Dietary niche constriction when invaders meet natives: evidence from freshwater decapods

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Abstract

1. Invasive species are a key driver of global environmental change, with frequently strong negative consequences for native biodiversity and ecosystem processes. Understanding competitive interactions between invaders and functionally similar native species provides an important benchmark for predicting the consequences of invasion. However, even though having a broad dietary niche is widely considered a key factor determining invasion success, little is known about the effects of competition with functionally similar native competitors on the dietary niche breadths of invasive species.

2. We used a combination of field experiments and field surveys to examine the impacts of competition with a functionally similar native crab species on the population densities, growth rates and diet of the globally widespread invasive red swamp crayfish in an African river ecosystem.

3. The presence of native crabs triggered significant dietary niche constriction within the invasive crayfish population. Further, growth rates of both species were reduced significantly, and by a similar extent, in the presence of one another. In spite of this, crayfish maintained positive growth rates in the presence of crabs, whereas crabs lost mass in the presence of crayfish. Consequently, over the three year duration of the study, crab abundance declined at those sites invaded by the crayfish, becoming locally extinct at one.

4. The invasive crayfish had a dramatic effect on ecosystem structure and functioning, halving benthic invertebrate densities and increasing decomposition rates four-fold compared to the crabs. This indicates that replacement of native crabs by invasive

crayfish likely alters the structure and functioning of African river ecosystems significantly.

5. This study provides a novel example of the constriction of the dietary niche of a successful invasive population in the presence of competition from a functionally similar native species. Our finding highlights the importance of considering both environmental and ecological contexts in order predict and manage the impacts of invasive species on ecosystems.

Key words: diet breadth, community structure, ecosystem functioning, interspecific competition, invasive species, *Procambarus clarkii*, stable isotopes, field experiment.

Introduction

The increasingly rapid spread of biological invaders in recent decades (*e.g.* Ricciardi, 2006; Jackson & Grey, 2013) is a key driver of global environmental change with major implications for biodiversity and ecosystem functioning (Chapin *et al.*, 2000; Gurevitch & Padilla, 2004; Pejchar & Mooney, 2009). Invasive species can have dramatic and often irreversible effects on ecosystem services, frequently with considerable economic implications (Pejchar & Mooney, 2009; Walsh *et al*., 2016), particularly in aquatic ecosystems, which tend to be especially susceptible (Rahel & Olden, 2008). They can change fundamental ecological processes from the level of the individual to the whole ecosystem (Peltzer *et al.*, 2010; Penk *et al.* 2015, 2016), and frequently alter the distribution of native species via a range of competitive interactions, predation pressure and/or habitat degradation (Mack *et al.*, 2000; Simon & Townsend, 2003; Hooper *et al.*, 2005). Classic invasion theory (Elton, 1958) predicts that a successful invader can establish itself in an unoccupied niche or displace similar native species by overlapping their niche and eventually out-competing them for limited resources. Having a generalist diet is a common trait of successful invaders, allowing them to opportunistically exploit diverse resources in novel environments and competitively exclude native species (Snyder & Evans, 2006). Hence, the decline of native species following an invasion is often a consequence of direct interspecific competition for resources (*e.g.* Porter & Savignano, 1990; Olsson *et al.*, 2009).

Classic niche theory predicts that species occupy a larger niche in the absence of interspecific competition (Hutchinson 1957; Van Valen 1965). Hence, competing invasive and native species would be expected to occupy smaller niches than their allopatric counterparts (Bolnick *et al.*, 2010). However, increased competition for resources might necessitate an increase in dietary niche breadth in order to maintain energy requirements

(Svanbäck and Bolnick 2007). Empirical evidence indicates that interspecific competition can cause the niche widths of consumers to increase or decrease depending on the context but the reason for this variation is still unclear (Araújo *et al.,* 2011). Despite these apparently contradictory processes (Araújo *et al.,* 2011), the dietary niche breadth of invasive and native competitors has rarely been examined, even though it is likely a key factor in determining invasion success and predicting impacts of invaders on biodiversity (*e.g.* Jackson & Britton, 2013; Penk *et al.* 2015).

Some of the most destructive freshwater invaders are crayfish (Lodge *et al.,* 2012), which can alter ecosystem structure and processes by, for example, homogenising biotic assemblages and altering rates of both primary production and decomposition (Stenroth & Nyström, 2003; Renai & Gherardi, 2004; Gherardi & Acquistapace, 2007; Jackson *et al.*, 2014). Ecologists have yet to examine fully the range of ecological mechanisms underpinning the impacts of invasive crayfish on ecosystem structure and functioning (Lodge *et al.*, 2012). The red swamp crayfish (*Procambarus clarkii*) is a particularly important invader due to its global distribution (Capinha *et al.*, 2011) and the severe impacts it has on ecosystems (Klose and Cooper, 2012; Jackson *et al.,* 2014). In the 1960s, the species was introduced to multiple locations throughout East Africa for aquaculture (Harper *et al.*, 2002), where its effects remain largely unknown. This widespread introduction of crayfish in the region has led to encroachment on the range of many native freshwater crab species, several of which are endangered and endemic (Cumberlidge *et al.*, 2009). Indeed, crayfish have replaced crabs as the primary food source of African clawless otters in some Kenyan rivers (Ogada, 2006), providing indirect evidence that they are becoming more abundant and outcompeting crabs. Crabs and crayfish are both benthic omnivores with similar feeding mechanisms. They frequently occupy similar functional roles as shredders driving detrital processing (Nyström *et al.*, 1996; Dudgeon, 1999; Dobson *et al.*, 2002; Lancaster *et al.*, 2008) and, consequently, the introduced crayfish might be expected to be functionally redundant (*sensu* Naeem, 1998). However, even morphologically similar species can vary significantly in their effects on ecosystems (O'Connor & Bruno, 2007; Matthews *et al.*, 2011; Jackson *et al.*, 2014; Penk *et al.*, 2015). Furthermore, highly invasive species tend to be more voracious than their native counterparts (Haddaway *et al.*, 2012; Alexander *et al.*, 2014), implying that red swamp crayfish could cause considerable alteration to ecosystem structure and processes were they to replace native crabs.

Using a combination of field experiments and surveys, we examined interactions between the globally widespread invasive red swamp crayfish and a native crab, *Potamonautes loveni,* and compared their impacts on the structure and functioning of a Kenyan river ecosystem. We quantified dietary niche breadth in experimental and natural populations of both species in allopatry and sympatry by analysis of carbon and nitrogen stable isotopes from muscle tissue, which provides information on dietary preferences integrated over time. We then obtained quantitative measures of total foraging niche space at the population level using methods that incorporate individual variation of stable isotope ratios (Layman *et al.*, 2007a; Newsome *et al.*, 2007; Jackson *et al.*, 2011). We hypothesised that (i) the invasive crayfish has stronger per-capita effects on ecosystem structure and functioning than the native crab and (ii) the invasive crayfish and native crabs will have a larger niche breadth when present together.

Materials and Methods

Study system

The River Malewa is the primary tributary of Lake Naivasha (catchment area 1750 km^2) in Kenya's Rift Valley in East Africa. Red swamp crayfish were introduced to Lake Naivasha in 1970 and subsequently spread throughout the catchment as a result of further introductions and natural dispersal, leading to their intrusion upon the range of a native river crab, *P. loveni* (Foster & Harper, 2007). The native range of *P. loveni* extends from Eastern Kenya into Western Uganda (Cumberlidge, 2008).

Experimental design

We conducted two field experiments in the River Malewa near Gilgil (0°31 5' 5.42" S, 36° 24' 3.33" E) at a site at the crayfish invasion front where both species were present. The first experiment took place in April 2009 and the second in March 2010. Both experiments were of 28 days duration and comprised the same two fixed factors in a fully-factorial design: the presence of the native crab (two levels: present and absent) and the presence of red swamp crayfish (two levels: present and absent). The experiments differed, however, in both the level of replication (experiment 1: $n = 4$; experiment 2: $n = 6$) and the range of response variables that were quantified (Table 1).

We manipulated the presence of our target organisms using steel-framed cages (Fig. S1). The cages had a 0.315 m^2 solid base surrounded fully by stainless steel mesh (5 mm aperture) to regulate the presence of crayfish and crabs and allow the free movement of other smaller invertebrates, algae and organic matter. The cages were 30 cm in height. The entire base of each cage was covered with pooled and well-mixed pebble and gravel substratum from the adjacent river bed and a native macrophyte (Family Scrophulariaceae, ~5 g fresh weight) was added to simulate natural habitat. A 400 cm^2 tray was also filled with well-mixed river substratum and inoculated with benthic invertebrates from a uniform kick sample taken from the experimental site. The cages were fully submerged for the duration of the experiment.

Crayfish and crabs used in the experiment were collected from allopatric populations in the River Malewa. Experimental cages belonging to all treatments containing decapods comprised four adult individuals of crabs (mean individual biomass [± S. D.]: 7.4 ± 1.9 g) and/or crayfish (mean individual biomass [± S. D.]: 7.9 ± 2.2 g), with a combined biomass approximating 30 g fresh weight (range: 25.7 – 37.7 g; total decapod biomass within experimental cages did not vary among treatments: ANOVA, $F_{2,12} = 0.66$, $P = 0.53$). The density of decapods within our experimental cages (12.7 individuals m^{-2}) was within the range of natural densities of both species at each of our survey locations (Harper *et al.* 2002). Males and females were represented equally in all experimental treatments, although we only used individuals of the same sex within each enclosure. The weight (g) and size [carapace length (cephalic groove to the end of the rostrum) in crayfish and carapace width (at the widest point] in crabs)] of all individuals was recorded before addition to the enclosures. Where both crabs and crayfish were present together, treatments contained two individuals of both species, all of similar biomass. Results from substitutive experiments that manipulate density and biomass, such as we use here, can be sensitive to the selected total mixture density (Inouye, 2001). However, they can effectively quantify the extent to which the measured outcome is a consequence of the mixture components (in our case, presence or absence of crayfish and crabs at natural densities). Comparison of the treatment with crayfish present and crabs absent with the treatments without crayfish allowed us to quantify the effect of the invader on the ecosystem, while comparison of the single species treatments with the two-species treatment allowed us to quantify the effect of interspecific competition on crayfish and crab growth and diet. Our four treatment combinations (crayfish only; crabs only; crayfish and crabs; neither crayfish nor crabs) were assigned to cages placed along a 40 m stretch of the river following a randomised block design. The cage mesh was cleaned every four days to remove debris, and at the same time we checked for survival of crabs and crayfish. Survival rates were 100% throughout the second field experiment but some crab mortality occurred in the last week of the first experiment. Hence, results of the first experiment were used only to explore aspects of ecosystem functioning (Table 1). Unfortunately, two enclosures were damaged during the second experiment and were omitted from analyses (Table 1).

Experiment sampling protocol

We quantified leaf litter breakdown using plastic mesh bags (aperture 5 mm) containing a known mass (~ 2.5 g) of air-dried leaf litter (from a native riparian shrub, *Dovyalis abyssinica*) fastened to the side of each cage at the start of the experiments. The leaf litter remaining in each mesh bag after 72 hours (to avoid total decomposition of material) was washed and then dried at 60ºC to constant weight. The exponential decay rate coefficient (k) was calculated for each treatment as a measure of the rate of leaf litter breakdown as:

$$k = \frac{\log_e\left(\frac{M_t}{M_0}\right)}{t}$$

where t is the duration of exposure (in days), M_0 is the initial dry mass (in grams) and M_t is the dry mass at time t (Hieber & Gessner, 2002).

We measured epilithic algal standing stock by placing a terracotta tile (10 x 10 cm) in each cage at the start of the experiment. Tiles were removed on the final day and all biofilm was washed off and filtered through GF/C filters (Whatman®, Maidstone, UK) before adding

15 ml of 90% acetone. Chlorophyll *a* concentration of the filtrate, quantified following Jeffery and Humphrey (1975), was used as a measure of periphyton biomass. We quantified the benthic invertebrates in the cages at the end of the experiment by removing, counting and identifying all organisms in the trays that were filled with substrate from the experimental site at the commencement of the experiment. All invertebrates were stored in 70% ethanol prior to identification (to genus) and enumeration.

On the final day of each experiment, crayfish and crabs were removed from the enclosures and their total mass recorded. Measurements of total fresh mass were used to calculate per capita growth rates over the duration of the experiment to compare growth in allopatry and sympatry. All individuals were then frozen overnight and thawed before dissecting a portion of muscle from the tail of crayfish and the abdomen of crabs for the analysis of stable isotopes. The duration of the experiment (28 days) allowed sufficient time for crayfish and crab muscle tissue to equilibrate with their diet in experimental conditions at warm river temperatures (15 to 20 ^{o}C; Fantle *et al.*, 1999; Fry *et al.*, 2003; McIntyre & Flecker, 2006). We also collected epilithic algae, macrophytes, detritus and dominant benthic invertebrate species from the experimental location for stable isotope analysis. All tissue samples were oven-dried at 60^{o}C, ground using an agate pestle and mortar and 0.6 to 1.0 mg weighed into 6 x 4 mm tin cups using a microbalance. Stable carbon and nitrogen isotope analyses were carried out using an elemental analyser (Flash EA 1112 series, Thermo-Finnigan, Waltham, Massachusetts, USA) coupled to a continuous flow isotope ratio mass spectrometer (Finnigan MAT Delta^{Plus}, Thermo-Finnigan, Waltham, Massachusetts, USA). Secondary standards (sucrose for carbon; ammonium sulphate for nitrogen) with known relation to international standards (Pee Dee Belemnite for carbon; nitrogen in air for nitrogen) were used as reference materials. Cyclohaxonone-2,4-Dinitrophemylhydrazone was used as an internal standard and resulted in typical precision of < 0.1‰ for carbon and < 0.3% for nitrogen.

Finally, upon completion of the first field experiment, the guts were dissected from 5 randomly selected individual crayfish from each treatment and stored in 50% ethanol. A Novex Holland® Microscope at x10 magnification was then used to separate vegetation and invertebrate contents before drying to constant weight to calculate the relative proportion of plant to animal material ingested by each individual.

Field surveys

We examined the distribution of both crabs and crayfish at four sites in the River Malewa, located approximately 10, 30, 35 and 40 km upstream of Lake Naivasha, in 2008, 2009 and 2010. We quantified the abundance of adult crayfish and crabs on 3 to 8 occasions at each site in each year over a 6-week period, using a series of crayfish traps of 5 mm mesh, baited with fish pellets and left for between 1 and 2 hours. All crayfish and/or crabs were removed and counted and we used the catch per unit effort (CPUE; number of individuals per trap per hour) to quantify relative abundance among sites. Samples (n = 6 to 18) of a selected common size range of crabs (26 - 35 mm carapace width) and crayfish (31 - 45 mm carapace length) from all sites on all sampling occasions were prepared for stable isotope analysis as described previously. Epilithic algae, macrophytes, detritus and dominant benthic invertebrate species were also collected from all the sites for subsequent stable isotope analysis.

Data analyses

We used analysis of variance (ANOVA) to test for independent and combined effects of crayfish and crabs on algal biomass, rates of leaf litter breakdown, trophic niche widths (see below), total invertebrate abundance and invertebrate taxon richness. We measured leaf litter breakdown in both field experiments (Table 1) and tested for differences between experiments by incorporating experiment number as an additional random factor. There was no difference between the two experiments and this random effect was then removed to maximise the power of the subsequent analysis. The Tukey procedure was used to make post-hoc comparisons among levels of significant terms. We used permutational multivariate analysis of variance (PERMANOVA; Anderson *et al.*, 2008) to test for effects of our experimental manipulations on the structure of invertebrate assemblages using the PERMANOVA+ add-in to PRIMER® version 6.1 (PRIMER-E Ltd, Plymouth, UK). These analyses were performed with 9999 permutations of the residuals under a reduced model (McArdle & Anderson, 2001; Anderson *et al.*, 2008) and were based on Bray-Curtis similarity matrices calculated from log (X + 1)-transformed abundance data. Similarity percentages (SIMPER; Clark & Warwick, 2001) analysis was used to determine the contribution of each benthic invertebrate taxon to the pairwise Bray-Curtis dissimilarities between experimental treatments. All analyses were balanced and variables were transformed where necessary prior to analysis to homogenise variances.

The stable isotope-derived population metrics of carbon range (CR_b) and nitrogen range (NR_b) were used as measures of the trophic niche width of crabs and crayfish (Layman *et al.*, 2007b; Jackson *et al.*, 2012) in both the field experiments and field surveys. CR_b and NR_b were calculated as the Euclidean distance between the individuals with the lowest and highest $\delta^{13}C$ and $\delta^{15}N$ respectively and therefore reflect the total range of isotopic space used by a group of organisms. To enable comparison among variables and to account for small sample sizes, the metrics were bootstrapped (*n* = 10000; indicated with a subscript '$_b$') based on the minimum sample sizes (2 individuals in the field experiment [in the enclosures containing 2 crabs and 2 crayfish – each measurement was therefore replicated independently five times (Table 1)] and 6 individuals in the field surveys [at field sites with declining crab numbers]). We then used ANOVA to test for differences in the trophic niche width of crayfish and crabs when together and apart in the field experiment. However, given that one of our experimental treatments contained no crayfish or crabs, and could not therefore provide measurements of trophic niche widths of either species, our statistical model testing for differences in trophic niche width comprised two fixed factors: species (two levels: crabs and crayfish) and the presence of interspecific competition with a functionally similar species (two levels: competition and no competition). For the field survey data, we tested for correlations between our metrics of trophic niche width of each species and the corresponding CPUE of its functionally similar competitor. To ensure comparability in the isotopic data among survey sites and years, we used PERMANOVA to test for any effect of site or year on the stable isotopic signature of putative resources (biofilm, macrophytes, detritus and dominant invertebrate taxa). We found similar stable isotope values of putative resources both among survey sites and years (Table S1), indicating that any differences in trophic niche width between crayfish and crabs were attributable to actual dietary variation.

Results

Field experiments

There was a significant interaction between the presence of crayfish and crab on rates of leaf litter breakdown (ANOVA; $F_{1,36} = 12.66$, $P = 0.001$). Rates of breakdown were significantly higher in the cages containing only crayfish compared with those containing none of the manipulated consumers (control treatment). In contrast, cages containing crabs were similar to those in the control treatment, while cages containing both crayfish and crabs had intermediate effect on breakdown rates (Fig. 1). The latter result indicates that the presence of crabs did not alter the per capita effects of crayfish on leaf litter breakdown rates. Neither crabs nor crayfish affected the standing stock of epilithic algae.

Crayfish reduced the density of benthic invertebrates (ANOVA, $F_{1,16} = 9.39$, $P = 0.007$, Fig. 2) and altered their multivariate structure significantly (PERMANOVA; pseudo-$F_{1,17} = 6.05$, $P = 0.004$). The latter result was driven primarily by reductions in the density of hydropsychid caddis flies (Trichoptera) together with an increase in the density of oligochaete worms (Table 2). In contrast, crabs had no effect on the density or multivariate structure of benthic invertebrate assemblages. However, both crabs and crayfish reduced the taxon richness of benthic invertebrates significantly, irrespective of the presence or absence of the other decapod consumer species (ANOVA; crayfish: $F_{1,16} = 6.76$, $P = 0.019$; crabs: $F_{1,16} = 4.84$, $P = 0.043$; Fig. 2).

The nitrogen range (NR_b) of both crabs and crayfish was reduced significantly in the presence of the other functionally similar species (ANOVA; $F_{1,17} = 4.64$, $P = 0.046$; Fig. 3A), but there was no effect of the presence of crab or crayfish on the carbon range (CR_b; Fig. 3B) of the other species. Gut content analysis revealed that the relative contribution of animal and plant material to the diet of crayfish did not change in the presence of crabs (45.5 ± 17.7 % and 46.8 ± 9.8 % animal material in sympatric and allopatric populations, respectively).

Per capita growth rates of both crabs and crayfish were reduced significantly by the presence of the other species compared with a similar biomass of conspecifics (ANOVA; $F_{1,48} = 6.64$, $P = 0.013$; Fig. 4). Both crabs and crayfish experienced similar reductions in both absolute (ANOVA; species*competition interaction: $F_{1,48} = 0.003$, $P = 0.96$) and relative ($F_{1,48} = 0.02$, $P = 0.9$) growth rates due to the presence of the other species. However, growth rates of crayfish were significantly higher than those of crabs ($F_{1,48}$ = 10.63, P = 0.002). Thus, even though their growth rates were reduced significantly in the presence of crabs, crayfish still gained significant biomass over the course of the experiment. In contrast, crabs generally lost biomass when present together with crayfish (Fig. 4).

Field surveys

Crabs and crayfish were found coexisting at the two middle sampling sites (Sites 2 and 3) of the survey for at least two of the three study years (Fig. 5). Both sites showed a similar trend from 2008 to 2010 of crayfish CPUE increasing simultaneously with a decline in crab CPUE. In fact, crabs appeared to be locally extinct at Site 2 by 2010, while the crayfish population was seven times larger compared with the previous year. In contrast, only crayfish were present at the most downstream of our survey sites, whereas only crabs were found at the most upstream location throughout the study period (Fig. 5).

We found significant inverse correlations between the abundance of crabs and both the nitrogen (NR_b; r_{11} = -0.67, P = 0.018; Fig. 6A) and carbon (CR_b; r_{11} = -0.80, P = 0.002; Fig. 6B) range of crayfish over the four sites. However, neither measure of crab trophic niche width correlated significantly with the abundance of crayfish (CR_b: r_{11} = -0.54, P = 0.071; NR_b: r_{11} = -0.53, P = 0.074).

Discussion

In 1958, Elton proposed that invasive species can out-compete similar native competitors by occupying a broader niche. This classic mechanism of invasion was exemplified recently by Olsson *et al.* (2009) and Ercoli *et al.* (2014), showing that trophic niche breadth of an invasive crayfish (*Pacifastacus leniusculus*) was double or treble that of a native crayfish (*Astacus astacus*). Indeed, it is typically reported that invasive species occupy a broad niche and suppress the niche of similar natives (*e.g.* Human & Gordon, 1996; Thomson, 2004). Conversely, we found that competition between invasive crayfish and native crabs resulted in reduction in the diet breadth of both species. In our field experiments, the presence of interspecific competition between crayfish and crabs caused a decline in the nitrogen range of both species and our field surveys revealed that both the carbon and nitrogen ranges of the invasive crayfish correlated inversely with the abundance of crabs. While it has been shown that invaders can alter their feeding behaviour in the presence of native species (*e.g.* Harrington *et al.*, 2009), our study provides a novel example of the constriction of the dietary niche of a successful invasive population in the presence of competition from a functionally similar native species.

Invasive species regularly outcompete and reduce the growth rate of native species (*e.g.* Smith, 2005; Riley, 2009; Britton *et al.*, 2011). However, we found strong and apparently symmetric interspecific competition, measured in terms of biomass change, between the invasive crayfish and native crabs. Growth rates of crayfish individuals were reduced in the presence of crabs compared to in the presence of a similar biomass of conspecifics, implying that interspecific competition was significantly greater than intraspecific competition. This is consistent with the presence of significant interspecific aggression, which we observed repeatedly during the study, causing reductions in foraging efficiency of both species when present together. Such aggressive behaviour between species is frequently greater than aggression with conspecifics (Polo-Cavia *et al.*, 2011). Even though both absolute and relative reductions in growth rates were similar for both decapod consumers, crayfish still exhibited positive per capita growth rates in the presence of crabs, whereas crabs generally lost mass in the presence of the invasive crayfish. This likely contributed to the decline in crab abundance at sites invaded by crayfish. Invasive crayfish have outcompeted native crayfish across North America and Europe by triggering similar declines in growth rates of natives (Hill & Lodge, 1999; Dunn *et al.*, 2009; Nakata & Goshima, 2006). Yet, as far as we are aware, this is the first study to test experimentally for interspecific competition between native crabs and introduced crayfish, despite numerous overlapping populations in both Europe and Africa (*e.g.* Barbaresi & Gherardi, 1997; Foster & Harper, 2007; du Preez & Smit, 2013).

As omnivores, crayfish and crabs can survive when a resource is limited by shifting their diet to alternative resources to compensate (Tillberg *et al.*, 2007; Grey & Jackson, 2012). This is advantageous when exploiting niches with novel resources, which may explain the successful widespread distribution of some invasive crayfish and crab species (Capinha *et al.*, 2011). Flexibility in diet choice does not necessarily imply a wide niche breadth because in some scenarios it may benefit the consumer to focus on one abundant but under-used resource (Popa-Lisseanu *et al.*, 2007). The observed reduction in crayfish and crab diet breadth in the presence of interspecific competition could be a result of increased dietary specialisation and hence a consequent decline in the variation in diet choice of individuals (Bolnick *et al.*, 2010). Alternatively, the isotopic variability could be reduced due to individuals becoming more generalist and therefore reducing the variation among the diets of each individual (Bolnick *et al.*, 2010). Examination of gut contents revealed no significant overall shift in the diets of crayfish in the presence of crabs. Therefore, that we found significant reductions in the trophic niche breadth of crayfish populations in the presence of crabs in both the field experiments and field surveys indicates that, although the overall dietary preferences of crayfish were not altered in the presence of crabs, the individuals within the crayfish population were tending to feed in a more similar manner. These results were consistent across both the field experiments and field surveys, strongly supporting the robustness and generality of this finding. The presence of the crabs appears to have triggered dietary homogenisation within the crayfish population. Crabs exhibited a significant decline in diet breadth only in the experiments and not in the field surveys. This inconsistency in results perhaps suggests less flexibility in diet choice of crabs compared to the crayfish.

Since the crayfish and crab species in our study ecosystem are both relatively large decapod Crustacea, individuals of each of the same biomass might be expected to have similar effects on ecosystem structure and functioning. Both species are considered important shredders yet invasive crayfish had a considerably greater influence on detrital processing in our field experiments, quadrupling rates of leaf litter breakdown compared to native crabs. Analysis of gut contents demonstrated that this was due to direct consumption; indeed, leaf litter is considered to be an important part of crayfish diet when available (Bobeldyk & Lamberti, 2008). Some invasive predators consume native shredders, causing a trophic cascade whereby leaf litter decomposition is reduced, but via omnivory, crayfish can decouple this trophic cascade by feeding directly both on shredders and the leaf litter itself (Jackson *et al.* 2014).

Previous studies have found that functionally similar sympatric crab species can interact to moderate one another’s impact due to consumer redundancy (Griffen & Byers, 2008). However, we found intermediate leaf litter breakdown rates in the combined species treatment in our field experiment suggesting there was no consumer interaction, as was also found for pairs of crayfish in the United Kingdom (Jackson *et al.*, 2014). We also found that the invasive crayfish significantly altered benthic community structure and approximately halved invertebrate densities compared with the native crabs. These latter findings are consistent with previous studies on invasive crayfish in Europe (Stenroth & Nyström, 2003; Haddaway *et al.*, 2012; Moorhouse *et al.*, 2013). In contrast, native crabs had no effect on the structure or density of benthic assemblages, which were similar to those in the experimental units containing no decapod consumers. In spite of the similarities between these decapod crustaceans, results from our field experiments suggest that replacement of the native crabs by the invasive crayfish will considerably alter both the structure and functioning of African river ecosystems. Moreover, these shifts in ecosystem structure and functioning may even have facilitated indirectly the replacement of the native crabs by the crayfish by reducing suitable habitat for the crabs (Parker *et al.*, 1999) by, for example, removing leaf litter as refugia. Such changes also have the potential to alter key ecosystem services such as fishery production and water quality, both of which are extremely important in this semi-arid region of East Africa. Many river crabs in East Africa are already highly endangered (Cumberlidge *et al.*, 2009) and local biodiversity will only become increasingly impaired as crayfish spread or are introduced further in both rivers and lakes (Lodge *et al.*, 2005).

In contrast to classic invasion theory, here we have shown that competition with a native species can drive niche constriction in invader populations without impairing invasion success. Interactions between native crabs and invasive crayfish caused a decline in the dietary niche width of both species but this only resulted in a reduction in performance in the native crabs. We conclude that both environmental context and species interactions need to be considered in order to predict invasion potential and the impacts of invasive species on ecosystems.

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Data Accessibility

All data from the field experiments and surveys are available in the Online Supporting Information associated with this paper.

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Supporting Information

The following supporting information is available for this article online:

Figure S1. The design of the experimental cages

Table S1. Results of PERMANOVA testing for an effect of survey site and year on the stable isotope signature of putative resources of crabs and crayfish.

Table S2. Mean (± s.e.) decomposition rates, benthic invertebrate densities, benthic invertebrate taxon richness and chlorophyll a concentrations on tiles in each treatment across both field experiments.

Table S3. Carbon (CR_b) and nitrogen (NR_b) ranges of crayfish and crab populations in each experimental enclosure (Field Experiment 2).

Table S4. Change in crayfish and crab individual body mass in the experimental treatments (mean ± s.e.).

Table S5. Crayfish and crab catch per unit effort (CPUE), carbon (CRb) and nitrogen (NRb) range in the field surveys.

Tables

Table 1. Response variables quantified during the two field experiments. The number of replicate experimental units is shown in parentheses.

Experiment 1 (April 2009)	**Experiment 2 (March 2010)**
Litter breakdown rates (*n* = 4)	Litter breakdown rates (*n* = 6)
Algal biomass (*n* = 4)	Benthic invertebrate assemblage structure (*n* = 5)
	Stable isotope analysis (crayfish [crabs absent]: *n* = 6 [24 individuals]; crabs [crayfish absent]: *n* = 5 [20 individuals]; crayfish [crabs present]: *n* = 5 [10 individuals]; crabs [crayfish present]: *n* = 5 [10 individuals])

Table 2. Results of SIMPER analysis indicating the five benthic invertebrate taxa affected most strongly by the presence of crayfish.

Taxon	**Mean density in crayfish absence (density m^{-2})**	**Mean density in crayfish presence (density m^{-2})**	**Contribution to dissimilarity (%)**	**Cumulative contribution (%)**
Hydropsychidae	96.4	49.1	63.6	63.6
Oligochaeta	5.9	8.2	10.8	74.4
Heptageniidae	9.1	2.3	8.2	82.6
Baetidae	5.5	0.5	6.4	89.0
Heptageniidae	4.6	0.9	5.7	94.7

Figure legends

Fig. 1. Leaf litter breakdown rates (mean + s.e.) in the experimental cages, measured as exponential decay rate coefficients (*k*). Letters (a, b, c) indicate groups of treatments that are statistically indistinguishable from each other ($P > 0.05$).

Fig. 2. Total density (A) and taxon richness (B) of benthic invertebrate assemblages in the experimental cages (mean + s.e.). Figure insets show effects of crayfish and/or crab presence (A: absent, P: present) where either had significant main effects ($P < 0.05$).

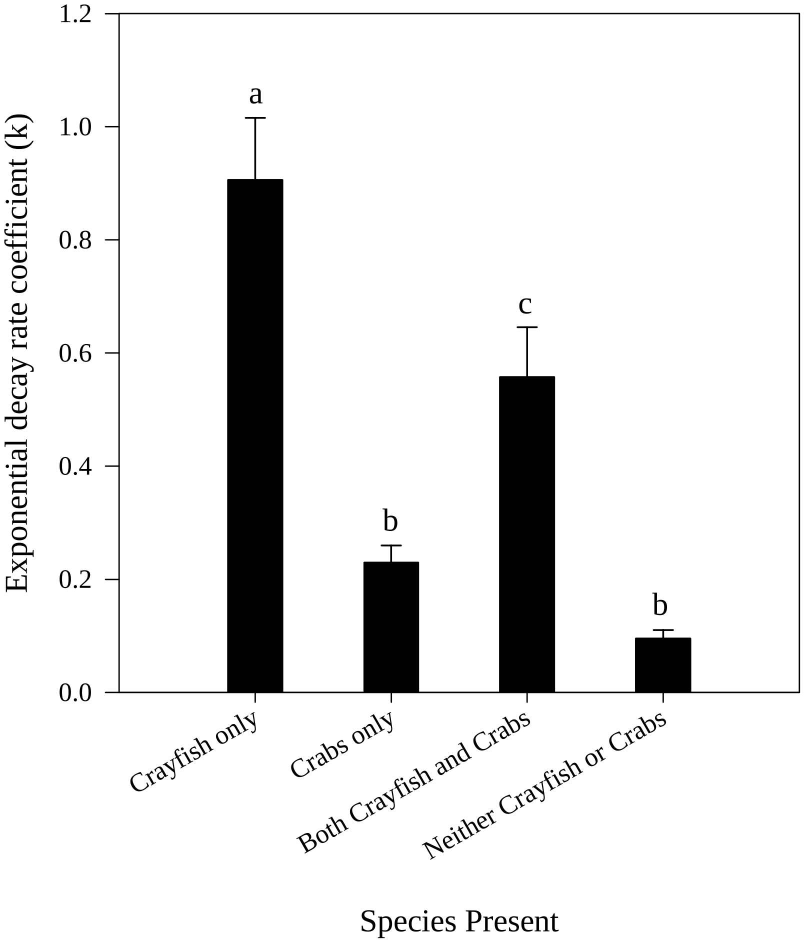
Fig. 3. The nitrogen (A) and carbon (B) range of crayfish and crabs in our experimental treatments (mean + s.e.). Figure inset shows the effect of the presence (C) and absence (NC) of interspecific competition on both species where significant main effects were detected ($P < 0.05$).

Fig. 4. Change in crayfish and crab individual body mass in our experimental treatments (median boxed by first and third quartiles). Figure inset shows the effect of the presence (C) and absence (NC) of interspecific competition on both species where significant main effects were detected ($P < 0.05$).

Fig. 5. Catch per unit effort (CPUE) of crayfish (black circles) and crabs (open circles) from 2008-2010 based on multiple trapping sessions at four sites (mean ± s.e.). The distance indicated on the graphs refers to the total distance upstream from the lake. Note the different scale on the Y-axis for Site 1. The decrease in crayfish CPUE at the latter site, the most downstream site adjacent to Lake Naivasha, is consistent with concurrent patterns within the lake, and is likely a consequence of competition with a more recent invader, the common carp (*Cyprinus carpio*), to the lake ecosystem at the time of study (Jackson *et al.*, 2012).

Fig. 6. Relationships between crab CPUE and the nitrogen range (A) and carbon range (B) of crayfish.

Figures



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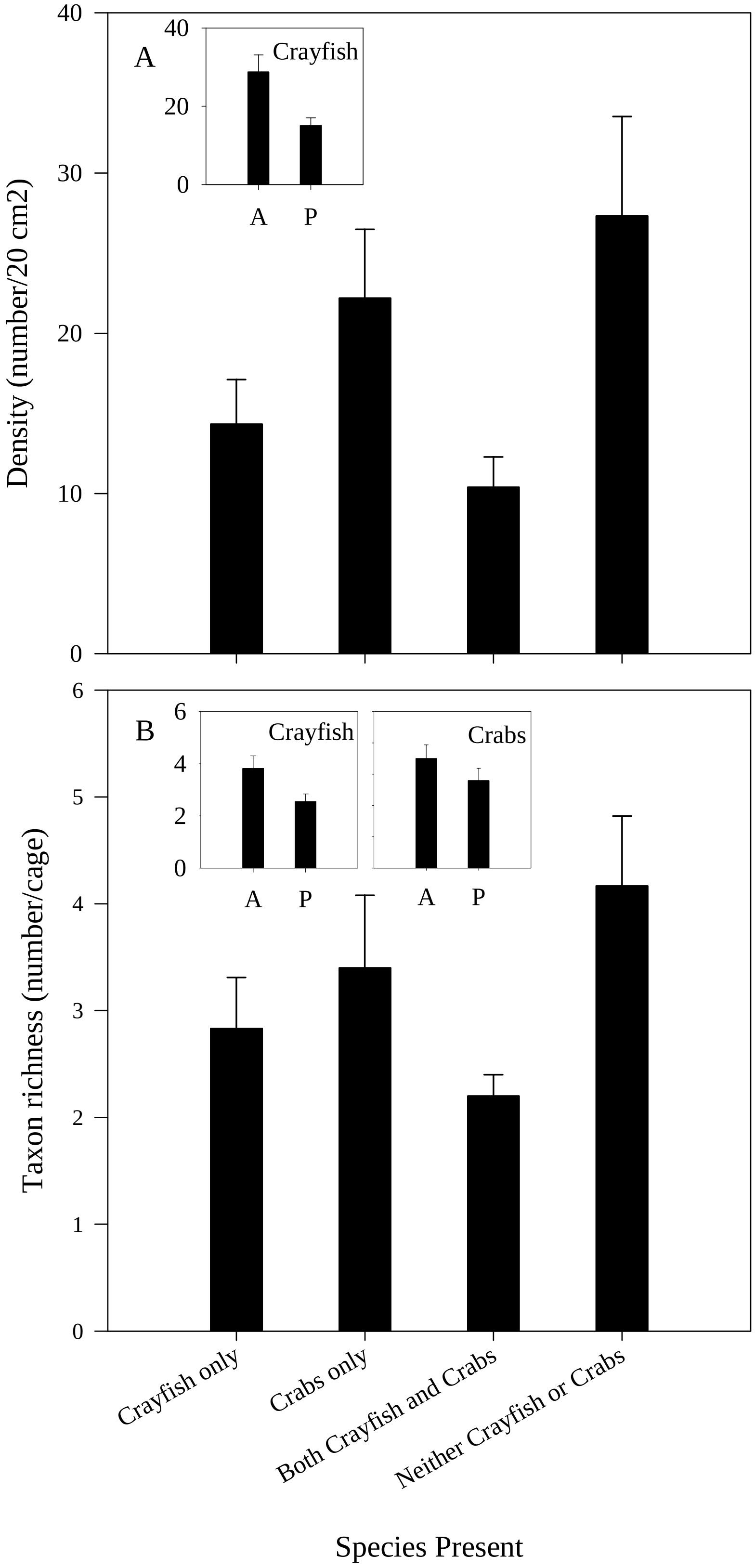

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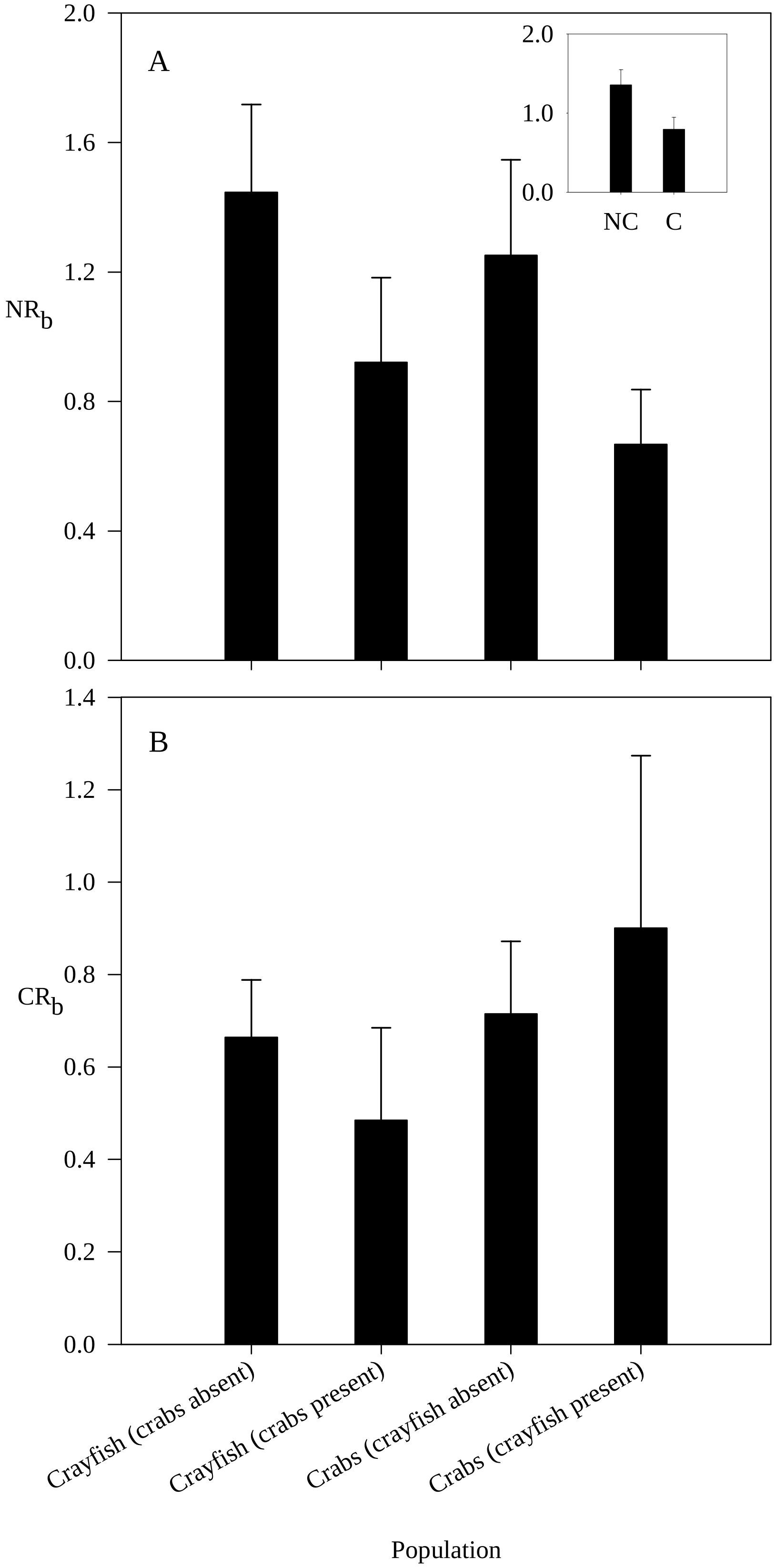

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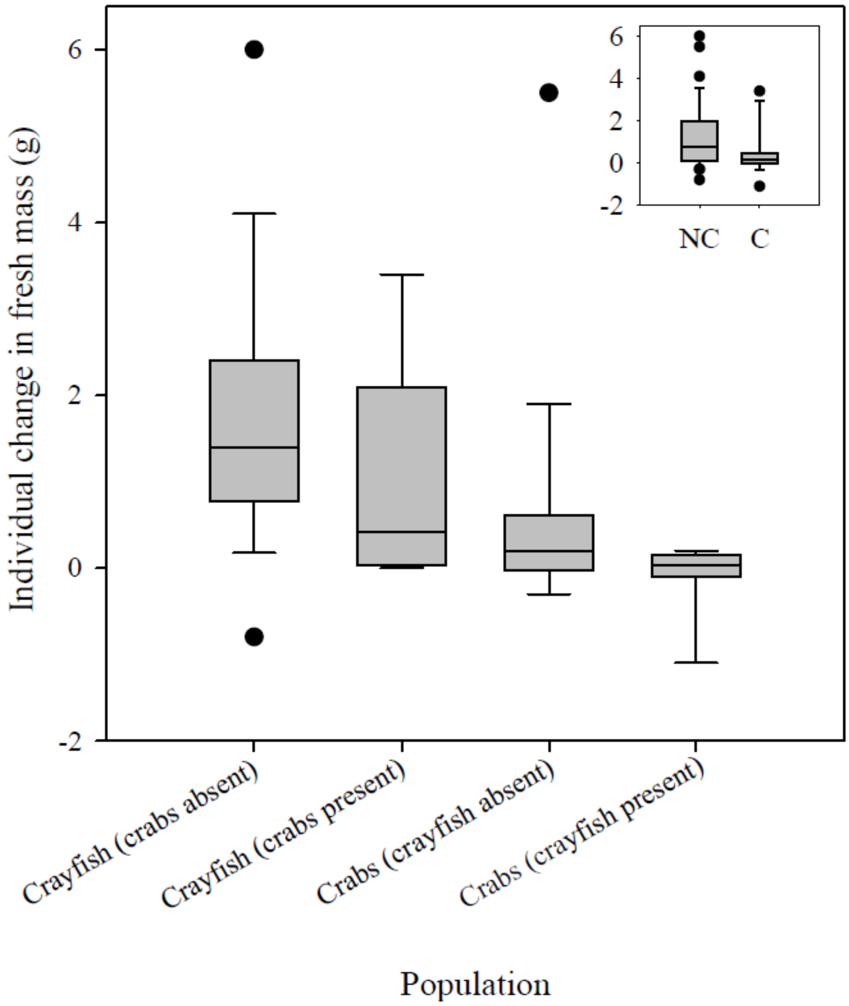

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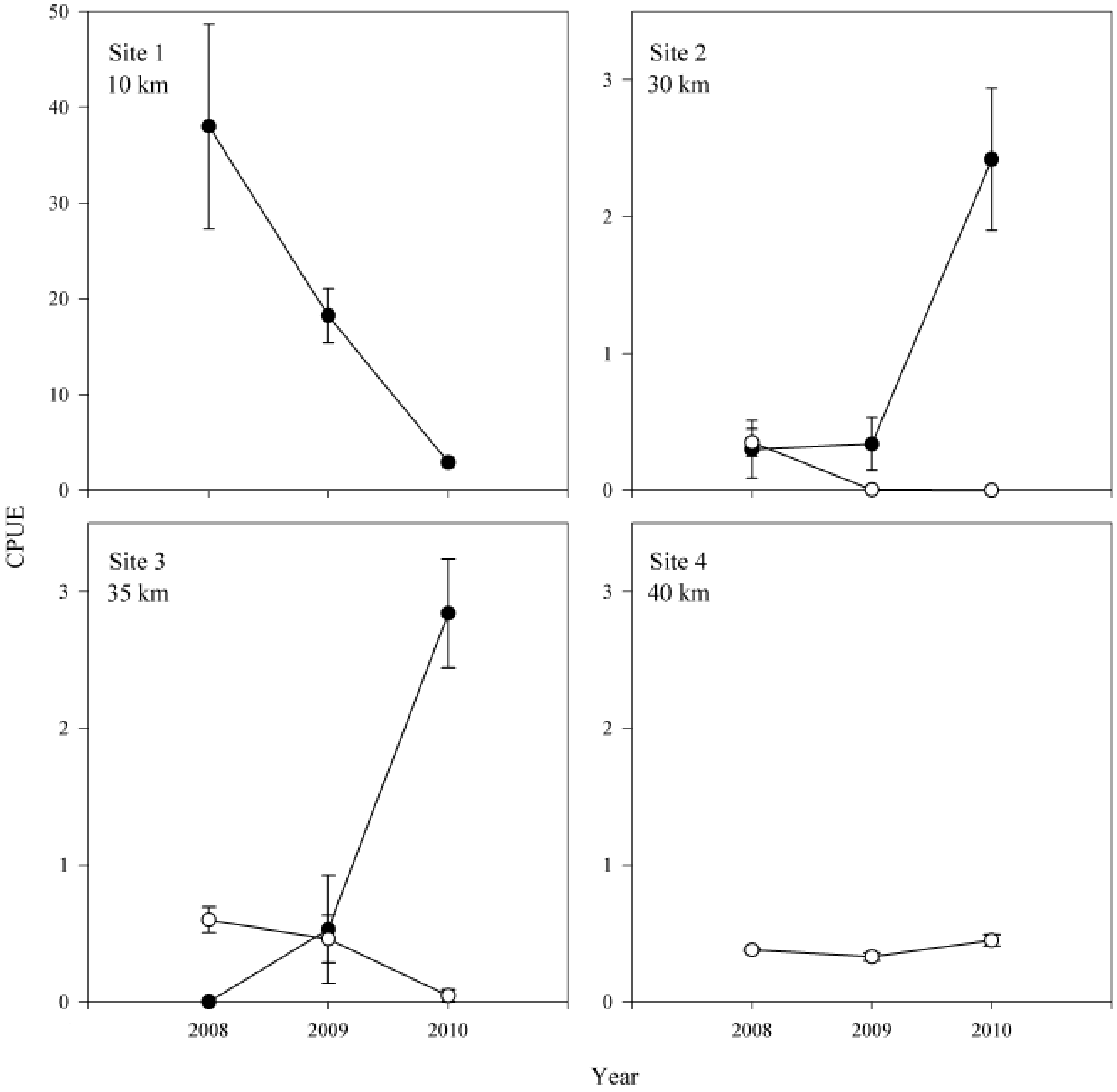

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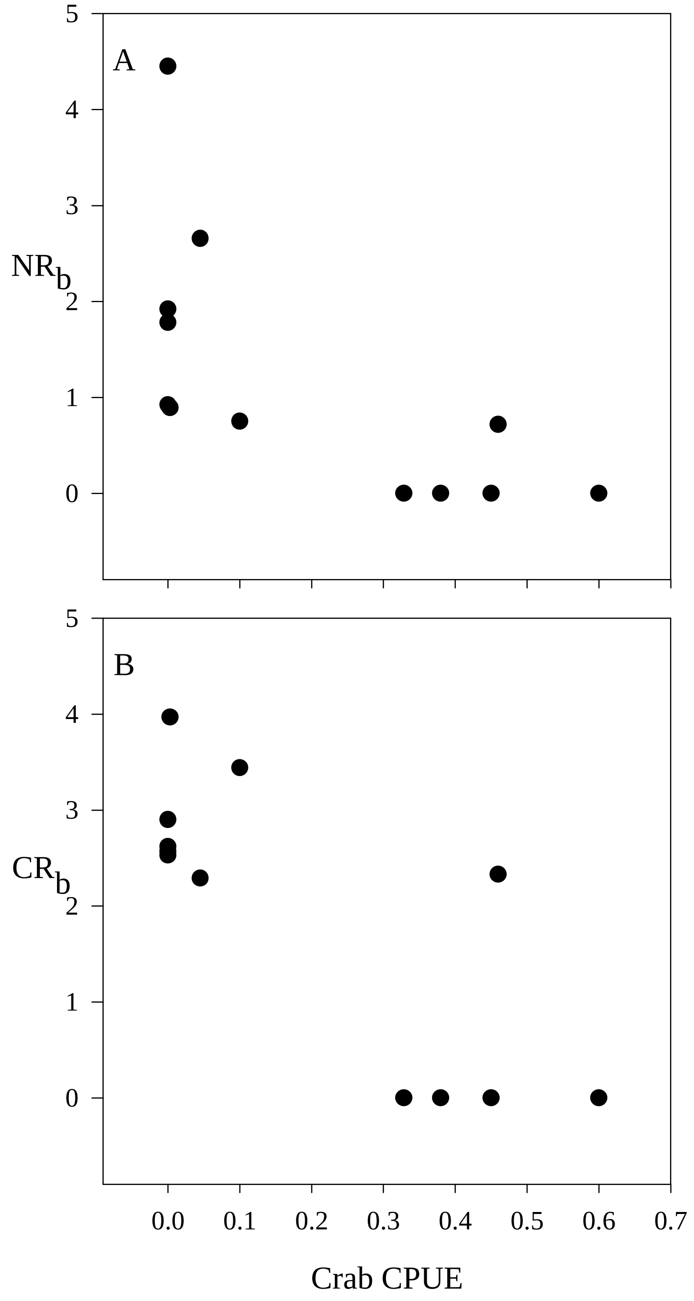

Fig. 6. Jackson *et al.*