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# Impacts of Cattle on the Vegetation Structure of Mangroves

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## **Abstract**

Across the globe coastal wetlands have been lost and degraded due to agriculture. Here we test hypotheses that there are differences in vegetation structure of the mangrove *Avicennia marina* at locations with or without cattle in the lower Shoalhaven River Estuary in New South Wales, Australia. We sampled the pneumatophores, seedlings, saplings, and trees within the mangrove forest and landward of the forest where cattle are most active. Areas with cattle had fewer trees, and their lowest branches were more than 2 m above the ground, giving trees an umbrella-shaped morphology. Although abundances of saplings and seedlings were highly variable among locations, plants at both stages were shortest along the landward side of the forest in the presence of cattle and seedlings were bushier, suggesting consumption of the apical shoots. A reduction in pneumatophore density and the highest proportion of branched pneumatophores occurred along the landward side of the forest in the presence of cattle, indicating impacts of trampling. Prospects for regeneration of the mangroves in the presence of cattle appear limited due to grazing, physical disturbance and trampling across multiple life history stages. Livestock paddocks should be fenced to exclude cattle and prevent degradation of these coastal intertidal habitats.

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## **Impacts of Cattle on the Vegetation Structure of Mangroves**

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23 **Abstract**

24 Across the globe coastal wetlands have been lost and degraded due to agriculture. Here we  
25 test hypotheses that there are differences in vegetation structure of the mangrove *Avicennia*  
26 *marina* at locations with or without cattle in the lower Shoalhaven River Estuary in New  
27 South Wales, Australia. We sampled the pneumatophores, seedlings, saplings, and trees  
28 within the mangrove forest and landward of the forest where cattle are most active. Areas  
29 with cattle had fewer trees, and their lowest branches were more than 2 m above the ground,  
30 giving trees an umbrella-shaped morphology. Although abundances of saplings and seedlings  
31 were highly variable among locations, plants at both stages were shortest along the landward  
32 side of the forest in the presence of cattle and seedlings were bushier, suggesting  
33 consumption of the apical shoots. A reduction in pneumatophore density and the highest  
34 proportion of branched pneumatophores occurred along the landward side of the forest in the  
35 presence of cattle, indicating impacts of trampling. Prospects for regeneration of the  
36 mangroves in the presence of cattle appear limited due to grazing, physical disturbance and  
37 trampling across multiple life history stages. Livestock paddocks should be fenced to exclude  
38 cattle and prevent degradation of these coastal intertidal habitats.

39

40 **Key words:** *Avicennia marina*, grazing, herbivory, recruitment, saltmarsh, trampling

41

## 42 **Introduction**

43 Across the globe mangrove forests and other coastal wetlands are under particular threat of  
44 habitat loss from mariculture and urbanisation (Spalding et al. 1997; Valiela et al. 2001;  
45 Alongi 2002; Lee et al. 2006), but the threat of agriculture, and specifically livestock grazing,  
46 has received relatively little attention despite rapidly growing food production with  
47 expanding human populations and the often obvious impacts on the plants themselves (e.g.  
48 Bridgewater and Cresswell 1999; Dahdouh-Guebas et al. 2006; Hoppe-Speer et al. 2015; He  
49 and Silliman 2016; Kauffman et al. 2016). Although mangrove loss has been primarily linked  
50 to agriculture through land clearing (e.g. Abuodha and Kairo 2001), degradation of mangrove  
51 ecosystems can occur indirectly through use of adjacent land for livestock farming or directly  
52 through use of mangrove forests and saltmarsh as paddocks for grazing, movement and  
53 resting of livestock (He and Silliman 2016; Wood et al. 2017).

54 In riparian and terrestrial habitats, it is widely recognised that livestock farming can have  
55 substantial impacts on the biotic, geomorphic, and hydrological environment (Wilson 1990;  
56 Trimble and Mendel 1995; Belsky et al. 1999; Robertson and Rowling 2000). Habitat  
57 damage due to livestock in riparian ecosystems is particularly concentrated (e.g. Fleischner  
58 1994), and it thus might be predicted that impacts due to cattle grazing and trampling in the  
59 unconsolidated sediments of estuarine habitats might be substantial (Fouda and Ali-  
60 Muharrami 1995). Although there is a relatively long history of studies examining the  
61 impacts of grazing in salt marshes (Ranwell 1961; Reimold et al. 1975; Bakker 1985;  
62 Andresen et al. 1990; Levin et al. 2002; Di Bella et al. 2014), comparatively little is known  
63 about the direct and indirect effects of livestock on mangrove forests (e.g. Dahdouh-Guebas  
64 et al. 2006; He and Silliman 2016). In coastal saltmarsh habitats grazing and trampling by  
65 sheep, cattle, and horses can reduce the abundance and diversity of plants (e.g. Jensen 1985;  
66 Turner 1987; Tessier et al. 2003). For example, Zedler et al. (1995), working in temperate

67 Australian saltmarshes, proposed that depressions in the soil created by cattle trampling  
68 might alter plant community composition by favouring species more suited to edaphic  
69 conditions under this disturbance agent. Observations of grazing on mangroves have been  
70 recorded for a diverse range of species (e.g. camels: Fouada and Al-Muharrami 1995; cattle:  
71 Yang et al. 2014; sheep: Hogarth 1999; goats: Hoppe-Speer et al. 2015; wallabies and  
72 kangaroos: Hutchings and Saenger 1987; pigs: Hoppe-Speer et al. 2015; water buffalo:  
73 Dahdouh-Guebas et al. 2006), and mangrove leaves have been considered as cattle feed (see  
74 Morton 1965). The relatively few investigations of impacts of livestock in mangroves have  
75 noted the fragmentation of forests due to the creation of pathways, alterations to vegetation  
76 structure, and changes to soil conditions (Dahdouh-Guebas et al. 2006; Yang et al. 2014;  
77 Hoppe-Speer et al. 2015).

78 In Australia, cattle have been recognised as a significant agent of disturbance at land-water  
79 interfaces in riparian habitats (Jansen and Robertson 2001). Along the coast of New South  
80 Wales (NSW), Australia, it is common for saltmarsh to have been cleared for conversion to  
81 pasture or used directly for grazing (Adam 2002; Daly 2013). In the lower Shoalhaven River  
82 estuary, NSW, extensive areas of coastal land have been cleared for dairy farming (Umwelt  
83 2005, 2006), with pasture often leading directly into the intertidal landscape comprised of a  
84 complex of open mud, saltmarsh and mangroves. Many paddocks are left unfenced to give  
85 cattle access to saltmarsh and mangroves as a source of water, forage, and shade (Umwelt  
86 2005, 2006). Consequently, livestock activity associated with coastal dairy farming has been  
87 identified as a significant factor contributing to the loss of ecologically important saltmarsh  
88 (Coast Saltmarsh is listed as an Endangered ecological community under the NSW  
89 Biodiversity Conservation Act 2016 and Subtropical and Temperate Coastal Saltmarsh is  
90 listed as a Vulnerable ecological community under the Commonwealth Environment  
91 Protection and Biodiversity Conservation Act 1999 in Australia) and mangrove habitat

92 (Marine Vegetation, including mangroves and saltmarsh plants) has been protected under the  
93 NSW Fisheries Management Act 1994) (see Daly 2013).

94 The aim of our investigation was to assess the damage to mangrove vegetation associated  
95 with unrestricted cattle access to mangrove forests in the lower Shoalhaven River estuary.

96 We quantified differences in the vegetation structure across multiple life history stages (trees,  
97 saplings, seedlings) and structural elements (size, branches, leaves, roots) of the mangrove  
98 *Avicennia marina* at locations with or without cattle. At each location we focused on two key  
99 zones across the intertidal landscape with differential activity of cattle: within the mangrove  
100 forest where cattle are less active and along the landward side of the forest between the  
101 mangroves and the pasture where cattle are most active. We thus predicted that mangrove  
102 vegetation would be most heavily impacted along the landward side of the mangrove forest at  
103 locations with cattle. Our approach documenting impacts across the various life history stages  
104 will help to identify which life history stage and demographic process might limit forest  
105 regeneration and thus guide effective conservation strategies for these protected estuarine  
106 habitats.

## 107 **Methods**

### 108 *Region and locations studied*

109 The study was done from June to August (winter) of 2006 in mangrove forests of the lower  
110 Shoalhaven River estuary (34°52'30" S, 150°42'50" E), east of Nowra on the south coast of  
111 NSW, Australia. The estuary extends from Nowra Bridge to Shoalhaven and Crookhaven  
112 Heads and has a catchment area of 21 km<sup>2</sup> with an extensive floodplain (Umwelt 2005,  
113 2006). The intertidal landscape in the estuary is comprised of mangrove forests fringing the  
114 rivers, and saltmarshes bordering the landward sides of the mangrove forests. The majority of  
115 land is zoned for agriculture and used for dairy farming. Clearing for agriculture and

116 extensive erosion of the riverbanks has substantially reduced the area of estuarine vegetation:  
117 the remaining mangroves and saltmarsh vegetation covers areas of 3.5 km<sup>2</sup> and 1.5 km<sup>2</sup>,  
118 respectively (Umwelt 2005, 2006).

119 Four locations with mangrove forests were chosen along the lower Shoalhaven River estuary:  
120 two locations (Regatta Island, Ryan's Creek) were private dairy farming properties where  
121 cattle had unrestricted access to mangroves due to the absence of fencing, and two (Berry's  
122 Bay, Comerong Island) were control (or reference) locations that, to our knowledge, have  
123 never and certainly not within decades been accessed by cattle. Locations were spatially  
124 independent and separated by at least 2 km. The mangrove forests in the region are  
125 comprised of two tree species which are both approaching their global southern range limits:  
126 the larger *A. marina* and the smaller *Aegiceras corniculatum*, but *A. marina* is the dominant  
127 species. At locations with cattle present, saltmarsh vegetation landward of the mangrove  
128 forest was severely degraded, with cover restricted to small and isolated patches of the grass  
129 *Sporobolus virginicus*, the chenopods *Suaeda australis* and *Sarcocornia quinqueflora*, the  
130 native rush *Juncus kraussii* and the non-indigenous, invasive rush *J. acutus* (see Harvey et al.  
131 2010).

132 Regatta Island was converted into a dairy farm in the early 1900s and is a fourth-generation  
133 dairy farm. The landward-facing edge of the island forms a protected inlet with the mainland.  
134 Along this edge, the upper paddocks of the farm have been fenced off from cattle and have  
135 dense mangroves. The lower paddocks of the farm, where the study was done, are not fenced  
136 and mangroves are noticeably less dense. In these lower paddocks a permanent population of  
137 20 to 25 heifers are rotated through daily for grazing. Ryan's Creek is a permanent agistment  
138 and the number of cattle present is variable. At the time of sampling there were 15 head of  
139 cattle rotating through the paddocks. Importantly, at both of these locations the cattle are



140 rotated through relatively small paddocks (estimated at roughly 0.12 to 0.14 km<sup>2</sup> including  
141 the intertidal landscape, but the area used is variable and calculating an accurate long-term  
142 stocking rate is not possible), with mangrove forest extending roughly 400 m alongshore, and  
143 thus there is the potential for substantial impact. In each paddock, cattle have access to  
144 pasture, which transitions into the intertidal landscape dominated by patches of saltmarsh  
145 vegetation and then mangroves with an intertidal extent ranging from 50 m to 100 m. At both  
146 locations, cattle roamed throughout the intertidal landscape and were observed walking and  
147 resting in and along the landward side of the mangrove forests, as well as consuming  
148 mangrove vegetation (B. Coulthart personal communication; H. Shuttleworth personal  
149 observation).

150 The location at Comerong Island was at the northern part of the island in the Comerong  
151 Island Nature Reserve, created in 1986. At this location the intertidal landscape is comprised  
152 from seaward to landward of mangrove forest, saltmarsh and then swamp-oak forest  
153 dominated by *Casuarina glauca*. The location at Berry's Bay was on Crown Land and more  
154 impacted by humans than the Comerong Island location: some of the upper saltmarsh had  
155 been claimed as private land and there was evidence of illegal dumping of rubbish, but  
156 sampling was not done in these disturbed areas. At both locations, an area with mangrove  
157 forest extending roughly 400 m alongshore was selected, to parallel the alongshore extent of  
158 the locations with cattle.

### 159 *Sampling design*

160 At each of the four locations, a sampling area with mangrove forest extending 150 to 200 m  
161 alongshore was selected to occupy the central area at the location. This area was divided into  
162 two intertidal zones: one within the upper (or landward) part of the mangrove forest (the  
163 lower part of the mangrove forest adjacent to the river was not used) and one along the

164 landward edge of the forest where there is a complex of open mud, mangroves and patches of  
165 saltmarsh vegetation. These zones were delineated by the boundary where the mangrove  
166 forest with complete canopy cover transitions landward to a mud, mangrove and saltmarsh  
167 complex. To ensure comparable areas were being sampled among locations, tidal heights  
168 were used to determine zonal boundaries, and this was done by measuring water depth along  
169 the landward edge of the forest at each location during specific times of the tidal cycle. These  
170 two zones were also distinguished because cattle roaming the intertidal landscape occurred  
171 more frequently and were more active along the landward side of the mangrove forest than  
172 within the mangrove forest where there are more trees and mud is less consolidated (B.  
173 Coulthart personal communication; H. Shuttleworth personal observation). Although cattle  
174 activity could not be quantified outside of personal observations, we nevertheless predicted  
175 that not only would there be differences between locations with or without cattle, but that  
176 these differences would be more pronounced along the landward edge of the mangroves than  
177 within the mangrove forest.

178 At each location, two sites were selected in each of the two zones, and each site covered 10 m  
179 of intertidal extent and stretched 50 m alongshore, giving a sampling area of 500 m<sup>2</sup> for each  
180 site and 2000 m<sup>2</sup> for each location. Sites were separated by at least 15 m and positioned  
181 where there was sufficient intertidal extent for sampling and away from areas with obvious  
182 disturbance that changed the nature of the sampling area. Sites within the mangrove forest  
183 (referred to as “mangrove forest”) were located in upper part of the forest, and extended 10 m  
184 seaward from the landward edge of the mangrove forest. Sites along the edge of the  
185 mangrove forest (referred to as “mangrove edge”) extended 10 m landward from the  
186 landward edge of the mangrove forest. To account for edge effects, a 5 m band running along  
187 the forest boundary and separating these two zones was excluded from sampling.

188 *Sampling variables*

189 Cattle may directly impact *A. marina* and its capacity for persistence and regeneration  
190 through trampling, other physical disturbance (e.g. breakage of branches) and grazing effects.  
191 To assess these potential effects, mangrove vegetation was quantified by measuring the  
192 production of aboveground roots (i.e. pneumatophores) and the sizes of individual plants  
193 across various life history stages (trees, saplings, seedlings). Trees were classified as  
194 individuals >150 cm tall and with a crown >1 m<sup>3</sup>, saplings as individuals up to 150 cm tall  
195 with lateral branches but not forming canopy, and seedlings as single-stemmed individuals ≤  
196 50 cm tall (see Clarke and Allaway 1993; Minchinton 2001). Plants > 50 cm tall almost  
197 always had lateral branches. Classification of trees and saplings is difficult, however, because  
198 size and life history stage are not necessarily correlated. For example, short plants with thick  
199 trunks would be classified as saplings, but these apparently stunted plants appear much older  
200 and may be capable of reproducing.

201 Aboveground root production was measured by the densities and heights of pneumatophores.  
202 At each site, the densities of live pneumatophores were estimated by counting their numbers  
203 in ten, 1 m<sup>2</sup> (1 m × 1 m) randomly located quadrats. A separate record was kept of the  
204 number that were branched, an indicator of damage from trampling in mangrove habitats (see  
205 Ross 2006). Some pneumatophores had characteristic assemblages of epiphytic algae (see  
206 King and Wheeler 1984), but the occurrence of these algae was sporadic and not quantified.  
207 In each quadrat, the heights of five randomly selected unbranched pneumatophores were  
208 measured from their bases at the mud surface to their tips. Seedling densities were estimated  
209 in ten, 2 m<sup>2</sup> (1 m × 2 m) quadrats in each site. The heights and numbers of leaves for 50  
210 randomly selected seedlings were quantified across these quadrats. The heights of seedlings  
211 were measured from the base of the stem at the mud surface to the tip of the stem. Sapling

212 and tree densities were estimated in two, 100 m<sup>2</sup> (10 m × 10 m) randomly selected quadrats  
213 in each site. The height of 20 randomly selected saplings, measured from the base of the  
214 trunk at mud surface to top of the plant, was recorded in each site. The sizes of trees were  
215 estimated by measuring circumference (or girth, G) of their central stems (or trunks) at 130  
216 cm above the ground (G<sub>130</sub>) for (where available) 20 randomly selected trees at each site  
217 (Brokaw and Thompson 2000). Trees had relatively straight, single-stemmed trunks and,  
218 consequently, we did not encounter the problem associated with estimating tree girth for  
219 multiple-stemmed mangrove trees (see Dahdouh-Guebas and Koedam 2006). On each tree,  
220 the height of the lowest branch was used as an indicator of consumption and physical  
221 disturbance of mangrove vegetation by cattle, and this was measured as the vertical distance  
222 from the base of the trunk at the mud surface to the base of the lowest branch with live  
223 foliage (i.e. excluding dead branches).

#### 224 *Statistical analyses*

225 A three-factor, nested analysis of variance (ANOVA) was used to determine differences in  
226 the effect of cattle (fixed factor: present, absent), zone (fixed factor: mangrove forest,  
227 mangrove edge) and location (random factor nested within cattle treatments) for each of the  
228 sampling variables. For each sampling variable, the mean value of estimates was calculated  
229 for each site. These means for each site were then used as replicates (n=2 sites for each zone  
230 at each location) in the ANOVA. Following significant cattle by zone interactions in  
231 ANOVA, Student-Newman Keuls (SNK) multiple comparisons tests were done to determine  
232 the location of differences among these four treatments. Data were transformed as necessary  
233 to reduce variance heterogeneity (see Table 1). There were no trees at one site at Regatta  
234 Island and, therefore, to balance the design we used G<sub>130</sub> and lowest branch height of the

235 other site and reduced the degrees of freedom in the residual by one (Quinn and Keogh  
236 2002).

## 237 **Results**

238 There were stark differences in the vegetation structure of *A. marina* in the presence of cattle  
239 and, as predicted, these were most pronounced along the landward side of the mangrove  
240 forest where cattle are most active. Throughout the intertidal landscape there were  
241 substantially fewer trees where cattle were present (Fig. 1a, Table 1a). Within the mangrove  
242 forest, almost twice as many trees occurred in the absence than in the presence of cattle, and  
243 this difference was most pronounced along the landward edge of the forest where trees were  
244 scarce ( $< 5$  per  $100 \text{ m}^2$ ) (Fig. 1a, b). Nevertheless, trees on the landward side of the forest  
245 with cattle were approximately double the girth of those in the mangrove forest, whereas the  
246 reverse pattern was evident in the absence of cattle (Fig. 1b, Table 1b). There were also  
247 striking differences in tree morphology: where cattle were present the lowest tree branches  
248 were at least 2 m above the ground, likening their shape to an open umbrella, whereas in the  
249 absence of cattle branches were on average only 34 cm above the mud (Fig. 1c, Table 1c).

250 Densities of saplings were highly variable among locations, primarily due to extremely few  
251 saplings at Ryan's Creek where cattle were present, and saplings were at greater densities  
252 along the landward side than within the mangrove forest (Fig. 1d, Table 1d). Saplings were,  
253 however, consistently shorter in the presence than in the absence of cattle and shortest along  
254 the edge of the mangrove forest with cattle present, particularly at Regatta Island where  
255 saplings appeared stunted (Fig. 1e, Table 1e).

256 The abundance of seedlings, like saplings, was extremely variable among locations, with  
257 large numbers at Comerong Island and few at Ryan's Creek (Fig. 1d, f, Table 1f).  
258 Nevertheless, seedlings were consistently taller in the mangrove forest than along its

259 landward edge (Fig. 1g, Table 1g). In general, at both locations with cattle, seedlings were  
260 least abundant and shortest along the landward side of the forest, and these short seedlings  
261 had the greatest numbers of leaves compared to similar areas in the absence of cattle and in  
262 the mangrove forest in the presence of cattle (Fig. 1f, g, h, Table 1f, g, h).

263 Areas where cattle roamed the landward side of the mangrove forest were associated with  
264 prominent differences in the abundance and morphology of pneumatophores (i.e. aerial roots)  
265 compared to all other areas. Along the edge of the forest, there were on average six times  
266 more pneumatophores and proportionally fewer branched pneumatophores in the absence  
267 than in the presence of cattle, although pneumatophore heights were similar (Fig. 1i, j, k,  
268 Table 1i, j, k). Moreover, at locations with cattle, areas along the landward side of the forest  
269 had fewer pneumatophores and these were shorter and more branched than in the mangrove  
270 forest (Fig. 1i, j, k, Table 1i, j, k). In contrast, within the mangrove forest the density and  
271 percentage of pneumatophores that were branched was similar in the presence or absence of  
272 cattle, although pneumatophores were taller in areas with cattle (Fig. 1i, j, k, Table 1i, j, k).

## 273 **Discussion**

274 There were dramatic differences in the vegetation structure of *A. marina* between areas with  
275 or without cattle, providing strong evidence for direct impacts of grazing and trampling by  
276 cattle in the mangrove environment. Although experimental manipulation of cattle would be  
277 needed to attribute causal links, observations of cattle trampling pneumatophores and  
278 consuming mangrove leaves coupled with the conspicuous and unusual differences in  
279 morphology of trees, saplings and pneumatophores provide compelling evidence of the  
280 impacts of cattle (see He and Silliman 2016).

281 Trees were dramatically reduced in abundance at both locations with cattle, and the few and  
282 more isolated trees on the landward side of the mangrove forest were large and mature

283 individuals, that were shaped like open umbrellas with the lowest branches and canopy  
284 consistently 2 m above the substratum. Fewer trees likely translate to a loss of production and  
285 associated carbon storage (Kauffman et al. 2016). This tree morphology reflects the height at  
286 which cattle can consume leaves and cause physical damage to lower branches, and others  
287 have observed similar characteristic grazing lines within mangrove forests (e.g. Hoppe-Speer  
288 et al. 2015). This altered morphology was also obvious in the mangrove forest with cattle  
289 present, although more variable among trees, suggesting that cattle graze mangroves in the  
290 upper part of the forest but do not have as large an impact on tree abundance as on the  
291 landward side. This loss in structural complexity of the mangrove trees might negatively  
292 influence a diverse array of taxa that depend on mangroves for shelter, nesting and food.

293 Saplings showed similar results to trees, with reduced densities in the presence of cattle, but  
294 only at Ryan's Creek. Along the landward side of the forest at both locations with cattle, but  
295 particularly at Regatta Island, the majority of saplings appeared stunted and old, with thick  
296 trunks and short branches with compact foliage and tightly clustered leaves around the central  
297 stem, likely reflecting suppression of growth and morphological changes due to sustained  
298 grazing of apical shoots (e.g. Dahdouh-Guebas et al. 2006). At Ryan's Creek some plants had  
299 unusual morphology indicative of cattle grazing, with long elongated central stems with  
300 clumps of leaves at heights  $> 1.7$  m (as well as low to the ground), resembling lollipops. It  
301 thus appears that grazing by cattle was reducing the abundance and size of saplings,  
302 preventing their transition into trees.

303 Similar to patterns of abundance for trees, there were few seedlings in areas with cattle along  
304 the landward side of the mangrove forest (Hoppe-Speer et al. 2015). Trampling by livestock  
305 in saltmarshes has been shown to reduce establishment of seedlings due to a loss in soil  
306 structure increasing the likelihood of small marsh plants being uprooted (Jensen 1985; Turner

307 1987; Tessier et al. 2003; Wasson and Woolfolk 2011). In addition to trampling, cattle were  
308 also likely grazing on mangrove seedlings because, similar to the stunting of saplings, they  
309 were shorter and had more leaves in these areas, suggesting a compensatory response to  
310 breakage of the apical shoot (Strauss and Agrawal 1999). Alternatively, limited natural  
311 production or supply of propagules to this area or unfavourable soil conditions might have  
312 reduced seedling establishment (e.g. Minchinton 2001). Unravelling these multiple  
313 explanations requires further testing. Regardless, in areas with cattle present there were few  
314 seedlings available for forest regeneration.

315 The small number of pneumatophores along the landward edge of the forest is likely  
316 associated with the scarcity of trees in this area coupled with trampling by cattle. Studies  
317 have shown that trampling by humans can bend, break and eventually detach  
318 pneumatophores (Skilleter 1996; Ross 2006), and cattle are likely having similar effects.  
319 Indeed, reductions in abundance and branching of pneumatophores have been linked to  
320 increased human disturbance and an indicator of trampling disturbance in mangrove forests  
321 (see Skilleter 1996; Ross 2006), and the percentage of branched pneumatophores was greatest  
322 in these landward regions with cattle. Reduced abundance and increased deformity of aerial  
323 roots may diminish the capacity of mangrove saplings and trees to exchange gases in  
324 physiologically stressful low oxygen environments, trap sediments and prevent coastal  
325 erosion, and provide habitat for epiphytic macroalgae and associated gastropods (e.g.  
326 Skilleter and Warren 2000; Chapman et al. 2005).

327 There appears extremely limited capacity for mangrove regeneration along the landward side  
328 of forest because while cattle remain in these relatively small paddocks there will be  
329 sustained impacts (Wasson and Woolfolk 2011). Indeed, all life history stages of the  
330 mangrove *A. marina* appeared influenced by cattle access and grazing. The scarcity of



331 seedlings along the landward edge of the forest at both locations and the lack of saplings at  
332 Ryan's Creek suggest that establishment of seedlings or successful transition to the sapling  
333 stage due to consumption or trampling by cattle are limiting demographic processes.

334 Importantly, seedlings with cotyledons attached were present, indicating that there is at least  
335 some dispersal of propagules into these areas and suggesting that edaphic conditions remain  
336 suitable for establishment (Minchinton 2006). Nevertheless, dispersal of *A. marina* is often  
337 highly localised (e.g. Clarke 1993) and the presence of few mature trees along the landward  
338 side of the mangrove forest indicates that there might be limited prospects for natural forest  
339 regeneration from local populations (Robertson and Rowling 2000). Seedlings that made the  
340 transition into saplings, such as those at Regatta Island, were stunted, suggesting suppression  
341 of growth by grazing cattle. Consequently, the continued presence of cattle, even at reduced  
342 stocking densities, is likely to prevent natural regeneration of the mangrove vegetation along  
343 the landward side of mangrove forests.

344 Assuming that tidal levels and hydrodynamic and edaphic conditions are suitable for natural  
345 regeneration, as appears to be the case, fencing to exclude cattle access should promote  
346 natural regeneration of these areas by eliminating the direct impacts of grazing and trampling  
347 (see Fleischner 1994, Dahdouh-Guebas et al. 2006), particularly for mangrove *A. marina*  
348 which is generally a robust and resilient mangrove species. The influence of fencing on the  
349 indirect effects of cattle living in paddocks adjacent to coastal waterways, such as potential  
350 impacts of elevated sedimentation and nutrients, cannot be predicted, but investigations in  
351 riparian habitats highlight positive changes to water quality and sedimentation among other  
352 parameters (Belsky et al. 1999; Sovell et al. 2000). Natural regeneration of mangroves under  
353 such disturbance conditions is predicted to be slow (e.g. Ross 2006), particularly due to  
354 limitations on recruitment, but planting of *A. marina* seedlings would accelerate this process  
355 and has already proven successful in this catchment by members of Shoalhaven Riverwatch.

356 Fencing provides benefits to farmers by preventing stock losses (e.g. when cattle get stuck in  
357 the mud), reducing land erosion and thus improving land value (Staton and O’Sullivan 2006).  
358 At a minimum, fencing should aim to regenerate the interconnected mangrove, saltmarsh and  
359 swamp oak forest complex across the coastal landscape, protecting listed Endangered  
360 Ecological Communities and Marine Vegetation (Daly 2013). Once cattle are excluded,  
361 monitoring forest regeneration, including habitat structure, associated biota, as well as  
362 changes to edaphic and hydrodynamic conditions, would inform future conservation  
363 strategies by quantifying the speed and full extent of mangrove regeneration.

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365

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502



**Table 1.** Analyses of (a) tree densities, (b) tree girths at 130 cm ( $G_{130}$ ), (c) tree lowest branch heights (lbh), (d) sapling densities, (e) sapling heights, (f) seedling densities, (g) seedling heights, (h) seedling leaf numbers, (i) pneumatophore densities, (j) pneumatophore heights, and (k) percentage of pneumatophores that were branched for two sites in each of two zones (within the mangrove forest: F, along the landward edge of the mangrove forest: E) at each of two locations in the presence (P: RC=Ryan's Creek, RI=Regatta Island) or absence (A: BB=Berry's Bay, CI=Comerong Island) of cattle. Cattle and Zone are fixed factors and Location is a random factor and nested within cattle. Data were transformed as indicated. Results of Student-Newman-Keuls (SNK) tests for effects of significant interactions. MS=estimate of mean squares. NT=not tested due to significant interactions; NS=not significant, \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

		Trees			Saplings		Seedlings			Pneumatophores		
		a. Density	b. $G_{130}$	c. lbh	d. Density	e. Height	f. Density	g. Height	h. Leaf no.	i. Density	j. Height	k. Branched
Source	d.f. for $F$ ratio	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS
Cattle: C	1, L(C)	5148.1*	1.994 NS	12.184**	43.29 NS	1140.2*	13.85 NS	2.33 NS	1.69 NT	61281 NT	10.86 NT	45.08 NT
Location(C): L(C)	2, R	104.3 NS	0.1654 NT	0.115 NS	57.03*	58.6 NS	5.26***	4.32 NS	0.46 NS	9260*	9.06 NS	4.90 NS
Zone: Z	1, L(C) $\times$ Z	3969.0*	0.3279 NT	0.226 NS	17.11*	251.0 NS	0.86 NS	99.50*	0.64 NT	26929 NT	5.36 NT	20.89 NT
C $\times$ Z	1, L(C) $\times$ Z	169.0 NS	0.8581 NS	0.040 NS	0.91 NS	103.6 NS	0.75 NS	40.64 NS	3.80*†	15240*	12.85*	21.36*†
L(C) $\times$ Z	2, R	189.3 NS	0.3909*	0.112 NS	0.69 NS	85.5 NS	0.51 NS	3.99 NS	0.40 NS	556 NS	0.14 NS	1.69 NS
Residual: R		237.8	0.070	0.222	1.07	46.8	0.13	33.97	0.51	2077	4.95	3.87
d.f. in Residual		8	7	7	8	8	8	8	8	8	8	8
Transformation		None	ln ( $x+1$ )	None	sqrt ( $x+1$ )	None	ln ( $x+1$ )	None	None	None	None	None
SNK			BB: F > E CI: F = E RC: F < E RI: F < E						F: A = P E: A < P A: F = E P: F < E	F: A = P E: A > P A: F = E P: F > E	F: A < P E: A = P A: F = E P: F > E	F: A = P E: A < P A: F = E P: F < E

†To increase the power of the test for the main effect of interest, C  $\times$  Z, the estimate of means squares used in the denominator of the  $F$ -ratio is a pooled estimate from the mean squares of the L(C)  $\times$  Z interaction and the residual, and then the effect of C  $\times$  Z were tested with 1 and 10 d.f. (see Winer et al. 1991 for pooling procedures).

## Figure Legends

**Fig 1.** Mean ( $\pm$ se) (a) tree densities, (b) tree girths at 130 cm ( $G_{130}$ ), (c) tree lowest branch heights (lbh), (d) sapling densities, (e) sapling heights, (f) seedling densities, (g) seedling heights, (h) seedling leaf numbers, (i) pneumatophore densities, (j) pneumatophore heights, and (k) percentage of branched pneumatophores for two sites in each of two zones (within the mangrove forest: Forest, along the landward edge of the mangrove forest: Edge) at each of two locations in the presence (RC=Ryan's Creek, RI=Regatta Island) or absence (BB=Berry's Bay, CI=Comerong Island) of cattle.

