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1 **The intertidal benthic community of mangrove dominated**
2 **estuaries: the ecological implications of a decoupled**
3 **habitat.**

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21 **Abstract**

22 The benthic infauna of mangrove forests have received little research despite their importance in
23 regulating ecological processes and nutrient cycling. The majority of studies of benthic community in
24 mangrove systems have either focused on the adjacent tidal flats, or areas with high density of
25 pneumatophores without entering within the forest, giving a misleading impression that mangrove
26 infauna community is understood in detail. To fill the knowledge gap we investigated the
27 composition and distribution of benthic taxa across a tidal gradient in two meso-tidal tropical
28 estuarine mangrove forests in north Queensland, Australia. We used a 10 cm corer to sample inside
29 the mangrove forest and on the adjacent tidal flat. Taxonomic composition was vastly different
30 between the tidal flat and the mangrove forest. In fact, although peracarid (e.g. amphipods)
31 characterized the community of tidal flats, they were never recorded within the forest. The
32 contrasting community composition likely denotes contrasting ecological role of the two habitats. In
33 particular, because peracarids are a key component of juvenile fish diets, their absence within the
34 forest probably limits foraging opportunities for many juvenile fish within the forest, while their
35 dominance on adjacent tidal flats suggests that these are likely to be the key feeding areas.

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39 **Key words:** Marine Invertebrate, *Rhizophora stylosa*, feeding ground, tidal flat, mangrove function

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43 **Introduction**

44 The importance of benthic invertebrate fauna in regulating environmental processes in marine
45 ecosystems is indisputable. They influence structural complexity, nutrient recycling and sediment
46 bioturbation, and provide trophic linkages between primary producers and higher consumers
47 (Underwood 2000, Coen et al. 2007, Queirós et al. 2013, McPhee et al. 2015). As a result of their
48 trophic roles, benthic invertebrate communities are often instrumental in regulating the composition
49 and distribution of fish at higher trophic levels by providing bottom-up control (Grebmeier et al. 2006,
50 Davis et al. 2014). Moreover, benthic invertebrates are often used as key indicators for the assessment
51 of environmental changes, and their composition and density can be used to detect habitat
52 degradation (Dufrene & Legendre 1997, Dauvin 2007). Due to their importance in the ecology of
53 estuarine and coastal systems, many studies have focussed on understanding the factors influencing
54 benthic invertebrate distribution, and on determining hotspots of benthic biodiversity (Connell 1972,
55 Bredenhand & Samways 2009, Sheaves et al. 2016).

56 In coastal and estuarine systems, the highest densities and richness of benthic fauna usually occur in
57 the intertidal zone, with subtidal areas often depauperate due to constant predatory pressure
58 (Gilinsky 1984, Little 2000, França et al. 2009, Sheaves et al. 2016). In tropical regions the higher
59 intertidal zone is often occupied by mangrove forests, thereby splitting the intertidal into two distinct
60 biotopes (i.e. the flat, and the forest). Nonetheless, the majority of research on benthic communities
61 in tropical intertidal systems has focussed on tidal flats, with fewer studies conducted within the
62 mangrove forest itself (Dittmann 1995, Dittmann & Vargas 2001, Bosire et al. 2004, Gladstone-
63 Gallagher et al. 2014); largely due to the difficulty of working within structurally complex mangrove
64 forests. Additionally, most of the knowledge regarding invertebrate fauna within mangrove forests
65 has come from the study of larger epibenthic taxa, such as crabs, large whelks and sessile bivalves
66 (Wells 1983, Lee 1998, Koch & Wolff 2002, Macintosh et al. 2002, Bosire et al. 2008, Rajpar & Zakaria
67 2014

68 This gives the impression that mangroves forest invertebrate communities are well studied, and
69 unique when compared to the tidal flats.

70 However, mangrove infauna, particularly those of smaller sizes, are underrepresented in the literature
71 (Checon et al 2017) and because of their different characteristics are likely to respond different to the
72 different habitats.

73 Additionally, the studies that have been conducted within mangrove forests focussed on systems with
74 contrasting biological and biophysical attributes, leading to results that are difficult to reconcile. For
75 instance, in a southern Florida microtidal *Rhizophora* forest, benthic infauna were more abundant
76 within the mangroves than in any adjacent habitat, with a mean density of about 35 000 individual
77 per square meter (Sheridan 1997). In contrast, in a temperate New Zealand mesotidal *Avicennia* forest
78 the pattern was reversed, with just a few hundred organisms per square meter within the forest (Ellis
79 et al. 2004). Such contrasting results are expected when comparing studies conducted in forests with
80 widely different environmental settings and mangrove species. Indeed, the overall paucity of well
81 defined studies that have assessed infauna communities within mangrove forests makes it hard to
82 find studies that are really comparable.. Mangrove forest infauna community is unlikely to resemble
83 the one of the adjacent tidal flat because of differences in inundation period and because unfavourable
84 dissolved oxygen (DO) dynamics within mangrove forests probably limits their utilisation by many
85 benthic taxa (Mattone and Sheaves 2017). Because DO is influenced by factors that are likely to act
86 differently based on location within the estuary (e.g. within the forest, on tidal flats, subtidal areas)
87 (Mattone and Sheaves 2017), its effect on the benthic community, and how benthos communities are
88 shaped would also differ. Consequently, a broad understanding of the nature of the infauna of
89 mangrove forests and their role within these systems is lacking.

90 A deeper understanding of the benthic community composition of mangrove forests is important in
91 evaluating and understanding the services provided to organisms by mangroves. For instance, there
92 is a general consensus that mangrove forests are important feeding grounds for juvenile fish.

93 However, the scientific evidence to support this paradigm is not convincing, with studies reporting
94 contrasting evidence (e.g. Huxham et al. 2004, Tse et al. 2008). This is because most studies that focus
95 on determining the value of mangroves as fish feeding grounds have based their assessment on
96 analyses of fish diets, or more recently stable isotope analysis (SIA) of fish (Cocheret De La Morinière
97 et al. 2003, Lugendo et al. 2007, Baker et al. 2014). However, the temporal resolution of both
98 techniques complicates interpretation. While dietary studies provide detailed information on prey
99 consumed, they do not indicate when and where the prey were ingested (Lugendo et al. 2007). This is
100 a problem when mangroves and adjacent tidal flats are only metres apart. There is an even greater
101 problem with SIA, because SIA integrates over time periods of days to months, and material (both in
102 the form of animal moving and organic matter transported in the water) can move between the forest
103 and flats, making it very hard to determining the extent to which a carbon signature reflects feeding
104 inside the mangrove forest versus feeding on prey utilising exported mangrove carbon (Bouillon et al.
105 2008).

106 Benthic communities influence nutrient cycles, both by providing important food sources (Baker &
107 Sheaves 2005) and by reworking the sediment leading to recycling of nutrients within the system
108 (Bertics et al. 2010). Consequently, an improved understanding of the benthic community of
109 mangrove forest would also improve our understanding of the extent and nature fish reliance on
110 mangrove resources. This is because knowing what taxa occur within mangrove forests, and their
111 distribution across forests, enhances our ability to infer their ecological role within the system. For
112 instance, from dietary studies we know that many estuarine juvenile fish tend to feed heavily on small
113 crustaceans, particularly peracarids (i.e. amphipods, tanaids, mysids) (Salini et al. 1990, Baldoa &
114 Drake 2002, Nanjo et al. 2008), therefore, if mangrove forests are important feeding grounds for
115 juvenile fish, we would expect high densities of peracarids within mangrove forests. Alternatively, if
116 some key prey taxa do not occur within mangrove forests, but only on the adjacent tidal flats, we
117 would be able to conclude that those taxa mainly acquire their food on adjacent tidal flats rather than
118 mangroves. In order to improve our understanding on the benthic ecology of mangrove forests, and

119 how this influences mangrove functions and processes, this study investigates the composition and
120 distribution of benthic taxa across a tidal gradient in two meso-tidal tropical estuarine *Rhizophora*
121 *stylosa* forests.

122

123 **Materials and Methods**

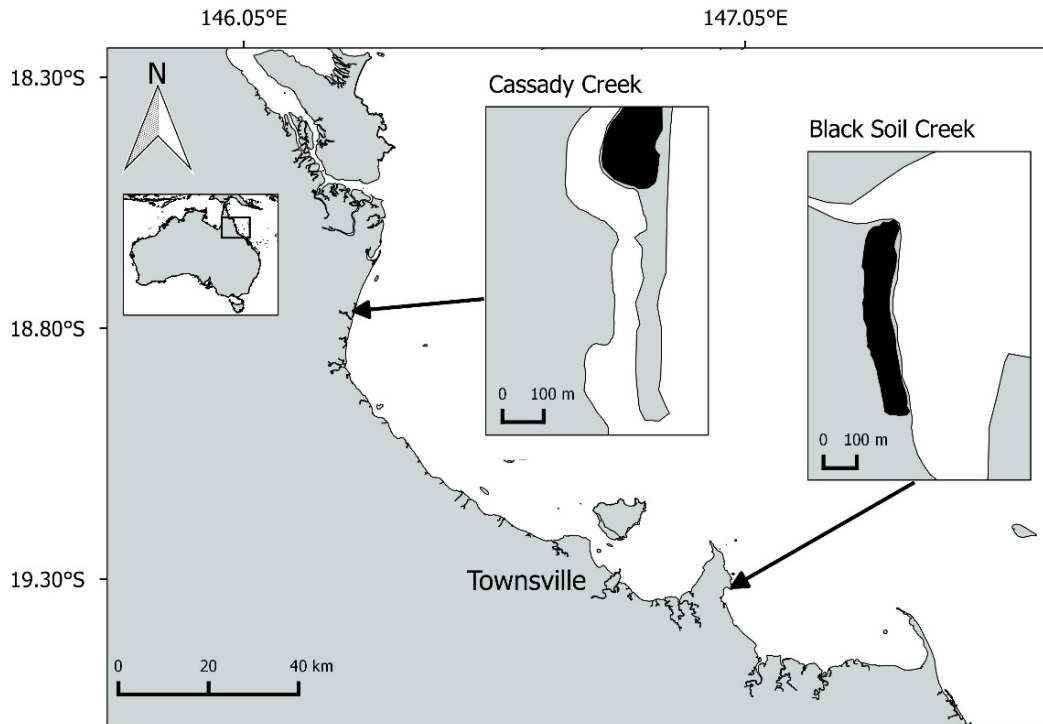
124 *Study Location*

125 The study was conducted in two estuaries, Blacksoil Creek (19.29806 S, 147.04083 E) and Cassady
126 Creek (18.74166 S, 146.28916 E), in tropical northeast Queensland, Australia (Fig. 1). Both estuaries
127 have a tidal range of approximately 4 m and are surrounded by thick mangrove forests dominated to
128 seaward by *Rhizophora stylosa*, with sparse occurrences of *Avicennia marina*, and with *Ceriops* spp.
129 dominating the landward margin of the forests. There is little urban or agricultural development in the
130 immediate vicinity of either study location; therefore direct human impact on the study sites is low.
131 Additionally, Blacksoil Creek is located within the Bowling Green Bay National Park, ensuring minimal
132 impact (Scheltinga et al. 2005). Both creeks are approximately 6 km long and have episodic freshwater
133 input that peaks during the wet season (November to March). Cassady Creek is located within the wet
134 tropics and has a relatively higher annual rainfall (averaging 1500-2000 mm a year) than Blacksoil
135 Creek, which is located in the dry tropics (averaging annual rainfall between 1000-1500 mm).

136 The Blacksoil Creek sampling area consisted of a small *R. stylosa* forest approximately 600 m in length
137 that extends landward for approximately 60 m. The sediment within the forest was firm mud rich in
138 organic matter. The Cassady Creek sampling location was approximately 160 m in length and extended
139 approximately 60 m landward. The sediment was also firm, but comprised a mix of mud and sand,
140 with less organic detritus than at Blacksoil Creek. Both forests had high levels of root webbing and
141 thick canopy cover (more than 80%). Both study locations are within the first kilometre upstream of
142 the mouth of the estuary and have similar elevations. Both forests are exposed during low tides and
143 neap high tides and inundation starts when tides exceed 2.6 m above lower astronomical tide (LAT)

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147 **Figure 1:** Map of the study sites, Blacksoil Creek and Cassidy Creek. The black shaded area represents
148 the Rhizophora forests that were sampled, tidal connection begins when the tide exceeds 2.6 m above
149 LAT.

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157 *Data Collection*

158 Samples were collected at Cassady Creek in February, April, August and December of 2014 and in
159 January 2015. Blacksoil Creek was sampled in July, September and October 2014. Two additional
160 sampling events were conducted at Cassady Creek because it was the initial site where preliminary data
161 were collected to determine sampling protocols. Therefore, while data collected with different
162 methods were discarded, the samples that utilized the same techniques as in the main study were
163 retained. Sampling was conducted using a corer of 10 cm diameter, and sampling standardised by only
164 utilising samples that reached a depth of at least 20 cm. Samples were taken inside the forest, at 10
165 m from the seaward forest edge (Edge) and again at 40 m from the seaward boundary (Inner). Six
166 replicate samples were collected at each distance approximately 5-10m apart. These were transported
167 to the laboratory within 3 hours where they were sieved through a 0.5 mm mesh and animals sorted
168 alive when possible. Following preliminary analysis, sampling was extended to the tidal flat, with
169 samples collected 1 m outside the forest edge (Flat). The additional sampling distance was introduced
170 at both study locations during the final two sampling trips. In total, 120 sediment samples were
171 collected. Animals extracted from the samples were identified to the lowest possible taxonomic level,
172 however, because the benthic infauna of mangroves in north Queensland is not well known, many
173 specimens were only identifiable to Family or Order level.

174 At each location and distance, four additional core samples of 5 cm diameter and 20 cm depth, were
175 collected and transported to the laboratory for assessment of sediment size and organic matter
176 content. All sediment samples were washed in fresh water to remove salt. Sediment size composition
177 was determined by drying samples at 105°C, weighed and filtered through a series of stacked sieves
178 of decreasing mesh size (coarse sand > 1 mm, medium sand = 250 µm – 1 mm, fine sand = 60 µm –
179 250 µm, and mud = < 60 µm)). The content of each sieve was weighed and the relative proportion of
180 material from each size calculated. The percentage organic content of the sediment was measured

181 by loss on ignition (Dean Jr 1974) by burning 5 grams of dried sediment in a muffle furnace at 500°C
182 for 8 hours and estimating organic content from the difference in mass.

183 *Data Analysis*

184 Sediment size and organic matter content were normalised before a principal component analysis
185 (PCA) was carried out to describe similarities in sediment composition between locations and
186 distances from the forests edge.

187 A two-way factorial ANOVA was performed on invertebrate data expressed as densities (individuals
188 $m^{-2} = ind. m^{-2}$) followed by square root transformation, to assess if there were detectable differences
189 in total animal density between the two locations and across the three distances (i.e. Flat, Edge, Inner).
190 Only one sample was removed from the dataset as it was considered an outlier.

191 An Indicator species analysis was performed on the benthic invertebrate density data to identify what
192 taxa are indicators of each locations (i.e. Blackoil Creek, Cassady Creek) and distance across the forest
193 (i.e. Flat, Edge, Inner).

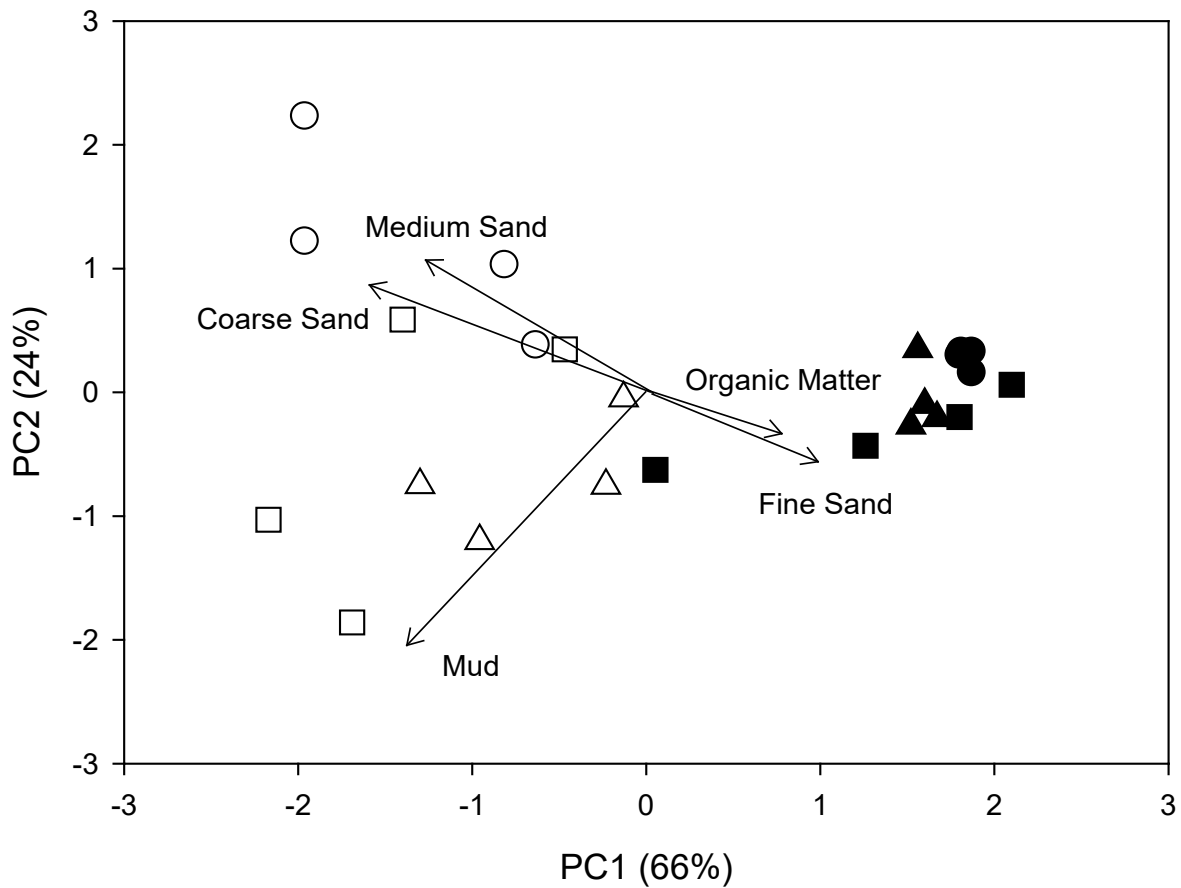
194 Non-metric Multidimensional Scaling Analysis (nMDS), using a Bray-Curtis similarities, was used to
195 analyse density data ($Ind. m^{-2}$) to identify changes in benthic composition between distances within
196 the forests (Edge, Inner), and across all sampling events. Replicates were pooled to minimize the effect
197 of benthos patchiness, with every sampling event included in this analysis. Invertebrate taxa were
198 grouped into major taxonomic groups and only taxa which occurred in more than 5 % of samples were
199 retained for analysis. The use of broad taxonomic groups rather than genus and species was
200 considered acceptable because, using this approach, little information regarding spatial differences
201 between sites and locations is lost, while information about the functional role of the taxa is preserved
202 (Chapman 1998). Additionally, due to the poor knowledge of the infauna of mangroves in north
203 Queensland, many specimens were only identifiable to Family or Order level. Brachyuran crustaceans
204 were excluded from the analysis because their high mobility and ability to retreat into deep burrows
205 invariably introduces inconsistency into their representation in core samples (Sheaves et al. 2016).

206 Data were log (x+1) transformed prior to nMDS to down-weight the effect of highly abundant taxa,
207 thereby preventing ordination outcomes being determined by just a few influential taxa. Then the
208 data were row standardized to emphasise taxonomic composition. Loading vectors of taxa with
209 correlation > 0.5 with the ordination space were super-imposed on the nMDS to identify taxa most
210 influential in the ordination. Analysis of Similarity (ANOSIM) was performed on the Bray-Curtis
211 similarity matrix to quantitatively compare the differences in benthic assemblages between locations
212 and distances.

213 The ANOVA and Indicator Species Analysis were conducted using R open source software (RCoreTeam
214 2017), employing the “indicspecies” package (De Caceres and Legendre 2009) for the correspondence
215 analysis. The nMDS, ANOSIM and PCA were carried out using Primer E (Clarke 2006).

216 **Results**

217 The PCA generated from sediment grain size and organic matter data shows strong differentiation
218 between the two study locations (Fig. 2). Sediment composition at Blacksoil Creek is relatively
219 homogeneous among replicates, characterised by fine sand and organic matter. In contrast, samples
220 from Cassady Creek display more variability, with a mix of coarse and medium sand characterizing the
221 samples collected in the Flat, while the Edge is mostly characterized by mud. The Inner area is less
222 consistent and features both sediment types.



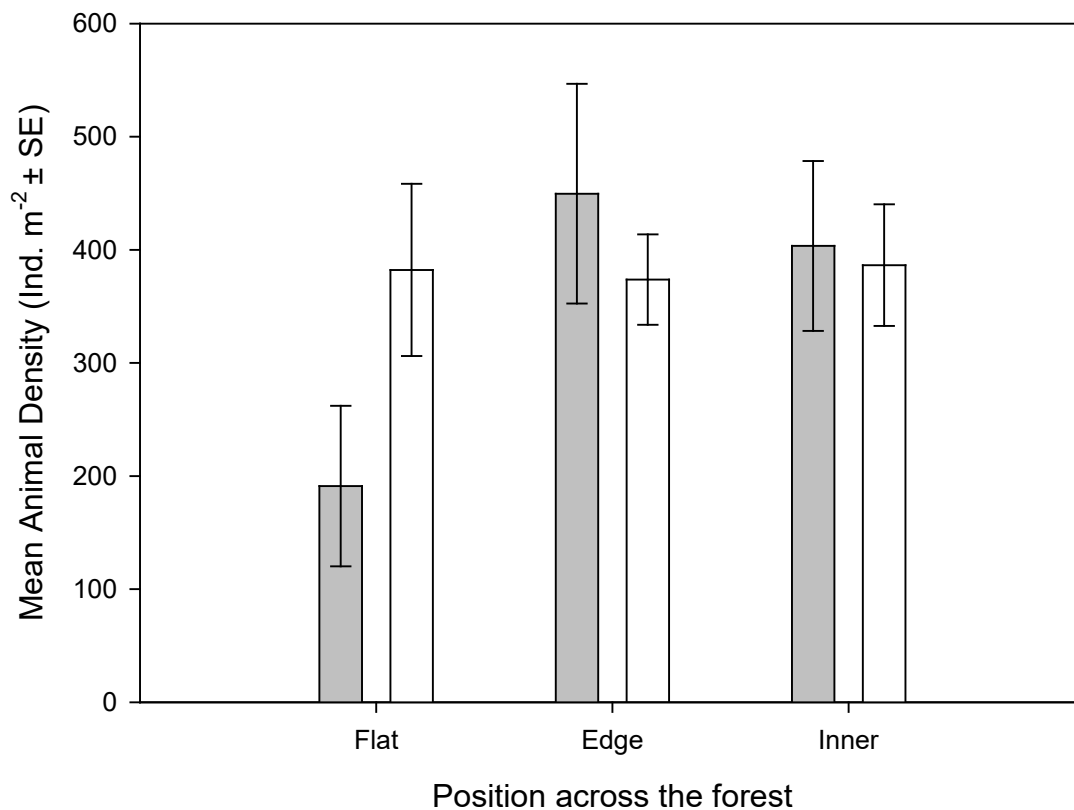
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224 **Figure 2:** *Principal Component Analysis for the sediment size and organic matter at the two study*
 225 *locations (Black = Blacksoil Creek, White = Cassady Creek,) and three positions across the intertidal*
 226 *gradient (Circle = Flat, Triangle = Edge, Square = Inner).*

227

228 The relative density of animals was similar between Blacksoil Creek and Cassady Creek, with both
 229 locations displaying relatively low animal densities, averaging approximately 350 ind. m⁻² (Fig. 3).
 230 Similarly, the density of animals based on their position across the tidal gradient (Flat, Edge, Inner) did
 231 not reveal any trends. The factorial ANOVA failed to detect any differences in density among distances
 232 or between locations ($F_{2,106} = 0.947$, $p = 0.391$).

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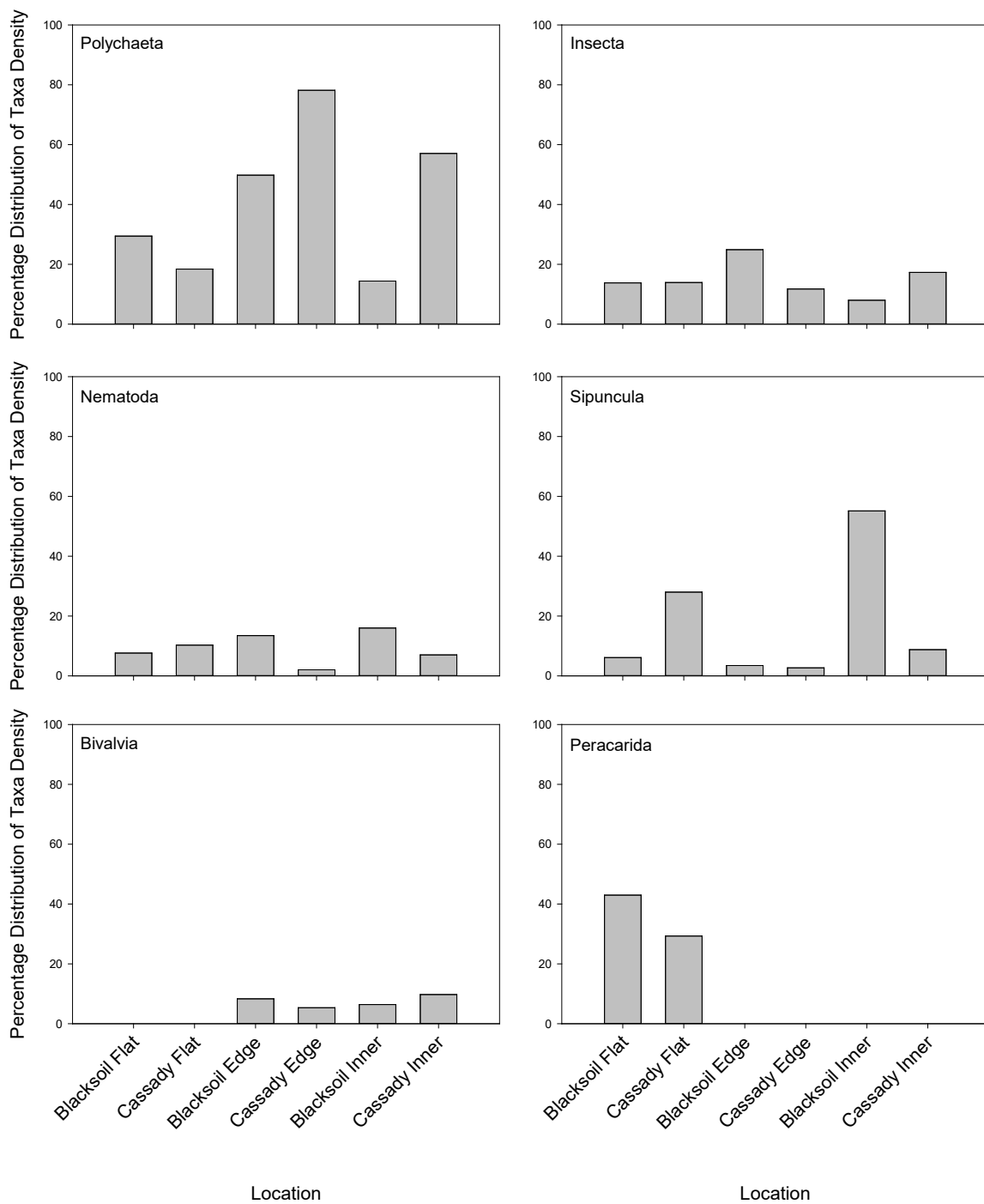
235 **Figure 3:** Mean animal density (\pm SE) between the three positions across the intertidal gradient (Flat,
 236 Edge, Inner) at the two locations (Dark Grey = Blacksoil Creek, White= Cassady Creek).

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240 Regardless of the similarity in densities between locations and distances across the mangrove forest,
 241 there were clear differences in taxonomic composition (Fig. 4). Despite Peracarida crustaceans
 242 representing a large proportion of the taxa community on the flats at Blacksoil Creek and Cassady
 243 Creek (40% and 30 % respectively), they were not recorded inside the forest at either location during
 244 the study. The taxa most consistently represented at both locations were insects and polychaetes,
 245 with the latter dominating the assemblages within the forests. The only exception was Blacksoil Creek,
 246 where sipunculids were the dominant taxa in the Inner forest (contributing more than 50% to the
 247 entire animal composition).



248

249 **Figure 4:** Percentage contribution of taxa density between the two estuaries at the positions across the
 250 intertidal gradient (Flat, Edge, Inner).

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257 The Indicator Species Analysis has found three taxa, namely Peracarida, Sipuncula and Polychaeta, can
 258 be indicative of a particular site or combination of sites (Table 1). However, only peracarids had a
 259 specificity of 1, meaning that they are only found in the specified sites. The Polychaete are considered
 260 indicative taxa for almost all sites except Blacksoil Inner, however this is likely due to the
 261 overwhelmingly density of Sipunculids at that site. Sipunculids are highly indicative of Blacksoil Creek
 262 inside the forest and Cassady creek Flat.

263

264 **Table 1:** *Indicator Species Analysis, the X represent the location and position across the tidal gradient*
 265 *where the taxa is an indicator. The taxa in bold represent a taxa that is only found in the sites where it*
 266 *also act as indicator. Only significant taxa are reported.*

Taxa	Blacksoil			Cassady			Result	
	Flat	Edge	Inner	Flat	Edge	Inner	Statistic	p value
Peracarida	X			X			0.447	0.007
Sipuncula		X	X	X			0.683	0.001
Polychaete	X	X		X	X	X	0.744	0.018

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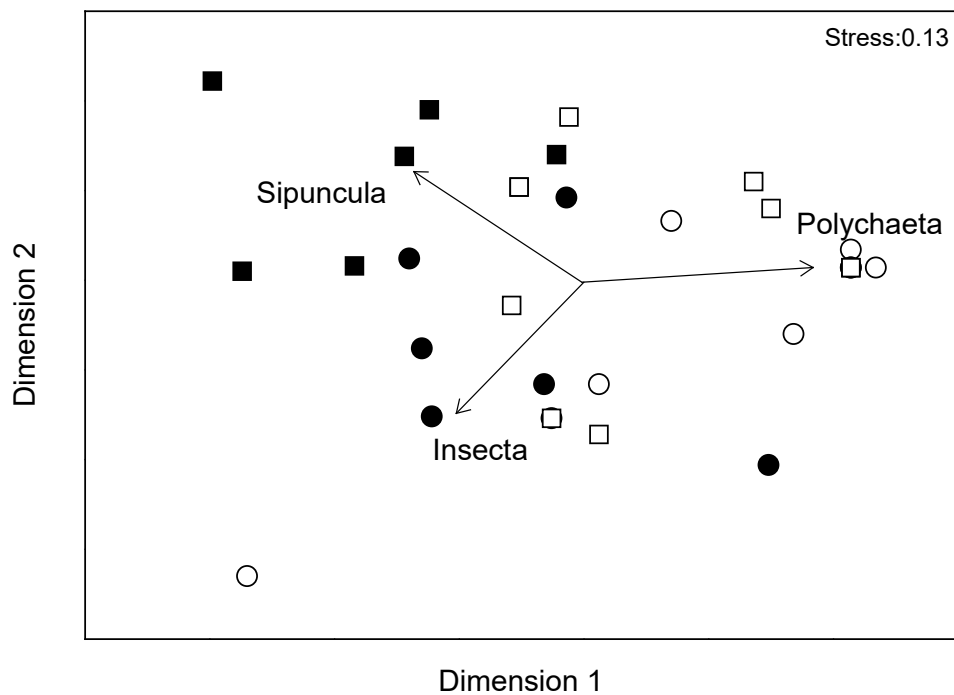
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271 The nMDS ordination of species composition within the two study forests revealed variability among
272 data points within groups, rather than well-defined clusters (Fig. 5). Despite that, there is a clear
273 separation between most Blacksoil Creek and Cassady Creek samples, highlighting the variability of
274 the benthos. The split in assemblages, based on location, were further supported by ANOSIM ($R=0.54$,
275 $p<0.001$). Despite an apparent separation between the Inner and Edge at Blacksoil Creek the position
276 within the forest (i.e. Edge or Inner) does not appear to greatly influence the benthic community
277 (ANOSIM $R=0.06$, $p>0.05$). When the loading vectors of the most correlated taxa are superimposed,
278 it is clear the majority of the trend is correlated with changes in dominance of the three main
279 taxonomic groups; Polychaetes dominating the benthic composition at Cassady Creek, Sipunculids at
280 Blacksoil Creek, and insects found in half the samples at both locations and both distances within the
281 forests. The community seems to be constant throughout the year, with no cluster structure related
282 to sampling events. Consequently, these data are not presented.

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287 *Figure 5: nMDS for the ordination of taxa composition, constructed using Bray-Curtis similarity matrix*
 288 *on transformed (log x+1) and row standardized data, between the two estuaries (Black= Blacksoil*
 289 *Creek, White = Cassady Creek) and the two distances within the forest (Circle= 10 m, Square= 40 m).*
 290 *Each symbol represents 3 pooled replicates. Loading vectors for taxa correlated >0.5 with the two*
 291 *dimensional space are displayed on the nMDS ordination.*

292

293

294 Discussion

295 *Macro-benthic composition of estuarine mangrove forests*

296 Benthic macrofauna density was relatively constant between the study locations and the three
 297 positions across the intertidal gradient; however composition differed between the two forests. This
 298 is largely attributable to the higher occurrences of sipunculids at Blacksoil Creek. Sipunculids are non-
 299 selective detritus feeders (Beesley et al. 2000). Their dominance at Blacksoil Creek may be a response
 300 to higher levels of organic matter in the sediment evident in the PCA, that are likely to provide greater
 301 food availability for non-selective detritus feeders.

302 No substantial variations in benthic composition were detected within the mangrove forests between
303 the two distances (Edge and Inner). However, although high concentrations of peracarids were
304 observed on the Flats, they were absent within the mangrove forests. These strong faunal differences
305 between the mud-flat and the forest cannot be attributed to the sediment characteristics alone, as
306 the PCA for the sediment composition did not reveal any substantial variations in substrate across the
307 intertidal gradient. Furthermore, Peracarida are generally found in high abundance in both sandy and
308 muddy substrates (Swennen et al. 1982, Dittmann 2000, Sheaves et al. 2016). Previous studies provide
309 inconsistent information with respect to the ability of peracarids to colonise mangrove forests
310 (Schrijvers et al. 1995, Sheridan 1997, Dittmann 2001, Alfaro 2006). This may be because the different
311 studies were conducted at sites dominated by different mangrove species, located at different
312 latitudes, and influenced by different tidal regimes.

313 Physical variability is an important driver of faunal distributions in tropical Australian estuaries
314 (Sheaves 1996, 1998, Johnston et al. 2007), and it has recently been identified that in both fringing
315 and basin mangrove forests, dissolved oxygen (DO) regularly falls to hypoxic levels during tidal
316 disconnection (Knight et al. 2013, Mattone and Sheaves 2017). DO is likely to be a limiting factor for
317 many biota, and exposure to very low oxygen for prolonged periods of time is likely to impact the
318 fauna composition. In fact, Mattone and Sheaves (2017) found that water in mangrove forests at
319 Blacksoil Creek are often exposed to DO as low as 5 % saturation, particularly in remnant pools during
320 tidal disconnection. This likely explains the lack of peracarids within the forest, as experimental
321 investigations and field observation have both found that this taxonomic group has a very low
322 tolerance to hypoxia (Davis 1975, Rabalais et al. 2002). In contrast, sipunculids are capable of
323 oxyconforming; adapting their metabolic rate according to DO availability (Lombardo et al. 2014), with
324 many species (e.g. *Dendrostomum cymodoceae*, *Phascolosoma arcuatum*) able to switch to anaerobic
325 metabolism and survive several days in anoxic conditions (Edmonds 1957, Ip et al. 1992). Such
326 adaptations would allow them to survive the periodic low DO of mangrove forests, allowing their high
327 occurrence within Blacksoil forest.

328 The absence of a number of taxa within mangrove forests, that were common on the flats, suggest we
329 need to revise our understanding of how benthic organisms take advantage of macro-tidal mangrove
330 forests. If a forest provides shelter from predation (e.g. birds and fish) and shade from the tropical
331 heat (attractants), low DO levels are still likely inhibit many taxa from colonising the forest, resulting
332 in a benthic community characterized by highly DO tolerant species. This is also likely to influence the
333 way other taxa, such as crabs, utilise mangrove forests. In fact, many of the grapsid and ocypodid crabs
334 that characterize mangrove forests (Koch & Wolff 2002) display semi-terrestrial behaviour (Takeda et
335 al. 1996), that may represent an adaptation to low DO during tidal disconnection.

336

337 *Ecological implications*

338 Understanding the distribution of benthic organisms across estuarine mangrove forests is critical to
339 evaluating the roles played by mangroves in the ecology of tropical estuaries. Mangrove forests are
340 usually considered valuable feeding grounds for juvenile fish (Aburto- Oropeza et al 2008). Although
341 we did not directly sample fish during this study, the lack of some benthic organisms (particularly
342 peracarids) within mangrove forests suggest that for many species, in particular juveniles, feeding
343 opportunities may be limited within the forest compared to adjacent habitats (e.g. intertidal flats).
344 This has implications for revaluing the 'mangrove forests as feeding ground' paradigm. Nonetheless,
345 mangrove forests could still be important for specialist species that target particular taxa known to be
346 abundant within the forest, such as *Lutjanus argentimaulatus*, and *Acanthopagrus* spp., that can feed
347 extensively on crabs (Sheaves & Molony 2000), or insect feeding specialists (e.g. *Toxotes* spp.) because
348 mangroves are rich in both invertebrate groups (Koch & Wolff 2002, Burrows 2003). Interestingly,
349 Sheaves et al (2016) found that *Acanthopagrus pacificus* was among the taxa most commonly found
350 within mangroves in northern Australia, while other taxa were less common than previously believed.
351 Additionally, other studies in Australia (Vance et al. 1996, Smith & Hindell 2005) and New Caledonia
352 (Dubuc in review) have revealed low level of mangrove forest utilization by fish, most of which were

353 concentrated within the first few metres of the forest. This supports our expectations based on the
354 benthic infauna community of mangrove forests.

355

356 This study has highlighted some important gaps in our current understanding of the both the benthic
357 fauna of mangrove systems and of the functioning of tropical mangrove ecosystems. The high
358 variability in benthic composition across habitats, both inside and outside mangrove forests, and
359 between estuaries, suggests more in-depth research is necessary before we fully understand how both
360 basal and higher trophic groups use these systems, what services different habitats provide, and
361 precisely which factors influence benthic communities. We focused on *Rhizophora* forests in this
362 study, however it seems obvious that a study in forests dominated by different mangrove species
363 would likely reveal further variations in benthic communities. Understanding this variability is likely to
364 be of great importance for the protection and management of mangrove ecosystems, particularly in
365 the face of environmental change (Sheaves et al. 2007, Gehrke et al. 2011).

366

367

368 A list of species presence is available at ICESJMS online

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