

1 Hydroperiod is the main driver of the spatial pattern of dominance in
2 mangrove communities

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14
15 **ABSTRACT**

16 **Aim** Many mangrove communities form bands parallel to the shoreline with each community
17 dominated by a single species. However, the key determinants of mangrove species
18 distribution across the intertidal zone are not well understood. We aimed to quantify the
19 relationship between species' dominance and the hydroperiod (defined as the duration of
20 inundation in a year), soil salinity and the salinity of inundating water for three dominant
21 species: *Sonneratia alba*, *Rhizophora stylosa* and *Ceriops tagal*.

22 **Location** An extensive (20,000 ha), largely intact mangrove forest in northern Australia, of
23 some note as mangrove forests are threatened globally.

24 **Methods** We related species dominance to the explanatory variables by applying two
25 statistical modelling approaches: Generalised Linear Models (GLMs), where a set of
26 competing models were evaluated; and Boosted Regression Tree models (BRTs), an
27 approach able to automatically capture interactions and nonlinear relationships between
28 variables.

29 **Results and main conclusions** Both GLM and BRT models achieved strong predictive
30 performance for all species based on cross-validation, with ROCs above 0.85 for all species,
31 and 88% of deviance explained for *S. alba*, 42% for *R. stylosa* and 35% for *C. tagal*. All
32 models indicated that the hydroperiod was the key variable influencing distribution, followed
33 by soil salinity. The salinity of inundating water was the least informative variable in the
34 models. Ecological space, determined by gradients in hydroperiod and soil salinity, was
35 partitioned between the three species with little overlap. As anticipated changes in sea level
36 will alter the hydroperiod, our findings are critical for global forecasting of future
37 distributions of mangrove communities, and for the design of mitigation and adaptation
38 measures.

39

40 *Key words:* boosted regression tree; BRT; generalized linear model; GLM; hydroperiod;
41 salinity; sea level rise; species dominance; species distribution; statistical models; tidal
42 regime

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46 **INTRODUCTION**

47 Mangrove forests perform a critical role in maintaining a high diversity and abundance of fish
48 in near-by reefs and seagrass meadows, store more carbon than most other forest types
49 worldwide, and provide coastal protection from erosion caused by storm surge and tsunamis
50 (Costanza *et al.*, 1997; Mumby *et al.*, 2004; Danielsen *et al.*, 2005; Donato *et al.*, 2011).

51 Mangrove forests are threatened globally, due to clearing for aquaculture, agriculture, urban
52 and industrial development (Giri *et al.* 2011; Valiela *et al.*, 2001). Future sea levels are
53 forecast to increase from 0.18 to 1.8 m by 2100 (Nicholls *et al.*, 2007; Rahmstorf *et al.*, 2007)
54 with the potential to strongly affect mangrove forests. Sound management decisions and our
55 understanding of mangrove ecology depend on characterizing the key factors influencing the
56 distribution of mangrove species across the intertidal zone.

57 Many mangrove communities form bands parallel to the shoreline with each community
58 dominated by a single species (Snedaker, 1982; Smith III, 1992). This striking spatial
59 patterning of dominance, often referred to as “zonation” has been investigated using both
60 field observations and glasshouse experiments, and although the spatial patterning in bands is
61 simple, the relationship between mangrove species distribution and environmental drivers is
62 complex (see for reviews Snedaker, 1982; Smith III, 1992; Krauss *et al.*, 2008). The key
63 environmental drivers proposed for mangrove species distribution include the salinity of the
64 soil and inundating water (Ball, 1988a; Ukpong, 1991; Ball & Pidsley, 1995; Bunt, 1996), the
65 hydroperiod (Watson, 1928; Krauss *et al.*, 2006), other soil physicochemical properties such
66 as phosphorous and nitrogen, pH, redox potential and sulphides (McKee, 1993; Matthijs *et*
67 *al.*, 1999; Feller *et al.*, 2003; Krauss *et al.*, 2006) and biotic interactions (Ball, 1988b; Clarke,
68 2004).

69 Of these proposed environmental drivers of mangrove species distribution and dominance,
70 the influence of salinity on mangrove species physiology and distribution has received the
71 greatest research effort. However, it has been difficult to link the physiological response of
72 species to their observed distribution within mangrove forests. For example, Ball and Pidsley
73 (1995), Smith III (1988) and Ukpong (1991) found that experimentally determined growth
74 optima did not match the soil salinity of areas occupied by the taxa within mangrove forests.
75 Furthermore, correlations between soil salinity and species patterning have been
76 demonstrated for only about one-third of mangrove species studied (Matthijs *et al.*, 1999;
77 Lovelock *et al.*, 2005). Likewise, the salinity of inundating water along rivers was not shown
78 to strongly relate to the observed spatial patterning of mangrove species (Bunt, 1996), and the
79 relationship between plant species distribution or dominance and soil physicochemical
80 properties such as phosphorous, nitrogen, pH, redox potential and sulphides is inconsistent
81 (McKee, 1993; Matthijs *et al.*, 1999; Feller *et al.*, 2003; Krauss *et al.*, 2006).

82 Biological factors have also been proposed to influence mangrove zonation, and two of these
83 hypotheses have been explored, and rejected. The first proposed that tidal sorting of
84 propagules resulted in zonation (Rabinowitz, 1978), and was later disproven by several other
85 studies including Sousa *et al.* (2007). The second hypothesis proposed that the selective
86 predation of propagules by crabs caused the observed zonation and was supported at some
87 locations but not at other, equally well zoned, locations (Smith *et al.*, 1989; McGuinness,
88 1997). Finally, competition between mangrove species has been proposed (Ball, 1988b;
89 Clarke, 2004), and tested in glasshouse experiments (Cardona-Olarte *et al.*, 2006). Cardona-
90 Olarte and colleagues showed that two mangrove species responded differentially to
91 treatments of salinity and hydroperiod (tidal and fixed flooding), and that one species had a
92 competitive advantage over the other under low to mild stress by hydroperiod and salinity,
93 but that this advantage was reduced under the high salinity and fixed flooding treatments.

94 Where competitive interactions between species occur, the portion of an environmental
95 gradient occupied by a species represents the realized niche of that species (Hutchinson,
96 1959; Austin & Smith, 1989).

97 Hydroperiod has been largely overlooked in studies of the spatial distribution of mangrove
98 species occurrence and dominance. The hydroperiod is the proportion of time a location is
99 inundated (here called duration of inundation), and is determined by elevation, tidal
100 frequency and amplitude. The influence of hydroperiod on mangrove distribution is still
101 poorly known (Krauss *et al.*, 2006), despite being proposed as a key factor more than 80
102 years ago (Watson, 1928). Experimental treatments simulating natural tidal amplitudes
103 showed that species grew at different rates under different treatments (Ellison & Farnsworth,
104 1997; Chen *et al.*, 2005; He *et al.*, 2007). For example, He *et al.* (2007), reported differing
105 biomass, mortality and carbon allocation to roots, stems and leaves among mangrove species;
106 and species ranked by experimentally determined inundation tolerance matched the pattern of
107 species distribution for that location. Furthermore, differing growth responses and mortality
108 to elevation (and therefore hydroperiod) were reported for seven species (Kitaya *et al.*, 2002).
109 However, little variation in mortality, establishment and growth rates was found among five
110 species planted at low and high elevation sites (Clarke, 2004).

111 Species distribution models (SDMs) are a collection of statistical modelling approaches
112 widely used to characterise and forecast plant and animal distributions (Zimmermann *et al.*,
113 2010). However, we are unaware of studies using these techniques to investigate mangrove
114 species distributions and their ecological drivers. While statistical models (such as SDMs) do
115 not demonstrate the physiological or mechanistic basis for species distribution or dominance,
116 experimental approaches, such as glasshouse trials, are limited because the complexity of a
117 natural forest ecosystem cannot be replicated. As previous studies have indicated a mismatch
118 between the experimentally identified salinity optima (or tolerance) and the natural

119 distribution of mangrove species (eg. Smith III, 1988; Ball & Pidsley, 1995), applying these
120 statistical modelling approaches provides a useful way to investigate the relationship between
121 species distribution and environmental conditions. Strong correlations identified in the field
122 can be used for two broad purposes: firstly to identify which causal relationships to test
123 experimentally, and secondly, to provide a basis for predictions of the global implications of
124 sea level rise on mangroves ecosystems.

125 In this study we use spatially explicit statistical models to quantify the relationship between
126 the spatial patterning of mangrove species' dominance and hydroperiod, soil salinity and
127 water salinity. We derived the duration of inundation experienced at field sites from high
128 precision, remotely sensed LiDAR (Light Detection and Ranging) data, and this is the first
129 time such data have been used to explore the drivers of mangrove distribution. Our specific
130 goals were to rank the influence of hydroperiod, soil salinity and water salinity on the
131 dominance of three mangrove tree species, to identify interactions between variables and to
132 characterise the partitioning of environmental gradients between species. We specifically aim
133 to assess the influence of hydroperiod against other variables representing water salinity and
134 soil salinity.

135

136 **METHODS**

137 **Study site**

138 The study was conducted in the mangrove forest (20, 400 ha) of Darwin Harbour in northern
139 Australia (Fig. 1), a relatively undisturbed system representative of mangrove systems in the
140 tropics (Brocklehurst & Edmeades, 1996). Such undisturbed forests are of note because
141 mangrove forests are a globally threatened ecosystem (Valiela *et al.*, 2001). Extensive
142 clearing particularly in the Asia-Pacific region (including Australia) has substantially reduced
143 the extent of mangrove forests (Valiela *et al.*, 2001). Darwin Harbour has semidiurnal, macro

144 tides up to 8 m, with mean spring and neap tides of approximately 6 and 3 m, respectively
145 (Williams *et al.*, 2006). The upstream reaches of the harbour have low water salinity during
146 the wet season due to fresh water run off and high salinity in the dry season due to the
147 concentration of salts via evaporation (Williams *et al.*, 2006). The maximum daily
148 temperatures range from 30.5 to 33.3 °C, and the average annual rainfall of 1728 mm falls
149 during the wet season from November to March (Australian Bureau of Meteorology, 2011).

150 **Focal species**

151 We investigated the relationship between the spatial patterning of dominance of three
152 mangrove tree species *Sonneratia alba* Sm., *Rhizophora stylosa* Griff and *Ceriops tagal* Perr
153 and a set of explanatory variables. These species were selected because they each form
154 mono-specific communities in Darwin Harbour that are clearly evident from aerial
155 photographs. Furthermore, these taxa dominate 82% of the mangrove forest as shown in
156 maps produced by Brocklehurst and Edmeades (1996). *Ceriops tagal* dominates
157 approximately 44% of the forest area, followed by the *R. stylosa* with 33%, and finally *S.*
158 *alba* covering 5% (Brocklehurst & Edmeades, 1996).

159 These taxa have large geographical ranges; *Sonneratia alba* and *C. tagal* are distributed along
160 the eastern coast of Africa, through Asia and northern Australia to the Pacific, and *R. stylosa*
161 occurs throughout Asia, northern Australia and the Pacific (Duke, 2006). Throughout their
162 biogeographic distribution *C. tagal* usually occupies down-stream to intermediate estuarine
163 locations of the high to mid intertidal zone, *R. stylosa* the down-stream estuarine areas in the
164 mid to low intertidal and *S. alba* the down-stream areas of estuaries at the lowest tidal
165 elevations (Duke 2006). Experiments have shown the growth optima (measured as net
166 assimilation rate) across a gradient in salinity to be 25% of sea water for both *R. stylosa* and
167 *S. alba* (Clough, 1984; Ball & Pidsley, 1995), and at 50% for *C. tagal* (Aziz & Khan, 2001).

168 Field experiments indicated differing flood tolerance, with *S. alba* reported as more flood
169 tolerant than *C. tagal* (Kitaya et al., 2002).
170 Although recent work elevated *C. tagal* (Perr.) C. B. Rob var. *tagal* and *C. tagal* var.
171 *australis* C. T. White to the rank of species, discrimination between the two taxa is difficult
172 without fertile material (Duke, 2006; Sheue et al., 2009). Therefore, in this study these taxa
173 are referred to by their basyonym, *Ceriops tagal* Perr.

174 **Sampling methods**

175 A total of 201 sites were surveyed throughout Darwin Harbour, at least 100 meters apart (Fig.
176 1). Access constrained site selection and a map of the mangrove communities was used to
177 target areas to survey (Brocklehurst & Edmeades, 1996). We ensured a broad geographic
178 spread of sites and site selection was stratified by vegetation type shown in maps of the
179 Darwin Harbour mangoves (Brocklehurst & Edmeades, 1996). Sites were selected *a priori*
180 within three mapped vegetation types, each dominated by one of the focal species. To ensure
181 sampling along the full gradients of soil and water salinity and the hydroperiod, an additional
182 43 sites were surveyed in areas not dominated by any of the three focal species. To avoid
183 disturbed areas near industrial complexes and the city of Darwin, no sites were located on the
184 north eastern side of East Arm. Where access to sites was constrained the sites were located
185 as near to the selected location as possible. We recorded a site as dominated by one of the
186 focal species where it contributed 70% or more to the total basal area. Forty three sites were
187 dominated by *S. alba*, 59 dominated by *R. stylosa* and 56 by *C. tagal*. At each site we
188 calculated the basal area (at 1.3m) of all tree species present using angle count sampling with
189 two basal sweeps, 20 m apart, using a basal wedge (Bitterlich Gauge, factor 0.25 for all sites).

190 **Explanatory variables**

191 The explanatory variables selected for this study were the hydroperiod, soil salinity and three
192 measurements of water salinity (dry season, wet season and the annual range in water
193 salinity). The hydroperiod was selected as it has been long over looked as a possible factor
194 and its role is poorly known (Krauss *et al.*, 2008); and soil salinity and water salinity were
195 included as the physiological effects of salinity on mangrove species are well established and
196 generally regarded as an important influence on mangrove species establishment and growth
197 (Snedaker, 1982; Smith III, 1992; Krauss *et al.*, 2008). Other physicochemical soil properties
198 were not explicitly included as their relationship to mangrove species distribution is weak and
199 inconsistent (Smith III, 1992; Krauss *et al.*, 2008).

200 To record soil salinity, soil samples were collected from the centre of each site, at a depth of
201 15-20 cm from the surface of the soil using a Russian-D sampler (where sites were reached
202 on foot) or a custom made underwater corer (where sites were reached by boat). Soil samples
203 were air dried, Milli-Q water added at a 1:5 soil to water ratio, shaken for one hour and
204 allowed to settle following Rayment and Higginson (1992). The conductivity of the
205 supernatant was measured with a conductivity probe (Activon model 301, Activon Scientific,
206 Sydney, Australia) at an ambient temperature of 25°C in $\text{mS}\cdot\text{cm}^{-1}$ and converted to salinity in
207 parts per thousand (ppt).

208 Salinity values of the inundating water during the wet season and dry season were derived
209 from interpolated surfaces for Darwin Harbour created from 222 locations sampled during the
210 dry season and 674 locations sampled during the wet season between March 2009 and June
211 2010 (unpublished data Aquatic Health Unit, NT Government). Water salinity was measured
212 with hydrolabs (Datasonde4a and DS5X, both from Hydrolab, Colorado, USA) 0.2 m below
213 the water surface in parts per thousand (ppt). The two seasonal water salinity surfaces were
214 created using diffusion interpolation (based on a heat diffusion equation) in ArcGIS (v10,
215 ESRI 2011). Values of water salinity were extracted from these surfaces for each of the 201

216 field sites. An additional water salinity variable was calculated by taking the difference
217 between dry season and wet season salinity, and represents the range in water salinity. Before
218 fitting to the models, the three water salinity variables were tested for correlations and as they
219 were highly correlated (Pearson's product moment correlations > 0.9 , $p < 0.001$), we selected
220 only the wet season water salinity variable to fit to the models as it had a greater range of
221 values across the harbour (5 to 31.25 ppt) in comparison with the dry season (33.00 to 37.07
222 ppt).

223 Hydroperiod was calculated from the elevation above sea level for each site derived from
224 remotely sensed LiDAR data collected for Darwin Harbour in 2009. The LiDAR product we
225 used had been processed to remove noise and represents ground elevation only and has
226 vertical accuracy of 0.01 ± 0.15 m, and a horizontal resolution of 0.21 m (Temby, 2009). The
227 LiDAR elevations were converted from Australian Height Datum to Darwin Port Datum
228 (Lowest Astronomical Tide) by subtracting 4.105 m (Australian Baseline, 2011). Tidal
229 heights in Darwin Harbour, recorded every 20 minutes for a year by the Darwin tidal gauging
230 station, were grouped into 1 cm elevation classes (D. Williams, unpublished data). The tide
231 heights for a year were used to incorporate the annual, monthly and seasonal variation in tidal
232 amplitude for the study area. We calculated the duration of inundation for each elevation
233 class, which ranged from 0% (never inundated) to 100% (always inundated), then matched
234 the elevation of each survey site (as indicated by LiDAR) to the vertical elevation class and
235 extracted the percent of time each survey site is inundated.

236

237 **Statistical analyses**

238 Sets of statistical models were developed to describe the probability of dominance by *C.*
239 *tagal*, *R. stylosa* or *S. alba*. We modelled the dominance of these species, rather than species

240 distribution, because it is the dominance that produces the banded patterning of mangrove
241 forests. Statistical models relate the response variable (the dominance or non-dominance of
242 each species) to the set of explanatory variables (soil salinity, wet season water salinity and
243 hydroperiod). To ensure robust model inference the explanatory variables fitted to the models
244 should be independent and before fitting these three explanatory variables to models, they
245 were tested for pair wise correlations with Pearson's product moment correlations.

246 We used two statistical modelling approaches, Generalised Linear Models (GLMs) and
247 Boosted Regression Tree (BRT) models to increase our confidence in the inference arising
248 from the statistical analyses and to exploit the strengths of the two approaches: the
249 interpretability of GLMs and the ability to automatically capture interactions and complex
250 nonlinear relationships of BRT models (De'ath, 2007; Elith *et al.*, 2008). As the data used in
251 this study are binary and follow a Bernoulli distribution, a logit link function was used in the
252 models (McCullagh & Nelder, 1983). Three variables were fitted to GLMs using all
253 combinations of linear, quadratic terms and interaction terms and the best model selected
254 based on Akaike's Information Criteria (AIC, Akaike, 1974). AIC is a measure of the
255 parsimony of models based on a trade off between deviance reduction and the number of
256 parameters fitted in the model. A full list of the GLM models fitted is provided as
257 Supplementary Material. GLMs were developed using R, and the package 'stats' (v 2.13.1; R
258 Development Core Team, 2011).

259 BRT models are a machine learning tool that combines two algorithms (Breiman, 1996;
260 De'ath, 2007). The first generates trees by recursive binary splits, with explanatory variables
261 and split points selected to minimize prediction errors. The second algorithm, called boosting,
262 combines the trees produced by the first algorithm. The first tree is fitted to the data, the
263 second tree is fitted to the residuals of the first tree, the third tree is fitted to the residuals of
264 the second tree, and so on. Each tree selected for fitting is the one that produces the greatest

265 reduction in deviance. Interactions between explanatory variables are controlled by setting
266 the tree complexity where a value of one does not allow any interactions between variables.
267 The relative importance of each variable, within a model, is reported by calculating the
268 number of times the variable is selected as the basis for a bifurcation by the fitting algorithm
269 and scaled out of 100 (Elith et al. 2008). A tree complexity of three was used to allow some
270 interaction between variables fitted to the model. The models were developed with a learning
271 rate set to produce a minimum of 1000 trees using code from Elith *et al.* (2008) and the gbm
272 library (Ridgeway, 2006) in R (vers 2.13.1; R Development Core Team, 2011).

273 We calculated two cross validated model performance metrics, the Area Under Curve (AUC)
274 and the percent of deviance explained for the GLMs and BRT models (Guisan &
275 Zimmermann, 2000; Pearce & Ferrier, 2000). The AUC combines the trade off between
276 sensitivity (the true positive proportion) against the false positive proportion (Swets, 1988).
277 An AUC score of 0.5 indicates that the model will correctly rank sites that are actually
278 dominated by the focal species above sites not dominated by the focal species 50% of the
279 time, and an AUC of 0.7 indicates the minimum acceptable accuracy of prediction (Pearce &
280 Ferrier, 2000). The deviance explained by the model shows the goodness of fit between
281 modelled and observed values, and reflects the match between actual and predicted frequency
282 of dominance of the focal species (Ferrier & Watson, 1997). The deviance explained is null
283 deviance minus residual deviance scaled by the null deviance, where the null deviance is the
284 deviance of the model with only the intercept fitted, and residual deviance is the deviance
285 remaining unexplained by the model when predictor variables are fitted (Guisan &
286 Zimmermann, 2000). We used ten-fold cross validation, whereby the data were randomly
287 partitioned into ten subsets, the models fitted to nine of the ten subsets and accuracy
288 determined by comparing model predictions to the tenth subset of held out data (Stone,
289 1974). This process was cycled through until each model had been fitted and tested ten times.

290 As model predictions were tested against the held out portion of data during the cross
291 validation procedure and not on the data used for fitting the model the assessment of model
292 performance is more realistic than testing on the data used to fit the models. AICs are
293 provided for the GLMs but not for the BRT models as they rely on degrees of freedom which
294 cannot be calculated for complex modelling approaches such as BRT (Elder, 2003).

295 **RESULTS**

296 The mean hydroperiod differed among sites dominated by each species (Fig. 2). Sites
297 occupied by *S. alba* had the longest mean hydroperiod (inundated 68.8% of the year), *R.*
298 *stylosa* had an intermediate hydroperiod (20.7%) and *C. tagal* had the shortest hydroperiod
299 (5.1%). The mean soil salinity associated with each species shows a different pattern, with *S.*
300 *alba* occupying sites with the lowest soil salinity (27.04 ppt), followed by *C. tagal* (32.61
301 ppt) and *R. stylosa* in the sites with the highest mean soil salinity (38.61 ppt) (Fig. 2). The
302 salinity of the inundating water was greater at sites dominated by *S. alba* than sites dominated
303 by the other two species, with a mean wet season water salinity of 25.05 ppt for *S. alba*, and
304 21.42 and 21.23 ppt for *R. stylosa* and *C. tagal* respectively.

305 The three explanatory variables (soil salinity, wet season water salinity and hydroperiod)
306 were tested for pair wise correlation with Pearson's product moment correlation and found to
307 be uncorrelated (p-values > 0.05). Therefore, all three were fitted to the models. The BRT
308 models outperformed the GLMs for two of the three species as AUC scores were higher for
309 *R. stylosa* and *C. tagal* BRT models (Table 1). The percent of deviance explained indicated
310 that GLMs with quadratic and interaction terms had a performance similar to that of the BRT
311 models (Table1). More deviance was explained by the GLM than the BRT for *S. alba* (86.1%
312 GLM, 79.2% BRT), far more by the BRT model than by the GLM for *R. stylosa* (25.6%

313 GLM, 42.4% BRT) and a similar amount by both the models of *C. tagal* dominance (34.2%
314 GLM, 31.4% BRT).

315 Model performance was strong for all three species (Table 1), showing that the variables
316 included in the models explain much of the relationship between the environment and species
317 dominance. Hydroperiod was identified as significant in the GLMs of all three species
318 ($p < 0.01$), while water salinity was not significant in any of them (Table 1). For the BRT
319 models, hydroperiod was also the most important variable for species dominance for all
320 species (relative variable importance ranged from 48.6 to 90.1), followed by soil salinity (7.5
321 to 46.3) and finally wet season water salinity (2.4 to 5.2) (Fig. 3).

322 The plots of the fitted functions of the BRT models show that *S. alba* dominance was
323 dependent on both hydroperiod and soil salinity, while the other two species were less
324 influenced by soil salinity (Fig. 3). The probability of dominance by *S. alba* peaked when the
325 hydroperiod was above 40% of the time, whereas *R. stylosa* peaked between about 10 and
326 30% and *C. tagal* showed a peak when inundation was below about 10%. Thus each species
327 occupies a different portion of the gradient in the duration of inundation. A less distinct
328 relationship is shown between the probability of species dominance and soil salinity (Fig. 3).
329 *Sonneratia alba* had a higher probability of dominance with low soil salinity (0 to 35 ppt),
330 while for *R. stylosa* the opposite relationship was found, where the probability of dominance
331 is higher when soil salinity is above 30 ppt. There was a weak relationship between *C. tagal*
332 dominance and soil salinity.

333 The relationship between species dominance and the explanatory variables was generally
334 shown to be similar in the BRT fitted functions (Fig. 3) and the values of the GLM
335 parameters (Table 2). In the GLMs, the quadratic term for hydroperiod was significant and
336 negative for *S. alba* and *R. stylosa* showing that although there is a positive relationship with
337 hydroperiod, once the duration of inundation is high the probability of dominance declines.

338 *Ceriops tagal* dominates vegetation at higher elevations and is positively associated with soil
339 salinity (as shown by the significant positive values in the GLM, Table 2), but the probability
340 of dominance declines with high soil salinity, as indicated by the significant negative value of
341 the quadratic soil salinity term. In contrast, the BRT models showed no decline in the
342 probability of *C. tagal* dominance with higher soil salinity.

343 The probability of dominance by the three mangrove species, as determined by the duration
344 of the hydroperiod and soil salinity is represented in 3-dimensional plots in Fig. 4. These
345 plots illustrate the strong relationship between dominance of *S. alba* and both hydroperiod
346 and soil salinity. *Sonneratia alba* is highly unlikely to dominate areas where the duration of
347 inundation is less than 40% and soil salinity exceeds about 35 ppt, as shown in Fig. 4a. Both
348 *R. stylosa* and *C. tagal* dominance are less influenced by soil salinity than *S. alba*, and there
349 is a very marked increase in probability of dominance of these species along the gradient in
350 the duration of hydroperiod (Fig. 4b, c). The gradient in hydroperiod is partitioned between
351 the species as locations inundated more than 40% of the time more likely to be dominated by
352 *S. alba*, locations inundated 10-40% *R. stylosa* dominates and locations with a hydroperiod of
353 less than 10% are more likely to be dominated by *C. tagal*.

354 Interactions between hydroperiod and soil salinity and between hydroperiod and water
355 salinity were significant in the GLMs for *R. stylosa* and *C. tagal* (Table 2). *Ceriops tagal*
356 dominance had a negative relationship with hydroperiod and a positive relationship with soil
357 salinity, but the effects of hydroperiod was not so marked at high soil salinity. The GLM's for
358 *S. alba* contained no significant interaction terms, and hydroperiod had, by far, the strongest
359 relationship with *S. alba* dominance.

360 **DISCUSSION**

361 The analyses presented here provide unique insight into mangrove ecology because they
362 provide, for the first time, spatially explicit statistical models quantifying the relationship
363 between dominant mangrove species and a set of candidate explanatory variables which
364 includes the hydroperiod derived from LiDAR data. Thus, they fill an important gap in the
365 empirical study of mangrove ecology. Species dominance was most influenced by the
366 hydroperiod followed by soil salinity and these relationships were nonlinear. The least
367 influential variable was salinity of inundating water, concurring with previous studies (Bunt,
368 1996; Takaki *et al.*, 2003). The mangrove species partitioned the gradient in hydroperiod, and
369 to a lesser extent, the gradient in soil salinity. We found that *C. tagal* had the greatest
370 probability of dominance at locations where the hydroperiod was less than 10%, *R. stylosa*
371 between 10 and 40%, and *S. alba* dominated areas inundated more than 50% of the time.
372 Experiments investigating the growth of mangrove seedlings under a range of hydroperiods
373 found that in low elevation treatments, most *C. tagal* seedlings died within a year while the *S.*
374 *alba* seedlings survived (Kitaya *et al.* 2002). This agrees with our study, that *S. alba*
375 dominates areas with the greatest hydroperiod (low elevations), while *C. tagal* dominated
376 locations with the lowest duration of inundation (high elevations).

377 In our study the hydroperiod was the most important explanatory variable in the models of
378 mangrove dominance. There are two mechanisms by which the hydroperiod acts to influence
379 mangrove growth and therefore distribution. First, the direct effects of flooding reduce the
380 oxygen available to roots and reduce the rate of aerobic metabolism and water use efficiency
381 (Naidoo, 1985; McKee, 1996). Secondly, phytotoxins such as reduced forms of iron,
382 manganese and sulphides build up in flooded, anoxic soils, and these affect plant growth by
383 inhibiting photosynthetic gas exchange and root oxygen (Nickerson and Thibodeau, 1985;
384 Youssef & Saenger, 1998; McKee, 1993). Studies have shown a differential growth response
385 of mangrove species to flooding treatments without separating the direct effects of inundation

386 and the effects of soil phytotoxins (eg He et al. 2007). McKee (1993) separated the effects of
387 inundation and sulphide and found that growth and biomass allocation differed between two
388 mangrove species. The statistical modelling of the spatial distribution of mangrove dominants
389 applied here illustrates that there is no need to partition the direct effect of flooding from the
390 accumulation of soil phytotoxins as the hydroperiod controls both these mechanisms.

391 We found that the gradient in hydroperiod was clearly partitioned between the focal species,
392 with less decisive partitioning of the gradient in soil salinity. As our data were collected from
393 the distribution of taxa in a natural ecosystem, the partitioning of the gradients reported here
394 are based on observations of a sub-set of the realized niche, not the fundamental niche *sensu*
395 Hutchinson (1959), see also Colwell and Rangel (2009). We specify ‘subset’ because the
396 species only dominate some fraction of the sites that they occupy. Therefore, the statistical
397 models implicitly include the effects of competition between the species. The steep decline in
398 *C. tagal* dominance when the hydroperiod exceeds 10% could be related to competition with
399 *R. stylosa* rather than a threshold in physiological tolerance to inundation (Fig. 3). There are
400 few studies on the effects of hydroperiod and interspecific competition (Cardona-Olarte *et al.*,
401 2006), but these are needed to partition the effects of competition from the direct
402 physiological effects of hydroperiod.

403 Our findings allow a reinterpretation of the substantial, and often conflicting literature on the
404 effect of salinity on mangrove distribution across intertidal areas. Mangrove species have a
405 range of morphological and physiological adaptations to saline environments (Parida & Jha,
406 2010) and the differences in salt tolerance between taxa lead to differential growth rates with
407 increasing salinity (Ball, 1988a; Smith III, 1988; Ball & Pidsley, 1995). However, previous
408 studies have not been able to demonstrate a link between the demonstrated physiological
409 response of taxa and their observed distribution within mangrove forests. For example,

410 optimum salinity for growth of mangrove species in glasshouse experiments did not
411 correspond to species' distribution along a natural salinity gradient (Smith III, 1988; Ball &
412 Pidsley, 1995). Our results suggest that the hydroperiod overwhelms the effects of soil
413 salinity on plant physiology and explains the previously reported weak and inconsistent
414 relationship between soil salinity and species patterning (Matthijs *et al.*, 1999; Lovelock *et*
415 *al.*, 2005).

416 For Darwin Harbour there were no correlations between the explanatory variables fitted to
417 the models (i.e. among soil salinity, wet season water salinity and hydroperiod). Across a
418 single transect it is possible for soil salinity to be inversely related to the hydroperiod as
419 evaporation concentrates the salts at locations of higher elevation (Smith, 1992). However,
420 when a study area is considered in its entirety in all directions across the landscape then
421 correlations between soil salinity and elevation are lost. Soil salinity is also determined by the
422 salinity of the inundating water which varies from fresh to sea water depending on location
423 along an upstream to downstream axis, and also by distance to local fresh water inputs from
424 runoff and springs (Duke *et al.*, 1998). In addition, soil salinity can also greatly vary with
425 depth, for example, a single location can range from 10 to 50 ppt at different depths
426 (Marchand *et al.*, 2004). Thus soil salinity has a high spatial variability (in three dimensions:
427 upstream downstream, elevation above sea level, and with depth of soil) and high temporal
428 variability on daily (tidal), seasonal (rainfall and tidal) and yearly cycles. The ecological
429 rationale for the action of the hydroperiod is sufficient to explain the lack of correlation
430 between soil salinity, hydroperiod and water salinity for Darwin Harbour.

431 The statistical modelling approach applied here provides a powerful technique for
432 quantifying relationships between species dominance and explanatory variables. Such species
433 distribution models are widely used in ecology, although this is the first example for a

434 mangrove ecosystem. Mangrove field work is difficult and can be dangerous where saltwater
435 crocodiles occur (e.g. northern Australia), and we advocate reanalysing existing datasets
436 using the statistical approaches used here to test the generality of the patterns and
437 relationships we have presented in this study. Exploring existing datasets in new ways may
438 prompt further insights into mangrove dominance, community assembly and distribution.
439 While species distribution models are commonly used to model species occurrence, we
440 provide a novel approach by modelling the distribution of species dominance. Modelling the
441 spatial dominance of keystone species in other vegetation types may lead to new insights into
442 the processes structuring communities.

443 The most important implication of our findings about the primacy of the hydroperiod in
444 influencing the spatial patterning of species dominance, is that under conditions of sea level
445 rise we can expect extensive spatial restructuring of mangrove communities within the
446 forests. Such restructuring may have a cascade of effects on coastal erosion, fisheries and
447 carbon sequestration. This study hinges on the use of LiDAR data which have not yet been
448 collected for many areas supporting mangrove forest, for example in the developing world
449 and in the vast, remote areas of northern Australia. LiDAR has a high vertical precision (to
450 within 1 cm) and a fine grain (1x1m tiles) enabling detailed forecasts of the spatial changes in
451 mangrove distribution. However, such datasets are massive (the whole of Darwin Harbour
452 mangrove forest LiDAR is in excess of 6 GB) and the ability of software to handle them
453 efficiently or to handle them at all could limit spatial analyses.

454 The relationships we have quantified can be used to forecast the spatial shift in species
455 dominance in response to sea level rise, critical for planning coastal development and
456 infrastructure, fisheries management, mangrove rehabilitation projects and management
457 activities directed towards mitigation and adaptation to sea level driven changes. Our findings

458 indicate that future experimental studies that aim to identify influences on mangrove species
459 distributions should focus on the hydroperiod rather than the effects of salinity.

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466

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642

643

644 **BIOSKETCH:** Beth Crase is a tropical botanist interested in spatial analysis and statistical
645 modelling within landscape ecology and biogeography, with a particular focus on forecasting
646 the impacts of sea level rise on coastal plant communities.

647

648 **Table 1. Performance metrics for GLM and BRT models of *Sonneratia alba*, *Rhizophora***
 649 ***stylosa* or *Ceriops tagal* dominance in Darwin Harbour, northern Australia. Ten-fold**
 650 **cross-validation scores are provided for AUC and percent of deviance explained (% DE)**
 651 **± standard error (s.e.). The first five GLMs are a standard set of models provided for**
 652 **each species, and the sixth model is the best of a set of 91 GLMs as indicated by**
 653 **Akaike’s information criteria (AIC), marked by an asterisk. GLMs were fitted with all**
 654 **combinations of the explanatory variables: hydroperiod (h), soil salinity (s) and wet**
 655 **season water salinity (w), quadratic term (denoted by superscript 2) and interactions**
 656 **between variables (denoted by a colon). All models fitted are shown in**
 657 **SUPPLEMENTARY MATERIAL. BRT models are the final two models illustrated**
 658 **and were fitted with all explanatory variables, with and without interactions between**
 659 **the variables. AIC scores are not able to be calculated for BRT models**

660

Model	Mean AUC ± s.e.	Mean % DE ± s.e.	AIC
<i>Sonneratia alba</i> ~			
GLM:			
Hydroperiod (h)	0.95 ± 0.02	60.2 ± 0.9	87.4
soil salinity (s)	0.54 ± 0.04	0.2 ± 0.03	212.3
water salinity (w)	0.63 ± 0.05	5.0 ± 0.2	202.4
h + s + w	0.98 ± 0.01	71.3 ± 0.8	68.2
h+s+w+h ² +s ² +w ² +h:s +h:w+w:s	0.99 ± 0.01	88.2 ± 0.5	45.6
h + s + h ² *	0.99 ± 0.04	86.1 ± 0.4	37.4

BRT:

no interactions	0.99 ± 0.01	77.9 ± 6.3	n.a.
interactions	0.99 ± 0.01	79.2 ± 5.8	n.a.

Rhizophora stylosa ~

GLM:

hydroperiod	0.31 ± 0.03	0.2 ± 0.1	246.9
soil salinity	0.70 ± 0.66	7.7 ± 0.5	228.8
water salinity	0.53 ± 0.03	0.3 ± 0.1	248.6
h + s + w	0.73 ± 0.03	8.6 ± 0.5	230.9
h+s+w+h ² +s ² +w ² +h:s +h:w+w:s	0.81 ± 0.03	26.9 ± 0.3	199.4
h + s + w + h ² + h:s + h:w *	0.86 ± 0.02	25.6 ± 0.8	195.8

BRT:

no interactions	0.89 ± 0.03	41.6 ± 7.1	n.a.
interactions	0.90 ± 0.02	42.4 ± 3.6	n.a.

Ceriops tagal ~

GLM:

hydroperiod	0.73 ± 0.04	15.2 ± 0.4	205.9
soil salinity	0.56 ± 0.06	0.8 ± 0.1	240.1
water salinity	0.54 ± 0.05	0.5 ± 0.1	240.7
h + s + w	0.76 ± 0.05	17.3 ± 0.5	205.4
h+s+w+h ² +s ² +w ² +h:s +h:w+w:s	0.82 ± 0.04	35.1 ± 0.2	175.8
h + s + w + h ² + s ² + h:s + h:w *	0.85 ± 0.02	34.2 ± 0.6	172.9

BRT:

no interactions 0.84 ± 0.02 28.7 ± 4.7 n.a.

interactions 0.88 ± 0.02 31.4 ± 5.0 n.a.

661

662

663 **Table 2. The estimated coefficient values (\pm standard error) of the best models, as**
 664 **indicated by Akaike's Information Criterion (AIC) for the GLMs of *Sonneratia alba*,**
 665 ***Rhizophora stylosa* and *Ceriops tagal* dominance in Darwin Harbour. Interactions**
 666 **between variables denoted by a colon and quadratic terms by a superscript 2. n.s.**
 667 **indicates values not significant at $p < 0.05$**

668

Coefficient	<i>S. alba</i>	<i>R. stylosa</i>	<i>C. tagal</i>
intercept	-21.36 \pm 6.89	-2.76 \pm 0.77	-1.06 \pm 0.88
hydroperiod	0.96 \pm 0.28	0.30 \pm 0.07	-0.97 \pm 0.27
soil salinity	-0.77 \pm 0.25	0.06 \pm 0.04 n.s.	0.54 \pm 0.14
water salinity		0.02 \pm 0.02 n.s.	-0.03 \pm 0.03 n.s.
hydroperiod ²	-0.007 \pm 0.002	-0.003 \pm 0.001	0.002 \pm 0.001 n.s.
soil salinity ²			-0.02 \pm 0.01
hydroperiod:soil salinity		0.007 \pm 0.003	0.02 \pm 0.01
hydroperiod:water salinity		-0.007 \pm 0.002	0.02 \pm 0.01

669

670

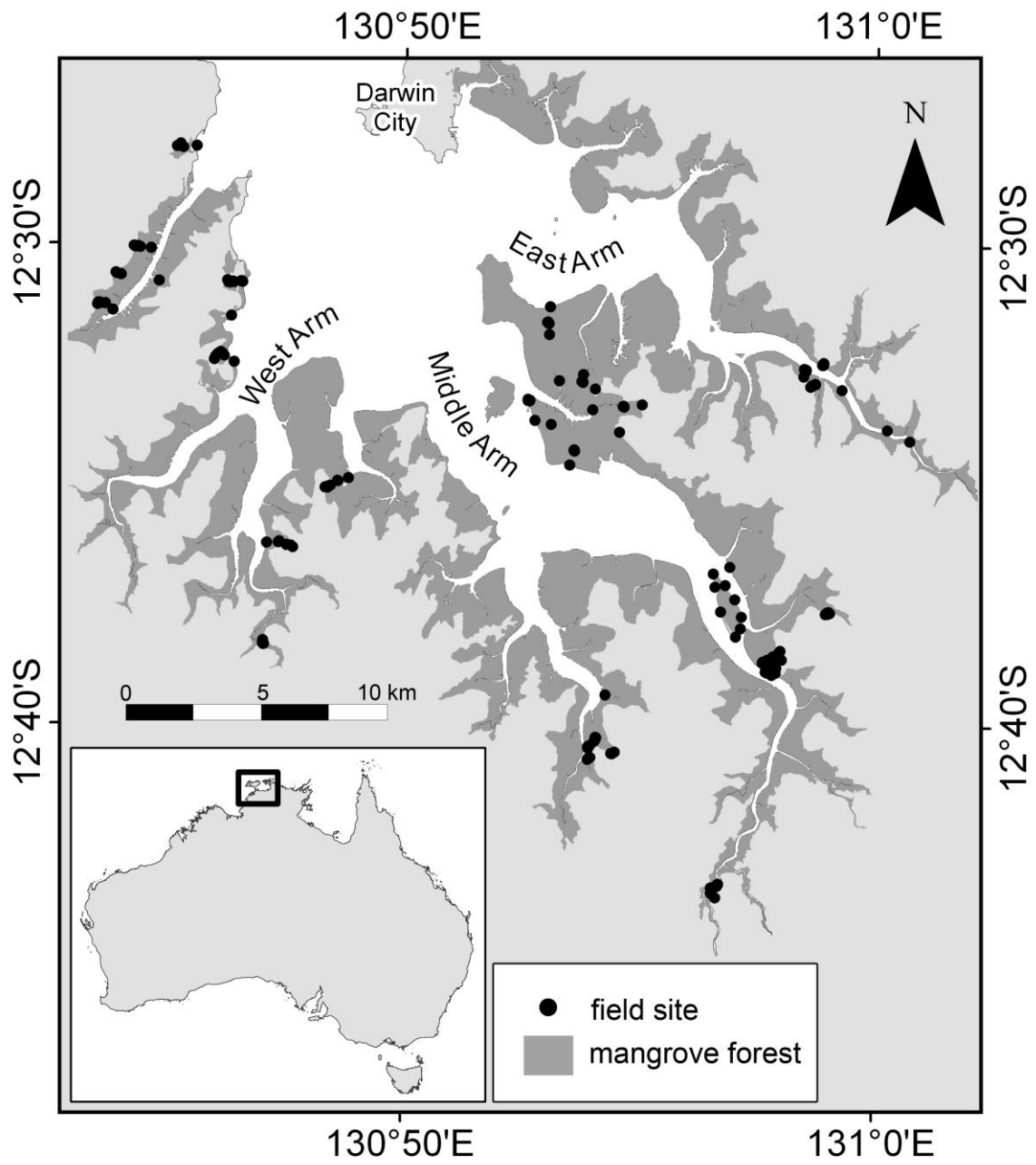
671 **Figure 1** Map of the study area showing the extent of the mangrove forest in Darwin
672 Harbour, northern Australia and location of sites surveyed. Inset map of Australia indicates
673 the location of Darwin Harbour.

674 **Figure 2** Mean, standard error (indicated by boxes) and 95% confidence intervals (indicated
675 by whiskers) for the explanatory variables (hydroperiod, soil salinity and wet season water
676 salinity) at sites dominated by *Sonneratia alba* (43 sites), *Rhizophora stylosa* (59 sites) and
677 *Ceriops tagal* (56 sites) in Darwin Harbour.

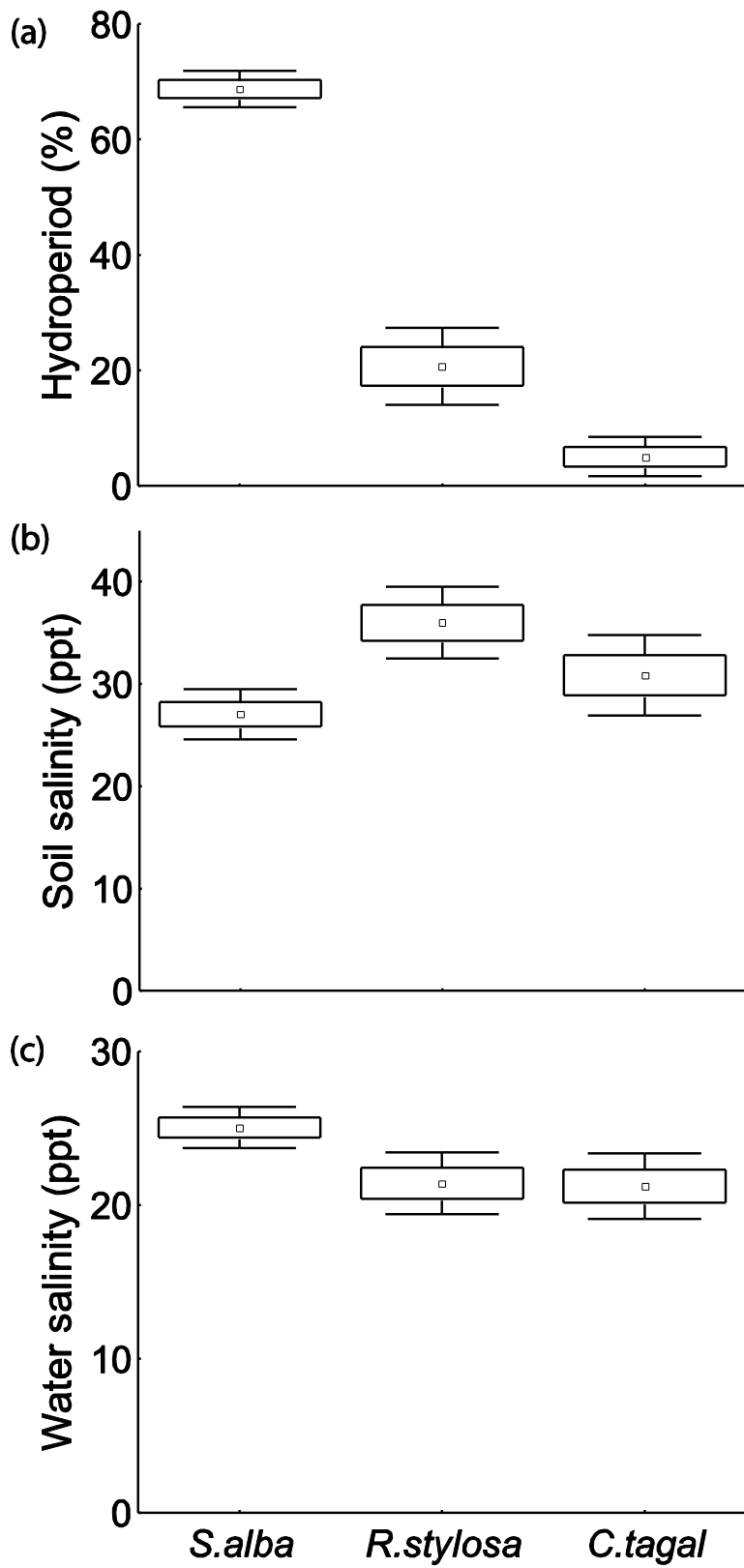
678 **Figure 3** Partial dependence plots from BRT models, showing the relationship between the
679 probability of dominance of *Sonneratia alba*, *Rhizophora stylosa* or *Ceriops tagal*, and the
680 explanatory variables: hydroperiod (percent of time inundated), soil salinity (parts per
681 thousand, ppt) and the salinity of the inundating water in the wet season (ppt), for Darwin
682 Harbour. Relative variable importance represents the number of times a variable is selected
683 for splitting in the BRT algorithm and is scaled out of 100 (shown on each panel)

684 **Figure 4** Plots showing the relationship between the probability of dominance of (a)
685 *Sonneratia alba*, (b) *Rhizophora stylosa* or (c) *Ceriops tagal*, along two gradients:
686 hydroperiod (percent of time inundated) and soil salinity (ppt), as derived from the BRT
687 models for Darwin Harbour.

688



691 **Figure 1**

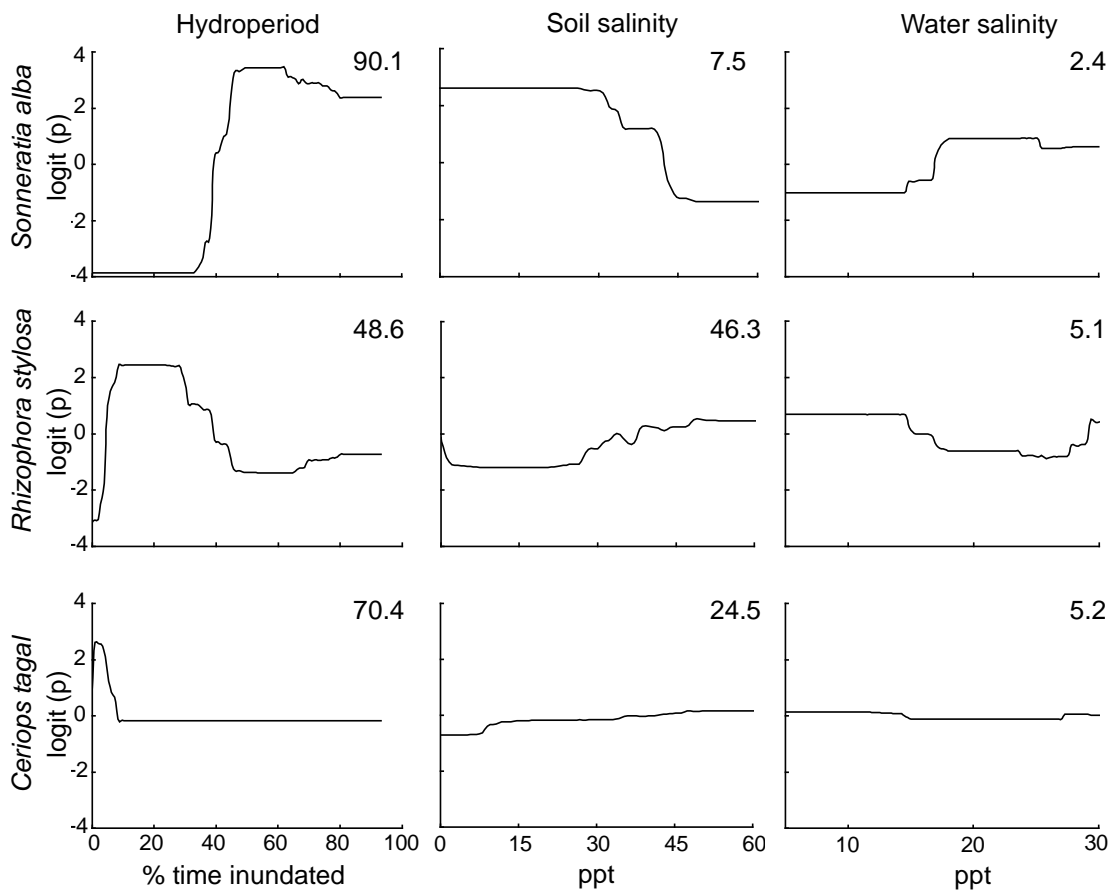


694

695 **Figure 2**

696

697

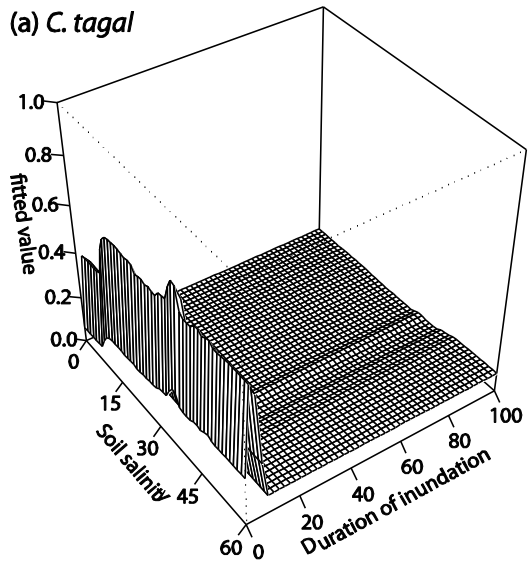


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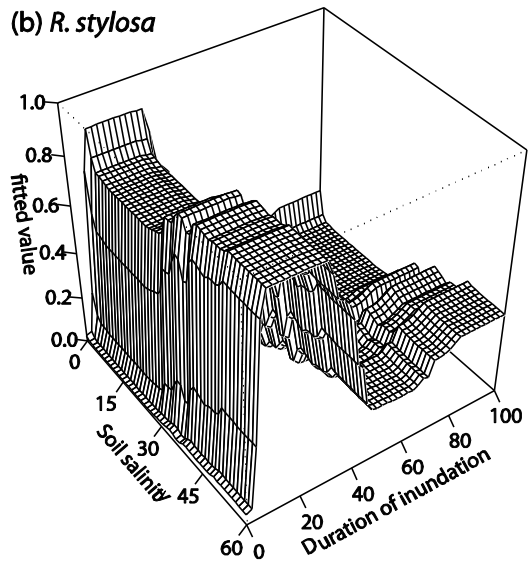
699

700 **Figure 3**

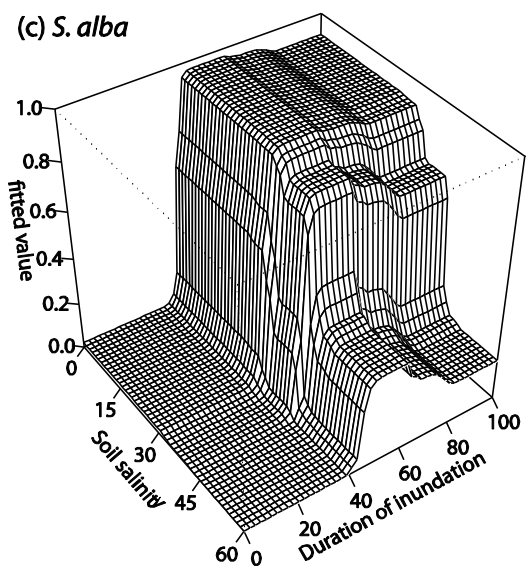
(a) *C. tagal*



(b) *R. stylosa*



(c) *S. alba*



701

702 **Figure 4**



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