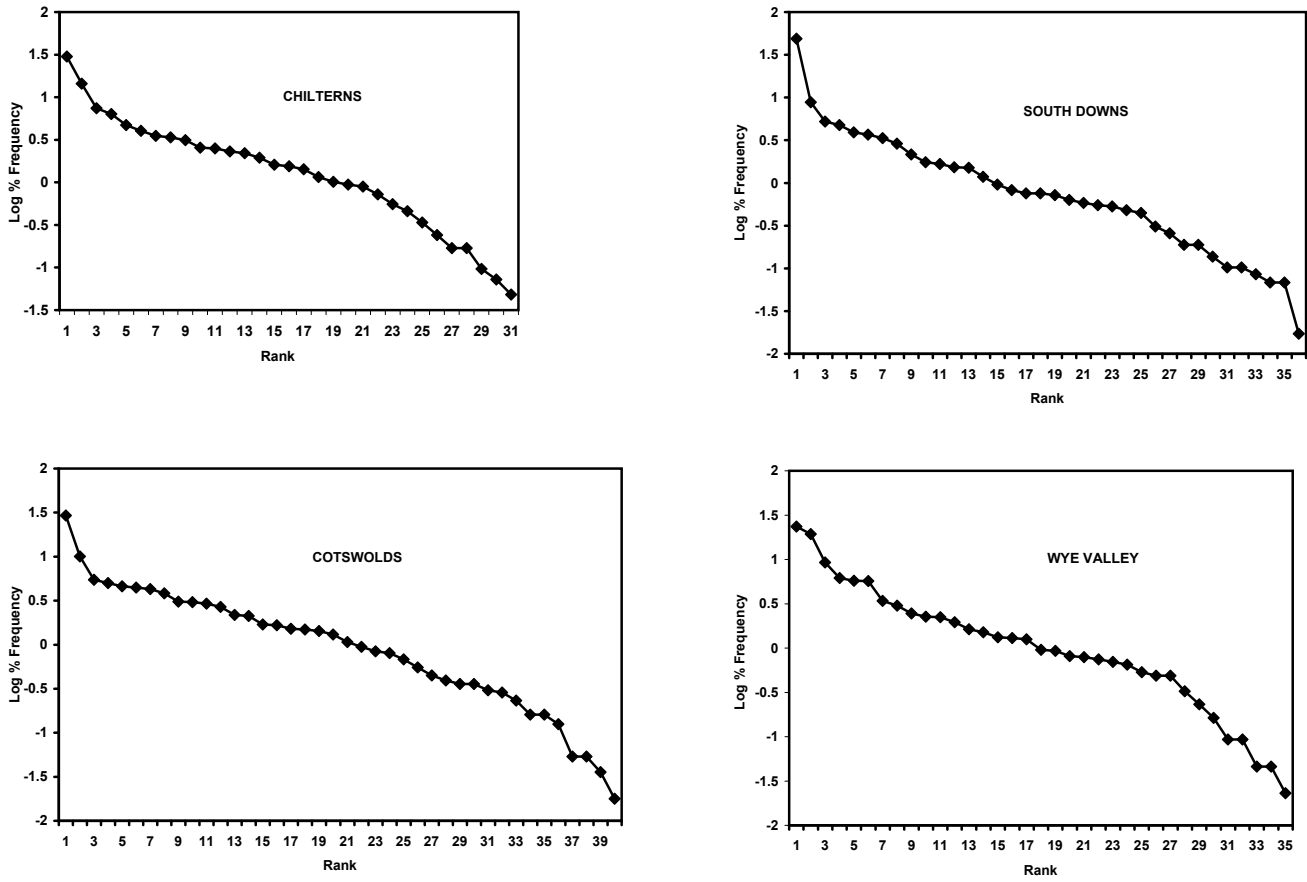


Figure 2 The logarithmic rank/ abundance relationships for each area, abundance given as the percentage of all individuals represented by each species.

tiation in the faunas, as shown by Whittaker's Index and its variant I_{\max} . The values are low, and are similar within each area. Overall, the value is slightly higher for Whittaker's Index itself, but not for its variant, I_{\max} . This reflects a degree of differentiation between regions, but the Cotswolds contain nearly all the species recorded overall. Table 4 shows the missing, and the unique, species in each area. Only the South Downs contain species not found in the Cotswolds sites: one, *Oxychilus draparnaudi*, is an anthropochorous species found in a single site close to a village. DCL has recorded it in other Cotswold woods. Another, *Vertigo substriata*, represented by a single shell, appears entirely anomalous, but the third, *Helicodonta obvolvata*, is genuinely confined, in Britain, to the South and Hampshire Downs (Kerney, 1999: 199).

Site-by-site comparisons of faunal similarity using the Nei Index confirm the homogeneity of the fauna in these woodlands (Table 5). They also show, however, that there is a slight, but signifi-

cant, geographical effect: on average, sites from the same area resemble each other more than they do those from elsewhere. This clustering is illustrated in Figure 3, which orders the sites by their similarities to the two least similar sites, first as between the Cotswolds and the Chilterns, and second as between the Wye valley and the South Downs. In both cases, although there is overlap between areas, there is a clustering by area. There is also a division between the chalk and harder limestone substrates. Ecologically, the Cotswolds and Wye valley sites used for ordering are relatively wet, while the Chilterns and South Downs sites are dry slopes. The Chilterns site (Chinnor 1) is in secondary woodland (see above, p. 14).

The Nei Index comparisons of the faunas of each area as a whole show even higher levels of similarity (Table 6). This implies that some of the differences between areas on a site-by-site basis are due to differences in the frequency of occurrence of species present in both. Inspection

Table 2 The number of sites in which each snail species was found in each area, and overall, ordered by overall frequency.

Species	CHIL				TOTAL	CHIL				TOTAL
	SD	COTS	WV	TOTAL		SD	COTS	WV	TOTAL	
<i>Carychium tridentatum</i>	7	8	7	30	3	6	8	7	24	
<i>Cochlicopa lubrica</i>	7	8	7	30	7	7	8	1	23	
<i>Ena obscura</i>	7	8	7	30	0	6	7	6	19	
<i>Discus rotundatus</i>	7	8	7	30	5	8	1	5	19	
<i>Vitrea pellucida</i>	7	8	7	30	0	3	8	7	18	
<i>Vitrea contracta</i>	7	8	7	30	3	5	4	6	18	
<i>Aegopinella pura</i>	7	8	7	30	5	2	4	5	16	
<i>Aegopinella nitidula</i>	7	8	7	30	0	8	5	1	14	
<i>Oxychilus cellarius</i>	7	8	7	30	4	4	5	0	13	
<i>Cochlodina laminata</i>	7	8	7	30	0	3	6	2	11	
<i>Clausilia bidentata</i>	7	8	7	30	3	4	2	1	10	
<i>Acicula fusca</i>	6	8	7	29	2	0	5	1	8	
<i>Cepaea hortensis</i>	7	8	5	28	0	0	4	4	8	
<i>Pomatias elegans</i>	7	8	4	27	0	8	0	0	8	
<i>Oxychilus alliarius</i>	6	7	6	27	0	0	6	0	6	
<i>Oxychilus helveticus</i>	6	7	7	27	0	0	2	2	4	
<i>Acanthinula aculeata</i>	6	5	7	26	0	1	2	1	4	
<i>Euconulus fulvus</i>	6	8	4	26	0	0	2	0	2	
<i>Cepaea nemoralis</i>	7	4	7	26	1	0	1	0	2	
<i>Punctum pygmaeum</i>	4	6	7	25	1	0	1	0	2	
<i>Trichia hispida</i>	6	6	7	25	0	1	0	0	1	
<i>Oxychilus draparnaudi</i>					0	1	0	0	1	

Table 3 Totals and site means (with standard errors) for snail species in each area, and the values of Whittaker's Index (I), and snail species in the richest sites and the values of I_{\max}

	Chilterns	South Downs	Cotswolds	Wye valley	Overall
Total species	31	36	40	35	43
Mean/site	24.6 +/-0.6	27.6 +/-0.5	30.9 +/-0.8	26.6 +/-0.5	27.5 +/-0.5
I	1.26	1.30	1.30	1.31	1.56
Richest site	26	29	35	28	35
I_{\max}	1.19	1.24	1.14	1.25	1.23

Table 4 Species missing from, and species unique to, each area studied.

Chilterns	South Downs	Cotswolds	Wye valley
Species missing			
<i>Carychium minimum</i>	<i>Carychium minimum</i>	<i>Vertigo substriata</i>	<i>Succinea putris</i>
<i>Succinea putris</i>	<i>Succinea putris</i>	<i>Oxychilus draparnaudi</i>	<i>Cochlicopa lubricella</i>
<i>Azeca goodalli</i>	<i>Columella edentula</i>	<i>Helicodonta obvolvata</i>	<i>Vertigo substriata</i>
<i>Vertigo substriata</i>	<i>Abida secale</i>		<i>Abida secale</i>
<i>Ena montana</i>	<i>Ena montana</i>		<i>Ena montana</i>
<i>Phenacolimax major</i>	<i>Phenacolimax major</i>		<i>Oxychilus draparnaudi</i>
<i>Nesovitrea hammonis</i>	<i>Monacha cantiana</i>		<i>Monacha cantiana</i>
<i>Oxychilus draparnaudi</i>			<i>Helicodonta obvolvata</i>
<i>Macrogastra rolphii</i>			
<i>Zenobiella subrufescens</i>			
<i>Helicodonta obvolvata</i>			
<i>Arianta arbustorum</i>			
Species unique			
	<i>Vertigo substriata</i>	<i>Succinea putris</i>	
	<i>Oxychilus draparnaudi</i>	<i>Ena montana</i>	
	<i>Helicodonta obvolvata</i>		

of table 2, above, shows that there are indeed such differences, but except for extreme cases, the number of sites in each area is too small to expect statistically significant results. 21 species (down to, and including, *Trichia hispida* in table 2) occur in at least half of all the sites in each area. Among the remainder, there are some which are either restricted to one area where they are relatively frequent (*H. obvolvata* on the South Downs, *Ena montana* on the Cotswolds), or are missing or very infrequent in one area but frequent

elsewhere (*Arianta arbustorum* and *Zenobiella subrufescens* on the Chilterns, *Helix aspersa* on the Cotswolds, *Trichia striolata* and *Cochlicopa lubricella* in the Wye valley, perhaps *Lauria cylindracea* on the South Downs). Those left are either very rare, or do not show very clear patterns.

Given the standardized sampling, it is also possible to consider abundance. Inspection of Appendix 2 shows that numbers of many species vary greatly between sites, even in the same area. We have therefore examined the rank order of

Table 5 Mean values (%) and standard errors of the Nei Index for site-by-site comparisons. For reference, the overall mean similarity between sites is 82.5 +/- 0.25.

	Chilterns	South Downs	Cotswolds	Wye valley
Chilterns	86.7 +/- 1.1	80.4 +/- 0.6	80.8 +/- 0.6	79.8 +/- 0.6
South Downs		86.0 +/- 0.6	81.1 +/- 0.6	79.6 +/- 0.6
Cotswolds			87.9 +/- 0.7	83.5 +/- 0.5
Wye valley				87.3 +/- 0.7

Table 6 Values of the Nei Index (%) for area-by-area comparisons, using the whole recorded snail fauna of each.

AREAS	South Downs	Cotswolds	Wye valley
Chilterns	83.8	88.0	85.0
South Downs		87.0	90.1
Cotswolds			93.5

abundance in each area relative to that obtained overall. Ranking orders are, not surprisingly, correlated between areas, but some species show marked deviations from their overall position in particular areas. Table 7 shows cases where the deviation is at least eight ranking positions, arranged by area, and the remainder, where the evidence for differences between areas is much less.

The Correspondence Analysis demonstrates even more clearly than presence and absence data the degree of geographical differentiation. Table 8 shows the basic data: the first three axes explain more than half of all the variation in composition. CA makes it possible to place both sites and species on the axes. Figure 4 (a and b) shows the distribution of sites and species on the first two axes. For sites, the first axis opposes the Cotswolds to the South Downs, with the wettest Cotswolds sites (Workman’s Wood and Siccaridge) having high negative scores. The Chilterns, the Wye Valley, and the drier Cotswolds sites are intermediate. The sec-

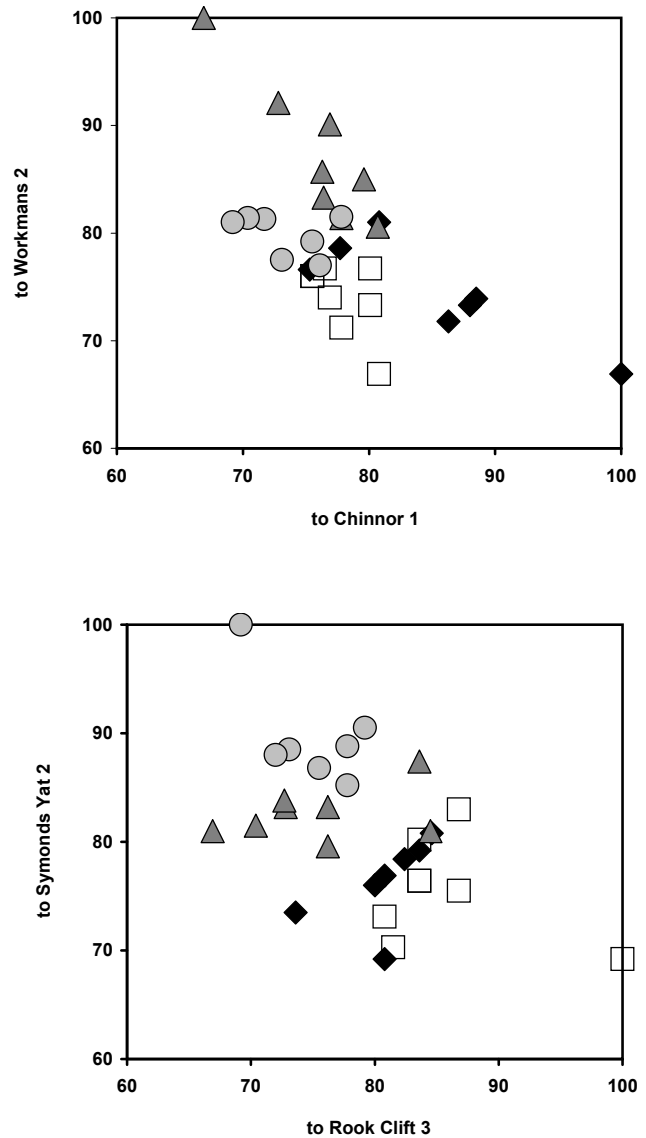


Figure 3 Ordering of sites by their Nei similarities, (a) to Workman’s Wood 2 and Chinnor 1, (b) to Symonds Yat 2 and Rook Clift 3. In both cases, the comparisons are with the least similar sites in the array. Squares = South Downs; diamonds = Chilterns; circles = Wye Valley; triangles = Cotswolds.

ond axis opposes the Cotswolds to the Chilterns. Scores on this axis correlate well with species richness ($R = 0.668, P < 0.001$). It can be seen that if samples from the South Downs are excluded, scores on these first two axes are strongly correlated. Both axes reflect the fact that the faunas of the Wye Valley and of the Chilterns are, essentially, reduced versions of that of the Cotswolds, whereas that of the South Downs is more distinctive. On both axes, the drier Cotswolds sites (Midger, Rough Park and Pope’s Wood) are scarcely distinguishable from Wye Valley sites.

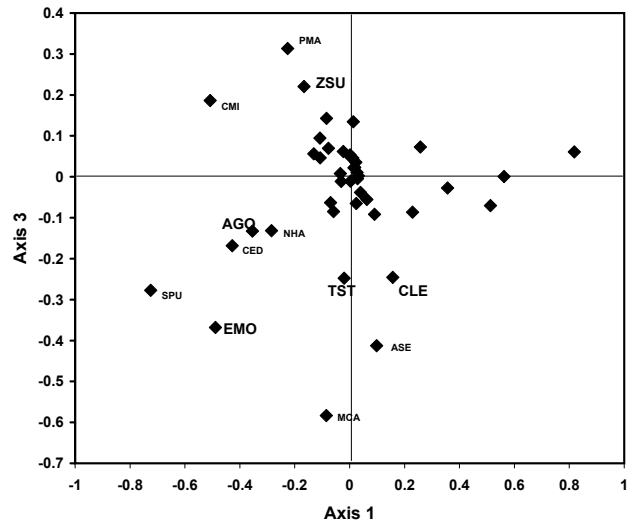
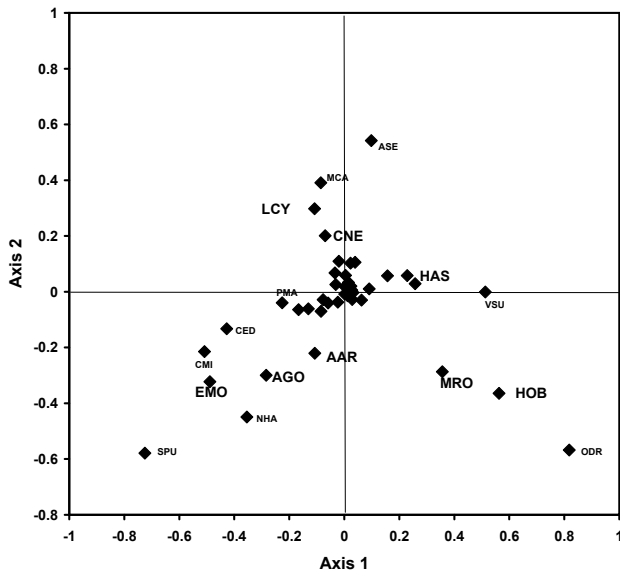
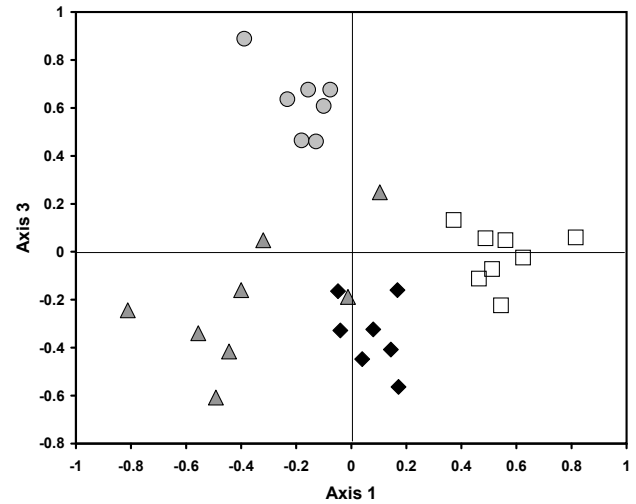
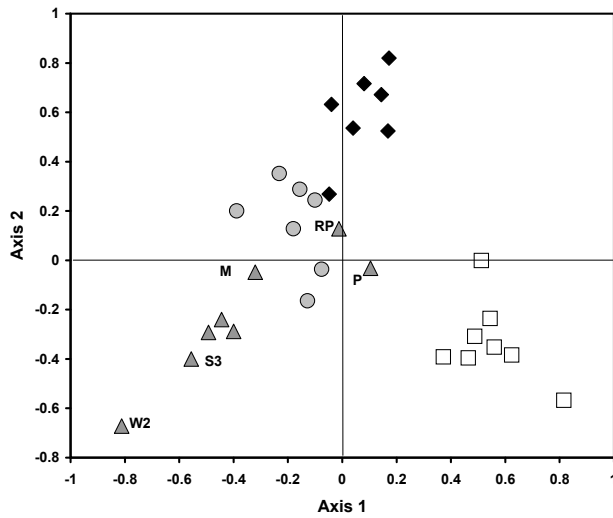


Figure 4 The location of sites (above) and species (below) on the first two axes of the Correspondence Analysis. For sites, symbols as in Figure 3. For Cotswold sites, W2 = Workman's Wood 2, S3 = Siccaridge 3, M = Midger, RP = Rough Park, and P = Pope's Wood (see text). For species, outliers are identified, using larger font for common, and smaller for rare species as follows: AAR = *Arianta arbustorum*, AGO = *Azeca goodalli*, ASE = *Abida secale*, CED = *Columella edentula*, CMI = *Carychium minimum*, CNE = *Cepaea nemoralis*, EMO = *Ena montana*, HAS = *Helix aspersa*, HOB = *Helicodonta obvolvata*, LCY = *Lauria cylindracea*, MCA = *Monacha cantiana*, MRO = *Macrogastra rolpheii*, NHA = *Nesovitrea hammonis*, ODR = *Oxychilus draparnaudi*, PMA = *Phenacolimax major*, SPU = *Succinea putris*, and VSU = *Vertigo substriata*.

Figure 5 The location of sites (above) and species (below) on the first and third axes of the Correspondence Analysis. For sites, symbols as in figure 3. For species, conventions as in figure 4, with the addition of: CLE = *Cochlicopa lubricella*, TST = *Trichia striolata*, and ZSU = *Zenobiella subrufescens*.

For species (Figure 4b), most cluster close to the origin (the 0,0 intersection), and are clearly contributing to similarity rather than difference among sites. Among the more abundant species, *E. montana* and *H. obvolvata*, species unique to the Cotswolds and the South Downs respectively, clearly contribute significantly to area differences. Others, not so restricted, also contribute by differential abundance: *Azeca goodalli* and *A. arbustorum* for the Cotswolds, *Macrogastra rolpheii* for the South Downs, and, to a lesser extent, *L.*

Table 7 Differences in rank of abundance by area relative to the aggregate of all samples, for all species represented by more than 30 individuals, and present in at least three areas. *H. obvolvata* and *E. montana* are each present in only one area, but are represented there by more than 30 individuals. Asterisked species are missing from the Chilterns.

Eight or more ranks above aggregate rank							
Chilterns		South Downs		Cotswolds		Wye valley	
<i>E. obscura</i>	+9	<i>M. rolphii</i>	+14	<i>A. goodalli</i>	+12	<i>V. crystallina</i>	+10
<i>C. nemoralis</i>	+8	<i>H. aspersa</i>	+14	<i>A. arbustorum</i>	+8	<i>Z. subrufescens</i>	+9
<i>C. lubricella</i>	+8	(<i>H. obvolvata</i>)		(<i>E. montana</i>)		<i>T. hispida</i>	+9
Eight or more ranks below aggregate rank							
<i>M. rolphii</i> *	-15	<i>L. cylindracea</i>	-21	<i>L. cylindracea</i>	-17.5	<i>T. striolata</i>	-24
<i>V. contracta</i>	-13	<i>C. nemoralis</i>	-17.5	<i>H. aspersa</i>	-11.5	<i>P. elegans</i>	-11
<i>A. goodalli</i> *	-12	<i>P. pygmaeum</i>	-12			<i>M. rolphii</i>	-9
<i>A. arbustorum</i> *	-10	<i>T. striolata</i>	-12			<i>C. laminata</i>	-8
<i>P. pygmaeum</i>	-10						
<i>A. aculeata</i>	-8						
<i>A. pura</i>	-8						
Species showing less or no difference in area ranks relative to aggregate							
<i>C. tridentatum</i>		<i>O. cellarius</i>		<i>C. hortensis</i>		<i>H. lapicida</i>	
<i>D. rotundatus</i>		<i>A. fusca</i>		<i>V. pellucida</i>			
<i>C. bidentata</i>		<i>O. helveticus</i>		<i>E. fulvus</i>			
<i>A. nitidula</i>		<i>C. lubrica</i>		<i>O. alliarius</i>			

cylindracea and *Cepaea nemoralis* for the remainder. A number of less abundant species also occupy outlying positions, and it is noticeable that those with negative scores on both axes (Cotswolds associated) include wetland species, while those with positive values on axis 2 are frequently encountered in open, drier habitats.

Figure 5 shows the positions of sites and species on axes 1 and 3. Even the third axis produces some geographical pattern, in this case separating Wye Valley sites from the remainder. *Z. subrufescens* seems to be the only abundant species contributing positively to this segregation, but the position of the rarer *Phenacolimax* major also plays a part. It is noticeable that both species associated with openness and disturbance (*Monacha cantiana*, *Trichia striolata*, *Cochlicopa lubricella*), and those associated with wetter conditions (*Succinea putris*, *A. goodalli*, *Columella edentula*) score negatively.

Table 9 shows the frequency of occurrence of slugs by area and overall. Four species, two of which are aggregates, were encountered in 70% or more of the sites. Of the remainder, the two

most frequent show differing patterns, *Limax maximus* being rare in the Wye valley, while *Deroceras reticulatum* occurs much more often on limestone than on chalk. *Deroceras laeve* is restricted to sites with some wetland vegetation in the Cotswolds. *Limax cinereoniger* and *Arion fasciatus* are most frequent in the Wye valley, which lacks any of the remainder, which are mostly introduced species with anthropochorous tendencies. As shown below (page..), the inventories of slugs are far from complete.

The snail species represented by ancient shells only are mostly associated with open habitats (Appendix 3), and they are much more frequent in the Chilterns than elsewhere. In the Cotswolds, the ancient *Vallonia* sp. shells could be *V. pulchella*. Along with those of *Vertigo pygmaea*, they were extracted from wetland litter within Workman's Wood sites.

SOUTH DOWNS: COMPARISON WITH EARLIER WORK
Cameron (1973) sampled 44 1000m² woodland sites on the South and Hampshire Downs. Of

Table 8 Basic data for the Correspondence Analysis.

Axes	1	2	3	4	Total Inertia
Eigenvalues	0.089	0.068	0.049	0.028	0.401
Cumulative % Variance explained	22.2	39.3	51.5	58.4	

these, 24 were made in scarp woodlands similar to those reported here. Our sites lie roughly in the middle of the area covered by the earlier survey. Table 10 shows comparative data from the two surveys. Taking into account the two species found off the scarp in the 1970s, the difference in the total fauna is not large, but the difference in mean richness per site is greater: nine species (33%), slightly less if the failure to segregate *Cochlicopa* in 1973 is taken into account. Site faunas are more heterogeneous in the earlier survey, as indicated by the higher value of Whittaker's index. Both unique species in the early survey are atypical for woodland; most of those found only on the later occasion are infrequent. Many species are more frequent in the second sur-

vey; for *Vitrea crystallina*, *Oxychilus helveticus*, *Helicigona lapicida*, *H. obvoluta* and *A. arbustorum* occurrence has more than doubled in proportion. Among slugs (data not shown), there is no clear pattern, but *L. cinereoniger* was recorded more frequently in the earlier survey, and *Lehmannia marginata* less frequently.

COTSWOLDS: COMPARISONS WITH EARLIER WORK

In addition to his published accounts (Long, 1969 and 1980), DCL has surveyed a number of Cotswold woods, usually presenting reports for English Nature or the Gloucestershire Wildlife Trust. A comparison of these data with those of RADC and BMP was used by Cameron and Pokryszko (2005) in discussing sampling methods. The eight sites recorded here lie in five woodland nature reserves, the smallest of which is Siccaridge Wood at 25 ha. In Pope's Wood, DCL records come from a number of visits, but do not represent a detailed survey. In the other four, however, visits, usually in more than one year, were planned to sample many parts of each reserve. DCL has also added earlier records made by himself and others. Most records come from visual searching, but litter was examined from some places within each.

Table 9 The number of occurrences of slugs by area and overall.

	CHILT	SD	COTS	WV	Total
<i>Arion ater</i> agg.	7	8	7	5	27
<i>Arion subfuscus</i>	7	8	8	7	30
<i>Arion circumscriptus</i>	4	7	6	5	22
<i>Arion fasciatus</i>	0	1	1	4	6
<i>Arion hortensis</i> agg.	7	8	8	7	30
<i>Limax maximus</i>	3	6	5	1	15
<i>Limax cinereoniger</i>	0	1	1	5	7
<i>Lehmannia marginata</i>	7	7	8	7	29
<i>Boettgerilla pallens</i>	0	2	1	0	3
<i>Tandonia sowerbyi</i>	2	0	2	0	4
<i>Tandonia budapestensis</i>	0	1	0	0	1
<i>Deroceras laeve</i>	0	0	2	0	2
<i>Deroceras reticulatum</i>	1	1	6	7	15
<i>Deroceras panormitanum</i>	0	2	0	0	2
Total	8	12	12	9	14

Table 10 Comparison of the results of Cameron (1973) for 24 scarp woodland sites on the South Downs with the South Downs sites of this study. The asterisks highlight the non-segregation of *C. lubrica* and *C. lubricella* in the earlier study. *N. hammonis* and *Z. subrufescens* were found in non-scarp woodlands in the earlier study.

	Cameron 1973	This study
No. of sites	24	8
No. of species (total)	31*	36
Mean no. of species /site	18.6 +/- 0.45	27.6 +/- 0.50
Whittaker's Index	1.67	1.30
Richest site	23	29
Whittaker, I_{\max}	1.35	1.24
Species in 75%+ of sites	13 (42%)	25 (69%)
Unique species	<i>A. secale</i> (2) <i>M. cantiana</i> (1)	<i>A. goodalli</i> (3) <i>C. lubricella</i> * (4) <i>V. substriata</i> (1) <i>L. cylindracea</i> (2) <i>N. hammonis</i> § (1) <i>O. draparnaudi</i> (1) <i>Z. subrufescens</i> § (3)

Table 11 shows the comparative data. There is a very substantial difference in the recorded slug fauna, indicating the inefficiency of single visits to small patches. The differences in number of snail species are much less marked, even reversed in the case of Pope's Wood, where a thorough survey had not been done previously, and in each case the RADC/BMP survey has found species not previously recorded. Inspection of DCL's detailed lists by patches within each reserve show that many of the species recorded by him, but not by RADC/BMP do not occur near the sample sites chosen by them. Some, including *Candidula intersecta*, *Helix pomatia*, *Monacha cantiana*, *Abida secale* and *Ashfordia granulata*, were found mainly on edges, in openings or in stream-side vegetation; *Columella aspera* was found on a high and unusually acid part of Siccaridge Wood. *P. major* was not found in Siccaridge Wood at the time of DCL's major survey (2001), and has not been seen there since the 1980s. Conversely, the absence of *L. cylindracea*, *E. montana*, *Helix aspersa* and *H. lapicida* from a number of RADC/BMP sites probably reflect accidents of sampling. A combination of similar accidents and the searching of larger quantities of litter can account for most species found by RADC/BMP and not earlier. An exception is *Oxychilus helveticus*; this

large, easily found species was absent or very localised in early records made by DCL, but was present in his most recent surveys.

DISCUSSION

SAMPLING ISSUES

The evidence presented above suggests that the site inventories are nearly complete as regards snails. Comparison with earlier detailed surveys by DCL in the Cotswolds suggests that one or two species may have been missed from some sites. The habitats sampled are particularly easy to work, having high abundance. Using exactly the same techniques, Cameron and Pokryszko (2004) were unable to distinguish between genuine heterogeneity and sampling error in oligotrophic sites in the Białowieża Forest (eastern Poland), where sample sizes were only around 100-150 individuals. The problem becomes even more acute in some studies in oligotrophic tropical forests (de Winter and Gittenberger, 1999; Schilthuizen and Rutjes, 2001).

Less rigorous sampling can give rise to spurious heterogeneity, and underestimates of very local richness, even in such favourable habitats. Cameron (1973) clearly underestimated site diver-

Table 11 Records for each wood made by DCL, and by RADC/BMP in the Cotswolds. Numbers in brackets indicate the number of RADC/BMP sites included in the wood. The table also shows the species recorded uniquely by one or the other, and the aggregate total number of species recorded for each woodland reserve.

	Siccaridge	Workman's	Pope's	Rough Park	Midger
Snails DCL	41	38	26	30	33
Snails RC/BP	37 (3)	33 (2)	29 (1)	31 (1)	28 (1)
Total Records	44	40	30	34	34
DCL only	<i>Abida secale</i> <i>Columella aspera</i> <i>Phenacolimax major</i> <i>Ashfordia granulata</i> <i>Candidula intersecta</i> <i>Helix aspersa</i> <i>Helix pomatia</i>	<i>Oxyloma pfeifferi</i> <i>Vertigo substriata</i> <i>Abida secale</i> <i>Lauria cylindracea</i> <i>Candidula intersecta</i> <i>Helicigona lapicida</i> <i>Helix aspersa</i>	<i>Ena montana</i>	<i>Lauria cylindracea</i> <i>Arianta arbustorum</i> <i>Helix aspersa</i>	<i>Ena montana</i> <i>Nesovitrea hammonis</i> <i>Candidula intersecta</i> <i>Monacha cantiana</i> <i>Helicigona lapicida</i> <i>Helix aspersa</i>
RC/BP only	<i>Carychium minimum</i> <i>Cochlicopa lubricella</i> <i>Ceciliooides acicula</i>	<i>Cochlicopa lubricella</i> <i>Oxychilus helveticus</i>	<i>Acicula fusca</i> <i>Oxychilus helveticus</i> <i>Zenobiella</i> <i>subrufescens</i> <i>Helix aspersa</i>	<i>Cochlicopa lubricella</i> <i>Oxychilus helveticus</i> <i>Ceciliooides acicula</i> <i>Cepaea hortensis</i>	<i>Lauria cylindracea</i>
Slugs DCL	16	12	10	11	15
Slugs RC/BP	10	9	6	4	6
Total records	16	12	10	11	16
DCL only	<i>Boettgerilla pallens</i> <i>Tandonia</i> <i>budapestensis</i> <i>Arion flagellus</i> <i>Arion silvaticus</i> <i>Arion hortensis</i> seg. <i>Arion intermedius</i>	<i>Arion silvaticus</i> <i>Arion intermedius</i> <i>Tandonia</i> <i>budapestensis</i>	<i>Arion silvaticus</i> <i>Arion hortensis</i> seg <i>Arion intermedius</i> <i>Limax maximus</i>	<i>Arion ater</i> agg. <i>Arion flagellus</i> <i>Arion silvaticus</i> <i>Arion intermedius</i> <i>Limax cinereoniger</i> <i>Limax maximus</i> <i>Deroceras</i> <i>reticulatum</i>	<i>Arion flagellus</i> <i>Arion circumscriptus</i> <i>Arion silvaticus</i> <i>Arion hortensis</i> seg <i>Arion intermedius</i> <i>Tandonia sowerbyi</i> <i>Tandonia</i> <i>budapestensis</i> <i>Limax cinereoniger</i> <i>Deroceras laeve</i> <i>Deroceras reticulatum</i>
RC/BP only					<i>Arion fasciatus</i>
Total species all records	60	52	40	45	50

sity, and overestimated heterogeneity between sites. However, his results gave similar levels of heterogeneity to those reported in many other studies in northern Europe (Cameron, 1995); inspection of some of these, for example Körnig (1966), suggests that the same problems affect the results. Conversely, our results give reassurance that more qualitative approaches, with multiple samples taken over time in, for example, a nature reserve, will provide very good inventories of rather larger areas than single sites as used by us. This is especially the case for slugs, as demonstrated by the comparison between the small site/single visit strategy of RADC/BMP and the repeated visits and extended visual searches of DCL in the Cotswolds.

The aim of this study was to determine the richness and composition of snail faunas in forest plots containing as many of the known microhabitats of snails as possible. Site selection was certainly not random within the chosen areas, and inspection of DCL's detailed studies within woodland blocks of 25 ha or more shows that many small sites within them are poorer than those reported here. The detection of micro-environmental variation affecting snail species' occurrence and abundance would require a much finer grain of sampling. Nevertheless, it is worth noting that, among these rather standardized sites, the first two axes of the Correspondence Analysis explain nearly 40% of variation in the data, and can be related to ecological differences between sites and areas. This compares well with the 35% of variation explained by these axes in Labaune and Magnin's (2001 and 2002) study of snail faunas on the Grand Luberon, Provence, which involved much smaller sites (25 m²), a much wider range of environments, and greater overall heterogeneity between sites. Similarly, Kiss and Magnin (2003) found the first two axes explained only 28% of variation between sites in a Mediterranean environment; sampling strategy was similar to that of Labaune and Magnin. Our nearly complete inventories reveal rather subtle differences between very similar faunas, which might be drowned by statistical "noise" in less intensive surveys.

GEOGRAPHICAL AND ECOLOGICAL PATTERNS

When compared with other studies, the major feature of these snail faunas is their uniformity. This is well illustrated by the low values of both

variants of Whittaker's index, the very high values of the Nei index, and by the clustering of most species around the origin in the Correspondence Analysis. In this respect, within area variation as measured by the Nei index is matched by the richest of three forest types in the Białowież a forest: *Tilio-Carpinetum* forest sites, all within 15 km of each other, have a mean Nei index of 86.7%, almost identical to the within area indices reported here (Cameron and Pokryszko, 2004). We have evidence (Pokryszko and Cameron, 2005 and unpublished) that this level of uniformity is typical among northern European sites from the same (eutrophic) forest type within a few tens of kilometres of each other, provided sample sizes are adequate. What is more remarkable is the similarity between areas. In this respect, the British fauna is unusual; distance decay in similarity (Nekola and White, 1999) is more rapid in other parts of northern Europe (Pokryszko and Cameron, 2005).

Nevertheless, there is coherent variation between areas and sites. Both on presence and absence data (Nei index), and using abundance (CA and rank differences), there is a geographical pattern in composition. The evidence suggests that this is mostly due to ecological differences between areas, rather than to geographical range limits. National Atlas data (Kerney, 1999) show that only *H. obvolvata* is geographically restricted to a single area. Subfossil, Holocene, records show that it was once more widespread, reaching the Cotswolds (Kerney, 1999). *Z. subrufescens* is missing from our Chilterns sites, and this may have a geographical, or climatic cause: the species is generally absent in the east of England, and the nearest record in the Atlas is c. 50 km to the west. *E. montana*, recorded here only in the Cotswolds, is known from hectads adjacent to our sites on the South Downs and the Chilterns. Indeed, there are old and more recent records from the South Downs and adjacent Hampshire Downs as there are for *P. major* (Chatfield, 1981; Dalglish, unpublished notebooks, M. Willing and T. Wimbleton, unpublished); *M. rolphii* is known within a similar distance of the Chiltern sites, where it was absent. *V. substriata*, and some other wetland species not found in our Cotswolds sites, are known from DCL's surveys there (Long, 1969 and unpublished).

The limited differences between areas seem to be caused mainly by a few ecological or historical

factors. The presence of forested wetland adds a few species not found elsewhere. This contributes to the exceptional richness of some Cotswold sites; drier sites in that area are indistinguishable, apart from the presence of *E. montana*, from those in the Wye Valley. Some of the latter had wetland vegetation, but this was associated with proximity to the river Wye itself. In contrast to the small springs and streams in Cotswold woods, such areas are prone to total inundation in river floods, and are also subject to considerably more human disturbance. Variation in frequency and abundance may sometimes have a climatic connection; *M. rolphii*, missing from the Chilterns, declines rapidly in abundance and frequency from a maximum on the South Downs, through the Cotswolds to the Wye Valley, and *Z. subrufescens* shows the reverse pattern.

The nature of human modification, and the age of the habitat in its present form are also significant. The Chilterns series are the most disturbed and secondary. They are, marginally, the poorest, and have the greatest frequencies and abundance of species tolerating open and disturbed conditions. Nevertheless, around three quarters of all species recorded in the study were found there, and supposed anthropophobes such as *A. fusca* were frequent. Kerney (1968) suggested that the restricted distribution of *E. montana* in southern England might be accounted for by local summer temperatures. In our study, it appeared to be associated strongly with ancient coppice (most conspicuously in Siccaridge Wood). Sites on the South Downs and Chilterns are predominantly beech high forest, and have been so for some time. The species is also found in ancient hedges (Kerney, 1999: 112), in which coppiced species such as hazel are often present; its rather patchy distribution within its British range may thus also reflect different patterns of forest management on calcareous soils.

These patterns, revealed by intensive and adequate sampling, show that the differences between areas are caused by variation in the occurrence and abundance of relatively few species. The majority are common to all areas, and, as Boycott (1934) pointed out, are species capable, in the damp, Atlantic climate of Britain, of living in more open and disturbed habitats than the original forests. A minority are invasive species that have become naturalised.

SCALE AND SPECIES RICHNESS

In this study, the difference between the numbers of snail species in individual 400 m² plots, and in clusters of such sites within a few kilometres of each other is slight. When comparisons are made with the richest single sites, the differences are even less. This suggests that quite small areas can contain most of the locally available forest fauna. The same appears to be true for other north European forests under eutrophic or calcareous conditions (Pokryszko and Cameron, 2005). The work of Schmid (1966), on the Spitzberg near Tübingen, shows that this may be true for much smaller areas, with up to 35 species (including slugs) being found in single 1m² quadrats; figures of more than 20 were frequent. The same phenomenon is recorded in N. American forest faunas (Nekola and Smith, 1999) The maximum site richness recorded here (35 snail species, in Siccaridge Wood 1), and the average for the Cotswolds (more than 30), are amongst the highest recorded at this scale in N. Europe, being significantly exceeded only in some parts of the Polish Carpathians and Sudetes (Pokryszko and Cameron, 2005 and unpublished).

In this respect, our results can be compared with those of Meyrick and Preece (2001), who found that some English mid- Holocene forest faunas preserved in tufas were consistently richer than recorded modern faunas. There is an irresolvable problem of scale in this comparison; our inventories refer to relatively large areas, recording presence only in one year, while individual tufa samples refer to a much smaller area, but encompass perhaps up to 100 years of accumulation (R. C. Preece, personal communication). The numbers and identities of forest species are very similar when a comparison is made with the modern Cotswolds fauna overall, but at site level, modern faunas often lack the wooded wetland component, and always lack species, such as *Vertigo antiwertigo*, *V. moulinsiana* and *Zonitoides nitidus* that are wetland specialists. Forested wetland has certainly declined, largely as a result of human activity, and active tufas in Britain are no longer found, at least on the scale of those of the mid-Holocene. Thus species such as *Leiostyla anglica* and *Vertigo substriata* are now very local and rare in this kind of wood. More mysteriously, some non-wetland species present in mid Holocene tufas both in Northamptonshire

(Meyrick and Preece, 2001), Kent (Preece and Bridgland, 1999) and elsewhere are also missing from these modern faunas, for example *Vallonia costata* and *Vertigo pusilla*. Both can be found in some English woods (RAD Cameron, unpublished), and are not infrequent in similar forest types elsewhere in Europe (Pokryszko and Cameron, 2005). The tally of species missing or very rare in modern faunas suggests that the environment around these tufas was often both wetter and more open, at least in parts, than that of modern, managed, closed canopy forest (cf. Bishop, 1981).

While these species have declined, or become locally extinct, there have been a number of later additions. Thus *H. aspersa*, a Roman introduction, and *O. helveticus*, possibly also introduced, are now quite frequent members of forest faunas, but were missing from mid Holocene tufa sites. DCL's surveys, spread over more than 30 years, suggest that the spread of the latter species is very recent in some areas. Again, more mysteriously, *Azeca goodalli* is relatively abundant in some modern faunas, but is absent from the mid Holocene samples.

As noted above, the high level of maximum site richness does not imply an even distribution of species throughout a larger block of forest; sites in this study were selected to offer as full a range of microhabitats as possible. It does reinforce the point, made by Boycott (1934) and reinforced powerfully by Waldén (1981), that where all appropriate microhabitats are present, the whole fauna will be too, and that variation between sites is mostly the result of impoverishment in sites lacking certain features. There are very few species specialising in oligotrophic conditions; in Britain, *Zonitoides excavatus*, not present in any of our calcareous sites, is the best known example, but *Columella aspera*, and in N.E. Europe, *Vertigo ronneyensis*, may be other examples (Pokryszko, 1990; von Proschwitz, 1993). *C. aspera* was recorded in one unusually oligotrophic part of Siccaridge Wood by DCL.

At a larger scale, the richness of some woodlands in England is not far short of some famous global examples (Emberton, 1995), and such woods appear to contain nearly all the geographically available species which can survive in that habitat. The richest single block included in this study is the 25 ha Siccaridge Wood. 44 snail species have been recorded from it; with slugs,

the total rises to 60. This represents nearly half the known terrestrial fauna of Britain, including all introduced and open habitat species. The Cotswold woods as a whole are even richer; in the five woods considered here, there are 63 species. Considering other woodlands nearby, we can add seven more: *Pyramidula rupestris* from Frith Wood (DCL), *Euconulus alderi* (a wetland species) from Three Groves (DCL), *Leiostryla anglica* from Cranham Wood (Long, 1969) and *Cerneuella virgata*, *Milax gagates* and *Malacolimax tenellus* from Witcombe Wood (Cameron, 1984, and Boycott, 1934), though the last named has not been seen since the 1920s. There is a similar ancient record (1920) of *Spermodea lamellata* from Upton St. Leonards; this species has very few known locations in S. England. This represents virtually the whole of the available British forest fauna; most of the few species missing are those with geographical ranges excluding the Cotswolds.

Some species in this fauna are not "natural" inhabitants of British forests, being introduced species. Some of these, like *Candidula intersecta*, *Cerneuella virgata* and *Monacha cantiana* are more typical of open habitats, where they are now widespread. They appear to colonise woodland edge, or to occupy cleared patches. Others, like *H. aspersa*, *H. pomatia*, and *O. helveticus* appear to be fully integrated in the woodland fauna, though they occur in other habitats too. Amongst slugs the list might be longer, but we lack a fossil record. *Boettgerilla pallens* is certainly a recent invader (first recorded in Britain in 1972); it has penetrated ancient forests not only in Britain, but also elsewhere in Europe. Some *Tandonia*, *Milax* and *Deroceras* species are notorious agricultural pests, and most of the *Arion* species are abundant outside woodland.

There are also a few species here that are native, but not normally found under full canopy cover. *A. secale* and *P. rupestris* are principally rock-dwellers, and can be found on Cotswold limestone grassland. They occur sporadically in the woods, usually in rather open patches. The finds of long dead shells probably represent short periods of local clearance or opening of the canopy. *Vallonia costata*, found dead in Rough Park, is typical of grassland, but is frequently found in dry, rocky and rather open woodland.

While the Cotswolds appear to hold the richest forest faunas in Britain, other areas are not far

behind. 47 species, including slugs, have been recorded from a 25 ha wood in S. Yorkshire, which lacks significant wetland (Cameron, 1999), and inspection of other surveys suggests that similar local faunas could be found elsewhere (e.g. Wardhaugh, 1996). Such high diversity sites are known elsewhere in northern Europe (Waldén, 1981; Cameron and Pokryszko, 2004), far from the sources of post-glacial colonists. They may offer clues as to the ways in which local (syntopic) molluscan diversity is formed.

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REFERENCES

- BISHOP MJ 1981 Quantitative studies on some living British wetland mollusc faunas. *Biological Journal of the Linnean Society of London* **15**: 299-326.
- BOYCOTT AE 1934 The habitats of land Mollusca in Britain. *Journal of Ecology* **22**: 1-38.
- CAMERON RAD 1973 Some woodland mollusc faunas from southern England. *Malacologia* **14**: 355-370.
- CAMERON RAD 1984 Witcombe Wood revisited. *Conchologists' Newsletter* **91**: 227-229.
- CAMERON RAD 1995 Patterns of diversity in land snails: the effects of environmental history. In A C van Bruggen, S M Wells & Th C M Kemperman (eds) *Biodiversity and conservation of the Mollusca* 187-204 Backhuys, Leiden
- CAMERON RAD 1999 The slugs and snails of Anston Stones Wood. *Sorby Record* **35**: 24-27.
- CAMERON RAD & POKRYSZKO BM 2004 Land mollusc faunas of Białowieża Forest (Poland), and the character and survival of forest faunas in the North European Plain. *Journal of Molluscan Studies* **70**: 149-164.
- CAMERON RAD & POKRYSZKO BM 2005 Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. *Journal of Conchology* **38**: 529-547.
- CHATFIELD J 1981 Field meeting in Selbourne. *Conchologists' Newsletter* **76**: 292-293.
- EMBERTON KC 1995 Land snail community morphologies of the highest diversity sites of Madagascar, North America and New Zealand, with recommended alternatives to height-diameter plots. *Malacologia* **36**: 43-66.
- KERNEY MP 1968 Britain's fauna of land Mollusca and its relation to the post-glacial thermal optimum. *Symposia of the Zoological Society of London* **22**: 273-291.
- KERNEY MP 1999 *Atlas of the land and freshwater molluscs of Britain and Ireland*. Harley Books, Colchester.
- KISS L & MAGNIN F 2003 The impact of fire on some Mediterranean land snail communities and patterns of post-fire recolonization. *Journal of Molluscan Studies* **69**: 43-53.
- KÖRNIG G 1966 Die Molluskengesellschaften des mitteldeutschen Hügellandes. *Malakologische Abhandlungen Staatliches Museum für Tierkunde Dresden* **1**: 1-112.
- LABAUNE C & MAGNIN F 2001 Land snail communities in Mediterranean upland grasslands: the relative importance of four sets of environmental and spatial variables. *Journal of Molluscan Studies* **67**: 463-474.
- LABAUNE C & MAGNIN F 2002 Pastoral management vs. land abandonment in Mediterranean uplands: impact on land snail communities. *Global Ecology and Biogeography* **11**: 237-245.
- LEGENDRE L & LEGENDRE P 1984 *Ecologie numérique*. Masson et Presses de l'Université du Québec, Paris, Québec.
- LONG DC 1969 A small bog in Cranham Wood. *Conchologists' Newsletter* **30**: 111-113.
- LONG DC 1980 Workman's Wood. *Conchologists' Newsletter* **73**: 221-225.
- MABEY R 1996 *Flora Britannica*. Sinclair-Stevenson, London.
- MEYRICK RA & PREECE RC 2001 Molluscan successions from two Holocene tufas near Northampton, English Midlands. *Journal of Biogeography* **28**: 77-93.
- NEKOLA JC & SMITH TM 1999 Terrestrial gastropod richness in Wisconsin carbonate cliff communities. *Malacologia* **41**: 253-269.
- NEKOLA JC & WHITE PS 1999 Distance decay of similarity in biogeography and ecology. *Journal of Biogeography* **26**: 867-878.
- POKRYSZKO BM 1990 The Vertiginidae of Poland (Gastropoda: Pulmonata: Pupilloidea) - a systematic monograph. *Annales Zoologici* **43**: 133-257.
- POKRYSZKO BM & CAMERON RAD 2005 Geographical variation in the composition and richness of forest snail faunas in northern Europe. *Records of the Western Australian Museum supplement* **68**: 115-132.
- PREECE RC 1998 Mollusca p. 158-212 In: Preece RC & Bridgland DR (eds) *Late Quaternary environmental change in North-west Europe: excavations at Holywell Coombe, South-east England*. Chapman & Hall, London.
- PREECE RC & BRIDGLAND DR 1999 Holywell Coombe, Folkestone: a 13,000 year history of an English chalkland valley. *Quaternary Science Reviews* **18**: 1075-1125.
- PROSCHWITZ T von 1993 Habitat selection and distri-

- bution of ten vertiginid species in the province of Dalsland (SW. Sweden). *Malakologische Abhandlungen Staatliches Museum für Tierkunde Dresden* **16**:177-212.
- SCHILTHUIZEN M & RUTJES HA 2001 Land-snail diversity in a square kilometre of tropical rainforest in Sabah, Malaysian Borneo. *Journal of Molluscan Studies* **67**: 417-423.
- SCHMID G 1966 Die Mollusken des Spitzbergs. *Natur und landschaftsschutzgebiete Baden Württemberg* **3**: 596-701.
- SOLEM A 1984 A world model of land snail diversity and abundance. In: Solem, A. and van Bruggen A.C. (eds) *World-wide snails* pp. 6-22. E.J. Brill/ W. Backhuys, Leiden.
- SOUTHWOOD TRE & HENDERSON PA 2000 *Ecological Methods*. Blackwell, Oxford.
- TER BRAAK CFJ & SMILAUER P 1998 CANOCO reference manual and user's guide to CANOCO for Windows. *Software for canonical community ordination, version 4* Microcomputer Power, Ithaca, NY
- WALDÉN HW 1981 Communities and diversity of land molluscs in Scandinavian woodlands. I. High diversity communities in taluses and boulder slopes in SW Sweden. *Journal of Conchology* **30**: 351-372.
- WARDHAUGH AA 1996 The terrestrial molluscan faunas of some woodlands in north-east Yorkshire, England. *Journal of Conchology* **35**: 313-328.
- DE WINTER AJ & GITTENBERGER E 1998 The land snail fauna of a square kilometre patch of rainforest in southwestern Cameroon: high species richness, low abundance and seasonal fluctuations. *Malacologia* **40**: 231-250.

APPENDIX 1

Details of the sites sampled in this study.

CHILTERNNS

Aston Rowant 1. SU739976. 25.04.03. Steep N-facing slope. Beech dominant, with sycamore, yew and horse chestnut in the canopy, dog's mercury dominant in the field layer. Much exposed chalk and flint, much fallen timber. Site crossed by old trackways.

Aston Rowant 2. SU744980. 25.04.03. Steep W-facing slope. Canopy a mixture of sycamore, ash and beech. Field layer mixed, with dog's mercury, bluebell, bramble and ivy. Much exposed chalk and flints, many cut logs and signs of recent management.

Chinnor 1. SP765007. 26.04.03. Steep NW-facing slope. Coppice and some standards, with sycamore, hazel, ash and hawthorn. Much bare ground, with nettles the most abundant herb. Small dead branches only.

Chinnor 2. SP764003. 26.04.03. Moderate W-facing slope. Beech dominant, with ash, yew and holly. Field layer with ivy, woodruff, sanicle and primrose, but much bare ground. Fallen timber mostly small branches.

Chinnor 3. SU763999. 26.04.03. Steep W-facing slope. Beech dominant, with cherry, yew and sycamore. Field layer mixed, with woodruff, violets, sanicle and dog's mercury. Canopy partly opened, many dead and fallen trees.

Chinnor 4. SU753989. 26.03.04. Moderate W-facing slope. Decaying beechwood: old beeches with younger sycamore, ash and hazel. Field layer with much bare ground, ivy, dog's mercury and some woodruff. Sparse fallen timber. Many paths across area.

Chinnor 5. SP770010. 26.04.03. Steep NE-facing slope. Disturbed woodland with Norway maple, cherry and ash. Field layer mostly bare soil with patches of dog's mercury. Small fallen timber only. Signs of recent interplanting.

SOUTH DOWNS

Buriton 1. SU736198. 27.04.03. Steep N-facing slope. Beech, field maple, elder, ash. Field layer damp with clematis, ferns, dog's mercury. Much old rotting timber. Clearly disturbed in past, near old chalk pit.

Buriton 2. SU737197. 27.04.03. Steep NE-facing slope. Beechwood with some very old trees, and some sycamore and ash. Field layer: dog's mercury, garlic, hartstongue fern. Some fallen trees.

Buriton 3. SU739197. 27.04.03. Steep NW-facing slope. Beechwood with old trees and fallen timber, some sycamore and elm. Ground: partly bare, with dog's mercury and garlic. Appears drier than 1 or 2.

Harting 1. SU790183. 28.04.03. Steep WNW-facing slope. Few big live beech trees, some ash and hazel, with a lot of large, rotten fallen timber. Field layer: dog's mercury, and brambles, with much bare ground..

Harting 2. SU758197. 28.04.03. Steep N-facing slope. Nearly pure managed beechwood, much bare ground and dog's mercury, little fallen timber.

Rook Cliff 1. SU819182. 28.04.03. Steep NW-facing slope. Old beeches and revived coppice including *Tilia*. Ground: dog's mercury, primrose, garlic. Some bare ground, unstable due to coppicing activity. Many logs.

Rook Cliff 2. SU 818182. 28.04.03. Mostly N-facing, steep-to-gentle slope around and above spring. Mature beech with yew and elm. Much bare ground with thick litter, dog's mercury, garlic, and some *Chrysosplenium* near the spring.

Rook Cliff 3. SU818183. 28.04.03. Steep E-facing slope. Beechwood, with yew, ash, elm, clematis and some hazel coppice. Ground: bare, or with dog's mercury and garlic. Modest amounts of fallen timber.

COTSWOLDS

Siccaridge 1. SO932034. 02.05.03. Moderate NW-facing slope. Hazel coppice with some ash and elm. Beech litter on ground from higher

up. Field layer: some bare, plus dog's mercury, wild garlic, bluebells and moss. Small fallen/cut timber only.

Siccaridge 2. SO931033. 02.05.03. Moderate NNW-facing slope. Very similar to site 1, but with more logs and larger ash trees. Some stony ground, with dog's mercury, garlic and wood anemone.

Siccaridge 3. SO934032. 02.05.03. Gentle S-facing slope and some flat ground. Very mixed canopy, with ash, birch, beech and some hazel coppice. Bare ground (c. 30%) and garlic, dog's mercury, bluebells and old man's beard. Much fallen timber.

Workman's Wood 1. SO902108. 01.05.03. Gentle S-facing slope, down to streamside. Beechwood (some alder by stream, also *Chrysosplenium*). Much small fallen or cut timber. Some bare ground, also dog's mercury, garlic, wood anemone and nettle.

Workman's Wood 2. SO904113. 01.05.03. Gentle SE-facing slope, down to springs and small wetland patch. Managed beechwood, with some ash and sycamore. Some small fallen timber. Bare ground and dog's mercury, garlic, and sedges and *Chrysosplenium* around springs.

Pope's Wood. SO874131. 01.05.03. Gentle NW-facing slope. Beech, with some sycamore, elm and hazel. c. 30% bare ground, and ivy, dog's mercury, wood anemone, bluebell, woodruff. Some small rocks and logs.

Rough Park. SO885135. 01.05.03. Moderate to steep NNW-facing slope. Nearly pure beechwood, but with some hazel coppice at base of plot. Rather open, with much regeneration. Not much fallen timber. Stony ground, with dog's mercury, bluebell, wood anemone, woodruff and brambles. A lot of ivy.

Midger Wood. ST797895. 02.05.03. Gentle NE-facing slope. Coppice with standards (oak/hazel), with some ash and field maple. Deep clay soil with very few stones. Ground: dog's mercury, garlic, bluebell wood anemone and brambles.

WYE VALLEY

Lady Park Wood 1. SO548144. 29.04.03. Steep NE-facing slope with cliffs and talus. Beech, ash,

field maple and coppiced hazel. Ground: some bare, dog's mercury, moss. Some small timber.

Lady Park Wood 2. SO547145. 29.04.03. Base of high N-facing cliffs. Elm, large-leaved lime, beech, ash, hawthorn, hazel. Rocks. Dog's mercury, hart's tongue fern, other ferns, ivy and mosses.

Lady Park Wood 3. SO549143. 29.04.03. Gentle N-facing slope and some flat ground. Some very small crags. Alder on flat ground, and ash, beech and coppiced hazel. Ground: some waterlogged patches; dog's mercury, garlic and wood anemone. Some fallen timber.

Highbury Wood 1. SO539092. 30.04.03. Gentle NE-facing slope, with relics of quarrying. Beech, large-leaved lime, sycamore, ash. Rocks and debris. Ground: a little bare, and dog's mercury, garlic, hart's tongue fern and other ferns. Small dead timber only.

Highbury Wood 2. SO538089. 30.04.03. Steep W-facing slope, with small crags and talus. Very mixed canopy with large-leaved lime, beech, yew, ash, cherry, holly and elm. Much bare ground, with dog's mercury and garlic. Some large fallen timber.

Symond's Yat 1. SO564162. 30.04.03. (Devonian Sandstone). Steep E-facing slope. Very diverse wood with evidence of coppicing and disturbance. Large-leaved lime, beech, ash and field maple. Lots of stones and rocks, some from old walls. Mosses, dog's mercury, garlic, herb paris. Some fallen timber.

Symond's Yat 2. SO571157. 30.04.03. N-facing cliffs, with talus and flatter ground below. Mainly large-leaved lime, with beech above (contributing to litter) and some ash. Dense ground cover of dog's mercury, garlic, *Chrysosplenium* and ferns, including hart's tongue. Much dead timber.

APPENDIX 2 (pages 33-36)

The numbers of each species collected, given by area and site. Sites are identified by the first letter of their name, followed by a number where relevant (Appendix 1). Freq = number of sites in which the species occurred.

CHILTERNERS	A1	A2	C1	C2	C3	C4	C5	Total	freq
Species									
<i>Pomatias elegans</i>	7	25	12	21	26	83	21	195	7
<i>Acicula fusca</i>	24	4	0	10	7	33	3	81	6
<i>Carychium minimum</i>	0	0	0	0	0	0	0	0	0
<i>Carychium tridentatum</i>	481	100	26	66	187	105	282	1247	7
<i>Succinea putris</i>	0	0	0	0	0	0	0	0	0
<i>Azeca goodalli</i>	0	0	0	0	0	0	0	0	0
<i>Cochlicopa lubrica</i>	5	10	33	2	3	10	4	67	7
<i>Cochlicopa lubricella</i>	0	0	9	1	0	2	2	14	4
<i>Columella edentula</i>	2	0	0	0	1	0	0	3	2
<i>Vertigo substriata</i>	0	0	0	0	0	0	0	0	0
<i>Abida secale</i>	0	0	4	0	0	0	0	4	1
<i>Lauria cylindracea</i>	0	0	8	43	75	6	14	146	5
<i>Acanthinula aculeata</i>	8	3	0	3	4	26	4	48	6
<i>Ena montana</i>	0	0	0	0	0	0	0	0	0
<i>Ena obscura</i>	20	34	25	4	6	46	5	140	7
<i>Punctum pygmaeum</i>	8	6	0	0	3	6	0	23	4
<i>Discus rotundatus</i>	129	103	112	71	56	80	46	597	7
<i>Vitrina pellucida</i>	3	2	28	2	3	16	5	59	7
<i>Phenacolimax major</i>	0	0	0	0	0	0	0	0	0
<i>Vitrea crystallina</i>	7	0	1	0	0	2	0	10	3
<i>Vitrea contracta</i>	6	5	10	1	2	11	4	39	7
<i>Nesovitrea hammonis</i>	0	0	0	0	0	0	0	0	0
<i>Aegopinella pura</i>	25	7	10	12	8	27	7	96	7
<i>Aegopinella nitidula</i>	17	8	32	11	5	31	26	130	7
<i>Oxychilus cellarius</i>	12	20	26	8	13	10	15	104	7
<i>Oxychilus alliarius</i>	6	0	5	6	3	8	2	30	6
<i>Oxychilus helveticus</i>	15	15	25	8	0	14	14	91	6
<i>Oxychilus draparnaudi</i>	0	0	0	0	0	0	0	0	0
<i>Euconulus fulvus</i>	11	1	1	9	13	0	2	37	6
<i>Cecilioides acicula</i>	2	0	2	0	0	3	0	7	3
<i>Cochlodina laminata</i>	72	49	20	34	61	18	10	264	7
<i>Macrogastrea rolphii</i>	0	0	0	0	0	0	0	0	0
<i>Clausilia bidentata</i>	23	3	19	6	17	4	34	106	7
<i>Monacha cantiana</i>	0	0	2	0	0	0	0	2	1
<i>Zenobiella subrufescens</i>	0	0	0	0	0	0	0	0	0
<i>Trichia striolata</i>	16	63	58	39	33	13	85	307	7
<i>Trichia hispida</i>	7	7	13	3	0	6	6	42	6
<i>Helicodonta obvolvata</i>	0	0	0	0	0	0	0	0	0
<i>Arianta arbustorum</i>	0	0	0	0	0	0	0	0	0
<i>Helicigona laticida</i>	2	3	0	2	0	0	0	7	3
<i>Cepaea nemoralis</i>	10	36	23	11	16	35	36	167	7
<i>Cepaea hortensis</i>	3	10	3	3	2	9	34	64	7
<i>Helix aspersa</i>	0	0	2	2	4	6	5	19	5
Total snail species	26	22	26	25	23	26	24	31	
Total individuals	921	514	509	378	548	610	666	4146	
Total species +slugs	33	27	32	30	28	30	30	39	

SOUTH DOWNS	B1	B2	B3	H1	H2	R1	R2	R3	Total	freq
Species										
<i>Pomatias elegans</i>	33	15	13	45	35	29	39	68	277	8
<i>Acicula fusca</i>	23	5	12	12	4	7	14	12	89	8
<i>Carychium minimum</i>	0	0	0	0	0	0	0	0	0	0
<i>Carychium tridentatum</i>	161	528	276	517	219	105	651	397	2854	8
<i>Succinea putris</i>	0	0	0	0	0	0	0	0	0	0
<i>Azeqa goodalli</i>	0	3	0	5	0	0	3	0	11	3
<i>Cochlicopa lubrica</i>	1	4	10	4	7	4	5	9	44	8
<i>Cochlicopa lubricella</i>	3	0	2	3	3	0	0	0	11	4
<i>Columella edentula</i>	0	0	0	0	0	0	0	0	0	0
<i>Vertigo substriata</i>	0	0	0	0	0	0	0	1	1	1
<i>Abida secale</i>	0	0	0	0	0	0	0	0	0	0
<i>Lauria cylindracea</i>	0	2	0	3	0	0	0	0	5	2
<i>Acanthinula aculeata</i>	28	20	6	12	3	0	0	0	69	5
<i>Ena montana</i>	0	0	0	0	0	0	0	0	0	0
<i>Ena obscura</i>	3	3	4	2	20	7	1	4	44	8
<i>Punctum pygmaeum</i>	2	10	3	4	3	0	4	0	26	6
<i>Discus rotundatus</i>	104	75	70	38	56	30	62	78	513	8
<i>Vitrina pellucida</i>	7	8	2	3	4	3	2	2	31	8
<i>Phenacolimax major</i>	0	0	0	0	0	0	0	0	0	0
<i>Vitrea crystallina</i>	8	15	5	1	0	4	0	4	37	6
<i>Vitrea contracta</i>	14	31	21	6	16	8	20	10	126	8
<i>Nesovitrea hammonis</i>	0	0	0	0	0	4	0	0	4	1
<i>Aegopinella pura</i>	44	34	24	40	17	14	25	30	228	8
<i>Aegopinella nitidula</i>	36	18	25	19	22	37	18	20	195	8
<i>Oxychilus cellarius</i>	13	13	23	23	5	8	9	8	102	8
<i>Oxychilus alliarius</i>	4	8	7	0	7	6	10	0	42	7
<i>Oxychilus helveticus</i>	3	6	0	3	9	6	5	16	48	7
<i>Oxychilus draparnaudi</i>	4	0	0	0	0	0	0	0	4	1
<i>Euconulus fulvus</i>	1	7	5	1	2	6	4	2	28	8
<i>Cecilioides acicula</i>	2	1	4	0	0	0	0	1	8	4
<i>Cochlodina laminata</i>	7	6	14	21	51	48	40	28	215	8
<i>Macrogastera rolpheii</i>	63	9	22	16	26	14	15	3	168	8
<i>Clausilia bidentata</i>	18	10	4	34	103	60	35	41	305	8
<i>Monacha cantiana</i>	0	0	0	0	0	0	0	0	0	0
<i>Zenobiella subrufescens</i>	0	0	3	1	0	2	0	0	6	3
<i>Trichia striolata</i>	1	3	9	0	9	5	4	3	34	7
<i>Trichia hispida</i>	0	4	2	2	0	5	2	3	18	6
<i>Helicodonta obvolvata</i>	25	18	15	18	5	5	8	3	97	8
<i>Arianta arbustorum</i>	3	3	2	0	19	2	3	0	32	6
<i>Helicigona lapicida</i>	0	0	1	2	0	8	3	1	15	5
<i>Cepaea nemoralis</i>	0	0	0	1	3	0	1	1	6	4
<i>Cepaea hortensis</i>	10	10	3	15	24	12	7	7	88	8
<i>Helix aspersa</i>	6	3	10	12	8	12	2	3	56	8
Total snail species	28	29	29	29	26	27	27	26	36	
Total individuals	627	872	597	863	680	451	992	755	5837	
Total species +slugs	35	34	34	37	32	33	33	31	48	

COTSWOLDS	S1	S2	S3	W1	W2	P	R	M	Total	freq
Species										
<i>Pomatias elegans</i>	21	13	20	24	11	20	55	6	170	8
<i>Acicula fusca</i>	11	10	9	8	23	3	7	2	73	8
<i>Carychium minimum</i>	0	0	3	0	10	0	0	0	13	2
<i>Carychium tridentatum</i>	142	233	169	365	356	89	248	40	1642	8
<i>Succinea putris</i>	0	0	2	0	7	0	0	0	9	2
<i>Azeqa goodalli</i>	12	42	34	10	16	0	0	8	122	6
<i>Cochlicopa lubrica</i>	8	10	30	22	11	2	3	9	95	8
<i>Cochlicopa lubricella</i>	2	2	0	2	0	0	2	1	9	5
<i>Columella edentula</i>	5	1	1	0	8	0	0	2	17	5
<i>Vertigo substriata</i>	0	0	0	0	0	0	0	0	0	0
<i>Abida secale</i>	0	0	0	0	0	0	2	0	2	1
<i>Lauria cylindracea</i>	7	10	1	0	0	0	0	2	20	4
<i>Acanthinula aculeata</i>	9	20	54	52	30	25	35	14	239	8
<i>Ena montana</i>	53	28	13	15	8	0	2	0	119	6
<i>Ena obscura</i>	6	4	2	5	2	12	13	3	47	8
<i>Punctum pygmaeum</i>	11	50	19	17	32	5	18	12	164	8
<i>Discus rotundatus</i>	53	68	72	91	69	68	98	43	562	8
<i>Vitrina pellucida</i>	6	3	5	12	2	9	5	3	45	8
<i>Phenacolimax major</i>	0	0	0	2	1	2	2	0	7	4
<i>Vitrea crystallina</i>	15	4	3	10	26	6	13	16	93	8
<i>Vitrea contracta</i>	20	50	23	71	35	17	26	15	257	8
<i>Nesovitrea hammonis</i>	2	0	0	0	20	0	0	0	22	2
<i>Aegopinella pura</i>	16	28	31	80	40	28	39	18	280	8
<i>Aegopinella nitidula</i>	18	30	30	20	19	5	16	35	173	8
<i>Oxychilus cellarius</i>	9	39	31	25	17	2	11	16	150	8
<i>Oxychilus alliaris</i>	2	9	5	4	3	5	4	6	38	8
<i>Oxychilus helveticus</i>	7	4	3	8	0	5	5	21	53	7
<i>Oxychilus draparnaudi</i>	0	0	0	0	0	0	0	0	0	0
<i>Euconulus fulvus</i>	3	11	7	26	24	3	6	5	85	8
<i>Cecilioides acicula</i>	1	0	0	0	0	0	2	0	3	2
<i>Cochlodina laminata</i>	38	37	16	32	26	35	37	28	249	8
<i>Macrogastra rolphii</i>	2	3	1	0	0	12	7	0	25	5
<i>Clausilia bidentata</i>	19	25	14	73	67	40	14	54	306	8
<i>Monacha cantiana</i>	1	0	0	0	0	0	0	0	1	1
<i>Zenobiella subrufescens</i>	1	3	3	4	2	1	2	4	20	8
<i>Trichia striolata</i>	75	35	23	15	12	9	40	5	214	8
<i>Trichia hispida</i>	7	6	6	4	2	4	2	0	31	7
<i>Helicodonta obvolvata</i>	0	0	0	0	0	0	0	0	0	0
<i>Arianta arbustorum</i>	23	4	4	21	16	8	0	4	80	7
<i>Helicigona lapicida</i>	4	2	0	0	0	8	2	0	16	4
<i>Cepaea nemoralis</i>	4	8	3	3	7	11	41	6	83	8
<i>Cepaea hortensis</i>	13	6	8	8	9	8	1	7	60	8
<i>Helix aspersa</i>	0	0	0	0	0	3	0	0	3	1
Total snail species	35	32	32	29	31	29	31	28	40	
Total individuals	626	798	645	1029	911	445	758	385	5597	
Total species +slugs	44	39	40	36	39	35	35	34	52	

WYE VALLEY	L1	L2	L3	H1	H2	S1	S2	Total	freq
Species									
<i>Pomatias elegans</i>	35	5	6	0	0	8	0	54	4
<i>Acicula fusca</i>	4	7	4	3	2	7	14	41	7
<i>Carychium minimum</i>	5	0	0	0	0	0	5	10	2
<i>Carychium tridentatum</i>	275	198	57	85	128	71	198	1012	7
<i>Succinea putris</i>	0	0	0	0	0	0	0	0	0
<i>Azeza goodalli</i>	0	0	0	10	2	0	0	12	2
<i>Cochlicopa lubrica</i>	14	7	9	4	7	8	7	56	7
<i>Cochlicopa lubricella</i>	0	0	0	0	0	0	0	0	0
<i>Columella edentula</i>	0	3	0	0	0	0	0	3	1
<i>Vertigo substriata</i>	0	0	0	0	0	0	0	0	0
<i>Abida secale</i>	0	0	0	0	0	0	0	0	0
<i>Lauria cylindracea</i>	4	114	0	0	24	8	95	245	5
<i>Acanthinula aculeata</i>	10	17	7	16	30	19	31	130	7
<i>Ena montana</i>	0	0	0	0	0	0	0	0	0
<i>Ena obscura</i>	6	3	5	4	4	1	9	32	7
<i>Punctum pygmaeum</i>	12	18	2	25	11	3	25	96	7
<i>Discus rotundatus</i>	145	137	141	82	77	100	148	830	7
<i>Vitrea pellucida</i>	2	11	6	11	8	8	19	65	7
<i>Phenacolimax major</i>	0	1	2	1	0	0	3	7	4
<i>Vitrea crystallina</i>	9	36	16	9	12	16	8	106	7
<i>Vitrea contracta</i>	25	42	40	19	14	45	62	247	7
<i>Nesovitrea hammonis</i>	0	0	1	0	0	0	0	1	1
<i>Aegopinella pura</i>	27	40	36	38	36	48	40	265	7
<i>Aegopinella nitidula</i>	19	20	23	22	19	24	20	147	7
<i>Oxychilus cellarius</i>	13	6	15	11	10	31	11	97	7
<i>Oxychilus alliarius</i>	0	3	9	4	11	5	3	35	6
<i>Oxychilus helveticus</i>	6	15	8	14	25	9	7	84	7
<i>Oxychilus draparnaudi</i>	0	0	0	0	0	0	0	0	0
<i>Euconulus fulvus</i>	14	5	0	1	0	0	1	21	4
<i>Ceciloides acicula</i>	0	0	0	0	0	2	0	2	1
<i>Cochlodina laminata</i>	6	1	2	24	8	3	26	70	7
<i>Macrogastra rolpheii</i>	0	0	0	4	0	0	0	4	1
<i>Clausilia bidentata</i>	42	22	60	90	49	69	65	397	7
<i>Monacha cantiana</i>	0	0	0	0	0	0	0	0	0
<i>Zenobiella subrufescens</i>	2	4	3	3	10	4	4	30	7
<i>Trichia striolata</i>	0	2	0	0	0	0	0	2	1
<i>Trichia hispida</i>	15	0	2	20	11	2	7	57	6
<i>Helicodonta obvolvata</i>	0	0	0	0	0	0	0	0	0
<i>Arianta arbustorum</i>	2	0	5	4	1	1	15	28	6
<i>Helicigona lapicida</i>	3	7	2	2	2	0	5	21	6
<i>Cepaea nemoralis</i>	4	5	2	11	11	4	3	40	7
<i>Cepaea hortensis</i>	1	3	8	12	10	0	0	34	5
<i>Helix aspersa</i>	2	7	2	3	9	0	0	23	5
Total snail species	27	28	27	28	26	24	26	35	
Total individuals	702	739	473	532	531	495	831	4303	
Total species +slugs	34	35	33	36	34	30	32	44	

APPENDIX 3.

The occurrence of slugs, and of snails represented only by ancient shells, given by area and site. Conventions as in Appendix 2.

CHILTERN

SLUGS	A1	A2	C1	C2	C3	C4	C5	Freq.
<i>Arion ater</i> agg.	X	X	X	X	X	X	X	7
<i>Arion subfuscus</i>	X	X	X	X	X	X	X	7
<i>Arion circumscriptus</i>	X	X	X				X	4
<i>Arion fasciatus</i>								0
<i>Arion hortensis</i> agg.	X	X	X	X	X	X	X	7
<i>Limax maximus</i>	X			X	X			3
<i>Limax cinereoniger</i>								0
<i>Lehmannia marginata</i>	X	X	X	X	X	X	X	7
<i>Boettgerilla pallens</i>								0
<i>Tandonia sowerbyi</i>			X				X	2
<i>Tandonia budapestensis</i>								0
<i>Deroceras laeve</i>								0
<i>Deroceras reticulatum</i>	X							1
<i>Deroceras panormitanum</i>								0
Total slugs	7	5	6	5	5	4	6	8
Total species	33	27	32	30	28	30	30	39
ANCIENT SHELLS								
<i>Pyramidula rupestris</i>								0
<i>Vertigo pygmaea</i>	X			X		X		3
<i>Abida secale</i>		X	X				X	3
<i>Pupilla muscorum</i>	X		X			X	X	4
<i>Vallonia costata</i>								0
<i>Vallonia excentrica</i>	X	X	X			X	X	5
<i>Vallonia</i> sp.								0
<i>Helicella itala</i>		X	X	X		X	X	5
Total	3	3	4	2	0	4	4	5

SOUTH DOWNS

SLUGS	B1	B2	B3	H1	H2	R1	R2	R3	Freq
<i>Arion ater</i> agg.	X	X	X	X	X	X	X	X	8
<i>Arion subfuscus</i>	X	X	X	X	X	X	X	X	8
<i>Arion circumscriptus</i>	X		X	X	X	X	X	X	7
<i>Arion fasciatus</i>				X					1
<i>Arion hortensis</i> agg.	X	X	X	X	X	X	X	X	8
<i>Limax maximus</i>	X		X		X	X	X	X	6
<i>Limax cinereoniger</i>				X					1
<i>Lehmannia marginata</i>	X	X		X	X	X	X	X	7
<i>Boettgerilla pallens</i>	X	X							2
<i>Tandonia sowerbyi</i>									0
<i>Tandonia budapestensis</i>				X					1
<i>Deroceras laeve</i>									0
<i>Deroceras reticulatum</i>			X						1
<i>Deroceras panormitanum</i>	X	X							2
Total slugs	8	6	6	8	6	6	6	6	12
Total species	35	34	34	37	32	33	33	31	48
ANCIENT SHELLS									
<i>Pyramidula rupestris</i>									0
<i>Vertigo pygmaea</i>									0
<i>Abida secale</i>									0
<i>Pupilla muscorum</i>				X					1
<i>Vallonia costata</i>								X	1
<i>Vallonia excentrica</i>									0
<i>Vallonia</i> sp.									0
<i>Helicella itala</i>									0
Total	0	0	0	1	0	0	0	1	2

COTSWOLDS

SLUGS	S1	S2	S3	W1	W2	P	R	M	Freq
<i>Arion ater</i> agg.	X	X	X	X	X	X		X	7
<i>Arion subfuscus</i>	X	X	X	X	X	X	X	X	8
<i>Arion circumscriptus</i>	X		X	X	X	X	X		6
<i>Arion fasciatus</i>								X	1
<i>Arion hortensis</i> agg.	X	X	X	X	X	X	X	X	8
<i>Limax maximus</i>	X	X	X		X			X	5
<i>Limax cinereoniger</i>			X						1
<i>Lehmannia marginata</i>	X	X	X	X	X	X	X	X	8
<i>Boettgerilla pallens</i>				X					1
<i>Tandonia sowyerbyi</i>	X	X							2
<i>Tandonia budapestensis</i>									0
<i>Deroceras laeve</i>	X				X				2
<i>Deroceras reticulatum</i>	X	X	X	X	X	X			6
<i>Deroceras panormitanum</i>									0
Total slugs	9	7	8	7	8	6	4	6	12
Total species	44	39	40	36	39	35	35	34	52
ANCIENT SHELLS									
<i>Pyramidula rupestris</i>						X			1
<i>Vertigo pygmaea</i>					X				1
<i>Abida secale</i>									0
<i>Pupilla muscorum</i>									0
<i>Vallonia costata</i>							X		1
<i>Vallonia excentrica</i>									0
<i>Vallonia</i> sp.				X	X				2
<i>Helicella itala</i>									0
Total	0	0	0	1	2	1	1	0	4

WYE VALLEY

SLUGS	L1	L2	L3	H1	H2	S1	S2	Freq
<i>Arion ater</i> agg.	X	X		X	X	X		5
<i>Arion subfuscus</i>	X	X	X	X	X	X	X	7
<i>Arion circumscriptus</i>	X		X	X	X		X	5
<i>Arion fasciatus</i>		X		X	X	X		4
<i>Arion hortensis</i> agg.	X	X	X	X	X	X	X	7
<i>Limax maximus</i>	X							1
<i>Limax cinereoniger</i>		X	X	X	X		X	5
<i>Lehmannia marginata</i>	X	X	X	X	X	X	X	7
<i>Boettgerilla pallens</i>								0
<i>Tandonia sowerbyi</i>								0
<i>Tandonia budapestensis</i>								0
<i>Deroceras laeve</i>								0
<i>Deroceras reticulatum</i>	X	X	X	X	X	X	X	7
<i>Deroceras panormitanum</i>								0
Total slugs	7	7	6	8	8	6	6	9
Total species	34	35	33	36	34	30	32	44
ANCIENT SHELLS:	NONE							