

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

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19 **Running head:** Niche constriction and invasion success

20 **Abstract**

- 21 1. Invasive species are a key driver of global environmental change, with frequently
22 strong negative consequences for native biodiversity and ecosystem processes.
23 Understanding competitive interactions between invaders and functionally similar
24 native species provides an important benchmark for predicting the consequences of
25 invasion. However, even though having a broad dietary niche is widely considered a
26 key factor determining invasion success, little is known about the effects of
27 competition with functionally similar native competitors on the dietary niche breadths
28 of invasive species.
- 29 2. We used a combination of field experiments and field surveys to examine the impacts
30 of competition with a functionally similar native crab species on the population
31 densities, growth rates and diet of the globally widespread invasive red swamp
32 crayfish in an African river ecosystem.
- 33 3. The presence of native crabs triggered significant dietary niche constriction within the
34 invasive crayfish population. Further, growth rates of both species were reduced
35 significantly, and by a similar extent, in the presence of one another. In spite of this,
36 crayfish maintained positive growth rates in the presence of crabs, whereas crabs lost
37 mass in the presence of crayfish. Consequently, over the three year duration of the
38 study, crab abundance declined at those sites invaded by the crayfish, becoming
39 locally extinct at one.
- 40 4. The invasive crayfish had a dramatic effect on ecosystem structure and functioning,
41 halving benthic invertebrate densities and increasing decomposition rates four-fold
42 compared to the crabs. This indicates that replacement of native crabs by invasive

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

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

50

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

53 **Introduction**

54 The increasingly rapid spread of biological invaders in recent decades (*e.g.* Ricciardi,
55 2006; Jackson & Grey, 2013) is a key driver of global environmental change with major
56 implications for biodiversity and ecosystem functioning (Chapin *et al.*, 2000; Gurevitch &
57 Padilla, 2004; Pejchar & Mooney, 2009). Invasive species can have dramatic and often
58 irreversible effects on ecosystem services, frequently with considerable economic
59 implications (Pejchar & Mooney, 2009; Walsh *et al.* 2016), particularly in aquatic
60 ecosystems, which tend to be especially susceptible (Rahel & Olden, 2008). They can change
61 fundamental ecological processes from the level of the individual to the whole ecosystem
62 (Peltzer *et al.*, 2010; Penk *et al.* 2015, 2016), and frequently alter the distribution of native
63 species via a range of competitive interactions, predation pressure and/or habitat degradation
64 (Mack *et al.*, 2000; Simon & Townsend, 2003; Hooper *et al.*, 2005). Classic invasion theory
65 (Elton, 1958) predicts that a successful invader can establish itself in an unoccupied niche or
66 displace similar native species by overlapping their niche and eventually out-competing them
67 for limited resources. Having a generalist diet is a common trait of successful invaders,
68 allowing them to opportunistically exploit diverse resources in novel environments and
69 competitively exclude native species (Snyder & Evans, 2006). Hence, the decline of native
70 species following an invasion is often a consequence of direct interspecific competition for
71 resources (*e.g.* Porter & Savignano, 1990; Olsson *et al.*, 2009).

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

77 (Svanbäck and Bolnick 2007). Empirical evidence indicates that interspecific competition can
78 cause the niche widths of consumers to increase or decrease depending on the context but the
79 reason for this variation is still unclear (Araújo *et al.*, 2011). Despite these apparently
80 contradictory processes (Araújo *et al.*, 2011), the dietary niche breadth of invasive and native
81 competitors has rarely been examined, even though it is likely a key factor in determining
82 invasion success and predicting impacts of invaders on biodiversity (*e.g.* Jackson & Britton,
83 2013; Penk *et al.* 2015).

84 Some of the most destructive freshwater invaders are crayfish (Lodge *et al.*, 2012),
85 which can alter ecosystem structure and processes by, for example, homogenising biotic
86 assemblages and altering rates of both primary production and decomposition (Stenroth &
87 Nyström, 2003; Renai & Gherardi, 2004; Gherardi & Acquistapace, 2007; Jackson *et al.*,
88 2014). Ecologists have yet to examine fully the range of mechanisms underpinning the
89 impacts of invasive crayfish on ecosystem structure and functioning (Lodge *et al.*, 2012). The
90 red swamp crayfish (*Procambarus clarkii*) is a particularly important invader due to its global
91 distribution (Capinha *et al.*, 2011) and the severe impacts it has on ecosystems (Klose and
92 Cooper, 2012; Jackson *et al.*, 2014). In the 1960s, the species was introduced to multiple
93 locations throughout East Africa for aquaculture (Harper *et al.*, 2002), where its effects
94 remain largely unknown. This widespread introduction of crayfish in the region has led to
95 encroachment on the range of many native freshwater crab species, several of which are
96 endangered and endemic (Cumberlidge *et al.*, 2009). Indeed, crayfish have replaced crabs as
97 the primary food source of African clawless otters in some Kenyan rivers (Ogada, 2006),
98 providing indirect evidence that they are becoming more abundant and outcompeting crabs.
99 Crabs and crayfish are both benthic omnivores with similar feeding mechanisms. They
100 frequently occupy similar functional roles as shredders driving detrital processing (Nyström

101 *et al.*, 1996; Dudgeon, 1999; Dobson *et al.*, 2002; Lancaster *et al.*, 2008) and, consequently,
102 the introduced crayfish might be expected to be functionally redundant (*sensu* Naeem, 1998).
103 However, even morphologically similar species can vary significantly in their effects on
104 ecosystems (O'Connor & Bruno, 2007; Matthews *et al.*, 2011; Jackson *et al.*, 2014; Penk *et*
105 *al.*, 2015). Furthermore, highly invasive species tend to be more voracious than their native
106 counterparts (Haddaway *et al.*, 2012; Alexander *et al.*, 2014), implying that red swamp
107 crayfish could cause considerable alteration to ecosystem structure and processes were they
108 to replace native crabs.

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

121

122 **Materials and Methods**

123 *Study system*

124 The River Malewa is the primary tributary of Lake Naivasha (catchment area 1750 km²)
125 in Kenya's Rift Valley in East Africa. Red swamp crayfish were introduced to Lake Naivasha
126 in 1970 and subsequently spread throughout the catchment as a result of further introductions
127 and natural dispersal, leading to their intrusion upon the range of a native river crab, *P. loveni*
128 (Foster & Harper, 2007). The native range of *P. loveni* extends from Eastern Kenya into
129 Western Uganda (Cumberlidge, 2008).

130 *Experimental design*

131 We conducted two field experiments in the River Malewa near Gilgil (0°31' 5" 5.42" S,
132 36° 24' 3.33" E) at a site at the crayfish invasion front where both species were present. The
133 first experiment took place in April 2009 and the second in March 2010. Both experiments
134 were of 28 days duration and comprised the same two fixed factors in a fully-factorial design:
135 the presence of the native crab (two levels: present and absent) and the presence of red
136 swamp crayfish (two levels: present and absent). The experiments differed, however, in both
137 the level of replication (experiment 1: $n = 4$; experiment 2: $n = 6$) and the range of response
138 variables that were quantified (Table 1).

139 We manipulated the presence of our target organisms using steel-framed cages (Fig. S1).
140 The cages had a 0.315 m² solid base surrounded fully by stainless steel mesh (5 mm aperture)
141 to regulate the presence of crayfish and crabs and allow the free movement of other smaller
142 invertebrates, algae and organic matter. The cages were 30 cm in height. The entire base of
143 each cage was covered with pooled and well-mixed pebble and gravel substratum from the
144 adjacent river bed and a native macrophyte (Family Scrophulariaceae, ~5 g fresh weight) was

145 added to simulate natural habitat. A 400 cm² tray was also filled with well-mixed river
146 substratum and inoculated with benthic invertebrates from a uniform kick sample taken from
147 the experimental site. The cages were fully submerged for the duration of the experiment.

148 Crayfish and crabs used in the experiment were collected from allopatric populations in
149 the River Malewa. Experimental cages belonging to all treatments containing decapods
150 comprised four adult individuals of crabs (mean individual biomass [\pm S. D.]: 7.4 ± 1.9 g)
151 and/or crayfish (mean individual biomass [\pm S. D.]: 7.9 ± 2.2 g), with a combined biomass
152 approximating 30 g fresh weight (range: 25.7 – 37.7 g; total decapod biomass within
153 experimental cages did not vary among treatments: ANOVA, $F_{2,12} = 0.66$, $P = 0.53$). The
154 density of decapods within our experimental cages (12.7 individuals m⁻²) was within the
155 range of densities reported for both species from nearby locations (Harper *et al.* 2002). Males
156 and females were represented equally in all experimental treatments, although we only used
157 individuals of the same sex within each enclosure. The weight (g) and size [carapace length
158 (cephalic groove to the end of the rostrum) in crayfish and carapace width (at the widest
159 point] in crabs)] of all individuals was recorded before addition to the enclosures. Where both
160 crabs and crayfish were present together, treatments contained two individuals of both
161 species, all of similar biomass. Results from substitutive experiments that manipulate density
162 and biomass, such as we use here, can be sensitive to the selected total mixture density
163 (Inouye, 2001). However, they can effectively quantify the extent to which the measured
164 outcome is a consequence of the mixture components (in our case, presence or absence of
165 crayfish and crabs at natural densities). Comparison of the treatment with crayfish present
166 and crabs absent with the treatments without crayfish allowed us to quantify the effect of the
167 invader on the ecosystem, while comparison of the single species treatments with the two-
168 species treatment allowed us to quantify the effect of interspecific competition on crayfish

169 and crab growth and diet. Our four treatment combinations (crayfish only; crabs only;
170 crayfish and crabs; neither crayfish nor crabs) were assigned to cages placed along a 40 m
171 stretch of the river following a randomised block design. The cage mesh was cleaned every
172 four days to remove debris, and at the same time we checked for survival of crabs and
173 crayfish. Survival rates were 100% throughout the second field experiment but some crab
174 mortality occurred in the last week of the first experiment. Hence, results of the first
175 experiment were used only to explore aspects of ecosystem functioning (Table 1).
176 Unfortunately, two enclosures were damaged during the second experiment and were omitted
177 from analyses (Table 1).

178 *Experiment sampling protocol*

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

$$185 \quad k = \frac{\log_e \left(\frac{M_t}{M_0} \right)}{t}$$

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

188 We measured epilithic algal standing stock by placing a terracotta tile (10 x 10 cm) in
189 each cage at the start of the experiment. Tiles were removed on the final day and all biofilm

190 was washed off and filtered through GF/C filters (Whatman[®], Maidstone, UK) before adding
191 15 ml of 90% acetone. Chlorophyll *a* concentration of the filtrate, quantified following
192 Jeffery and Humphrey (1975), was used as a measure of periphyton biomass. We quantified
193 the benthic invertebrates in the cages at the end of the experiment by removing, counting and
194 identifying all organisms in the trays that were filled with substrate from the experimental site
195 at the commencement of the experiment. All invertebrates were stored in 70% ethanol prior
196 to identification (to genus) and enumeration.

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

214 were used as reference materials. Cyclohexanone-2,4-Dinitrophenylhydrazone was used as
215 an internal standard and resulted in typical precision of < 0.1‰ for carbon and < 0.3% for
216 nitrogen.

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

222 *Field surveys*

223 We examined the distribution of both crabs and crayfish at four sites in the River
224 Malewa, located approximately 10, 30, 35 and 40 km upstream of Lake Naivasha, in 2008,
225 2009 and 2010. We quantified the abundance of adult crayfish and crabs on 3 to 8 occasions
226 at each site in each year over a 6-week period, using a series of crayfish traps of 5 mm mesh,
227 baited with fish pellets and left for between 1 and 2 hours. All crayfish and/or crabs were
228 removed and counted and we used the catch per unit effort (CPUE; number of individuals per
229 trap per hour) to quantify relative abundance among sites. Samples ($n = 6$ to 18) of a selected
230 common size range of crabs (26 - 35 mm carapace width) and crayfish (31 - 45 mm carapace
231 length) from all sites on all sampling occasions were prepared for stable isotope analysis as
232 described previously. Epilithic algae, macrophytes, detritus and dominant benthic
233 invertebrate species were also collected from all the sites for subsequent stable isotope
234 analysis.

235

236

237 *Data analyses*

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

256 The stable isotope-derived population metrics of carbon range (CR_b) and nitrogen range
257 (NR_b) were used as measures of the trophic niche width of crabs and crayfish (Layman *et al.*,
258 2007b; Jackson *et al.*, 2012) in both the field experiments and field surveys. CR_b and NR_b
259 were calculated as the Euclidean distance between the individuals with the lowest and highest
260 $\delta^{13}C$ and $\delta^{15}N$ respectively and therefore reflect the total range of isotopic space used by a

261 group of organisms. To enable comparison among variables and to account for small sample
262 sizes, the metrics were bootstrapped ($n = 10000$; indicated with a subscript ‘_b’) based on the
263 minimum sample sizes (2 individuals in the field experiment [in the enclosures containing 2
264 crabs and 2 crayfish – each measurement was therefore replicated independently five times
265 (Table 1)] and 6 individuals in the field surveys [at field sites with declining crab numbers]).
266 We then used ANOVA to test for differences in the trophic niche width of crayfish and crabs
267 when together and apart in the field experiment. However, given that one of our experimental
268 treatments contained no crayfish or crabs, and could not therefore provide measurements of
269 trophic niche widths of either species, our statistical model testing for differences in trophic
270 niche width comprised two fixed factors: species (two levels: crabs and crayfish) and the
271 presence of interspecific competition with a functionally similar species (two levels:
272 competition and no competition). For the field survey data, we tested for correlations between
273 our metrics of trophic niche width of each species and the corresponding CPUE of its
274 functionally similar competitor. To ensure comparability in the isotopic data among survey
275 sites and years, we used PERMANOVA to test for any effect of site or year on the stable
276 isotopic signature of putative resources (biofilm, macrophytes, detritus and dominant
277 invertebrate taxa). We found similar stable isotope values of putative resources both among
278 survey sites and years (Table S1), indicating that any differences in trophic niche width
279 between crayfish and crabs were attributable to actual dietary variation.

280 **Results**

281 *Field experiments*

282 There was a significant interaction between the presence of crayfish and crab on rates of
283 leaf litter breakdown (ANOVA; $F_{1,36} = 12.66$, $P = 0.001$). Rates of breakdown were

284 significantly higher in the cages containing only crayfish compared with those containing
285 none of the manipulated consumers (control treatment). In contrast, cages containing crabs
286 were similar to those in the control treatment, while cages containing both crayfish and crabs
287 had intermediate effect on breakdown rates (Fig. 1). The latter result indicates that the
288 presence of crabs did not alter the per capita effects of crayfish on leaf litter breakdown rates.
289 Neither crabs nor crayfish affected the standing stock of epilithic algae.

290 Crayfish reduced the density of benthic invertebrates (ANOVA, $F_{1,16} = 9.39$, $P = 0.007$,
291 Fig. 2) and altered their multivariate structure significantly (PERMANOVA; pseudo- $F_{1,17} =$
292 6.05 , $P = 0.004$). The latter result was driven primarily by reductions in the density of
293 hydropsychid caddis flies (Trichoptera) together with an increase in the density of
294 oligochaete worms (Table 2). In contrast, crabs had no effect on the density or multivariate
295 structure of benthic invertebrate assemblages. However, both crabs and crayfish reduced the
296 taxon richness of benthic invertebrates significantly, irrespective of the presence or absence
297 of the other decapod consumer species (ANOVA; crayfish: $F_{1,16} = 6.76$, $P = 0.019$; crabs:
298 $F_{1,16} = 4.84$, $P = 0.043$; Fig. 2).

299 The nitrogen range (NR_b) of both crabs and crayfish was reduced significantly in the
300 presence of the other functionally similar species (ANOVA; $F_{1,17} = 4.64$, $P = 0.046$; Fig. 3A).
301 There was, however, no effect of the presence of crab or crayfish on the carbon range (CR_b ;
302 Fig. 3B) of the other species. Gut content analysis revealed that the relative contribution of
303 animal and plant material to the diet of crayfish did not change in the presence of crabs (45.5
304 ± 17.7 % and 46.8 ± 9.8 % animal material in sympatric and allopatric populations,
305 respectively).

306 Per capita growth rates of both crabs and crayfish were reduced significantly by the
307 presence of the other species compared with a similar biomass of conspecifics (ANOVA;
308 $F_{1,48} = 6.64$, $P = 0.013$; Fig. 4). Both crabs and crayfish experienced similar reductions in
309 both absolute (ANOVA; species*competition interaction: $F_{1,48} = 0.003$, $P = 0.96$) and relative
310 ($F_{1,48} = 0.02$, $P = 0.9$) growth rates due to the presence of the other species. However, growth
311 rates of crayfish were significantly higher than those of crabs ($F_{1,48} = 10.63$, $P = 0.002$).
312 Thus, even though their growth rates were reduced significantly in the presence of crabs,
313 crayfish still gained significant biomass over the course of the experiment. In contrast, crabs
314 generally lost biomass when present together with crayfish (Fig. 4).

315 *Field surveys*

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

323 We found significant inverse correlations between the abundance of crabs and both the
324 nitrogen (NR_b; $r_{11} = -0.67$, $P = 0.018$; Fig. 6A) and carbon (CR_b; $r_{11} = -0.80$, $P = 0.002$; Fig.
325 6B) range of crayfish over the four sites. However, neither measure of crab trophic niche
326 width correlated significantly with the abundance of crayfish (CR_b; $r_{11} = -0.54$, $P = 0.071$;
327 NR_b; $r_{11} = -0.53$, $P = 0.074$).

328

329 **Discussion**

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

345 Invasive species regularly outcompete and reduce the growth rate of native species (*e.g.*
346 Smith, 2005; Riley, 2009; Britton *et al.*, 2011). However, we found strong and apparently
347 symmetric interspecific competition, measured in terms of biomass change, between the
348 invasive crayfish and native crabs. Growth rates of crayfish individuals were reduced in the
349 presence of crabs compared to in the presence of a similar biomass of conspecifics, implying
350 that interspecific competition was significantly greater than intraspecific competition. This is
351 consistent with the presence of significant interspecific aggression, which we observed
352 repeatedly during the study, causing reductions in foraging efficiency of both species when

353 present together. Such aggressive behaviour between species is frequently greater than
354 aggression with conspecifics (Polo-Cavia *et al.*, 2011). Even though both absolute and
355 relative reductions in growth rates were similar for both decapod consumers, crayfish still
356 exhibited positive per capita growth rates in the presence of crabs, whereas crabs generally
357 lost mass in the presence of the invasive crayfish. This likely contributed to the decline in
358 crab abundance at sites invaded by crayfish. Invasive crayfish have outcompeted native
359 crayfish across North America and Europe by triggering similar declines in growth rates of
360 natives (Hill & Lodge, 1999; Dunn *et al.*, 2009; Nakata & Goshima, 2006). As far as we are
361 aware, this is the first study to test experimentally for interspecific competition between
362 native crabs and introduced crayfish, despite numerous overlapping populations in both
363 Europe and Africa (*e.g.* Barbaresi & Gherardi, 1997; Foster & Harper, 2007; du Preez &
364 Smit, 2013).

365 As omnivores, crayfish and crabs can survive when a resource is limited by shifting their
366 diet to alternative resources to compensate (Tillberg *et al.*, 2007; Grey & Jackson, 2012).
367 This is advantageous when exploiting niches with novel resources, which may explain the
368 successful widespread distribution of some invasive crayfish and crab species (Capinha *et al.*,
369 2011). Flexibility in diet choice does not necessarily imply a wide niche breadth because in
370 some scenarios it may benefit the consumer to focus on one abundant but under-used
371 resource (Popa-Lisseanu *et al.*, 2007). The observed reduction in crayfish and crab diet
372 breadth in the presence of interspecific competition could be a result of increased dietary
373 specialisation and hence a consequent decline in the variation in diet choice of individuals
374 (Bolnick *et al.*, 2010). Alternatively, the isotopic variability could be reduced due to
375 individuals becoming more generalist and therefore reducing the variation among the diets of
376 each individual (Bolnick *et al.*, 2010). Examination of gut contents revealed no significant

377 overall shift in the diets of crayfish in the presence of crabs. Therefore, that we found
378 significant reductions in the trophic niche breadth of crayfish populations in the presence of
379 crabs in both the field experiments and field surveys indicates that, although the overall
380 dietary preferences of crayfish were not altered in the presence of crabs, the individuals
381 within the crayfish population were tending to feed in a more similar manner. These results
382 were consistent across both the field experiments and field surveys, strongly supporting the
383 robustness and generality of this finding. The presence of the crabs appears to have triggered
384 dietary homogenisation within the crayfish population. Crabs exhibited a significant decline
385 in diet breadth only in the experiments and not in the field surveys. This inconsistency in
386 results perhaps suggests less flexibility in diet choice of crabs compared to the crayfish.

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

397 Previous studies have found that functionally similar sympatric crab species can interact
398 to moderate one another's impact due to consumer redundancy (Griffen & Byers, 2008).
399 However, we found intermediate leaf litter breakdown rates in the combined species
400 treatment in our field experiment suggesting there was no consumer interaction, as was also

401 found for pairs of crayfish in the United Kingdom (Jackson *et al.*, 2014). We also found that
402 the invasive crayfish significantly altered benthic community structure and approximately
403 halved invertebrate densities compared with the native crabs. These latter findings are
404 consistent with previous studies on invasive crayfish in Europe (Stenroth & Nyström, 2003;
405 Haddaway *et al.*, 2012; Moorhouse *et al.*, 2013). In contrast, native crabs had no effect on the
406 structure or density of benthic assemblages, which were similar to those in the experimental
407 units containing no decapod consumers. In spite of the similarities between these decapod
408 crustaceans, results from our field experiments suggest that replacement of the native crabs
409 by the invasive crayfish will considerably alter both the structure and functioning of African
410 river ecosystems. Moreover, these shifts in ecosystem structure and functioning may even
411 have facilitated indirectly the replacement of the native crabs by the crayfish by reducing
412 suitable habitat for the crabs (Parker *et al.*, 1999) by, for example, removing leaf litter as
413 refugia. Such changes also have the potential to alter key ecosystem services such as fishery
414 production and water quality, both of which are extremely important in this semi-arid region
415 of East Africa. Many river crabs in East Africa are already highly endangered (Cumberlidge
416 *et al.*, 2009) and local biodiversity will only become increasingly impaired as crayfish spread
417 or are introduced further in both rivers and lakes (Lodge *et al.*, 2005).

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

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432 **Data Accessibility**

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

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666

667 **Supporting Information**

668 The following supporting information is available for this article online:

669 **Figure S1.** The design of the experimental cages

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

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

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

677 **Table S4.** Change in crayfish and crab individual body mass in the experimental treatments
678 (mean \pm s.e.).

679 **Table S5.** Crayfish and crab catch per unit effort (CPUE), carbon (CR_b) and nitrogen (NR_b)
680 range in the field surveys.

681 **Tables**

682 **Table 1.** Response variables quantified during the two field experiments. The number of
683 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])

684

685 **Table 2.** Results of SIMPER analysis indicating the five benthic invertebrate taxa affected
 686 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

687

688

689 **Figure legends**

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

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

696 **Fig. 3.** The nitrogen (A) and carbon (B) range of crayfish and crabs in our experimental
697 treatments (mean + s.e.). Figure inset shows the effect of the presence (C) and absence (NC)
698 of interspecific competition on both species where significant main effects were detected ($P <$
699 0.05).

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

704 **Fig. 5.** Catch per unit effort (CPUE) of crayfish (black circles) and crabs (open circles) from
705 2008-2010 based on multiple trapping sessions at four sites (mean \pm s.e.). The distance
706 indicated on the graphs refers to the total distance upstream from the lake. Note the different
707 scale on the Y-axis for Site 1. The decrease in crayfish CPUE at the latter site, the most
708 downstream site adjacent to Lake Naivasha, is consistent with concurrent patterns within the
709 lake, and is likely a consequence of competition with a more recent invader, the common
710 carp (*Cyprinus carpio*), to the lake ecosystem at the time of study (Jackson *et al.*, 2012).

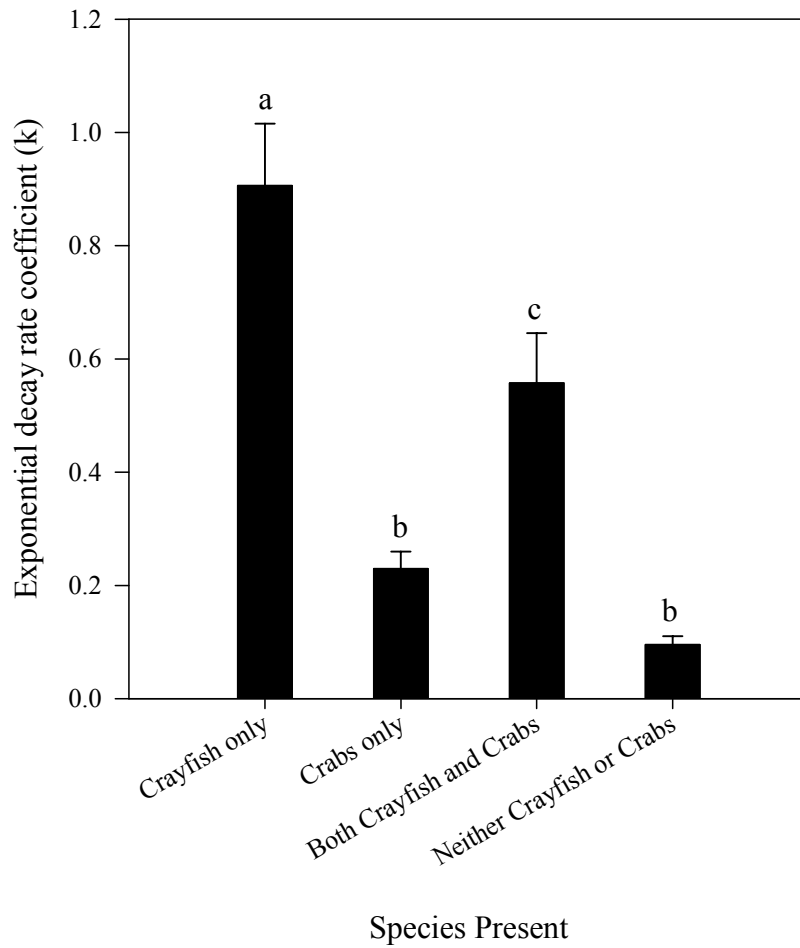
711 **Fig. 6.** Relationships between crab CPUE and the nitrogen range (A) and carbon range (B) of
712 crayfish.

713

714 **Figures**

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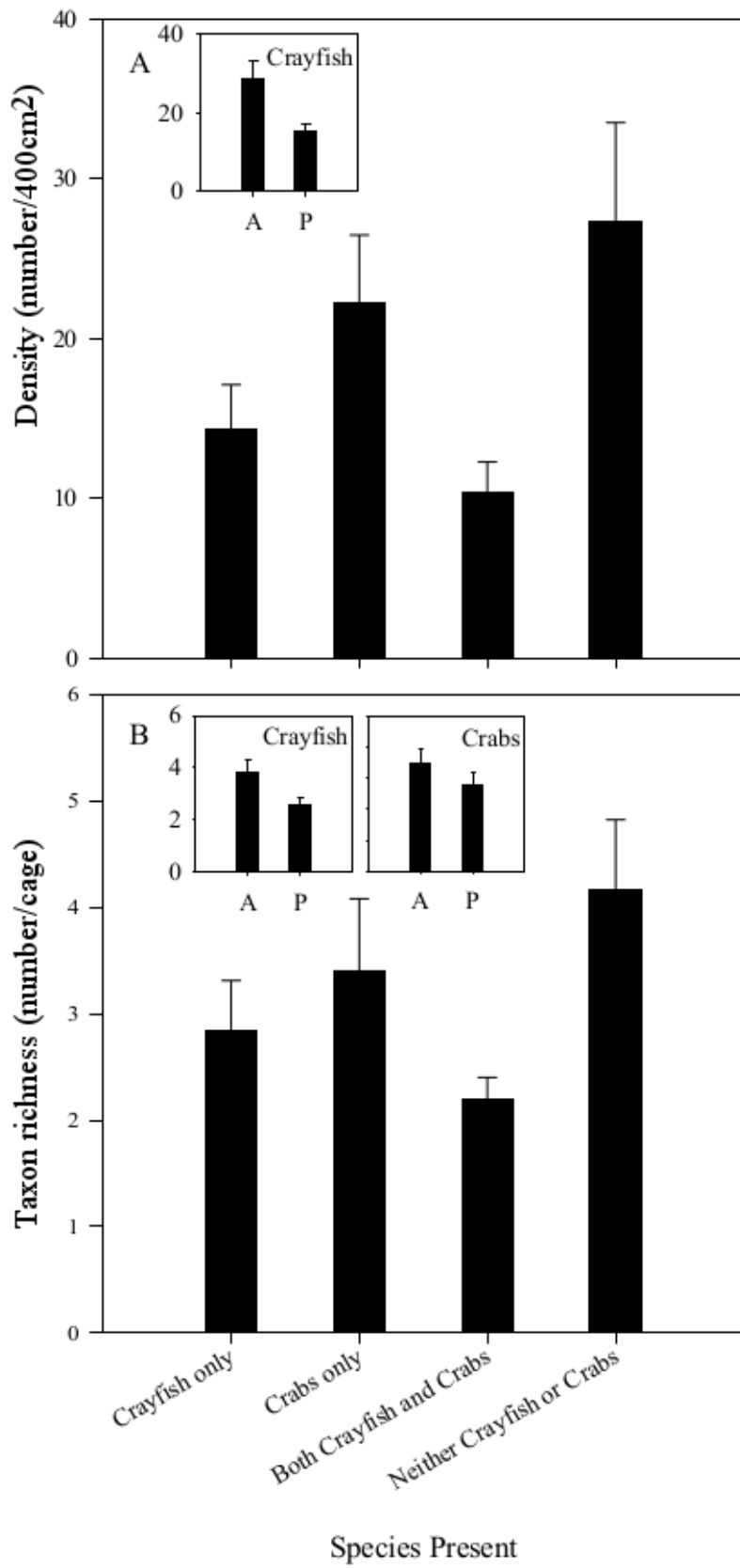
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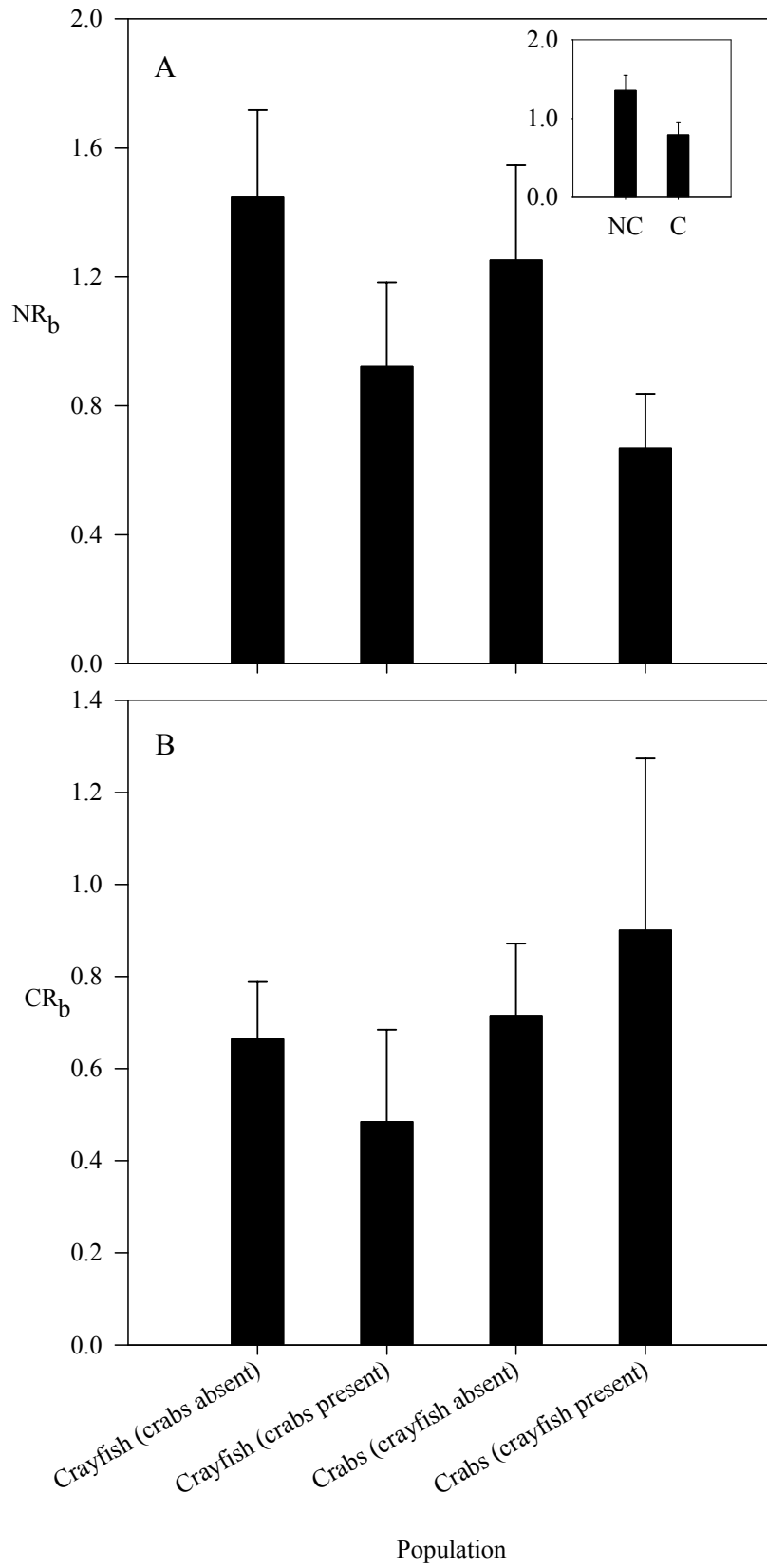
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Fig. 1. Jackson *et al.*





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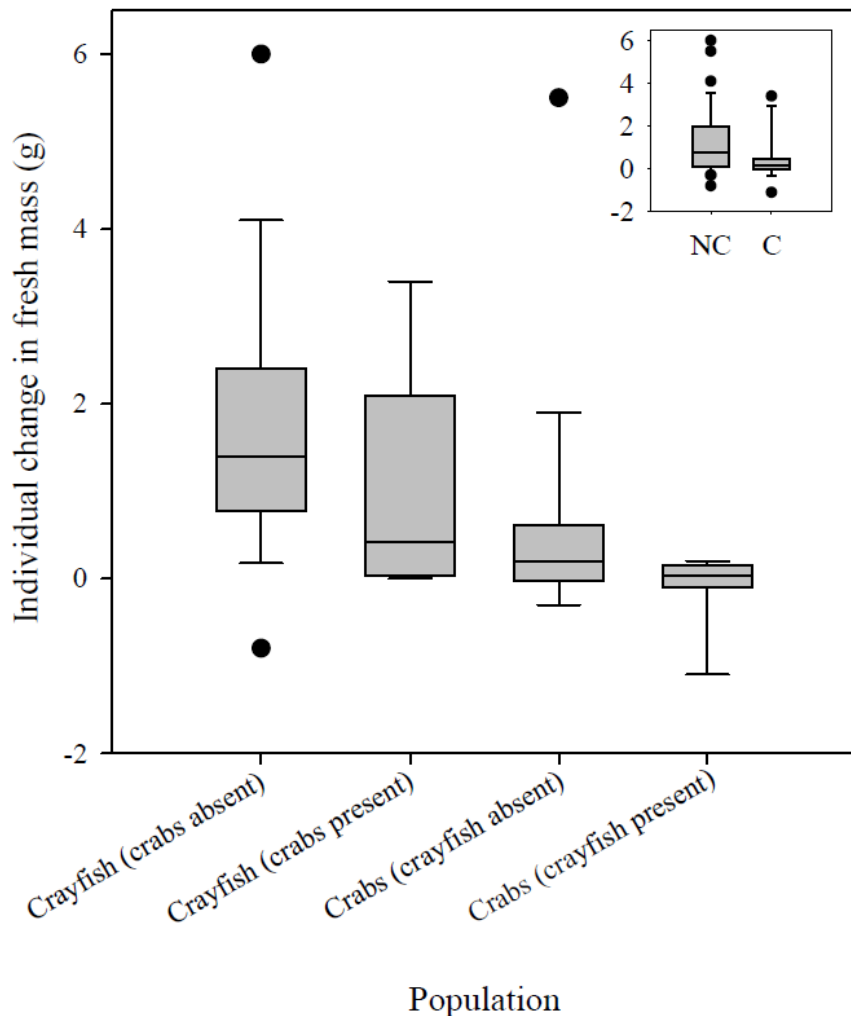
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Fig. 3. Jackson *et al.*

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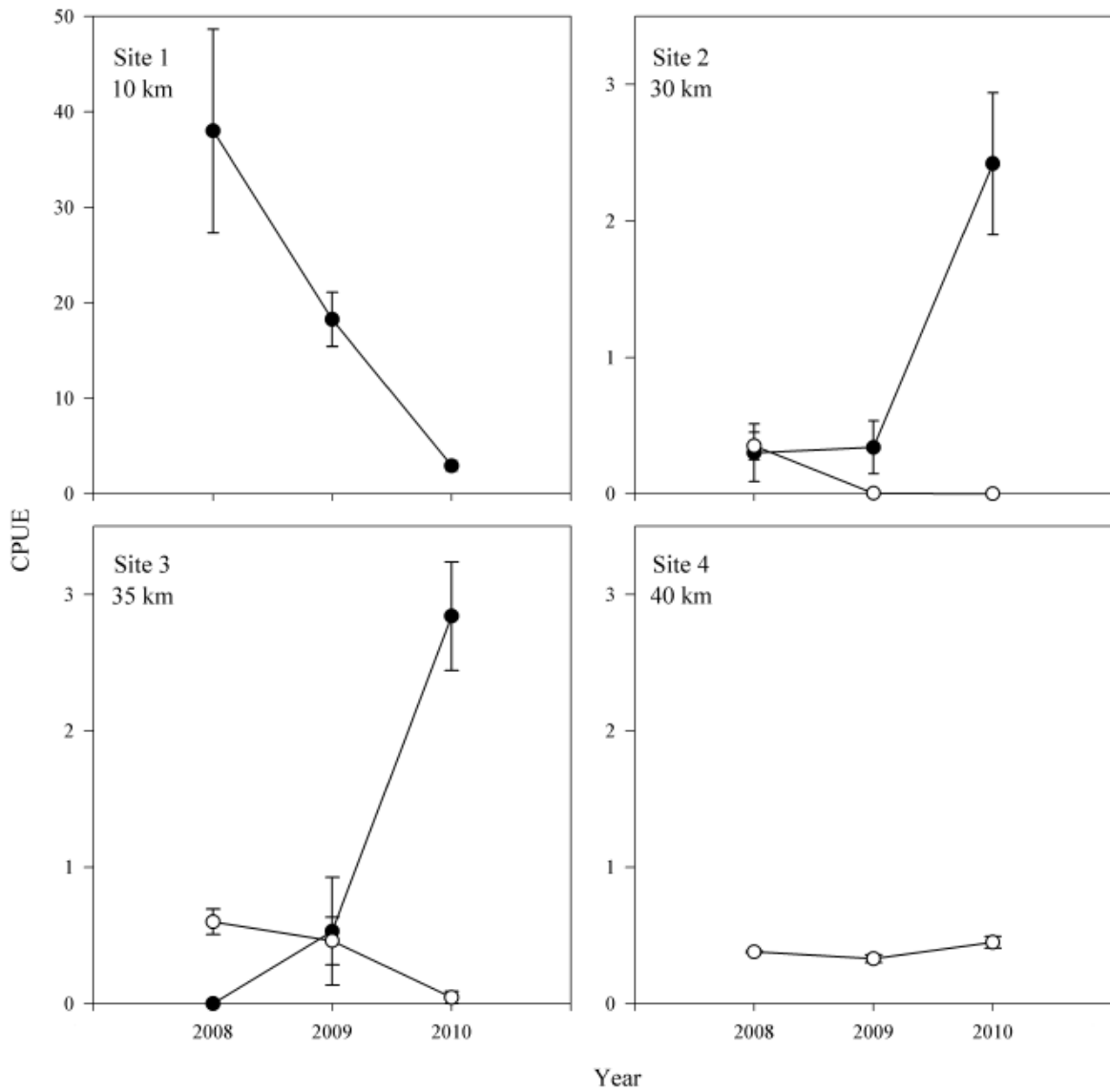
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Fig. 4. Jackson *et al.*

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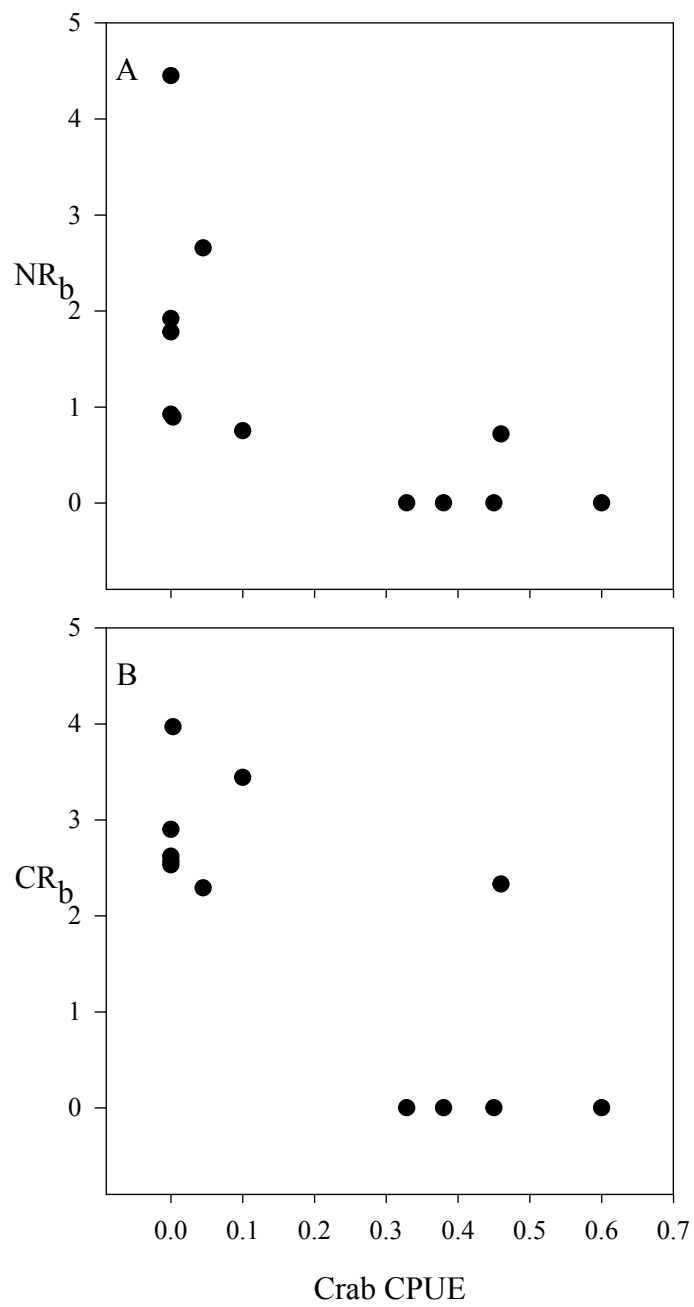
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Fig. 5. Jackson *et al.*



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Fig. 6. Jackson *et al.*