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Modelling both dominance and species distribution provides a more complete picture of changes to mangrove ecosystems under climate change

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## 22 **Abstract**

23 Dominant species influence the composition and abundance of other species present in  
24 ecosystems. However, forecasts of distributional change under future climates have  
25 predominantly focused on changes in species distribution and ignored possible changes in  
26 spatial and temporal patterns of dominance. We develop forecasts of spatial changes in both  
27 the distribution of species dominance, defined in terms of basal area and species occurrence,  
28 and species occurrence, in response to sea level rise, for three tree taxa within an extensive  
29 mangrove ecosystem in northern Australia. The current dominance and occurrence of the  
30 three taxa were modeled in relation to a set of environmental variables using Boosted  
31 Regression Tree (BRT) models. Distributional changes were forecast for sea level rises of 0.5  
32 and 1 m, under two scenarios of seedling establishment; unrestricted and highly restricted.  
33 While forecasts of spatial change were qualitatively similar for species occurrence and  
34 dominance, the models of species dominance exhibited higher metrics of model fit and  
35 predictive performance, and the spatial pattern of future dominance was less similar to the  
36 current pattern than was the case for the distributions of species occurrence. This highlights  
37 the possibility of greater changes in the spatial patterning of mangrove tree species  
38 dominance under future sea level rise. Under the restricted seedling establishment scenario,  
39 the area occupied by or dominated by a species declined between 42.1 and 93.8%, while for  
40 unrestricted seedling establishment, the area suitable for dominance or occurrence of each  
41 species varied from a decline of 68.4% to an expansion of 99.5%. As changes in the spatial  
42 patterning of dominance are likely to cause a cascade of effects throughout the ecosystem and  
43 result in changes in the distribution and abundance of dependent fauna, forecasting spatial  
44 changes in dominance provides new and complementary information in addition to that  
45 provided by forecasts of species occurrence.

47 As a result of human influence, the global climate has changed during the past century and is  
48 expected to continue to change for many hundreds of years (IPCC 2013). Climate is a  
49 primary driver of species distribution globally, and shifts in the spatial patterning of species  
50 in response to recent climate change have already been recorded for many plant and animal  
51 species (Parmesan & Yohe, 2003; Chen *et al.*, 2011). However, in coastal environments, over  
52 a short to medium term time-frame, climate-mediated sea level rise is likely to be more  
53 influential than the impacts of changing temperature, rainfall, and seasonality, per se.  
54 Between 1901-2010 sea level rise was  $1.7 \text{ mm.y}^{-1}$  (+/- 1 SD 1.5-1.9) for a total rise of 0.19 m  
55 (0.17-0.21), and is forecast to further rise between 0.18 and approximately 1 m by 2100  
56 (Church et al 2011; Rhamstorf *et al.*, 2011). Furthermore, impacts of sea level rise on coastal  
57 plant communities have already been recorded (IPCC 2013; Ellison, 1993; López-Medellin *et*  
58 *al.*, 2011). As sea level rise occurs over a vertical scale of mm to cm, high resolution  
59 elevation data are essential for forecasting changes. The actual change in distribution occurs  
60 across a smaller geographic extent under sea level rise mediated shifts, compared to climate  
61 mediated distributional shifts, though these small shifts can represent a very large shift  
62 proportional to a species' current range, which tend to be highly restricted to coastal areas.

63 Forecasts of future distributions of species are critical for informing management and  
64 adaptation responses to ensure optimal outcomes for conservation and provision of ecosystem  
65 services (Hannah *et al.*, 2007; Guisan *et al.*, 2013). A forecasting tool central to providing  
66 such predictions of species occurrence is species distribution modelling (SDM), also called  
67 niche modelling (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009; Zimmermann *et*  
68 *al.*, 2010). These are statistical modelling techniques that relate empirical observations of the  
69 current distribution of species to combinations of climatic, environmental and biotic

70 explanatory variables (Austin, 2002). The vast majority of forecasting (and hindcasting)  
71 studies focus on modelling the geographic distribution of the occurrence of individual species  
72 (for example Bakkenes *et al.*, 2002; Peterson *et al.*, 2002; Thomas *et al.*, 2004; Guisan *et al.*,  
73 2007; de Oliveira *et al.*, 2012), and forecasting plant community or vegetation type has also  
74 received some attention (Hilbert *et al.*, 2001; Ferrier & Guisan, 2006; Mokany & Ferrier  
75 2011; Rojas-Soto *et al.*, 2012). However, dominant species influence the occurrence and  
76 abundance of other species within the community (Whittaker, 1965). Therefore,  
77 understanding and forecasting changes in the spatial patterns of dominance may be critically  
78 important as changes in the distribution of dominant species can cause a cascade of effects on  
79 the other species present in the ecosystem. Despite this, forecasting changes in the spatial  
80 patterning of dominance has rarely been explored using SDMs (Meier *et al.*, 2011).

81 Dominance can be defined in a variety of ways, and the most appropriate definition may  
82 differ among ecosystems and the research questions posed. For example, dominance can be  
83 defined broadly as a measure of the relative importance of a plant species with respect to the  
84 degree of influence that the species exerts on other components of the community (Whittaker  
85 1965). This “degree of influence” can be difficult to quantify, especially for the below ground  
86 components of plant species (Daubenmire, 1968; Odum, 1971). Therefore metrics of  
87 dominance are more commonly derived from the above-ground portion (Daubenmire, 1968;  
88 Specht, 1970; Odum, 1971). Relative dominance is one such metric, and can also be defined  
89 in several ways, including, cover, basal area, frequency or biomass (Daubenmire, 1968;  
90 Odum, 1971). For this study, a species was designated as the dominant at sites when  
91 exceeding 50% of the total basal area (following Tiner 1999), although the dominant species  
92 in this case contributed > 66% of the basal area at all sites.

93 Forecasting changes in the spatial patterning of dominance can be a valuable tool for the  
94 following reasons. First, dominant species are used to classify habitat and vegetation types,  
95 and are used extensively in vegetation mapping and in some mapping applications informed  
96 by remotely sensed data (Skidmore, 2002; Thackway *et al.*, 2008; Neldner *et al.*, 2012);  
97 therefore useful datasets have already been compiled. Second, management options under  
98 environmental changes (i.e. climate change, sea level rise), but also disease, fire ecology and  
99 land use, are more easily explored for a few key species than for all species present. Third,  
100 changes in the dominance of a few species can be monitored more easily and with fewer  
101 resources than tracking the full floristic composition, and there are better opportunities for  
102 monitoring to be implemented via remote sensing. Finally, studies forecasting changes in the  
103 distribution of dominance under climate change and sea level rise can be used to infer a  
104 cascade of effects on other dependent species and thereby used to identify locations and  
105 ecosystems with a greater risk of unfavorable outcomes in response to a changing climate.  
106 Therefore, forecasting spatial patterns of dominance is a critical tool enabling impacts on  
107 ecosystem structure to be investigated.

108 Change in patterning of dominance in response to climate change, sea level rise or alteration  
109 of management activities has been explored in few instances. For example Meier *et al.*,  
110 (2011) evaluated patterns of distribution across climate gradients using co-occurrence  
111 patterns of a dominant species and three competing species. They forecast the current and  
112 future distribution of species under climate change and concluded that while the abundance  
113 of competitors strongly influenced abundance of the focal species under favorable  
114 environmental conditions, this link was weaker in unfavorable environments. Dullinger *et al.*,  
115 2005, investigated interactions among three tree species: pine, larch and spruce and found  
116 that pine affected spruce and larch differently. Their results suggest that spruce would be

117 favored at the expense of larch during expansion in suitable habitat of pine under climate  
118 change. Although SDMs were implemented to investigate interactions among species, no  
119 spatial predictions were produced. In addition, Pellissier *et al.*, 2010 studied a dominant shrub  
120 species (*Empetrum nigrum* ssp. *Hermaphroditum*, Ericaceae) and its influence on a range of  
121 non-dominant species. They concluded that including competitors or facilitators in SDMs  
122 improves model fit and therefore predictive power. A similar conclusion was reached by le  
123 Roux *et al.*, (2014) who incorporated data from three dominant species into community-level  
124 models as a surrogate for biotic interactions among species. They report that including  
125 dominant species in models improved the realism of modelled community composition and  
126 species richness. However, these studies did not forecast spatially explicit changes in the  
127 patterning of dominance of species under environmental change. So while there have been  
128 some studies investigating patterns of dominance in plant communities, spatial forecasts of  
129 changes in dominance under environmental change are rare and there is a need to explore  
130 how predicted changes in dominance differ from predicted changes in species occurrence  
131 using SDM techniques and other modelling approaches, such as community assembly  
132 models.

133 Mangrove forests may provide an ideal study system within which to investigate spatial  
134 patterns of dominance as they are frequently characterized by plant communities dominated  
135 by a single species (Smith, 1992; Snedaker, 1982). These mangrove plant communities often  
136 form bands parallel to shorelines or river banks, influenced by a gradient in the duration of  
137 inundation by water (Cruse *et al.*, 2013; Krauss *et al.*, 2006; Watson, 1928). While different  
138 mangrove plant species can be distributed throughout the mangrove forest, each community  
139 is usually dominated by a single species, and this dominance can extend to the development  
140 of monospecific stands (Smith, 1992; Snedaker, 1982). As mangroves occur within the  
141 intertidal zone they are highly sensitive to any change in sea level, therefore future climate

142 change is anticipated to strongly impact mangrove forests (Duke *et al.*, 2007, Gilman *et al.*,  
143 2008, Nicholls *et al.*, 2007). Empirical observations have shown that the distribution of  
144 mangrove forests across the intertidal zone has shifted in many locations over the past few  
145 decades (Ellison, 1993; Lucas *et al.*, 2002; Gilman *et al.*, 2007; Everitt *et al.*, 2010; López-  
146 Medellín *et al.*, 2011). However, few forecasts exist predicting mangrove forest shifts, or  
147 changes in the spatial patterning of mangrove species occurrence or communities (Doyle *et*  
148 *al.*, 2003; Record *et al.*, 2013, Quisthoudt *et al.* 2013).

149 Mangrove forests provide a range of highly valuable ecosystem services including habitat and  
150 breeding areas for fish, (Rönnbäck, 1999; Mumby *et al.*, 2004; Nagelkerken *et al.*, 2008),  
151 coastal protection from storm surge or tsunamis (Danielsen *et al.*, 2005), and carbon  
152 sequestration (up to five times more carbon per hectare than temperate boreal and tropical  
153 rainforests; Donato *et al.*, 2011; Siikamaki *et al.*, 2012). Any changes in the spatial  
154 distribution of dominance in response to sea level rise could strongly influence the presence  
155 and abundance of dependent fauna and alter ecosystem services provided by these forests.  
156 Few forecasts have been developed to determine the potential impact of sea level rise on the  
157 distribution of mangrove species, despite their high value in terms of economic products and  
158 ecosystem services. For this reason, and the fact that mangrove forests represent something of  
159 a 'model system' in terms of species dominance, these forests provide an ideal ecosystem  
160 within which to explore the magnitude and implications of future changes in the spatial  
161 patterning of dominance under conditions of higher sea level, and to compare predictions  
162 about changes in dominance with those for changes in the spatial distribution of species  
163 occurrence.

164 The aims of this paper are to (i) compare forecasts of species distribution in response to sea  
165 level rise using both occurrence and dominance as a dependent variable; and (ii) investigate

166 the potential for intensification of interspecific competition under sea level rise scenarios. We  
167 developed Species distribution models (SDMs) with binary (presence/absence, dominant/not-  
168 dominant) data collected within an extensive mangrove forest (20,000 ha) in northern  
169 Australia. The SDMs are then used to forecast species occurrence and dominance at high  
170 spatial resolution (25x25m pixel size) under future sea levels 0.5 and 1 m higher than the  
171 current sea level.

172

## 173 **Methods**

### 174 **Focal species and study area**

175 The study was conducted in the mangrove forest (approximately 20, 000 ha) of Darwin  
176 Harbor in northern Australia, focusing on *Sonneratia alba* Sm., *Rhizophora stylosa* Griff and  
177 *Ceriops tagal* Perr. These species were selected from among the 36 taxa recorded in the area,  
178 because they each form mono-specific communities in Darwin Harbor and dominate 82% of  
179 the mangrove forest, as shown in maps produced by Brocklehurst and Edmeades (1996).  
180 *Ceriops tagal* dominates approximately 44% of the forest area, followed by the *R. stylosa*  
181 with 33%, and finally *S. alba* covering 5% (Brocklehurst & Edmeades, 1996). These species  
182 occur throughout South-East Asia, northern Australia and the Pacific region, with *S. alba* and  
183 *C. tagal* additionally occurring in India, eastern Africa and Madagascar (Duke, 2006;  
184 Spalding *et al.*, 2010). In Darwin Harbor, *Sonneratia alba* usually dominates the low  
185 intertidal zone, *Rhizophora stylosa* the mid-intertidal and *Ceriops tagal* the high-intertidal  
186 zone (Crase *et al.* 2012). The presence or absence of the focal species was recorded at 201  
187 field sites during 2010/11, with each site located at least 100 meters apart and broadly  
188 distributed throughout the forest (Supplementary Material Figure SM1). The urban areas on

189 the north-eastern side of the harbor were avoided and sites were stratified by community type  
190 as previously mapped by Brocklehurst and Edmeades (1996).

191 A binary variable, dominance / non-dominance was recorded at each field site, with  
192 dominance defined as the species with the greatest basal area. For this study, a species was  
193 designated as the dominant at a site when it exceeds a minimum of 50% of the total basal  
194 area, following the U.S. forestry department guidelines presented in Tiner (1999). However,  
195 in this study the dominant species contributed more than 66% of the basal area at all sites,  
196 and more than 90% in about a third of sites. The approach developed here can not only be  
197 applied to other mangrove forests, but to any ecosystem with few dominant species, a  
198 situation common to many ecosystems, for example coral reefs, (Done, 1982; Aronson *et al.*,  
199 2002) and boreal forests (McCarthy 2001, see also Chapin *et al.*, 2004).

200 During the Holocene (6500-7000 yr bp) extensive mangrove forests developed across  
201 northern Australia in response to changes in sea-level and sediment deposition (Woodroffe *et*  
202 *al.*, 1985). Darwin harbor is a ria coast formed by post-glacial flooding of a dissected plateau,  
203 with two major rivers empty into the harbor (Semeniuk 1985). The study area is in a macro-  
204 tidal region with a tidal amplitude up to 8 m, and mean spring and neap tides of  
205 approximately 6 and 3 m, respectively (Williams *et al.*, 2006). Approximately 129,000  
206 people live in the township of Darwin on the north eastern portion of the harbor  
207 (Supplementary Material Figure SM1). The remaining coastline of the Northern Territory  
208 (NT), some 13,500 km in length, has very low anthropogenic impacts with the five largest  
209 towns being Nhulunbuy (population 3933), Galiwin'ku (2124), Maningrida (2068), Wadeye  
210 (1627) and Milingimbi (1081). Australia's population density is 3.07 km<sup>2</sup> whereas the  
211 Northern Territory is 0.4 per km<sup>2</sup> (Australian Bureau of Statistics 2014) and the mangrove  
212 forests that occur across the NT are largely unexploited.

213 The local geomorphology associated with the landward edge of the mangrove forest is a steep  
214 rise of approximately 1 m, and separates the tidally-influenced mangrove communities from  
215 the terrestrial vegetation. For forecasting distributional shifts in vegetation some of the  
216 adjacent terrestrial forest was included in the study area on the landward side of the  
217 mangrove forest. On the seaward side of the mangrove forest the study area was clipped  
218 where inundation exceeded 80% of the time as no mangrove trees were recorded beyond this  
219 level.

## 220 **Model development**

221 Three explanatory variables: slope, water salinity, and hydroperiod, previously identified as  
222 the key influences on the distribution of mangrove species dominance in Darwin Harbor  
223 (Crase *et al.*, 2012), were used to develop the distributional models for three focal species'  
224 occurrence and dominance. All variables were gridded at a resolution of 25x25 m, resulting  
225 in approximately 320,000 grid cells which is an extent and resolution appropriate for studies  
226 of sea level rise impacts in coastal areas. In contrast, studies forecasting distributional change  
227 in response to climate variables must be conducted across larger geographic extents but also  
228 utilize larger grid cell sizes. For example, grid cell sizes of between 4x4 km and 0.5x0.5  
229 degrees have been applied in climate impact studies resulting in forecasts across a few  
230 hundred to several hundred thousand grid cells (Bakkenes *et al.*, 2002; Peterson *et al.*, 2002;  
231 de Oliveira *et al.*, 2012). It is important to note that the present sea level rise study has a  
232 similar intensity to studies of climate change impacts, and we reiterate that the area of the  
233 study must match the environmental driver(s) as should the grain. Furthermore, the number  
234 of species must match with the research question and the ecosystem studied. As we focused  
235 on a scale appropriate for the main drivers within mangrove forests (ie a single harbor), we

236 did not include any climate variables. Across 20,000 ha of our study region there is no  
237 difference in climate variables such as rainfall or temperature.

238 The variable slope was calculated from elevation data. The elevation data were recorded from  
239 remotely sensed LiDAR data collected in 2009, for every m<sup>2</sup> in the Darwin Harbor mangrove  
240 forest, with a ground elevation vertical accuracy of  $0.01 \pm 0.15$  m and a horizontal resolution  
241 of 0.21 m (Temby, 2009). The variable salinity of the inundating water was derived from  
242 empirical measurements from 674 locations, surveyed during the wet season between March  
243 2009 and June 2010, and interpolated using a heat diffusion equation in ArcGIS (v10 ESRI  
244 2014) to produce salinity values for the whole harbor (unpublished data Aquatic Health Unit,  
245 NT Government). Water salinity was measured with two hydrolabs (Datasonde4a and DS5X,  
246 both from Hydrolab, Colorado, USA) 0.2 m below the water surface in parts per thousand  
247 (ppt). Hydroperiod, or duration of inundation, was calculated by resampling the 1x1m  
248 elevation above sea level from LiDAR elevation data (Temby, 2009) in 25x25 m grid cells,  
249 and relating the elevation to empirical tide gauge records (D. Williams, Northern Territory  
250 Government, unpublished data). Tidal data for a full calendar year were used in order to  
251 incorporate the annual, monthly and seasonal variation in tidal amplitude. Within the study  
252 area the hydroperiod ranged from 0% (never inundated) to 100% (always inundated).

253 Boosted Regression Tree (BRT) models are a machine learning approach used to develop  
254 species distribution models (SDMs) (Friedman *et al.*, 2000; De'ath, 2007; Elith *et al.*, 2008).  
255 They automatically model interactions between explanatory variables and are able to capture  
256 non-linear relationships between the response and explanatory variables. This has lead to  
257 strong performance of BRT models compared to other SDM modelling approaches (Elith *et*  
258 *al.*, 2006). The BRT models were developed using the gbm-package library (Ridgeway,  
259 2007; Ridgeway, 2010) and code from Elith *et al.*, (2008) in R (ver 2.13.1; R Core

260 Development Team, 2013). For the BRT models, a tree complexity of three was used to  
261 allow some interaction between the explanatory variables and the learning rate was set to  
262 produce a minimum of 1000 trees, with a bag fraction of 0.5.

263 Model performance was tested using the area under curve (AUC) of the receiver operating  
264 characteristic (ROC), which combines the trade-off between sensitivity (the true positive  
265 proportion) and the false positive proportion (Fielding & Bell, 1997). A model with an AUC  
266 score of 0.5 indicates that sites actually dominated by the focal species will only be  
267 accurately ranked above sites not dominated by the focal species 50% of the time, that is, it is  
268 no better than random (Swets, 1988). An AUC score above 0.7 indicates fair model  
269 performance and above 0.9 is considered excellent (Swets, 1988).

270 The deviance explained (also termed deviance reduction) by the model indicates the goodness  
271 of fit between modelled and observed values, and reflects the match between actual and  
272 predicted frequency of dominance of the focal species (Ferrier & Watson, 1997). Null  
273 deviance is the deviance of the model with only the intercept fitted, and residual deviance is  
274 the deviance remaining unexplained by the model when predictor variables are fitted. The  
275 deviance explained is null deviance minus residual deviance scaled by the null deviance  
276 (Guisan & Zimmermann, 2000). During the cross-validation procedure, the deviance  
277 explained was calculated on the held-out portion of data not used to fit the model, to ensure  
278 that model fitting and testing did not occur on the same data.

279 Performance metrics (AUC and percent of deviance reduction) were assessed with 10-fold  
280 cross-validation. The data were randomly partitioned into ten subsets, the models fitted to  
281 nine of the ten subsets (training data) and accuracy determined by comparing model  
282 predictions to the tenth subset (testing data) (Stone, 1974). This process was repeated until  
283 each model had been fitted and tested ten times. As model predictions were tested against the

284 held-out portion of data during the cross validation procedure (for both AUC and deviance  
285 explained) and not on the data used for fitting the model, the assessment of model  
286 performance is more realistic than testing on the data used to fit the models.

### 287 **Forecasting distributional change in response to sea level rise**

288 The BRT models of the current distribution of species and dominance of the focal species  
289 were used to forecast spatial changes in suitable habitat under two scenarios of sea level rise.  
290 The models produced a probability of occurrence (also referred to as habitat suitability), for  
291 every 25x25 m grid cell in the study area, thus producing a map of the species within Darwin  
292 Harbor at current sea level and for the two future sea levels (0.5 and 1 m). The current rate of  
293 sea level rise, averaged globally, is around 3.4 mm/y, although this rate varies spatially across  
294 the globe and is higher in the region between northern Australia and south-east Asia (Church  
295 *et al.*, 2004; Church & White, 2011). Tide gauge data for the northern coast of Australia  
296 shows that sea level rose in the harbor at a rate of 8.3 mm/y between 1992 and 2010, 2.4  
297 times the global average (Australian Baseline Sea Level Monitoring Project 2011). In  
298 addition, there is empirical evidence that sea level rise has accelerated in the past decade  
299 (Church *et al.*, 2011). This suggests that a 0.5 m rise in sea level is plausible by  
300 approximately 2050, and 1 m by 2100, for Darwin Harbor. While climate change forecasts  
301 indicate increased rainfall in equatorial regions (CSIRO & BOM, 2012), the potential  
302 changes in climatic variables, storm surge height and cyclone intensity were not examined  
303 here.

### 304 **Scenarios of seedling establishment**

305 Two scenarios of establishment of mangrove propagules were implemented which are  
306 conceptually similar to dispersal scenarios considered in terrestrial studies forecasting shifts

307 in species ranges (Thomas *et al.*, 2004; Engler *et al.*, 2009). In the first scenario, seedlings are  
308 assumed to be ineffective competitors against established trees, and therefore locations that  
309 become suitable under a higher sea level are not colonized if that location was previously  
310 occupied by another species. In the second scenario of establishment, propagules were  
311 assumed to disperse, establish and effectively compete against trees occupying locations that  
312 are currently unsuitable, but which become suitable under a higher sea level. Forecasts for  
313 species occurrence and dominance were developed for both scenarios. Over the medium term  
314 (20-50 years) it is expected that true seedling establishment will fall somewhere in between  
315 these two scenarios. However, mangrove seedling establishment is limited under a closed  
316 forest canopy (Clarke, 2004) and several species can only establish in canopy gaps (López-  
317 Hoffman *et al.*, 2007). Therefore, seedling establishment in locations that become suitable  
318 under sea level rise is likely to be limited when locations are already occupied by adult trees  
319 and may be directly related to the mortality rate of the incumbent adult trees. To explore the  
320 potential outcomes of asymmetric competition, forecasts of mangrove distribution should  
321 compare limited and unlimited scenarios of seedling establishment, in order to set the upper  
322 and lower bounds of possible range changes in response to sea level rise.

### 323 **Calculations of occurrence, overlap and instability**

324 The models were used to estimate a probability of species occurrence or dominance in every  
325 cell of the study area, at current and future sea levels. Although a threshold is usually selected  
326 to convert probabilities to 0 (absence) or 1 (presence), the threshold selected can influence  
327 calculations of occurrence (Liu *et al.*, 2005) and it is generally better to avoid arbitrary  
328 categorization of SDM predictions because it leads to unnecessary information loss  
329 (Calabrese *et al.*, 2014; Lawson *et al.*, 2014). We instead developed and applied threshold-

330 independent methods to estimate the number of cells occupied, the overlap between species,  
331 and a metric of stability (equations 1, 2 and 3).

332 The expected number of occupied cells under current ( $m = 0$ ) and future sea levels ( $m = 0.5$   
333 or 1) for the focal entity (species occurrence or dominance), was calculated by summing the  
334 probability of occurrence or dominance for all cells in the study area. This amounts to  
335 calculating the expected number of events arising from  $n$  binomial trials, each with event  
336 probability  $p_i$ , assuming the outcome of each trial is independent of the outcomes of all other  
337 trials:

$$338 \quad E_{occupied,m} = \sum_{i=1}^n p_{i,m} \quad \text{Equation 1}$$

339

340 where  $n$  is the number of cells in the study area, and  $p_{i,m}$  is the probability of occurrence of  
341 the focal entity in cell  $i$  of the study area at sea level  $m$ .

342 We then estimate the number of cells expected to be occupied by two species (or by two  
343 dominants), based on the predictions of two SDMs (or dominance models) for a given sea  
344 level rise scenario. This helps us to identify pairs of species for which future intense  
345 competition is likely. That is, if the expected area of overlapping ranges is high for one pair  
346 of species, and low for a different pair of species, then the former will be expected to be in  
347 higher competition than the latter under future conditions. Summing that product across all  
348 cells in the landscape gives the expected area of range overlap for that pair of species:

$$349 \quad E_{overlap,p,q,m} = \sum_{i=1}^n p_{i,m} \cdot q_{i,m} \quad \text{Equation 2}$$

350

351 where  $n$ ,  $i$  and  $m$  are as for Equation 1. This expected area of overlap can also be presented  
352 as a percentage of the total forested area. Intermediate probability of overlap predictions can  
353 be obtained at sites in which there is a moderately high probability of one species occurring  
354 and a moderately low probability of another species occurring, or at sites in which two  
355 species have intermediate probabilities of occurrence. Clearly, the latter case would represent  
356 more intense competition than the former. Therefore, this metric is primarily useful for  
357 identifying locations and pairs of species under strong interspecific competition because they  
358 are predicted to have simultaneously high individual occurrence (or dominance) probabilities  
359 at many places in the landscape, or over a large proportion of their expected (competition-  
360 free) future range. The metric does not provide any information about which species is  
361 dominant and which is dominated at any location or across the range.

362 A metric of instability ( $E_{instability}$ ) was calculated based on the assumption that species' with  
363 larger predicted *changes* in the probability of occurrence at different sea levels are more  
364 unstable compared to a species with smaller predicted changes in occurrence probabilities  
365 throughout the region. Therefore, this metric indicates the degree to which the predicted  
366 species' distributions are expected to change as the sea level rises. The index of instability  
367 was calculated by taking the absolute difference between the probability of occurrence of the  
368 focal (or dominant) species at current ( $p_{i,0}$ ) and future sea levels ( $p_{i,m}$ ), summed across all  
369 cells in the study area  $i$ ,

$$370 \quad E_{instability,m} = \sum_{i=1}^n |p_{i,0} - p_{i,m}| \quad \text{Equation 3}$$

371 where  $n$ ,  $i$  and  $m$  are as for Equation 1. The instability metric indicates how extensively  
372 species retreat from currently occupied areas, and/or invade newly suitable areas. Similarly,  
373 in the case of dominance, the metric indicates how much dominance changes (positively and

374 negatively) across the study region. It literally amounts to the expected number of cells (or  
375 hectares) that will switch state from occupied to unoccupied, or unoccupied to occupied  
376 based on the model predictions. The instability metric does not distinguish between range  
377 expansion, range contraction, or range shift; it simply highlights whether or not a species  
378 range is expected to change substantially or little. Species forecast to have large range  
379 contractions can be easily identified as potentially at risk under climate change. However,  
380 species with a forecast of range *expansion* may also be at risk of decline under changed  
381 environmental conditions because there is no guarantee that they will colonize areas forecast  
382 to be suitable. The  $E_{instability}$  metric allows us to explore a different quality of range shift, in  
383 addition to a simple quantification of contraction and enables the identification of species  
384 potentially at risk despite a predicted expansion into newly suitable areas.

385

## 386 **Results**

### 387 ***Model performance, variable importance and instability***

388 The BRT model performance metrics (ten-fold cross-validated AUC and deviance reduction)  
389 indicated that the modelled current distribution matched reasonably well the observed  
390 distribution for species occurrence and dominance, as AUC scores exceeded 0.82 in all cases  
391 (Table 1). The models of dominance had higher model performance than did the models of  
392 species occurrence. The models of *S. alba* occurrence and dominance had the highest AUC  
393 scores and the greatest proportion of deviance explained, followed by *R. stylosa* and finally  
394 by *C. tagal* (Table 1).

395 The rank importance of explanatory variables within the models were identical for species  
396 occurrence and dominance. Relative variable importance, measured by the proportion of  
397 times each explanatory variable was selected by the model-fitting algorithm, indicated that  
398 the hydroperiod was the most important variable in all models of species and dominance  
399 (range 68.5 – 88.1, Table 1), with slope the second most important variable in most models  
400 (range 6.1 – 17.4) and salinity of the inundating water the least important variable (range 5.4  
401 – 15.8).

402 Partial plots illustrate the relationship between the response variable (species occurrence or  
403 dominance) and the explanatory variable of interest, with the other explanatory variables set  
404 at their mean values. Partial plots of the most important variable, hydroperiod, illustrate a  
405 similar relationship between probability of species occurrence or dominance (Figure 1). For  
406 example, for *S. alba*, the probability of species occurrence and dominance increased sharply  
407 when hydroperiod exceeded approximately 35% (Figure 1a, b), while for *R. stylosa*, the  
408 probability of species occurrence and dominance was highest between approximately 10 -  
409 30% (Figure 1c, d). The probability of occurrence or dominance of *C. tagal* peaked when  
410 hydroperiod was between approximately 8 – 15 % of the time (Figure 1e, f). Salinity of the  
411 inundating water and slope were not influential variables, and partial plots are available in the  
412 Supplementary Material (Figure SM2, SM3).

413 Species dominance was less stable through time than species occurrence as indicated by  
414 higher *Einstability* values for all focal taxa, suggesting greater spatial changes in dominance  
415 under future sea levels compared to changes in species' distributions (Table 2). *Rhizophora*  
416 *stylosa* had a higher metric of instability compared to *S. alba* and *C. tagal* due to the large  
417 expansion of *R. stylosa* into areas that become suitable after sea level rise, and the loss of area  
418 to invading *S. alba*.

419 ***Forecasts of decline and expansion under two establishment scenarios***

420 The area of forest suitable for species occurrence or dominance changed with each increment  
421 in sea level rise and differed substantially between the two seedling establishment scenarios  
422 (Figure 2). When the establishment of mangrove seedlings is restricted, seedlings cannot  
423 establish in areas already occupied, and the predicted area suitable declined for all mangrove  
424 taxa. *Sonneratia alba*, which occurs along the seaward fringe of the mangrove forest, is  
425 forecast to decline by 42.7-48.2%, *R. stylosa* by 44.1-47.7% and *C. tagal*, the most inland  
426 taxon, by 92.1-93.8% (Figure 2 a, c, e), after a sea level rise of 1 m.

427 Under the second establishment scenario where propagules are able to establish in any newly  
428 suitable area only *C. tagal* is forecast to decline after a 1 m sea level rise (by 47.6-68.4%). In  
429 contrast, *S. alba* is forecast to expand by 17.4 -20.2%, relative to the area occupied under  
430 current sea levels, and *R. stylosa* expands by 82.6-99.5% (Figure 2 b, d, f).

431 ***Change in probability of occurrence with sea level rise***

432 The change in probability of occurrence was mapped for the area under each sea level rise  
433 scenario and shows an increase in the area suitable for *R. stylosa* and *S. alba* and a decline in  
434 area suitable for *C. tagal*. Maps of the probability of occurrence were similar for species  
435 occurrence (Figure 3 a) and dominance (Figure 3 b) at a macro level, and are presented here  
436 for Wood's Inlet, an 8 by 8 km portion of the full 20,000 ha forest at Darwin harbor.  
437 Locations with a high habitat suitability for species occurrence at current sea levels became  
438 slightly less suitable after a 1 m sea level rise (Figure 4 a, b, c). This is shown by the high  
439 frequency of cells in portion (i) of Figure 4. Habitat suitability for *C. tagal* and *R. stylosa*  
440 dominance changed little under conditions of sea level rise (Figure 4, e, f), as the greatest  
441 frequency of cells occur along the 1:1 line in Figure 3. In contrast, *S. alba* dominance

442 suitability increased slightly after a 1 m of sea level rise (Figure 4 d), as indicated by the high  
443 frequency of cells in portion (iv) of the figure.

#### 444 ***Invasion and intensity of competition***

445 There was little overlap in area suitable for more than one species (for either occupation or  
446 dominance), with most combinations of species showing less than 5% overlap (Area of  
447 overlap as a % of forested area, Supplementary Material Table SM1). The greatest overlap  
448 was forecast between the species distribution for *R. stylosa* and *C. tagal* (12.3 and 11.3% at  
449 0.5 and 1 m sea level rise, respectively).

450 Although there was little overlap in forecasts of future suitable habitat between the species,  
451 this does not reflect the intensity of competition between the species currently occupying a  
452 location and a species invading that location as it becomes suitable for colonization after sea  
453 level rise. Thus, some of the habitat that becomes suitable for colonization by *S. alba* (the  
454 low-intertidal species) under sea level rise occurs within the current distribution of *R. stylosa*  
455 (the mid-intertidal species). That may not appear as a zone of competition in the overlap  
456 statistics if such a site was predicted to be unsuitable for *R. stylosa* under the future sea level  
457 scenario. Likewise, some of the habitat suitable for *R. stylosa* colonisation after a 1 m sea  
458 level rise is currently occupied by *C. tagal* (the high-intertidal species). Competition between  
459 the occurrence of *S. alba* and *R. stylosa* is expected to be low, as a high frequency of  
460 locations highly suitable for *R. stylosa* at current sea level, have low probabilities of *S. alba*  
461 occurrence after a 1 m rise in sea level (Supplementary Material Figure SM4). A similar  
462 pattern was found for future competition between the *S. alba* and *R. stylosa*.

463

#### 464 **Discussion**

465 Extensive future shifts in the distribution of species occurrence and dominance within the  
466 mangrove forest of Darwin Harbor were forecast in this study, as indicated by the metrics of  
467 instability and changes in the area occupied with increments of sea level rise. Change in the  
468 area forecast to be suitable under the scenarios of sea level rise was similar for species  
469 occurrence and for dominance, when considered on a taxon by taxon basis. For example, the  
470 area suitable for the occurrence of *S. alba* expands, as does the area suitable for dominance  
471 by *S. alba*. However, the metrics of instability indicate that the spatial distribution of habitat  
472 suitable for species dominance is likely to change more than a species' distribution. The  
473 landward edge of the *S. alba* and *R. stylosa* distribution is forecast to shift inland, in  
474 concordance with empirical studies reporting increases in mangrove extent along the  
475 landward margins in the Pacific region, Australia and the USA (Lucas *et al.*, 2002; Manson *et*  
476 *al.*, 2003; Gilman *et al.*, 2007; Everitt *et al.*, 2010). However, the current distribution in  
477 Darwin Harbor of *C. tagal*, the most landward of the mangrove species, is adjacent to a steep  
478 rise of approximately 1 m that separates the tidally influenced mangrove forest from coastal  
479 vine thicket, a terrestrial forest type (Brocklehurst & Edmeades, 1996). This steep rise  
480 restricts the expansion of *C. tagal* further inland under sea level rises of 0.5 and 1 m,  
481 assuming no physical change in this barrier due to wave action or changes in sedimentation  
482 patterns. It is possible that rising sea levels will erode these coastal geomorphological  
483 features (Zhang *et al.*, 2004); however, this is likely to occur over relatively long time  
484 periods, creating a bottleneck in suitable habitat for *C. tagal*. Detailed analyses of processes  
485 contributing to movement of sediments and change to geomorphology is beyond the scope of  
486 the present study but should be considered in future studies.

487 ***Changes in spatial patterning and differences in model accuracy***

488 Models of dominance outperformed models of species occurrence, as measured by the AUC  
489 scores and percent of deviance explained, suggesting that dominance within mangrove forests  
490 can be more accurately modeled than species occurrence (Table 1). In the way that we have  
491 defined dominance, distribution models for dominance are likely to indicate areas of core  
492 suitability where a species has a strong competitive advantage over other species. The models  
493 of dominance implemented here tend to ignore areas of marginal suitability which are more  
494 likely to be ‘sink’ habitat (*sensu* Pulliam 1988). It is not surprising, therefore, that dominance  
495 models do slightly better than models of species occurrence which seek to explain patterns of  
496 occurrence across a full range of suitability. For this reason, we expect our main finding, that  
497 models of dominance outperform models of occurrence, will often apply in other ecosystems.  
498 By reducing the set of positive cases to locations in which a species is dominant, rather than  
499 simply occurring, dominance modelling may generally be more reliable than occurrence  
500 modelling; though this conjecture requires additional testing. This in no way detracts from the  
501 value of SDMs based on occurrence data, because they are produced for a different purpose.  
502 Nonetheless, we maintain that modelling and predicting dominance patterns provides a better  
503 indication of a species’ future competitive advantage, information that complements  
504 predictions of occurrence. Modelling changes in dominance in response to sea level rise,  
505 climate change or other environmental changes enables the potential changes in species  
506 occurrence and dominance to be contrasted. The method of modelling dominance that we  
507 present here provides an additional approach to be considered alongside modelled species  
508 occurrence, community distribution, species dissimilarity and species richness (Lobo *et al.*,  
509 2002; Ferrier & Guisan 2006; Algar *et al.*, 2009; Rojas-Soto *et al.*, 2012), in order to provide  
510 a more complete picture of the magnitude and spatial patterning of climate change and other  
511 impacts. The dominance modelling approach taken here can be applied within any system

512 dominated by a few taxa, for example, coral reefs, (Done, 1982; Aronson *et al.*, 2002) and  
513 boreal forests (McCarthy 2001, see also Chapin *et al.*, 2004).

514 While our study was conducted at a regional scale with a fine grain, appropriate for  
515 forecasting impacts of sea level rise, the underlying mechanisms responsible for patterns of  
516 dominance and species occurrence are general. For example, while different mangrove tree  
517 species occur in different locations across the world, a characteristic pattern of dominance,  
518 referred to as zonation, has been widely recorded (Snedaker, 1982; Smith, 1992). For  
519 mangrove forests, species distribution and dominance across the inter-tidal zone are strongly  
520 influenced by a steep gradient in hydroperiod (Crase *et al.*, 2013). For other plant  
521 communities we expect the processes leading to spatial patterns in species occurrence,  
522 abundance and dominance to be similar.

### 523 *Comparison of the seedling establishment scenarios*

524 Forecasting studies implement two simplifying assumptions about seedling or propagule  
525 dispersal scenarios: restricted (null) or unrestricted (universal), (Araújo *et al.*, 2004; Thomas  
526 *et al.*, 2004), or select one of the two assumptions (Araújo *et al.*, 2011; Rapacciuolo *et al.*,  
527 2012; Rojas-Soto *et al.*, 2012). There have been calls to incorporate more realistic dispersal  
528 distances into forecasts, however it is unclear whether this extra complexity translates to  
529 more accurate forecasts given the additional uncertainty it introduces. When Urban *et al.*  
530 (2012) incorporated more realistic dispersal limitations into forecasts, they found that species  
531 with the greatest dispersal distance tracked climate change and outcompeted species with low  
532 dispersal ability. In addition, Fordham *et al.* (2012) reported that the trailing and leading  
533 edges of range shifts were most sensitive to assumptions about dispersal dynamics and  
534 habitat patch structure, which in many cases are not well understood and are therefore  
535 difficult to accurately parameterize. Incorporating dispersal dynamics was reported to

536 improve the accuracy of forecasts using simulated data (Pagel & Schurr, 2012) and for  
537 modelling the distribution of 21 Alpine plant species (Boulangeat *et al.*, 2012). Although in  
538 contrast, Engler *et al.*, (2009) reported little difference between forecasts of species'  
539 distribution for unrestricted dispersal and more realistic dispersal scenarios. These studies  
540 indicate that some species are likely to be very sensitive to assumptions with respect to  
541 dispersal scenarios.

542 In the present study, we have assumed that the propagules of all three focal species can  
543 disperse to all locations suitable for colonization, but that seedling establishment was either  
544 unrestricted or restricted. Unrestricted dispersal is realistic for the mangrove taxa we studied  
545 given the scale of the study area (a single harbor) and the extensive distribution of the taxa  
546 throughout South-East Asia and the Pacific region (Ellison *et al.*, 1999; Spalding *et al.*,  
547 2010). However, realistic assumptions about mangrove species' seedling establishment are  
548 more difficult to identify. We bounded the problem by implementing two highly contrasting  
549 scenarios (unrestricted or restricted seedling establishment), and report that the forecasts of  
550 suitable habitat differed greatly between these two scenarios. This indicates a key research  
551 priority to better understand competition and establishment dynamics in mangroves. Over  
552 the short to medium term (one or two generations) the restricted-establishment scenario is the  
553 more realistic of the two scenarios for mangrove forests, as empirical evidence shows that the  
554 establishment of mangrove seedlings in a closed forest canopy is very limited (Clarke, 2004;  
555 López-Hoffman *et al.*, 2007). Areas that become suitable under a higher sea level cannot be  
556 colonized by seedlings due to asymmetric competition with the already established adult  
557 trees. In the longer term (three or more generations), however, the unrestricted establishment  
558 scenario is more realistic, as canopy gaps are produced by natural tree mortality and  
559 disturbance mechanisms such as cyclones and lightning strikes. These gaps provide

560 opportunities for colonization by mangrove seedlings (Smith III *et al.*, 1994), and enable all  
561 areas with a suitable hydroperiod to eventually be colonized. However, depending on the  
562 realized rate of sea-level rise, bottle-necks due to limited recruitment under canopies may  
563 prove to be a serious threat to the viability of some species in the region and the ecosystem  
564 services they provide. Additional studies are required to provide a better understanding of  
565 how these competitive dynamics may play out.

### 566 ***Intensity of competitive interactions***

567 Each species (or dominant) occupies a specific, delineated, segment of the gradients  
568 influencing distribution, as indicated by the small overlap in forecasts of spatial extent  
569 (Supplementary Material Table SM1). However, as sea levels rise, locations already  
570 occupied by *C. tagal*, the landward species, become more suitable for *R. stylosa*, the mid-  
571 intertidal species. Areas currently suitable for *R. stylosa*, will, likewise, become more suitable  
572 for *S. alba*, the seaward species. To summarize, *S. alba* will invade *R. stylosa*, which invades  
573 *C. tagal*, as the hydroperiod increases under sea level rise. Species invasions lead to increased  
574 interspecific competition. More intense competitive interactions are forecast between *S. alba*  
575 (invader) and *R. stylosa* (occupier), than between *R. stylosa* (invader) and *C. tagal* (occupier).  
576 Future experimental studies within the mangrove forests experiencing high rates of sea level  
577 rise, such as Darwin harbor and other areas in South-East Asia (Church *et al.*, 2004; Church  
578 & White, 2011), may improve understanding of processes that govern rates of replacement of  
579 one species with another and the intensity of competition between the occupying species and  
580 the invading species. Though given the predicted rates of sea level rise there is little time for  
581 detailed, in-situ empirical or experimental studies on competitive dynamics between  
582 mangrove species. Consequently, seeking conservation adaptation options that are robust to  
583 uncertainties about competitive dynamics should be the highest priority in the short term

584 (Wintle *et al.* 2011; Mills *et al.* 2014). An important short-term strategy is to seek climate  
585 adaptation options that provide tolerable outcomes under the widest range of possible future  
586 environmental conditions and ecosystem responses.

### 587 ***Modelling assumptions and alternative modelling approaches***

588 For the purposes of modeling the distribution of dominance, we consider dominance to be a  
589 special case of site occupancy, whereby the species not only occurs at a site but thrives and  
590 out-competes other species such that it becomes the dominant species, according to the  
591 particular definition of dominance used. By modeling dominance in the way that we model  
592 occurrence (using SDM approaches), we assume the theoretical link between niche theory  
593 and distribution modeling also holds when dominance is the ~~in~~dependent variable, and that  
594 the statistical properties of dominance, as an ~~in~~dependent variable, satisfy all of the regular  
595 assumptions required of the modeling method used. Modelling dominance is theoretically  
596 coherent, as we interpret the dominance niche as simply a narrower version of the  
597 Hutchinsonian realized niche modeled in SDMs, and is, therefore amenable to modeling in  
598 the same way. To the extent that it is reasonable to model a categorical (dominant or not)  
599 version of a continuous measure (proportion of the total basal area), the method implemented  
600 here satisfies all of the statistical assumptions required for the use of BRT (i.e. independent  
601 and identically distributed (IID) residuals, normality in the transformed dependent variable,  
602 and correct measurement of variables). As is the case for many variables of interest to  
603 ecologists and biologists, there remains much to explore about the properties and best ways to  
604 model dominance as a dependent variable in regression. However, our approach to modeling  
605 dominance provides valuable inference and insights into the way species and communities  
606 will change under changing environmental conditions.

607 Although excellent model performance was achieved with the modelling approach  
608 implemented here, model realism could be improved by incorporating demographic  
609 information such as rates of dispersal, establishment, mortality and interspecific competitive  
610 interactions. These demographic processes could be incorporated within an SDM-mechanistic  
611 hybrid approach (Kearney & Porter, 2009) or by developing spatially explicit mechanistic  
612 approaches, such as cellular automata or individual-based modelling (Clark & Bullock,  
613 2007; Berger *et al.*, 2008; Potvin & Dutilleul, 2009). Other insights into this ecosystem  
614 might be produced by models derived from assembly rules for communities, for example  
615 linked alpha and beta diversity models (Mokany *et al.*, 2011), and from joint species  
616 distribution models or multinomial approaches (eg McInery & Purves, 2011; Pollock *et al.*,  
617 2014). It while is plausible that important ecological processes could occur at thresholds that  
618 differ from the one we selected (50% basal area), and an exploration of this would require  
619 data on, not just the dominant species, but the full complement of species present in the  
620 ecosystem. In addition, modelling a continuous form of dominance, perhaps using abundance  
621 or cover measures, could be achieved with currently available statistical modelling methods,  
622 though the availability of such data are rare. These more complex approaches could be used  
623 to test the conclusions drawn from species distribution models, and help understand the  
624 processes underpinning shifts in distribution, in particular, the lag between locations  
625 becoming suitable and colonization of those suitable areas. A challenge lies in the collection  
626 and collation of empirical data to parameterize such models.

## 627 ***Conclusions***

628 Models of species dominance are an additional tool providing a more complete picture of the  
629 impacts of climate change on community composition and structure, without the  
630 implementation of complex nor data hungry modelling approaches. Overlap between areas

631 forecast to be suitable for dominance can indicate locations where competitive interactions  
632 intensify and could be utilized to select field monitoring sites. While, in this study, the total  
633 area of change forecast was similar for species occurrence and dominance, the spatial  
634 patterning differed. By focusing on the locations in which a species is dominant, rather than  
635 simply occurring, dominance modelling may be generally more reliable than occurrence  
636 modelling. In addition, modelling and predicting dominance patterns provides a better  
637 indication of future competitive advantage, which differs from and is complementary to  
638 predictions of occurrence. Forecasts of changes in habitat suitability for dominance under an  
639 altered climate could offer critical insight into impacts within other ecosystems and lead to  
640 more robust management and resource allocation decisions.

641

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## 649 **Biosketch**

650 Beth Crase has research interests in spatial ecology with a focus on tropical ecosystems. Her  
651 current research focuses on forecasting impacts of sea level rise and climate change on  
652 species' distributions; estimations of species loss from habitat fragmentation and developing  
653 new tools to improve implementation of statistical models used in forecasting studies.

654

655 **Author contributions:** B.C., A.L., B.W. and P.V. conceived the ideas; B.C. analyzed the  
656 data; and B.C. lead the writing, with all authors contributing.

657

658

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940 Zimmermann NE, Edwards TC, Graham CH, Pearman PB, Svenning JC (2010) New trends  
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943

944 Table 1. Model performance metrics, ten-fold cross-validated Area Under Curve (AUC) and  
 945 percent of deviance explained (DE), for models of species occurrence of *Sonneratia alba*,  
 946 *Rhizophora stylosa* or *Ceriops tagal* and for the dominance of these focal taxa, in Darwin  
 947 Harbor, northern Australia. s.e. indicates the standard error of the mean. Relative importance  
 948 (RI) of variables was derived from the proportion of times each variable was selected by the  
 949 model fitting algorithm, scaled out of 100.

Model	Model performance metrics:		RI for explanatory variables:		
	AUC $\pm$ s.e.	DE (%) $\pm$ s.e.	Hydro-period	Slope	Water salinity
<i>Sonneratia alba</i>					
Species	0.95 $\pm$ 0.03	62.26 $\pm$ 0.07	79.3	15.3	5.4
Dominant	0.98 $\pm$ 0.01	70.19 $\pm$ 0.06	88.1	6.1	5.9
<i>Rhizophora stylosa</i>					
Species	0.85 $\pm$ 0.03	28.21 $\pm$ 0.06	78.6	14.9	6.5
Dominant	0.91 $\pm$ 0.03	43.80 $\pm$ 0.08	78.0	8.0	14.0
<i>Ceriops tagal</i>					
Species	0.82 $\pm$ 0.03	22.58 $\pm$ 0.05	69.2	17.4	13.4
Dominant	0.86 $\pm$ 0.03	28.81 $\pm$ 0.09	68.5	15.7	15.8

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952

953 Table 2. Percent of the area occupied at current sea levels that is forecast to be unstable at  
 954 future sea levels ( $E_{instability}$  as a percent of  $E_{occupied}$ ), followed in parenthesis by  $E_{instability}$ , for  
 955 *Sonneratia alba*, *Rhizophora stylosa* and *Ceriops tagal*, species and dominants, in Darwin  
 956 Harbor, northern Australia. The metric of instability includes areas of both contraction and  
 957 expansion into new areas under future sea levels, therefore, the values as a proportion of  
 958 current area can exceed 100%.

	<b>Sea level rise (m)</b>	<i>S. alba</i>	<i>R. stylosa</i>	<i>C. tagal</i>
Species	0.50	25.7 (23095)	70.0 (109563)	41.5 (79098)
	1	55.1 (10761)	119.8 (63994)	66.8 (49111)
Dominance	0.50	41.0 (29025)	83.6 (150963)	65.4 (97349)
	1	83.8 (14212)	139.0 (90798)	96.0 (66305)

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960

961 Figure 1. Partial plots showing the probability of occurrence (left column) or dominance  
962 (right column) of *Sonneratia alba* (a, b), *Rhizophora stylosa* (c, d) and *Ceriops tagal* (e, f)  
963 across a gradient in hydroperiod, for Darwin Harbor, northern Australia, with mean (black  
964 line) and 95% confidence (grey lines) for 1000 bootstrapped samples and Relative variable  
965 Importance (R.I.) shown in top right corner of each panel.

966

967 Figure 2. The percentage change under a no establishment scenario (left panels a, c, e) and a  
968 complete establishment scenario (right panels b, d, f), forecast for sea level rise of 0.5 and 1  
969 m, for *Sonneratia alba*, *Rhizophora stylosa* and *Ceriops tagal* species occurrence and for  
970 dominance by these taxa, for Darwin Harbor, northern Australia. The expected number of  
971 cells occupied ( $E_{occupied}$ ) at higher sea levels expressed as a percent of the  $E_{occupied}$  at current  
972 sea level, following equation 1. Vertical dashed line indicates zero change.

973

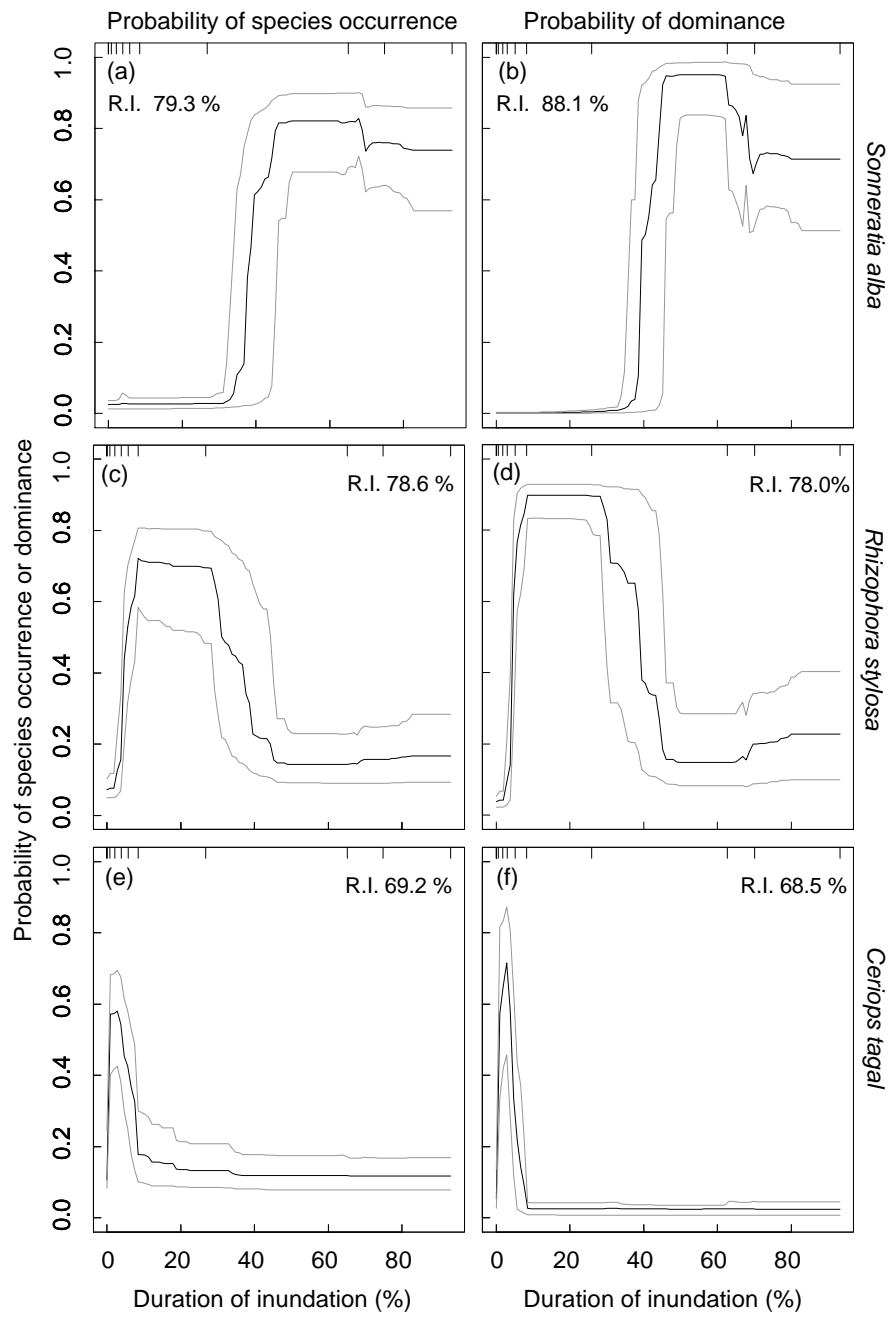
974 Figure 3 Mapped probability of (a) species occurrence and (b) species dominance, for  
975 *Sonneratia alba*, *Rhizophora stylosa* and *Ceriops tagal*, for Wood's Inlet (8x8 km area),  
976 Darwin Harbor, northern Australia, at current sea level and forecasts after sea level rises  
977 (s.l.r.) of 0.5 and 1 m.

978

979 Figure 4 Probability of occurrence of *Sonneratia alba*, *Rhizophora stylosa* and *Ceriops tagal*  
980 species occurrence (upper row a-c) and dominance (lower row d-f), at current sea level (y-  
981 axis) plotted against the probability of occurrence after a 1 m sea level rise (s.l.r, x-axis), as a  
982 2-dimensional histogram, for Darwin Harbor, northern Australia. Each axis is divided into 50  
983 equal bins and point color indicates the frequency of cells classed into each bin. Lower panel

984 repeats panel (a) shows a solid 1:1 line and two dashed lines as guides for interpretation. Sites  
985 falling on the solid line have the same habitat suitability (i.e. probability of occurrence) at  
986 current sea level and after a 1 m rise in sea level (thus  $E_{instability} = 0$ ).  $E_{instability}$  increases with  
987 more points farther away from the solid 1:1 line, to reach maxima at the top left and bottom  
988 right of the graph. (i) habitat suitability is high at current sea level, and lower after a 1 m s.l.r.  
989 indicating a contraction in suitable area; (ii) indicates the frequency of cells with a high  
990 habitat suitability at current sea level and an even higher habitat suitability at 1 m s.l.r., hence  
991 an expansion in suitable area; (iii) low habitat suitability at current sea levels, which further  
992 declines after 1 m s.l.r.; and (iv) low habitat suitability at current sea level, which increases  
993 after a 1 m s.l.r.. The values plotted in the lower panel are for the habitat suitability for the  
994 species, *Sonneratia alba*.

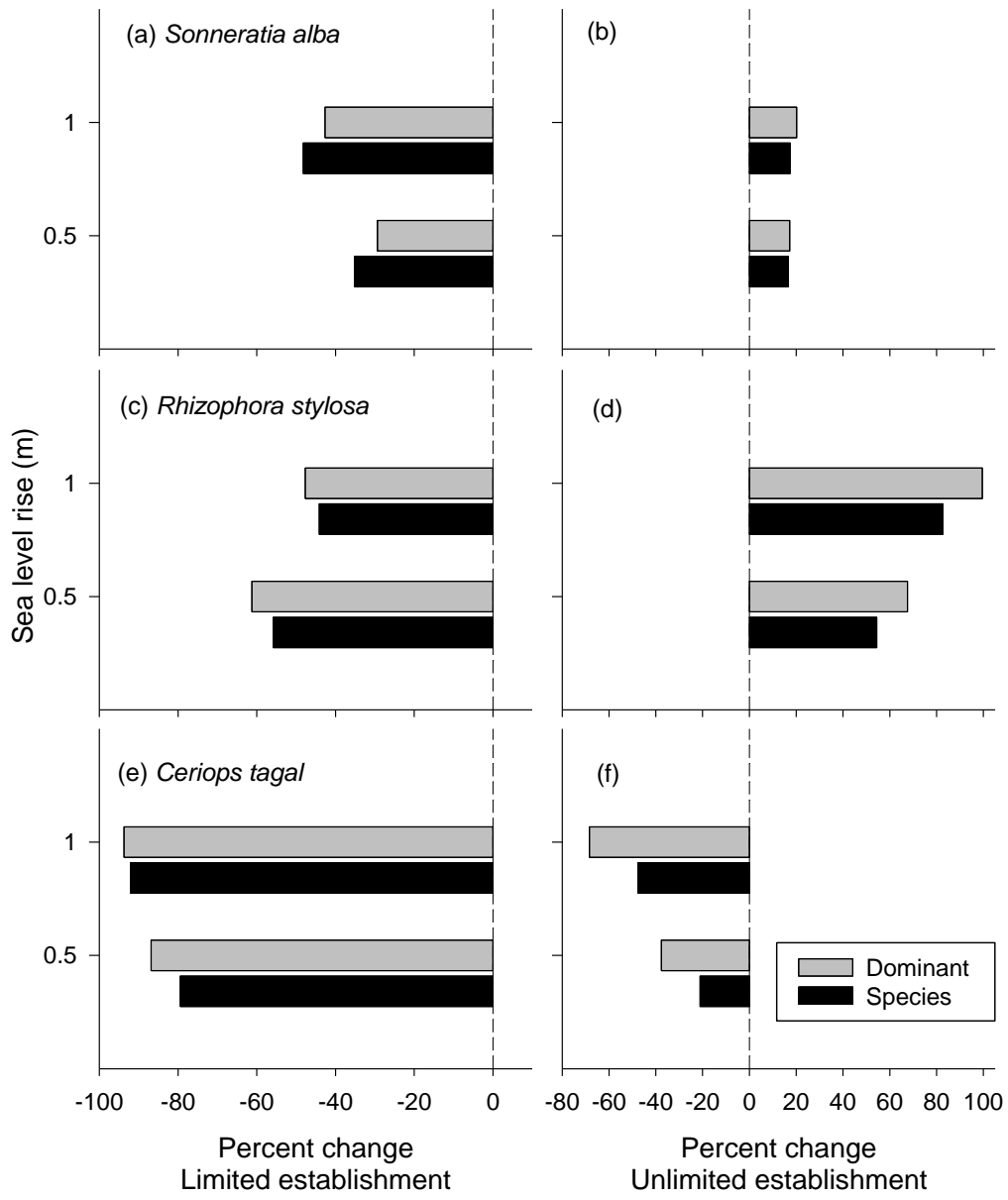
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999 Figure 1.



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1001 Figure 2.

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