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

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Abstract

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

Introduction

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

Forecasts of future distributions of species are critical for informing management and adaptation responses to ensure optimal outcomes for conservation and provision of ecosystem services (Hannah *et al.*, 2007; Guisan *et al.*, 2013). A forecasting tool central to providing such predictions of species occurrence is species distribution modelling (SDM), also called niche modelling (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009; Zimmermann *et al.*, 2010). These are statistical modelling techniques that relate empirical observations of the current distribution of species to combinations of climatic, environmental and biotic explanatory variables (Austin, 2002). The vast majority of forecasting (and hindcasting) studies focus on modelling the geographic distribution of the occurrence of individual species (for example Bakkenes *et al.*, 2002; Peterson *et al.*, 2002; Thomas *et al.*, 2004; Guisan *et al.*, 2007; de Oliveira *et al.*, 2012), and forecasting plant community or vegetation type has also received some attention (Hilbert *et al.*, 2001; Ferrier & Guisan, 2006; Mokany & Ferrier 2011; Rojas-Soto *et al.*, 2012). However, dominant species influence the occurrence and abundance of other species within the community (Whittaker, 1965). Therefore, understanding and forecasting changes in the spatial patterns of dominance may be critically important as changes in the distribution of dominant species can cause a cascade of effects on the other species present in the ecosystem. Despite this, forecasting changes in the spatial patterning of dominance has rarely been explored using SDMs (Meier *et al.*, 2011).

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

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

Change in patterning of dominance in response to climate change, sea level rise or alteration of management activities has been explored in few instances. For example Meier *et al.,* (2011) evaluated patterns of distribution across climate gradients using co-occurrence patterns of a dominant species and three competing species. They forecast the current and future distribution of species under climate change and concluded that while the abundance of competitors strongly influenced abundance of the focal species under favorable environmental conditions, this link was weaker in unfavorable environments. Dullinger *et al.,* 2005, investigated interactions among three tree species: pine, larch and spruce and found that pine affected spruce and larch differently. Their results suggest that spruce would be favored at the expense of larch during expansion in suitable habitat of pine under climate change. Although SDMs were implemented to investigate interactions among species, no spatial predictions were produced. In addition, Pellissier *et al.*, 2010 studied a dominant shrub species (*Empetrum nigrum* ssp. *Hermaphroditum*, Ericaceae) and its influence on a range of non-dominant species. They concluded that including competitors or facilitators in SDMs improves model fit and therefore predictive power. A similar conclusion was reached by le Roux *et al.*, (2014) who incorporated data from three dominant species into community-level models as a surrogate for biotic interactions among species. They report that including dominant species in models improved the realism of modelled community composition and species richness. However, these studies did not forecast spatially explicit changes in the patterning of dominance of species under environmental change. So while there have been some studies investigating patterns of dominance in plant communities, spatial forecasts of changes in dominance under environmental change are rare and there is a need to explore how predicted changes in dominance differ from predicted changes in species occurrence using SDM techniques and other modelling approaches, such as community assembly models.

Mangrove forests may provide an ideal study system within which to investigate spatial patterns of dominance as they are frequently characterized by plant communities dominated by a single species (Smith, 1992; Snedaker, 1982). These mangrove plant communities often form bands parallel to shorelines or river banks, influenced by a gradient in the duration of inundation by water (Crase *et al.*, 2013; Krauss *et al.*, 2006; Watson, 1928). While different mangrove plant species can be distributed throughout the mangrove forest, each community is usually dominated by a single species, and this dominance can extend to the development of monospecific stands (Smith, 1992; Snedaker, 1982). As mangroves occur within the intertidal zone they are highly sensitive to any change in sea level, therefore future climate change is anticipated to strongly impact mangrove forests (Duke *et al.*, 2007, Gilman *et al.*, 2008, Nicholls *et al.*, 2007). Empirical observations have shown that the distribution of mangrove forests across the intertidal zone has shifted in many locations over the past few decades (Ellison, 1993; Lucas *et al.*, 2002; Gilman *et al.*, 2007; Everitt *et al.*, 2010; López-Medellin *et al.*, 2011). However, few forecasts exist predicting mangrove forest shifts, or changes in the spatial patterning of mangrove species occurrence or communities (Doyle *et al.*, 2003; Record *et al.*, 2013, Quisthoudt *et al.* 2013).

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

The aims of this paper are to (i) compare forecasts of species distribution in response to sea level rise using both occurrence and dominance as a dependent variable; and (ii) investigate the potential for intensification of interspecific competition under sea level rise scenarios. We developed Species distribution models (SDMs) with binary (presence/absence, dominant/not-dominant) data collected within an extensive mangrove forest (20,000 ha) in northern Australia. The SDMs are then used to forecast species occurrence and dominance at high spatial resolution (25x25m pixel size) under future sea levels 0.5 and 1 m higher than the current sea level.

Methods

Focal species and study area

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

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

During the Holocene (6500-7000 yr bp) extensive mangrove forests developed across northern Australia in response to changes in sea-level and sediment deposition (Woodroffe e*t al.*, 1985). Darwin harbor is a ria coast formed by post-glacial flooding of a dissected plateau, with two major rivers empty into the harbor (Semeniuk 1985). The study area in in a macro-tidal region with a tidal amplitude up to 8 m, and mean spring and neap tides of approximately 6 and 3 m, respectively (Williams *et al.*, 2006). Approximately 129,000 people live in the township of Darwin on the north eastern portion of the harbor (Supplementary Material Figure SM1). The remaining coastline of the Northern Territory (NT), some 13,500 km in length, has very low anthropogenic impacts with the five largest towns being Nhulunbuy (population 3933), Galiwin’ku (2124), Maningrida (2068), Wadeye (1627) and Milingimbi (1081). Australia’s population density is 3.07 km^2 whereas the Northern Territory is 0.4 per km^2 (Australian Bureau of Statistics 2014) and the mangrove forests that occur across the NT are largely unexploited.

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

Model development

Three explanatory variables: slope, water salinity, and hydroperiod, previously identified as the key influences on the distribution of mangrove species dominance in Darwin Harbor (Crase *et al.*, 2012), were used to develop the distributional models for three focal species' occurrence and dominance. All variables were gridded at a resolution of 25x25 m, resulting in approximately 320,000 grid cells which is an extent and resolution appropriate for studies of sea level rise impacts in coastal areas. In contrast, studies forecasting distributional change in response to climate variables must be conducted across larger geographic extents but also utilize larger grid cell sizes. For example, grid cell sizes of between 4x4 km and 0.5x0.5 degrees have been applied in climate impact studies resulting in forecasts across a few hundred to several hundred thousand grid cells (Bakkenes e*t al.*, 2002; Peterson *et al.*, 2002; de Oliveira *et al.*, 2012). It is important to note that the present sea level rise study has a similar intensity to studies of climate change impacts, and we reiterate that the area of the study must match the environmental driver(s) as should the grain. Furthermore, the number of species must match with the research question and the ecosystem studied. As we focused on a scale appropriate for the main drivers within mangrove forests (ie a single harbor), we did not include any climate variables. Across 20,000 ha of our study region there is no difference in climate variables such as rainfall or temperature.

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

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

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

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

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

Performance metrics (AUC and percent of deviance reduction) were assessed with 10-fold cross-validation. The data were randomly partitioned into ten subsets, the models fitted to nine of the ten subsets (training data) and accuracy determined by comparing model predictions to the tenth subset (testing data) (Stone, 1974). This process was repeated until each model had been fitted and tested ten times. As model predictions were tested against the held-out portion of data during the cross validation procedure (for both AUC and deviance explained) and not on the data used for fitting the model, the assessment of model performance is more realistic than testing on the data used to fit the models.

Forecasting distributional change in response to sea level rise

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

Scenarios of seedling establishment

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

Calculations of occurrence, overlap and instability

The models were used to estimate a probability of species occurrence or dominance in every cell of the study area, at current and future sea levels. Although a threshold is usually selected to convert probabilities to 0 (absence) or 1 (presence), the threshold selected can influence calculations of occurrence (Liu *et al.*, 2005) and it is generally better to avoid arbitrary categorization of SDM predictions because it leads to unnecessary information loss (Calabrese *et al.*, 2014; Lawson *et al.*, 2014). We instead developed and applied threshold-independent methods to estimate the number of cells occupied, the overlap between species, and a metric of stability (equations 1, 2 and 3).

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

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

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

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

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

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

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

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

where *n*, *i* and *m* are as for Equation 1. The instability metric indicates how extensively species retreat from currently occupied areas, and/or invade newly suitable areas. Similarly, in the case of dominance, the metric indicates how much dominance changes (positively and negatively) across the study region. It literally amounts to the expected number of cells (or hectares) that will switch state from occupied to unoccupied, or unoccupied to occupied based on the model predictions. The instability metric does not distinguish between range expansion, range contraction, or range shift; it simply highlights whether or not a species range is expected to change substantially or little. Species forecast to have large range contractions can be easily identified as potentially at risk under climate change. However, species with a forecast of range *expansion* may also be at risk of decline under changed environmental conditions because there is no guarantee that they will colonize areas forecast to be suitable. The $E_{instability}$ metric allows us to explore a different quality of range shift, in addition to a simple quantification of contraction and enables the identification of species potentially at risk despite a predicted expansion into newly suitable areas.

Results

Model performance, variable importance and instability

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

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

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

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

Forecasts of decline and expansion under two establishment scenarios

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

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

Change in probability of occurrence with sea level rise

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

Invasion and intensity of competition

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

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

Discussion

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

Changes in spatial patterning and differences in model accuracy

Models of dominance outperformed models of species occurrence, as measured by the AUC scores and percent of deviance explained, suggesting that dominance within mangrove forests can be more accurately modeled than species occurrence (Table 1). In the way that we have defined dominance, distribution models for dominance are likely to indicate areas of core suitability where a species has a strong competitive advantage over other species. The models of dominance implemented here tend to ignore areas of marginal suitability which are more likely to be 'sink' habitat (*sensu* Pulliam 1988). It is not surprising, therefore, that dominance models do slightly better than models of species occurrence which seek to explain patterns of occurrence across a full range of suitability. For this reason, we expect our main finding, that models of dominance outperform models of occurrence, will often apply in other ecosystems. By reducing the set of positive cases to locations in which a species is dominant, rather than simply occurring, dominance modelling may generally be more reliable than occurrence modelling; though this conjecture requires additional testing. This in no way detracts from the value of SDMs based on occurrence data, because they are produced for a different purpose. Nonetheless, we maintain that modelling and predicting dominance patterns provides a better indication of a species' future competitive advantage, information that complements predictions of occurrence. Modelling changes in dominance in response to sea level rise, climate change or other environmental changes enables the potential changes in species occurrence and dominance to be contrasted. The method of modelling dominance that we present here provides an additional approach to be considered alongside modelled species occurrence, community distribution, species dissimilarity and species richness (Lobo *et al.*, 2002; Ferrier & Guisan 2006; Algar *et al.*, 2009; Rojas-Soto *et al.*, 2012), in order to provide a more complete picture of the magnitude and spatial patterning of climate change and other impacts. The dominance modelling approach taken here can be applied within any system dominated by a few taxa, for example, coral reefs, (Done, 1982; Aronson *et al.*, 2002) and boreal forests (McCarthy 2001, see also Chapin *et al.*, 2004).

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

Comparison of the seedling establishment scenarios

Forecasting studies implement two simplifying assumptions about seedling or propagule dispersal scenarios: restricted (null) or unrestricted (universal), (Araújo *et al.*, 2004; Thomas *et al.*, 2004), or select one of the two assumptions (Araújo *et al.*, 2011; Rapacciuolo *et al.*, 2012; Rojas-Soto *et al.*, 2012). There have been calls to incorporate more realistic dispersal distances into forecasts, however it is unclear whether this extra complexity translates to more accurate forecasts given the additional uncertainty it introduces. When Urban *et al.* (2012) incorporated more realistic dispersal limitations into forecasts, they found that species with the greatest dispersal distance tracked climate change and outcompeted species with low dispersal ability. In addition, Fordham *et al.* (2012) reported that the trailing and leading edges of range shifts were most sensitive to assumptions about dispersal dynamics and habitat patch structure, which in many cases are not well understood and are therefore difficult to accurately parameterize. Incorporating dispersal dynamics was reported to improve the accuracy of forecasts using simulated data (Pagel & Schurr, 2012) and for modelling the distribution of 21 Alpine plant species (Boulangeat *et al.*, 2012). Although in contrast, Engler *et al.*, (2009) reported little difference between forecasts of species' distribution for unrestricted dispersal and more realistic dispersal scenarios. These studies indicate that some species are likely to be very sensitive to assumptions with respect to dispersal scenarios.

In the present study, we have assumed that the propagules of all three focal species can disperse to all locations suitable for colonization, but that seedling establishment was either unrestricted or restricted. Unrestricted dispersal is realistic for the mangrove taxa we studied given the scale of the study area (a single harbor) and the extensive distribution of the taxa throughout South-East Asia and the Pacific region (Ellison *et al.*, 1999; Spalding *et al.*, 2010). However, realistic assumptions about mangrove species' seedling establishment are more difficult to identify. We bounded the problem by implementing two highly contrasting scenarios (unrestricted or restricted seedling establishment), and report that the forecasts of suitable habitat differed greatly between these two scenarios. This indicates a key research priority to better understand competition and establishment dynamics in mangroves. Over the short to medium term (one or two generations) the restricted-establishment scenario is the more realistic of the two scenarios for mangrove forests, as empirical evidence shows that the establishment of mangrove seedlings in a closed forest canopy is very limited (Clarke, 2004; López-Hoffman *et al.*, 2007). Areas that become suitable under a higher sea level cannot be colonized by seedlings due to asymmetric competition with the already established adult trees. In the longer term (three or more generations), however, the unrestricted establishment scenario is more realistic, as canopy gaps are produced by natural tree mortality and disturbance mechanisms such as cyclones and lightning strikes. These gaps provide opportunities for colonization by mangrove seedlings (Smith III *et al.*, 1994), and enable all areas with a suitable hydroperiod to eventually be colonized. However, depending on the realized rate of sea-level rise, bottle-necks due to limited recruitment under canopies may prove to be a serious threat to the viability of some species in the region and the ecosystem services they provide. Additional studies are required to provide a better understanding of how these competitive dynamics may play out.

Intensity of competitive interactions

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

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

Modelling assumptions and alternative modelling approaches

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

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

Conclusions

Models of species dominance are an additional tool providing a more complete picture of the impacts of climate change on community composition and structure, without the implementation of complex nor data hungry modelling approaches. Overlap between areas forecast to be suitable for dominance can indicate locations where competitive interactions intensify and could be utilized to select field monitoring sites. While, in this study, the total area of change forecast was similar for species occurrence and dominance, the spatial patterning differed. By focusing on the locations in which a species is dominant, rather than simply occurring, dominance modelling may be generally more reliable than occurrence modelling. In addition, modelling and predicting dominance patterns provides a better indication of future competitive advantage, which differs from and is complementary to predictions of occurrence. Forecasts of changes in habitat suitability for dominance under an altered climate could offer critical insight into impacts within other ecosystems and lead to more robust management and resource allocation decisions.

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Biosketch

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

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

REFERENCES

Algar AC, Kharouba HM, Young ER, Kerr JT (2009) Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods. *Ecography*, **32**, 22-33.

Aronson RB, Macintyre IG, Precht WF, Murdoch TJT, Wapnick CM (2002) The expanding scale of species turnover events on coral reefs in Belize, *Ecological Monographs*, **72,** 233-249.

Araújo MB, Cabeza M, Thuiller W, Hannah L, Williams PH (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology*, **10**, 1618-1626.

Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. *Ecology Letters*, **14**, 484-492.

Austin MP (1990) Community theory and competition in vegetation. In Grace, J.B. & Tilman, D. (Eds.) *Perspectives on plant competition.* San Diego, CA, Academic Press, pp. 215-238.

Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, **157**, 101-118.

Australian Baseline (2011) *Australian Baseline Sea Level Monitoring Project File, Information and Instructions, IDO71014 (Northern Territory),* Australian Bureau of Meteorology. http://www.bom.gov.au/oceanography/projects/ abslmp/data /data.shtml (Accessed 19/01/2014)

Australian Bureau of Statistics (2014) http://www.abs.gov.au/websitedbs/ censushome.nsf/home /data?opendocument&navpos=200 (Accesssed 25/09/2014)

Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, **8**, 390-407.

Berger U, Rivera-Monroy VH, Doyle TW et al (2008) Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review. *Aquatic Botany* **89**: 260-274.

Boulangeat I, Gravel D, Thuiller W (2012) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, **15**, 584-593.

Brocklehurst P, Edmeades B (1996) The mangrove communities of Darwin Harbour. *Department of Lands, Planning and Environment, Resource Capability Assessment Branch*, Northern Territory Government.

Calabrese JM, Certain G, Kraan C, Dormann CF (2014). Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecology and Biogeography*, **23**, 99-112.

Chapin, FS, Callaghan TV, Bergeron Y, *et al* (2004) Global change and the boreal forest: Thresholds, shifting states or gradual change? *Ambio*, **33**, 361-365.

Chen IC, Hill JK, Ohlemuller R., Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024-1026.

Church J, White N (2011) Sea-Level Rise from the Late 19th to the Early 21st Century. *Surveys in Geophysics*, **32**, 585-602.

Church JA, White NJ, Coleman R, Lambeck K, Mitrovica JX (2004) Estimates of the regional distribution of sea level rise over the 1950-2000 period. *Journal of Climate*, **17**, 2609-2625.

Clark B, Bullock S (2007) Shedding light on plant competition: Modelling the influcnce of plant morphology on light capture (and vice versa). *Journal of Theoretical Biology*, **244**: 208-217.

Clarke PJ (2004) Effects of experimental canopy gaps on mangrove recruitment: lack of habitat partitioning may explain stand dominance. *Journal of Ecology*, **92**, 203-213.

Crase B, Liedloff AC, Wintle BA (2012) A new method for dealing with residual spatial autocorrelation in species distribution models. *Ecography*, **35**, 879-888.

Crase B, Liedloff AC, Vesk PA, Burgman M, Wintle BA (2013) Hydroperiod is the main driver of the spatial pattern of dominance in mangrove communities. *Global Ecology & Biogeography*, **22**, 806-817.

CSIRO & BOM (2012) *State of the Climate*. Canberra, Australia. http://www.csiro.au/Outcomes /Climate/Understanding/State-of-the-Climate-2012.aspx

Danielsen F, Sørensen MK, Olwig MF *et al.* (2005) The Asian tsunami: A protective role for coastal vegetation. *Science,* **310**, 643-643.

Daubenmire R (1968) *Plant communities: A textbook of plant synecology*. Harper & Row, New York.

De'ath G (2007) Boosted trees for ecological modeling and prediction. *Ecology,* **88**, 243-251.

de Oliveira G, Araújo MB, Rangel TF, Alagador D, Diniz JAF. (2012) Conserving the Brazilian semiarid (Caatinga) biome under climate change. *Biodiversity and Conservation*, **21**, 2913-2926.

Donato DC, Kauffman, JB, Murdiyarso D, Kurnianto S, Stidham M, Kanninen M (2011) Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, **4**, 293-297.

Done TJ (1982) Patterns in the distribution of coral communities across the Central Great Barrier Reef. *Coral Reefs*, **1**, 95-107.

Doyle TW, Girod GF, Books MA (2003) Modeling mangrove forest migration along the southwest coast of Florida under climate change. In: *Intergrated assessment of the climate change impacts on the Gulf Coast Region*, Eds. Ning ZH, Turner RE, Doyle TW, Abdollahi D. GRCCC and LSU Graphic Services, Baton Rouge, LA, US.

Duke NC (2006) *Australia's Mangroves,* University of Queensland Press, Brisbane, Australia.

Duke NC, Meynecke JO, Dittmann S *et al.* (2007) A world without mangroves? *Science*, **317**, 41-42.

Dullinger S, Dirnbock T, Kock R, Hochbichler E, Englisch T, Sauberer N, Grabherr G (2005) Interactions among tree-line conifers: differential effects of pine on spruce and larch. *Journal of Ecology*, **93**: 948-957.

Gilman EL, Ellison J, Duke NC, Field C (2008) Threats to mangroves from climate change and adaptation options: A review. *Aquatic Botany,* **89**, 237-250.

Guisan A, Zimmermann NE, Elith J, Graham CH, Phillips S, Peterson AT (2007) What matters for predicting the occurrences of trees: Techniques, data, or species' characteristics? *Ecological Monographs*, **77**, 615-630.

Elith J, Graham CH, Anderson RP *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography,* **29**, 129-151.

Elith J, Leathwick JR (2009) Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology & Systematics,* **40**, 677-697.

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802-813.

Ellison AM, Farnsworth EJ, Merkt RE (1999) Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography*, **8**, 95-115.

Ellison JC (1993) Mangrove retreat with rising sea-level, Bermuda. *Estuarine, Coastal and Shelf Science*, **37**, 75-87.

Engler R, Randin CF, Vittoz P, Czaka T, Beniston M, Zimmermann NE, Guisan A (2009) Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography*, **32**, 34-45.

Everitt JH, Yang C, Judd FW, Summy KR (2010) Use of archive aerial photography for monitoring black mangrove populations. *Journal of Coastal Research*, **26**, 649-653.

Ferrier S, Guisan A (2006) Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, **43**, 393-404.

Ferrier S, Watson G (1997) *An evaluation of the effectiveness of environmental surrogates and modelling techniques in predicting the distribution of biological diversity.* New South Wales Parks and Wildlife, Biodiversity Group, Environment Australia, Sydney, Australia.

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation,* **24**, 38-49.

Fordham DA, Akçakaya HR, Araújo MB *et al.* (2012) Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Global Change Biology,* **18**, 1357-1371.

Friedman JH, Hastie T, Tibshirani R (2000) Additive logistic regression: A statistical view of boosting. *The Annals of Statistics,* **28**, 337-407.

Gilman E, Ellison J, Coleman R (2007) Assessment of mangrove response to projected relative sea-level rise and recent historical reconstruction of shoreline position. *Environmental Monitoring and Assessement*, **124**, 105-130.

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling,* **135**, 147-186.

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013) Predicting species distributions for conservation decisions. *Ecology Letters*, **16**, 1424-1435.

Hannah L, Midgley G, Andelman S, Araújo M, Hughes G, Martinez-Meyer E, Pearson R, Williams P (2007) Protected area needs in a changing climate. *Frontiers in Ecology and the Environment,* **5**, 131-138.

Hilbert DW, Ostendorf B, Hopkins, MS (2001) Sensitivity of tropical forests to climate change in the humid tropics of north Queensland. *Austral Ecology*, **26**, 590-603.

IPCC (2013) Climate Change 2013: The physical science basis. *Working group contribution to the fifth assessment report of the intergovernmental panel on climate change*.

Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334-350.

Keddy PA (2001) *Competition.* (2nd edition) Kluwer, Dordrecht.

Krauss KW, Doyle TW, Twilley RR, Rivera-Monroy VH, Sullivan JK (2006) Evaluating the relative contributions of hydroperiod and soil fertility on growth of south Florida mangroves. *Hydrobiologia,* **569**, 311-324.

Lawson CR, Hodgson JA, Wilson RJ, Richards SA (2014) Prevalence, thresholds and the performance of presence-absence models. *Methods in Ecology and Evolution*, **5**, 54-64.

Levin S (1992) The problem of pattern and scale in ecology. *Ecology*, **73**:1943-1967.

Le Roux PC, Pellissier L, Wisz MS, Luoto M (2014) Incorporating dominant species as proxies for biotic interactions strengthens plant community models. *Journal of Ecology*, 102, 767-775.

Liu CR, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography,* **28**, 385-393.

Lobo JM, Lumaret JP, Jay-Robert P (2002) Modelling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. *Global Ecology & Biogeography*, **11**, 265–277.

López-Hoffman L, Ackerly DD, Anten NPR, Denoyer JL, Martinez-Ramos M (2007) Gap-dependence in mangrove life-history strategies: a consideration of the entire life cycle and patch dynamics. *Journal of Ecology*, **95**, 1222-1233.

López-Medellin X, Ezcurra E, González-Abraham C, Hak J, Santiago LS, Sickman JO (2011) Oceanographic anomalies and sea-level rise drive mangrove inland in the Pacific coast of Mexico. *Journal of Vegetation Science,* **22**, 143-151.

Lucas RM, Ellison JC, Mitchell A, Donnelly B, Finlayson M, Milne AK (2002) Use of stereo aerial photography for quantifying changes in the extent and height of mangroves in tropical Australia. *Wetlands Ecology and Management*, **10**, 161-175.

Manson FJ, Loneragan NR, Phinn SR (2003) Spatial and temporal variation in distribution of mangroves in Moreton Bay, subtropical Australia: a comparison of pattern metrics and change detection analyses based on aerial photographs. *Estuarine, Coastal and Shelf Science*, **57**, 653-666.

McCarthy, J (2001) Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environmental Reviews,* **9**, 1-59.

McInerny GJ, Purves DW (2011) Fine-scale environmental variation in species distribution modelliing: regression dilution, latent variables and neighbourly advice. *Methods in Ecology and Evolution*, **2**: 248-257.

Meier, E.S., Edwards, T.C., Kienast, F., Dobbertin, M. & Zimmermann, N.E. (2011) Competition patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of Fagus sylvatica. *Journal of Biogeography*, **38:** 371–382.

Mills M, Nicol S, Wells J A, Lahoz-Monfort JJ, *et al.* (2014) Minimizing the cost of keeping options open for conservation in a changing climate. *Conservation Biology*, **28**, 646-653.

Mokany K and Ferrier S (2011). Predicting impacts of climate change on biodiversity: a role for semi-mechanistic community-level modelling. *Diversity and Distributions* **17**, 374–80.

Mumby PJ, Edwards AJ, Arias-González JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CCC, Llewellyn G

(2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, **427**, 533-536.

Nagelkerken I, Blaber SJM, Bouillon S, Green P, Haywood M, Kirton LG, Meynecke JO, Pawlik J, Penrose HM, Sasekumar A, Somerfield PJ (2008) The habitat function of mangroves for terrestrial and marine fauna: A review. *Aquatic Botany,* **89**, 155-185.

Neldner VJ, Wilson BA, Thompson EJ, Dillewaard HA (2012) *Methodology for Survey and Maping of Regional Ecosystems and Vegetation Communities in Queensland*. Queensland Herbarium, Brisbane.

Nicholls RJ, Wong PP, V Burkett *et al.* (2007) Coastal systems and low-lying areas. IPCC 4th assessement.

Odum EP (1971) *Fundamentals of ecology*. W.B. Suanders Co., Philadelphia.

Pagel J, Schurr FM (2012) Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography,* **21**, 293-304.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.

Pellissier L, Brathen KA, Pottier J, Randin CF, Vittoz P, Dubuis A, Yoccoz NG, Alm T, Zimmermann NE, Guisan A (2010) Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography*, **33**, 1004-1014.

Peterson AT, Ortega-Huerta MA, Bartley J, Sánchez-Cordero V, Soberón J, Buddemeier RH, Stockwell DRB (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature,* **416**, 626-629.

Pollock LJ, Tingley R, Morris WK, Golding N, O'Hara RB, Parris KM, Vesk PA, McCarthy MA (2014) Understanding co-occurrence by modelling species simultaneously with a

Joint Species Distribution Model (JSDM) *Methods in Ecology and Evolution* **5**, 397-406.

Potvin C, Dutilleul P (2009) Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity. *Ecology*, **90**, 321-327.

Pulliam HR (1988) Sources, sinks and population regulation. *American Naturalist*, **132**, 652-661.

Quisthoudt K, Adams J, Rajkaran A, Dahdouh-Guebas F, Koedam N, Randin CF (2013) Disentangling the effects of global climate and regional land-use change on the current and future distribution of mangroves in South Africa. *Biodiversity and Conservation*, **22**, 1369-1390.

Rahmstorf S, Perrette M, Vermeer M (2011) Testing the robustness of semi-empirical sea level projections. *Climate Dynamics*, **39**, 861-875.

R Development Core Team (2012) *R: A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Switzerland.

Rapacciuolo G, Roy DB, Gillings S, Fox R, Walker K, Purvis A (2012) Climatic associations of British species distributions show good transferability in time but low predictive accuracy for range change. *Plos One*, **7**, e40212.

Record S, Charney ND, Zakaria RM, Ellison AM (2013) Projecting global mangrove species and community distributions under climate change. *Ecosphere*, **4**, 34.

Ridgeway G (2007) *Generalized Boosted Models: A guide to the gbm package*. CRAN.

Ridgeway G (2010*) 'gbm' package*. CRAN.

Rojas-Soto OR, Sosa V, Ornelas JF (2012) Forecasting cloud forest in eastern and southern Mexico: conservation insights under future climate change scenarios. *Biodiversity and Conservation*, **21**, 2671-2690.

Rönnbäck P (1999) The ecological basis for economic value of seafood production supported by mangrove ecosystems. *Ecological Economics*, **29**, 235-252.

Semeniuk, V. 1985 Mangrove environment of Port Darwin, Northern Territory: The physical framework and habitats. *Journal of the Royal Society of Western Australia*, **67**, 81-97.

Siikamaki J, Sanchirico JN, Jardine SL (2012) Global economic potential for reducing carbon dioxide emissions from mangrove loss. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 14369-14374.

Skidmore A (2002) *Environmental modelling with GIS and remoge sensing*. Taylor & Francis, London.

Smith TJ (1992) Forest Structure. In: *Tropical Mangrove Ecosystems.* Ed. Roberston AI, Alongi DM). American Geophysical Union, Washington D.C.

Smith III TJ, Robblee MB, Wanless HR, Doyle TW (1994) Mangroves, hurricanes, and lightning strikes. *Bioscience*, **44**, 256-262.

Snedaker SC (1982) *Mangrove species zonation: why?* Dr W. Junk, The Hague, The Netherlands.

Spalding M, Kainuma M, Collins L (2010) *World Atlas of Mangroves*. Earthscan, London.

Specht RL (1970) Vegetation. *The Australian Environment* (ed. by G.W. Leeper). Melbourne University Press, Melbourne.

Stone M (1974) Cross-validatory choice and assessment of statistical predictions. *Journal of the Royal Statistics Society, Series B,* **36**, 111-147.

Swets JA (1988) Measuring the accuracy of diagnostic systems. *Science*, **240**, 1285-1293.

Temby O (2009) *Project report for aerial LiDAR survey of Darwin and surrounds,* Fugro Spatial Solutions Pty Ltd, Perth, Australia.

Thackway R, Neldner BJ, Bolton MP (eds) (2008) *Vegetation*. CSIRO Publishing, Melbourne.

Tiner RW (1999) *Wetland indicators: A guide to wetland identification, delineation, classification and mapping*, CRC Press, Florida.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. *Nature*, **427**, 145-148.

Urban MC, Tewksbury JJ, Sheldon K (2012) On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B*, **279**, 2072-2080.

Watson JC (1928) Mangrove forests of the Malayan peninsula. *Malayan Forest Records*, **6**, 1-275.

Whittaker RH (1965) Dominance and diversity in land plant communities. *Science*, **147**, 250-260.

Williams D, Wolanski E, Spagnol S (2006) Hydrodynamics of Darwin Harbour. In: *The environment in Pacific Harbours*, Ed. Wolanski E. The Hague, The Netherlands, Springer.

Wintle BA, Bekessy SA, Keith DA *et al.* (2011) Ecological-economic optimization of biodiversity conservation under climate change. *Nature Climate Change* **1**, 355-359.

Woodroffe CD, Mulrennan ME, Chappell J (1993) Estuarine infill and coastal progradation, southern Van Diemen Gulf, Northern Australia. *Sedimentary Geology* **83**, 257-275.

Zhang K, Douglas BC, Leatherman SP (2004) Global warming and coastal erosion. *Climatic Change*, **64**, 41–58.

Zimmermann NE, Edwards TC, Graham CH, Pearman PB, Svenning JC (2010) New trends in species distribution modelling. *Ecography*, **33**, 985-989.

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

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

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

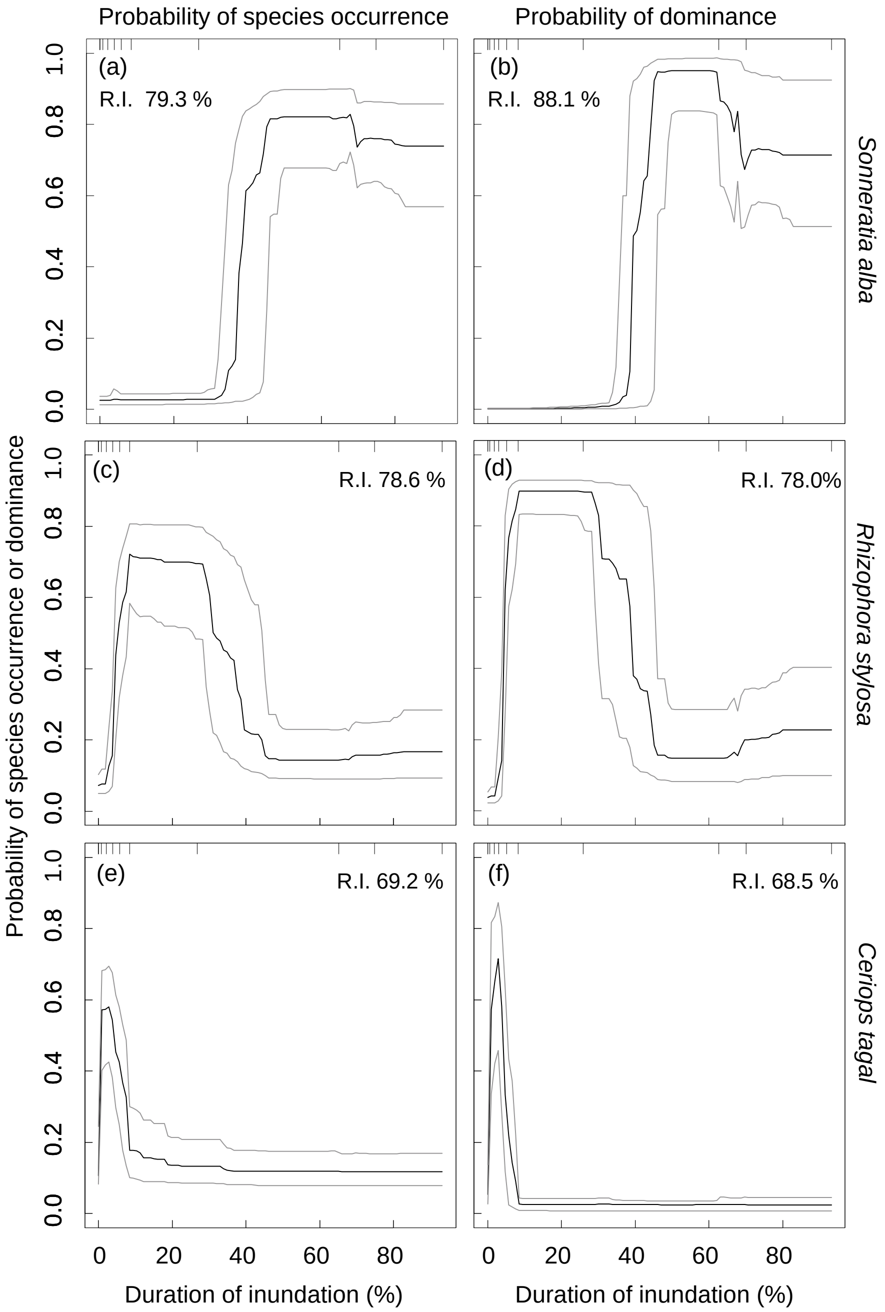
	Sea level rise (m)	***S. alba***	***R. stylosa***	***C. tagal***
Species	0.50	25.7 (23095)	70.0 (109563)	41.5 (79098)
	1	55.1 (10761)	119.8 (63994)	66.8 (49111)
Dominance	0.50	41.0 (29025)	83.6 (150963)	65.4 (97349)
	1	83.8 (14212)	139.0 (90798)	96.0 (66305)

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

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

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

Figure 4 Probability of occurrence of *Sonneratia alba*, *Rhizophora stylosa* and *Ceriops tagal* species occurrence (upper row a-c) and dominance (lower row d-f), at current sea level (y-axis) plotted against the probability of occurrence after a 1 m sea level rise (s.l.r, x-axis), as a 2-dimensional histogram, for Darwin Harbor, northern Australia. Each axis is divided into 50 equal bins and point color indicates the frequency of cells classed into each bin. Lower panel repeats panel (a) shows a solid 1:1 line and two dashed lines as guides for interpretation. Sites falling on the solid line have the same habitat suitability (i.e. probability of occurrence) at current sea level and after a 1 m rise in sea level (thus $E_{instability} = 0$). $E_{instability}$ increases with more points farther away from the solid 1:1 line, to reach maxima at the top left and bottom right of the graph. (i) habitat suitability is high at current sea level, and lower after a 1 m s.l.r. indicating a contraction in suitable area; (ii) indicates the frequency of cells with a high habitat suitability at current sea level and an even higher habitat suitability at 1 m s.l.r., hence an expansion in suitable area; (iii) low habitat suitability at current sea levels, which further declines after 1 m s.l.r.; and (iv) low habitat suitability at current sea level, which increases after a 1 m s.l.r.. The values plotted in the lower panel are for the habitat suitability for the species, *Sonneratia alba*.



Probability of species occurrence
Probability of dominance
(a)
R.I. 79.3 %
(b)
R.I. 88.1 %
(c)
R.I. 78.6 %
(d)
R.I. 78.0%
(e)
R.I. 69.2 %
(f)
R.I. 68.5 %
Sonneratia alba
Rhizophora stylosa
Ceriops tagal
Probability of species occurrence or dominance
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
Duration of inundation (%)

Figure 1.

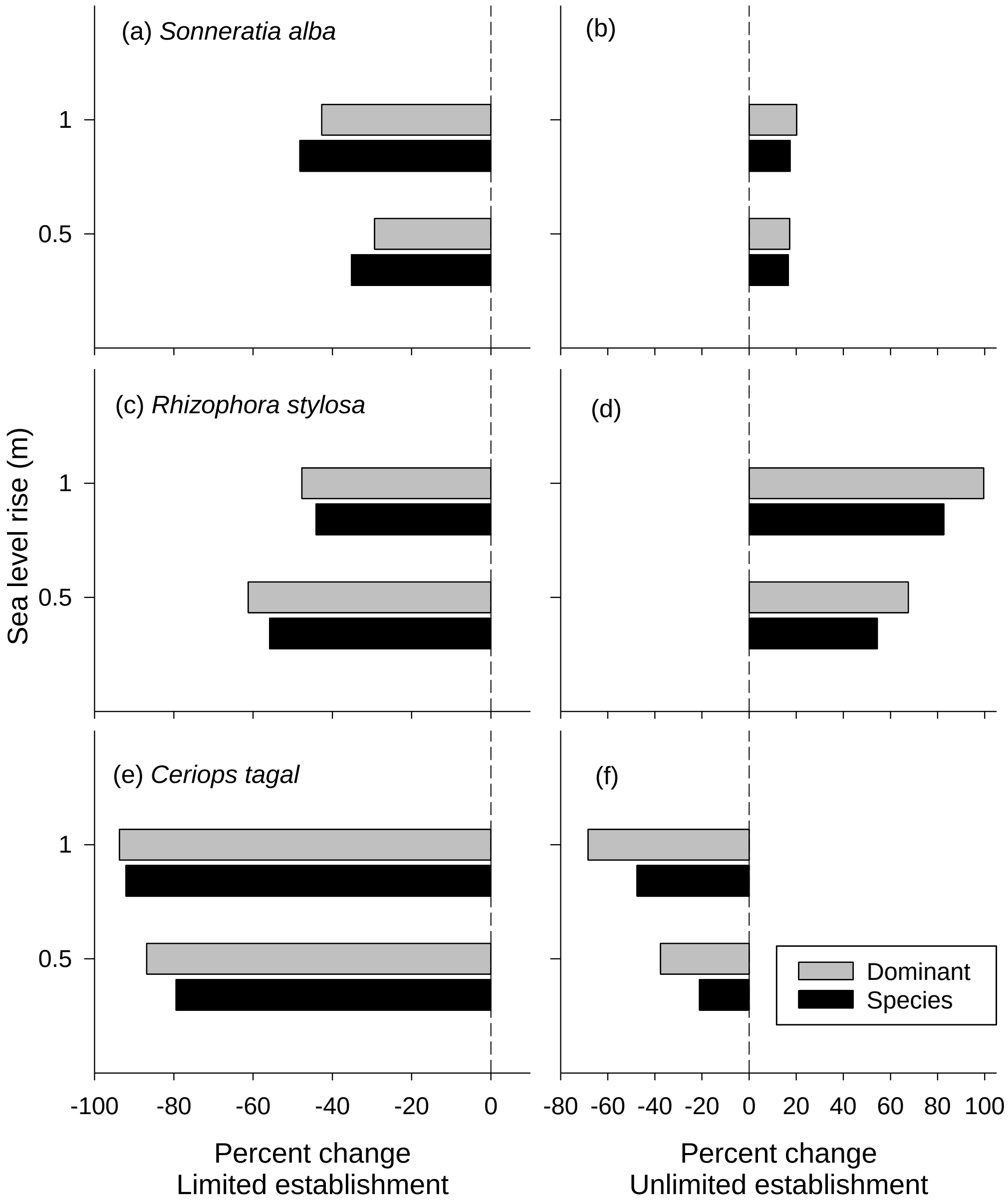

(a) *Sonneratia alba*
(b)
(c) *Rhizophora stylosa*
(d)
(e) *Ceriops tagal*
(f)
Sea level rise (m)
1
0.5
-100
-80
-60
-40
-20
0
-80
-60
-40
-20
0
20
40
60
80
100
Percent change
Limited establishment
Percent change
Unlimited establishment
Dominant
Species

Figure 2.