

## Geographical variation in the composition and richness of forest snail faunas in northern Europe

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**Abstract** – The forest snail fauna of northern Europe originated from post-glacial colonization from the south. While it is regionally poor (c. 150 species, excluding slugs), individual localities (clusters of sample sites within a few km of each other) can be rich by global standards (up to 57 species). Distance decay in faunal similarity is very gradual in lowland regions, but Carpathian faunas are sharply differentiated, and hold the most endemics. British faunas are remarkably uniform. Very little of this differentiation is due to congeneric replacement; it results mostly from shifts in the richness of whole families. Clausiliids in particular predominate in the Carpathians and adjacent areas, but this is not reflected in the apparent density of individuals: as species richness increases, average abundance of each declines. In general, small species are more widely distributed than large ones. Although the richest localities are found in the Carpathians, regional variation in local richness is slight. Substrate has significant effects: oligotrophic areas have poorer and more locally variable faunas. At a slightly larger scale, areas of less than 100 km<sup>2</sup> holding more than 60 species can be found in many parts of the region (even more when slugs are included); the richest such patches hold about half the whole regional forest fauna. Comparison with limited data from regions further south shows that although they have much richer regional faunas, local communities are no richer than those of the north. Distance decay is much more rapid. These results are discussed, with global comparisons, in terms of the ways in which molluscan communities are assembled and structured.

**Key words:** Land snail faunas, N. Europe, species richness and composition

### INTRODUCTION

At the largest scale, the pattern of land snail distribution in Europe is well known (Kerney, Cameron and Jungbluth, 1983; Falkner, Bank and von Proschwitz, 2001). There is an increase in species richness from north to south, and to a lesser extent from west to east (Cameron, 2004). These large-scale patterns have many causes. More southerly areas offer a wider range of habitats, each with its own fauna; they also hold more restricted endemics, the ranges of which reflect the distribution of glacial refugia during the Pleistocene. By contrast, large-scale variation in northern faunas reflects differential movement from refugia, sometimes over long distances, as well as ecological constraints (Hausdorf and Hennig, 2003). While arctic-alpine faunas survived the later phases of the Pleistocene in the north, moving northward or upward as the climate ameliorated, forest faunas in areas north of the major mountain ranges are composed of immigrants that have arrived from the south in the last 10,000 years.

This large-scale pattern does not persist at much smaller scales (Cameron, 2004). Within forests, local faunas (in areas of 1 km<sup>2</sup> or less) do not show the same degree of latitudinal variation in richness. Some forest faunas north of the mountain ranges, for example on the Spitzberg, Tübingen (Schmid, 1966), in Białowieża Forest (Cameron and Pokryszko, 2004), or in the Cotswolds (Cameron, Pokryszko and Long, in press), have levels of richness approaching those found in the famous subtropical sites in New Zealand studied by Solem and colleagues (Solem, 1984; Solem, Climo and Roscoe, 1981; see also comments in Emberton, 1995).

These issues of local relative to regional composition and richness have both theoretical (Srivastava, 1999), and conservation (Reid, 1998) significance. They also relate to Solem's (1984) analysis of global patterns in land mollusc diversity.

In an earlier paper (Cameron and Pokryszko, 2004), we noted the rather slow rate of distance decay in similarity in faunas (Nekola and White, 1999) on non-calcareous soils in the North European

Plain. In this paper, we examine the pattern of variation in North European forest faunas as a whole, including those in mountainous areas and on limestone, where the richest faunas are to be found. We do this by comparing small areas of relatively uniform environments. We look at both richness and composition, and relate them both to Pleistocene/Holocene environmental changes, and to ecological constraints.

Although there is an extensive literature relating to local faunas in many European countries, variations in sampling methods and efficiency, and in the sizes and uniformity of the areas surveyed often make direct comparisons hazardous. We have therefore relied heavily on data collected by ourselves, using standard protocols, supplementing it with others where the sampling regime appears adequate, and where better geographical coverage was required. Although we discuss them briefly, we have excluded slugs from our formal analyses, as inspection of both our own data, and those of others, demonstrates that the sampling methods used are not adequate for them (Cameron, Pokryszko and Long, in press).

### SAMPLING METHODS, THE CHOICE OF STUDIES AND ANALYSIS

Our own studies consist of clusters of samples made from 400 m<sup>2</sup> plots within a few km of each other, and within forest; edges or ecotones being excluded (Cameron and Pokryszko, 2004). Within each plot, two people searched by eye for one hour, and 10 litres of litter was collected, and sieved and searched in the laboratory. All living and fresh specimens were identified and counted.

Our own studies are confined to southern England, to the south and east of Poland, and to the Ukrainian Carpathians. To increase the geographical coverage, we have included data from studies elsewhere in N. Europe (Table 1). In each case, it is possible to assemble a list of forest species resulting from sampling in more than one site, within a restricted district, using comparably effective sampling. We have excluded data relating to non-forest sites, and in the case of data from Körnig (1966), we have considered only the three sites in which the sampling regime appears to resemble our own. We have excluded species recorded as long dead shells only.

Analysis of between plot and other local variation in richness and composition will be presented elsewhere. For the purposes of analysis here, we have examined the composition of each cluster, combining all the plots involved. While biased sampling error (missing some species present) cannot be eliminated, we are satisfied that such errors are small when results from our plots are combined in this way (Cameron and Pokryszko,

2005). For some analyses, confined to our own data, we consider mean levels of recorded abundance per site.

Although all clusters are in forest, there is considerable ecological variation both within and between them. As Waldén (1981) has shown, in any one locality the richest single plots contain most of the species; poorer plots lose species, but do not, in general, gain others specialising in oligotrophic conditions. One exception to this occurs when some plots sampled include forested wetland (e.g. Cameron and Pokryszko, 2004). Thus we also consider the richest single plot within each cluster as an indication of syntopic richness, the  $\alpha$  diversity of Whittaker (Southwood and Henderson, 2000). In some studies not made by us it is not possible to extract data for the richest single plot, and plot sizes vary (sometimes unspecified) between studies. We use the modified Whittaker's Index,  $I_{\max}$ , the ratio of the number of species recorded for the locality to the number in the richest plot as an indicator of the uniformity of the fauna (Koleff, Gaston and Lennon, 2003). The conventional index uses the mean number of species per plot (Southwood and Henderson, 2000) as the divisor; inspection of the data suggests that this will be influenced by the inclusion of poor individual plots, which differ merely in having a reduced fauna.

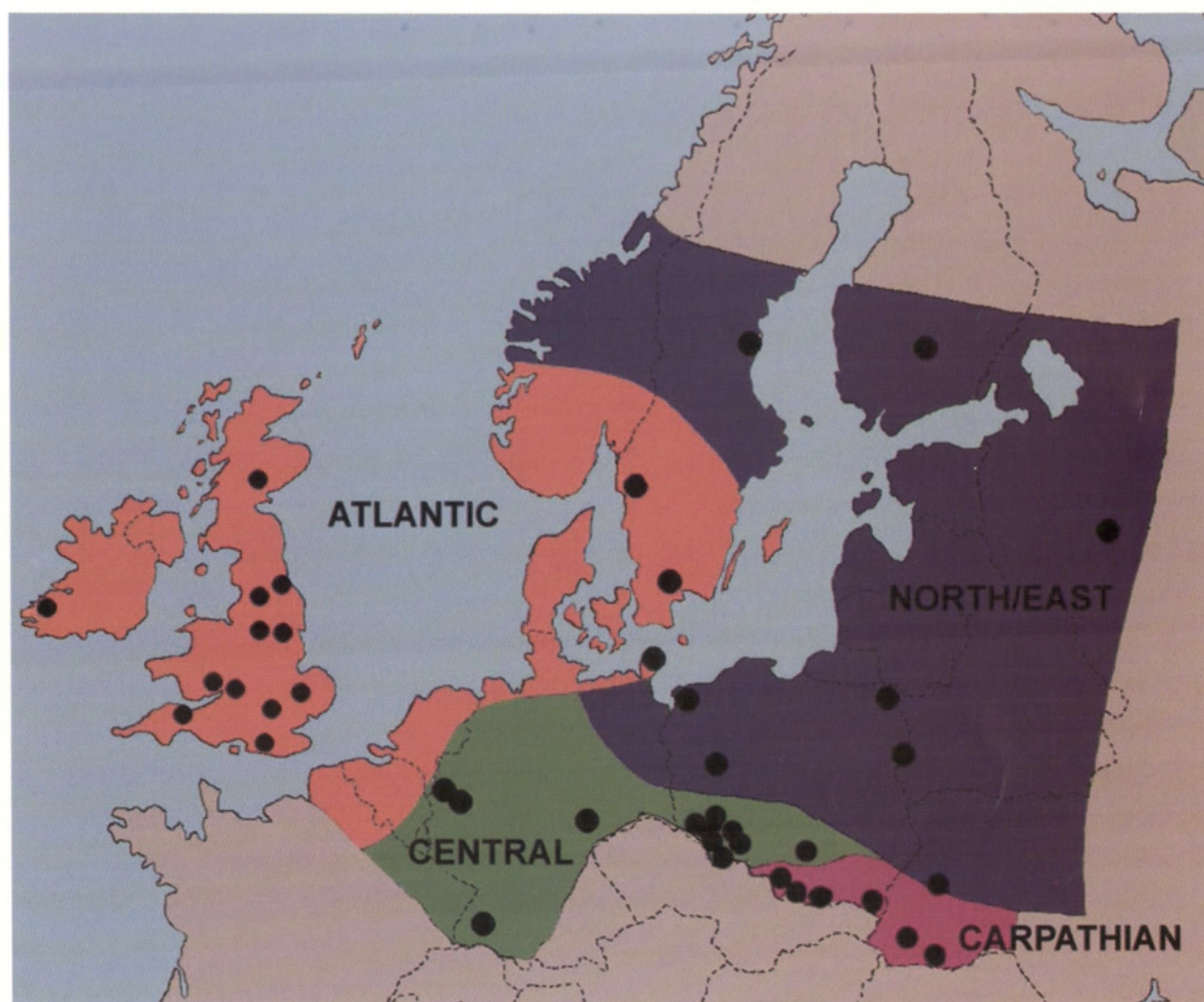
Faunal similarity has been compared in two ways:

1. Site by site comparison using the Nei index:  $I_N = \text{number of species in common} / \text{geometric mean of the species present at each site}$ . This index is very similar to the familiar Jaccard index, but compensates in part for differences in the species richness at each site, and lacks the undesirable concave decay curve associated with single step changes in species held in common.
2. Site by site comparison using both presences and absences in relation to the whole array of 129 species, to estimate the significance of any associations, whether positive or negative (Cameron and Cook, 2001). The derived index gives the number of standard deviations separating the observed association and that expected by chance, given the number of species found at each site. Values in excess of 2.0 are formally significant.

### THE AREA COVERED AND THE SPECIES ARRAY

Figure 1 shows the distribution of localities included in our analyses. All are north of the watershed formed by the Alps, the Böhmer Wald, the Sudetes and the Carpathians, except for the two localities (Ugol'ka and Kuziy) in the Ukrainian Carpathians. Within this area, also including the





**Figure 1** The position of localities used in this paper. Note that some spots include more than one locality.

northern half of France, there are c. 195 species of snail (slugs excluded), using the species identities, nomenclature and distributions given in Kerney, Cameron and Jungbluth (1983). There are two exceptions to the latter: included in the list for Kuziy (Ukraine) is *Mastus bielzi* (Kimakowicz, 1890), a species absent from the area covered by Kerney *et al.* (1983) (Grossu, 1955), and in both Kuziy and Ugol'ka there is an unidentified *Vestia* species (Clausiliidae), clearly distinct from all other *Vestia* in the array.

Of these 195 species, 48 have open wetland, alpine or xerophile habitat preferences, and are unlikely to be found inside true forest. Of the 147 species remaining, the samples we consider contain 129 (87%). Table 2 shows the missing species. Of the 18 involved, 13 are basically Alpine, 3 are extreme westerners, one is an anomalous endemic (W. Germany), and one extends from the Czech Republic to a single site in S.W. Poland. Overall, 10 species were recorded in one locality only, and 9 species in only two. Based on this, the Chao

estimator (Southwood and Henderson, 2000) indicates that there might be c. 6 species present but missed in our array. Our own samples contain 108 species, 73% of all forest species, and 84% of those included here. The array is thus reasonably representative of the fauna of the region as a whole.

## RESULTS

Table 1 gives the details for each of the 46 localities we consider. A presence/absence table is available in electronic form from the authors.

### Faunal Similarities

Figure 2 shows the dendrogram of affinities given by the Nei index. There is a manifest grouping of localities, which conforms to a geographical pattern. In order to examine general trends, four major regions are recognised, separated at the 50% affinity level: Atlantic, North and East, Central, and Carpathian. Within each, geographically coherent subregions can be distinguished (Figure 2). Mean

**Table 1** Details of the localities used. Ref. No. = locality numbers used in figure 1 and in the text. Long = degrees east of 10 degrees west. Subs = substrate: N, non-eutrophic; E, eutrophic; L, exposed limestone. No. of Sites = number of plots considered. Best plot = greatest number of species recorded in a single plot.  $I_{\max}$  = modified Whittaker's index (see text). C/P = unpublished data of the authors. M/P = unpublished data of T. Maltz and B.M. Pokryszko. \*Cameron and Pokryszko (2004), data from sources given in that paper. All species data exclude slugs.

Ref. No.	Location	Country	Lat	Long*	Subs	No. of Sites	No. of species	Best Plot	$I_{\max}$	Source
1	South Bluffs	Sweden	63.0	28.0	E	2	21	19	1.11	Andersson (1961)
2	Hyperite Hills	Finland	62.1	35.5	E	21	23	n/a	n/a	Valovirta (1968)
3	Meadow woods	Sweden	57.0	25.0	N	24	30	21	1.43	Wäreborn (1968)
4	Talus slopes	Sweden	57.9	22.0	E	6	43	34	1.26	Waldén (1981)
5	Cork woods	Ireland	52.0	0.5	N	11	29	20	1.45	Bishop (1977)
6	Perth woods	Scotland	56.8	6.6	N	5	30	25	1.20	Waldén (unpublished)
7	Perth woods	Scotland	56.8	6.6	L	4	30	26	1.15	Cameron and Greenwood (1992)
8	N. Yorks	England	54.5	9.3	E	17	36	28	1.29	Wardhaugh (1996)
9	Malham	England	54.1	7.8	L	4	34	27	1.26	Cameron (1978)
10	Dark Peak	England	53.3	8.2	N	17	31	24	1.29	Tattersfield (1990)
11	White Peak	England	53.3	8.2	L	21	31	25	1.24	Tattersfield (1990)
12	Anston, S. Yorks	England	53.4	8.8	L	5	33	27	1.22	Cameron (1999)
13	Cambridge	England	52.2	9.9	E	6	28	24	1.17	Paul (1978)
14	Wye Valley	England	51.8	7.4	L	7	35	28	1.25	C/P
15	Cotswolds	England	51.7	7.8	L	8	40	35	1.14	C/P
16	Chilterns	England	51.7	9.1	L	7	31	26	1.19	C/P
17	South Downs	England	50.9	9.1	L	8	36	29	1.24	C/P
18	Somerset	England	51.2	6.7	E	6	33	22	1.50	Bishop (1976)
19	Rügen	Germany	54.5	23.5	E	6	36	31	1.16	Körnig (1980)
20	Kottenforst, Bonn	Germany	50.8	17.0	N	12	28	20	1.40	Bless (1977)
21	Siebengeberg, Rhine	Germany	50.8	17.0	E	18	35	28	1.25	Hässlein (1961)
22	Spitzberg, Tübingen	Germany	48.5	19.0	L	n/a	36	n/a	n/a	Schmid (1966)
23	Hügellandes	Germany	51.0	12.0	L	3	36	34	1.06	Körnig (1966)
24	Książ	Poland	50.8	26.3	E	5	48	36	1.33	M/P
25	Góra Milek	Poland	51.1	26.0	L	4	38	29	1.31	C/P
26	Wąwóz Myśluborski	Poland	51.2	26.2	E	5	37	29	1.28	C/P
27	Bardo	Poland	50.6	26.6	E	5	42	25	1.68	C/P
28	Młynowiec	Poland	50.4	26.8	N	3	29	23	1.26	C/P
29	Muszkowice	Poland	50.7	27.1	L	4	34	32	1.06	C/P
30	Ojców	Poland	50.2	29.6	L	4	43	36	1.19	C/P, Dzieczkowski (1972)
31	Babia Góra	Poland	49.6	29.4	E	3	35	35	1.00	Dzieczkowski (1972)
32	Tatra	Poland	49.2	29.8	L	4	38	35	1.09	Dzieczkowski (1972)
33	Pieniny	Poland	49.3	30.4	L	6	57	40	1.42	Dzieczkowski (1972), Szybiak (2000)
34	Pieniny	Poland	49.3	30.4	L	7	54	42	1.29	C/P
35	Podlipowiec	Poland	49.3	30.4	N	8	48	30	1.60	C/P
36	Bieszczady Mts	Poland	49.2	32.4	E	10	50	38	1.32	Sulikowska-Droz (in press)
37	W. Baltic coast	Poland	54.0	25.0	N	6	33	22	1.50	*Cameron and Pokryszko (2004)
38	Wielkopolski N. P.	Poland	52.2	27.0	N	6	34	24	1.42	*Cameron and Pokryszko (2004)
39	Białowieża	Poland	52.7	33.8	E	17	45	32	1.41	Cameron and Pokryszko (2004)
40	Hańcza	Poland	54.3	32.8	N	8	26	18	1.44	C/P
41	L'viv	Ukraine	49.8	34.0	E	n/a	46	n/a	n/a	Sverlova (2000)
42	L'viv	Ukraine	49.8	34.0	N	3	27	17	1.59	C/P
43	Kuziy	Ukraine	48.1	34.1	L	5	40	30	1.33	C/P
44	Ugol'ka	Ukraine	48.4	33.9	L	7	38	27	1.41	C/P
45	Valdai Hills	Russia	57.5	43.0	E	n/a	40	n/a	n/a	Shikov (1981)
46	Valdai Hills	Russia	57.5	43.0	E	n/a	45	n/a	n/a	Shikov (1982)

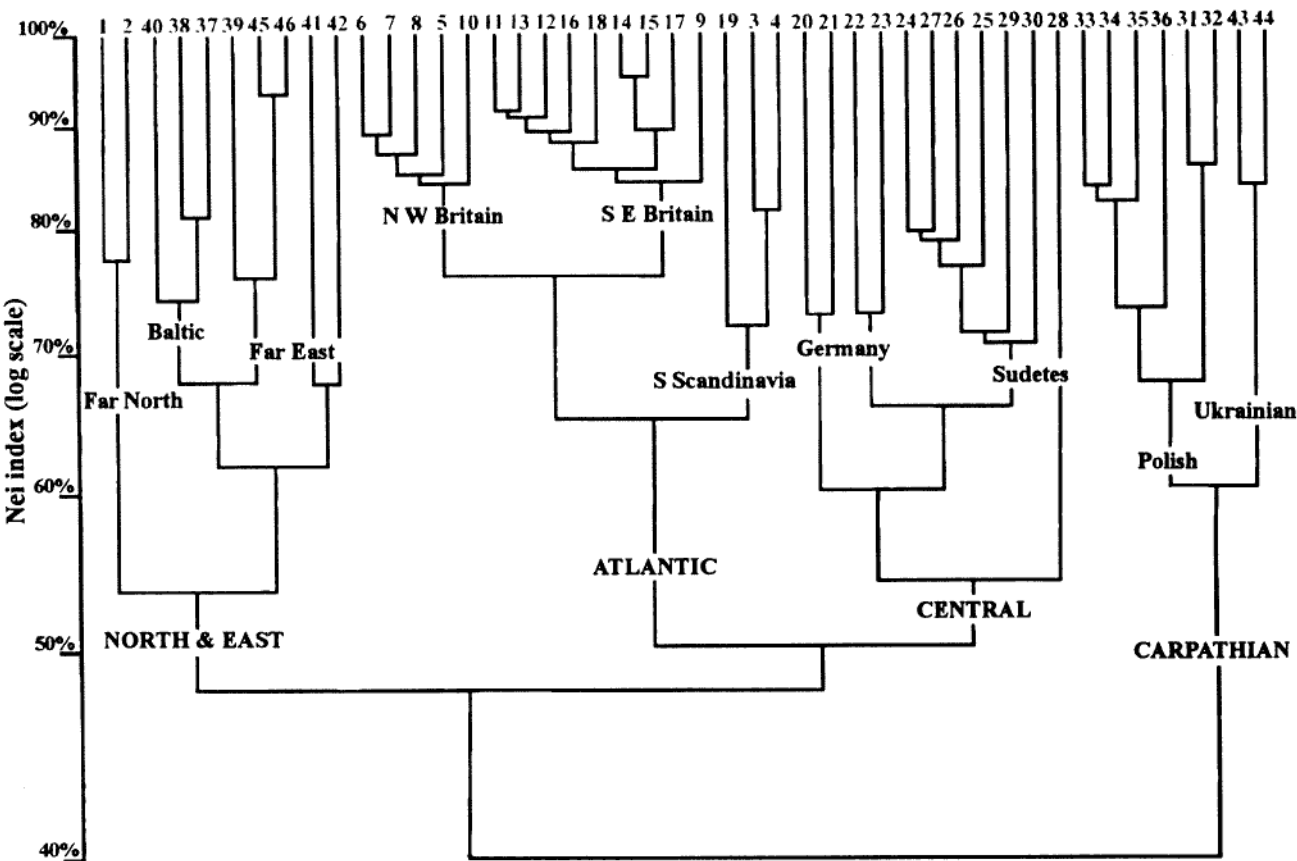


Figure 2 An UPGMA dendrogram of affinities between localities, using the Nei index (see text).

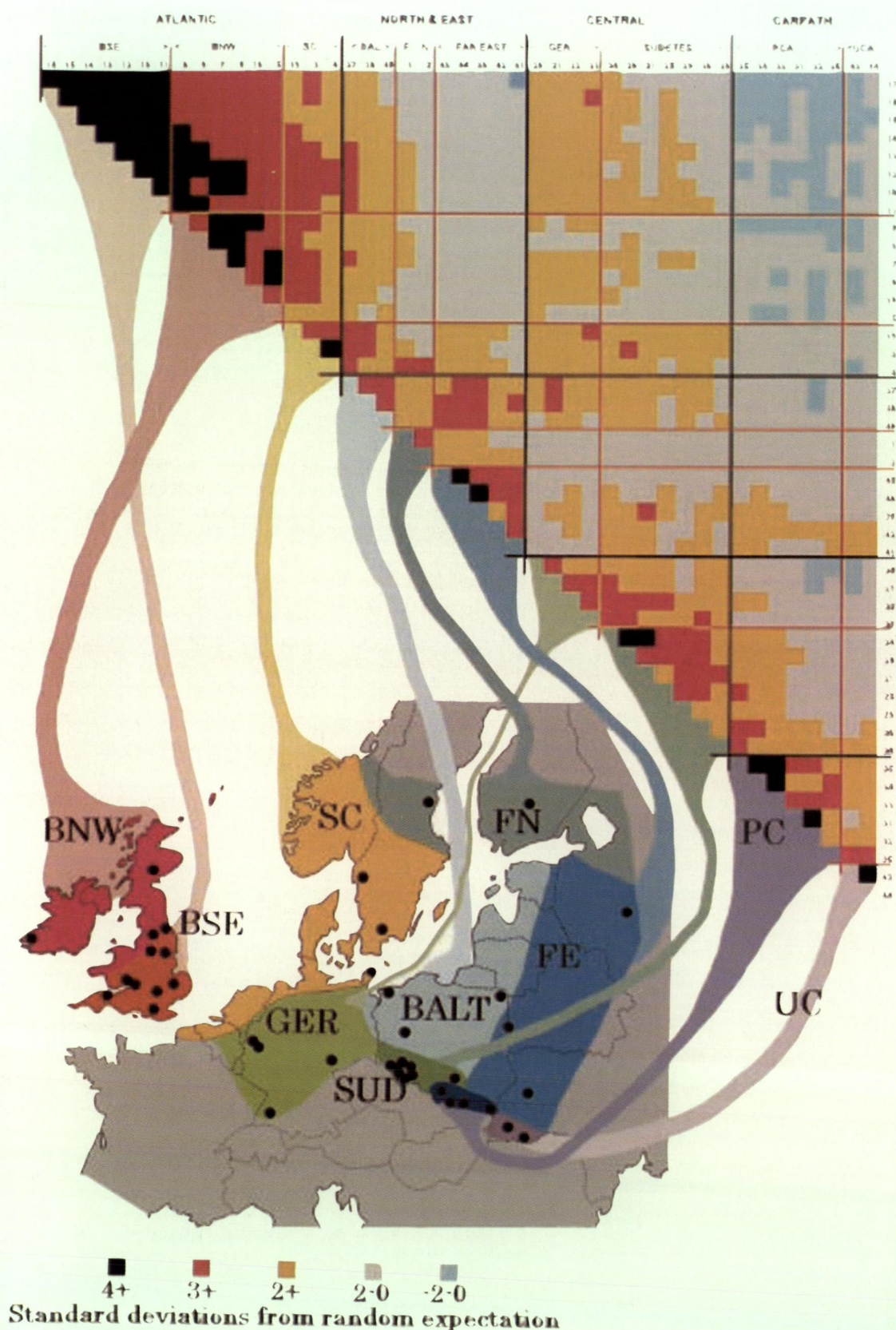
Table 2 Forest snails in N. Europe not found in the studies used here.

<i>Acicula lineata</i>	Rare N of Alps (Alpine)
<i>Acicula dupuyi</i>	France only: just into the N. half.
<i>Orcula dolium</i>	Rare N of Alps (Black Forest)
<i>Pagodulina pagodula</i>	Alsace/Lorraine only N of Alps
<i>Aegopinella ressmanni</i>	S.E. Bavaria only
<i>Clausilia fimbriata</i>	Alpine foreland of S. Germany only
<i>Charpentieria ornata</i>	Just gets into S. Poland
<i>Pseudofusulus varians</i>	Alpine foreland, S. Germany
<i>Neostyriaca corynodes</i>	Alpine foreland, S. Germany
<i>Bulgarica vetusta</i>	Isolated German relict pops only
<i>Elona quimperiana</i>	Brittany endemic
<i>Hygromia limbata</i>	Western France only (intro in UK)
<i>Trichia suberecta</i>	Relict in S. Germany (Alpine)
<i>Trichia graminicola</i>	One locality endemic, W. Germany
<i>Trichia villosa</i>	S. Germany only (Alpine)
<i>Chilostoma cingulatum</i>	Alpine: scattered relicts in S. Germany
<i>Cepaea sylvatica</i>	Jura/Alpine: just into S.W. Germany.

similarities within each region are greater than those between them (Table 3).  
Figure 3 shows the degrees of association given by the second index, with samples ordered, within the regions and subregions identified above, to maximise the amount of order in the array. The two indices are highly correlated ( $r = 0.923$ ). In both cases, it is apparent that the major axis of difference is between the British Isles at one extreme, and the

Carpathians at the other. Negative, but non-significant, associations are recorded for many comparisons between these regions. The two other regions are intermediate.  
The extent to which this axis explains variation can be seen by ordering the localities in terms of their affinities to the two most different (Figure 4). While the Carpathian and British Isles localities form distinct groups, the remainder are mixed.





**Figure 3** The matrix of associations given by the Cameron and Cook (2001) index in relation to subregions (see text). Localities are ordered among the subregions identified by the Nei index so as to give the greatest consistency in pattern. Values of the index are colour coded in the figure. Values of  $>2$  (+ or -) are formally significant at  $P < 0.05$ . No correction has been made for number of tests, as it is the pattern rather than the significance level that is relevant. Locality reference numbers are given across the top, and at the right. BNW = British Isles northwest; BSE = British Isles southeast; SC = Southern Scandinavia; GER = Germany; BALT = Baltic; FN = Far north; FE = Far east; SUD = Polish Sudetes; PC = Polish Carpathians; UC = Ukrainian Carpathians.

**Table 3** Mean values ( $\pm$  Standard Errors) of the Nei index in locality-by-locality comparisons within and between the major groupings identified (see text).

	Atlantic	Central	North/East	Carpathian
Atlantic	74.7 $\pm$ 0.81	50.6 $\pm$ 0.48	47.4 $\pm$ 0.77	31.8 $\pm$ 0.51
Central		63.6 $\pm$ 1.18	47.8 $\pm$ 0.88	47.6 $\pm$ 1.23
North/East			62.7 $\pm$ 1.59	43.4 $\pm$ 1.24
Carpathian				66.7 $\pm$ 1.98

**Table 4** Mean levels of similarity (Nei) amongst localities in the British Isles, and along the Carpathian Chain (see text).

	No. of Localities	Mean Similarity	Variance	F <sub>105, 91</sub>
British Isles	14	79.4	54.8	2.54
Carpathian Chain	15	59.2	139.1	P < 0.001

There are, however, distinct signs of geographical trends amongst them. Ojców (locality 30) for example, on limestone north of Kraków, connects the Carpathian and Sudetes faunas. The outlying position of the Far North sites (1 and 2) reflects, in part, their low species richness. There are clear east-west trends in both Central and North and East regions. Apart from these broad geographical trends, it is evident that there are differences in the amount of variation within regions; although covering a much larger geographical area, faunas in the British Isles are much more uniform than those in the Carpathians, and, indeed, show greater affinity to faunas close to the Carpathians, than the latter do to the Carpathian faunas themselves. This relative uniformity in the lowlands is illustrated by the two isocline maps in Figure 5. A far larger area has faunas that have high affinity to that of western Ireland than those showing high affinities to the fauna of the Tatra.

This difference is emphasised by considering samples in the two areas for which we have the most, and the most reliable data, the British Isles

and the whole Sudetes-Carpathian ridge. Both have samples extending over the same distance, c. 650 km, north-south in the former, WNW to ESE in the latter. Table 4 shows that the Sudetes-Carpathian localities differ more amongst themselves, and also that the variance in degree of affinity is greater, indicating a geographical pattern within the region. Faunas in the Sudetes, c. 300 km from the main Carpathians, are as different from them as they are from the fauna in W. Ireland, c. 1,800 km away.

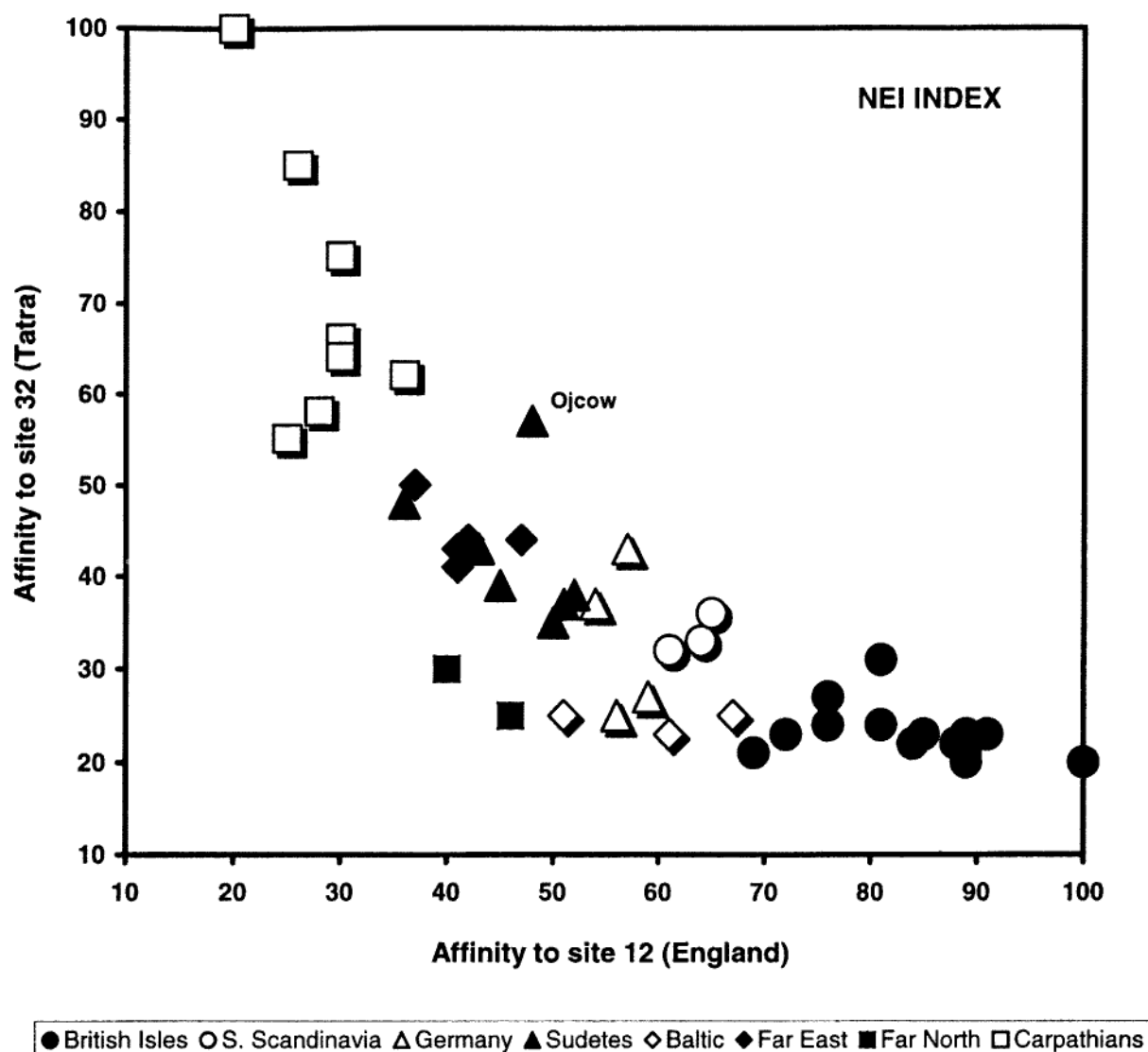
Despite the rather arbitrary nature of the two intermediate groups defined above, Central and North and East, shown clearly in Figure 4, we have retained them in many of the analyses that follow.

**Taxonomic Composition**

Of the 129 species considered here, eleven are universal, or nearly so, occurring in more than 80% of all localities, and in at least 50% of the localities in each major region considered separately (Table 5). With the exception of *Cochlodina laminata*, a clausiliid, they are all small litter-dwelling species. A further 20 species are also found in all four

**Table 5** Universal species, occurring in 50%+ of the localities in each region, and in 80%+ of all localities (% frequencies).

	Atlantic	Central	North/East	Carpathian	Total occurrences
<i>Euconulus fulvus</i>	100	100	100	100	46
<i>Punctum pygmaeum</i>	94	100	100	100	45
<i>Carychium tridentatum</i>	100	100	80	100	44
<i>Acanthinula aculeata</i>	100	91	90	100	44
<i>Columella edentula</i>	94	91	100	87	43
<i>Aegopinella pura</i>	100	100	70	100	43
<i>Cochlicopa lubrica</i>	100	100	100	50	42
<i>Vitrina pellucida</i>	100	82	90	62	40
<i>Nesovitrea hammonis</i>	100	82	100	50	40
<i>Cochlodina laminata</i>	82	82	90	100	40
<i>Vitrea crystallina</i>	100	82	80	62	39



**Figure 4** Localities ordered on their similarities (Nei index) to Locality 12 (Yorkshire, UK), and to Locality 32 (Tatra, Poland). These are the two most dissimilar localities (see text). Ojcow (marked) lies between the Sudetes and the Carpathians proper.

regions, but at low frequencies in at least one. Of these, however, seven are missing from the British Isles localities within the Atlantic region.

At the other extreme, 27 species are recorded from three or fewer localities, and cannot, therefore, be present in all four regions. While most of these are native forest species that are rare or geographically restricted, a few are introduced species, or are not normally found under full forest cover. Despite the "noise" that such species may introduce, our analyses refer always to the full set of species recorded. The varying number of localities available in each subregion is an additional analytical constraint.

As expected, the distribution of species amongst the localities reflects what is known of their geographical distributions. Some are more restricted in our localities than their geographical range necessitates, but in general the fit is good. Thus, of

the 72 species in the array not recorded in the British localities, only eight are known from Britain, though a further three are recorded in Holocene deposits (Kerney, 1999). When the subregions delimited in figures 2 and 3 are considered individually, 23 species are found in one only, while 7 are found in all ten. Of the 99 remaining species, only five show incoherent distributions in our localities, and in one of these, *Vitrea subrimata*, incoherence reflects a genuinely disjunct range (Kerney *et al.*, 1983). While it is not surprising that the Far North (represented also by only two localities) is species-poor, this is also true of the Baltic relative to the neighbouring lowland subregions, Germany, S. Scandinavia and the Far East. The two Carpathian subregions hold far more unique species individually and combined than any other subregion or adjacent pair, followed by the British subregions combined, reflecting the pattern shown earlier.



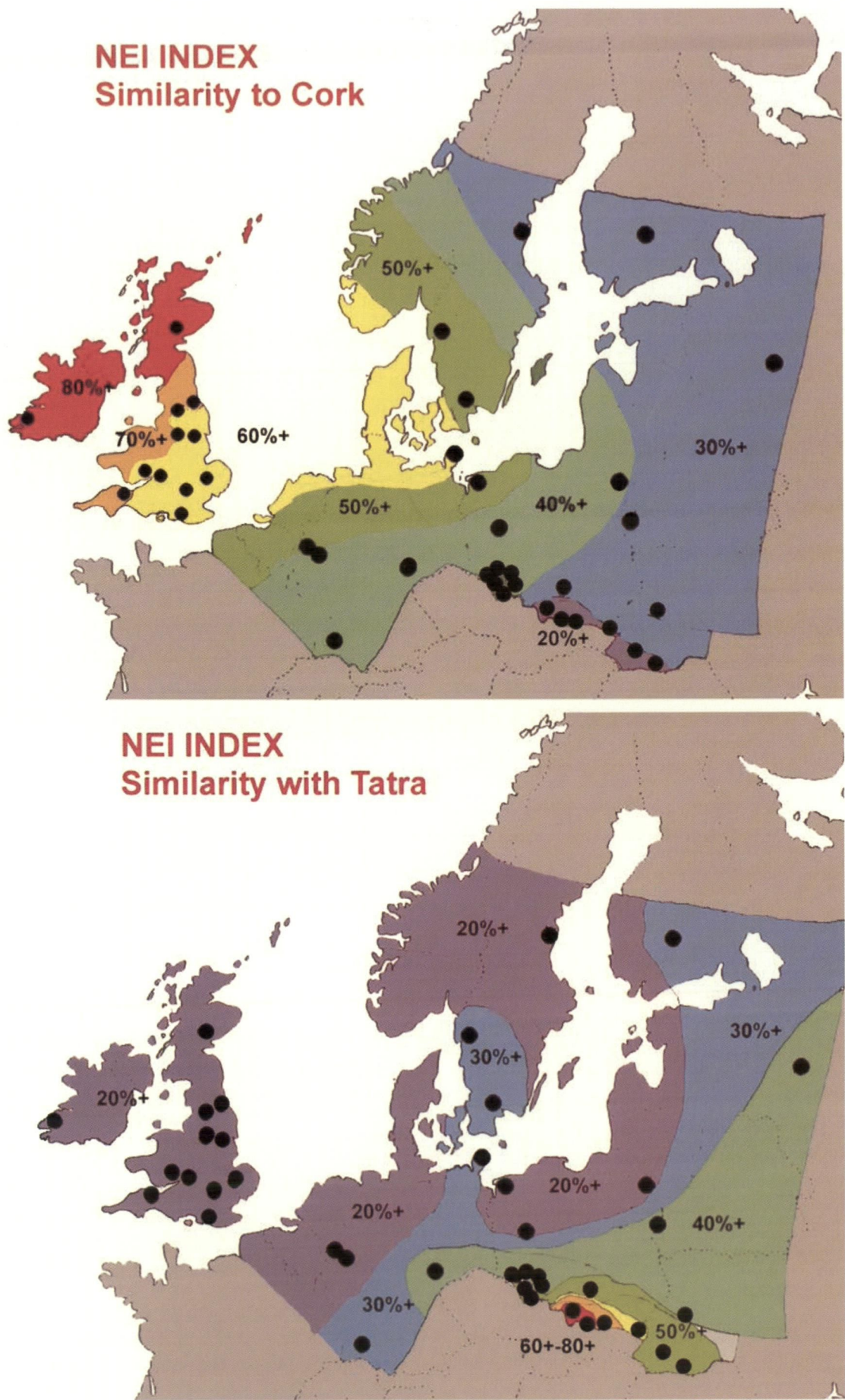


Figure 5 Isocline maps of Nei similarities to (a) Locality 5, Cork, Ireland, and (b) Locality 32, Tatra, Poland.

**Table 6** A. Unique species by Region, arranged in order of decreasing frequency of occurrence. Asterisks: for Atlantic, species not unique to British Isles, i.e. also/only in S. Scandinavia; for Central, species found only in the Polish Sudetes, i.e. in the Carpathian Chain. B. Species occurring in more than one region, but at least 2.5 times as frequent in the one labelled than in any other.

A			
Atlantic	Central	North/East	Carpathian
<i>Lauria cylindracea</i> *	<i>Clausilia parvula</i>	<i>Perforatella rubiginosa</i>	<i>Vitrea transsylvanica</i>
<i>Oxychilus helveticus</i>	<i>Eucobresia diaphana</i>	<i>Columella columella</i>	<i>Argna bielzi</i>
<i>Perforatella subrufescens</i>	<i>Causa holosericum</i> *	<i>Cochlicopa nitens</i>	<i>Oxychilus orientalis</i>
<i>Trichia striolata</i>	<i>Sphyradium doliolum</i> *		<i>Semilimax kotulae</i>
<i>Helix aspersa</i>	<i>Vitrinobrachium breve</i>		<i>Vestia gulo</i>
<i>Pomatias elegans</i>	<i>Cochlodina costata</i> *		<i>Vestia turgida</i>
<i>Acicula fusca</i>	<i>Macrogastra lineolata</i>		<i>Vestia sp.</i>
<i>Spermodea lamellata</i> *			<i>Balea fallax</i>
<i>Zonitoides excavatus</i>			<i>Balea stabilis</i>
<i>Euconulus alderi</i> *			<i>Mastus bielzi</i>
<i>Leiostyla anglica</i>			<i>Trichia villosula</i>
<i>Monacha cantiana</i>			<i>Trichia bielzi</i>
<i>Ashfordia granulata</i>			<i>Trichia lubomirskii</i>
<i>Phenacolimax major</i>			<i>Trichia bakowskii</i>
<i>Vertigo angustior</i> *			<i>Drobacia banatica</i>
			<i>Acicula perpusilla</i>
			<i>Oxychilus inopinatus</i>
			<i>Carpathica calophana</i>
B			
Atlantic	Central	North/East	Carpathian
<i>Azeza goodalli</i>	<i>Helicodonta obvolvata</i>	<i>Nesovitrea petronella</i>	<i>Aegopinella epipedostoma</i>
<i>Oxychilus alliarius</i>	<i>Balea biplicata</i>	<i>Vallonia pulchella</i>	<i>Oxychilus glaber</i>
<i>Vitrea contracta</i>		<i>Vallonia costata</i>	<i>Vitrea subrimata</i>
<i>Cecilioides acicula</i>		<i>Vertigo pygmaea</i>	<i>Eucobresia nivalis</i>
<i>Balea perversa</i>		<i>Vertigo ronneyensis</i>	<i>Acicula parcelineata</i>
<i>Clausilia bidentata</i>		<i>Zoogenetes harpa</i>	<i>Discus perspectivus</i>
		<i>Oxyloma elegans</i>	<i>Ruthenica filigrana</i>
		<i>Zonitoides nitidus</i>	<i>Macrogastra tumida</i>
		<i>Perforatella bidentata</i>	<i>Macrogastra latestriata</i>
		<i>Euomphalia strigella</i>	<i>Perforatella dibothrion</i>
			<i>Perforatella umbrosa</i>
			<i>Trichia unidentata</i>
			<i>Faustina faustinum</i>

Because some subregions contain very few localities, however, detailed analysis is restricted to the faunas of each major region, to get a better balance in the numbers of localities involved. 43 species are restricted to one region, and a further 31 are much more frequent in one region than in any others (Table 6). The species confined to, or predominant in, the Carpathians are mostly those with limited Carpathian or Alpine-Carpathian distributions. In the Atlantic region, however, while there are genuine western endemics such as *A. fusca*, *L. anglica*, *A. granulata* and *P. subrufescens*, there are also introduced species of southern origin, such as *H. aspersa*, *M. cantiana* and *O. helveticus*. Those in the Central region include species with Alpine or circum-Alpine centres of distribution, but in the North and East region only four of the 13

species shown in Table 6 are restricted to the far north or east, or have Arctic-Alpine ranges. The remainder are widespread, but not typical of forests elsewhere; six have wetland affinities, while the other three are often found in the open.

Species with restricted distributions are not randomly distributed with respect to the family-level groups involved. Table 7 presents details of distribution overall, and for the four most speciose of such groups, which between them account for 86 species (67% of the total). It also shows the distribution of species in relation to maximum shell dimension. The same figures are also given for the British Isles and the Carpathian Chain.

Disparities between regions are most evident in the case of the Clausiliidae, where the Carpathian region is richest, and has the most unique species. It

**Table 7** The distribution of numbers of species by region, overall, and in the British Isles and the Carpathian Chain, for the four largest family groups, and for species with maximum shell dimension above or below 5 mm (Vitrinidae excluded). Asterisked figures indicate the presence of known introductions: the helicoids *Helix aspersa* and *Monacha cantiana* in Britain, and the zonitids *Oxychilus helveticus* and *O. draparnaudi*, the former in Britain, the latter both in Britain and the Polish Sudetes.

	Tot	Atl	Cent	N/E	Carp	B.I.	C.Ch.
No.of localities	46	17	11	10	8	14	15
<b>All Species</b>							
Species Present	129	73*	79*	71	81	56	97
Unique species	43	15*	7	3	18	10*	21
<b>Clausiliidae</b>							
Present	24	9	14	13	17	5	20
Unique	8	0	3	0	5	0	6
Richest loc.	-	8	8	11	16	4	16
Mean/loc.	-	2.94	5.63	5.30	10.88	2.36	8.60
Standard Error	-	0.42	0.41	1.22	0.95	0.22	0.84
<b>Helicoidea</b>							
Present	29*	15*	16	14	20	11	23
Unique	12*	5*	1	1	5	5*	6
Richest loc.	-	9	14	10	11	9	14
Mean/loc.	-	6.53	8.90	4.90	8.00	6.57	8.73
Standard Error	-	0.44	0.86	0.87	0.78	0.52	0.72
<b>Zonitidae s.l.</b>							
Present	24*	13*	17*	13	16	12*	20*
Unique	6*	2	0	0	4	1*	4
Richest loc.	-	10	12	10	12	10	12
Mean/loc.	-	8.24	7.82	5.10	9.50	8.36	9.00
Standard Error	-	0.18	0.62	0.72	0.60	0.20	0.51
<b>Vertiginidae</b>							
Present	9	8	4	7	4	4	4
Unique	2	1	0	1	0	0	0
Richest loc.	-	8	3	6	4	3	4
Mean/loc.	-	2.65	2.10	4.2	2.75	2.00	2.67
Standard Error	-	0.45	0.34	0.42	0.31	0.23	0.21
<b>Less than 5 mm</b>							
Present	36	27	19	24	22	22	23
Unique	11	6	1	1	3	2	3
<b>More than 5 mm</b>							
Present	85	44	56	46	54	32	68
Unique	28	8*	4	2	14	7*	17

also has much the richest single locality, and the highest mean per locality. When examined in detail, it is apparent that both the Atlantic and North and East regions are geographically heterogeneous for this family: in the former, richness is concentrated in S. Scandinavia, and not in the British Isles, while in the latter, the Far Eastern localities are far richer than those in the Far North or in the Baltic.

A similar, though not so extreme, pattern can be seen in the Helicoidea, especially if the two introduced species restricted here to the British Isles are discounted. At the level of single localities, however, the Central region is the richest, due to some exceptional faunas in the Polish Sudetes.

By contrast, the Zonitidae show rather little regional variation in richness, and a low proportion of unique species. The same is broadly true at

locality level. In the Vertiginidae, with many fewer species, a different pattern emerges: richness is greatest in the Atlantic and North and East regions. As with Clausiliidae, the Atlantic region is heterogeneous, with rich vertiginid faunas concentrated in S. Scandinavia. Overall, the number of vertiginid species increases northward (species on latitude:  $r = 0.517$ ,  $p < 0.001$ ).

Of these four groups, members of the Clausiliidae and Helicoidea are all relatively large; Vertiginidae are all very small, while Zonitidae span a wide range. The last two sections of Table 7 compare the distributions of species with shells more or less than 5 mm in maximum dimension, excluding Vitrinidae, for which this may not be a good measure (Hausdorf and Hennig, 2003). The ratio of large to small species present does not vary



**Table 8** Data on mean abundance per plot, and % of all specimens for Clausiliidae and Helicoidea, and (% only) for *Punctum pygmaeum* (P) and Vertiginidae in relation to the number of species involved. Subs = substrate as in table 1; No. = number of species; Mean = mean number of individuals per plot; % = % of all individuals per locality; Mean/sp = mean number of individuals per species present.

Locality	Clausiliidae					Helicoidea				P	Vertiginidae	
	Subs	No.	Mean	%	Mean/sp	No.	Mean	%	Mean/sp	%	No.	%
ENGLAND												
Chilterns	L	2	52.9	8.9	26.4	7	86.9	14.7	12.4	0.6	1	0.1
South Downs	L	3	86.0	11.8	28.7	9	44.0	6.1	4.9	0.4	1	0.02
Cotswolds	L	3	73.1	10.4	24.4	9	63.5	9.1	7.1	2.9	1	0.03
Wye Valley	L	3	67.3	10.9	22.4	8	34.6	5.6	4.3	2.2	1	0.1
Means		2.75	69.8	10.5	25.4	8.25	57.2	8.9	6.9	1.5	1	0.06
SUDETES												
Góra Miłek	L	6	71.2	20.1	11.9	10	63.2	12.9	6.3	11.6	2	1.0
Muszkowice	L	4	125.0	23.8	31.2	11	47.7	9.0	4.3	1.4	1	3.5
Ojców	L	7	93.5	8.9	13.4	7	78.5	7.5	11.2	11.1	3	4.9
Myśliborski	E	6	31.2	7.5	5.2	7	35.2	8.4	5.0	21.0	3	8.5
Bardo	E	5	30.4	3.7	6.1	14	47.6	5.8	3.4	30.8	3	11.8
Młynowiec	N	6	41.0	11.5	6.8	4	14.3	4.0	3.6	14.2	3	15.0
Means		5.67	65.5	12.6	12.6	8.83	47.7	7.9	5.4	11.8	2.5	7.4
CARPATHIANS												
Pieniny	L	13	52.3	12.9	4.0	11	89.6	22.2	8.1	16.3	3	6.7
Ugol'ka	L	8	50.7	22.7	6.3	6	45.0	20.2	7.5	4.4	3	0.7
Kuziy	L	8	38.6	9.42	4.8	8	49.2	12.0	6.2	4.9	3	0.7
Podlipowiec	E	11	30.0	10.9	2.7	10	36.1	13.1	3.6	17.8	3	5.6
Means		10.0	42.9	14.0	4.3	8.75	55.0	16.9	6.3	10.3	3	3.4
EASTERN												
Białowieża	E	11	33.5	12.1	3.1	8	24.6	9.0	3.1	9.7	4	4.7
L'viv	N	5	32.7	18.9	6.5	5	37.7	21.8	7.5	0.2	3	11.2

significantly between regions, although it is smallest in the Atlantic and North and East. It is significantly smaller in the British Isles relative to the Carpathian Chain ( $\chi^2 = 3.8$ ,  $p < 0.05$ ). In terms of unique species, three of the seven large species in the British Isles are introduced. If these are discounted, it is evident that the Carpathian Chain holds a higher proportion of large, unique species. In contrast, the Atlantic region holds the largest number of small species, and of small uniques; The British Isles hold virtually the same number of small species as the whole Carpathian Chain.

### Relative Abundance

Data analysed above relate to presence and absence from localities. In the case of our own studies, a standardised sampling methodology, while not giving true density estimates, enables us to compare both the number of specimens of species collected per plot, and the percentage of all shells in a plot that belong to any species or higher taxon. While very crude, such figures enable us to look at changes in abundance between localities and regions.

Table 8 gives these data for selected groups of species from our own standardised studies. Amongst Clausiliidae, the pattern of species richness reflects the overall analysis above, but the

recorded abundance of the Family, whether expressed as numbers per plot, or as a percentage of all shells, does not (for the relationship between percentage of all shells and number of species,  $r^2 = 0.0012$ ). Although substrate clearly influences recorded abundance, and increases variance, mean abundance per species declines as richness increases. This relationship is shown in Figure 6; it is strong and highly significant ( $P < 0.001$ ).

By contrast, no clear trends can be seen amongst Helicoidea in terms of species richness, abundance, or percentage of the fauna, although the influence of substrate on recorded abundance is again visible. Data for *Punctum pygmaeum* and for the Vertiginidae show that both are much less abundant in the British Isles than in the overwhelming majority of the Polish and Ukrainian sites, even when the number of species of the latter is taken into account. Other universal species fluctuate without obvious geographical pattern, though substrate again affects recorded abundances.

### Species Richness and Hotspots

Table 1 shows the number of species recorded at each locality, the number of species recorded in the richest plot (where the latter data are available), and some environmental data. The latter reflect the

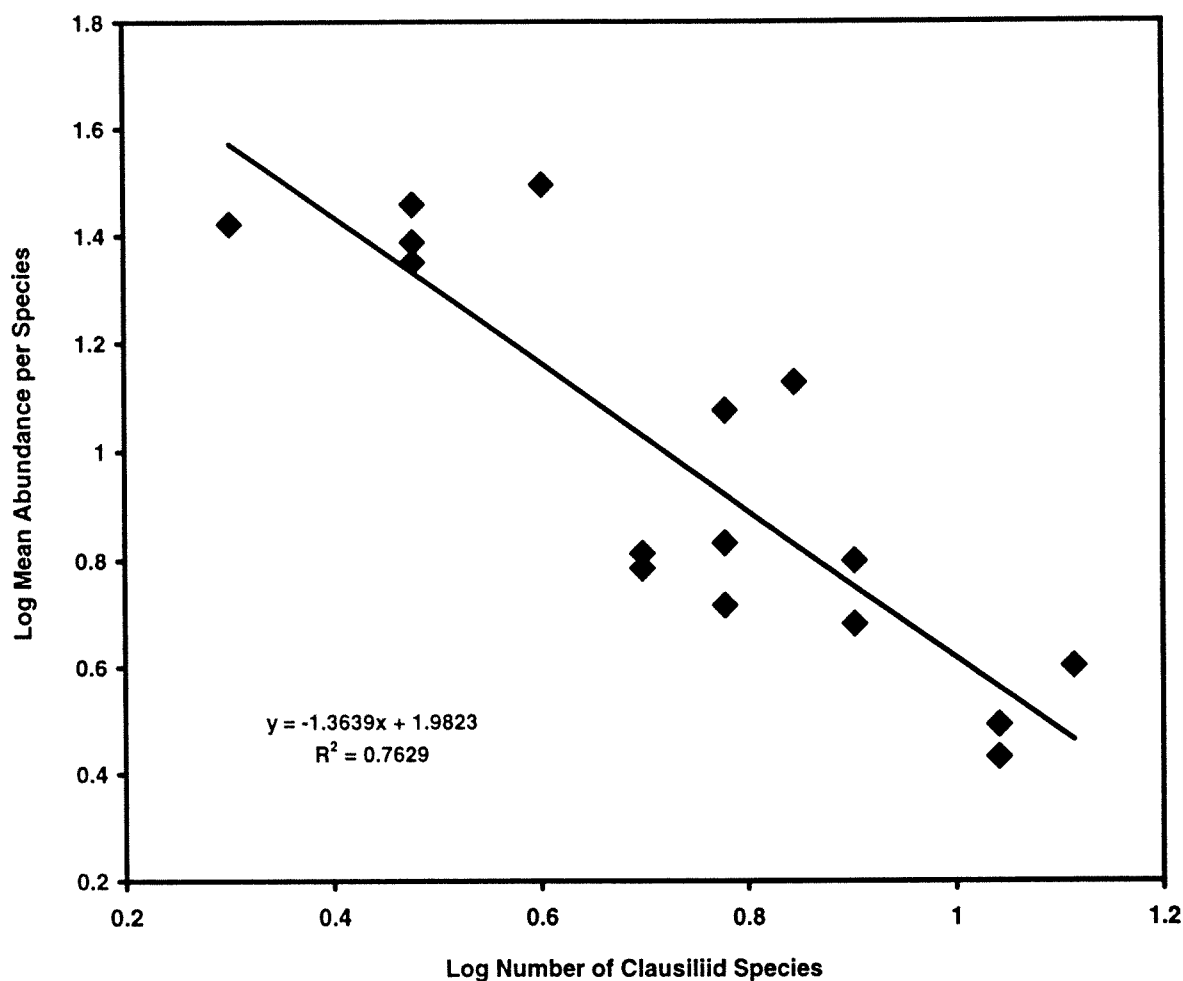


Figure 6 The logarithmic relationship between mean per plot abundance of individual clausiliid species and the number of clausiliid species in all localities sampled by the authors (Table 8).

general status of the forest types in each locality. Although there are formally significant relationships between species richness and both latitude (increase southwards) and longitude (increase eastwards), inspection of the data shows that the former is heavily influenced by the two, species-poor, localities in the Far North, and is not significant without them. The latter, though significant, accounts for only a small proportion of the total variance ( $r^2 = 0.141$ ).

The maximum locality richness is to be found in the Polish Carpathians east of the Tatra (L 33–36). Of other localities, only Książ (L 24) in the Sudetes equals any of them. Of the three other localities that approach closely, L'viv (L 41) and Valdai (L 45) represent rather large areas, and both they and the third, Białowieża (L 39) include wet alder forests, missing from all but locality 36 in the Polish Carpathian series. Except for the poor faunas in the extreme north (L 1 and 2), no other clear geographical pattern emerges.

Omitting the localities above, there are signs that the local environment influences richness. The mean number of species in non-eutrophic localities is  $29.7 \pm 0.8$ , significantly lower than that for

eutrophic ( $36.2 \pm 1.7$ ), or for limestone ( $35.7 \pm 0.9$ ) localities. This effect is comparatively slight, reflecting the choice of the most favourable plots in non-eutrophic regions.

The pattern in the richest single plots is much the same. While the Carpathian group contains the richest plots, all other regions have individual plots with 32–36 species (Table 1). The mean value of  $I_{\max}$  is  $1.295 \pm 0.024$ ; on average, the richest plot in a locality contains 77% of the species found. There is no consistent geographical variation in its value, nor does it vary with species richness ( $r^2 = 0.022$ ). As with richness, however, there is a relationship with substrate; the mean is higher in non-eutrophic localities than in eutrophic or limestone based ones (non-eutrophic, mean  $1.41 \pm 0.04$ , eutrophic mean  $1.28 \pm 0.05$ , limestone mean  $1.22 \pm 0.03$ ). Plots vary more in composition within non-eutrophic localities than do those in richer places.

At both plot and at locality levels, therefore, the faunas of Polish Carpathian forests appear to be the richest in this particular array, although the difference between these faunas and some others is not great.

Where localities used in this study are close

together, or we can add supplementary data from other, less precise studies, it is possible to consider the richness of forest faunas at a larger scale, c. 100 km<sup>2</sup>. In the Pieniny region of the Carpathians, we can add data from Urbański (1939) to those from localities 33–35 to give a total of 69 forest dwelling snail species, 53% of all the species in our array. In the two other areas of similar size for which we have such data, the totals are lower: 49 species each in Białowieża (Cameron and Pokryszko, 2004), and the Cotswolds (Cameron, Pokryszko and Long, in press). Some areas of the Polish Sudetes and of southern Germany are probably comparable (Pokryszko and Cameron, unpublished; Schmid, 1966). The proportional differences seen here alter when slugs are also considered.

### Slugs

Although slugs were found in all the studies used here, there are good reasons to think that their inventories are far less complete than for snails, and that they vary in completeness between localities. The evidence suggests that locality species richness is greatest in the west, and particularly in Britain. Thus, where we have data from several visits, some British localities have 13–16 species (Cameron, 1999 and unpublished; Long, unpublished; Wardhaugh, 1996). By comparison, the Białowieża Forest has seven (Cameron and Pokryszko, 2004), and the Pieniny forests in the Carpathians eight. These differences, and the restricted geographical distribution of some Carpathian species (e.g. *Bielzia coerulans*) will increase the degree of geographical differentiation in faunal composition, and decrease the differences in locality species richness seen when only snails are considered. In particular, the greater number of slug species in the west tends to cancel out the trend for increased richness in the east.

## DISCUSSION

### Coverage, Reliability and Human Influence

The studies used here include the great majority of forest dwelling species recorded in the region. Nevertheless, it is significant that most of those missing have Alpine affinities; only one locality is near the Alpine foreland. From accounts available (e.g. Favre, 1927), it appears that forest faunas from below 1,000m a.s.l. do not differ from their lowland counterparts as much as do those from the Carpathians.

It is inevitable that the results presented are subject to sampling error: species present will have been missed. The amalgamation of results from neighbouring plots, and the large sizes of the resulting samples should minimise this (Cameron and Pokryszko, 2005). Where the results of many

previous general surveys are available, the locality lists presented here seem to contain the great majority of the available forest fauna. The greatest caution is required when considering oligotrophic localities, where sample sizes are generally smaller (Cameron and Pokryszko, 2004).

While all samples come from forests, there are, of course, ecological differences between them. In particular, some, but not all localities include riverine or floodplain forest; there is a considerable range of altitude involved, and there is a climatic gradient from oceanic in the west to continental in the east.

The whole of northern Europe has been subject to intensive human activity for thousands of years. We have carried out or chosen studies in areas retaining elements of natural forest vegetation, and the evidence from Quaternary studies is that, in general, faunas have survived in such areas (Evans, 1972; Wiktor, 1974; Alexandrowicz, 1997). Nevertheless, the influence of this activity is perceptible. In the west, and particularly in Britain, the principal effect in the context of our studies is the occurrence of introduced but naturalised species. More seriously, it seems likely that a combination of aerial pollution, grazing pressure and some climatic change has impoverished forest faunas in the Baltic subregion as used here (Cameron and Pokryszko, 2004); the absence or scarcity of clausiliids in many plots in this region is probably due to this.

In the context of the discussion that follows, it should be noted that all these factors tend to increase the degree of difference among localities. Since it is the relative uniformity in both composition and richness that characterises these faunas in comparison with others, they are unlikely to lead to false contrasts.

### Patterns and Processes

The pattern of high local, but low regional species richness reported here reflects a very limited amount of geographical differentiation. At the extreme, within the British Isles, it is scarcely perceptible above the "noise" of sampling error, and involves only a few species. Over distances of 2,000 km or more, faunas away from the mountains retain Jaccard index similarities in the range 27–35% (Cameron and Pokryszko, 2004). Even along the Sudetes-Carpathian chain, it is much less than that recorded in many other parts of the world. Over this c. 650 km length, the mean Nei index is 59%, equivalent to a Jaccard index of c. 40%. Over shorter distances in the Aegean region, Jaccard is around 20–25% (Cameron, Mylonas and Vardinoyannis, 2000), while over 610 km in Tanzanian coastal forests it is only 11% (Tattersfield, 1998). Similar rapid turnover occurs in the Kimberley region of Western Australia (Solem, 1985, 1988, 1991; Solem



and McKenzie, 1991; Cameron, 1992)), and along the eastern seaboard of Australia (Stanisic, 1994; Moritz *et al.* 2001).

By contrast, faunas from the Great Lakes region of N. America show a pattern similar to that seen in N. Europe (Nekola and Smith, 1999; Nekola, 2003); Individual forest localities can hold a high proportion of the regionally available forest fauna. It seems clear that this pattern is related to the post-glacial immigrant status of the forest fauna in both cases, as distinct from regions in which most of the fauna has survived *in situ*, albeit sometimes in scattered refugia.

The geographical variation seen in the N. European faunas is mainly at the level of higher taxa; rather little of it is caused by allopatric ranges of ecologically equivalent congeners (Hausdorf and Hennig, 2003). Thus, there are many more species of Arionidae in the west than in the east, of Vertiginidae in the north than in the south, and of Clausiliidae in the Carpathians and Far East than elsewhere. The extent to which this reflects family-level adaptations to differing present climates, as opposed to being the product of varying composition amongst source faunas remains to be determined. Amongst Clausiliidae, our own studies suggest that the density or biomass of clausiliids is as high in British forests as it is in the Carpathians. In the latter, resources or niches are more finely partitioned simply because more species are available. By contrast, some widespread taxa (e.g. *Punctum pygmaeum*, some *Vertigo* species) show substantial differences in frequency and abundance between parts of the region, even though they occur throughout, suggesting ecological constraints. The existence of such constraints is also suggested by known range contractions since the mid-Holocene temperature maximum in N. Europe (Ložek, 1982, Kerney, 1999), though some of these may be a product of human disturbance.

This contrasts with some patterns elsewhere. In the Aegean (Mylonas *et al.*, 2004), and in the Kimberley region of Western Australia (Solem 1988, 1991; Solem and McKenzie, 1991; Cameron, 1992), much of the difference between localities is accounted for by allopatric replacement by congeners: local "non-adaptive" radiations (Gittenberger, 1991). These tend to be concentrated amongst larger species with rather specific environmental requirements: Camaenidae in the Kimberley, Clausiliidae (*Albinaria*), Enidae (*Mastus*) and some Helicoidea in the Aegean. The case of *Albinaria* is particularly instructive: amongst at least 26 species present on Crete, individual localities (all of similar habitat) hold only one or two species. In the Carpathians, with a clausiliid fauna of c. 20 species, 16 were found in the richest locality, and 10 in the richest 400 m<sup>2</sup> plot. Three species from the same genus often coexist.

Both the Aegean and the Kimberley are situated in areas where the effect of desiccation at intervals in the Pliocene and Pleistocene (coupled with tectonic and sea level changes in the Aegean) can be implicated in the fragmentation of ranges and consequent differentiation. In areas where climatic shifts have had less drastic effects, the patterns are rather different. Thus Solem, Climo and Roscoe (1981) for North Island New Zealand, and Stanisic (1994) for eastern Australian forests, attribute the high levels of both local and regional diversity to a gradual build up of sympatric diversity as a consequence of isolation by distance and subsequent back colonisation. In these cases, as in the very rich faunas of tropical rainforests reported in Cameroon (de Winter and Gittenberger, 1998) and in Borneo (Schilthuizen and Rutjes, 2001), there are many coexisting species in the same families and genera, and they are often small, litter-dwelling species such as Punctidae and Charopidae. In East Africa, both patterns coexist (Tattersfield, 1998). This is demonstrated elegantly in the case of *Gulella* species (Streptaxidae), where are often unique to particular forest localities, but such localities may hold many coexisting species. In the Kimberley, Solem (1985) has demonstrated some resource partitioning amongst coexisting camaenids; such work has started amongst Carpathian clausiliids (Sulikowska-Drozd, *in press*). In general, though, we have little information on possible interactions between closely related, but coexisting, species.

In terms of species richness, it is remarkable that these European forests, non-existent only 10,000 years ago, achieve levels of locality and plot richness not far short of those recorded in more stable regions with millions of years accumulation of diversity. *Contra* Solem (1984), this richness is genuinely syntopic, as reflected by low values of  $I_{max}$ ; indeed, individual square metre quadrats have been recorded with up to 35 species, including slugs (Schmid, 1966). Present habitats are manifestly favourable. In most cases, the locality faunas contain the overwhelming majority of the fauna known to occur in the vicinity. We are thus unable to say whether more species could be packed in if they were available locally. Further south in Europe, where regional diversity increases, it would appear that, even in forests of comparable character, locality species richness remains much the same (Table 9). In the case of the Czech Republic, we have an area that was also deforested in the full-glacial; faunas here are essentially part of the N. European assemblage. Further south, many new species are encountered, but richness is no higher.

There are further implications to this pattern. The uniformity of British faunas, not accompanied by any noticeable impoverishment at locality level,

**Table 9** Snail species richness in forest localities south of the study area. In the case of Flasar (1995) (\*) it is hard to allocate the fauna as between a locality, or the equivalent of one of our plots (see text). Site = richness of the best site/plot without obvious anthropogenic alteration. New = number of species in the array considered not found in any studies used by us. Sites considered by Giusti *et al.* (1985) are separated by more than 100 km (Ap = Apennines). Dashes indicate that the localities or plots are not directly comparable with the data from N. Europe.

	Locality	Site	New	Source
<b>Czech Rep.</b>				
Moravia	37*	*	0	Flasar, 1995
Bohemia	–	28	1	Hlaváč and Horsák, 2002
Bohemia	–	34	1	Hlaváč <i>et al.</i> 2002
Bohemia	–	30	1	Flasar, 1971
<b>Italy</b>				
Pre-alp to Ap	48	24	23	Giusti <i>et al.</i> , 1985
Novara	42	22	8	Bishop, 1980
<b>Croatia</b>				
Medvednica	39	21	15	Štamol, 1991
Velika Kapela	36	–	18	Nikolic and Štamol, 1990

shows that many species, in disparate families, can disperse over large distances in a relatively short time. We may suspect that Carpathian faunas are richer in, for example, Clausiliidae, because distances from sources were shorter, and more species established simultaneously. Early arrivals might pre-empt niche space further north or west. Bearing in mind the short time span involved, we cannot be sure that the patterns we see are stable; changes (now grossly affected by human disturbance) may have been taking place as the initial influx of colonists interacted. Over similar time-spans, it seems that dispersal of species from refuges in the Kimberley, or in the Aegean, was hindered by encountering congeners. Hindrance might be due to conventional competition, or to the disadvantage of being a minority colonist amongst closely related but genetically unsuitable mating partners.

In this context, it is worth noting that many of the smallest litter dwelling species are capable of uniparental reproduction (Whitney, 1938; Morton, 1954; Baur, 1987 and 1989; Bulman, 1990; Pokryszko, 1990). Build up of congeneric sympatric diversity in low latitudes often involves such species. It also occurs in relatively oligotrophic localities, where low density and patchy distributions might allow a complex metapopulation structure to develop, permitting more coexistence than is possible in dense and continuous populations (Cameron *et al.*, 2003). Given appropriate rates of speciation, migration and

local extinction, such metapopulations can allow the coexistence of many ecologically identical species (Hubbell, 2001). Whatever the actual determinants of local diversity turn out to be, the N. European forest fauna shows us that when suitable habitats appear, they can be colonised in a geologically short time, over considerable distances, and to levels of local diversity which are high in a global context.

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