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HETEROGENEITY OF MOLLUSC COMMUNITIES BETWEEN AND WITHIN FOREST FRAGMENTS IN A MUCH MODIFIED FLOODPLAIN LANDSCAPE

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Abstract: The Rhine floodplain is much modified by human land use. What used to be the hardwood zone of the large floodplain nowadays holds only a few isolated, recent (mostly < 60 years) forest patches. The aim of the study was to check if the circumstances favoured homogeneity of the snail communities, usually observed within floodplains, or if heterogeneity prevailed. We inventoried molluscs (presence-absence) in 21 sites within and 18 sites adjacent to a stretch of the Lower Rhine floodplain (total 39 sites). Communities from eight of the sites were quantitatively sampled for within-site analyses. Species turnover occurred with distance from the Rhine, partially along with lateral habitat turnover. Introduced species mainly occurred in young forests, in similar numbers within and beyond the floodplain. Old forests beyond the floodplain had a small number of introduced species and a small between-site heterogeneity, suggesting strong habitat filters (selection of species by environmental conditions) which might be associated with the prevalence of detritus-derived food. The occasionally flooded sites had the longest scatter along the first NMDS axis, indicating a local differentiation without a longitudinal gradient. The young forests that were occasionally inundated and those that were never flooded shared many species, resulting in the lack of significant differences based on the presence-absence data. The damp, regularly flooded forests differed from the occasionally inundated ones and the ones beyond the floodplain. Flooding introduces drift material and species to the sites. The drift is associated with an initially increased within-site heterogeneity. During the years after the flooding event, the within-site homogeneity of communities increases (suggesting local selection of species) in tandem with an increase in the between-site differences (local selection plus stochastic extinctions).

Key words: afforestation, drift dispersal, habitat fragmentation, introduced species, land use, snail fauna

INTRODUCTION

Floodplains are biodiversity hotspots but they are often densely populated and, consequently, subject to significant land cover changes along with hydrological degradation. Schnitzler (1994) regards the Rhine and its floodplain as the probably most severely destroyed riparian landscape in Europe, with many implications for further conservation of the floodplains' hardwood forests. As in other regions, river regulation, ground water depletion and forest fragmentation are major issues, but they are very pronounced along this large river that has been a major travel and trade thoroughfare for at least two millennia. Preservation and reactivation of the few remaining floodplain fragments are priorities for the environmental protection actions along the Rhine (e.g. LUBW 2010).

Mollusc communities vary among forests of different inundation frequency (e.g. Körnig 1966, Kerkhoff 1989, Horáčková et al. 2014), and have been suggested as indicators of duration of inundation episodes (e.g. Follner & Henle 2006). Gastropods have been shown to respond to floodplain degradation within a few years, with euryoecious species invading, and species with a high moisture requirements disappearing from floodplain forests which lose contact with the ground water table (e.g. Čejka 1997). Habitat changes in floodplains bring about impoverishment of gastropod communities (e.g. Horáčková et al. 2014). Already Steusloff (1950) noted that suitable habitats for snail groups such as door snails had almost completely disappeared in the hostile matrix of the anthropogenic agricultural steppe on the Lower Rhine. According to Geyer & le Roi (1912) only four clausiliid species can be found in the lowlands of the Rhineland: *Cochlodina laminata, Clausilia bidentata, Alinda biplicata* and *Laciniaria plicata*. Hence, one aim of our study was to check if the intensive land use had further depleted clausiliid richness during the last century. Consequently, we focussed on potential clausiliid habitats, namely forests and forest-like vegetation.

Floodplain habitats are considered to have an increased connectivity due to flooding. Passive transport by drift is one of the well-recognised pathways of gastropod dispersal (Dörge et al. 1999). Flooding enhances richness through passive dispersal, but the positive effect of drift on local species richness is of short duration (Ilg et al. 2009). The temporary character of the effect might be associated with habitat filtering, resulting in reduced or hampered colonisation success of maladapted species, but also with local effects of species interactions (Wilson 1992).

Continued connectivity due to flooding can compensate for local extinctions and favour similarity among communities along the floodplain. The floodplain mollusc fauna has indeed been reported to be more homogeneous through space than that of the adjacent landscape (Myšák & Horsák 2011). This increased homogeneity, however, has been found for a smaller river in an altered, but not that much transformed floodplain landscape. It remains unclear if drift enhances homogeneity of gastropod communities under much modified conditions as well. Habitat fragmentation, for example, limits plant seed dispersal by drift (e.g. Markwith et al. 2014).

Because of drift effect, we hypothesised that regularly inundated sites should be much richer in species than occasionally inundated sites, or sites beyond the floodplain. The presence of non-native species might be an indicator of passive dispersal and habitat accessibility. Given that passive dispersal is enhanced by flooding and that many non-native taxa utilise river corridors for dispersal (e.g. Thébauld & Debussche 1991, Thomas et al. 2006, Säumel & Kowarik 2010), we expected to find a higher per site richness of introduced gastropods in forest patches within the floodplain than in those beyond the floodplain. Furthermore, we attempted to check if a higher homogeneity of gastropod communities could be achieved within the floodplain under the much modified conditions of the region.

MATERIAL AND METHODS

REGIONAL INVENTORY, SURVEY SITES

Presence-absence data were compiled from 39 localities in the environs of Cologne, Germany (Fig. 1), where a shallow rift valley forms the so-called Cologne embayment through which the Rhine flows. For the sake of simplicity, all the inventory sites are called "forests" although they are subject to severe anthropogenic disturbance and habitat fragmentation. Most tree stands are plantations and too small to buffer edge effects that in the region can extend up to 250 m into the forests (Kappes et al. 2009); some have patches with a canopy closure of only 50–60%. The regional climate is characterised by an Atlantic influence with a tendency towards mild winters, and a comparatively high annual mean temperature (10–12°C) at 600–900 mm annual precipitation (data for 1981–2010; LANUV 2015). The natural vegetation includes mainly willow-dominated stands in the longer and regularly flooded softwood zone, and mixed broadleaved forests mainly with *Fraxinus excelsior, Acer* spp., *Carpinus betulus, Quercus robur, Tilia cordata, Cerasus avium* and occasionally *Fagus sylvatica* in the only briefly and irregularly inundated hardwood zone. The beech marks the transition to the uppermost levels where mesic beech-oak forests grow on more acidic soils (pH usually << 5). However, most of the forest patches originate from afforestation with more or less natural sets of tree species. Some plantations contain alien tree species such as *Quercus palustris* and/or *Q. rubra*. The floodplain can harbour additional forest types such as alder carrs. However, alder carrs require wet soils and are virtually absent because (1) stagnant waters such as oxbows are basically lacking and (2) tributary brooks from the slopes of the Ville Ridge and the Bergisches Land mostly flow through artificial subterranean channels in the densely populated floodplain with intensive agriculture, and with decreasing groundwater levels. To illustrate the potential mollusc composition of alder

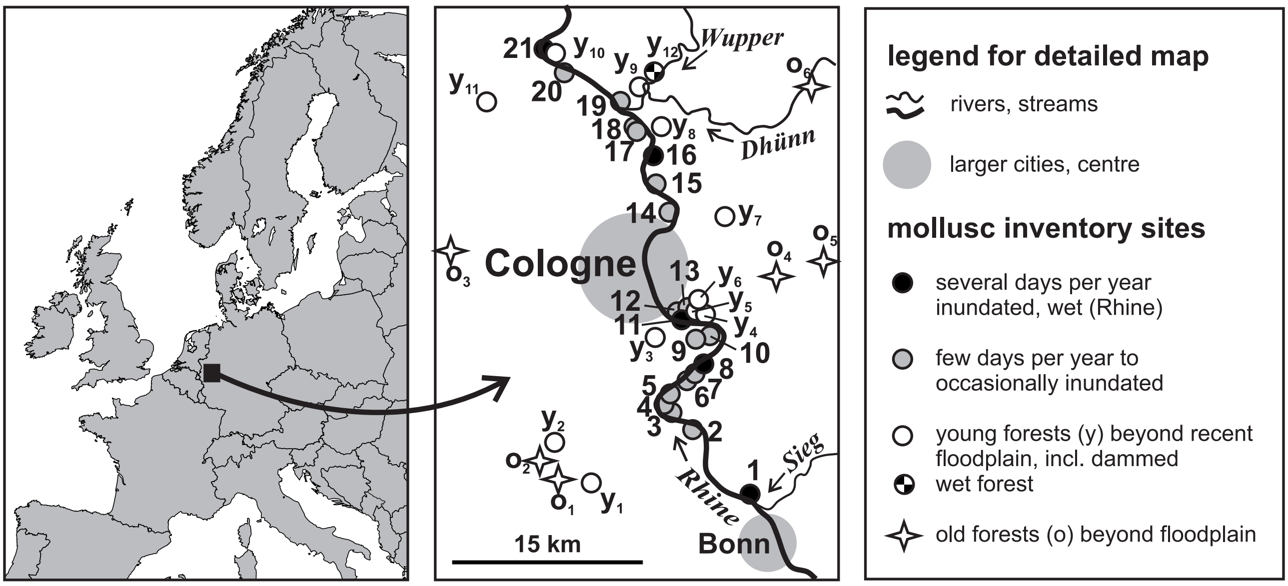

Fig. 1. Location of the mollusc inventory sites. For explanations of forest groups see text

carrs in that region, a forest at the lower stretch of a tributary river was included (*Fraxinus*-dominated interspersed with *Alnus*, site y_{12}) in the study; it receives moisture from a small brook and probably also from local ground water discharge.

The Lower Rhine usually has flood peaks in winter and spring when heavy rains coincide with thaw in the low mountain ranges. In cold water terrestrial gastropods survive for a longer time than in warmer water (KÜNKEL 1930). Nevertheless, summer floods may also occur, though such floods are more typical of the Upper Rhine (SCHNITZLER 1994, BUNDESANSTALT FÜR GEWÄSSERKUNDE 2015). The hardwood zone is thus mostly inundated in winter, but with few exceptions the forests are not flooded on an annual base. The continuing incision of the straightened river into the old floodplain deposits increasingly decouples the hardwood zone from floodplain dynamics.

Several forest types were studied: (1) regularly flooded forests (softwood forest zone, *Salicetum* s.l., black circles in Fig. 1), (2) occasionally flooded forests (≤1 hygrophilous species, hardwood forest zone, *Fraxinetum* s.l., grey circles in Fig. 1), (3) young forests beyond the recent floodplain (white circles in Fig. 1) and (4) old-growth (beech-oak) forests beyond the floodplain (white crosses in Fig. 1). Within class 3, one forest was constantly wet (*Fraxino-Alnetum*) and was thus treated separately (y_{12}).

A square of, or equalling to, 50×50 m, as for example used in forest biodiversity inventories (e.g. FISCHER et al. 2009), was surveyed in each locality, except the eight forests that were quantitatively sampled (see below). These eight forests were searched on two different dates to account for the smaller square. For the presence-absence lists, low vegetation (where present), tree trunks, piles of driftwood, fallen logs, etc. were searched, along with five litres of mixed detritus sample (leaf litter and/or decaying herbs) that were checked for microsnails. Species which could be identified in the field were released. Although most habitats were artificial and their role in biodiversity conservation and metapopulation dynamics is unclear, this proportion might be significant because wooded habitats sustain many snail species, even if these habitats are rare (STEUSLOFF 1950, ANHUT 1977). To reduce a potential bias resulting from passive dispersal (especially of empty shells) by drift, only live individuals and empty shells with fresh-looking periostracum were included in the analysis. The field work was mainly carried out in the growing seasons of 2010 and 2011, the Ville ridge sites were surveyed in 2012 and 2013. Classification of the species as being "introduced" follows the regionalised list in KOBIALKA et al. (2009).

QUANTITATIVE STUDY

Eight of the forest localities were quantitatively sampled. We noted environmental parameters (canopy closure, cover by different vegetation strata, amount of deadwood, pH of topsoil) for each locality to provide more detailed information on the habitats and to facilitate comparisons or meta-analyses.

The forests which were selected for quantitative analysis were sampled in the spring and summer of 2010, with some additional visual sampling in the spring of 2014. We focussed on a square of 20×20 m in each locality, as proposed for forest snail sampling (CAMERON & POKRYSZKO 2005). Species richness (alpha diversity) and abundance were estimated from ground cover samples (decaying herbs and leaf litter) from eight random plots in each of the eight localities. Each plot covered 50×50 cm, or 0.25 m^2; two square metres per locality were sampled. Besides, tree trunks and fallen logs were visually searched for gastropods. These species were added to the species lists of the localities, but not to calculations such as of the Bray-Curtis matrix (see below).

STATISTICS

For the analysis, forests were classified according to the habitat type as specified above. To scrutinise feed-backs from species richness, forests from classes 1 to 3 (non-inundated old-growth forests were excluded) were classified in three categories according to their species richness (<20, 20–24, ≥25 species). The classes were compared using ANOVA with post-hoc test (Tukey HSD for unequal n).

The presence-absence-data were transformed to a Sørensen similarity matrix to depict community similarities between sites using non-metric multidimensional scaling (NMDS). The spatial configuration with the lowest stress value was selected (minimum stress of 0.12 occurred in 21 of 25 runs) and plotted. The more similar the communities of two sites were, the closer their position in the plot. The species composition in the occasionally flooded forests (≤1 hygrophilous species, grey circles in Fig. 1) was then compared with that of the regularly flooded wet forests, and the young and old non-flooded forests. The wet forest y_{12} could not be compared because n = 1 for that habitat type, displaying no heterogeneity, and causing insufficient permutations. For the forest classes, the Sørensen index matrix was used to calculate the multivariate dispersion index (MVDISP). The MVDISP value describes the multivariate variability between replicate samples and hence is a measure of heterogeneity of the community, and reflects Whittaker's (1960) spatial variation in communities between samples, or beta-diversity. The more heterogeneous or homogenous the replicates of a given class are, the higher or lower the MVDISP value of that class, respectively. Increases in heterogeneity often derive from stochastic changes in the species composition of samples which are caused by habitat stress such as physical disturbance or pollution (Warwick & Clarke 1993). Multivariate dispersion is a sensitive metric for environmental impact assessment (e.g., Bevilacqua et al. 2012).

The MVDISP value is independent from the actual species composition. To test compositional differences between the three major forest classes, group similarity and overlap were quantified from the Sørensen matrix with the analysis of similarity procedure with 999 permutations, where possible (ANOSIM, in Primer 5). Similar analyses were performed for within-site heterogeneity in the eight quantitatively surveyed forests. Here, a Bray-Curtis similarity matrix was calculated from the log(x+1)-transformed data from the eight replicates (n = 64 in total). The matrix was then used to calculate the MVDISP values and to perform the ANOSIM.

RESULTS

TARGET TAXA RETRIEVAL

We were able to retrieve all four clausiliid species that had been mentioned for the floodplain a century ago. *Alinda biplicata, Cochlodina laminata, Laciniaria plicata,* and *Clausilia bidentata* were observed in 20, 13, two and one of the 21 floodplain sites, respectively (Table 1). In addition, *Macrogastra lineolata* was found in the floodplain (one site). The richest sites in terms of Clausiliidae had four species, with one site located in the floodplain and thus receiving drift input (site 7) and one site being a wet forest on calcium-rich soil, located outside the floodplain (site y_{12}).

SPECIES RICHNESS

In total, 73 mollusc species were found (Table 1). The maximum species richness was 33 and 49 taxa per site (sites 21 and y_{12}, respectively), whereas the minimum value was 15 (sites 6, 15 and 20). The forest type had no significant effect on the species richness in the sites. The old-growth forests and young forests harboured 20.3 ± 4.0 and 21.9 ± 3.5 species per site, respectively (mean and standard deviation). The occasionally flooded forests held 21.0 ± 4.8, and the wet regularly flooded forests 26.4 ± 4.8 species per site. Although the latter had a somewhat higher species richness, a lack of difference could not be rejected (ANOVA: F = 2.3; p = 0.097, adjusted R^2 = 0.094).

INTRODUCED SPECIES

Introduced species can be viewed as general indicators of habitat disturbance and dispersal into habitats. Out of the 73 species, five species (6.8%) are regarded as introduced. The maximum richness of alien species was three per site (sites 12, 13, 14, 19 and y_7). The forest type influenced the occurrence of introduced species: the old-growth forests had significantly fewer introduced species, in both absolute and relative terms (Fig. 2). A prominent example of the forest class specificity is the invasive slug *Arion lusitanicus* auct. non Mabille which was found in all

Table 1. Species (in alphabetical order) from the inventory sites along the Lower Rhine. For localities see Fig. 1. a – affinity to aquatic habitats: w – aquatic, h – highly hygrophilous; i – introduced according to the regionalised list (Kobialka et al. 2009). Note that forest y_{12} (*Fraxino-Alnetum*) differs from the other young forests in hydrology

Species	a	i	Floodplain		Non-floodplain	
			Salicetum s.l.	*Fraxinetum* s.l.	Young (y)	Old (o)
Acanthinula aculeata (O. F. Müller, 1774)			1,21	2,4,5,9,12–14,17–19	1–3,5–7,9,11,12	1–5
Aegopinella nitidula (Draparnaud, 1805)			1,11,21	2–7,9,10,12–14,17–20	1–12	1–5
Aegopinella pura (Alder, 1830)			–	–	2,6,11,12	5
Alinda biplicata (Montagu, 1803)			1,8,16,21	2–7,9,10,12–15,17–20	1,3–12	–
Arianta arbustorum (Linnaeus, 1758)			1	17	10,12	–
Arion distinctus J. Mabille, 1868			1,8,16,21	2–7,9,10,12–14,18–20	1–12	–
Arion fuscus (O. F. Müller, 1774)			1	4,9,17	3,6,11,12	1–3,5,6
Arion hortenis A. Férussac, 1819			–	4,13	3–5,8	–
Arion intermedius Normand, 1852			–	4,9,17	1,2,6,9–12	1–6
Arion lusitanicus auct. non J. Mabille, 1868		i	1,8,11,16,21	2–7,9,10,12–15,17–20	1–12	4
Arion rufus (Linnaeus, 1758)			–	–	–	1–6
Arion silvaticus Lohmander, 1937			1,8,21	2,4,5,9,17,19	1–3,6,8,10–12	1–6
Arion subfuscus (Draparnaud, 1805)			–	–	–	2–4,6
Boettgerilla pallens Simroth, 1912			8,21	2–5,9,12–14,17–19	1–8,11,12	2–4,6
Carychium minimum O. F. Müller, 1774	h		11,16	–	12	–
Carychium tridentatum (Risso, 1826)			1,8,11,16,21	4,9,12,14,17–19	1–4,6,7,9,11,12	2–4
Cecilioides acicula (O. F. Müller, 1774)			–	3	4	–
Cepaea hortensis (O. F. Müller, 1774)			21	4,7,10,12,13,17,19,20	2,3,6,8–12	3
Cepaea nemoralis (Linnaeus, 1758)			1,8,11,16,21	2–7,9,10,12–15,18–20	1,3–5,7–9,12	–
Clausilia bidentata (Strøm, 1765)			–	17	6,7,11,12	2,3
Cochlicopa lubrica (O. F. Müller, 1774)			1,8,11,16,21	2,5–7,9,10,12,13,15,18–20	1,3–10,12	–
Cochlodina laminata (Montagu, 1803)			1,11,21	2,5,7,9,10,12–14,17,18	1,2,11,12	1,3,4
Columella aspera Waldén, 1966			–	–	–	5,6
Columella edentula (Draparnaud, 1805)			–	9,13,17	12	2–4
Deroceras invadens (Reise et al., 2011)		i	1,8,11,16,21	2,3,5–7,9,10,12–15,18–20	3–5,7–9,12	–
Deroceras laeve (O. F. Müller, 1774)	h		11,16	–	12	–
Deroceras reticulatum (O. F. Müller, 1774)			1,8,11,16,21	2–7,9,10,12,13,15,19,20	3–5,10,12	–
Discus rotundatus (O. F. Müller, 1774)			1,8,21	2,4–7,9,10,12–14,17,19	1–12	1–6
Euconulus praticola (Reinhardt, 1883)	h		–	–	12	–
Euconulus fulvus (O. F. Müller, 1774)			1,16,21	9,13	11,12	1–3,5,6
Eucobresia diaphana (Draparnaud, 1805)	h		1	17	–	–
Fruticicola fruticum (O. F. Müller, 1774)			8,11,21	7,10,15,19,20	–	–
Galba truncatula (O. F. Müller, 1774)	w		21	–	12	–
Gyraulus albus (O. F. Müller, 1774)	w		11,16	–	–	–
Helix pomatia Linnaeus, 1758			1	2,7,13	1–4	–
Laciniaria plicata (Draparnaud, 1801)			–	5,7	–	–
Lehmannia marginata (O. F. Müller, 1774)			–	–	–	1–6
Lehmannia valentiana (A. Férussac, 1822)		i	–	12,13	7	–
Limax cinereoniger Wolf, 1803			–	–	–	2–6
Limax maximus Linnaeus, 1758			1	2,4,7,9,12,13,17,18	1–6,9,11,12	3–5
Lucilla singleyana (Pilsbry, 1889)		?	–	–	2	2
Macrogastra attenuata lineolata (Held, 1836)			–	7	12	–
Malacolimax tenellus (O. F. Müller, 1774)			–	–	–	1–3,5,6
Merdigera obscura (O. F. Müller, 1774)			1,21	2,13,14,18,19	3,4,6	–
Monacha cartusiana (O. F. Müller, 1774)		i	–	19	–	–
Monachoides incarnatus (O.F. Müller, 1774)			1,8,11,21	3–7,9,10,12,13,15,17,19	1–4,6,9–12	2–6
Nesovitrea hammonis (Strøm, 1765)			21	2,4,5,7,9,12–15,17–19	2–12	1–6
Oxyloma elegans (Risso, 1826)	h		8,11	–	–	–
Oxychilus alliarius (J. S. Miller, 1822)			–	–	–	1
Oxychilus cellarius (O. F. Müller, 1774)			8,21	4,12,18,19	1,5,6,9,11,12	1–6

Table 1. Continued

Species	a	i	Floodplain		Non-floodplain	
			Salicetum s.l.	*Fraxinetum* s.l.	Young (y)	Old (o)
Oxychilus draparnaudi (H. Beck, 1837)			1,8	2,3,5–7,9,12,13,15,17–20	2–8,12	–
Paralaoma servilis (Shuttleworth, 1852)		i	–	14	–	–
Phenacolimax major (A. Férussac, 1807)			–	–	1,2	1–3
Pisidium casertanum casertanum (Poli, 1791)	w		–	–	12	–
Pisidium obtusale (Lamarck, 1818)	w		–	–	12	–
Pseudotrichia rubiginosa (Rossm., 1838)	h		1,8,11,16,21	–	–	–
Punctum pygmaeum (Draparnaud, 1801)			1,21	4,5,7,9,12,13,17–19	1–12	1–6
Succinea putris (Linnaeus, 1758)	h		1,8,11,16,21	–	12	–
Succinella oblonga (Draparnaud, 1801)	h		8,11,21	15,19	12	–
Trochulus hispidus (Linnaeus, 1758)			1,8,11,16,21	2,3,5–7,9,12–15,18–20	1,3–8,10–12	–
Trochulus striolatus (C. Pfeiffer 1828)	h		1,8,11,16,21	7	–	–
Vallonia costata (O. F. Müller, 1774)			8	2,3,5–7,10,13,15,17,19,20	3–10,12	–
Vallonia excentrica Sterki, 1893			21	3,5,10,13,15,18,20	3,4	–
Vallonia pulchella (O. F. Müller, 1774)			–	–	12	–
Vertigo antivertigo (Draparnaud, 1801)	h		–	–	12	–
Vertigo pusilla O. F. Müller, 1774			–	9	12	–
Vertigo pygmaea (Draparnaud, 1801)			8,16	15,19	12	–
Vertigo substriata (Jeffreys, 1833)	h		–	–	12	–
Vitrea contracta (Westerlund, 1871)			–	–	11,12	–
Vitrea crystallina (O. F. Müller, 1774)			11,16,21	1,5	1,6,11,12	2,3
Vitrina pellucida (O. F. Müller, 1774)			8,11,16,21	3–7,9,10,12,13,17,18,20	2–4,6,7,9–12	1–4
Vitrinobrachium breve (A. Férussac, 1821)			8,11,16,21	2,3,5–7,9,10,12–14,18,19	3–5,8–10,12	–
Zonitoides nitidus (O. F. Müller, 1774)	h		1,8,11,16,21	–	12	–

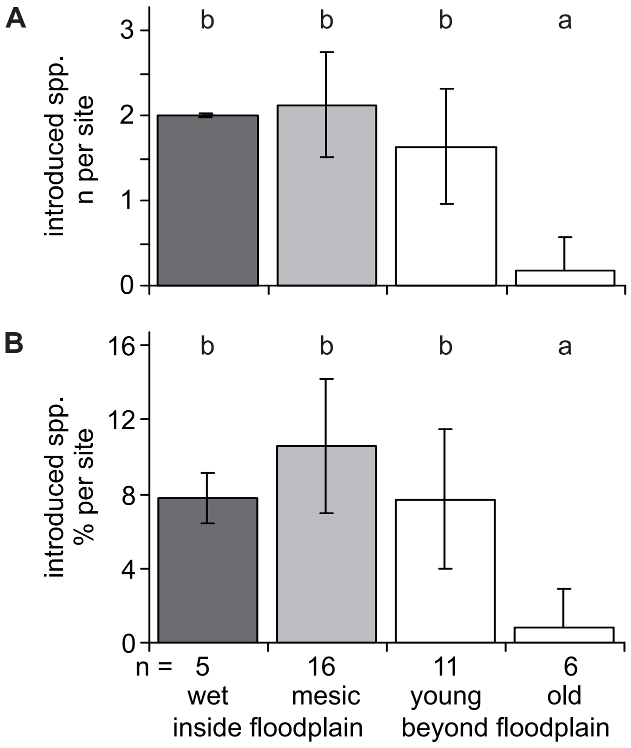

Fig. 2. A – per-site numbers of introduced species; B – proportion of introduced species (mean with standard deviation) depending on forest type. Shared letters indicate lack of difference between richness groups (ANOVA with post-hoc Tukey HSD for unequal n); n = number of sites

the recent forests, but only in one of the old forest sites (Table 1). Its density ranged from just detectable by visual search (Table 2) to eight specimens in the quantitative plots (Table 3).

Because the old-growth forests differed in many respects from the recent forests, the analysis of the relation between the overall species richness and introduced species focussed on the invasion-sensitive recent forests. Here, ANOVA revealed that the overall species richness per site did not predict differences in the number of introduced species (< 20, 20–24 and ≥ 25 total species: 2.1 ± 0.6, 1.7 ± 0.6, and 2.0 ± 0.6 introduced species, respectively; Tukey HSD for unequal n: not significant). As a consequence, the proportion of introduced species decreased with overall species richness (< 20, 20–24 and ≥ 25 total species: 12.8 ± 3.6, 8.1 ± 2.7, and 7.0 ± 2.3% of introduced species, respectively; Tukey HSD for unequal n: grouping b – a – a).

COMPOSITIONAL DIFFERENCES BETWEEN GROUPS AND SITES

The compositional similarities among the sites were illustrated in a non-metric multidimensional scaling plot (NMDS, Fig. 3A). Axis 1 of the NMDS plot roughly corresponds to faunal changes that are associated with the distance of the sites from the Rhine River (Fig. 3B), from the upper and middle ter-

Table 2. Species lists from quantitatively studied sites 6 and 5. Light grey: additional species from visual sampling 2010, dark grey: additional species from supplementary visual sampling 2014

Locality number	6	5
Sampling dates	2010.07.02 (suppl. qual.: 2014.05.01)	2010.07.02 (suppl. qual. 2014.05.01)
Dominant tree species	*Acer pseudoplatanus, Tilia cordata*	*Fraxinus excelsior, Acer pseudoplatanus*
Canopy/bush/herb/moss cover %	70/20/10/20	60/20/60/10
Deadwood volume (m^3/ha)	1.7	2.1
Mean pH	5.6	4.6
Coordinates	50°51'26.3"N, 7°01'24.9"E	50°50'45.2"N, 7°00'02.0"E

Subsamples	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Cochlicopa lubrica (O. F. Müller, 1774)	0	0	1	0	0	0	0	0	▓	▓	▓	▓	▓	▓	▓	▓
Acanthinula aculeata (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	▓	▓	▓	▓	▓	▓	▓	▓
Vallonia costata (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
Vallonia excentrica Sterki, 1893	–	–	–	–	–	–	–	–	░	░	░	░	░	░	░	░
Cochlodina laminata (Montagu, 1803)	–	–	–	–	–	–	–	–	0	1	0	0	0	0	3	0
Alinda biplicata (Montagu, 1803)	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0
Laciniaria plicata (Draparnaud, 1801)	–	–	–	–	–	–	–	–	░	░	░	░	░	░	░	░
Punctum pygmaeum (Draparnaud, 1801)	–	–	–	–	–	–	–	–	░	░	░	░	░	░	░	░
Discus rotundatus (O. F. Müller, 1774)	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0
Vitrea crystallina (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	0	0	0	0	1	0	0	0
Oxychilus draparnaudi (H. Beck, 1837)	▓	▓	▓	▓	▓	▓	▓	▓	░	░	░	░	░	░	░	░
Aegopinella nitidula (Draparnaud, 1805)	0	0	0	1	1	0	0	1	0	1	1	0	0	5	1	0
Nesovitrea hammonis (Strøm, 1765)	–	–	–	–	–	–	–	–	░	░	░	░	░	░	░	░
Vitrinobrachium breve (A. Férussac, 1821)	0	0	0	0	0	0	1	0	0	3	0	0	1	1	0	0
Vitrina pellucida (O. F. Müller, 1774)	2	1	1	3	0	1	0	1	1	1	0	0	0	3	2	1
Boettgerilla pallens Simroth, 1912	–	–	–	–	–	–	–	–	▓	▓	▓	▓	▓	▓	▓	▓
Deroceras reticulatum (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	0	0	0	0	0	1	0	0
Deroceras invadens (Reise et al., 2011)	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
Arion lusitanicus auct. non J. Mabille, 1868	░	░	░	░	░	░	░	░	0	2	0	1	0	0	2	2
Arion silvaticus Lohmander, 1937	–	–	–	–	–	–	–	–	▓	▓	▓	▓	▓	▓	▓	▓
Arion distinctus J. Mabille, 1868	▓	▓	▓	▓	▓	▓	▓	▓	░	░	░	░	░	░	░	░
Trochulus hispidus (Linnaeus, 1758)	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░
Monachoides incarnatus (O. F. Müller, 1774)	0	1	1	0	0	0	0	1	1	0	1	2	0	0	1	1
Cepaea nemoralis (Linnaeus, 1758)	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░
No of species per subsample	1	2	3	2	2	2	1	3	2	6	3	2	2	4	6	3
No of individuals per subsample	2	2	3	4	2	2	1	4	2	9	3	3	2	10	10	4
No of species (total)								15								24
No of individuals per 1 m^2								10								22

race old growth sites on the left to the recent floodplain sites on the right. Sites 4 and 17 have an unexpected position in the NMDS plot (Fig. 3B). These two sites are located closer to the Rhine than would be predicted from the faunal turnover of the other localities along the first NMDS axis. Consequently, their faunal composition seems to be more typical of non-inundated forests.

The turnover with distance from the Rhine is associated with the spatial distribution of specific taxa. The few old forests that remained at a distance from the Rhine harbour typical forest species such as *Limax cinereoniger* or *Malacolimax tenellus*. The sites which are so close the Rhine that they are regularly moistened by inundations have additional taxa such as *Perforatella rubiginosa* and *Trochulus striolatus*. The irregularly inundated forests and the young forests beyond the floodplain are between these two extremes. They share many species, and only few species are exclusively or more often found in the irregularly inundated forests than in the young forests beyond the floodplain (e.g. *Fruticicola fruticum*, see Table 1).

Consequently, the group separations were not always clear. The young forests with and without occasional inundation shared very many species, resulting in overlapping circles in the NMDS (Fig. 3A). This overlap corresponds to the lack of significant compositional between-group difference in the analysis of similarities for the young mesic forests with and without occasional inundations (ANOSIM, p = 0.161). Consequently, the NMDS and ANOSIM

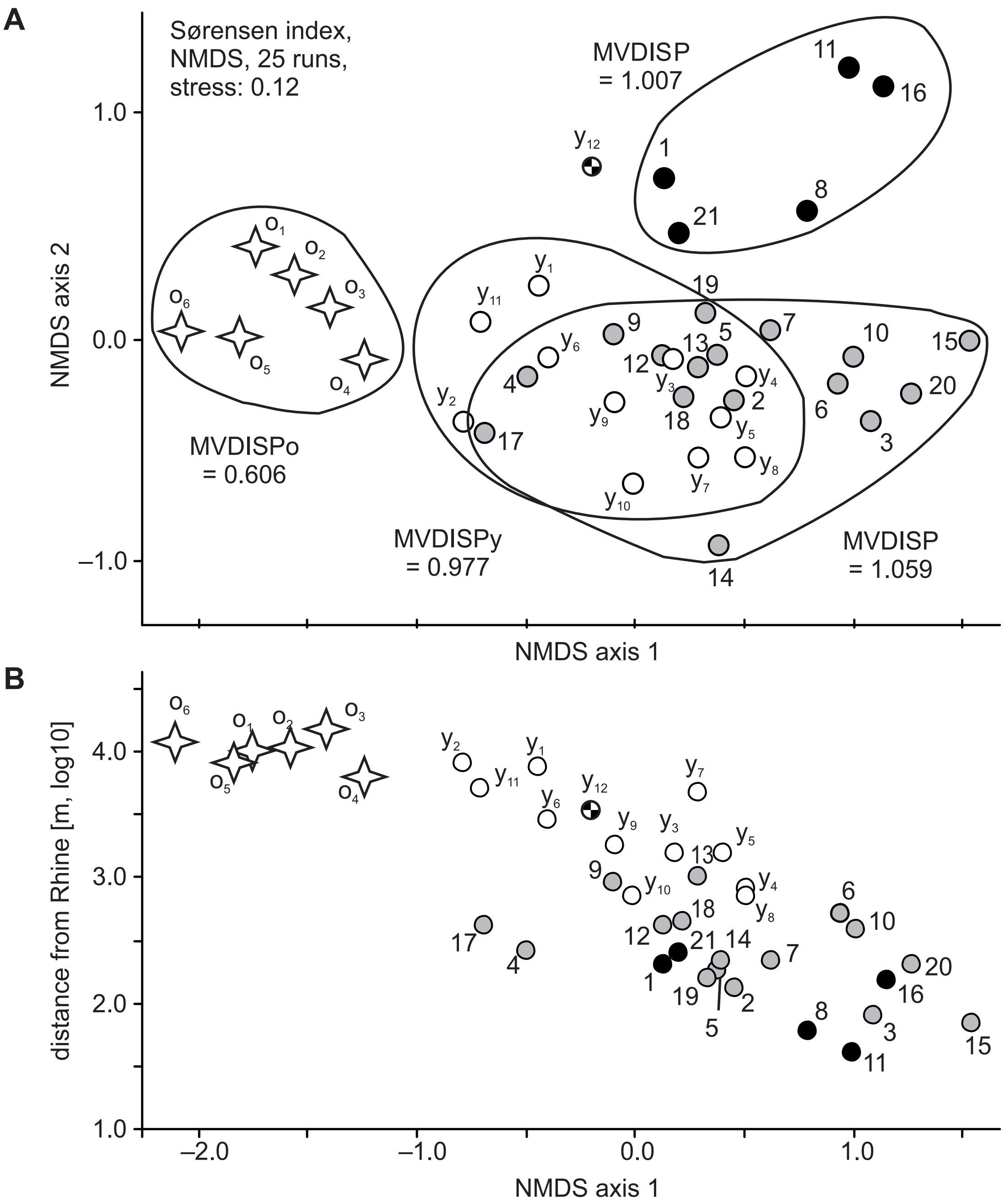

Fig. 3. A – 2D-plot of nonmetric multidimensional scaling (NMDS) of the Sørensen similarities between the inventory sites, MVDISP values indicate overall heterogeneity within groups of sites (groups are encircled); B – Axis 1 of NMDS plot in A partially accounts for the distance [log-transformed] from the Rhine River. Distances of 2.0 and 4.0 equal 100 m and 10 km, respectively. For site codes see caption to Fig. 1

identified three groups of forests ($p < 0.005$), namely (1) wet, regularly inundated (2) young mesic, independent of occasional inundation, and (3) old-growth forests (see Fig. 3A). At the group level, differences for pairs with the single wet forest outside the floodplain (site y_{12}) are likely, but could not be calculated.

In quantitative terms, site y_{12} did indeed differ from the other seven sites (ANOSIM, all $p < 0.003$; compare Fig. 4A–H). In general, the analysis of similarities found more differences between sites than potential overlaps ($p < 0.04$, usually $p < 0.01$). There were five exceptions: compositional differences were marginal for sites 6 and 21 ($p = 0.06$) and sites 5 and 21 ($p = 0.05$), whereas compositional overlaps were likely for sites 5 and 6 ($p = 0.25$), for 12 and 21 ($p = 0.21$) and for 9 and 21 ($p = 0.67$). To sum up, most similarities arose in pairwise comparisons with the site that most recently received drift input (21), whereas similarities between the hardwood fragments were unusual.

Table 3. Species lists from quantitatively studied sites 12 and 7. Light grey: additional species from visual sampling 2010, dark grey: additional species from supplementary visual sampling 2014

Locality number	12	7
Sampling date	2010.07.04 (suppl. qual.: 2014.06.12)	2010.07.02 (suppl. qual.: 2014.05.01)
Dominant tree species	*Fagus sylvatica, Fraxinus excelsior, Tilia cordata, Acer pseudoplatanus*	*Fraxinus excelsior, Fagus sylvatica, Tilia cordata, Acer pseudoplatanus*
Canopy/bush/herb/moss cover %	70/50/30/5	80/20/10/0
Deadwood volume (m³/ha)	5.0	9.3
Mean pH	5.5	5.7
Coordinates	50°54'15.1"N, 6°59'48.9"E	50°51'50.4"N, 7°01'35.3"E

Subsample	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Carychium tridentatum (Risso, 1826)	23	5	1	0	0	9	1	0	–	–	–	–	–	–	–	–
Cochlicopa lubrica (O. F. Müller, 1774)	0	1	0	0	0	0	0	0	1	0.4	0	2	0	0	1	0
Vallonia costata (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	0	1	0	0	0	0	0	0
Acanthinula aculeata (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	–	–	–	–	–	–	–	–
Cochlodina laminata (Montagu, 1803)	0	0	0	0	5	0	4	2	1	0	0	1	1	3	3	2
Macrogastra attenuata lineolata (Held, 1836)	–	–	–	–	–	–	–	–	0	0.1	0	0	0	0	0.1	0
Laciniaria plicata (Draparnaud, 1801)	–	–	–	–	–	–	–	–	0	0.1	0	0	0	0.1	0	0
Alinda biplicata (Montagu, 1803)	18	4	0	1	0	6	5	1	14	39	0	7	2	4	13	5
Punctum pygmaeum (Draparnaud, 1801)	5	1	0	0	0	2	2	0	1	0	0	0	0	0	0	0
Discus rotundatus (O. F. Müller, 1774)	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0
Oxychilus cellarius (O. F. Müller, 1774)	0	0	0	0	0	1	0	0	–	–	–	–	–	–	–	–
Oxychilus draparnaudi (H. Beck, 1837)	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0
Aegopinella nitidula (Draparnaud, 1805)	6	2	0	0	1	2	19	1	0	2	0	0	0	0	0	0
Nesovitrea hammonis (Strøm, 1765)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Vitrinobrachium breve (A. Férussac, 1821)	3	0	1	9	1	8	7	1	4	13	0	10	0	0	6	4
Vitrina pellucida (O. F. Müller, 1774)	░	░	░	░	░	░	░	░	0	54	0	1	0	4	25	4
Boettgerilla pallens Simroth, 1912	░	░	░	░	░	░	░	░	–	–	–	–	–	–	–	–
Limax maximus Linnaeus, 1758	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░
Lehmannia valentiana (A. Férussac, 1822)	▓	▓	▓	▓	▓	▓	▓	▓	–	–	–	–	–	–	–	–
Deroceras reticulatum (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
Deroceras invadens (Reise et al., 2011)	1	0	0	0	0	0	0	0	░	░	░	░	░	░	░	░
Arion lusitanicus auct. non J. Mabille, 1868	1	0	1	0	0	1	3	2	0	1	0	0	0	0	0	0
Arion distinctus J. Mabille, 1868	1	0	0	0	0	1	0	1	░	░	░	░	░	░	░	░
Fruticicola fruticum (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	▓	▓	▓	▓	▓	▓	▓	▓
Trochulus hispidus (Linnaeus, 1758)	▓	▓	▓	▓	▓	▓	▓	▓	0	0.1	0.1	0	0	0	0	0.1
Trochulus striolatus (C. Pfeiffer, 1828)	–	–	–	–	–	–	–	–	0	0.4	0	0	0	0	0	0
Monachoides incarnatus (O. F. Müller, 1774)	0	0	0	1	0	0	0	0	4	1	0	0	0	0	0	0
Cepaea nemoralis (Linnaeus, 1758)	▓	▓	▓	▓	▓	▓	▓	▓	0	1	0	0	0	0	0	0
Cepaea hortensis (O. F. Müller, 1774)	░	░	░	░	░	░	░	░	▓	▓	▓	▓	▓	▓	▓	▓
Helix pomatia Linnaeus, 1758	–	–	–	–	–	–	–	–	0	1	0	0	0	0	0	0
no of species per subsample	9	5	3	3	3	10	10	7	6	15	2	5	2	4	6	5
no of individuals per subsample	59	13	3	11	7	32	44	9	25	115.1	1.1	21	3	11.1	48.1	15.1
no of species (total)								24								25
no of individuals per 1 m²								89								119.75

HETEROGENEITY BETWEEN GROUPS AND WITHIN SITES

Assemblage heterogeneity as an indicator of disturbance, or stress, was first calculated between sites within the forest groups. The heterogeneity was similar for the regularly inundated wet forests, the young irregularly inundated forests and the young forests beyond the Rhine floodplain (MVDISP value about 1). In contrast, the MVDISP value for the old forests was about 0.6, and thus much smaller than such values for the other three forest groups (see Fig.

3A). As only one constantly wet forest was surveyed, heterogeneity could not be compared on the group level.

The highest within-site heterogeneity was recorded for the regularly inundated site with patches of driftwood (site 21; MVDISP = 1.37; see Fig. 4A). In this site, supplementary visual search resulted in 15 additional species (Table 4). The within-site heterogeneity was smallest within the species-rich constantly wet forest (y_{12}; MVDISP = 0.48, see Fig. 4H), where only four additional species were found during the visual search (Table 5).

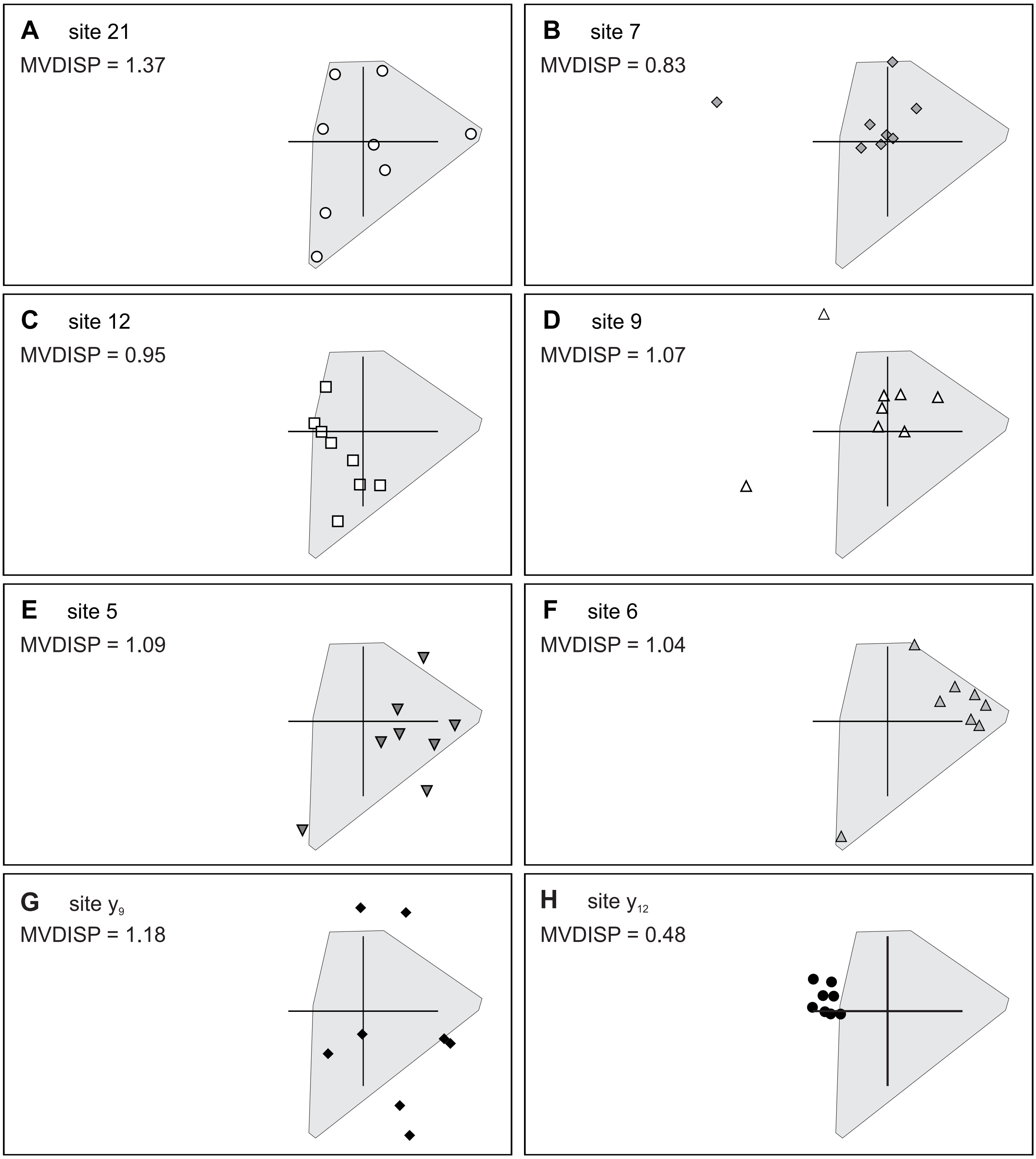

Fig. 4. NMDS plot for the quantitatively surveyed sites, with the eight replicates per site displayed for each site separately (A–H). NMDS was plotted from a Bray-Curtis similarity matrix that was calculated from log(x+1)-transformed data. Configuration with the lowest stress value was selected from 25 runs and was 0.2 for the original 2D plot (with n = 64). The cross marks the centre of ordination (0, 0) and spans from –1 to 1 for both axes. The grey shade is the envelope of site 21 in (A) that had drift input and hence was used as reference site for flooding.

Table 4. Species lists from quantitatively studied sites 21 and 9. Light grey: additional species from visual sampling 2010, dark grey: additional species from supplementary visual sampling 2014

Locality number	21	9
Sampling date	2010.07.03 (suppl. qual.: 2014.06.01)	2010.07.04 (suppl. qual.: 2014.06.12)
Dominant tree species	*Acer pseudoplatanus* with species rich admixture	*Quercus rubra, Quercus palustris, Fagus sylvatica*
Canopy/bush/herb/moss cover %	60/50/80/5	70/30/40/0
Deadwood volume (m^3/ha)	3.8	2.9
Mean pH	6.1	5.4
Coordinates	51°04'57.0"N, 6°51'38.1"E	50°53'11.4"N, 7°00'55.8"E

Subsample	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Carychium tridentatum (Risso, 1826)	0	0	0	0	0	0	2	0	░	░	░	░	░	░	░	░
Succinea putris (Linnaeus, 1758)	░	░	░	░	░	░	░	░	–	–	–	–	–	–	–	–
Succinella oblonga (Draparnaud, 1801)	░	░	░	░	░	░	░	░	–	–	–	–	–	–	–	–
Cochlicopa lubrica (O. F. Müller, 1774)	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Vallonia excentrica Sterki, 1893	░	░	░	░	░	░	░	░	–	–	–	–	–	–	–	–
Acanthinula aculeata (O. F. Müller, 1774)	0	0	0	0	1	0	0	0	0	1	2	0	3	1	4	0
Columella edentula (Draparnaud, 1805)	–	–	–	–	–	–	–	–	0	0	0	0	0	0	1	0
Vertigo pusilla O. F. Müller, 1774	–	–	–	–	–	–	–	–	0	0	0	1	0	0	0	0
Merdigera obscura (O. F. Müller, 1774)	░	░	░	░	░	░	░	░	–	–	–	–	–	–	–	–
Cochlodina laminata (Montagu, 1803)	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Alinda biplicata (Montagu, 1803)	0	0	1	2	2	1	9	0	0	10	5	0	1	9	1	2
Punctum pygmaeum (Draparnaud, 1801)	0	2	0	0	0	1	3	0	1	0	1	0	0	3	2	0
Discus rotundatus (O. F. Müller, 1774)	0	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0
Vitrea crystallina (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	–	–	–	–	–	–	–	–
Euconulus fulvus (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	░	░	░	░	░	░	░	░
Zonitoides nitidus (O. F. Müller, 1774)	0	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–
Oxychilus cellarius (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	–	–	–	–	–	–	–	–
Oxychilus draparnaudi (H. Beck, 1837)	–	–	–	–	–	–	–	–	▓	▓	▓	▓	▓	▓	▓	▓
Aegopinella nitidula (Draparnaud, 1805)	0	0	0	1	0	1	5	0	0	3	0	0	3	1	1	0
Nesovitrea hammonis (Strøm, 1765)	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0
Vitrinobrachium breve (A. Férussac, 1821)	0	2	1	0	0	1	4	1	0	0	0	0	1	0	0	0
Vitrina pellucida (O. F. Müller, 1774)	1	0	1	0	0	7	0	0	0	2	1	0	3	2	2	5
Boettgerilla pallens Simroth, 1912	▓	▓	▓	▓	▓	▓	▓	▓	░	░	░	░	░	░	░	░
Limax maximus Linnaeus, 1758	–	–	–	–	–	–	–	–	░	░	░	░	░	░	░	░
Deroceras reticulatum (O. F. Müller, 1774)	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0
Deroceras invadens (Reise et al., 2011)	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0
Arion lusitanicus auc. non J. Mabille, 1868	0	1	0	0	1	2	0	0	0	0	1	0	2	1	3	0
Arion fuscus (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	░	░	░	░	░	░	░	░
Arion silvaticus Lohmander, 1937	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
Arion distinctus J. Mabille, 1868	░	░	░	░	░	░	░	░	0	0	1	0	0	0	0	0
Arion intermedius Normand, 1852	–	–	–	–	–	–	–	–	░	░	░	░	░	░	░	░
Fruticicola fruticum (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	–	–	–	–	–	–	–	–
Trochulus hispidus (Linnaeus, 1758)	0	0	1	0	5	2	0	0	0	0	0	2	0	0	1	0
Trochulus striolatus (C. Pfeiffer, 1828)	0	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–
Pseudotrichia rubiginosa (Rossmässler, 1838)	▓	▓	▓	▓	▓	▓	▓	▓	–	–	–	–	–	–	–	–
Monachoides incarnatus (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	░	░	░	░	░	░	░	░
Cepaea nemoralis (Linnaeus, 1758)	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Cepaea hortensis (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	–	–	–	–	–	–	–	–
Helix pomatia Linnaeus, 1758	▓	▓	▓	▓	▓	▓	▓	▓	–	–	–	–	–	–	–	–
no of species per subsample	1	3	7	2	6	7	10	1	2	4	9	4	6	8	9	2
no of individuals per subsample	1	5	8	3	11	15	28	1	2	16	14	6	13	19	16	7
no of species (total)								33								27
no of individuals per 1 m^2								36								47

Table 5. Species lists from quantitatively studied sites y_9 and y_{12}. Light grey: additional species from visual sampling 2010, dark grey: additional species from supplementary visual sampling 2014

Locality number	y_9	y_{12}
Sampling date	2010.07.03 (suppl. qual.: 2014.06.01)	2010.07.03 (suppl. qual.: 2014.06.01)
Dominant tree species	*Acer pseudoplatanus, Fraxinus excelsior, Acer campestris*	*Fraxinus excelsior, Fagus sylvatica, Acer pseudoplatanus, Alnus glutinosa*
Canopy/bush/herb/moss cover %	80/40/20/5	60/50/60/15
Deadwood volume (m³/ha)	7.4	3.4
Mean pH	4.4	5.7
Coordinates	51°03'16.2"N, 6°57'55.3"E	51°04'03.0"N, 6°58'39.8"E

Subsample	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Galba truncatula (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	0	0,2	0	0	0	0	0	0
Carychium minimum O. F. Müller, 1774	–	–	–	–	–	–	–	–	0	23	0	2	4	0	0	0
Carychium tridentatum (Risso, 1826)	▓	▓	▓	▓	▓	▓	▓	▓	12	155	15	23	51	9	34	25
Succinea putris (Linnaeus, 1758)	–	–	–	–	–	–	–	–	0	0	0	0	0	0	0	3
Succinella oblonga (Draparnaud, 1801)	–	–	–	–	–	–	–	–	0	0	0	1	0	0	0	0
Cochlicopa lubrica (O. F. Müller, 1774)	0	1	0	0	0	0	0	0	6	2	12	2	15	1	2	0
Vallonia costata (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	0	0	1	4	0	0	0	0
Vallonia pulchella (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	0	0	0	0	0	1	0	0
Acanthinula aculeata (O. F. Müller, 1774)	3	0	0	0	0	0	0	0	0	13	5	0	11	2	3	0
Columella edentula (Draparnaud, 1805)	–	–	–	–	–	–	–	–	1	3	0	0	0	0	2	1
Vertigo antivertigo (Draparnaud, 1801)	–	–	–	–	–	–	–	–	░	░	░	░	░	░	░	░
Vertigo pusilla O. F. Müller, 1774	–	–	–	–	–	–	–	–	1	0	0	0	0	0	0	0
Vertigo substriata (Jeffreys, 1833)	–	–	–	–	–	–	–	–	0	0	0	0	0	0	1	0
Vertigo pygmaea (Draparnaud, 1801)	–	–	–	–	–	–	–	–	1	0	1	2	0	0	0	0
Cochlodina laminata (Montagu, 1803)	–	–	–	–	–	–	–	–	2	3	0	2	0	1	0	8
Macrogastra attenuata lineolata (Held, 1836)	–	–	–	–	–	–	–	–	6	2	0	1	2	0	0	5
Clausilia bidentata (Strøm, 1765)	–	–	–	–	–	–	–	–	0	0	1	0	1	0	0	2
Alinda biplicata (Montagu, 1803)	1	0	0	0	0	0	0	0	31	13	13	17	7	1	3	21
Punctum pygmaeum (Draparnaud, 1801)	2	0	0	0	0	0	0	2	29	31	2	28	33	23	4	6
Discus rotundatus (O. F. Müller, 1774)	0	0	0	0	0	0	0	1	12	8	1	5	1	2	0	3
Vitrea crystallina (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	0	2	0	1	0	0	2	5
Vitrea contracta (Westerlund, 1871)	–	–	–	–	–	–	–	–	0	0	0	1	0	0	0	0
Euconulus fulvus (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	1	4	1	3	2	0	0	0
Euconulus praticola (Reinhardt, 1883)	–	–	–	–	–	–	–	–	▓	▓	▓	▓	▓	▓	▓	▓
Zonitoides nitidus (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	0	0	1	0	0	0	0	0
Oxychilus cellarius (O. F. Müller, 1774)	▓	▓	▓	▓	▓	▓	▓	▓	0	0	0	1	0	0	0	0
Oxychilus draparnaudi (H. Beck, 1837)	–	–	–	–	–	–	–	–	░	░	░	░	░	░	░	░
Aegopinella pura (Alder, 1830)	–	–	–	–	–	–	–	–	0	0	0	0	1	0	0	1
Aegopinella nitidula (Draparnaud, 1805)	1	2	0	1	0	0	0	1	1	5	2	4	0	4	4	0
Nesovitrea hammonis (Strøm, 1765)	4	0	1	0	1	1	2	4	3	5	1	0	4	2	1	0
Vitrinobrachium breve (A. Férussac, 1821)	1	0	0	0	0	0	0	0	1	0	3	0	0	1	1	0
Vitrina pellucida (O. F. Müller, 1774)	1	0	1	0	1	0	0	0	3	1	0	1	0	0	0	0
Boettgerilla pallens Simroth, 1912	–	–	–	–	–	–	–	–	0	0	0	0	0	1	0	0
Limax maximus Linnaeus, 1758	▓	▓	▓	▓	▓	▓	▓	▓	0	0	0	1	0	0	0	0
Deroceras laeve (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	0	1	0	0	0	0	0	0
Deroceras reticulatum (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	0	1	0	0	0	0	0	1
Deroceras invadens (Reise et al., 2011)	0	1	0	0	0	0	0	0	▓	▓	▓	▓	▓	▓	▓	▓
Arion lusitanicus auct. non J. Mabille, 1868	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Arion fuscus (O. F. Müller, 1774)	–	–	–	–	–	–	–	–	1	0	0	0	0	0	0	0
Arion silvaticus Lohmander, 1937	–	–	–	–	–	–	–	–	0	0	0	0	0	1	1	0
Arion distinctus J. Mabille, 1868	▓	▓	▓	▓	▓	▓	▓	▓	0	0	0	0	1	0	2	0
Arion intermedius Normand, 1852	▓	▓	▓	▓	▓	▓	▓	▓	0	0	0	1	1	0	2	1

Table 5. Continued

Trochulus hispidus (Linnaeus, 1758)	–	–	–	–	–	–	–	–	0	1	0	2	0	0	0	3
Monachoides incarnatus (O. F. Müller, 1774)	0	0	0	0	1	0	0	0	0	2	1	0	1	0	2	3
Arianta arbustorum (Linnaeus, 1758)	–	–	–	–	–	–	–	–	0	0	0	0	0	0	0	1
Cepaea nemoralis (Linnaeus, 1758)	▨	▨	▨	▨	▨	▨	▨	▨	1	0	0	0	0	0	0	1
Cepaea hortensis (O. F. Müller, 1774)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pisidium casertanum casertanum (Poli, 1791)	–	–	–	–	–	–	–	–	0	0,5	0	0	0	0	0	0
Pisidium obtusale (Lamarck, 1818)	–	–	–	–	–	–	–	–	0	0,3	0	0	0	0	0	0
no of species per subsample	8	3	2	1	3	1	2	4	17	22	16	21	15	13	16	17
no of individuals per subsample	14	4	2	1	3	1	3	8	112	276	61	103	135	49	65	90
no of species (total)								19								49
no of individuals per 1 m^2								18								446

DISCUSSION

FOCAL GROUPS: NATIVE DOOR SNAILS AND INVASIVE SPECIES

All four clausiliid species mentioned by GEYER & LE ROI (1912) were found. The most common clausiliid in our study was *Alinda biplicata*. *A. biplicata* is typical of floodplain forests also in other regions (e.g. KÖRNIG 1966, KERKHOFF 1989, WEDEL 1999, SULIKOWSKA-DROZD et al. 2013). The species, however, is not exclusively associated with forests; it also inhabits shrubs and tall herb stands (e.g. KAPPES et al. 2007). *Laciniaria plicata* was only observed in small numbers in the southern part of the study area. WEDEL (1999) suggests that *L. plicata* prefers rather undisturbed forests in the Upper Rhine floodplain. Our observations (HK, unpublished), however, indicate that it is not strictly bound to pristine forests: it occurs, for example, in forest-like habitats that originated from the former city park on the remains of the fortification of Landau in the Upper Rhine valley. Hence, its scarcity along the Lower River Rhine remains to be explained.

STEUSLOFF (1950) found *Balea perversa* and *Clausilia dubia* on old city walls and old trees of the Lower Rhine floodplain. Those were not sampled in our study. None of the species was found in the floodplain in recent years (unpublished data, mapping survey of NRW). The two species faced habitat loss during the last century (KOBIALKA et al. 2009).

In addition to the clausiliids that had been reported from the region so far, *Macrogastra lineolata* was found in the floodplain. *Macrogastra* species have been observed in hardwood forests of the Upper Rhine floodplain (e.g. WEDEL 1999: Kehl, STERN et al. 2014: Mainz), and floodplain forests of the Iller and Danube (e.g. KERKHOFF 1989). Consequently, *M. lineolata* might well belong to the typical floodplain fauna along the Lower Rhine. It may be speculated that, unlike *A. biplicata, Macrogastra* species are highly sensitive to anthropogenic disturbance and their absence is most probably the outcome of the significant habitat clearance and groundwater table depletion in the floodplain since the Middle Ages (SCHNITZLER 1994, KÜSTER 1999) and after the river straightening in the 18th century (SCHNITZLER 1994), respectively.

In contrast to native specialists that are negatively affected by land use, the occurrence of non-native taxa and the spread of invasive species are closely associated with human influence. Logging of the original floodplain forests can favour invasive species on the catchment area scale, as has been shown for riparian plant species (ŘEPKA et al. 2015). Two interesting findings of our study are two Mediterranean species, namely *Lehmannia valentiana* and *Paralaoma servilis*, which possibly undergo naturalisation in the highly modified floodplain and adjacent areas. Similarly, the frequently found door snail *A. biplicata* is considered to be regionally spreading (KOBIALKA et al. 2009) and thus can be regarded as a native invasive species.

GASTROPOD COMMUNITIES AND FOREST TYPES

We observed a substantial overlap in the snail species composition of the young inundated and non-inundated forests. Similarly, KÖRNIG (1966) found a gradual vegetational and faunal transition between floodplain hardwood forests and adjacent *Quercus-Carpinus-Tilia*-forests in central Germany. The overlap in our study concerned only the irregularly and briefly inundated forests.

The species richness per site was somewhat higher, but not significantly increased in more frequently inundated forests. Nevertheless, one of the two richest localities received regular drift input (site 21). Small-scale richness can increase temporarily after floods which imply substantial passive dispersal that includes maladapted taxa (Ilg et al. 2009). Comparing the two approaches, the presence-absence survey overestimated moisture in site 21, or the quantitative analysis was not sufficiently sensitive. Hygrophilous taxa may not be typical of the site that is transitional between the regularly inundated softwoods and the rarely inundated hardwoods. It may be speculated that in this specific locality hygrophiles are among the first taxa to vanish during times of low flooding recurrence.

Strikingly, the richest locality was not part of the highly modified Rhine floodplain. Here, the richness resulted from the rather stable, favourable conditions with a high soil pH and moisture. Soil moisture is known to affect snail and slug species abundance and turnover (e.g. Martin & Sommer 2004, Čejka et al. 2008, Čejka & Hamerlík 2009, Kappes & Schilthuizen 2014), as does inundation (e.g. Kerkhoff 1989, Horáčková et al. 2014, Kappes et al. 2014). The soils of the forests along the Rhine River are usually dry, among others because the ground water level has decreased along with the level of the river. Lowered ground water tables are known to affect riparian biodiversity (Čejka & Hamerlík 2009). Furthermore, smaller tributaries (brooks and small streams) have been directed to artificial subterranean channels in the studied region. Our survey thus barely covers (semi-)aquatic molluscs.

HOMOGENEITY IN THE HARDWOOD ZONE?

Faunal homogeneity was not achieved in the highly fragmented hardwoods. Our data suggest that the hardwood forest sites had a similarly composed drift input, as their species set was usually a subset of the site with the most recent drift event (site 21). The drift input favoured homogeneity of the fauna of the fragments within the floodplain, but it also contributed to heterogeneity of the assemblages on the plot level within a fragment, as was seen in site 21. Following drift, the samples within a fragment tended to homogenise in a site-specific way, and the communities then differed between sites.

In general, the same pattern can originate from different underlying processes (Magurran 2005, McGill et al. 2007). Heterogeneity after a homogenising dispersal event can, for example, result from (1) habitat/niche filtering where the environment selects the best adapted species, (2) random effects on reproduction success and/or extinctions, or (3) species interactions such as competition.

Habitat filtering may have acted on the stranded individuals if environmental properties differed between the sites. For example, some of the variability may have been caused by slight differences in the soil properties such as humus or sand content, or from differences in the tree species composition, canopy closure, and herb layer. Consistent, directed effects of habitat filtering in terms of species turnover could only be seen for the old-growth forests and the moist/wet forests. On the one hand, closed-canopy old-growth forests with a dominance of the detritus food chain, especially when subjected to calcium deficit, harbour a specific gastropod fauna (e.g. Kappes 2006, Kappes et al. 2009). On the other hand, wet floodplain forests contain hygrophilous and inundation-tolerant species (e.g. Kerkhoff 1989, Horáčková et al. 2014, Kappes et al. 2014).

Random effects such as stochastic extinctions following drift input can increase differences between the fragments. They might act at the community level as well as at the population level. Random genetic drift, for example, may underlie the marked between-population differences in *A. biplicata* despite the indications of a high overall gene flow between the forest fragments in the Elster/Saale floodplain (Hille et al. 2003). Also, drift input itself is expected to somewhat differ between patches and consecutive flooding events. Drift input, among other factors, depends on the presence and abundance of species in adjacent habitats and upstream origins along with hydrodynamics that influence the drift material uptake and deposition (e.g. Markwith et al. 2014). Furthermore, background densities during the colonisation process may vary. The background densities of residing individuals can affect the long-term outcome of post-dispersal species composition (Wilson 1992, and references therein). Some snails may endure flooding in situ, either hidden in the ground or crawling up tree trunks. Snails can survive a few hours to several days submerged, depending on the water temperature and species (Künkel 1930, Kerkhoff 1989). The vertical escape behaviour depends on the prevailing climatic conditions, but is typical of floodplain inhabiting species (Kerkhoff 1989).

Species interactions can further magnify the effects of different initial numbers of individuals, as Wilson (1992) illustrated with computer simulations of his metacommunity model for mosaics of fragments. Interactions can occur among gastropod species, but also with other taxa which act as predators, pathogens or parasites but were not part of our study (for review of snail enemies see Barker 2004). It can be assumed that the post-drift between-site differentiation was caused by a combination of different processes.

On a large scale, there is a question to which extent floodplain forests can be fragmented and still act as a stable metacommunity without any long-term species loss. Markwith et al. (2014) report disrupted drift dispersal in a study on plant seeds in fragmented floodplain habitats. Further reforestations and embankment deconstruction might to some extent help to revitalise the floodplain and increase its longitudinal and lateral connectivity which, in turn, can stabilise species richness not only of snails.

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