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SMALL-SCALE DISTRIBUTION OF TERRESTRIAL SNAILS: PATTERNS OF SPECIES RICHNESS AND ABUNDANCE RELATED TO AREA

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ABSTRACT

Although many studies have dealt with the spatial distribution of land-snail species and individuals, the effect of quadrat size on the interpretation of distributional patterns at small scales has rarely been investigated. We studied the spatial pattern of terrestrial snail distributions within a continuously sampled area of homogeneous habitat at very small scales (<1 m^2). The sampling was conducted in two contrasting habitat types: deciduous forests (29 sites) and treeless fens (23 sites) in Central Europe; each site consisted of three nested quadrats (25×25 cm^2, 50×50 cm^2 and 75×75 cm^2). On average the forest plots harboured higher numbers of species than fen plots and fen assemblages were composed of significantly smaller species in body volume. Numbers of species and individuals in smaller quadrats estimated from those present in larger ones often deviated significantly from those actually observed, showing frequently aggregated distribution of snails. These deviations were most marked for comparisons involving the smallest quadrats, whereas they almost disappeared in comparisons of large and middle-sized quadrats, both for species and individuals in both habitat types. Proportional deviances between collected and estimated numbers were always significantly higher for individuals than for species, with only one exception. Our results extend previous observations of land-snail spatial aggregations and they raise questions about environmental heterogeneity even in visually homogeneous areas or about possible biotic interactions among individual species. The steeper slope of the regression between area and numbers of species in log-log space from the smallest to the middle quadrat than from the latter to the largest quadrat, and the existence of several cases in which the observed richness was significantly greater than that predicted from rarefaction, suggest that even at this scale there are still idiosyncratic variations in the range of microhabitats available within quadrats.

INTRODUCTION

The spatial distribution of land-snail species and individuals at small scales has been the subject of many studies. These aimed to detect the effect of microhabitat conditions (Hylander *et al.*, 2005; Juřičková *et al.*, 2008), to study the patterns of dispersion and their changes among seasons and species (Cameron, 1982; Kuznik-Kowalska, 1998) and to investigate levels of species richness at different scales (Nekola & Smith, 1999; Cameron, 2004). Snails can reach high levels of species richness and abundance even within single quadrats (1 m^2 areas or less) (Schmid, 1966; Nekola & Smith, 1999; Coles & Nekola, 2007; Cernohorsky, Horsák & Cameron, 2010). There are often big differences in the numbers of species found among quadrats at the same site, and many studies reveal a nested or clustered spatial distribution: the richest quadrats contain nearly all the species present at the site (Waldén, 1981; Nekola & Smith, 1999; Szybiak *et al.*, 2009), even in apparently homogeneous habitats. Populations of any one species may be relatively evenly distributed among quadrats sampled, or be highly aggregated (Berry, 1966; Mason, 1970; Cameron, 1982; Kralka, 1986; Locasciulli & Boag, 1987). These patterns may be associated with the distribution of microhabitats (Waldén, 1981; Kralka, 1986; Hylander *et al.*, 2005; Juřičková *et al.*, 2008). They may also be influenced by season (Kuznik-Kowalska, 1998), time of day (e.g. Cameron, 1978) and spatial scale (size of quadrat) (Kunin, 1997; Bossuyt & Hermy, 2004).

While studies of life history or population density have of necessity used only specimens alive at the time of sampling, many more general faunal analyses include fresh empty shells

in assessments of species richness (see Cameron & Pokryszko, 2005). While this decreases the effects of seasonal variation in density and in spatial fluctuations in microhabitat quality over time, it may introduce other biases; shells persist for longer in calcium-rich environments (Kukla & Ložek, 1958; Millar & Waite, 1999; Menez, 2002; Pearce, 2008). Nekola & Smith (1999) found that a quadrat of 0.04 m^2 could harbour up to 62% of site richness, but quadrat richness declined sharply with distance from a carbonate cliff base. As empty shells were not separated in their study, it is not clear to what extent differential shell preservation accounted for the steep decline of species richness at this scale within their sites.

Rather few faunistic studies have distinguished empty shells and live individuals (Mason, 1970; Cameron & Morgan-Huws, 1975; Cameron, 1982; Kralka, 1986; Cernohorsky *et al*., 2010), yet studies of microhabitat use clearly require the use of live specimens only. Long-dead empty shells increase the chances of including species that no longer live in the plot or site; they may indeed provide a signal of environmental changes (Cameron & Morgan-Huws, 1975). As there was considerable local turnover in species over time at the smallest observed scale in a study of calcareous fens (Cernohorsky *et al*., 2010), old shells may even-out these local fluctuations; equally, they may be moved passively from the precise location in which they lived.

The aggregation of species and individuals in favourable microsites raises both practical issues of sampling strategy, and more fundamental issues of understanding the factors influencing distribution and abundance. While there is pragmatic guidance related to sampling to produce site inventories (Cameron & Pokryszko, 2005), the influence of quadrat size on the interpretation of patterns of distribution at small scales has rarely been studied (Kunin, 1997; Bossuyt & Hermy, 2004). There are no studies on the effect of varying quadrat size in a completely nested sampling routine using living individuals only. In this paper, we analyse spatial distribution of land snail species and individuals, quantitatively sampled at very small scales, comparing nested plots of 25 × 25 cm^2, 50 × 50 cm^2 and 75 × 75 cm^2. Results from larger plots were used to estimate results from smaller, and compared with results actually obtained; differences were used to examine small-scale heterogeneity in richness and abundance. We compare and contrast results from two habitats: treeless fens and temperate deciduous forest. We expected more even distributions in fen habitats than those recorded in forests, due to the much lower variability in size of species present in the former (Schamp, Horsák & Hájek 2010). We use our data to investigate the behaviour of species/area relationships at very small scales. Leitner & Rosenzweig (1997) suggest that such relationships are a by-product of sampling effects. As body size variation is important in terms of snail species coexistence and can play significant role in structuring land snail communities (Schamp *et al*., 2010), we also consider the effects of species' size on the patterns shown.

MATERIAL AND METHODS

Study area and sites

The study was conducted in fen and forest habitats in the Czech Republic and Slovakia (Central and Eastern Europe). Sampling of fens was carried out in the Western Carpathian flysch belt; altogether 29 sites were sampled. The sampling sites were selected to reflect the whole mineral-poor to mineral-rich gradient (details given by Hájek *et al*., 2006; Cernohorsky *et al*., 2010), the most important gradient for fen communities (Hájek *et al*., 2006). Forest samples were collected at 23 sites in Moravia (eastern Czech Republic). These localities varied in their soil moisture and calcium content and in the composition of the tree layer. Such environmental factors were found to be the most important for forest snail assemblages (e.g. Wäreborn, 1969; Juřičková *et al*., 2008). For both fen and forest habitats, we sampled a comparable number of sites within three categories, defined by calcium concentration (for fen sites) and both calcium content and humidity (for forest sites). Thus, we obtained three groups of sites that differed in species richness and abundances with only few overlaps: 9 forest and 10 fen sites favourable for snails, 9 and 10 moderately favourable sites and 5 and 9 unfavourable sites.

Data collection and analysis

Data were collected from 52 plots; only one plot was sampled per site to ensure independence of each. Sampling took place during the summer (from June to September) when the majority of terrestrial gastropods are active. Each plot consisted of three nested quadrats (25 × 25 cm^2, 50 × 50 cm^2 and 75 × 75 cm^2), placed within a visually homogenous habitat in terms of substrate and vegetation. The smallest quadrat was placed in the upper left corner of the largest quadrat with side edges oriented in the north–south direction. All herbaceous vegetation, mosses, twigs, litter and loose topsoil from these quadrats were collected. Fen plots were cut just below ground level using a sharp knife and completely removed along with vegetation and topsoil; the litter and topsoil in the entire area of forest plots were collected from the surface down to a depth at which the soil became difficult to remove (*c*. 2-5 cm). Snails from fen habitats were then extracted using the 'wet sieving method' (Horsák, 2003), while forest samples were sieved (8-mm mesh) using the standard sieving method (Ložek, 1956) and larger snails that did not go through the sieve were carefully separated in the field and kept for identification. The shells thus collected were dried in the laboratory and sorted by eye, or under a stereoscopic dissection microscope. Slugs were not included into our analyses, as their activity and the probability of detection depend strongly on weather conditions (Rollo, 1991) and our sampling methods are not suitable for slug collecting. Empty shells were also omitted and only live individuals (i.e. shells with a visible, dried body inside) were counted for analysis. All recorded individuals were identified, using the nomenclature of Horsák *et al*. (2010). To get estimates of the species-pool at each site and to compare how effectively sampled quadrats capture the whole array of the habitat, we sampled the surroundings of the quadrats at each site. For these purposes, in forest sites we chose the combination of visual searching and volume method as recommended by Cameron & Pokryszko (2005). This sampling was carried out within a radius of 10 m from the sampling quadrats and the volume was comparable with the volume taken from the middle quadrat of 50 × 50 cm^2. To obtain information about the entire fauna of the fen habitats, we randomly collected 12 litres of the upper-fen layer from an area of 16 m^2 around the quadrats (details given by Cernohorsky *et al*., 2010). The largest quadrats contained on average more than 80% of species found at the entire site (Cernohorsky *et al*., 2010; E. Svobodová, unpubl.).

From the largest plot we estimated numbers of individuals and species for the two smaller plots and compared these estimates with the actual numbers recorded. The same was done using the middle plot as a starting point for the estimates. The estimation of individual numbers was based simply on numbers per unit area recorded at different quadrat sizes. To test differences between numbers of collected and estimated individuals, we used the χ^2 goodness-of-fit test. The statistical tests for differences in numbers of collected and estimated species compared the observed number of species in a smaller plot with 10 000 estimates of species number based on rarefaction of the sample recorded in a larger plot to generate the

Table 1. Numbers of live snail individuals and species recorded at three nested quadrats in 23 forest and 29 fen sites.

	Forests				Fens			
	Minimum	Mean	Median	Maximum	Minimum	Mean	Median	Maximum
Individuals								
25 × 25 cm	0	13	6	68	1	14	10	58
50 × 50 cm	3	71	51	389	8	54	34	193
75 × 75 cm	15	173	102	895	22	113	67	381
Species								
25 × 25 cm	0	4	4	13	1	4	4	8
50 × 50 cm	1	9	7	21	2	7	7	12
75 × 75 cm	2	11	8	26	2	8	9	14

expected number of species in a collection of individuals actually recorded in a smaller plot. If the number of collected species was smaller or higher than 95% of rarefaction estimations, then it was considered to be significantly different from the number of species in this quadrat expected from a random sample of species in a larger quadrat.

We used the absolute values of the coefficient of variation for pairs of estimated and collected numbers to compare proportional deviations between numbers of species and individuals, scales and habitats sampled. A Mann–Whitney U test was performed to test the significance of these differences.

For both habitats we constructed frequency histograms of species' body volumes. The volume of each species was calculated using the formula of McClain & Nekola (2008). Shell dimensions were compiled from available literature (Ložek, 1956; Wiktor, 2004); body-size values taken from the literature represent objective, species-level measures of potential size (e.g. Schamp & Aarssen, 2009). To test differences in species' body sizes between two studied habitats, we calculated medians for all localities and compared them using the Mann–Whitney U test. The same test was done for the comparison of all individuals from both habitats. Since these data relate to adult individuals, these medians will overestimate size, but given the magnitude of differences between the habitats it is unlikely that they arise from any difference in the proportion of adults between them.

RESULTS

Altogether, we recorded 3987 live individuals of 55 species and 3276 individuals of 36 species at all studied forest and fen quadrats, respectively (Appendices 1 and 2). The average forest $75 \times 75\ cm^2$ quadrat captured 173 individuals and 11 species, compared with 113 individuals and 8 species recorded on average in the same-sized quadrat in fens (Table 1).

Within fens the numbers of individuals collected in the smallest plots tended to be slightly greater than those estimated on the basis of area from the largest quadrats, but there were significant deviations in both directions (Fig. 1). For species, the numbers found in the smallest quadrats were frequently, but not always, significantly lower than those predicted by rarefaction from the largest (Fig. 2), with some significant differences in the opposite direction. When numbers of species in the middle-sized quadrats were estimated from those in the largest, the differences between observed and expected values were less marked. There were only four significant deviations and the coefficient of determination was higher in middle-sized to largest quadrat comparison ($r^2 = 0.92$) than in those between the smallest and larger quadrats ($r^2 = 0.73$-0.75), also indicating a lower level of deviation between collected and estimated numbers in the former comparison. Figure 2 also shows that many of these deviations also occur when the smallest and middle quadrats are compared.

In forests, the observed numbers of individuals in the smallest quadrats tended to be lower than predicted from the largest, and eight of these differences are significant (Fig. 1). However, the estimates for middle quadrats from the largest were more similar, with only one plot having significantly lower density of snails than expected under the assumption of even distribution. As in fens, however, observed species richness in the smallest quadrat was generally lower than predicted by rarefaction (Fig. 2); again the difference in predicted and observed richness was much less in the comparison of the intermediate quadrats compared with the largest, and again the coefficient of determination was higher than in the smallest/largest comparison.

In both habitats, medians of proportional deviance between collected and estimated numbers were always significantly higher for individuals than for species (U test, $P < 0.05$), except for the estimation made from the middle to the smallest quadrats in fens (U test, $P = 0.10$). As shown above, deviations between collected and estimated numbers of both species and individuals were smallest in the estimations made from the largest to the middle quadrats, both in fens and in forests (Table 2). There was no significant difference in these deviations among forests and fens (U test, $P > 0.68$).

As expected, the median number of species recorded in each habitat increased with quadrat size. Although the number of points available is very small, it is possible to calculate conventional log S/log A regressions (Table 3). Although not testable, it can be seen that the slopes overall are similar and relatively steep (see Discussion) and the slopes between the smallest and middle-sized quadrats are steeper than those between the middle and the largest.

Fen plots were occupied by significantly smaller snail species than forest plots ($P \ll 0.001$, U test, Fig. 3), as calculated from the largest plot size. Body size of the median adult individual of forest plots was $90.9\ mm^3$, whereas in the fen fauna it was only $8.8\ mm^3$. Snail individuals from forest plots were significantly larger than those of fens (U test, $P = 0.008$).

DISCUSSION

In this study we investigated spatial distribution of land snail assemblages of two contrasting habitat types: treeless spring fens and deciduous forests. The smallest quadrats in both habitats had numbers of individuals and species that often deviated significantly from those estimated based on data collected in the largest quadrats. There is a bias in these deviations, with more showing smaller numbers of species recorded than estimated. These deviations were more marked, although not significantly so, in fens than in forests, despite the fact that species

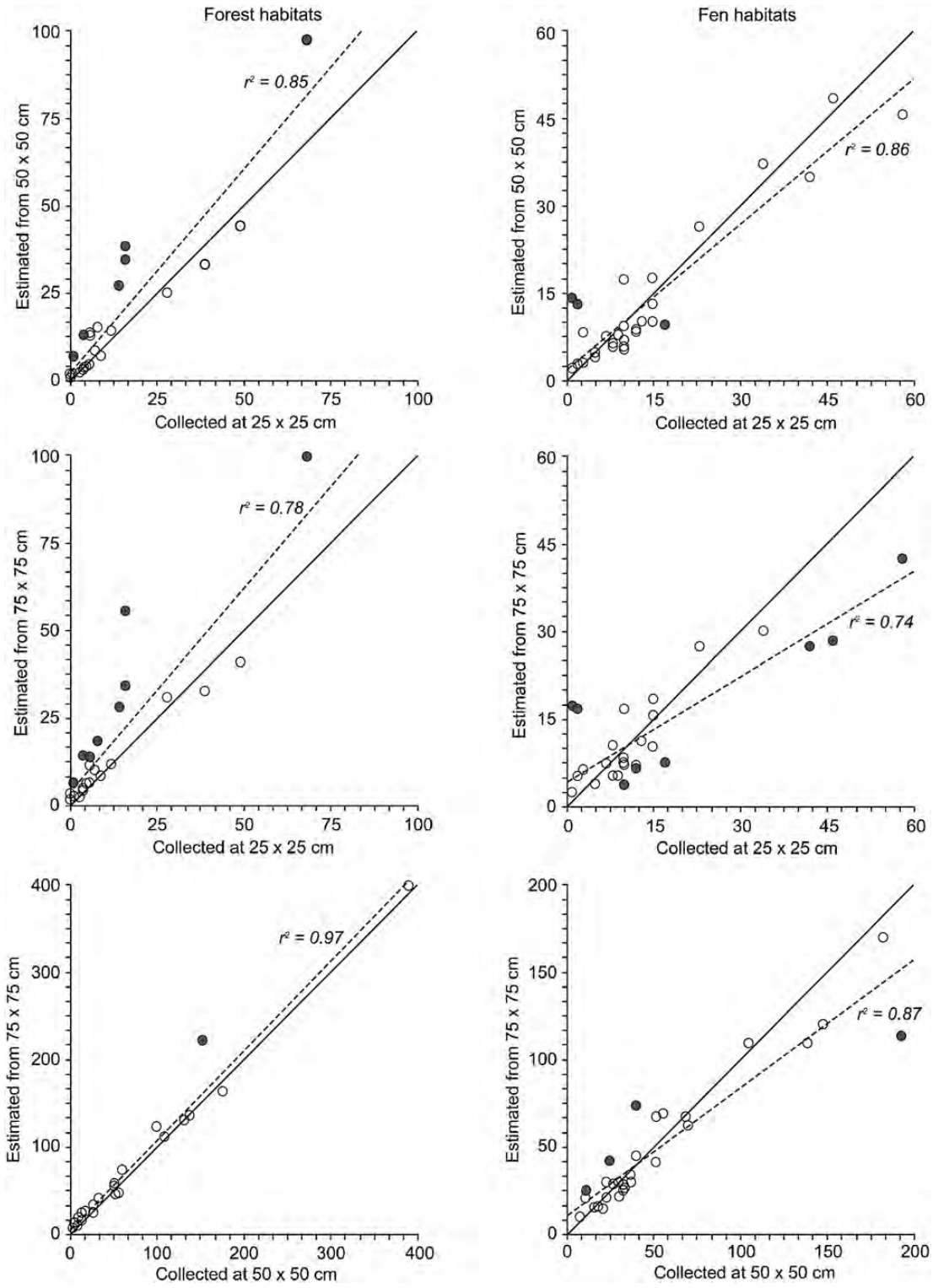

Figure 1. Comparison between observed and estimated numbers of snail individuals for fen and forest habitats sampled at three nested quadrat sizes. Significantly different pairs of observed and estimated numbers are marked by full circles (χ^2 test, $P < 0.05$). The solid line shows the line of perfect fit; the dashed line is the linear regression between observed and estimated numbers, which is shown as an illustrative comparison of individual site dispersion within the array.

in fens are on average smaller than in forests, and show less variation in size among species. Large species often occur at densities of <5 individuals per square metre and any aggregative behaviour might lead to marked deviations at this scale. On the other hand, the scale of microhabitat heterogeneity experienced by very small species may match the quadrat size used here. Certainly, in studies using the same size of quadrat ($0.0625\ m^2$), but with quadrats placed at random in a larger area, tiny fen species show an immense range of variation in both the numbers of individuals and species recorded in each

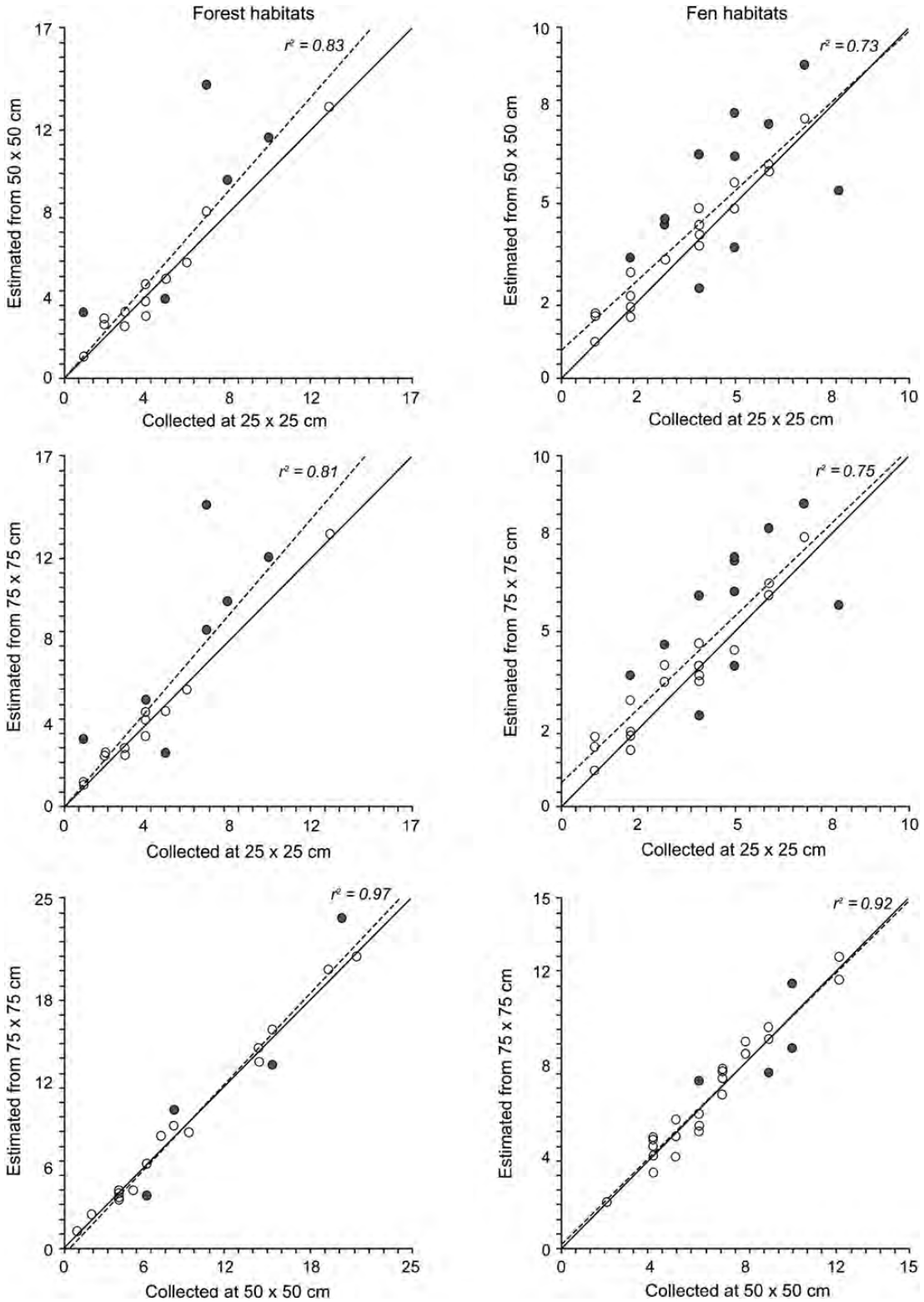

Figure 2. Comparison between observed and estimated numbers of snail species for fen and forest habitats sampled at three nested quadrat sizes. Significantly different pairs of observed and estimated numbers are marked by full circles (based on rarefaction of the larger plot sample, see Material and Methods for details). The solid line shows the line of perfect fit; the dashed line is the linear regression between observed and estimated numbers, which is shown as an illustrative comparison of individual site dispersion within the array.

quadrat (Cameron, 2003). In contrast, though expected from the ratios of quadrat sizes, these deviations were much less marked in the comparison of intermediate sized quadrats and the largest, as consistently documented by the values of the coefficient of variation (Table 2) and coefficient of determination (Figs 1 and 2). Thus it seems that the patterns of distribution

Table 2. Median values and interquartile ranges (in parentheses) of the coefficients of variation between estimated and collected numbers of individual snails and of species at three scales (quadrat sizes 75 × 75 cm, 50 × 50 and 25 × 25 cm): 50/25, an estimate of the smallest from the intermediate quadrat; 75/25, of the smallest from the largest quadrat and 75/50, of the intermediate from the largest quadrat.

	50/25	75/25	75/50
Individuals			
Forests	0.370 (0.240–0.743)	0.370 (0.194–0.753)	0.162 (0.071–0.359)
Fens	0.261 (0.143–0.532)	0.420 (0.250–0.683)	0.213 (0.104–0.280)
Species			
Forests	0.126 (0.026–0.227)	0.171 (0.052–0.208)	0.086 (0.040–0.149)
Fens	0.187 (0.054–0.400)	0.208 (0.072–0.343)	0.083 (0.039–0.141)

Table 3. Log-log regressions of median numbers of snail species on quadrat area, for fens and forests, overall and between adjacent quadrat sizes.

Regression	Slope	Intercept
Fens		
All points	0.325	1.006
Smallest to intermediate	0.404	1.088
Intermediate to largest	0.165	0.944
Forests		
All points	0.373	0.106
Smallest to intermediate	0.404	1.088
Intermediate to largest	0.310	1.032

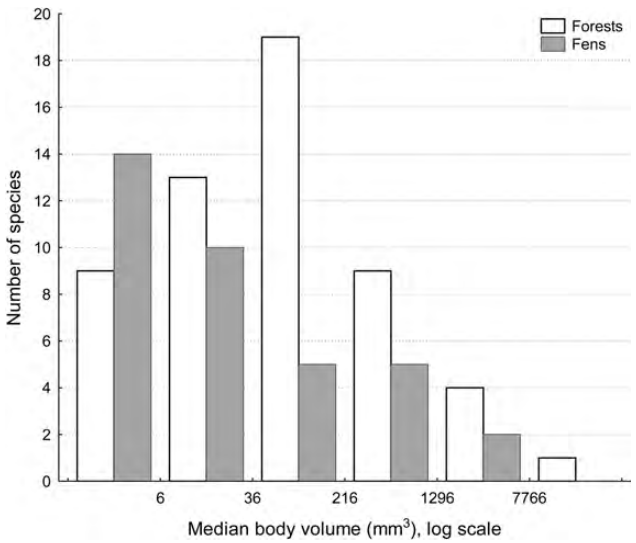

Figure 3. Frequency histogram of body volumes for forest and fen land-snail species.

at the scale of the middle- and largest-sized quadrats were very similar both for species and individuals. Any heterogeneity within a habitat at this scale (<1 m^2) would appear to be at a smaller scale. The proportional deviations are always greater for individuals than for species, suggesting that there is variation in suitability for snails in general.

A number of conclusions follow from these results. While it would be wrong to estimate the faunal richness and composition of a larger site, even of apparently uniform habitat, from a single quadrat of 1 m^2 or less, it is evident that much smaller quadrats will show much greater variation in richness and composition. Hence, very small quadrats may be needed to detect the nature of microhabitats that determine the distribution and abundance of snails at these scales. Cernohorsky *et al.*, (2010) showed that it is at this smallest scale that the effects of including empty shells in any analysis are greatest, imposing a spurious uniformity; microhabitat suitability may change over time and many such microhabitats of importance to snails are temporary (Kappes, 2005). Our results extend previous observations of land-snail spatial aggregations (e.g. Mason, 1970, Szybiak *et al.*, 2009) into continuously sampled areas of homogeneous habitats. This raises questions about environmental heterogeneity even in visually homogeneous areas, and about possible biotic interactions among individual species. As many sites show a rather even distribution of both individuals and species at larger scales, fine-scale heterogeneity of habitat conditions is a probable explanation of aggregated distribution at least in some sites.

The bias towards estimating a greater number of species in the smallest quadrats than were actually found suggests that different species have different habitat requirements, and that not all of these are to be found in any one small quadrat. Although there are many studies suggesting a strong element of nestedness in the local distribution of land snails (Waldén, 1981; Hylander *et al.*, 2005), these are based on quadrats placed at random in a larger area, or on qualitative assessment. We can hypothesize that if a larger area is completely sampled in smaller segments, many such segments will lack species present in others and *vice versa*.

Although its existence as a general phenomenon is questioned (Tjørve & Tjørve, 2011), the 'small island effect' (Lomolino, 2000; Lomolino & Weiser, 2001), whereby very small islands do not conform to a broader species/area relationship but display idiosyncratic features dependent on the range of habitats present, has been generalized to a 'small area effect'. Removing the sampling effort effect, species richness is largely independent of area until a particular threshold is exceeded, and this threshold is body-size dependent (Azovsky, 2011). Different upper limits of the small area effect were found for some island land snail assemblages or other taxa of soil macrofauna (Triantis *et al.*, 2006). A more conventional analysis using birds (Rosenzweig, 1995) suggests that at very small scales relative to the size and mobility of the organisms under study, the slope of the species/area curve is steeper than at larger scales, because increasing area relates to the inclusion of a greater range of species-specific habitat features and flattens out when most of these are represented in the areas considered (Storch *et al.*, 2012). Our data tend to support this more orthodox pattern; the log S-log A regressions based on median richness (based, however, on a very small number of points) are steeper than those derived from studies of snails at larger scales (Cameron, 2004), and the slope is steeper between the smallest and intermediate quadrats than between the latter and the largest, though this is more marked in the fens than in the forest. However, there are individual cases in which the observed richness is significantly greater than that predicted from rarefaction. This suggests that at this scale there are still idiosyncratic variations in the range of microhabitats available within the smallest quadrat. Cameron (2002) found a very wide scatter of richness at this quadrat size of 25 × 25 cm^2, even within the same site and habitat. It appears that although there is a conventional species/area relationship at this scale, the variance among individual samples is very high; it is this variance that suggests that the small area effect cannot be dismissed outright. Consistent with our findings, no small area effect was obtained for lumbricid earthworms and the species/area curve at small scales was somewhat steeper (Williamson,

Gaston & Lonsdale, 2001). Thus our study confirms the view of the small area effect as an idiosyncratic phenomenon of limited effect (Williamson *et al*., 2002; Triantis *et al*., 2006). In our study the effect of small-scale habitat heterogeneity diminished between the intermediate and largest quadrat size; differences in observed richness were as predicted from a rarefaction model. This has consequences for inventories of snail species, because sampling higher numbers of small areas can bring more complete inventories than sampling one large plot of the same area. This is in agreement with the finding of Cameron & Pokryszko (2005) that volume methods can bring more complete inventories than sampling based on quadrat samples, as volume samples are composed of high number of very small 'quadrat samples'.

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REFERENCES

AZOVSKY, A.I. 2011. Species–area and species–sampling effort relationships: disentangling the effects. *Ecography*, **34**: 18–30.

BERRY, A.J. 1966. Population structure and fluctuations in the snail fauna of a Malayan limestone hill. *Journal of Zoology*, **150**: 11–27.

BOSSUYT, B. & HERMY, M. 2004. Species turnover at small scales in dune slack plant communities. *Basic and Applied Ecology*, **5**: 321–329.

CAMERON, R.A.D. 1978. Differences in the sites of activity of co-existing species of land molluscs. *Journal of Conchology*, **29**: 273–278.

CAMERON, R.A.D. 1982. Life histories, density and biomass in a woodland snail community. *Journal of Molluscan Studies*, **48**: 159–166.

CAMERON, R.A.D. 2002. Some species/area relationships in the British land mollusc fauna and their implications. *Journal of Conchology*, **37**: 337–348.

CAMERON, R.A.D. 2003. Life-cycles, molluscan and botanical associations of *Vertigo angustior* and *Vertigo geyeri* (Gastropoda, Pulmonata: Vertiginidae). *Heldia*, **5**(7): 95–110.

CAMERON, R.A.D. 2004. From continents to quadrats: species/area relationships in land mollusc faunas. *Journal of Conchology Special Publication*, **3**: 39–54.

CAMERON, R.A.D. & MORGAN-HUWS, D.I. 1975. Snail faunas in the early stages of a chalk grassland succession. *Biological Journal of the Linnean Society*, **7**: 215–229.

CAMERON, R.A.D. & POKRYSZKO, B.M. 2005. Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. *Journal of Conchology*, **38**: 529–547.

CERNOHORSKY, N.H., HORSÁK, M. & CAMERON, R.A.D. 2010. Land snail species richness and abundance at small scales: the effect of distinguishing between live individuals and empty shells. *Journal of Conchology*, **40**: 233–241.

COLES, B.F. & NEKOLA, J.C. 2007. *Vertigo malleata*, a new extreme calcifuge land snail from the Atlantic and Gulf coastal plains of the U.S.A. (Gastropoda, Vertiginidae). *Nautilus*, **121**: 17–28.

HÁJEK, M., HORSÁK, M., HÁJKOVÁ, P. & DÍTĚ, D. 2006. Habitat diversity of central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**: 97–114.

HORSÁK, M. 2003. How to sample mollusc communities in mires easily. *Malacologica Bohemoslovaca*, **2**: 11–14.

HORSÁK, M., JUŘIČKOVÁ, L., BERAN, L., ČEJKA, T. & DVOŘÁK, L. 2010. Komentovaný seznam měkkýšů zjištěných ve volné přírodě České a Slovenské republiky [Annotated list of mollusc species recorded outdoors in the Czech and Slovak Republics]. *Malacologica Bohemoslovaca*, (Suppl. 1): 1–37 (in Czech).

HYLANDER, K., NILSSON, C., JONSSON, B.G. & GÖTHNER, T. 2005. Differences in habitat quality explain nestedness in a land snail metacommunity. *Oikos*, **108**: 351–361.

JUŘIČKOVÁ, L., HORSÁK, M., CAMERON, R., HYLANDER, K., MÍKOVCOVÁ, A., HLAVÁČ, J.Č. & ROHOVEC, J. 2008. Land snail distribution patterns within a site: the role of different calcium sources. *European Journal of Soil Biology*, **44**: 172–179.

KAPPES, H. 2005. Influence of coarse woody debris on the gastropod community of a managed calcareous beech forest in western Europe. *Journal of Molluscan Studies*, **71**: 85–92.

KRALKA, R.A. 1986. Population characteristics of terrestrial gastropods in boreal forest habitats. *American Midland Naturalist*, **115**: 156–164.

KUKLA, J. & LOŽEK, V. 1958. K problematice výzkumu jeskynních výplní [On the problems of investigation of cave deposits]. *Československý kras*, **11**: 19–83 (in Czech).

KUNIN, W.E. 1997. Sample shape, spatial scale and species counts: implications for reserve design. *Biological Conservation*, **82**: 369–377.

KUZNIK-KOWALSKA, E. 1998. Seasonal changes in age structure of a land malacocenosis, with notes on clustered distribution of selected species. *Folia Malacologica*, **6**: 33–38.

LEITNER, W.A. & ROSENZWEIG, M.L. 1997. Nested species-area curves and stochastic sampling: a new theory. *Oikos*, **79**: 503–512.

LOCASCIULLI, O. & BOAG, D.A. 1987. Microdistribution of terrestrial snails (Stylommatophora) in forest litter. *Canadian Field Naturalist*, **101**: 76–81.

LOMOLINO, M.V. 2000. Ecology's most general, yet protean pattern: the species–area relationship. *Journal of Biogeography*, **27**: 17–26.

LOMOLINO, M.V. & WEISER, M.D. 2001. Towards a more general species–area relationship: diversity on all islands, great and small. *Journal of Biogeography*, **28**: 431–445.

LOŽEK, V. 1956. *Klíč československých měkkýšů [Key to Czechoslovak molluscs]*. Vydavatelstvo SAV, Bratislava (in Czech).

MASON, C.F. 1970. Snail populations, beech litter production and the role of snails in litter decomposition. *Oecologia*, **5**: 215–239.

McCLAIN, C.R. & NEKOLA, J.C. 2008. The role of local-scale processes on terrestrial and deep-sea gastropod body size distributions across multiple scales. *Evolutionary Ecology Research*, **10**: 129–146.

MENEZ, A. 2002. The degradation of land snail shells during the annual dry period in a Maditerranean climate. *Iberus*, **20**: 73–79.

MILLAR, A.J. & WAITE, S. 1999. Molluscs in coppice woodland. *Journal of Conchology*, **36**: 25–48.

NEKOLA, J.C. & SMITH, T.M. 1999. Terrestrial gastropod richness patterns in Wisconsin carbonate cliff communities. *Malacologia*, **41**: 253–269.

PEARCE, T.A. 2008. When a snail dies in the forest, how long will the shell persist? Effect of dissolution and micro-bioerosion. *American Malacological Bulletin*, **26**: 111–117.

ROLLO, C.D. 1991. Endogenous and exogenous regulation of activity in *Deroceras reticulatum*, a weather sensitive terrestrial slug. *Malacologia*, **33**: 199–220.

ROSENZWEIG, M.L. 1995. *Species diversity in time and space*. Cambridge University Press, New York.

SCHAMP, B., HORSÁK, M. & HÁJEK, M. 2010. Deterministic assembly of land snail communities according to species size and diet. *Journal of Animal Ecology*, **79**: 803–810.

SCHAMP, B.S. & AARSSEN, L.W. 2009. The assembly of forest communities according to maximum species height along resource and disturbance gradients. *Oikos*, **118**: 564–572.

SCHMID, G. 1966. Die Mollusken des Spitzbergs. *Natur und landschaftsschutzgebiete, Baden Würtemburg*, **3**: 596–701.

STORCH, D., KEIL, P. & JETZ, W. 2012. Universal species–area and endemics–area relationships at continental scales. *Nature*, **488**: 78–81.

SZYBIAK, K., BOSZYK, J., KORALEWSKA-BATURA, E. & GODYN, B. 2009. Small-scale distribution of wintering terrestrial snails in forest site: relation to habitat conditions. *Polish Journal of Ecology*, **57**: 525–535.

TJØRVE, E. & TJØRVE, K.M.C. 2011. Subjecting the theory of the small-island effect to Ockham's razor. *Journal of Biogeography*, **38**: 1834–1839.

TRIANTIS, K.A., VARDINOYANNIS, K., TSOLAKI, E.P., BOTSARIS, I., LIKA, K. & MYLONAS, M. 2006. Re-approaching the small island effect. *Journal of Biogeography*, **33**: 915–923.

WALDÉN, H.W. 1981. Communities and diversity of land molluscs in Scandinavian woodlands. I. High diversity communities in taluses and boulder slope in SW Sweden. *Journal of Conchology*, **30**: 351–372.

WÄREBORN, I. 1969. Land molluscs and their environments in an oligotrophic area in southern Sweden. *Oikos*, **20**: 461–479.

WIKTOR, A. 2004. Ślimaki lądowe Polski [Land snails of Poland]. Mantis, Olsztyn (in Polish).

WILLIAMSON, M., GASTON, K.J. & LONSDALE, W.M. 2001. The species–area relationship does not have an asymptote!. *Journal of Biogeography*, **28**: 827–830.

WILLIAMSON, M., GASTON, K.J. & LONSDALE, W.M. 2002. An asymptote is an asymptote and not found in species–area relationships. *Journal of Biogeography*, **29**: 1713.

APPENDIX I

List of all recorded snail species in all 23 studied forest plots. Body volume (V), number of occupied quadrats (P_{25}, 25 × 25 cm; P_{50}, 50 × 50 cm; P_{75}, 75 × 75 cm) and total number of recorded individuals (n_t) are given. Species are ordered by their volume (V); the nomenclature follows Horsák *et al.* (2010).

Species	V	P_{25}	P_{50}	P_{75}	n_t
Carychium minimum O.F. Müller, 1774	0.66	1	2	2	66
Carychium tridentatum (Risso, 1826)	0.73	6	8	8	556
Punctum pygmaeum (Draparnaud, 1805)	0.74	8	11	12	318
Columella edentula (Draparnaud, 1805)	1.70	0	1	3	14
Platyla polita (Hartmann, 1840)	2.07	0	5	6	60
Vitrea contracta (Westerlund, 1871)	3.44	2	3	3	25
Vallonia pulchella (O.F. Müller, 1774)	3.86	1	1	1	3
Acanthinula aculeata (O.F. Müller, 1774)	3.90	5	6	10	104
Vallonia costata (O.F. Müller, 1774)	4.02	0	1	1	4
Vitrea subrimata (Reinhardt, 1871)	6.82	3	5	5	218
Euconulus fulvus (O.F. Müller, 1774)	8.70	1	3	4	9
Cochlicopa lubricella (Rossmässler, 1835)	10.39	0	0	1	1
Vitrea crystallina (O.F. Müller, 1774)	11.58	6	8	9	408
Euconulus praticola (Reinhardt, 1883)	13.81	0	1	1	2
Vitrea diaphana (Studer, 1820)	14.66	1	5	5	40
Perpolita hammonis (Ström, 1765)	15.05	1	3	4	25
Cochlicopa lubrica (O.F. Müller, 1774)	16.83	2	5	5	71
Aegopinella pura (Alder, 1830)	16.99	5	9	10	573
Ruthenica filograna (Rossmässler, 1836)	18.08	2	4	4	44
Daudebardia rufa (Draparnaud, 1805)	18.11	3	4	5	75
Sphyradium doliolum (Bruguière, 1792)	18.56	1	2	3	45
Semilimax semilimax (J. Férussac, 1802)	29.17	1	3	4	31
Discus perspectivus (M. von Mühlfeld, 1816)	36.18	0	2	2	8
Cochlodina orthostoma (Menke, 1830)	48.32	0	0	1	1
Merdigera obscura (O.F. Müller, 1774)	49.28	1	1	1	8
Discus rotundatus (O.F. Müller, 1774)	50.19	6	7	9	80
Macrogastra plicatula (Draparnaud, 1801)	54.85	0	1	1	2
Vitrina pellucida (O.F. Müller, 1774)	57.29	3	6	7	150
Clausilia pumila C. Pfeiffer, 1828	61.57	1	5	5	35
Vestia turgida (Rossmässler, 1836)	94.59	1	1	1	69
Aegopinella minor (Stabile, 1864)	99.97	4	8	11	113
Cochlodina laminata (Montagu, 1803)	107.23	3	6	7	55
Oxychilus depressus (Sterki, 1880)	108.91	0	1	1	2
Alinda biplicata (Montagu, 1803)	109.25	2	7	10	112
Trochulus sericeus (Draparnaud, 1801)	127.05	0	0	1	1
Petasina unidentata (Draparnaud, 1805)	127.28	2	5	7	30
Trochulus hispidus (Linné, 1758)	135.72	3	5	6	92
Macrogastra ventricosa (Draparnaud, 1801)	136.19	0	3	3	20
Aegopinella epipedostoma iuncta Hudec, 1964	148.52	0	2	2	11
Perforatella bidentata (Gmelin, 1791)	161.57	0	1	1	2
Trochulus villosulus (Rossmässler, 1838)	170.24	0	1	1	35
Ena montana (Draparnaud, 1801)	251.57	0	1	3	5
Isognomostoma isognomostomos (Schröter, 1784)	279.48	0	1	1	8
Oxychilus cellarius (O.F. Müller, 1774)	299.35	4	6	7	32
Oxychilus glaber (Rossmässler, 1835)	334.83	0	1	1	4
Monachoides incarnatus (O.F. Müller, 1774)	623.23	8	16	18	172
Monachoides vicinus (Rossmässler, 1842)	709.25	2	7	10	40
Succinea putris (Linné, 1758)	994.84	1	2	2	63
Euomphalia strigella (Draparnaud, 1801)	1002.40	0	2	2	32
Faustina faustina (Rossmässler, 1835)	1100.19	1	2	3	16
Cepaea hortensis (O.F. Müller, 1774)	2325.06	0	2	3	10
Fruticicola fruticum (O.F. Müller, 1774)	2426.48	0	1	3	6
Arianta arbustorum (Linné, 1758)	3294.48	2	4	5	74
Aegopis verticillus (Lamarck, 1822)	7408.27	1	2	2	5
Helix pomatia Linné, 1758	29708.95	0	0	2	2

APPENDIX 2

List of all recorded snail species in 29 studied fen plots. Body volume (V), number of occupied quadrates (P_{25}, 25 × 25 cm; P_{50}, 50 × 50 cm; P_{75}, 75 × 75 cm) and total number of recorded individuals (n_t) are given. Species are ordered by their volume (V); the nomenclature follows Horsák *et al*. (2010).

Species	V	P_{25}	P_{50}	P_{75}	n_t
Carychium minimum O.F. Müller, 1774	0.66	6	13	15	307
Carychium tridentatum (Risso, 1826)	0.73	0	1	2	10
Punctum pygmaeum (Draparnaud, 1805)	0.74	3	10	14	61
Vertigo substriata (Jeffreys, 1830)	1.29	8	16	18	166
Vertigo pygmaea (Draparnaud, 1801)	1.33	6	11	13	143
Vertigo geyeri Lindholm, 1925	1.43	3	4	5	66
Vertigo angustior Jeffreys, 1830	1.49	6	8	9	330
Columella edentula (Draparnaud, 1805)	1.70	1	1	4	7
Columella aspera Waldén, 1966	2.09	1	1	2	4
Vertigo antivertigo (Draparnaud, 1801)	2.39	8	14	15	272
Vertigo moulinsiana (Dupuy, 1849)	3.40	3	3	3	45
Vallonia pulchella (O.F. Müller, 1774)	3.86	9	15	15	544
Vallonia costata (O.F. Müller, 1774)	4.02	0	0	1	1
Pupilla alpicola (Charpentier, 1837)	5.10	1	1	1	15
Euconulus fulvus (O.F. Müller, 1774)	8.70	4	10	12	64
Vitrea crystallina (O.F. Müller, 1774)	11.58	0	1	1	1
Euconulus praticola (Reinhardt, 1883)	13.81	5	7	8	86
Vitrea diaphana (Studer, 1820)	14.66	0	1	1	1
Perpolita hammonis (Ström, 1765)	15.05	14	21	23	383
Cochlicopa lubrica (O.F. Müller, 1774)	16.83	15	25	26	437
Daudebardia brevipes (Draparnaud, 1805)	18.11	1	1	1	1
Daudebardia rufa (Draparnaud, 1805)	18.11	1	1	2	6
Semilimax semilimax (J. Férussac, 1802)	29.17	3	4	4	51
Perpolita petronella (L. Pfeiffer, 1853)	32.26	1	1	1	2
Zonitoides nitidus (O.F. Müller, 1774)	52.86	1	1	2	8
Vitrina pellucida (O.F. Müller, 1774)	57.29	0	1	3	3
Succinella oblonga (Draparnaud, 1801)	78.92	5	6	7	81
Pseudotrichia rubiginosa (Rossmässler, 1838)	112.25	0	1	1	14
Perforatella bidentata (Gmelin, 1791)	161.57	1	1	1	2
Plicuteria lubomirskii (Ślósarski, 1881)	316.67	0	3	6	13
Oxyloma elegans (Risso, 1826)	570.14	3	6	6	76
Monachoides incarnatus (O.F. Müller, 1774)	623.23	0	1	1	1
Succinea putris (Linné, 1758)	994.84	3	7	9	64
Euomphalia strigella (Draparnaud, 1801)	1002.40	0	0	1	2
Arianta arbustorum (Linné, 1758)	3294.48	0	1	1	1
Cepaea vindobonensis (A. Férussac, 1821)	6534.51	0	1	2	8