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Mollusc assemblages of Scandinavian fens: species composition in relation to environmental gradients and vegetation

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Little information exists about the ecological determinants of the mollusc species composition of Scandinavian fens. Therefore, we investigated water chemistry, hydrology, climate and vegetation composition of fens in southern and central Norway and in Sweden hosting mollusc assemblages. According to the results of the MDS ordination, variation in the mollusc composition was related to the hydrology of the studied sites, reflecting a transition from soligenous to topogenous fens. The second axis of the MDS reflected a complex gradient of mineral richness and climatic conditions. By analogy, cluster analysis revealed three main groups of sites, i.e. topogenous fens characterized by a frequent occurrence of *Vertigo lilljeborgi*, soligenous lowland fens characterized by *Cochlicopa lubrica* and *Nesovitrea hammonis*, and soligenous highland fens characterized by *Columella columella*. Results of the RDA closely resembled those of the MDS, suggesting that the selected explanatory variables defined mollusc assemblages well.

Introduction

The boreal zone of Scandinavia represents an exceptional European area where extensive groundwater-fed fens still remain intact and constitute a large proportion of all natural ecosystems (Pakarinen 1995, Joosten & Clarke 2002). In many other regions of the world, fens are among the most threatened ecosystems and have been severely altered or destroyed by human activities (e.g., agriculture and urban development; *see* Bedford & Godwin 2003, Grootjans *et al*. 2006, Middleton *et al*. 2006). At the same time, fens usually represent biodiversity hotspots, harboring a wide spectrum of rare, endangered and relict species (e.g., Amon *et al*. 2002, Wassen *et al*. 2005, Horsák & Cernohorsky 2008). In Scandinavia, the relatively low human impact along with specific features of climate, landscape topography and postglacial history have facilitated a development of various fen types, encompassing areas of great climatic contrasts and varying substantially along the gradient of mineral richness (Malmer 1986, Wheeler & Proctor 2000, Økland *et al*. 2001). Despite the prevailing crystalline bedrock, giving rise to mineral-poor *Sphagnum* fens in most of Fennoscandia (Tahvanainen 2004, Hájek *et al*. 2006), scattered calcareous outcrops support the development of mineral-rich brown-moss fens, sometimes even with calcium carbonate precipitation, such as in the Swedish provinces of Skåne and Jämtland (Malmer 1965, Sjörs 1965a). According to their hydrotopographic features, Scandinavian fens can be classified either as sloping soligenous systems, with a directional water flow through the sediment or up on the surface, or flat topogenous systems, usually located in terrain basins, with stagnant or very slowly flowing water (Rydin & Jeglum 2006).

Among a variety of different taxa, molluscs have been found to form extraordinarily diverse assemblages with unique species compositions in groundwater-fed fens, especially in those rich in calcium (Horsák & Hájek 2003). In Scandinavia, fens are among the habitats with the richest land snail fauna (Andersen & Halvorsen 1984, Nilsson 1987) and with a frequent occurrence of ecologically-sensitive fen specialists, such as *Vertigo genesii*, *V. geyeri* and *V. lilljeborgi* (Kerney *et al*. 1983, von Proschwitz 2003). These species are regarded as glacial relicts (e.g., Hausdorf & Hennig 2003, Schenková & Horsák 2013), as they were common and widespread in central Europe during the Late Glacial and Early Holocene (e.g., Ložek 1964). Nowadays, they are restricted to northern Europe and isolated refugia at lower latitudes, i.e. fens of a relict origin and historical continuity throughout the Holocene (Hájek *et al*. 2011, Schenková & Horsák 2013).

Owing to a high concentration of fen ecosystems along with a frequent occurrence of land snail habitat specialists, Scandinavia represents a perfect model territory for a large-scale study of fen mollusc fauna. Indeed, there has been a long tradition of faunistic malacological research in both Norway and Sweden, providing us with detailed knowledge about the distribution and ecology of individual species (e.g., Økland 1925, Kerney & Cameron 1979, Andersen & Halvorsen 1984, Waldén 1995, von Proschwitz 2003). However, studies focusing on fen ecosystems were mostly carried out locally, examining mollusc diversity and the occurrence of rare and threatened species in single counties or protected areas (comprehensive research was conducted by Ted von Proschwitz, e.g., von Prochwitz 1993, 1998, 2009, 2010, 2014). Little attention has been paid to comparisons on the assemblage scale, and only sparse information exists about the relationships between patterns in mollusc species composition and various environmental gradients. Much more effort has been put into ecological studies of fen mollusc assemblages in the temperate zone (e.g., Bishop 1981, Pokryszko 1993, Horsák & Hájek 2003, Ausden *et al*. 2005, Horsák *et al*. 2011, Schenková *et al*. 2014), where fens usually represent isolated and fragmented habitats of high conservation value (Grootjans *et al*. 2006). In Scandinavia, the only detailed study of fen mollusc ecology was conducted by Pokryszko (1993) in the Dovrefjell National Park in central Norway. Briefly summarizing the results, Pokryszko found a strong positive correlation between mollusc diversity and calcium richness, as also documented in studies of fen assemblages from central Europe (Horsák & Hájek 2003, Horsák *et al*. 2011). In addition, Pokryszko outlined differences in the species ecological optima along the mineral richness gradient (*see* also Horsák 2006), examined their altitudinal ranges (*see* also Solhøy 1976), and described prominent compositional differences between soligenous and topogenous fens, as also reported earlier by Nilsson (1987). However, to date there has been no attempt to associate environmental gradients with compositional changes in mollusc assemblages using a multidimensional approach.

To draw more general conclusions about factors affecting the composition of mollusc fauna in Scandinavian fens, we conducted a detailed ecological survey of mollusc assemblages in fens in southern and central Norway and Sweden. We attempted to cover a broad range of several key environmental characteristics, including water chemistry, climate and hydrological regime. The

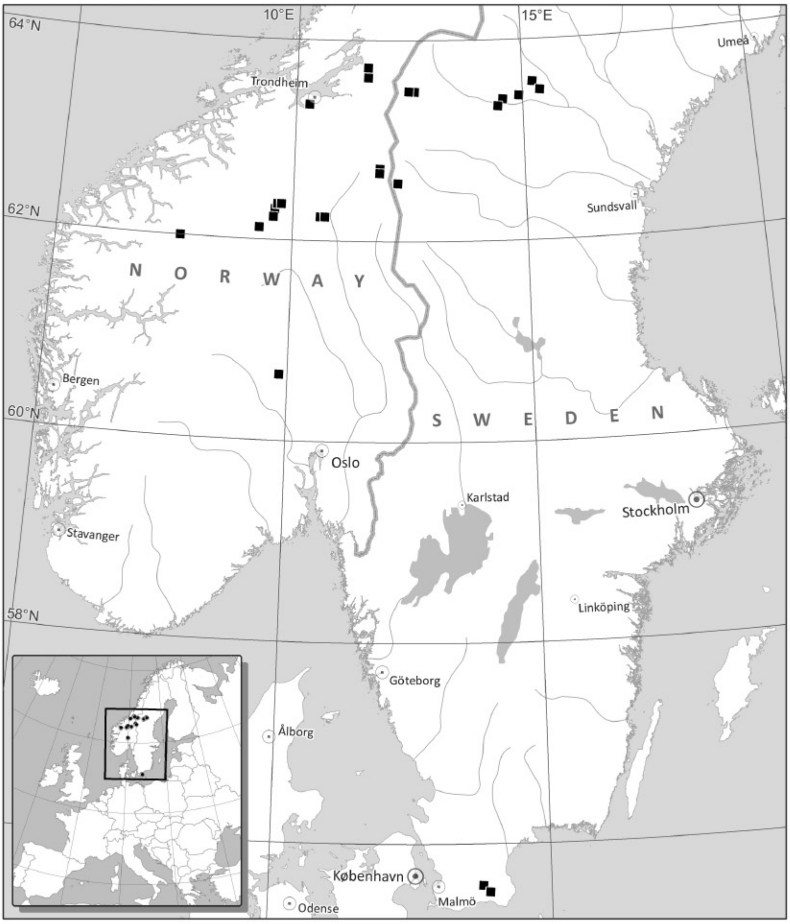

Fig. 1. Location of 40 sampling sites in the study area of southern and central Scandinavia.

aims of our study were (1) to find major gradients in composition of fen mollusc fauna and locate environmental factors related to these gradients, (2) to distinguish basic types of mollusc assemblages occurring in Scandinavian fens, and (3) to discuss specific features of the Scandinavian fen mollusc fauna when compared with those in other European countries.

Material and methods

Study area

The 40 study sites were situated in the southern and central parts of the Scandinavian Peninsula in Norway and Sweden between 55°31´–63°43´N and 09°17´–15°23´E (Fig. 1). The study area mostly falls within the boreal zone, with the exception of two sites situated on the southernmost coast of Sweden (Fig. 1) that belong to the temperate zone (Sjörs 1965b, Dierssen 1996). There are substantial contrasts between the mild, oceanic climate of the Norwegian coast and southernmost Sweden, and the rather continental climate of central Norway and Sweden, as also demonstrated by a broad range of mean annual temperature varying between –1.2 and 7.8 °C, and annual precipitation sums varying between 549 and 861 mm. The bedrock geology of the study area is very diverse, consequently influencing mineral concentrations in fen groundwater (Tahvanainen 2004). Quaternary glaciations contributed to the erosion of calcareous material down to the Precambrian crystalline bedrock, comprised mainly of acid granites and gneisses in a large part of the Fennoscandian Shield (e.g., Lahtinen 2012), which in turn led to the development of mineral-poor fens throughout the area (Tahvanainen 2004, Hájek *et al*. 2006). As such, calcium-poor conditions are hostile to the vast majority of European land snail fauna (Horsák 2006), we focused our sampling effort on regions with more varied bedrock geology in order to include all vegetation types along the mineral richness gradient, including calcareous tufa-forming fens (Hájek *et al*. 2006). Therefore, we sampled several sites situated in younger sedimentary bedrock in the Swedish provinces of Jämtland (Cambro-Silurian bedrock) and Skåne (Mesozoic and Tertiary bedrock), where calcareous sediments consisting mainly of sandstone, claystone, siltstone and limestone are preserved (Sjörs 1965a). A large proportion of the study sites were situated in the Scandinavian Mountains, where the bedrock is formed of a mixture of slightly transformed, highly metamorphosed as well as volcanic rocks of highly diverse calcium content (Ramberg *et al*. 2008).

Field work and explanatory variables

Field research was conducted in August 2006. At each study site we defined a sampling square of 16 m^2 from which one 12-liter sample was collected comprising the upper soil layer, including litter, bryophytes and herbaceous vegetation. This sample volume was found to sufficiently estimate the whole site's mollusc species pool (Cernohorsky *et al*. 2010). Coarse plant matter and fine inorganic particles were removed from the samples in the field using the wet sieving technique (Horsák 2003). After drying, shells were separated from the remaining sampled material under a dissecting stereomicroscope, identified to the species level and counted. Species nomenclature followed that of Horsák *et al*. (2013). In the same 16 m^2 plots, we recorded the occurrence and cover of plant species using the nine-grade Braun-Blanquet scale for both vascular plants and bryophytes (van der Maarel 1979).

Water conductivity and pH were measured in microsites optimally supplied with water in the central parts of each sampling plot, using portable instruments with automatic temperature compensation (PH119 and CM101, Snail Instruments, Beroun, Czech Republic). The readings were standardized to 20 °C. Conductivity caused by H$^+$ ions in acidic waters ($pH < 5.5$) was subtracted (Sjörs 1950). As water conductivity correlates with the amount of calcium and magnesium ions in fens (Sjörs & Gunnarsson 2002, Hájek *et al*. 2002), it can be used as a reliable approximation of calcium concentration (Horsák 2006). For each site, a set of basic climatic variables (mean January, July and annual temperatures; winter, summer and annual precipitation sums) was obtained using the WorldClim database ver. 1.4 (Hijmans *et al*. 2005) in the ArcGIS 8.3 program (ESRI 2003).

We used vegetation composition to classify the fens into five standard types according to Hájek *et al*. (2006), i.e. calcareous tufa-forming fens, extremely mineral-rich fens, mineral-rich *Sphagnum*-fens, moderately mineral-rich *Sphagnum*-fens and poor *Sphagnum* fens. In addition, we established the total cover of aquatic and semi-aquatic plant species requiring a stable water level at or above the apical parts of mosses in order to assess the water regime of each site; these were *Calliergon giganteum*, *Pseudocalliergon trifarium*, *Scheuchzeria palustris*, *Scorpidium scorpioides* and *Utricularia* spp.

Statistical analyses

Based on Spearman's correlations between all explanatory variables, we excluded four climatic variables as they were strongly correlated with other environmental characteristics ($r_s > 0.7$, $p << 0.001$), and compiled a parsimonious set of five explanatory variables that were used in the statistical analyses (Table 1). Four sites (mineral-poor *Sphagnum*-fens) were excluded from the analyses, as no molluscs were found there. Mollusc abundances were calculated from both live specimens and empty shells with entire periostracum. To reduce the influence of dominant species and suppress the effect of slower shell degradation at calcareous sites (Cernohorsky *et al*. 2010), abundances were ln-transformed ($\ln[x + 1]$) prior to all statistical analyses. Mollusc species recorded only as empty shells within the entire data set were excluded from the analyses, as they were regarded as inhabitants of adjacent areas, occurring only randomly at a few studied sites. Slugs (a total of two species) were also omitted, as the sampling method was not appropriate for assessing their occurrence at sites. Due to a few outliers, the percentage values of aquatic plant cover were also ln-transformed prior to the analyses.

To study compositional variation in mollusc assemblages, we subjected the data to indirect ordination analysis of metric multidimensional scaling (MDS, also known as principle coordinate analysis), based on the distance species-by-sites matrix calculated by the Bray-Curtis dissimilarity index, as a robust metric approach suited to revealing the major directions of compositional variation in ecological data (Faith *et al*. 1987). We used a broken-stick model (Peres-Neto *et al*. 2003) to evaluate the importance of ordination axes of mollusc MDS and determined that only the first two axes were appropriate for meaningful ecological interpretation. Five explanatory variables were linearly fitted into the two-dimensional ordination space and the fit was tested by 9999 permutations to investigate the relationships between the major compositional gradients in the mollusc data and known environmental predictors. Generalized additive models (GAMs) were used to estimate which mollusc species fit significantly ($p < 0.05$) into the two-dimensional ordination space, based on the ln-transformed abundances of mollusc species occurring at more than two sites. Those species that were significant according to GAMs were plotted into the ordination diagram. The same distance species-by-sites matrix was subjected to cluster analysis using a beta flexible method with a beta parameter set at a recommended value of –0.25 (Legendre & Legendre 2012). Environmental characteristics and numbers of mollusc species were visualized using box-and-whisker plots to characterize differences between the main clusters. Indicator species analysis (Dufrêne & Legendre 1997) was undertaken to identify species characterizing the main clusters revealed by cluster analysis, according to their relative frequencies and relative average abundances in the clusters.

To test what proportion of the overall variation in mollusc data could be explained by known environmental predictors, we conducted a distance-based redundancy analysis (distance-based RDA) of the distance species-by-sites matrix calculated by the Bray-Curtis dissimilarity index (Legendre & Anderson 1999). An automatic forward selection procedure and permutation test of 4999 permutations were carried out to identify a minimum subset of environmental predictors explaining a significant proportion of variation in the mollusc data. Variables were sequentially selected according to their contributions to the explained variation, and evaluated by comparing the AIC of the more complex model with the AIC of the simpler model. Procrustes analysis (Gower 1975) with a test of 9999 permutations (Jackson 1995) was used to test the similarity between the results of direct and indirect ordinations. Analogous to the mollusc data, vegetation data were also subjected to MDS using the Bray-Curtis dissimilarity index and further examined by GAMs in order to determine which plant species fit significantly ($p < 0.05$) into the two-dimensional ordination space, based on the ln-transformed percentage plant covers of spe-

Table 1. Descriptive statistics for the five variables used in the analyses and the numbers of mollusc species found at all 40 sampled sites.

	Mean	SD	Minimum	Lower quartile	Median	Upper quartile	Maximum
Water pH	6.4	0.7	4.0	6.1	6.5	6.9	7.7
Water conductivity (µS cm^{-1})	151.8	128.3	29.0	63.8	104.0	229.5	522.0
Aquatic plant cover (%)	13.39	21.7	0	0	3.0	19.0	88.5
Mean January temperature (°C)	–8.1	2.6	–11.0	–9.6	–9.2	–7.4	–0.1
Annual precipitation (mm)	719.2	126.2	549.0	565.8	748.0	775.5	953.0
All mollusc species	6.8	3.1	0	5.8	7.0	9.3	15.0
Land snail species	5.3	3.0	0	4.0	5.0	7.3	13.0
Aquatic mollusc species	1.5	1.2	0	1.0	1.0	2.0	5.0

cies occurring at more than four sites. Those species that were significant according to GAMs were plotted into the ordination diagram of the vegetation MDS in order to demonstrate the range of vegetation types covered in the present study (Appendix 1). Species nomenclature followed Tutin *et al*. (1964–1980) for vascular plants, and Hill *et al*. (2006) for bryophytes. All calculations were carried out in the R program (ver. 2.15.2, R Core Team 2012).

Results

In total, at the 40 study sites we recorded 42 mollusc species (31 land snails, 8 aquatic snails and 3 bivalves; *see* Appendix 2) represented by 3518 individuals. The number of species per site varied from 0 to 15, with a median value of 7 (Table 1).

Results from the MDS indicated that there were two major gradients in the compositional variation of mollusc assemblages, expressed as the first and the second ordination axes, explaining 28.4% and 19.6% of the total variation, respectively. All five explanatory variables were significantly associated with the variation in species composition (Table 2). The first axis was related to water pH and aquatic plant cover, whereas the second axis was related to water conductivity and annual precipitation (Table 2). Mean January temperature was associated with both ordination axes (Table 2). Cluster analysis distinguished 15 sites that could be characterized as topogenous fens from the remaining 21 sites, representing mostly soligenous fens (Fig. 2). Soligenous fens were further divided into a group of mostly lowland fens (cluster 2) and a group of highland fens situated in the Scandinavian Mountains (cluster 3). Cluster 1, i.e. topogenous fens, had low water pH and water conductivity values, a high percentage cover of aquatic plant species and a rich aquatic mollusc fauna (Fig. 3). *Pisidium obtusale* and *Vertigo lilljeborgi* were identified as indicator species for this cluster (Table 3 and Fig. 4), and several acidotolerant molluscs with an affinity for strongly waterlogged sites, such as *Galba truncatula*, *Pisidium casertanum* and *Succinea putris*, occurred with the highest frequency at sites in the first cluster as well (Appendix 2). Cluster 2, i.e. soligenous lowland fens, was characterized by the highest water conductivity values, the lowest annual precipitation and the richest land snail fauna (Fig. 3). Several land snails of various habitat preferences were identified as indicator species for this cluster (Table 3). The highest indicator values were obtained for *Cochlicopa lubrica* and *Nesovitrea hammonis* (Table 3 and Fig. 4). Sites in cluster 3, i.e. soligenous highland fens, had, in contrast to the previous cluster, lower water conductivity, January temperature and mollusc species richness, as well as higher annual precipitation (Fig. 3). These sites harbored cold-adapted land snail species typical of northern Europe, such as *Columella columella*, *Vertigo genesii* and *Vertigo modesta* (Figs. 2 and 4). *Columella columella* and *Nesovitrea petronella* were indicator species for this cluster, along with *V. genesii*, whose

Table 2. Regression coefficients between site scores on the first two axes of the mollusc metric multidimensional scaling (MDS) and five explanatory variables, the fit of each factor into the ordination space (the variation in the factor explained by site scores on the first two mollusc MDS axes in the multiple linear regression, and the significance (*p*) of the result based on 9999 permutations. Eigenvalues: first axis 2.778 and second axis 1.921, explaining 28.4% and 19.6% of the total variation in species data, respectively.

	Regression coefficients		r^2	*p*
	Mollusc MDS 1	Mollusc MDS 2		
Water pH	–0.871	–0.491	0.3625	0.0003
Water conductivity	–0.310	–0.951	0.5701	0.0001
Aquatic plant cover	0.894	0.447	0.3708	0.0004
Mean January temperature	0.644	–0.764	0.3426	0.0004
Annual precipitation	0.492	0.871	0.3761	0.0009

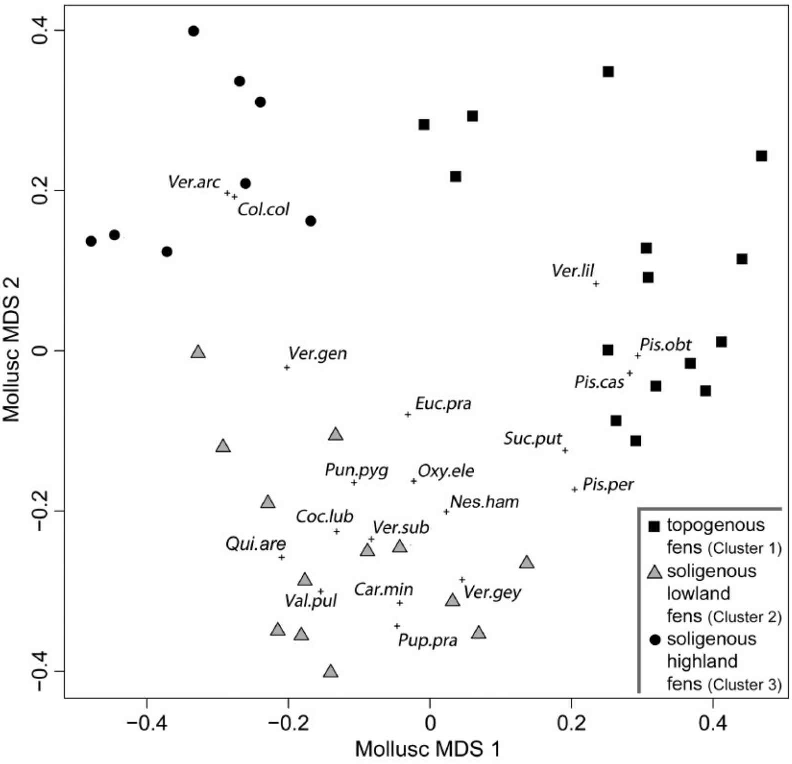

Fig. 2. MDS ordination plot of 36 mollusc assemblages with the positions of samples and species along the first and the second axes. Only species occurring at more than two sites and fitting significantly into the ordination space according to GAMs (*see* Methods for details) are shown. The classification of sites into three clusters corresponds to the results of cluster analysis. For species abbreviations *see* Appendix 1.

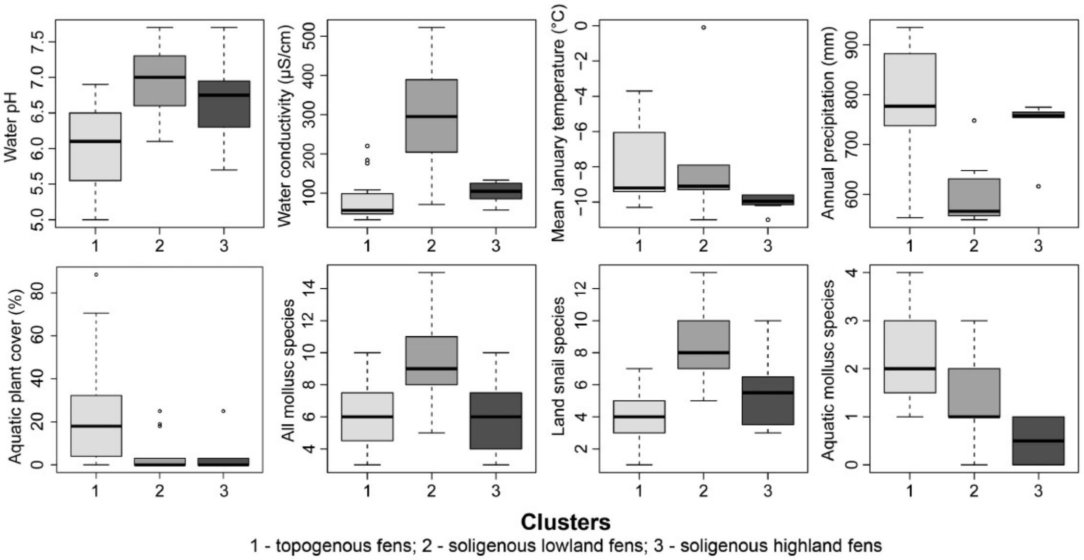

Fig. 3. Differences between the three main clusters revealed by cluster analysis in terms of explanatory variables and numbers of mollusc species. Each box-and-whisker shows median value, lower and upper quartile, minimum, maximum and outliers.

indicator value was also high for sites in cluster 2 as well (Table 3). Soligenous sites from clusters 2 and 3 had relatively high water pH values, low aquatic plant cover and poor occurrence of aquatic mollusc species as compared with topogenous sites in cluster 1 (Fig. 3).

Four standard fen types, which could be distinguished along the gradient of mineral rich-

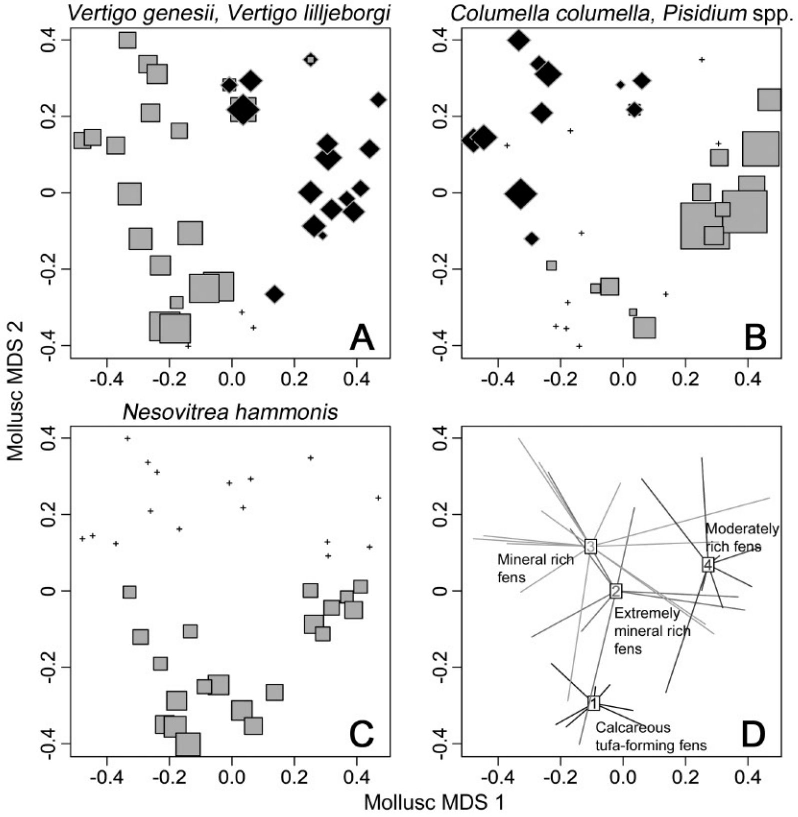

Fig. 4. Occurrence of selected mollusc species in 36 malacologically positive study sites arranged along the first and second axes of the mollusc MDS. The size of each symbol reflects the species' abundance at each site. (**A**) Grey squares = *Vertigo genesii*, black diamonds = *Vertigo lilljeborgi*. (**B**) Black diamonds = *Columella columella*, grey squares = *Pisidium* spp. (**C**) Grey squares = *Nesovitrea hammonis*. (**D**) Major fen types defined by vegetation composition visualized as a spider plot in the ordination diagram of mollusc MDS.

ness according to their vegetation composition, were plotted into the ordination diagram of the MDS to inspect the distribution of sites based on their mineral richness (Fig. 4D). Sites from

Table 3. Results of the indicator species analysis. For mollusc species with a significant indicator value ($p < 0.05$) in any of the three clusters revealed by cluster analysis, we show: indicator values based on relative frequencies and relative ln-transformed average abundances of species in the clusters (the values in boldface indicate the cluster in which the species has a maximum indicator value), and significance (p) of the result.

Species name	Indicator value			p
	Cluster 1: topogenous fens	Cluster 2: soligenous lowland fens	Cluster 3: soligenous highland fens	
Cochlicopa lubrica	0.00	**0.71**	0.11	0.001
Columella columella	0.02	0.02	**0.56**	0.003
Euconulus praticola	0.17	**0.44**	0.23	0.032
Oxyloma elegans	0.03	**0.50**	0.00	0.004
Nesovitrea hammonis	0.13	**0.72**	0.00	0.001
Nesovitrea petronella	0.06	0.07	**0.42**	0.013
Pisidium obtusale	**0.47**	0.00	0.00	0.002
Quickella arenaria	0.00	**0.38**	0.00	0.009
Vallonia pulchella	0.00	**0.46**	0.00	0.002
Vertigo genesii	0.01	0.33	**0.46**	0.024
Vertigo geyeri	0.00	**0.29**	0.00	0.037
Vertigo lilljeborgi	**0.85**	0.00	0.02	0.001
Vertigo substriata	0.01	**0.42**	0.01	0.008

opposite ends of the mineral richness gradient, i.e. calcareous tufa-forming fens and moderately rich *Sphagnum* fens (note that poor *Sphagnum* fens did not contain any molluscs), were separated from each other, thus representing clearly defined groups with relatively consistent species composition. In contrast, sites with intermediate calcium richness were rather scattered throughout the ordination diagram (Fig. 4D).

To investigate the importance of known environmental predictors with respect to the composition of the mollusc assemblages, we constructed a model in a distance-based RDA, comprising significant variables selected by an automatic forward selection procedure. All five environmental variables explained significant proportions of the overall variation in data about mollusc species composition. The highest effects were obtained for water conductivity (13.38%) and mean January temperature (12.53%), followed by aquatic plant cover, water pH and annual precipitation (Table 4). All the significant predictors together explained 42.78% of the overall variation. When plotted into the ordination diagram, the distribution of the sites and the three main clusters along the first two axes of the distance-based RDA closely resembled the pattern revealed by the MDS (cf. Figs. 2 and 5). Procrustes analysis confirmed a strong and significant correlation between the configurations of samples in the ordination spaces of the MDS and distance-based RDA (Procrustes $R = 0.839$, $p << 0.001$), indicating that we selected those explanatory variables (Table 4) that indeed determine compositional variation in Scandinavian fen mollusc assemblages, and that we did not fail to detect any important environmental factor.

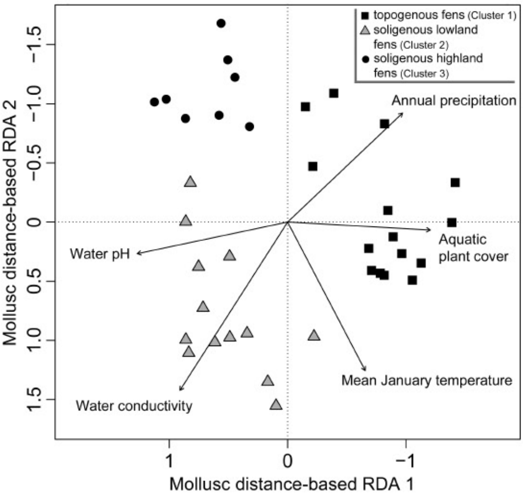

Fig. 5. Distance-based RDA ordination plot of 36 mollusc assemblages with the positions of samples along the first and second axes, together with explanatory variables contributing significantly to the explained variation in mollusc data according to forward selection with 4999 permutations (Table 4). The classification of sites into three clusters corresponds to the results of the cluster analysis.

Discussion

Interpretation of major gradients

Hydrology of the studied sites, expressed as the aquatic plant cover and reflecting the transition from soligenous to topogenous fens, was the best predictor of the main compositional variation in mollusc assemblages (Table 2 and Fig. 2). Aquatic plant species were confined to waterlogged fens on flat surfaces, and thus their percentage cover steeply dropped from topogenous towards soligenous fens (Fig. 3). By analogy, the ecological optima for all aquatic and strongly hygrophilous mollusc species were placed on the right-hand side of the ordination diagram, i.e. in topogenous fens (Fig. 2). Relating water pH to the hydrological gradient (Table 2) may seem ambiguous, considering that water pH usually

Table 4. Percentage variation in mollusc assemblages in 36 studied fens explained by each environmental variable in a distance-based RDA model (the pure effect of each variable is shown). Forward selection and permutation test with 4999 permutations were used to test the significance of the explained variation. The sum of the variation explained by the model accounted for 42.78% of the overall variation in the species data.

	Percentage of variation explained (pure effects)	*p*
Water conductivity	13.38	< 0.001
Mean January temperature	12.53	< 0.001
Aquatic plant cover	7.99	0.001
Water pH	4.88	0.005
Annual precipitation	4.00	0.016

approximates mineral richness gradient in fens (e.g., Gerdol 1995, Økland *et al*. 2001, Hájková *et al*. 2004) and correlates with water conductivity, which was, however, tightly associated with the second axis of the MDS (Table 2). Apparently, associating water pH with site's calcium richness may be misleading in particular cases, as water pH also reflects other environmental attributes of fen ecosystems (Vitt *et al*. 1995, Horsák 2006). For instance, pH increases with increasing water movement (Sparling 1966, Tahvanainen & Tuomaala 2003), which explains why sloping soligenous fens in cluster 3 had relatively high water pH (Fig. 3), independent of their calcium richness as estimated by water conductivity and vegetation composition.

The second axis of the MDS reflected a complex gradient of calcium richness and climatic conditions (Table 2). A strong negative relation between water conductivity and annual precipitation was mainly promoted by a distinction between the most calcareous fens, located in lowland areas with the lowest precipitation, and other less calcareous fens, located in areas with a more humid climate (Fig. 3). We do not expect precipitation affect mollusc assemblages directly, but rather by means of changes in fen water chemistry, as it has been documented that excessive rainfall lowers calcium concentrations due to dilution of upwelling groundwater by rainwater (Almendinger & Leete 1998, Hájek *et al*. 2002). Precipitation may further influence water table dynamics and hereby determine whether either peat mosses, or brown mosses predominate in the vegetation layer (Sekulová *et al*. 2013). These structural differences affect mollusc composition as well (Hájek *et al*. 2006).

Mean January temperature decreased along the second axis of the MDS, but the relation was not particularly strong (Table 2). Temperatures occurring during the coldest period of the year most likely represent a major factor limiting the distribution of terrestrial gastropods in northern Europe (Andersen & Halvorsen 1984, Hausdorf & Hennig 2003); however, we assume that a substantial number of the recorded mollusc species possessed rather broad climatic tolerance, and their occurrence was therefore more limited by the distribution of calcareous sedimentary bedrock than by climatic conditions. For instance, Nilsson (1987) documented a fen assemblage of 23 species, mostly identical to those in the present study, in a calcareous fen on dolomite bedrock 200 km north of the Arctic Circle (68°N). Thus, we suggest that calcium richness is the primary driving force of the compositional gradient expressed by the second axis of the MDS (Table 2), and temperature determines the presence or absence of several stenothermic species along the gradient. It should also be noted that the mean January temperature was chosen to represent a group of highly correlated climatic variables, so its effect on the studied assemblage composition could not, therefore, be quantified precisely. Thus, the January temperature could act as a proxy for more complex characteristics related to climate, such as the lengths of the dormant or active periods, the beginning of the breeding season, etc.

In direct ordination, water conductivity explained best the overall variation in the mollusc data (Table 4). Such a result may be ascribed to associations between conductivity and both major compositional gradients (Table 2). Although tightly linked to the second axis of the MDS, conductivity changed along the gradient of hydrology as well, as calcium is more readily extracted from bedrock on sloping surfaces of soligenous fens (Valovirta 1968). Evidently, the calcium-rich sites were soligenous, whereas the calcium-poor sites were topogenous (Fig. 3).

Compositional gradients and comparison with earlier studies

It is generally recognized that molluscs depend on calcium for their shell formation and reproduction (Wäreborn 1970, 1979), and that calcium richness accounts for the major compositional changes in mollusc assemblages in a variety of terrestrial habitats (e.g., Hylander *et al*. 2005, Sulikowska-Drozd & Horsák 2007, Juřičková *et al*. 2008). Likewise, in studies of spring fens in the Western Carpathians (Horsák & Hájek 2003) and Bulgaria (Horsák *et al*. 2011), calcium richness (or water conductivity as its proxy) was found to tightly correlate with the main direction of mollusc compositional variation. However, in central-European regions, the variation in calcium content often appears to be greater than the variation in other environmental factors, such as hydrology and climatic conditions. For instance, in Slovakia, well-preserved fens are almost entirely restricted to the Carpathian Mountains, whereas lowland fens have been mostly drained for agricultural purposes (Grootjans *et al.* 2013). Thus, there is great variation in sloping soligenous spring fens as compared with that of topogenous fens and, consequently, there are hardly any mollusc species associated exclusively with topogenous fens. In contrast, fens on the eastern Polish lowlands, developing on gentle slopes or plateaus of undulating post-glacial terrain, vary considerably in their hydrology (Wolejko *et al.* 2005) and the water regime was also found to explain the major compositional turnover of Polish fen mollusc fauna (Schenková *et al.* 2014).

Although multivariate statistics have never been applied to studies of mollusc assemblages in Scandinavian fens, earlier inspections of fens in the Torneträsk area (northern Sweden) (Nilsson 1987) and NP Dovrefjell (central Norway) (Pokryszko 1993) documented well-pronounced differences between topogenous and soligenous fens. Our results confirm that this pattern can be extrapolated to a larger geographical scale (Fig. 2) and, although we covered the entire mineral richness gradient of groundwater-fed fens (sensu Hájek *et al.* 2006), hydrology seemed to be the factor that best explained the major compositional gradient in Scandinavian mollusc assemblages (Table 2). Wide variation in species composition and its independence from calcium richness was particularly evident in intermediately mineral-rich sites, i.e. extremely mineral-rich fens and mineral-rich *Sphagnum* fens, which were scattered throughout the ordination diagram of the MDS (Fig. 4D). We presume that at sites of intermediate mineral richness, both hydrology and climate represent environmental filters determining mollusc composition. It is known that terrestrial snail species possess different ecological optima along the moisture gradient (Čejka & Hamerlík 2009, Hettenbergerová *et al.* 2013), and in northern Europe the same also holds true for climatic conditions, as there are several cold-adapted species preferentially inhabiting sites in relatively extreme environments (Solhøy 1976, Pokryszko 1993). In the Western Carpathians, by contrast, there is no analogous species turnover towards climatically harsher sites, as most species are thermophilous and restricted to sites with higher winter temperatures (Horsák & Cernohorsky 2008). Furthermore, the coldest regions are usually too acidic to support the occurrence of land snail species (Sekulová *et al.* 2013).

Species composition in Scandinavian fens

Following the gradient of hydrology, several mollusc species were tightly associated with either topogenous or soligenous fens. *Vertigo lilljeborgi* was found to represent a reliable indicator of topogenous fens (Table 3), presumably because of its strong preference for both mineral-poor and substantially waterlogged sites (e.g., von Proschwitz 2003, Schenková & Horsák 2013). Nilsson (1987) stated that *V. lilljeborgi* replaces *V. genesii* in topogenous fens, and such vicariance was also suggested by the present results (Fig. 4A). Similarly, Pokryszko (1993) showed that *V. lilljeborgi* was the most constant species in topogenous fens. An analogous affinity to topogenous fens was also observed for *Pisidium obtusale* (Table 3 and Fig. 4B), an exclusive inhabitant of stagnant water bodies lacking moving water (Meier-Brook 1975). Both Nilsson (1987) and Pokryszko (1993) indicated that *Columella columella* and *V. genesii* were species restricted to soligenous fens, which is in agreement with the present results (Table 3 and Fig. 4A). However, our findings do not concur with the observation of Pokryszko (1993) that *V. genesii* reaches its greatest abundances above 1000 m a.s.l., as it occurred along the whole altitudinal range of soligenous fens and was most abundant at lowland calcareous sites with tufa precipitation (Appendix 2). Apparently, sufficient calcium supply represents a factor limiting the occurrence of *V. genesii* in Scandinavia (von Proschwitz 2003), and Pokryszko (1993) did not sample any such calcareous sites similar to those in the present study. *Columella columella* was very clearly confined to higher altitudes than *V. genesii* (Fig. 4B), as it was never found below 700 m a.s.l. Along with *Vertigo modesta*, *C. columella* represented the only truly Arctic-Alpine species (Solhøy 1976) within our dataset. In soligenous lowland fens, the highest indicator values were obtained for *Cochlicopa lubrica* and *Nesovitrea hammonis* (Table 3). Such results may seem unexpected, considering that the soligenous lowland fens were on average very calcareous and these species are considered to have their ecological optima at sites of intermediate mineral richness (*C. lubrica*), or even shifted towards acid sites (*N. hammonis*; Martin & Sommer 2004, Horsák 2006). However, it has been previously observed that these species become more stenoecious and more calcium demanding as they approach their distribution limits in northern Europe (Andersen & Halvorsen 1984). At least for *N. hammonis*, such a pattern may be related to selective predation by *Aegopinella* species (Mordan 1977). In the Western Carpathians, where *Aegopinella* species frequently occur in mineral-rich fens, *N. hammonis* is virtually absent from these habitats (Horsák & Cernohorsky 2008). By contrast, in Scandinavia, *Aegopinella* species are absent or restricted to southern regions (Kerney *et al*. 1983) and *N. hammonis* is the most abundant in calcareous tufa-forming fens (Fig. 4C). Among the indicators of soligenous lowland fens, there was only one fen specialist, i.e. *Vertigo geyeri*. This supports observations of Solhøy (1976) and Pokryszko (1993), who described *V. geyeri* as a species limited to lower latitudes in Scandinavia. It also agrees with the recent finding of numerous populations of *V. geyeri* in well-preserved fens throughout central Europe, even in relatively warm lowland regions (Schenková *et al*. 2012).

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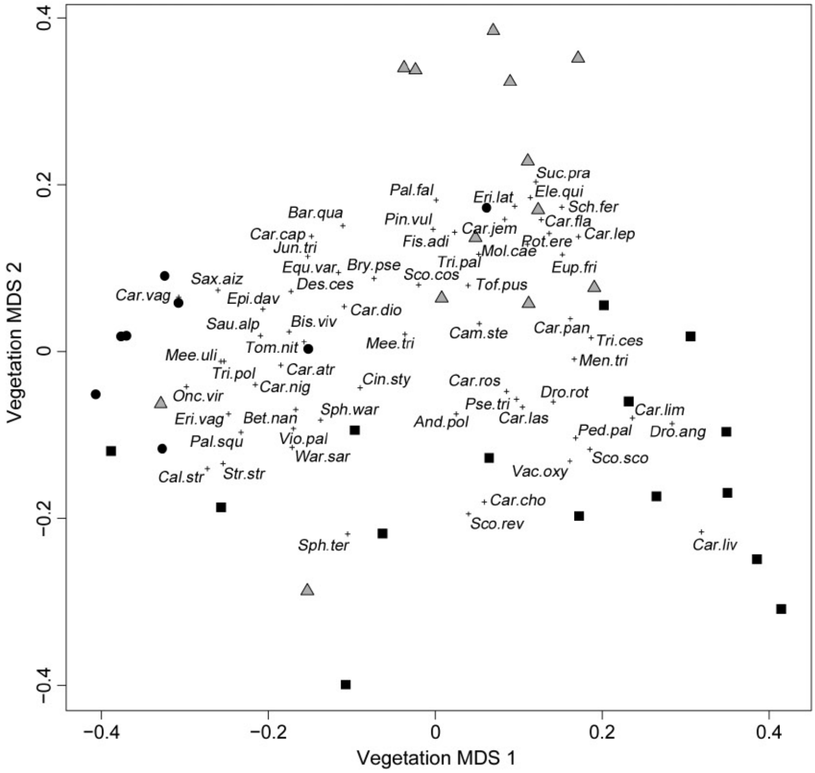

Appendix 1. MDS ordination plot of 36 vegetation relevés with the positions of samples and plant species along the first and second axes. Only species occurring at more than four sites and fitting significantly into the ordination space according to GAMs (*see* Methods for details) are shown. The classification of sites into three clusters corresponds to the results of the cluster analysis of mollusc assemblages (*see* Fig. 2). Species abbreviations: *And.pol = Andromeda polifolia, Bar.qua = Barbilophozia quadriloba, Bet.nan = Betula nana, Bis.viv = Bistorta vivipara, Bry. pse = Bryum pseudotriquetrum, Cal.str = Calamagrostis stricta, Cam.ste = Campylium stellatum, Car.atr = Carex atrofusca, Car.cap = Carex capillaris, Car.dio = Carex dioica, Car.fla = Carex flava, Car.cho = Carex chordorrhiza, Car.jem = Carex jemtlandica, Car.las = Carex lasiocarpa, Car.lep = Carex lepidocarpa, Car.lim = Carex limosa, Car.liv = Carex livida, Car.nig = Carex nigra, Car.pan = Carex panicea, Car.ros = Carex rostrata, Car.vag = Carex vaginata, Cat.nig = Catoscopium nigritum, Cin.sty = Cinclidium stygium, Des.ces = Deschampsia cespitosa, Dro. ang = Drosera anglica, Dro.rot = Drosera rotundifolia, Ele.qui = Eleocharis quinqueflora, Epi.dav = Epilobium davuricum, Equ.var = Equisetum variegatum, Eri.lat = Eriophorum latifolium, Eri.vag = Eriophorum vaginatum, Eup.fri = Euphrasia frigida, Fis.adi = Fissidens adianthoides, Jun.tri = Juncus triglumis, Mee.tri = Meesia triquetra, Mee.uli = Meesia uliginosa, Men.tri = Menyanthes trifoliata, Mol.cae = Molinia caerulea, Onc.vir = Oncophorus virens, Pal.squ = Paludella squarrosa, Pal.fal = Palustriella falcata, Ped.pal = Pedicularis palustris, Pin.vul = Pinguicula vulgaris, Pot.ere = Potentilla erecta, Pse.tri = Pseudocalliergon trifarium, Sau.alp = Saussurea alpina, Sax.aiz = Saxifraga aizoides, Sco.cos = Scorpidium cossoni, Sco.rev = Scorpidium revolvens, Sco.sco = Scorpidium scorpioides, Sch. fer = Schoenus ferrugineus, Sph.con = Sphagnum contortum, Sph.ter = Sphagnum teres, Sph.war = Sphagnum warnstorfii, Str.str = Straminergon stramineum, Suc.pra = Succisa pratensis, Tof.pus = Tofieldia pusilla, Tom.nit = Tomentypnum nitens, Tri.pal = Triglochin palustre, Tric.ces = Trichophorum cespitosum, Tri.pol = Tritomaria polita, Vac.oxy = Vaccinium oxycoccos, Vio.pal = Viola palustris, War.sar = Warnstorfia sarmentosa.*

Appendix 2. List of all recorded mollusc species. For each recorded species are shown: full species name; Freq. = frequency, i.e. number of sites in a particular cluster with the species present; Abund. = mean abundance of the species at those sites in a particular cluster with the species present; *n* = number of sites where species occurs. Species are listed alphabetically. Cluster 1: topogenous fens; Cluster 2: soligenous lowland fens; Cluster 3: soligenous highland fens. Abbreviations are shown for species plotted in the ordination diagram of the MDS (Fig. 2). Values of frequency and mean abundance are not stated for species that were excluded from the statistical analyses (*see* Material and methods).

Cluster		1		2		3		*n*
Number of sites in cluster		15		13		8		
Species name	Abbreviation	Freq.	Abund.	Freq.	Abund.	Freq.	Abund.	
Aegopinella pura		0	0	2	2.0	0	0	2
Arianta arbustorum		–	–	–	–	–	–	1
Carychium minimum	*Car.min*	0	0	3	27.0	0	0	3
Cochlicopa lubrica	*Coc.lub*	1	1.0	12	14.3	4	2.5	17
Columella columella	*Col.col*	3	3.0	2	18.5	6	11.8	11
Columella edentula		0	0	3	3.3	1	1.0	4
Discus ruderatus		–	–	–	–	–	–	1
Euconulus fulvus		0	0	2	3.0	0	0	2
Euconulus praticola	*Euc.pra*	10	5.3	12	13.2	7	3.0	29
Fruticicola fruticum		–	–	–	–	–	–	1
Oxyloma elegans	*Oxy.ele*	2	17.0	8	20.8	0	0	10
Nesovitrea hammonis	*Nes.ham*	7	7.6	13	13.0	0	0	21
Nesovitrea petronella		4	4.0	4	4.8	6	3.8	14
Punctum pygmaeum	*Pun.pyg*	1	1.0	4	2.5	3	1.0	8
Pupilla pratensis	*Pup.pra*	0	0	3	15.3	0	0	3
Quickella arenaria	*Qui.are*	0	0	5	12.6	0	0	5
Succinea putris	*Suc.put*	7	2.9	3	6.7	0	0	10
Vallonia pulchella	*Val.pul*	0	0	6	9.3	0	0	6
Vertigo angustior		0	0	1	1.0	0	0	1
Vertigo antivertigo		0	0	2	132.5	0	0	2
Vertigo modesta	*Ver.mod*	1	1.0	0	0	2	2.5	3
Vertigo genesii	*Ver.gen*	3	15.3	9	54.1	8	11.0	20
Vertigo geyeri	*Ver.gey*	1	1.0	4	26.0	0	0	5
Vertigo lilljeborgi	*Ver.lil*	15	8.2	1	6.0	2	1.5	18
Vertigo pygmaea		0	0	1	60	0	0	1
Vertigo substriata	*Ver.sub*	1	5.0	7	4.1	1	1.0	9
Vitrea contracta		0	0	1	12.0	0	0	1
Vitrea crystallina		0	0	1	16.0	0	0	1
Vitrina pellucida		0	0	0	0	1	1.0	1
Slugs								
Arion fuscus		–	–	–	–	–	–	3
Deroceras laeve		–	–	–	–	–	–	2
Aquatic snails								0
Anisus leucostoma		1	1.0	0	0	0	0	1
Anisus cf. *spirorbis*		–	–	–	–	–	–	1
Bathyomphalus contortus		2	3.5	0	0	0	0	2
Galba truncatula		14	17.7	9	24.0	4	13.3	27
Gyraulus acronicus		2	3.0	0	0	0	0	2
Radix labiata		–	–	–	–	–	–	1
Stagnicola fuscus		–	–	–	–	–	–	1
Valvata cristata		0	0	2	1.5	0	0	2
Bivalves								
Pisidium casertanum	*Pis.cas*	6	23.7	3	5.0	0	0	9
Pisidium obtusale	*Pis.obt*	7	26.6	0	0	0	0	7
Pisidium personatum	*Pis.per*	1	9.0	2	11.5	0	0	3