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An invasive species may be better than none: invasive signal and native noble crayfish have similar community effects

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1. Human activities have resulted in the decline of native crayfish and promoted the spread of invasive crayfish species in European fresh waters, threatening ecosystem structure and functioning.
2. We compared effects of native noble crayfish (*Astacus astacus*), invasive signal crayfish (*Pacifastacus leniusculus*) and of the absence of crayfish on leaf litter breakdown and invertebrate prey density and biomass in stream ecosystems.
3. In microcosm experiments, invertebrate shredder density was significantly reduced by crayfish presence but similarly affected by the two crayfish species. While crayfish did not directly influence leaf litter breakdown, their presence reduced litter decay rates through predation on invertebrate shredders (i.e. trophic cascade). These effects were again similar between native and invasive crayfish but differed among shredder prey species.
4. Field experiments confirmed that leaf litter breakdown was significantly reduced by crayfish. Although total invertebrate density was not affected by crayfish predation, species-specific effects were observed (e.g. Limnephilidae [Trichoptera] densities were reduced in the presence of crayfish) but did not differ between native and invasive species.
5. Our results show that crayfish can have strong, but species-specific, effects on invertebrate prey and indirect effects on leaf litter breakdown. Contrary to previous findings and popular belief, results also indicate that native noble crayfish and invasive signal crayfish have similar effects on stream communities. Hence, from a management perspective, it may be preferable to have invasive crayfish than no crayfish when impairment results in unsuitable habitats for native species.

Keywords: *Astacus astacus*, crayfish, invasive species, litter breakdown, *Pacifastacus leniusculus*

Introduction

Human activities promote the wide dispersion of species outside their native geographical range, and biological translocations are regarded as a significant component of global environmental changes (Vitousek *et al.*, 1997; Vilà *et al.*, 2009). Non-indigenous species can become invasive, potentially altering ecosystem structure and functioning and threatening native biological diversity (Lodge, 1993; Vitousek *et al.*, 1997; Rahel, 2002; Strayer *et al.*, 2006; Gherardi *et al.*, 2011; Strayer, 2012). Since

human-disturbed ecosystems are also at higher risk of biological invasions, continental fresh waters, often under constant pressure from human activities (e.g. pollution, irrigation, canalisation), are particularly vulnerable to invasive species (Ricciardi & Rasmussen, 1999; Dextrase & Mandrak, 2006; Strayer, 2010).

Crayfish are among the most translocated, either intentionally or accidentally, aquatic invertebrates worldwide (Hobbs, Jass & Huner, 1989; Strayer, 2010; Hudina *et al.*, 2012). For example, several North American crayfish species have been introduced into Europe,

posing a potential threat to native crayfish species and freshwater communities (Olsson *et al.*, 2009). Crayfish are the largest and among the longest lived invertebrate organisms in temperate fresh waters and are often present at high densities (Gherardi, 2006; Gherardi *et al.*, 2011). They play disproportionately important roles on community structure and energy flow via food webs (Momot, 1995; Nyström, Brönmark & Granéli, 1996). Crayfish can directly or indirectly modify habitat structure and alter the availability of resources to other species. For example, crayfish influence sediment distribution and organic matter breakdown rates (Creed & Reed, 2004; Usio & Townsend, 2004) and reduce fine particulate organic matter and inorganic sediment deposition and accumulation through bioturbation, thus modifying availability of interstitial habitats for smaller invertebrates included non-prey taxa (Zhang, Richardson & Negishi, 2004; Helms & Creed, 2005). Whether native or introduced, crayfish also constitute the main prey of numerous predator species, such as fish (Blake, 1995), birds (Rodriguez *et al.*, 2005) and mammals, including rare or endangered species like the otter *Lutra lutra* (Slater & Rayner, 1993; Freeman *et al.*, 2010).

In areas where no indigenous equivalent is present, the introduction of non-native crayfish species can have strong effects on ecosystem structure and function (Lodge & Lorman, 1987; Charlebois & Lamberti, 1996; Lodge *et al.*, 1998; Crawford, Yeomans & Adams, 2006; Gherardi & Acquistapace, 2007; Freeman *et al.*, 2010). While they clearly have direct effects on prey, altering their abundance and distribution, they may also indirectly modify interactions within communities, resulting in trophic cascades (Gherardi, 2007). Crayfish influence food webs at virtually all trophic levels (Lodge *et al.*, 1994; Whitley & Rabeni, 1997; Nyström, Brönmark & Granéli, 1999; Usio & Townsend, 2004; Bondar *et al.*, 2005). These effects can be accentuated when introduced species face low predation or competition pressure from native species and prey on taxa lacking defensive adaptations against the new species (Nyström *et al.*, 2001). Overall, resource acquisition by large invasive invertebrates creates new trophic relationships potentially leading to dramatic direct and indirect effects on ecosystems (Lodge, 1993; Woodward & Hildrew, 2001; Stenroth & Nyström, 2003). When invasive species replace indigenous crayfish, their behaviour and food intake should not be completely novel to colonised ecosystems (Gherardi *et al.*, 2011). However, invader effects may still be strong if they reach higher densities and/or larger size than native species (Strayer *et al.*, 2006; Gherardi, 2007; Gherardi *et al.*, 2011). Even at similar size and/or den-

sity, introduced species may display broader diet ranges, be more efficient predators and/or have higher resource intakes, thus exerting higher pressure on native communities than native crayfish (Nyström & Strand, 1996; Usio *et al.*, 2006; Haddaway *et al.*, 2012).

Evaluating the effects of native and invasive crayfish species in a particular ecosystem is thus essential to determine potential consequences of native crayfish extinction and/or invasion by non-native species. Invader effects often depend on abundance and distinctiveness in resources exploitation (i.e. how much invaders' effects differ from those of native species in the invaded community; Strayer *et al.*, 2006). If native and invasive species are substitutable, no significant changes in ecosystem structure or functioning should be observed at similar abundance/biomass (Walker, 1992; Lawton & Brown, 1993; Usio *et al.*, 2006). However, seemingly analogous species might still have different effects on ecosystems (Chalcraft & Resetarits, 2003; Jonsson & Malmqvist, 2003; Bjelke & Herrmann, 2005).

It is often suggested that alterations in crayfish assemblages, via loss of native species and/or introduction of exotic species, may have significant repercussions for native communities and ecosystem function (Schofield *et al.*, 2001). In this study, we tested the effects of crayfish on leaf litter breakdown and invertebrate communities in an oligotrophic stream ecosystem. We performed both field and laboratory experiments to quantify crayfish effects on basal resources and invertebrate consumers. We also compared effects of the native noble crayfish (*Astacus astacus* L.) and that of the species that most often replaces it, the introduced signal crayfish (*Pacifastacus leniusculus* Dana), on these resources.

Methods

Laboratory experiments

Study species, collection and experimental design. Native noble crayfish (*A. astacus*) and invasive signal crayfish (*P. leniusculus*) were captured using baited traps. *Astacus astacus* were collected in ponds near Loromontzey, north-eastern France (48°26'N, 6°21'E) and *P. leniusculus* in Lake Pont, eastern France (47°26'N, 4°21'E). Separate equipment was used to avoid possible transfer of crayfish plague between sites and from captured *P. leniusculus* to captured *A. astacus*. For the same reason, crayfish were kept separately (i.e. by species) in large holding tanks (500 L, 25 crayfish per tank) filled with continuously aerated tap water and fed regularly with frozen fish morsels.

Four prey species, two caddisfly larvae (Trichoptera, Limnephilidae) and two amphipod crustaceans (*Gammarus fossarum* and *G. roeseli*), were selected for their contrasting size, mobility and anti-predator defences. Limnephilidae have large, case-building larvae while adult amphipods are active swimmers. The two limnephilid larvae had similar sizes (mean dry body mass \pm SE = 27.1 ± 0.7 and 28.1 ± 0.8 mg, respectively) but build protective cases using different material (plant detritus versus sand) with potentially contrasting case resistance and vulnerability to predators. They are hereafter referred to as Limnephilidae sp.1 (plant detritus case) and Limnephilidae sp.2 (sand case). While *G. roeseli* can grow larger than *G. fossarum* (Pöckl, 1992), we selected amphipods of similar sizes for experiments ($1.0 \text{ cm} < \text{total body length} < 1.3 \text{ cm}$). Interspecific differences in vulnerability to predators may exist between the two amphipods (Bollache *et al.*, 2006). Invasive *G. roeseli* differ from native *G. fossarum* in the presence of three robust spines and a thicker, more resistant exoskeleton (Lagrue & Bollache, 2006), resulting in differences in amphipod mass at equivalent body length (mean dry body mass \pm SE = 5.2 ± 0.2 and 6.6 ± 0.2 mg for *G. fossarum* and *G. roeseli*, respectively). All four invertebrate species are shredders and participate actively in leaf litter breakdown (Tachet *et al.*, 2009). Limnephilidae were collected from the Suzon River ($47^{\circ}24'N$, $4^{\circ}53'E$) and amphipods from the Meuzin River ($47^{\circ}2'N$, $4^{\circ}59'E$). Invertebrates were captured using dip nets, taken to the laboratory and kept separately in 50-L containers filled with aerated water and alder [*Alnus glutinosa* (L.) Gaertn.] leaves for food prior to the laboratory experiments.

Laboratory microcosms were used to assess crayfish predation efficiency and prey intake at variable prey densities and to quantify predator effects on invertebrate density and litter breakdown. Aquaria ($30 \times 18 \times 20 \text{ cm}$) were filled with 10 L of aerated water and 5 cm of gravel substratum ($3 \text{ mm} < \text{Ø} < 4 \text{ mm}$). Temperature was maintained at 14°C under a 12-h light/12-h dark photoperiod. As both prey and crayfish species are mostly nocturnal, natural moonlight was reproduced using specially designed lamps («Night Glo, Exo Terra», 40 W, 220–240 V, 50 Hz) to avoid complete darkness.

Crayfish functional response. Differences in functional response of the two crayfish species to increasing prey densities were quantified and compared over 24 h using *G. fossarum* amphipods (total body length $>1 \text{ cm}$). Nine different initial prey densities (i.e. initial number of prey per aquarium) were used (4, 8, 12, 20, 30, 60, 100, 150

and 200), and 10 replicates per crayfish species per prey density were run.

An individual of either species of crayfish was first put in each aquarium and allowed to acclimatise for 6 h. Amphipod prey were then added, and after 24 h, surviving amphipods were counted and the crayfish measured (total body length from the tip of the rostrum to the end of the telson, to the nearest 1 mm) to control for possible predator size effects on prey consumption. Predator and prey individuals were used only once.

Amphipods can have cannibalistic tendencies, especially when deprived of food (Dick, 1995; MacNeil, Dick & Elwood, 1997). A control treatment was used to assess cannibalism effects on final prey numbers. At the highest density (200 *G. fossarum* per aquarium), 10 replicates were run with no predator to estimate prey mortality due to cannibalism.

Crayfish effects on prey mortality and litter breakdown. Interspecific differences between *A. astacus* and *P. leniusculus* effects on four different prey species and litter breakdown rate were quantified and compared over a 6-day period. Autumn-shed leaves of black alder (*A. glutinosa* Gaertn.) were provided as a food source in all treatments and used to determine leaf litter breakdown rates. This allowed testing for potential variations in cascading effects on leaf litter breakdown. Batches of air-dried alder leaves were weighed ($2 \pm 0.05 \text{ g}$), wetted, enclosed in nylon mesh bags (10 mm mesh size) and incubated for a week in water-containing organic matter debris from the Suzon River to allow for microbial colonisation and litter conditioning (Bärlocher & Kendrick, 1975). One leaf litter bag was placed in each aquarium at the beginning of each experiment.

All possible combinations of predator (no predator, *A. astacus* or *P. leniusculus*) and prey (no prey, Limnephilidae sp.1, sp.2, *G. fossarum* or *G. roeseli*) were tested (16 replicates per predator–prey combination). No predator–no prey combinations served as control and accounted for the combined physicochemical effects of water (i.e. leaching) and microorganisms (fungi and bacteria) on litter breakdown rate (Boulton & Boon, 1991). Predator-only and prey-only treatments were used to quantify litter consumption by each species.

In combinations including crayfish predators, one crayfish was added to each aquarium and allowed to acclimatise for 6 h. No prey, 20 Limnephilidae or 60 amphipods were then added to each aquarium. Initial numbers of prey were chosen to represent roughly equivalent prey biomass and reflect natural densities at sampling sites. After 6 days, remaining alder leaves

were rinsed with tap water, dried at 70 °C for 72 h and weighed to the nearest 0.01 g. Proportion of leaf mass remaining was expressed as the ratio of final to initial litter dry mass in each aquarium. Surviving prey were counted to determine prey mortality and then dried at 70 °C for 72 h and weighed (dry mass) to the nearest mg. Proportions of prey consumed (i.e. prey mortality) were expressed as the ratio between numbers of missing prey after 6 days and initial prey numbers.

Field experiments

Study site and experimental design. Field experiments were carried out in May 2011 in the Suzon River (47°24'14.45"N, 4°53'1.46"E), eastern France. This river is characterised by stable water levels (0.4 m mean depth, 0.5 m s⁻¹ mean velocity) and temperatures (12 °C mean water temperature) due to constant subterranean karstic input. It is heavily shaded by riparian forests and contains no aquatic macrophytes, and food webs are mostly based on terrestrial litter inputs.

Forty cages (50 × 30 × 20 cm) made of plastic wire netting (14 mm mesh size) were divided into three compartments of equal size. A PVC tube ($L = 15$ cm, $\varnothing = 4$ cm) was added to each compartment as a refuge for crayfish. One individual of *A. astacus* and one of *P. leniusculus* were measured and added in separate cage compartments. The third compartment did not contain a crayfish predator and was a control (no predator). Cages were deployed haphazardly in a single homogeneous 50-m stretch of the river and were maintained in position and in contact with the river substratum using iron rods.

Leaf litter breakdown. Crayfish effects and potential differences between crayfish species on litter breakdown rates were assessed using alder leaf litter bags. Batches of air-dried leaves were weighed (4 ± 0.05 g), wetted and enclosed in nylon mesh bags (10 mm mesh size). One alder leaf litter bag was fixed flat at the bottom of each cage compartment (40 bags per treatment, 120 in total). Cages were retrieved on three sampling dates to examine predator effects over time.

Thirteen cages were retrieved after 7 days, 13 after 14 days and the remaining 14 after 28 days. Leaf bags were immediately stored individually in plastic zip-lock bags and maintained at stream temperature during transport. In the laboratory, alder leaves were rinsed with tap water to remove sediment and exogenous organic matter. Remaining alder leaves were dried at 70 °C for 72 h and weighed to the nearest 0.01 g to estimate the proportion of litter mass remaining.

Fungal biomass. We tested for differences in fungal biomass in alder leaf litter among treatments as a potential confounding factor in leaf litter breakdown rate (Bärlocher & Kendrick, 1975). Leaf discs ($\varnothing = 1$ cm) cut from alder leaves from litter bags were immediately frozen (-20 °C) for fungal biomass determination. Five leaf discs per litter bag from the second and third sampling dates (i.e. 14 and 28 days of incubation) and three treatments (*A. astacus*, *P. leniusculus* and control) were used to determine ergosterol content as a measure of fungal biomass (Gessner, 2005). Leaf discs were freeze-dried and weighed to the nearest 0.1 mg before analysis. Ergosterol measurements were based on solid-phase extraction (cartridges Waters Oasis HLB, 60 mg, 3 mL) and high-performance liquid chromatography (Lecerf & Chauvet, 2008). Fungal biomass in alder litter was expressed as ergosterol mass (in μg) per gram of litter dry mass.

Invertebrate density and biomass. Leaf-colonising invertebrates were collected in a 0.5-mm-mesh sieve and preserved in 70% ethanol. They were later sorted, counted and identified to family (Tachet *et al.*, 2009). Invertebrates were then dried at 70 °C for 72 h and weighed (dry mass) to the nearest mg. Density and biomass were expressed per leaf litter bag.

Statistics

Laboratory experiments. An ANCOVA was used to test for potential differences in the number of prey eaten between the two crayfish species and the effects of prey density (i.e. initial prey number) on crayfish prey intake. Crayfish size was included as a covariate to control for possible effects of predator body size on prey intake. In addition, we used a nonlinear regression to fit a Hollings type II functional response equation to the data for each crayfish species: $N = N_0 a / (1 + N_0 a h)$, where N is the number of prey eaten, N_0 is the initial number of prey, a is the attack rate on prey, and h is prey-handling time. ANOVAs were used to test for the effects of predator (presence and species) on prey mortality and the combined effects of predator and prey (presence and species) on the proportion of leaf litter mass remaining. Proportions of prey consumed and litter mass remaining were transformed ($Y = \arcsin(\sqrt{X})$ where X is the proportion of prey consumed or leaf mass remaining) to meet parametric tests requirements. *Post hoc* tests (Tukey's HSD) were used when appropriate.

Field experiments. Nonlinear regression ($M = M_0 e^{-kt}$) of the proportion of leaf litter mass remaining (M) versus

time (t in days) was used to estimate exponential breakdown rates (k) of alder litter in the three treatments (control, *A. astacus* and *P. leniusculus*). The intercept M_0 was not fixed *a priori* to the theoretical value of 1 to achieve normally distributed residuals. An ANCOVA with incubation time (days) as a covariate was applied to test predator effects (i.e. crayfish presence and species) on litter breakdown rate. For the ANCOVA, proportion of litter mass remaining was ln-transformed to achieve a linear relationship with time.

A two-way ANOVA was run to test for effects of litter incubation time and crayfish treatment (i.e. crayfish presence and species) on fungal biomass. Finally, we used ANCOVAs to examine the effects of crayfish treatment and litter incubation time on invertebrate dynamics (density and biomass). Remaining leaf litter mass was included as a covariate to correct for change in habitat (leaf litter) availability to invertebrates due to litter breakdown. Invertebrate density and biomass were log-transformed before analyses to normalise the data. *Post hoc* tests (Tukey's HSD) were used when appropriate, and all tests were performed with a 0.05 type I error risk using STATISTICA Software 6.0 (StatSoft Inc., Tulsa, OK, USA).

Results

Laboratory experiments

Crayfish functional response. Predator size did not influence prey consumption ($F_{1,161} = 2.83$, $P = 0.095$). *Astacus astacus* consumed more prey than *P. leniusculus* ($F_{1,161} = 321.6$, $P < 0.0001$) although the magnitude of this interspecific difference changed with prey density (crayfish species \times prey density interaction: $F_{8,161} = 12.3$, $P < 0.0001$; Fig. 1). When initial prey density was above 60 *G. fossarum* per aquarium, there was no significant difference in the number of prey consumed by the two crayfish species (Tukey's HSD, d.f. = 161, all $P > 0.05$; Fig. 1). *Gammarus fossarum* cannibalism was minor compared with crayfish-induced mortality (Mann-Whitney *U*-test, $Z = 3.78$ and 3.55 , $P = 0.0002$ and $P = 0.0004$ compared with *A. astacus* and *P. leniusculus*, respectively; Fig. 1). The functional response of *A. astacus* to increasing prey density increased steeply and reached a higher asymptote than *P. leniusculus* (Fig. 1). Least-square estimate of model parameters indicated that attack rate ($a \pm SE$) and prey-handling time ($h \pm SE$) were three to four times higher in *A. astacus* (1.47 ± 0.25 and 0.017 ± 0.001) than in *P. leniusculus* (0.50 ± 0.11 and 0.004 ± 0.001).

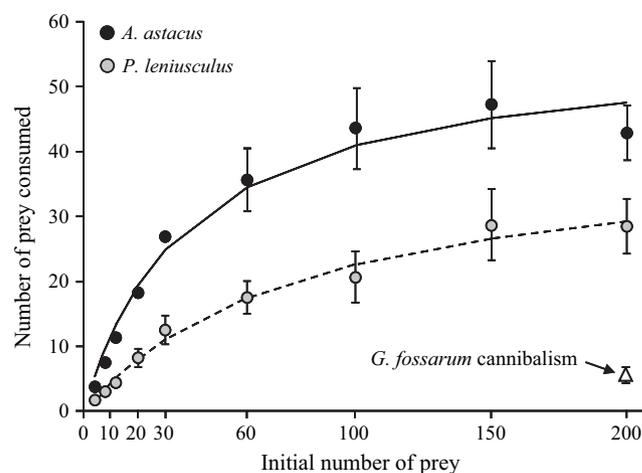


Fig. 1 Relationship between the initial number of prey (*Gammarus fossarum*) at the beginning of the 24-h experiment and the number of prey consumed (mean \pm SE) by *Astacus astacus* (native crayfish) and *Pacifastacus leniusculus* (invasive). Cannibalism (control) among prey (*G. fossarum*) in absence of predator was also estimated and is presented in the figure for comparison. Calculated Hollings type II response is also shown for each crayfish species.

Crayfish effects on prey mortality and litter breakdown. There was no size difference between crayfish species used in this experiment (ANOVA, $F_{1,152} = 0.71$, $P = 0.401$; mean size in cm \pm SE = 8.35 ± 0.07 and 8.44 ± 0.09 for *A. astacus* and *P. leniusculus*, respectively), so crayfish size was not considered in the following analyses.

Crayfish had a significant effect on prey mortality (ANOVA, $F_{2,181} = 201.3$, $P < 0.0001$). Native and invasive crayfish significantly increased mortality of all prey species compared with the respective control treatments (Tukey's HSD, d.f. = 171, all $P < 0.0001$; Fig. 2a). Mortality was significantly different among prey species (ANOVA, $F_{3,180} = 6.03$, $P = 0.0006$). In control treatments, mortality due to cannibalism did not differ among prey species (Tukey's HSD, d.f. = 171, all $P > 0.05$). Crayfish-induced mortality varied among prey species (Fig. 2a). In small, fast-swimming amphipod prey, proportions of *G. fossarum* and *G. roeseli* consumed were not different between crayfish species (Tukey's HSD, d.f. = 171, both $P > 0.05$; Fig. 2a). This is consistent with results obtained in the previous experiment on daily prey intake at similar prey density. Although crayfish-induced *G. roeseli* mortality seemed slightly lower than that of *G. fossarum* (Fig. 2a), differences in mortality between the two amphipod species were not significant (Tukey's HSD, d.f. = 171, both $P > 0.05$). Crayfish consumed significantly more large, case-building, Limnephilidae larvae sp.1 (plant detritus case) than amphipods (Tukey's HSD, d.f. = 171, all $P < 0.05$;

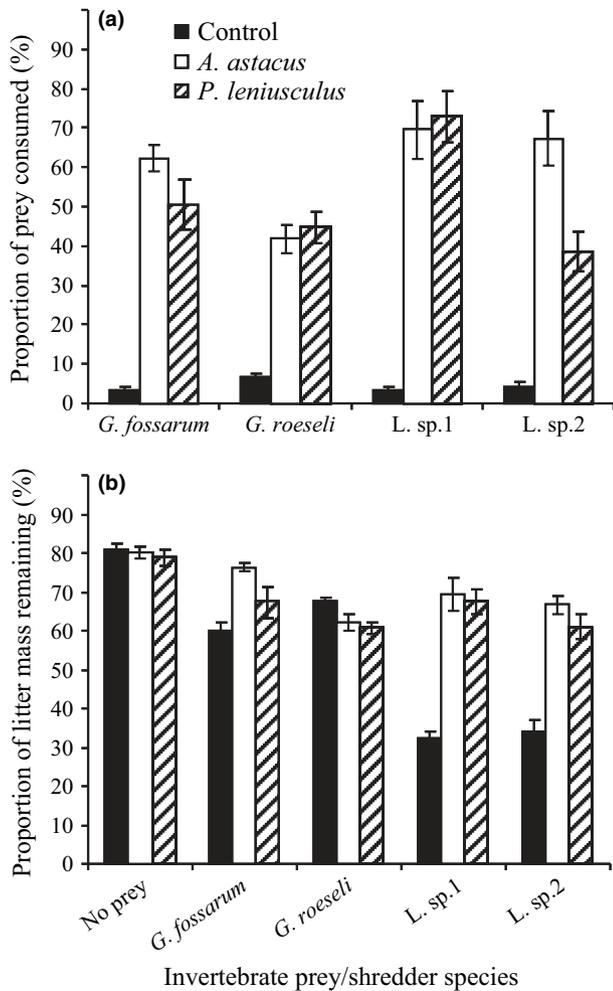


Fig. 2 (a) Proportion (%; mean \pm SE) of prey consumed in the three treatments (control, *Astacus astacus* and *Pacifastacus leniusculus*) for the four prey species. Rates of cannibalism among prey in the absence of predator are represented by the control treatments for each prey species. (b) Proportion (%; mean \pm SE) of alder (*Alnus glutinosa*) litter mass remaining at the end of the experiment in all predator-prey combinations. Leaching and conditioning effects on litter mass loss are represented by the control-no prey combination. 'L. sp.' corresponds to Limnephilidae species 1 (plant detritus case) and 2 (sand case).

Fig. 2a). Contrastingly, crayfish consumed as many Limnephilidae sp.2 (sand case) as amphipods (Tukey's HSD, d.f. = 171, all $P > 0.05$; Fig. 2a). *Astacus astacus* consumed significantly more Limnephilidae sp.2 than *P. leniusculus* (Tukey's HSD, d.f. = 171, $P = 0.0006$; Fig. 2a). Finally, case-building material (sand versus plant detritus) may have influenced the vulnerability of Limnephilidae larvae to predation by *P. leniusculus* (Tukey's HSD, d.f. = 171, $P < 0.0001$) but not by *A. astacus* (Tukey's HSD, d.f. = 171, $P = 1$; Fig. 2a).

Crayfish had a significant effect on alder litter breakdown (ANOVA, $F_{2,226} = 59.9$, $P < 0.0001$) although this

effect depended heavily on crayfish/prey combinations (ANOVA, crayfish \times prey interaction: $F_{8,220} = 19.9$, $P < 0.0001$; Fig. 2b). Proportion of litter mass remaining in Limnephilidae combinations was significantly higher in crayfish treatments than in the control (Tukey's HSD, d.f. = 213, all $P < 0.0001$; Fig. 2b) but not influenced by crayfish species (Tukey's HSD, d.f. = 213, all $P > 0.05$; Fig. 2b). Proportion of litter mass remaining in *G. fossarum* combinations was significantly higher in the presence of *A. astacus* treatment than in the control treatment (Tukey's HSD, d.f. = 213, $P = 0.0001$; Fig. 2b). However, there was no difference between *P. leniusculus* and control treatments (Tukey's HSD, d.f. = 213, $P = 0.273$; Fig. 2b). Contrastingly, the proportion of litter mass remaining in the presence of *G. roeseli* was not influenced by crayfish presence or species (Tukey's HSD, d.f. = 213, all $P > 0.05$; Fig. 2b). Crayfish alone did not seem to influence litter breakdown (i.e. proportion of leaf mass remaining; Tukey's HSD, d.f. = 213, both $P = 1$ for *A. astacus* and *P. leniusculus* compared with the no prey-no predator control; Fig. 2b).

All prey species significantly increased alder litter breakdown in the absence of crayfish predators (Tukey's HSD, d.f. = 213, all $P < 0.01$; Fig. 2b). Interspecific differences in litter breakdown abilities were detected among prey species (Fig. 2b). This trend was merely due to the significantly lower consumption rate of *G. roeseli* (mean \pm SE = 278 ± 13 mg litter g^{-1} *G. roeseli* per day) compared with the three other species (Tukey's HSD, d.f. = 56, all $P < 0.0001$; mean \pm SE = 417 ± 23 , 402 ± 10 and 380 ± 13 mg litter g^{-1} invertebrate per day for *G. fossarum* and Limnephilidae sp.1 and sp.2, respectively).

Field experiments

Leaf litter breakdown. Again, we found no size difference between crayfish species (ANOVA, $F_{1,80} = 0.82$, $P = 0.362$; mean size in cm \pm SE = 8.56 ± 0.08 and 8.37 ± 0.10 for *A. astacus* and *P. leniusculus*, respectively); thus, crayfish size was not considered in the following analyses.

Estimated exponential breakdown rates (k) revealed a significant influence of crayfish on litter breakdown (ANCOVA, crayfish species \times time interaction, $F_{2,74} = 3.74$, $P = 0.028$; $k \pm$ SE in per day = 0.062 ± 0.004 , 0.040 ± 0.004 and 0.035 ± 0.004 for control, *A. astacus* and *P. leniusculus* treatments, respectively). Alder leaf litter was broken down 1.5–1.8 times faster in the absence of crayfish. Crayfish effects on litter breakdown did not differ between the two species (Tukey's HSD, d.f. = 76, $P = 0.708$).

Fungal biomass. Ergosterol content in *A. glutinosa* leaf litter significantly increased between days 14 and 28 ($F_{1,67} = 44.4$, $P < 0.0001$). Crayfish had no effect on fungal biomass ($F_{2,66} = 0.85$, $P = 0.431$), and there was no interaction with time ($F_{2,66} = 0.007$, $P = 0.993$). Ergosterol contents were similar in leaf litter from the control, *A. astacus* and *P. leniusculus* treatments after 14 (mean \pm SE μg ergosterol per g leaf litter dry mass = 50.2 ± 3.9 , 54.2 ± 4.5 and 48.5 ± 3.9 , respectively) and 28 days (75.5 ± 5.6 , 80.6 ± 6.1 and 74.7 ± 4.6 , respectively).

Invertebrate density and biomass. Total invertebrate density in litter bags was slightly higher in the control than in crayfish treatments, although no significant difference was detected (Table 1 and Fig. 3a). After initial colonisation, total invertebrate density significantly decreased over time (Table 1 and Fig. 3a). Density remained stable between 7 and 14 days (Tukey's HSD, d.f. = 110, $P = 0.979$) but decreased sharply afterwards (Tukey's HSD, d.f. = 110, $P = 0.0001$). Crayfish and litter incubation time affected invertebrate prey densities in tax-specific ways (Table 1 and Fig. 3).

In case-bearing caddisfly larvae, crayfish significantly reduced Limnephilidae density while Sericostomatidae density was unaffected (Table 1 and Fig. 3c,d). However, Limnephilidae densities did not differ between *A. astacus* and *P. leniusculus* treatments (Tukey's HSD, d.f. = 110, $P = 0.085$; Fig. 3c). Both Limnephilidae and Sericostomatidae densities significantly decreased with litter incubation time (Table 1; Fig. 3c,d). *Gammarus fossarum* density was influenced only by incubation time (Table 1, Fig. 3b); amphipod densities were significantly lower after 28 days than after 7 and 14 days (Tukey's HSD, d.f. = 110, both $P = 0.0001$), regardless of predator treatment (Fig. 3b).

Crayfish presence slightly reduced larval Chironomidae (Diptera) and Leptophlebiidae (Ephemeroptera) den-

sities (Fig. 3e,f). However, predator effects were significant only on Leptophlebiidae (Table 1). Litter incubation time significantly affected both taxa densities but in contrasting ways (Table 1; Fig. 3e,f). Chironomidae density increased over time (i.e. among sampling dates; Tukey's HSD, d.f. = 110, all $P < 0.05$; Fig. 3e). Leptophlebiidae densities remained stable between 7 and 14 days (Tukey's HSD, d.f. = 110, $P = 0.993$) but decreased significantly afterwards (Tukey's HSD, d.f. = 110, $P = 0.0001$; Fig. 3f). Interaction between crayfish treatment and incubation time also had significant effects on Leptophlebiidae (Table 1). Leptophlebiidae density was significantly lower in the presence of crayfish than in the control only after 28 days (Tukey's HSD, d.f. = 110, $P = 0.028$ and 0.038 for *A. astacus* and *P. leniusculus*, respectively) but did not differ between the two crayfish treatments (Tukey's HSD, d.f. = 110, $P = 0.998$; Fig. 3f).

Crayfish significantly affected invertebrate biomass ($F_{2,117} = 10.3$, $P < 0.0001$; Fig. 4). Invertebrate biomass was significantly higher in the control (no crayfish) than in the presence of crayfish (Tukey's HSD, d.f. = 110, $P = 0.0008$ and $P = 0.0001$ for *A. astacus* and *P. leniusculus*, respectively; Fig. 4), but no difference was detected between the two crayfish species (Tukey's HSD, d.f. = 110, $P = 0.2$; Fig. 4). Incubation time had no significant effect on total invertebrate biomass ($F_{2,117} = 3.01$, $P = 0.053$; Fig. 4), and there was no significant interaction between leaf litter incubation time and crayfish treatment ($F_{4,115} = 0.2$, $P = 0.938$).

Discussion

Our results provide new experimental evidence of the strong potential of crayfish to affect leaf litter breakdown rate and invertebrate communities in oligotrophic streams, ecosystems highly dependent upon terrestrial organic matter inputs. Contrary to most previous experi-

Table 1 Results of ANCOVAs testing for crayfish effects on invertebrate density over time. Crayfish treatment (control, *Astacus astacus* and *Pacifastacus leniusculus*) and litter incubation time (7, 14 and 28 days) were included as fixed factors and litter mass remaining as a covariate. Invertebrate density (number of individuals per leaf litter bag) in leaf litter bags for the five most abundant taxa and all invertebrates (total) were the dependent variables

Invertebrate group	d.f.	<i>Gammarus fossarum</i>		Limnephilidae		Sericostomatidae		Leptophlebiidae		Chironomidae		Total	
		F	P	F	P	F	P	F	P	F	P	F	P
Litter mass remaining	1	0.01	0.924	3.45	0.066	8.34	0.005	6.26	0.014	0.75	0.390	0.04	0.842
Treatment	2	1.01	0.368	34.4	<0.0001	0.44	0.646	6.31	0.003	1.70	0.188	2.68	0.073
Time	2	5.98	0.003	11.2	<0.0001	5.34	0.006	8.98	0.0002	5.16	0.007	5.89	0.004
Treatment \times time	4	0.35	0.845	1.30	0.274	2.26	0.067	3.39	0.012	1.69	0.156	0.63	0.642

Significant P -values are in bold.

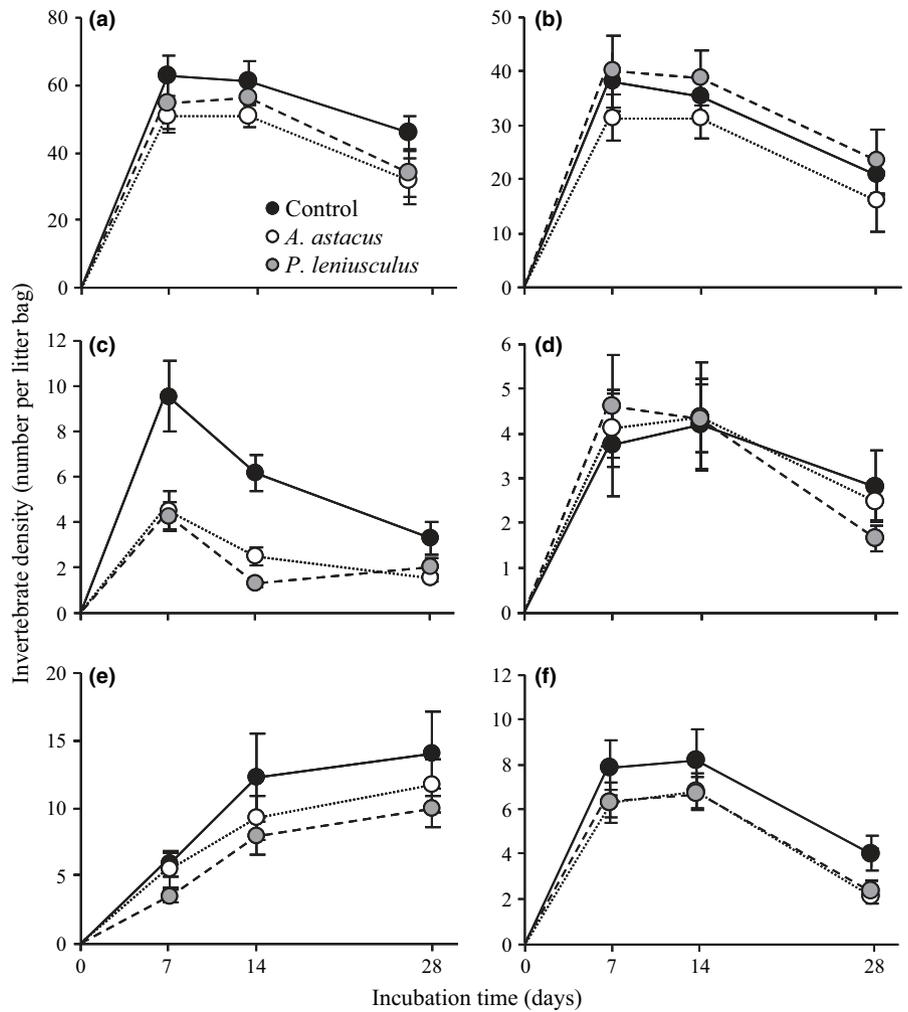


Fig. 3 Mean (\pm SE) density (number of individuals per leaf litter bag) of (a) all invertebrates (total density), (b) *Gammarus fossarum* (Amphipoda), (c) Limnephilidae (Trichoptera), (d) Sericostomatidae (Trichoptera), (e) Chironomidae (Diptera) and (f) Leptophlebiidae (Ephemeroptera) in alder (*Alnus glutinosa*) litter bags incubated in the three treatments; control (no crayfish), *Astacus astacus* (native crayfish) and *Pacifastacus leniusculus* (invasive).

ments, in which crayfish either did not affect (Usio & Townsend, 2004; Usio *et al.*, 2006) or enhanced litter breakdown (Usio & Townsend, 2001; Creed & Reed, 2004; Zhang *et al.*, 2004), we found that *P. leniusculus* and *A. astacus* negatively affected organic matter dynamics and did not seem to feed directly on terrestrial organic matter. These contrasting results may be due to species-specific crayfish diet or feeding behaviour, since a wide variety of species have been used in studies of leaf litter processing by crayfish.

Many crayfish, including *A. astacus* and *P. leniusculus*, have been shown to feed on leaf detritus, yet the proportion of plant detritus in crayfish diet and trophic niche width are highly variable among and within species (Momot, Gowing & Jones, 1978; Guan & Wiles, 1998; Schofield *et al.*, 2001; Helms & Creed, 2005; Usio *et al.*, 2006; Olsson *et al.*, 2009; Jackson *et al.*, 2014). Potential reasons for differences in documented crayfish effects on leaf litter breakdown include seasonal changes in crayfish diet (i.e. time of study; Capelli,

1980; Guan & Wiles, 1998; Gutiérrez-Yurrita *et al.*, 1998), intraspecific size/age-dependent diet preferences (i.e. ontogenic stage of crayfish used in experiments; Guan & Wiles, 1998) and habitat-specific food availability for crayfish (Alcorlo, Geiger & Otero, 2004). Generally, crayfish diet and niche widths are highly variable (Momot *et al.*, 1978; Olsson *et al.*, 2009; Jackson *et al.*, 2014). For example, crayfish tend to consume proportionally more animal prey in spring, corresponding to the time of our study, than in any other season and may overlook leaf litter as a food source during this period. By also consuming invertebrate prey and reducing shredder densities, crayfish may have an overall negative effect on leaf litter breakdown even though they also consume occasionally leaf material (Zhang *et al.*, 2004). Both *A. astacus* and *P. leniusculus* were observed manipulating leaf material and reaching into leaf bags in our experiments, but they seemed to be searching for hiding invertebrate prey rather than feeding on leaf material. Furthermore, *A. astacus* and *P. leniusculus* did not

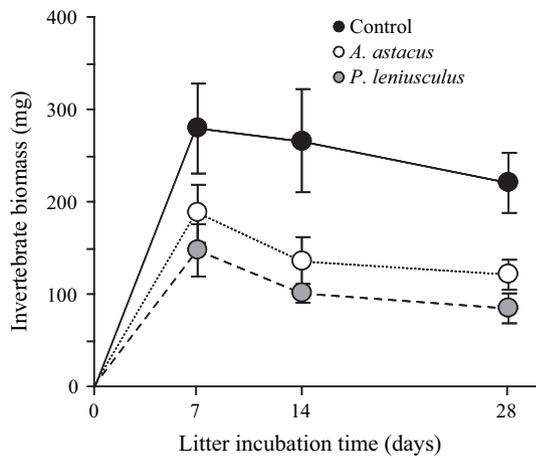


Fig. 4 Mean (\pm SE) biomass (mg per leaf litter bag) of all invertebrates (total biomass) in alder (*Alnus glutinosa*) litter bags incubated in the three treatments; control (no crayfish), *Astacus astacus* (native crayfish) and *Pacifastacus leniusculus* (invasive).

affect fungal biomass, suggesting that alder leaf litter was equally palatable to crayfish and other invertebrate shredders across all treatments. Litter quality being constant, crayfish effects on litter breakdown were therefore mostly indirect and mediated by invertebrate shredders.

Crayfish significantly reduced total invertebrate biomass and density of one of the main shredder taxa (Limnephilidae) in litter bags incubated in the field. Generally, invertebrate biomass and densities followed the same general pattern in crayfish and control treatments. A steep increase during the first 7 days was followed by a slow but steady decrease between 7 and 28 days, potentially due to a decrease in leaf litter mass (i.e. habitat) and quality (i.e. food). Contrastingly, chironomid larvae densities remained fairly constant during that time. Chironomidae densities may be affected by different factors. Chironomid larvae have limited dispersal abilities, colonising new habitat mainly through drift, and peak densities may take longer to reach. Furthermore, they are small collector gatherers and may depend less on leaf litter for food and habitat and be less affected by litter breakdown. Total invertebrate biomass and the density of large Limnephilidae were consistently and significantly higher in the absence of crayfish, likely causing the observed differences in litter breakdown rates among control and crayfish treatments.

Crayfish maintained some taxa at low densities, suggesting constant immigration controlled by stable crayfish effects. However, we could not determine to what extent low invertebrate densities in litter bags were due to prey consumption and/or non-consumptive (i.e.

reduced immigration, rapid emigration) effects of crayfish; the relative importance of these mechanisms likely varies among prey taxa. It is also possible that crayfish presence reduced invertebrate shredder consumption rates through predator-induced stress and anti-predator behavioural responses without influencing invertebrate densities (Schmitz, Krivan & Ovadia, 2004; Luttbeg & Kerby, 2005; Preisser, Bolnick & Benard, 2005; Peckarsky *et al.*, 2008). In the field experiment, crayfish presence may have induced high emigration rates in the relatively mobile prey like *G. fossarum*, maintaining constant immigration-emigration equilibrium and thus relatively stable invertebrate densities in litter bags over time. Overall, *A. astacus* and *P. leniusculus* effects differed among invertebrate taxa and seemed more pronounced on the large, slow-moving Trichoptera larvae, compared with the more mobile amphipods. Previous studies showed that large, slow or sedentary invertebrates are more vulnerable to direct crayfish predation (Nyström *et al.*, 1999; Usio, 2000; Usio & Townsend, 2004; Usio *et al.*, 2006, 2009). This trend was confirmed by our laboratory experiments where Trichoptera larvae were more vulnerable to crayfish predation than were amphipods.

Invasive crayfish are often assumed to have stronger effects on freshwater communities than their native counterparts (Usio *et al.*, 2009). Our results show that both *A. astacus* and *P. leniusculus* significantly affected organic matter breakdown rate and invertebrate densities and biomass. Although some differences were detected, *P. leniusculus* and *A. astacus* did not seem to markedly differ in their effects. Functional response of the native crayfish was slightly different from that of the invasive species over 24 h, at least at low prey densities, but that difference was not noticeable after 6 days in laboratory microcosms. Thus, over time and with no replacement of the prey, there was eventually no difference in the total number of prey consumed. Reduced leaf litter breakdown in *G. fossarum*-*A. astacus* compared with *G. fossarum*-*P. leniusculus* treatments may indicate a steeper reduction in *G. fossarum* prey numbers over time in the presence of *A. astacus* due to higher daily prey intake. Both crayfish species should decrease prey numbers exponentially over time according to the results of the daily prey intake experiment. However, prey depletion rate may be higher in the presence of *A. astacus* than *P. leniusculus*, and leaf litter breakdown should be reduced accordingly.

Our results also indicate that crayfish effects on prey and leaf litter breakdown are prey- and crayfish species specific. For example, 40–50% of *G. fossarum* and *G. roeseli* were consumed by crayfish, but leaf litter breakdown

was decreased only in the *G. fossarum* treatments. Daily intake of *G. roeseli* by crayfish may be lower than that of *G. fossarum* and thus reduce indirect effects of crayfish on litter breakdown. Anti-predator morphological defences seemed to marginally protect *G. roeseli* against both crayfish species, potentially giving it an advantage over *G. fossarum* in interspecific competition (Bollache *et al.*, 2006). Anti-predator efficiency of Limnephilidae larvae case was also species specific. The plant detritus case of Limnephilidae sp.1 did not offer much protection against either crayfish species. Comparatively, sand case of Limnephilidae sp.2 reduced predation by *P. leniusculus* but did not influence predation by *A. astacus* and could thus mediate interspecific differences in crayfish effects. However, field experiments showed little difference between crayfish species in their effects on prey and leaf litter breakdown.

Differences between the native and invasive species in their effects on invertebrate densities and leaf litter breakdown were minor, at least in our experimental microcosms and in small oligotrophic stream ecosystems. Whether small differences in crayfish effects between the two species were swamped by constant prey immigration and emigration and/or variable prey-specific effects of the two predators add up to the same overall trend cannot be determined here. *Astacus astacus* and *P. leniusculus* were previously shown to have similar niche width and food preferences, using available resources in a similar way and having comparable roles in a particular habitat (Nyström & Strand, 1996; Olsson *et al.*, 2009). However, it was also suggested that, compared with the native species, *P. leniusculus* may have higher per-capita food intake, thus exerting stronger predation pressure on some invertebrate taxa (Nyström *et al.*, 1999; Usio *et al.*, 2006; Haddaway *et al.*, 2012). Our data did not suggest higher predation rate on available prey by *P. leniusculus*, although it is difficult to extrapolate these results to invertebrate communities at larger spatial and temporal scales (Helms & Creed, 2005; Klose & Cooper, 2012).

Overall, for similar crayfish densities and size, effects of the invasive *P. leniusculus* on shredder prey densities and leaf litter breakdown rates were similar to those of the native *A. astacus*. Clearly, our results cannot be generalised or extrapolated to all important functions of crayfish in ecosystems and most likely underestimate levels of functional differences between the two crayfish species (Hector & Bagchi, 2007). Density/biomass, fecundity and/or growth rate and species-specific characteristics are also important ecological attributes to consider when investigating potential effects of invasive species

(Nyström *et al.*, 1999; Usio *et al.*, 2006; Gherardi *et al.*, 2011). Since invading species effects depend on their abundance and on their distinctiveness in resources exploitation from native species, invasion by *P. leniusculus* may still affect freshwater ecosystems at high densities (Strayer *et al.*, 2006; Strayer, 2012). Invader abundance often decreases after the acute invasion phase, and *P. leniusculus* effects on stream ecosystems may eventually become more similar to those of its native counterpart. Evidence suggests that 'new and dangerous' crayfish invaders may become 'old and integrated' when their population stabilises and local communities adjust to the coexistence with the invader (McCarthy *et al.*, 2006; Strayer *et al.*, 2006; Hesseselwerdt *et al.*, 2009; Hirsch, 2009). Crayfish species with different diets may also be functionally similar with respect to their community roles (Helms & Creed, 2005).

Native crayfish species are sensitive to water pollution, eutrophication and river bed modification. These factors have likely triggered the decline and disappearance of native crayfish from many human-impacted catchments (Weinländer & Füreder, 2009; Părvulescu, Pacioglu & Hamchevici, 2011; Svobodová *et al.*, 2012). Comparatively, invasive species are better at coping with changes caused by human activities, which frequently occur in highly eutrophic ecosystems, disturbed riverbeds or polluted habitats (Gherardi, 2006; Weinländer & Füreder, 2009, 2012; Svobodová *et al.*, 2012), and they often colonise habitats where native crayfish have disappeared (Gherardi, 2007). However, coexistence situations have been documented (Pöckl & Pekny, 2002; Westman, Savolainen & Julkunen, 2002), and some recent outbreaks of crayfish plague in native crayfish populations can be attributed to translocations of disease-carrying *P. leniusculus* (Vennerström, Söderhäll & Cerenius, 1998; Bohman, Nordwall & Edsman, 2006; Diéguez-Urbeondo, 2006). In most cases, however, *P. leniusculus* did not actually contact or compete with the native *A. astacus*. Consequently, their effects on colonised ecosystems are difficult to compare to those of *A. astacus* in natural conditions, since many streams are already disturbed and often deprived of native crayfish. Ecosystems may be closer to their original state with the invading *P. leniusculus* than with no crayfish at all. Positive effects of non-native crayfish, including the occupation of vacant niches within degraded habitats or the re-appearance of rare birds and mammals finding and adapting to a new abundant prey, have already been documented at local scales, although these effects are likely species specific

and may vary among non-native species (Ackefors, 1999; Holdich & Sibley, 2003).

Differences in diet, niche width, size and other biological characteristics among invasive crayfish species are likely to influence their effects on ecosystem structure and functioning (Jackson *et al.*, 2014). Crayfish impacts on native ecosystems should thus be investigated in context-specific ways before management decisions are taken (Westman & Savolainen, 2002; Strayer *et al.*, 2006; Degerman *et al.*, 2007; Ruokonen *et al.*, 2012). We still strongly believe that everything should be done to stop the spread of invasive crayfish when they threaten remnant native crayfish populations. However, when the successful translocation and recolonisation of native crayfish is impossible due to ongoing ecosystem perturbations (pollution, eutrophication, riverbed disturbance, crayfish plague, etc.), the question deserves to be asked: is the ecosystem really better off without invasive crayfish or is the invader the lesser of two evils? Given the importance of crayfish in ecosystem structure and functioning combined with the relatively poor state of fresh waters in Europe, the answer may need some thought. Local crayfish extinction can lead to major ecological changes in aquatic communities (Zhang *et al.*, 2004; Strayer, 2010). Crayfish can account for around 50% of the animal biomass in freshwater ecosystems, control the stock and processing rate of organic matter and constitute a significant part of fish, bird and/or mammal predator diets (Momot *et al.*, 1978; Haertel-Borer *et al.*, 2005). It is unlikely that any other native invertebrate species could substitute for crayfish ecological functions (Usio & Townsend, 2004). Overall, when introduced crayfish colonise ecosystems deprived of their native crayfish species by ecosystem degradation and their effects are similar to their native counterpart under similar conditions, then seeing the new crayfish establish and reoccupy the vacant niche may be the less bad situation. This is particularly important in the lights of new, developing management strategies that focus on conserving key ecological processes instead of specific, selected species and that look at maintaining ecosystem stability and resilience, thus preventing shifts to alternate stable states (Allen *et al.*, 2011).

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