LAND SNAIL SPECIES RICHNESS AND ABUNDANCE AT SMALL SCALES: THE EFFECTS OF DISTINGUISHING BETWEEN LIVE INDIVIDUALS AND EMPTY SHELLS

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Abstract *This paper considers the numbers of species and individuals of terrestrial snails in small plots (quadrats) of different sizes (0.0625 m², 0.25 m², 0.56 m²) in three types of treeless fen sites differing in mineral content; a good proxy for calcium content. It compares the results of considering only live individuals or of combining these with empty shells, a common practice in land snail faunistic studies. As expected, the numbers of both species and individuals increased with increasing mineral content and with sampling area, whether all shells or only live specimens were considered. In two of the three sizes of plots and all fen (mineral level) types there was a clear increase of species when empty shells were included. However, the pattern of the increase varied among the fen types. The greatest increase was observed at the smallest plot size in mineral-rich fens; the difference was less in the larger plots. By contrast, in calcium-poor sites the increase was lower and the numbers of species did not change at the largest plot-size. This differential preservation affects interpretation. In very calcium-rich sites, empty shells contribute significantly to a summary of the fauna in the plot over several years, and can improve the inventory efficiency of sampling, provided that very old or subfossil shells of species no longer living in the site can be excluded. However, when comparisons are made among sites with different soil chemistry, estimates of densities and relative abundances will be distorted, because shells decay at different rates among them. Hence, in any studies concerned with densities or spatial heterogeneity within sites it is necessary to distinguish between live individuals and empty shells.*

Key words *Fens, sampling quadrats, densities, species estimates*

Introduction

Determining the species composition and richness of an element of the fauna at a variety of scales is a fundamental requirement for understanding both patterns of distribution and the dynamics of local communities (Rosenzweig, 1995). For many invertebrates, this is a demanding requirement, as sampling problems are acute, especially at very small scales (for example, in single quadrats sampled once only). For terrestrial snails, the task is somewhat easier because most species can be identified by their shells, and hence empty shells provide evidence of occupation of the site. Although such shells must be excluded in studies of life history or population dynamics, they can be useful in compiling inventories. Hence, recommendations for sampling for inventory purposes encourage their inclusion (Rundell & Cowie, 2003; Cameron & Pokryszko, 2005), as this overcomes problems of seasonal variation in abundance and availability for sampling. Studies of microspatial distribution, however, could be distorted, as empty shells decay at different rates, both among species, and among sites (Millar & Waite, 1999; Menez, 2002; Pearce, 2008). Furthermore, old, often subfossil shells representing species no longer living on the site must be excluded from consideration, though these may provide a record of environmental change (Cameron & Morgan-Huws, 1975). However, not all studies of land snail faunas make this distinction between live animals and dead shells, nor do they give exact numbers for exact areas, but rather averages counted from many small areas.

This study was started to investigate the molluscan faunas of three fen types at three small scales. The ecological analysis of these results will be presented separately. It became apparent, however, that distinguishing individuals alive or dead at the time of sampling was necessary for correct interpretation. We present the results of this analysis, and discuss its significance for molluscan sampling. So far, no other study has done this for very small quadrats of different size and among sites differing in mineral richness.

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Material and Methods

Study area and sites The study was carried out in spring fens of the western Carpathian Mountains, in Slovakia and the Czech Republic. Spring fens are wetlands saturated by mineral-rich groundwater and characterized by vegetation dominated by sedges and mosses; this has low productivity and is nutrient limited (Grootjans *et al.*, 1996). The plant species composition is mainly influenced by the groundwater chemistry, especially pH and mineral richness (Hájek *et al.*, 2002), which reflect the bedrock chemistry (Rapant *et al.*, 1996). Bedrock in the Western Carpathians is varied, and hence the ground waters also vary in mineral richness, and especially in calcium. This gives rise to a mineral poor-rich gradient, the main ecological gradient of these habitats (Malmer, 1986; Hájek *et al.*, 2006). This gradient governs not only vegetation composition but also the species composition of algae, bryophytes, and molluscs (Horsák & Hájek, 2003; Poulíčková *et al.*, 2005).

Three types of fens differing in mineral richness and floral composition were studied. Mineral richness was estimated by measurements of pH and conductivity values of the groundwater. Mineral richness is closely correlated with the calcium content (Sjörs & Gunnarsson, 2002; Hájek *et al.*, 2005), the most important macronutrient for land snails (Dallinger *et al.*, 2001). Water conductivity and pH were measured in the micro-sites best supplied by water in small shallow holes dug in the central part of the spring, using portable instruments with automatic temperature compensation (CM 101 and PH 119, Snail Instruments, Beroun, Czech Republic). Readings were standardized to 20 °C.

The first fen type was extremely mineral-rich with tufa precipitation and pH values of 7.0–7.7 (median 7.2) and conductivity 360–709 µS cm^{-1} (median 567 µS cm^{-1}). The typical plant associations for this type of fen are *Carici flavae-Cratoneuretum* and *Caricetum davallianae*. The second fen type was moderately mineral-rich with pH of 6.7–7.3 (median 7.1), conductivity 279–486 µS cm^{-1} (median 336 µS cm^{-1}) and no tufa precipitation. The *Valeriano simplicifoliae-Caricetum flavae* association is typical. The third type was mineral-poor, with pH of 5.8–7.5 (median 6.0) and conductivity 60–282 µS cm^{-1} (median 110 µS cm^{-1}). This type of fen, with the occurrence of calcitolerant *Spaghnum* species, belongs to the *Sphagno warnstorfii-Tomenthypnion* alliance. Although it is referred to as mineral-rich *Sphagnum*-fen in the overall mire classification, it is mineral-poor relative to the two previous types, and supports only a few acid tolerant snail species (Horsák & Hájek 2003, Horsák & Cernohorsky 2008). Altogether, twenty-eight sites were sampled, of which ten were extremely mineral-rich (R), nine were moderately mineral-rich (MR), and nine were mineral-poor (P).

Data collecting and analyzing We sampled a set of three nested (the larger include the smaller) square quadrats in each site. The quadrats were 25×25 cm^2 (0.0625 m^2, henceforth referred to as plot S), 50×50 cm^2 (0.25 m^2, plot M), and 75×75 cm^2 (0.5625 m^2, plot L). Each plot was cut just below ground level, using a sharp knife, and removed along with the herbaceous vegetation, mosses, litter and the upper soil layer. To obtain information about the entire fauna of the site, we also randomly collected 12 litres of the upper-fen layer from an area of 16 m^2 around the plots. Molluscs were then extracted from all samples using the "wet sieving method" (Horsák, 2003), in which material from each sample is gradually washed through a bowl-shaped sieve (mesh size 0.5 mm) to remove fine soil. The coarse plant matter is then removed by hand. During the process of washing, empty shells, which are full of water from the fen, sink along with the live snails to the bottom of the sieve. After drying, shells were separated from the remaining material by hand-sorting under a stereo microscope and identified and counted, separating live animals and empty shells. Nomenclature follows Juřičková *et al.* (2001), with authorities given in Table 1. Slugs were not included in this study, as their activity depends largely on weather conditions (Rollo, 1991) and the sampling method used was not suitable to determine slug abundance (Oggier *et al.*, 1998).

The total species composition of each site was estimated from the combined sample from the plots and the 12 l sample. The percentage of the entire site's species richness detected by each plot size was calculated as: 1) the number of species found alive in each plot divided by the site's live species pool (in further text referred to as L_q/L_T); 2) the number of species found alive in each plot divided by all species (including empty shells as well as those found alive) of the site's species pool (as L_q/A_T); 3) the number of species found alive and dead in each plot divided by all species of the site's species pool (as A_q/A_T); 4) the number of species found alive and dead in each plot divided by the site's live species pool (as A_q/L_T). Mann-Whitney U tests were performed to test how plots of different sizes captured the site species pool as reflected by the above four percentages.

RESULTS

In total, 21,572 specimens were collected, of which 5,140 were alive. Table 1 lists the species, their frequency of occurrence in each fen type, and their average abundances as live and empty shell specimens. The total numbers of specimens in each plot size varied among fen types (Fig. 1). There are big differences in the proportions of live specimens between fen types. The median numbers of all recorded specimens were 13, 19, and 131 in the smallest plots (0.0625 m^2) for mineral-poor, moderately mineral-rich and extremely mineral-rich fens, respectively, but 8, 9, and 21, respectively for live snails only. Despite these differences, the number of specimens increased with increasing area in a similar way for all fen types.

The total number of species found alive was 40. Thirteen additional species were recorded

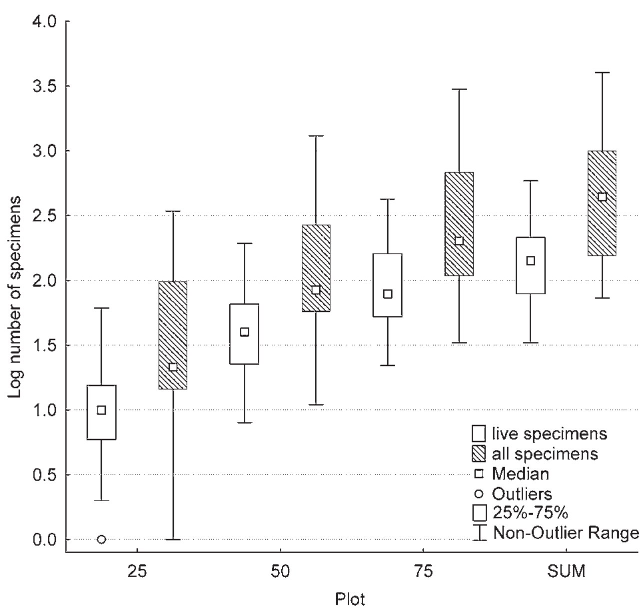

Figure 1 Variation in numbers of live specimens and all specimens (i.e. including species found alive as well as those found as empty shells) at different sized plots and at the entire site plotted together for all fen types. Explanations: 25, 25×25 cm^2; 50, 50×50 cm^2; 75, 75×75 cm^2; SUM, entire site.

as empty shells only, most of which were very uncommon (Table 1). Ten of these 13 were found in the rich fens (nine exclusively in this category), three in the medium fens and only one in the poor fens. As expected, the number of species increased with increasing area as well as with increasing mineral richness (Fig. 2). The number of species found was always greater when empty shells were included than when only live specimens were considered. This was most marked in the mineral-rich sites and within them in the smallest plot size. However, in mineral-poor sites these differences were small, and the median numbers of all species and live species in the whole site's species pool were equal (Fig. 2).

The efficiency with which each plot size captured the site's species pool varied among the three fen types and among the four methods of calculating efficiency: L_q/L_T, L_q/A_T, A_q/A_T and A_q/L_T (Fig. 3).

When empty shells were not included (L_q/L_T), the results were similar for all three types of fens. The smallest plot captured roughly half of the site species pool and the medium sized plot and largest plot capture about 70–80%. However when empty shells were added differences among the three fen types were revealed. In mineral-poor fens the results were similar to those obtained only with live snails; the smallest plot captured a relatively small proportion of the site's species, but even the medium sized plot captured almost all the site's species (on average only about two species fewer then found in the whole site). This was true for all calculations (L_q/L_T, L_q/A_T, A_q/A_T, and A_q/L_T), whether empty shells were included or not. For moderately mineral-rich and mineral-rich fens the situation was more complicated. For L_q/A_T (Fig. 3b), plots of moderately mineral-rich and mineral-rich fens were significantly less efficient at capturing the site species pool than those of mineral-poor fens (Mann-Whitney U test, $p < 0.05$). Plots M and L of mineral-rich fens were significantly more efficient at capturing the site's species when using A_q/A_T (Fig. 3c) than L_q/A_T (Fig. 3b) ($p < 0.05$), although this difference was not significant in moderately mineral-rich sites. Plots of all fen types captured the site species pool most efficiently when the A_q/L_T calculation was used (Fig. 3d). Plots of mineral-rich fens were the most efficient ($p < 0.05$) in comparison with mineral-poor and moderately mineral-rich fens.

Table 1 List of all recorded land snail species. For each species the number of sites at which it was found (F) and average abundances (the average number of specimens of the species expected at a site provided it is present at the site, from a sample the size of the largest plot (0.5625 m^2), plus the 12 litre sample) of live individuals (L) and empty shells (E) in each fen type are given. Species are arranged according to their total frequency (the last column). P, mineral-poor (nine sites); MR, moderately mineral-rich (nine sites); R, extremely mineral-rich (ten sites).

Individual group of sites		P			MR			R		**Total**
Species / their frequencies and abundances	**F**	**L**	**E**	**F**	**L**	**E**	**F**	**L**	**E**	**n. of sites**
Cochlicopa lubrica (O.F. Müller 1774)	6	36	31	9	193	569	10	624	1591	25
Perpolita hammonis (Ström 1756)	6	195	81	9	196	437	8	95	557	23
Carychium minimum O.F. Müller 1774	4	163	86	8	171	81	10	268	809	22
Punctum pygmaeum (Draparnaud 1801)	4	9	16	8	40	80	9	37	366	21
Vertigo substriata (Jeffreys 1833)	6	134	91	8	61	85	4	36	95	18
Vallonia pulchella (O.F. Müller 1774)	1	14	23	6	90	128	10	534	2570	17
Vertigo antivertigo (Draparnaud 1801)	3	4	6	7	74	113	7	318	1508	17
Vertigo pygmaea (Draparnaud 1801)	1	17	6	6	54	102	9	199	625	16
Carychium tridentatum (Risso 1826)	4	19	7	6	74	202	5	6	35	15
Succinea putris Linné 1758	4	45	16	8	76	114	3	6	12	15
Euconulus fulvus (O.F. Müller 1774)	3	48	52	7	25	87	3	8	73	13
Euconulus praticola (Reinhardt 1883)	3	40	45	2	21	19	7	49	430	12
Vertigo angustior Jeffreys 1830	~	~	~	3	46	87	9	412	1041	12
Vitrina pellucida (O.F. Müller 1774)	3	2	2	5	4	11	3	2	10	11
Columella edentula (Draparnaud 1805)	2	7	2	3	7	20	4	4	2	9
Succinella oblonga (Draparnaud 1801)	1	~	2	1	~	4	7	145	606	9
Oxyloma elegans (Risso 1826)	1	48	45	3	34	39	4	69	1727	8
Monachoides incarnatus (O.F. Müller 1774)	1	1	~	3	2	3	3	~	3	7
Plicuteria lubomirskii (Ślósarskii 1881)	1	1	1	2	3	3	4	11	14	7
Semilimax semilimax (Férussac 1802)	~	13	1	3	40	74	3	~	3	7
Daudebardia brevipes (Draparnaud 1805)	~	~	~	3	~	5	3	1	13	6
Vertigo geyeri Lindholm 1925	2	14	7	1	43	9	2	34	296	5
Zonitoides nitidus (O.F. Müller 1774)	~	~	~	~	~	~	4	11	108	4
Vitrea crystallina (O.F. Müller 1774)	~	2	~	1	1	2	2	9	21	4
Daudebardia rufa (Draparnaud 1805)	~	~	~	1	~	3	2	5	9	3
**Monachoides vicinus* (Rossmässler 1842)	~	~	~	2	~	2	1	~	2	3
Perforatella bidentata (Gmelim 1791)	~	~	~	1	2	3	2	2	16	3
Platyla polita (Hartmann 1840)	1	~	1	1	~	5	1	3	8	3
Pseudotrichia rubiginosa (A. Schmidt 1853)	~	~	~	~	~	~	3	25	283	3
Vallonia costata (O.F. Müller 1774)	~	~	~	1	~	1	2	1	19	3
Vertigo moulinsiana (Dupuy 1849)	~	~	~	~	~	~	3	70	314	3
Cepaea vindobonensis (Férussac 1821)	~	~	~	~	~	~	2	8	7	2
Columella aspera Waldén 1966	1	31	3	1	1	~	~	~	~	2
Euomphalia strigella (Draparnaud 1801)	~	~	~	~	~	~	2	2	6	2
**Vitrea contracta* (Westerlund 1871)	~	~	~	~	~	~	2	~	9	2
Vitrea diaphana (Studer 1820)	~	~	~	1	~	2	~	1	~	1
Acanthinula aculeata (O.F. Müller 1774)	~	~	~	~	~	~	1	6	11	1
Aegopinella pura (Alder 1830)	~	~	~	~	~	~	1	1	30	1
Arianta arbustorum (Linné 1758)	1	1	~	~	~	~	~	~	~	1
**Cepaea hortensis* (O.F. Müller 1774)	~	~	~	~	~	~	1	~	1	1
**Clausilia pumila* C. Pfeiffer 1828	~	~	~	~	~	~	1	~	5	1
**Cochlicopa lubricella* (Rossmässler 1835)	~	~	~	~	~	~	1	~	2	1
**Discus rotundatus* (O.F. Müller 1774)	~	~	~	1	~	1	~	~	~	1
**Faustina faustina* (Rossmässler 1835)	~	~	~	~	~	~	1	~	1	1
**Fruticicola fruticum* (O.F. Müller 1774)	~	~	~	~	~	~	1	~	5	1
**Oxychilus glaber* (Rossmässler 1835)	~	~	~	~	~	~	1	~	1	1
Perpolita petronella (L. Pfeiffer 1853)	1	2	14	~	~	~	~	~	~	1

Individual group of sites		P			MR			R		**Total**
Species / their frequencies and abundances	**F**	**L**	**E**	**F**	**L**	**E**	**F**	**L**	**E**	**n. of sites**
Pupilla alpicola (Charpentier 1837)	~	~	~	~	~	~	1	32	349	1
**Pupilla muscorum* (Linné 1758)	~	~	~	~	~	~	1	~	5	1
**Semilimax kotulae* (Westerlund 1871)	1	~	3	~	~	~	~	~	~	1
Trochulus hispidus (Linné 1758)	~	~	~	~	~	~	1	2	~	1
**Truncatellina cylindrica* (Férussac 1807)	~	~	~	~	~	~	1	~	1	1
**Vestia gulo* (E.A. Bielz 1859)	~	~	~	1	~	1	~	~	~	1

* - species recorded only as empty shells

Discussion

Mineral types and separating live individuals and empty shells When all shells are considered, mineral rich fen faunas appear to have much greater overall abundances than poorer fens. This appears at first sight to confirm the well-established belief that calcareous substrates support much higher densities, as well as greater diversity, than poorer sites. This study shows that although there is indeed a difference, the inclusion of empty shells exaggerates it. Abundance, and indeed the absolute number of shells retrieved influences the number of species detected (Cameron & Pokryszko, 2005). The inclusion of empty shells thus increases the chances of encountering the rarest species in the community (Rundell & Cowie, 2003), but also increases the chances of including species that no longer live in the plot or site, or that are merely accidental immigrants. This is important mainly in the mineral-rich fens, because in poor fens the lower pH values cause empty shells to dissolve relatively quickly, probably less than one year. Litter pH is one of the most important factors for shell decomposition since it was confirmed that lower pH increase the speed of shell dissolution (Claassen, 1998). Thus the difference between live species and all species is small in mineral-poor fens, especially when looking at species of the whole site (Fig. 3c), where the median number of live species was equal to the median number of all species. The greatest differences between the number of live species and all species were in mineral-rich fens and especially in the smallest plots (Fig. 2), which suggests that there is considerable local turnover in species over time at the smallest observed scale, but that old shells persist to even out these local fluctuations. The situation in moderately mineral-rich fens appears intermediate. These fens are sufficiently mineral-rich for development of species rich molluscan faunas but not enough for long-term persistence of empty shells.

All the above factors influenced how well each of the three plot sizes reflected the site species pool (Fig. 3). In mineral-poor fens the efficiency of how well plots captured the site species pool changed very little when empty shells were included (situation A_q/A_T), because as mentioned earlier, empty shells disappear quite rapidly in these fens due to lower pH values. Thus the smallest plot always captured a relatively small proportion of the site's species, and the medium sized plot always captured almost all of the site's species. This suggests that, at this scale, or grain, a medium plot contains nearly all the microhabitats required by the snail fauna; there are few species overall, and they are mostly very small. However, in moderately mineral-rich and mineral-rich fens differences did occur when empty shells were added, suggesting that there is a coarser grain of microhabitats, and that these are not spatially stable. Hence in the L_q/A_T comparison the medium sized plot (M) and largest plots (L) of moderately rich and rich sites captured the site's species significantly worse than those of mineral-poor sites ($p < 0.005$). This was expected, as many empty shells are present in both fen types and these increase the chances of finding rare species, and they may include accidental immigrants, the shells of which are preserved.

In the comparison A_q/A_T one would expect that plots would be more efficient at capturing the site's species than in situation L_q/A_T. This was true for mineral-rich fens (significantly more efficient than in situation L_q/A_T; $p < 0.05$), but not

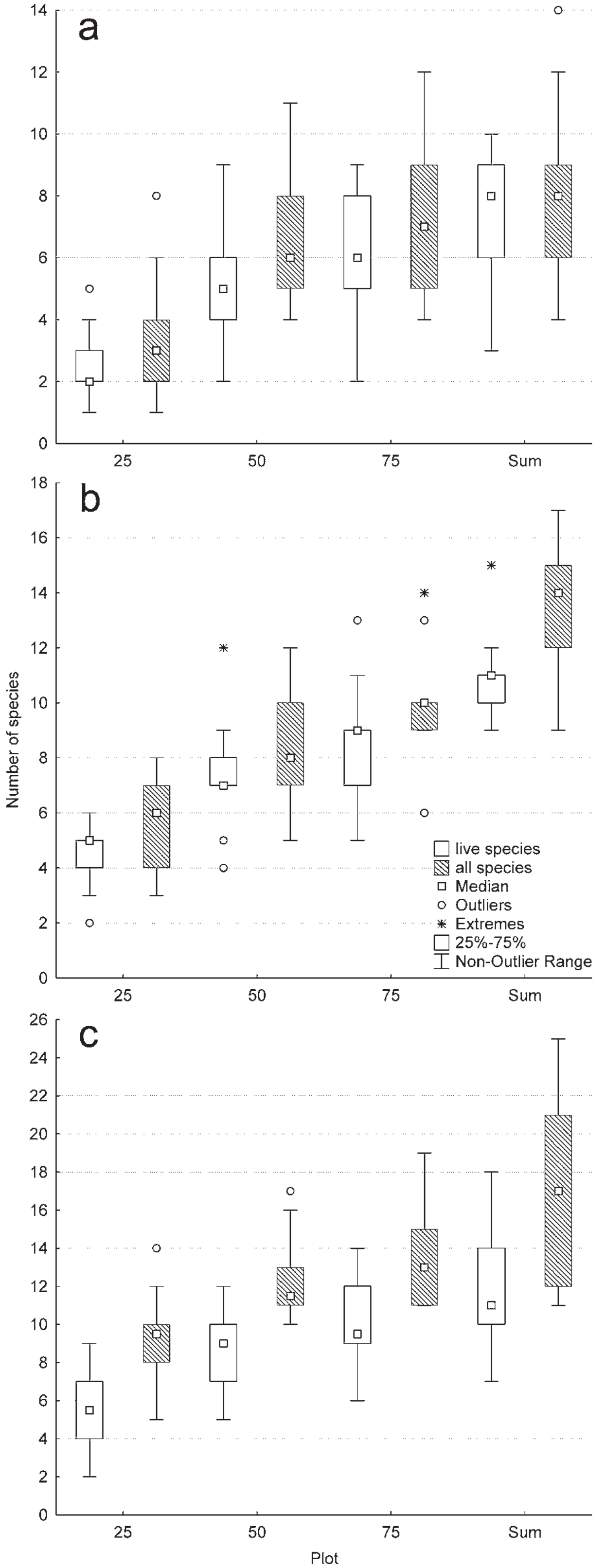

Figure 2 Variation in numbers of live species and all species (i.e. including live species as well as those found as empty shells) at different sized plots and at the entire site plotted together for (a) mineral-poor fens, (b) for moderately mineral-rich fens, (c) for mineral-rich fens.

for moderately rich fens. This lack of significant improvement in capturing the site species in moderately rich fens may be due to the rarity of species represented only by empty shells.

The fact that including dead shells improves the inventory estimate of the total living fauna is not surprising. However by including empty shells (Fig. 3), there is a risk of including species that are not currently living at the site, or in the particular plot within it. This must be considered especially when sampling sites where empty shells can persist for long periods of time, which is the case for rich calcareous fens. Presumably this will be true for other habitats as well (Rundell & Cowie, 2003), especially those rich in calcium.

How many species and individuals have been found in small plots Unfortunately, there are very few studies of the numbers of species and individuals in small areas, and that also obtain snails from the entire defined area, and that furthermore distinguish live individuals and empty shells. Generally, though, the number of species as well as the densities of live individuals and their ability to coexist in a small area increases under better conditions, such as higher calcium content. It has been suggested that competition is not a limiting factor for terrestrial snails, except in certain extreme habitats, and that the trend is that species with similar ecology tend to accumulate, rather than replace each other as conditions become more favourable (Boycott, 1934; Waldén, 1981; Hylander *et al.*, 2005).

Our results suggest that the densities are predominantly governed by mineral content and both average numbers of live individuals and species increased with mineral type of fens (Table 2). However, no quantitative studies giving numbers of live snails found in precisely defined areas have been carried out in fens so far. Our results may be compared only with other quantitative studies from different habitats. It appears that very few studies give figures both for live individuals and empty shells and refer these to a count representing the whole fauna at different scales. We were able to compile data from just five studies (Table 2). Unfortunately, these data came from very different habitats and also climatic zones which make any comparison conjectural. Thus, Table 2 presents only an overview on how many snail individuals and

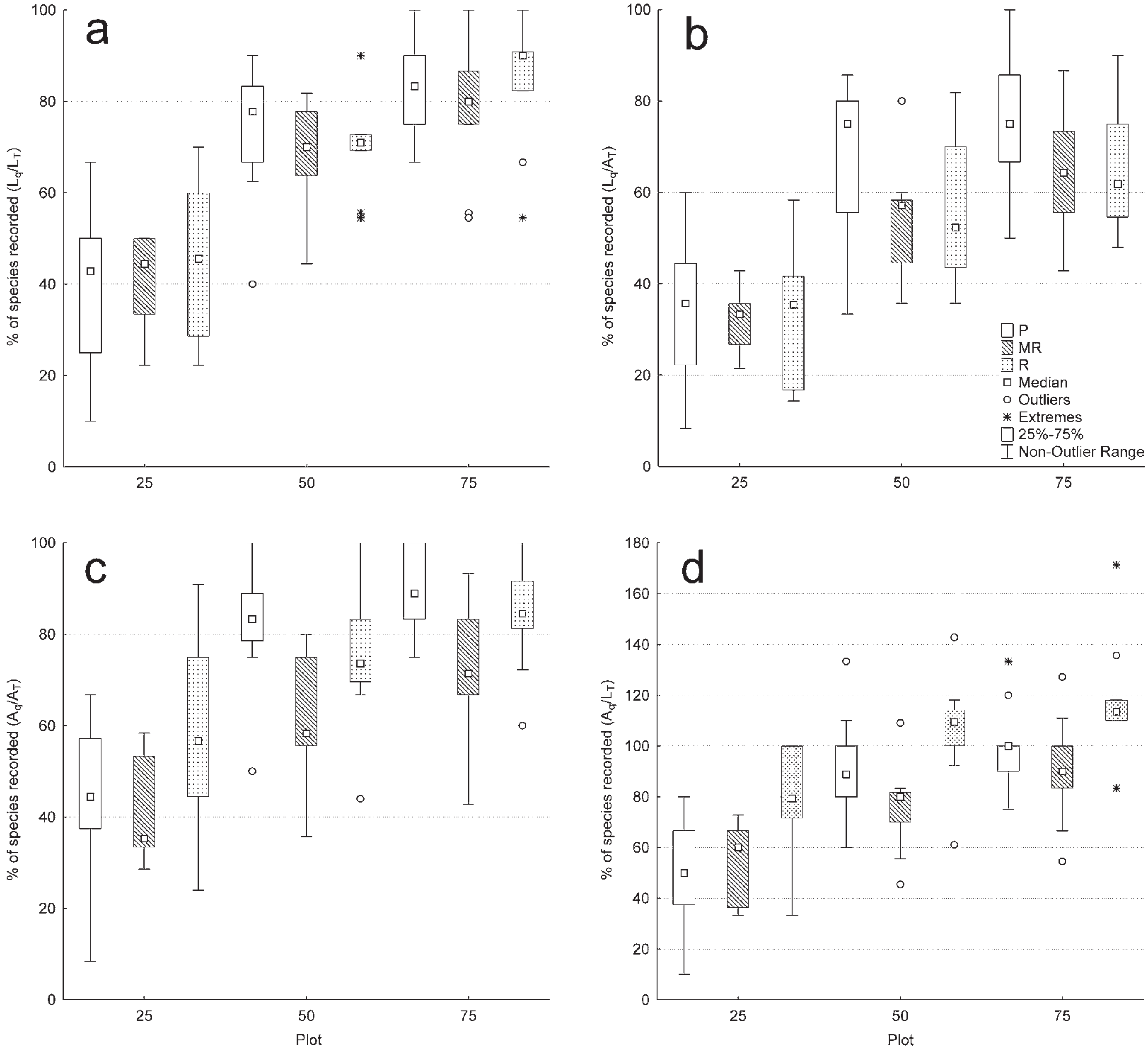

Figure 3 Variation in proportions, expressed as a percentage, of species retrieved in each of the four comparisons used (see text): (a) L_q/L_T, (b) L_q/A_T, (c) A_q/A_T and (d) A_q/L_T. Explanations: 25, 25×25 cm^2; 50, 50×50 cm^2; 75, 75×75 cm^2; SUM, entire site. Explanations: 25, 25×25 cm^2; 50, 50×50 cm^2; 75, 75×75 cm^2; P, mineral-poor fens; MR, moderately mineral-rich fens; R, mineral-rich fens.

species can co-exist in small and precisely defined plots.

Conclusions

When sampling spring fens and especially those that are mineral-rich, counting and identifying the empty shells as well as the live individuals improves the completeness of inventories. However it can also significantly bias our estimates, especially in the case of small plots, if we do not distinguish between live individuals and empty shells. This can lead to wrong interpretations of the results when the study includes sites differing in calcium content, or when heterogeneity of plots within a calcium-rich site is the subject of study.

Ackowledgements

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Table 2 Comparative average and maximum numbers of live specimens and species sampled at the entire defined plots of different habitats in Europe. Note that these studies (except Outeiro *et al.*, 1993; and for individuals also Millar & Waite, 1999) have provided numbers for a defined area, which was however defined by adding up the areas of smaller plots scattered across the site. In this respect the numbers, particularly for species, might be overestimates.

	Individuals		Species	
	Mean	Maximum	Mean	Maximum
Moravia and Slovakia	Present study / 0.25 m^2			
Poor fens	33	69	5	9
Moderately rich fens	35	68	7	12
Rich fens	80	193	9	12
South Germany	Martin & Sommer (2004b) / 0.25 m^2			
Grasslands	240	1035	9	19
Southwestern Germany	Martin & Sommer (2004a) / 0.25 m^2			
Woodlands	183	720	8	24
Central Spain	Outeiro *et al.* (1993) / 0.5 m^2			
Meadows	3	17	1	3
Shrubs	7	204	2	7
Woodlands	12	293	3	7
South England	Millar & Waite (1999) / 1 m2			
Coppice woodlands	152	1300	13	16
Central Sweden	Hylander *et al.* (2004) / 0.5 m^2			
Boreal riparian woodlands	69		8	

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