Biol Invasions (2008) 10:381–390
DOI 10.1007/s10530-007-9137-6

ORIGINAL PAPER

Response of ground-dwelling beetle (Coleoptera) assemblages to giant knotweed (*Reynoutria* spp.) invasion

Werner Topp · Heike Kappes · Frances Rogers

Received: 28 November 2006 / Accepted: 3 July 2007 / Published online: 25 July 2007

Abstract Giant knotweeds (*Reynoutria* spp.) are highly productive and aggressive invaders in riparian wetlands of Europe and North America. We sampled ground-dwelling beetles by pitfall traps from six sites comparing monotypic *Reynoutria* stands with the invaded native *Urtica*-dominated stands. Three sites were located in a semi-natural softwood forest and three sites were on a ruderal embankment. The analyses are based on a total of 13,244 individuals from 218 species. Location and site significantly influenced beetle assemblages. Moreover, there were pronounced differences between vegetation stands. The monotypic *Reynoutria* stands exhibited lower beetle abundance, species richness and rarefaction diversity irrespective of location. However, the negative effect on species richness, abundance and assemblage similarities were stronger on the transformed ruderal embankment than in the semi-natural softwood forest. *Reynoutria* invasion seems to influence microclimatic conditions. We found a higher abundance of silvicolous and a lower abundance of xerophilous ground beetles in the *Reyountria* stands than in the *Urtica*-dominated stands. Feeding guilds reacted differently to *Reynoutria* invasion that reduced the abundance of predators and herbivores but enhanced that of detritivores. Detritivores assumingly profit from the perennial presence of the large quantities of *Reynoutria* litter. We conclude that highly productive invaders pauperise the arthropod fauna and alter link strengths in trophic cascades shifting primary producer-based food webs to detritus-based food webs.

Keywords *Fallopia* · Rarefaction diversity · Trophic cascade · Ecosystem functioning · Carabidae · Staphylinidae · Microclimate · Functional group · Detritus-based food web

Introduction

Two species of the giant knotweeds (*Reynoutria*, syn. *Fallopia*, *Polygonum*), which are members of the Polygonaceae family, are highly invasive and are recognised as noxious weeds in areas of invasion. One species, *Fallopia japonica*, is native to Japan, Taiwan and northern China (Beerling et al. 1994). The other species, *Fallopia sachalinensis*, is native to the southern part of Sakhalin Island, the southern Kurile Islands, and the Japanese islands Hokkaido and Honshu (Sukopp and Starfinger 1995). Within their invasion area in Europe and North America both

W. Topp (✉) · H. Kappes
Department for Terrestrial Ecology, Institute for Zoology,
University of Cologne, Weyertal 119, Koln 50923,
Germany
e-mail: w.topp@uni-koeln.de

F. Rogers
Faculty of Life Sciences, University of Manchester,
Stopford Building, Oxford Road,
Manchester M13 9PT, UK

species are most common on sites disturbed by human activities such as industrial areas or roadsides situated in open grassland and forests as well and on sites with natural soil erosion such as river banks (Beerling et al. 1994, Sukopp and Starfinger 1995, Weston et al. 2005). *Fallopia sachalinensis* additionally invades semi-natural riparian sites (Pyšek and Prach 1993).

Stands of both *Reynoutria* species are remarkable for their height, leaf area and production values as summarised by Sukopp and Starfinger (1995): *Reynoutria sachalinensis* reaches a height of 2–4.5 m. The biomass can exceed 200 t/ha equalling an energy content of ~12,000 MJ/ha, which is above any other herbaceous vegetation. These extreme values are reached by daily height increments of up to 15 cm in early summer. The value of leaf area index is 21.0 which exceeds that of dense forests. The total cover of *Reynoutria* in areas of invasion is in the range of 95–100%. Native vegetation is mostly replaced. The only species able to persist within *Reynoutria* stands are spring geophytes (Beerling et al. 1994, Kappes et al., 2007). Outcompeting the native vegetation may be enhanced by allelolechemicals such as the anthraquinone compounds emodin and phycion which were isolated from roots of *R. sachalinensis* (Inoue et al. 1992).

The most common concern related to invasion are negative interactions between invaders and native species (Crooks 2002). In Europe, *Reynoutria* often establishes in herb-rich stands dominated by *Urtica dioica* (Sukopp and Starfinger 1995). When displacing *Urtica* stands, *Reynoutria* invasion is related to a decrease in soil pH and changes in habitat structure, including a reduced stem density (Kappes et al., 2007). In contrast to *Urtica*-dominated stands, *Reynoutria* stands provide a continuous detritus supply. *Reynoutria* continuously produces leaf litter as it drops the shaded leaves in the interior of the stands. Parts of the stem litter persist at least to the next growing season (Beerling et al. 1994).

Plant diversity is directly related to diversity of herbivore insects (Siemann 1998). Moreover, indigenous species such as nettles harbour a higher number of phytophagous insects (Davis 1983; Zabel and Tscharntke 1998) than the invasive *Reynoutria* (Zimmerman and Topp 1991; Beerling and Dawah 1993). Generally, assemblages of aerial insects associated with invasive vegetation considerably differ from those of native vegetation as invaders support lower abundance and species richness (Herrera and Dudley 2003).

Changes in the physical structure, nutrient cycling, productivity and food webs are substantial effects on ecosystems (Vitousek 1990; Crooks 2002; Zedler and Kercher 2004). These ecosystem changes should also affect ground-dwelling species of different trophic levels, although many of these arthropods are not as closely associated with vegetation as are aerial insects (Herrera and Dudley 2003). Among insects, beetles are the taxon with the highest species richness and include numerous ground-dwelling species with diversified feeding habits. Thus, beetles should be good indicators of the effects of plant invasions.

We studied ground-dwelling beetle assemblages and selected six pairs of *Urtica* dominated stands and invading *Reynoutria* stands growing in two different locations. One is a semi-natural softwood forest in which disturbance originates from natural processes such as erosion and sedimentation. The other is an artificial embankment in which human activities transformed late successional habitats into ruderal habitats. The goal of our study was to analyse changes in species richness, abundance and rarefaction diversity and in functional groups associated with *Reynoutria* invasion. We hypothesise that (1) the invader supports a lower species richness of ground-dwelling beetles, that (2) *Reynoutria* invasion especially affects herbivores and detritivores, and that (3) the impact of *Reynoutria* invasion on beetle assemblages is the same in the semi-natural softwood forest and the ruderal embankment because both habitats are subjected to disturbance by floodings.

Materials and methods

Study sites

We selected six sites in two different locations, a semi-natural softwood forest and a ruderal embankment of a canalised river (Table 1). The semi-natural softwood forest is located in the floodplain of the River Rhine at Düsseldorf–Urdenbach (sites 1–3). The herb layer is dominated by *U. dioica* stands, into which species such as *Angelica silvestris*, *Calystegia sepium*, *Cardamine amara*, *Galium aparine*, *Filipendula ulmaria*, *Lycopus europaeus*, *Ranunculus ficaria* and *Impatiens* species are interspersed. The herb

Table 1 Charactersitics of the two locations Urdenbach and Rheindorf

	Urdenbach	Rheindorf
Habitat	Semi-natural floodplain in abandoned meander	Embankment of canalised river
Vegetation	Softwood forest	Ruderal vegetation
Landscape structure	Flat with moist depressions, ponds and a brook	Steep shoreline, adjacent to levelled grasslands
Inundation	Direct through river floods	Direct through river floods
	Retention of heavy rains	

layer is invaded by both *Reynoutria sacchalinensis* and *Reynoutria japonica*. The semi-natural softwood forest is readily flooded after heavy summer rains and may be inundated for a couple of days to some weeks during floods of the River Rhine in the winter.

The ruderal embankment is characteristic for the severely disturbed floodplain of the lower River Wupper close to Leverkusen–Rheindorf (sites 4–6). The herb layer is dominated by *Urtica* stands into which a few other species such as *C. sepium*, *G. aparine* and *Lamium purpureum*, and some grasses such as *Agropyron repens* are interspersed. The herb layer is invaded by *R. japonica*. At Rheindorf, inundation of the three sites occurs only during winter floods.

Reynoutria has invaded the *Urtica*-dominated stands during the last decades. As *Reynoutria* established within the native *Urtica*-dominated stands, we used a paired design and compared the remaining *Urtica* stands with the stands of the invader *Reynoutria* in each of the sites.

Sampling

We used pitfall trapping to study the beetle fauna. We are aware that pitfall traps record activity densities rather than true abundances (Luff 1975; Baars 1979). As a consequence, abundance of hunting predators is overestimated when compared to other feeding guilds such as detritivores. Still, pitfall traps are a standard method in terrestrial ecology (Antvogel and Bonn 2001; Brose 2003). In each stand, five pitfall traps (white cups, diameter 85 mm, 2.5% formalin with detergent added) were placed at a distance of 5 m from each other and from the edge of the vegetation stand. Due to the invasion history, some stands of *Urtica* and *Reynoutria* were not continuously distributed. Instead they exhibited small corridors of the remaining *Urtica* or of the invading *Reynoutria* species. In these cases a stand comprised several patches to meet the above mentioned criterion of distances between pitfall traps and vegetation edges. *Urtica* patches covered areas between 100 and >3,000 m^2; *Reynoutria* patches covered areas sized 100–700 m^2.

The 60 pitfall traps were checked every fortnight. In early July, early August and late September heavy rainfalls resulted in the inundation of many pitfall traps in the semi-natural softwood forest. As beetles were lost, we also omitted the corresponding series of the other location for analyses. Data thus originated from 02 to 30 June, 14 to 28 July, 11 August to 22 September and 06 to 20 October 2005 for both locations.

Systematics of the beetles follow Freude et al. (1964–2004). Feeding guilds and ecological preference groups were assigned according to Koch (1989–1992).

Statistics

We pooled the data of the sampling dates (as described above) to yield higher numbers. Consequently, the analysis is based on five replicates per stand.

Rarefaction analyses were employed to standardise species richness for the number of individuals. We performed separate analyses for the two plant species and the two locations. Rarefaction diversity was calculated with EstimateS, Version 7.5.1 (Colwell 2005). To test if differences between the rarefaction curves were significant, we calculated z-values and one-tailed P-values based on the mean and the standard deviation of the S_{obs} value at the lowest number of individuals (with $n = 15$ samples).

Additionally, the rank order of species was plotted to visualise the influence of the vegetation on the relative abundance in each location. The threshold was set to a total of ≥ 20 individuals within each location.

We performed one-way ANOVAs for assessment of the effect of location on the beetle assemblages of the *Urtica*-dominated stands. Also, we employed one-way ANOVAs to test the effect of vegetation on the beetle assemblages for the two locations separately. In a further step, we performed a nested ANOVA. This method was chosen because of the hierarchical structure of the survey: each pair of vegetation stands was nested in site, and three sites were nested in each of the two different locations. The nested ANOVA was used to simultaneously test the influence of location, site and vegetation on the number of species and individuals. The nested ANOVA was run including the five subsamples per stand to account for within-stand variability. The variances of the abundances were stabilised using log(x + 0.5) transformation in the ANOVAs. The ANOVAs were performed with the programme package SPSS 11.0.

To further characterise the assemblages, we calculated the qualitative Sørensen indices and the quantitative Morisita–Horn indices (using EstimateS 7.5.1) for each combination of pitfall traps and entered the similarity matrices into an analysis of similarity (ANOSIM, programme package Primer 5.0). For testing, we classified four groups. Each group comprised the 15 pitfall traps per vegetation stand of each location. Relations between beetle assemblages were visualised in a detrended correspondence analysis (DCA). For the DCA, we pooled the five replicates of each stand. We only regarded those 96 species that had an abundance of ≥ 5 individuals. Abundances were log(x + 1)-transformed. Detrending was performed using second-order polynominals. The analysis focused on inter-species distances, using Hill's scaling to account for the long moisture gradient (Lepš and Šmilauer 2003). The DCA was performed using CANOCO for Windows 4.0.

Results

Differences between locations

In the two locations, a total of 13,244 beetles from 218 species were recorded. We collected 6,189 and 7,055 individuals in the semi-natural softwood forest and in the ruderal embankment, respectively.

Before dealing with the effects of the invasive *Reynoutria*, we compared the beetle assemblages from the *Urtica*-dominated stands of the two locations. The two locations differed in species assemblages. For example, some hygrophilus species, such as *Patrobus atrorufus*, *Carabus granulatus* and *Agonum micans* were trapped in high numbers in the semi-natural softwood forest (Table 2). The ruderal embankment of the canalised river was characterised by species such as *Drusilla canaliculata*, *Pterostichus melanarius*, *Barypeithes pellucidus* and *Phosphuga atrata* (Table 2).

A one-way ANOVA showed that the pitfall traps on the ruderal embankment caught significantly less carabid individuals ($F = 38.1$, $P < 0.001$) and staphylinid species ($F = 27.8$, $P < 0.001$), but more staphylinid individuals ($F = 85.5$, $P < 0.001$) than those in the semi-natural softwood forest. Also, there were less detritivorous individuals ($F = 19.4$, $P < 0.001$) but more herbivorous individuals ($F = 28.3$, $P < 0.001$) in the pitfall traps from the ruderal embankment.

Differences between *Urtica* and *Reynoutria* stands

Irrespective of location, both the total number of species and the total number of individuals were higher in the *Urtica*-dominated stands than in the *Reynoutria* stands (Table 2). A one-way ANOVA revealed that differences between vegetation stands were more pronounced on the ruderal embankment than in the semi-natural softwood forest. In both locations, there were less staphylinid individuals per pitfall trap in *Reynoutria* stands than in *Urtica*-dominated stands (softwood forest: $F = 5.2$, $P = 0.031$; ruderal embankment: $F = 10.1$, $P = 0.004$). On the ruderal embankment, there were also less beetle species ($F = 6.2$, $P = 0.019$) and less staphylinid species ($F = 8.3$, $P = 0.008$) per pitfall trap in *Reynoutria* stands than in *Urtica*-dominated stands.

Rarefaction analyses showed that overall beetle diversity was reduced in *Reynoutria* stands in both locations (Fig. 1, Table 2). However, the negative effect of *Reynoutria* stands was approximately twice as high in the softwood forest as on the ruderal embankment. At 2,941 individuals, the difference between the means was -18 ± 3 in the softwood forest ($z = -6.2$, $P < 0.001$), whereas the difference between the means was -8 ± 3 on the ruderal embankment ($z = -2.9$, $P = 0.002$).

In both locations, we found stand-specific beetle assemblages. Comparing rank orders of beetles from the semi-natural softwood forest visualised that the

Table 2 Species with a total of ≥ 40 individuals

	Guild	Softwood forest			Ruderal embankment		
		Urtica	*Reynoutria*	*P*	*Urtica*	*Reynoutria*	*P*
Drusilla canaliculata (Fabricius 1787)	p	6	1	n.s.	2,664	1,448	***
Patrobus atrorufus (Stroem 1768)	p	1,391	1,246	**	182	67	***
Limodromus assimilis (Paykull 1790)	p	193	440	***	142	471	***
Pterostichus strenuus (Panzer 1796)	p	208	172	n.s.	135	133	n.s.
Carabus granulatus Linnaeus 1758	p	186	174	n.s.	73	0	***
Phosphaenus hemipterus (Fourcroy 1785)	p	101	28	***	128	125	n.s.
Tachinus signatus Gravenhorst 1802	p	126	13	***	206	29	***
Pterostichus melanarius (Illiger 1798)	p	25	36	n.s.	132	169	*
Agonum micans (Nicolai 1822)	p	219	28	***	105	5	***
Atheta fungi (Gravenhorst 1806)	p	118	45	***	72	49	*
Agonum duftschmidi Schmidt 1994	p	45	65	n.s.	61	17	***
Barypeithes pellucidus (Boheman 1834)	h	1	2	n.s.	57	110	***
Pterostichus niger (Schaller 1783)	p	28	99	***	2	0	n.s.
Omalium rivulare (Paykull 1789)	d	30	71	***	8	2	n.s.
Poecilus versicolor (Sturm 1824)	p	1	0	n.s.	87	6	***
Oxytelus rugosus (Fabricius 1875)	d	37	45	n.s.	11	0	***
Stomis pumicatus (Panzer 1795)	p	10	4	n.s.	36	42	n.s.
Ocypus brunnipes (Fabricius 1781)	p	5	9	n.s.	15	62	***
Bembidion biguttatum (Fabricius 1779)	p	38	34	n.s.	14	0	***
Ocypus melanarius (Heer 1839)	p	21	6	**	25	23	n.s.
Oxyspelaphus obscurus (Herbst 1784)	p	18	31	n.s.	11	12	n.s.
Atomaria fuscicollis Mannerheim 1852	f	17	7	*	28	19	n.s.
Phosphuga atrata (Linnaeus 1758)	p	6	6	n.s.	36	22	n.s.
Loricera pilicornis (Fabricius 1775)	p	30	19	n.s.	7	0	**
Ancyrophorus flexuosus (Fairm.Lab. 1854)	p	3	50	***	2	0	n.s.
Bythinus burelli Denny 1825	p	28	26	n.s.	0	1	n.s.
Cidnorhinus quadrimaculatus (L. 1758)	h	17	1	***	34	2	***
Acrotrichis intermedia Gillm. 1845	f	32	6	***	10	1	**
Bembidion femoratum Sturm 1825	p	3	22	***	12	9	n.s.
Harpalus latus (Linnaeus, 1758)	p	1	0	n.s.	27	18	n.s.
Silpha tristis Illiger 1798	p	4	4	n.s.	35	1	***
Nebria brevicollis (Fabricius 1792)	p	1	35	***	3	1	n.s.
Individuals		3,248	2,941	***	3,998	3,057	***
Species		123	100	n.s.	152	96	***
Rarefaction diversity (at 2,941 individuals)		119	100	–	103	95	–

Classification of feeding guilds: *d* detritivore, *f* fungivore, *h* herbivore, *p* predator

The significance level of the χ^2-test is indicated as follows

n.s. $P > 0.05$

* $P \leq 0.05$

** $P \leq 0.01$

*** $P \leq 0.001$

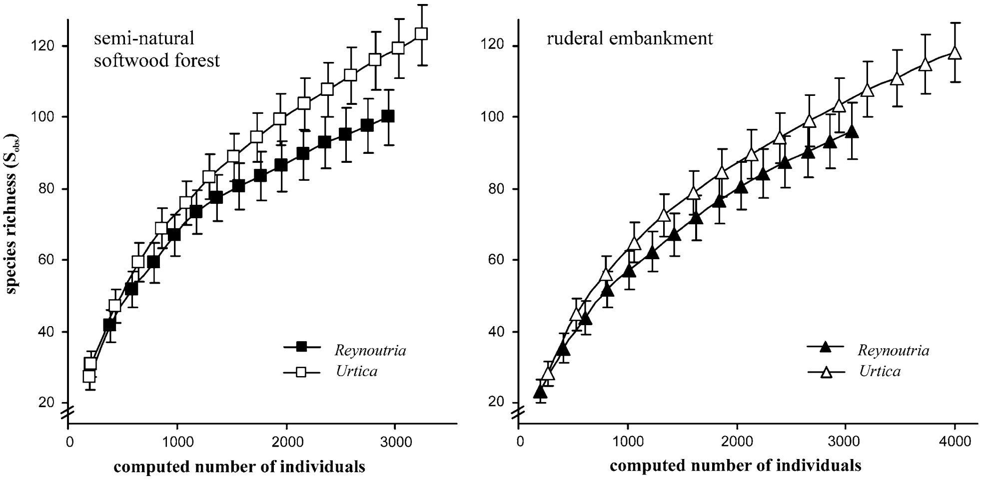

Fig. 1 Rarefaction analysis on the beetle fauna (S_{obs} with 95% confidence interval, 50 iterations) of the *Urtica*-dominated stands and the *Reynoutria* stands of the semi-natural softwood forest and the ruderal embankment

Urtica stands were preferred by *A. micans*, *Tachinus rufipes*, *Phosphaenus hemipterus*, *Acrotichis intermedia* and *Ocypus melanarius* (Fig. 2a). The *Reynoutria* stands were favoured by *Limodromus assimilis*, *Omalium rivulare*, *Pterostichus niger*, *Ancyrophorus flexuosus* and *Nebria bevicollis*. Rank orders of beetles from the ruderal embankment illustrate that the *Urtica* stand were preferred by *Tachinus signatus*, *A. micans*, *Poecilus versicolor*, *C. granulatus*, *Silpha tristis* and *Cidnorrhinus quadrimaculatus* (Fig. 2b). The *Reynoutria* stands were favoured by *L. assimilis*, *P. melanarius*, *B. pellucidus*, *Ocypus brunnipes*, *Omias mollinus* (Boh. 1834) and *Latridius nodifer* (Westw. 1839). The significance levels for the species with ≥ 40 individuals are given in Table 2.

In total, we observed a significanty increased number of detritivores ($\chi^2 = 5.7$), but decreased numbers of predators ($\chi^2 = 111.9$) and herbivores ($\chi^2 = 20.5$) in the *Reynoutria* stands (Fig. 3). The number of fungivores did not differ between vegetation stands ($\chi^2 = 2.4$).

Combined effects of location and vegetation

In a further step, we analysed the influence of location, site and vegetation in a nested ANOVA. Location and site usually had the most significant effect on the distribution pattern of the total number of individuals, species, feeding guilds and selected taxa (Table 3). However, there were three examples in which vegetation had the strongest influence. The two rove beetles *T. rufipes* and *Atheta fungi* preferred *Urtica* stands. Also, xerophilous ground beetles showed a high activity in the *Urtica* dominated stands of the ruderal embankment. In this location, xerophilous individuals made up 28% of the total number of ground beetles in the *Urtica* stands but only 5% in the *Reynoutria* stands. In the semi-natural softwood forest, the proportion of xerophilous beetles was <2% in both vegetation stands.

We found eight examples in which vegetation exhibited the second strongest influence: the species numbers and individuals of all Coleoptera, the three feeding groups of predators, fungivores and detritivores, the two ground beetles *L. assimilis* and *A. micans*, and the species numbers of Staphylinidae (Table 3). In seven cases, numbers were higher in *Urtica* stands. The only exception were detritivorous beetles that occurred in higher numbers in *Reynoutria* stands. The proportion of detritivorous beetles was about twice as high in the *Reynoutria* stands than in the *Urtica*-dominated stands (3 and 1.8%, respectively).

The qualitative Sørensen indices confirmed that species composition differed both between vegetation stands and between locations (ANOSIM, 999 Permutations: all $P \leq 0.002$). Similarly, the quantitative Morisita–Horn index confirmed dissimilarities between locations (all $P \leq 0.001$) and between the

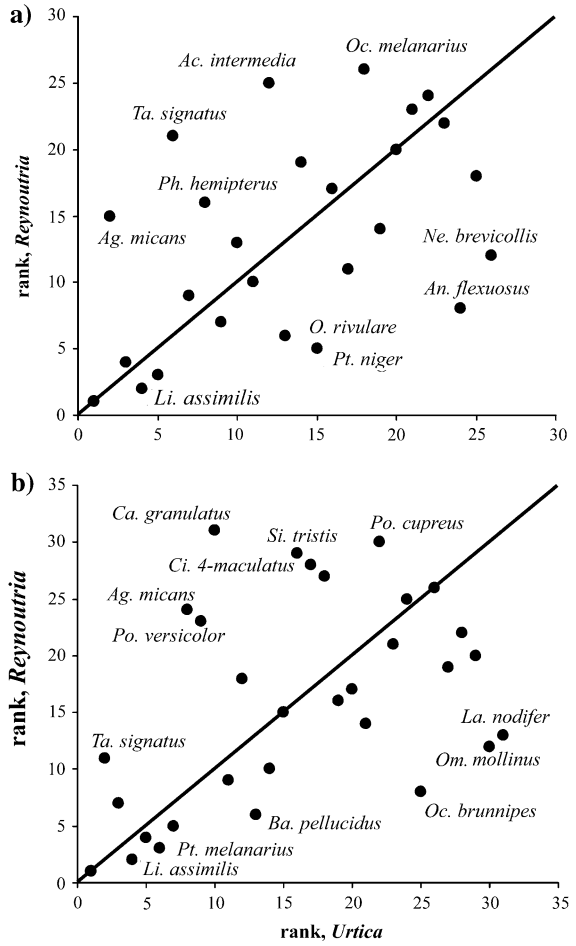

Fig. 2 Comparison of the ranks of the most abundant species (≥ 20 ind.) in the *Urtica*-dominated stands and the *Reynoutria* stands of **a** the semi-natural softwood forest and **b** the ruderal embankment. Deviations above or below the *line* indicate a higher prevalence in *Urtica*-dominated stands or *Reynoutria* stands, respectively. Strongly deviating species are identified with genus names abbreviated to the first two digits

vegetation stands on the ruderal embankment ($P = 0.003$). However, Morisita–Horn indices could not separate between the vegetation stands of the softwood forest ($P = 0.104$).

The specific assemblages of the locations and the plant stands were illustrated in a DCA (Fig. 4). The Eigenvalues of the first and the second axis were 0.32 and 0.11, respectively. The first two axes cover 50.2% of the total variance. The Eigenvalues of higher axes were lower than 0.07 and only marginally contributed to the entire model. Figure 4 shows that the gradient described by axis 1 separated the beetle assemblages of the two locations. Axis 2 describes a gradient that separates the beetle assemblages from the two plant species.

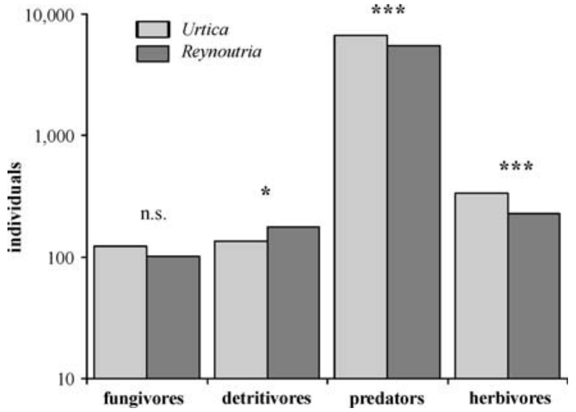

Fig. 3 Total abundance of the feeding groups in the two vegetation stands. The significance level of the χ^2-test is indicated as follows: n.s.$P > 0.05$; *$P \leq 0.05$; ***$P \leq 0.001$

Discussion

Differences between locations

Many beetles species are highly specialised and thus are valuable indicator species for habitat quality assessment (Boháč and Fuchs 1991; Boscaini et al. 2000; Bonn and Schröder 2001). As a consequence, the assemblages of the semi-natural softwood forest and those of the ruderal embankment were well separated. The habitat preferences of the dominant species reflect the differences between the locations. The prevalence of hygrophilous species is typical for close to natural wetland conditions (Günther and Assmann 2005). The hygrophilous ground beetle *P. atrorufus* that dominated the assemblages in the semi-natural softwood forest prefers moist floodplain forests, whereas the myrmecophagous rove beetle *D. canaliculata* commonly inhabits dry ruderal places (Koch 1989–1992). Thus, the severe transformation of the floodplain along the lower River Wupper is mirrored in the beetle assemblages. The effects of site are due to the small-scale heterogeneity that is typical of floodplain habitats (Robinson et al. 2002). Small-scale habitat preferences have for example been found for soil moisture and ground beetles (Antvogel and Bonn 2001) and the amount of detritus and rove beetles of the genus *Stenus* (Betz 1998).

Table 3 Nested ANOVA on the influence of location (loc), site and vegetation (veg) on the beetles

	Loc		Loc(site)		Loc(site(veg))		Model		R^2
	F	P	F	P	F	P	F	P	
Coleoptera									
Species	10.1	0.003	**9.2**	**1×10^{-5}**	7.1	2×10^{-5}	8.1	9×10^{-8}	0.651
Individuals	2.1	0.149	**7.5**	**9×10^{-5}**	5.3	3×10^{-4}	5.8	7×10^{-6}	0.571
Predators	1.1	0.299	**6.2**	**6×10^{-4}**	4.6	0.001	4.9	5×10^{-5}	0.527
Fungivores	**13.2**	**7×10^{-4}**	1.6	0.195	3.1	0.012	3.5	0.001	0.443
Detritivores	**86.8**	**2×10^{-12}**	1.5	0.217	3.6	0.005	10.4	2×10^{-9}	0.705
Herbivores	**64.1**	**2×10^{-10}**	10.9	2×10^{-6}	2.7	0.026	11.2	6×10^{-10}	0.720
Lampyridae	**24.3**	**1×10^{-5}**	4.7	0.003	2.3	0.047	5.2	3×10^{-5}	0.543
Curculionidae	**88.0**	**2×10^{-12}**	14.1	1×10^{-7}	2.4	0.045	14.4	1×10^{-11}	0.768
Carabidae									
Species	8.7	0.005	**4.9**	**0.002**	3.0	0.013	4.2	2×10^{-4}	0.491
Individuals	**139**	**9×10^{-16}**	23.0	1×10^{-10}	6.8	3×10^{-5}	24.7	4×10^{-16}	0.850
Silvicolous	84.0	4×10^{-12}	**30.5**	**1×10^{-12}**	11.3	8×10^{-8}	24.9	4×10^{-16}	0.851
Hygrophilous	**151**	**2×10^{-16}**	22.7	1×10^{-10}	6.8	3×10^{-5}	25.7	2×10^{-16}	0.855
Xerophilous	8.2	0.006	3.6	0.012	**4.2**	**0.002**	4.3	2×10^{-4}	0.499
Pa. atrorufus	**300**	**3×10^{-22}**	7.2	1×10^{-4}	4.3	0.002	32.2	2×10^{-18}	0.881
Li. assimilis	6.2	0.016	**27.9**	**5×10^{-12}**	15.3	1×10^{-9}	19.0	7×10^{-14}	0.813
Pt. strenuous	39.8	8×10^{-8}	**18.7**	**3×10^{-9}**	5.8	1×10^{-4}	13.6	3×10^{-11}	0.757
Ca. granulatus	**297**	**3×10^{-22}**	4.2	0.006	2.3	0.052	29.8	1×10^{-17}	0.872
Pt. melanarius	26.9	4×10^{-6}	**15.1**	**5×10^{-8}**	8.0	5×10^{-6}	12.3	1×10^{-10}	0.738
Ag. micans	**151**	**2×10^{-16}**	2.9	0.030	14.0	4×10^{-9}	22.5	3×10^{-15}	0.837
Staphylinidae									
Species	**63.1**	**3×10^{-10}**	1.8	0.155	2.7	0.024	7.8	1×10^{-7}	0.642
Individuals	**241**	**2×10^{-20}**	10.4	4×10^{-6}	6.1	9×10^{-5}	29.0	2×10^{-17}	0.869
Ta. signatus	2.8	0.101	3.3	0.019	**15.2**	**1×10^{-9}**	9.7	6×10^{-9}	0.691
At. fungi	11.0	0.002	0.7	0.588	**9.8**	**5×10^{-7}**	6.6	2×10^{-6}	0.601

Species were tested, if $n \geq 200$ individuals. Bold numbers indicate the factor with the lowest P-value

$df = 1, 4, 6$ and 11 for loc, loc(site), loc(site(veg)) and model, respectively

Differences between *Urtica* and *Reynoutria* stands

Differences between vegetation stands resulted from different aspects of bottom-up effects. Food quality and quantity are known to structure insect assemblages (Strong et al. 1984). *Cidnorhinus quadrimaculatus*, for example, solely feeds on *Urtica* (Lohse 1983). The preference of the malacophagous silphid *P. atrata* for *Urtica* stands may be because snails are less abundant in *Reynoutria* stands (Kappes et al., 2007). Also, *Reynoutria* litter harbours a distinct microfungal assemblage (Beerling et al. 1994). These fungi may be of low palatability for species such as *T. signatus* and *Acrotrichis intermedia* that are at least partially fungivorous (Koch 1989–1992).

The effects on species richness, abundance and assemblage similarities were more pronounced on the ruderal embankment. We thus assume that the two vegetation stands strongly differ in physical characteristics especially in disturbed habitats. Microclimate is one factor known to influence the distribution pattern of species. The higher incidence of silvicolous species such as *L. assimilis* and *O. brunnipes* and the lower abundance of xerophilous individuals suggest that the microclimate in the *Reynoutria* stands of the ruderal embankment partially mimics that of forest habitats.

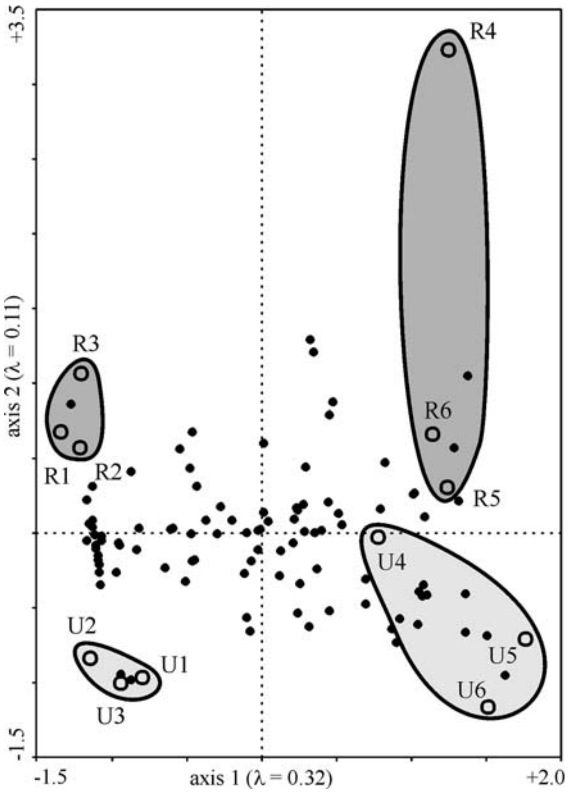

Fig. 4 Biplot of the DCA of the beetle fauna from the *Urtica*-dominated stands (*U*) and the *Reynoutria* stands (*R*) of the semi-natural softwood forest (sites 1–3) and the ruderal embankment (sites 4–6). The *circles* comprise the vegetation stands of each location. The *black dots* represent the species scores (96 species with ≥ 5 ind.)

Theories on biodiversity predict a higher number of animal species, and a higher diversity in species-rich vegetation (Siemann 1998; Siemann et al. 1998). Our results on the lower beetle species richness and rarefaction diversity in the monospecific *Reynoutria* stands are in accordance with these theories. *Reynoutria* invasion consequently poses a threat to the species-rich *Urtica*-dominated floodplain habitats. According to Siemann et al. (1998) there is no effect of plant diversity on arthropod abundance. However, we also found negative effects of *Reynoutria* stands on total beetle abundance and both herbivores and predators.

Detritivore beetles were the only feeding group that had a higher abundance in *Reynoutria* stands. Similarly, the relative share of the detritivorous diplopods and isopods increases in *Reynoutria* stands (Kappes et al., 2007). Detritivores seemed to have profited from the increased productivity and the resulting high-detritus supply throughout the year. Our results on detritivore abundance also coincide with those of Levin et al. (2006), who observed a shift from an algae-based food web to a detritus-based food web following codgrass invasion in a coastal wetland. Obviously, highly productive invaders such as *Reynoutria* alter link strengths in trophic cascades shifting primary producer-based food webs to detritus-based food webs.

Acknowledgements Mrs. Birgit Schmitz (ULB Düsseldorf) issued the sampling permission for the nature reserve at Urdenbach (AZ 68/21-ULB-SZ). Furthermore, we are grateful to Rebecca Lay and Katrin Thelen for assistance during the field work and to two anonymous referees for valuable comments.

References

Antvogel H, Bonn A (2001) Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. Ecography 24:470–482

Baars MA (1979) Catches in pitfall traps in relation to mean densities of carabid beetles. Oecologia 41:25–46

Beerling DJ, Dawah HA (1993) Abundance and diversity of invertebrates associated with *Fallopia japonica* (Houtt. Ronse Decrane) and *Impatiens glandulifera* (Royle): two alien plant species in the British Isles. Entomologist 112:127–139

Beerling DJ, Bailey JP, Conolly AP (1994) *Fallopia japonica* (Houtt.) Ronse Decraene. J Ecol 82:959–979

Betz O (1998) Comparative studies on the predatory behaviour of *Stenus* spp. (Coleoptera: Staphylinidae): the significance of its specialized labial apparatus. J Zool Lond 244:527–544

Boháč J, Fuchs R (1991) The structure of animal communities as bioindicators of landscape deterioration. In: Jeffrey DW, Madden B (eds) Bioindicators and environmental management. Academic, Prague, pp 165–178

Bonn A, Schröder B (2001) Habitat models and their transfer for single and multispecies groups: a case study of carabids in an alluvial forest. Ecography 24:483–496

Boscaini A, Franceschini A, Maiolini B (2000) River ecotones: carabid beetles as a tool for quality assessment. Hydrobiologia 422/423:173–181

Brose U (2003) Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? Oecologia 135:407–413

Colwell RK (2005) EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. Persistent URL <purl.oclc.org/estimates>

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166

Davis BNK (1983) Insects on nettles. Naturalists' handbooks 1. Cambridge University Press, Cambridge

Freude H, Harde KW, Lohse GA (1964–2004) Die Käfer Mitteleuropas, vol 1–14. Goecke and Evers, Krefeld

Günther J, Assmann T (2005) Restoration ecology meets carabidology: effects of floodplain restitution on ground beetles (Coleoptera, Carabidae). Biodivers Conserv 14:1583–1606

Herrera AM, Dudley TL (2003) Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. Biol Invasions 5:167–177

Inoue M, Nishimura H, Li H-H, Mizutani J (1992) Allelochemicals from *Polygonum sachalinense* Fr. Schm. (Polygonaceae). J Chem Ecol 18:1833–1840

Kappes H, Lay R, Topp W (2007) Changes in different trophic levels of litter-dwelling macrofauna associated with giant knotweed invasion. Ecosystems. doi:10.1007/s10021-007-9052-9

Koch K (1989–1992) Die Käfer Mitteleuropas: Ökologie, vol 1–3. Goecke and Evers, Krefeld

Lepš J, Šmilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge

Levin LA, Neira C, Grosholz ED (2006) Invasive cordgrass modifies wetland trophic function. Ecology 87:419–432

Lohse GA (1983) Ceutorhynchinae. In: Freude H, Harde KW, Lohse GA (eds) Die Käfer Mitteleuropas, vol 11. Goecke and Evers, Krefeld, pp 180–253

Luff ML (1975) Some features influencing the efficiency of pitfall traps. Oecologia 19:345–357

Pyšek P, Prach K (1993) Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. J Biogeogr 20:413–420

Robinson CT, Tockner K, Ward JV (2002) The fauna dynamic riverine landscapes. Freshw Biol 47:661–677

Siemann E (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 79:2057–2070

Siemann E, Tilman D, Haarstad J, Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. Am Nat 152:738–750

Strong DR, Lawton JH, Southwood TRE (1984) Insects on plants. Community patterns and mechanisms. Blackwell, London

Sukopp H, Starfinger U (1995) *Reynoutria sachalinensis* in Europe and in the far east: a comparison of the species ecology and its native and adventive distribution range. In: Pyšek P, Prach K, Rejmanek M, Wade M (eds) Plant invasions—general aspects and special problems. SPB Academic Publ., Amsterdam, pp 151–159

Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13

Weston LA, Barney JN, DiTommaso A (2005) A review of the biology and ecology of three invasive perennials in New York State: Japanese knotweed (*Polygonum cuspidatum*), mugwort (*Artemisia vulgaris*) and pale swallow-wort (*Vincetoxicum rossicum*). Plant Soil 277:53–69

Zabel J, Tscharntke T (1998) Does fragmentation of *Urtica* habitats effect phytophagous and predatory insects differentially? Oecologia 116:419–425

Zedler JB, Kercher S (2004) Causes and consequences of invasive plants in wetlands: opportunities, opportunists and outcomes. Criti Rev Plant Sci 23:431–452

Zimmermann K, Topp W (1991) Anpassungserscheinungen von Insekten an Neophyten der Gattung *Reynoutria* (Polygonaceae) in Zentraleuropa. Zool Jahrb Syst Ökologie Tiere 118:377–390