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Research

Predicting community rank-abundance distributions under current and future climates

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Understanding influences of environmental change on biodiversity requires consideration of more than just species richness. Here we present a novel framework for understanding possible changes in species' abundance structures within communities under climate change. We demonstrate this using comprehensive survey and environmental data from 1748 woody plant communities across southeast Queensland, Australia, to model rank-abundance distributions (RADs) under current and future climates. Under current conditions, the models predicted RADs consistent with the region's dominant vegetation types. We demonstrate that under a business as usual climate scenario, total abundance and richness may decline in subtropical rainforest and shrubby heath, and increase in dry sclerophyll forests. Despite these opposing trends, we predicted evenness in the distribution of abundances between species to increase in all vegetation types. By assessing the information rich, multidimensional RAD, we show that climate-driven changes to community abundance structures will likely vary depending on the current composition and environmental context.

Keywords: abundance, evenness, macroecology, southeast Queensland, SAD, species abundance distribution, species richness, vegetation

Introduction

Understanding the drivers of diversity remains a key challenge in ecology, and is becoming increasingly important as organisms respond to rapid climate change (Parmesan et al. 1999, Walther et al. 2005). Almost all projections of diversity, both spatial and temporal, have focused on species richness derived from species occurrence data. For example, spatial models of richness across broad geographic extents have been developed for birds (Davies et al. 2007, Rahbek et al. 2007, Distler et al. 2015), reptiles (Lewin et al. 2016, Rodrigues et al. 2017), invertebrates (Lobo et al. 2002, Overton et al. 2009) and plants (Steinmann et al. 2009, Cramer and Verboom 2017, Fricker et al. 2015), with



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projections also made under future climates (Currie 2001, Thuiller et al. 2005). However, it has been suggested that richness alone is a poor proxy for diversity (Hurlbert 1971) as it fails to describe the abundance patterns that define ecological communities (Stirling and Wilsey 2001, Wilsey et al. 2005).

Models of species richness rarely acknowledge that richness is intrinsically linked to, and constrained by, overall community abundance – there cannot be more species than the total number of individuals. While this is unlikely to be an issue in models using large grain sizes, it is relevant to data collected at plot scales (e.g. sub-hectare forest plots) where abundances of some species can be low, and adding or removing a relatively small number of individuals may greatly increase the chance of altering richness (Dornelas et al. 2011). Focusing on richness alone also fails to consider one of the universal laws of ecology: that virtually all communities contain many uncommon and few common species (Tokeshi 1993, McGill et al. 2007). A number of indices (i.e. Simpson’s and Shannon’s diversity) have been developed to compare community structure among sites, however these are known to oversimplify community-level abundance patterns and it has been recommended that full community-level abundance patterns are used when comparing across sites (see Matthews and Whittaker 2015, and references therein). Understanding the relative abundances of species (e.g. community evenness) provides additional useful information relating to important ecological processes, such as competition (Whittaker 1965, Rajaniemi 2011). However, due to influences from important environmental variables (e.g. fire, drought, storms) – sometimes with complicated interactions – species abundances can be difficult to predict accurately. A continued focus on richness alone may mask important changes to species abundance distributions under future climates. For example, even if richness remains relatively constant, the abundance of many species might nevertheless shift dramatically, with consequences for longer-term population persistence (Ehrlén and Morris 2015).

The rank-abundance distribution (RAD), where all species in a community are ranked from most to least abundant, provides a more holistic representation of communities than richness alone (Whittaker 1965). Rank abundance distributions can be used to describe any community where the abundance of each species is recorded and can be summarised using three simple components: 1) the total number of individuals within a community (abundance), 2) the total number of species in the community (richness) and 3) the allocation of individuals among species (evenness). These three RAD components can be modelled sequentially as functions of environmental covariates (Foster and Dunstan 2010) allowing for spatial predictions that respect their inherent conditionality. The concept of the RAD has featured prominently in the literature since the 1940s (Fisher et al. 1943, Preston 1948), and a steady-state non-linear distribution of abundances within a community is a fundamental assumption of neutral theory (Hubbell 2001). There has been some concerted effort to examine the form of these distributions in more detail across large regions and environmental gradients (Dunstan and Foster 2011, Arellano et al. 2017), however

their consideration in biogeography is lacking and there have been specific calls for greater consideration of RADs in large-scale analyses (Matthews et al. 2017). Despite the enormous potential of abundance distributions to reveal new insights about the drivers of multiple community attributes, and for predicting and interpreting community responses to environmental change (Fig. 1), RADs have not yet been spatially

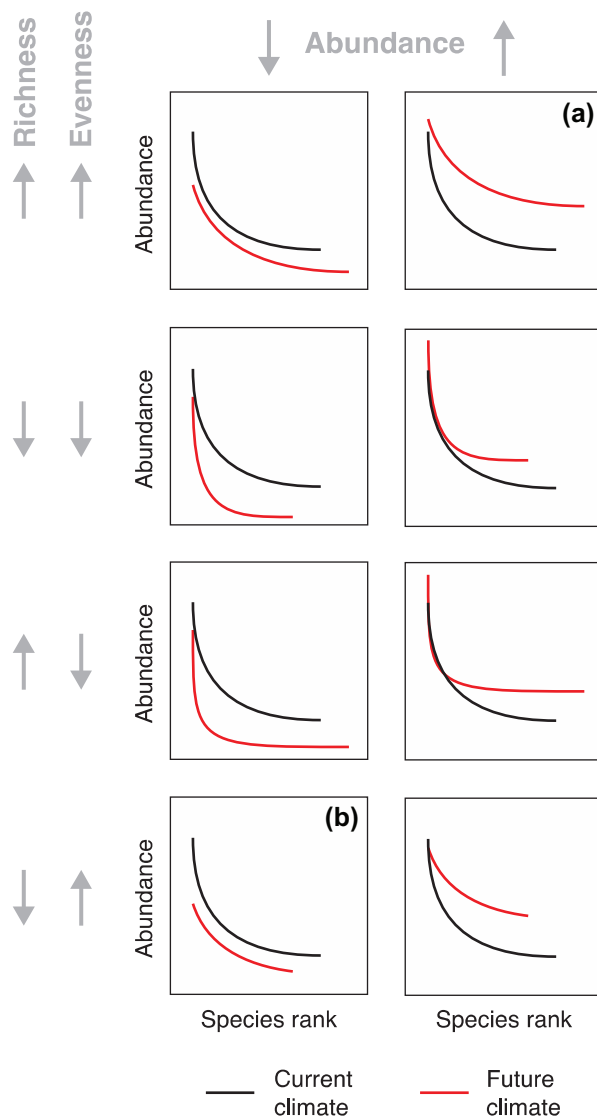


Figure 1. Conceptual representation of the different ways in which community rank-abundance distributions (RADs) may shift in response to climate change. The relationship between the three RAD components; abundance, richness and evenness; can be inferred by a distinctive RAD curve. Climate change could impact communities, and therefore their RADs, by driving changes to these three components from a current RAD (black lines) to future RADs (red lines). Two possible changes in RADs under climate change are highlighted for Southeast Queensland: (a) an increase in abundance, richness and evenness characteristic of a shift from dry sclerophyll to wet sclerophyll or rainforest; and (b) a decrease in abundance and richness with an increase in evenness, characteristic of a shift from rainforest to a sclerophyll-type (or simpler rainforest) communities.

projected across any terrestrial system, nor have temporal changes in RADs been predicted under future climates.

In this study, we use an extensive woody plant community dataset from southeast Queensland, Australia, to project the three RAD components – abundance, richness and evenness – under current and future climates at a fine spatial resolution across this large and diverse region (vegetation ranging from subtropical rainforest to sclerophyll woodlands and shrublands). Given the region’s climate is expected to become warmer and drier in the future (Dowdy et al. 2015), our overall hypothesis is that substantial changes in RADs will be predicted under future climates, but that the nature of these changes will vary with environmental context. Specifically, in response to climate change we expect areas currently dominated by open sclerophyll forests and woodlands to experience ‘woody thickening’ (Bowman et al. 2001, Russell-Smith et al. 2004, Macinnis-Ng et al. 2011), resulting in increased overall abundance and richness (e.g. Fig. 1a).

Material and methods

Study region

Our study region is the portion of the southeast Queensland (SEQ) bioregion that falls within the state of Queensland, Australia (Fig. 2a) (Thackway and Cresswell 1995). SEQ covers the section of the eastern coastline from the New South

Wales border (ca 28.1°S) to ca 20 km NW of Gladstone (ca 23.8°S) and extends west to the Great Dividing Range. SEQ covers ca 6.1 M ha, of which 21% is protected as national parks and state forests (Dept of National Parks, Sport and Racing 2014). There are substantial environmental gradients in the region, with forested mountains exceeding 1300 m in elevation to lowland coastal areas supporting shrubby heathlands. Temperature, radiation, precipitation and precipitation seasonality increase from south to north, and temperature seasonality increases with distance from the coast. Based on broad vegetation categories derived from the Queensland Herbarium’s Regional Ecosystem Classification (Accad et al. 2013) (Supplementary material Appendix 1), remaining intact vegetation in SEQ is dominated by sclerophyll woodlands (2.2 M ha) with smaller proportions of rainforest (0.3 M ha) and shrub-dominated heathland (0.1 M ha) (Fig. 2b, c). We conducted our analyses on a three second (ca 90 m) resolution spatial grid over the region.

Woody plant community data

Our starting dataset was the Queensland Herbarium’s COR-VEG floristic survey data (Lawson 2006, Neldner et al. 2012). We used CORVEG’s comprehensive one-off surveys (‘secondary sites’) where the percent foliage cover of each vascular plant species was recorded in multiple height strata along a central 50 m transect. All species present in the plot, but not recorded on the transect, were recorded in their

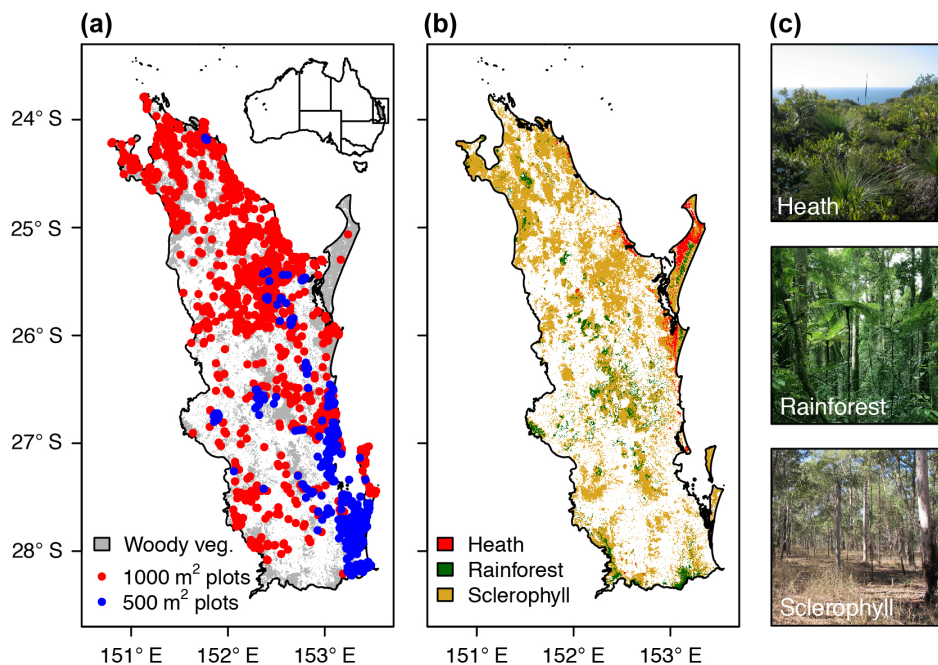


Figure 2. Southeast Queensland (SEQ) is a 6.1 M ha area on the east coast of Australia and contains 2.6 M ha of mapped extant native woody vegetation. (a) Existing survey data of woody plants at 1748 locations were used in our analyses with plot sizes of either 1000 m² (n=1276) or 500 m² (n=472). (b) The remnant woody vegetation of SEQ consists mainly of sclerophyll forest and woodlands, with areas of rainforest occurring where conditions are suitable, while heath occurs primarily in coastal areas (areas in white are non-woody vegetation or modified by humans). (c) Typical examples of heath, rainforest and sclerophyll communities present in SEQ (rainforest photo by Brandon Clark, heath and sclerophyll by authors).

appropriate strata and assigned an arbitrarily low cover value of 0.1% (Neldner et al. 2012). Surveys were conducted in 1000 m² (50 × 20 m) plots until 1997, and 500 m² (50 × 10 m) thereafter, but importantly, the central 50 m transect along which abundances were measured remained consistent across plot sizes.

The original dataset contained 3799 sites, but for the purposes of our analyses we only included sites that measured full floristic composition [$n=1748$ (abundance model) and 1276 (richness and evenness models), see below]. We limited our study to woody species because they contribute most to community biomass across the region and because herbaceous species can be highly ephemeral or present but not visible (e.g. below-ground storage organs). Sites that fell outside areas of mapped woody vegetation (as defined in the Queensland Herbarium's Broad Vegetation Group classification at a scale of 1:1 M, Supplementary material Appendix 1) were also excluded. Within the selected sites, we limited our analyses to vegetation > 1 m in height (i.e. excluding small shrubs and seedlings) because cover of species below 1 m were highly variable and strongly influenced by stochastic demographic processes (e.g. patchy seedling recruitment) and local scale natural disturbances such as fire, resulting in 910 species in our analyses.

Densities of each species in each site were estimated from crown cover data (originally collected in multiple strata along each site's central 50 m transect) and other environmental and species-level variables using a generalised additive mixed-effects model (McCarthy et al. 2016). The model was parameterised using detailed cover and abundance data comprising 610 individual 'species in strata' level measurements collected across 30 additional unbiased and systematically-selected sites (analysis presented in McCarthy et al. 2016). The model performed well with an adjusted R^2 of 0.57. Because the central 50 m transect from which abundance was estimated was identical between the two CORVEG plot sizes (1000 m² and 500 m²), we used the same method to estimate stem densities for the 500 m² sites (also expressed as stems per 1000 m²). These additional data were used to increase the sample size for the abundance model but were not included in the richness and evenness models because richness generally does not scale linearly with area (Gotelli and Colwell 2001). Total woody plant abundances for each site were obtained by summing predictions for each species. These were then expressed on a common scale of stems per 1000 m² to correspond with the richness data which were calculated directly from the 1000 m² site survey data. For our RAD modelling, a total of 1748 sites were used to parameterise the abundance model and 1276 sites were used to parameterise the richness and evenness models (Fig. 2a).

Environmental data

We collated 32 spatially complete environmental variables covering our study region; of these, 12 were climate variables, 14 were soil and geological variables and six were vegetation variables (plant growth indices, fire frequency and maximum

canopy height; Supplementary material Appendix 2). For the climate variables and plant growth indices, we applied the three second (ca 90 m) Shuttle Radar Topographic Mission digital elevation model of SEQ in ANUCLIM 6.1 (Xu and Hutchinson 2010) (with default spline surfaces) to derive these variables across our spatial grid. The remaining environmental variables (soil, geology, etc.) were obtained or derived from various sources (Supplementary material Appendix 2). Given our intention to demonstrate the potential of RAD modelling for predicting community changes, rather than comparing predictions from multiple climate models, we investigated only the CanESM2 general circulation model (GCM) at the representative concentration pathway (RCP) 8.5 for the year 2090. This is a robust GCM for predicting Australian climate (Williams et al. 2014, Moise et al. 2015) and provides an indication of future climates in the absence of serious action on climate change (i.e. a 'business as usual' climate scenario). All environmental variables were standardised (mean = 0, standard deviation = 1) prior to analyses and future climate variables were standardised using the mean and standard deviation of present day variables. To prevent unrealistic predictions into an unsampled climate future, we clamped the extremes (maximum and minimum values) of the standardised variables to the extremes of their current equivalents. This conservative approach primarily affects small parts of the region that currently possess the most extreme climates and was implemented to reduce extrapolation into unsampled climates where predictions can become unrealistic, especially when employing models with polynomial predictors.

Modelling and prediction

We modelled the three elements of the RADs in each community (i): total abundance (N_i), species richness (S_i) and species relative abundances (n_i , as a vector of abundances), under current climate conditions. As described by Foster and Dunstan (2010), the joint distribution of these three attributes in community can then be modelled sequentially:

$$\Pr(N_i, S_i, n_i) = \Pr(N_i) \Pr(S_i | N_i) \Pr(n_i | N_i, S_i) \quad (1)$$

Total abundance (N_i) is modelled first as a function of environmental variables using a generalised linear model (GLM) with negative binomial errors. Species richness (S_i , conditional on N_i) is then modelled as a function of ln-transformed N_i and environmental variables using a GLM with errors following a negative binomial distribution truncated at the total number of individuals. Relative abundance (n_i , conditional on N_i and S_i) is a vector of length S_i and represents the number of each species at a site (summing to N_i). It is modelled last as a multinomial distribution (see Foster and Dunstan 2010 for details) and is conditional on ln-transformed N_i and ln-transformed S_i . Evenness (η_i) is derived from the initial slope of the RAD curve and ranges from zero (highly even sites) to $-\infty$ (highly uneven, e.g. monodominant sites). More specifically, it is the derivative of the unstandardised

probability function for the most abundant (first ranked) species at each site (Foster and Dunstan 2010).

Each of the three RAD components were modelled using the 'RAD' package (ver. 0.3) for R (ver. 3.3.1) (R Core Team). Linear and quadratic relationships were considered for environmental explanatory variables and, consistent with subsequent applications of this technique (Dunstan and Foster 2011), model selection was conducted using forward selection based on Akaike information criterion (AIC). While other model selection procedures would have been preferred, such as model averaging to account for model uncertainty, the computational requirements and time required to fit the RAD models (especially across large datasets) made alternative approaches impractical. Some quadratic relationships showed poorly informed trends near the limits of the data and we excluded such terms from the forward selection procedure. While this approach is somewhat subjective, we placed greater importance on preventing extreme and poorly supported predictions than on model selection driven solely by AIC (Gelman and Hill 2007). As many of the 32 environmental variables exhibited some level of collinearity, variables with an absolute Pearson's correlation of ≥ 0.6 with a previously selected variable were not considered in subsequent model selection rounds. Variables were added until improvements in AIC became less than two AIC units (Burnham and Anderson 2002). All two-way interactions between the selected linear terms were then tested using the same forward selection procedure.

Predictions of N , S , and η were made for all 3 351 637 grid cells of mapped woody vegetation of SEQ, under both current and future climates. Standard errors were obtained by performing 500 bootstrap samples (Supplementary material Appendix 5) on the predictions from the distribution of the models' coefficients to take into account parameter uncertainty and sampling variation (Foster and Dunstan 2010). For each of the component RAD models we implemented a k -fold cross-validation using only the 1000 m² sites that were used in all three models (N , S , η). Sites were randomly ascribed to 10 evenly sized subsamples. In each of 10 iterations, one subsample was withheld as validation data and the remaining 90% of sites were used to train the models of N , S , and η . This ensured that every site was used for validation once. The accuracy of RAD models and the cross-validation exercise were assessed using the root mean square error (RMSE) and median proportional error (MPE, determined as the median of the absolute prediction error divided by the observed values across all sites). When assessing RMSEs, Pielou's evenness was substituted for η in the evenness models as it can be readily calculated during our model validation for both predicted (model generated) and measured (survey site) relative abundances. However, we present η in our projections of evenness to maintain consistency with previous applications of the RAD modelling technique.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.90tc8>> (McCarthy et al. 2017).

Results

RAD models and cross-validation

The final model of total abundance for woody plant communities in SEQ included four quadratic relationships, four linear relationships and three two-way interactions (Supplementary material Appendix 6, 7). Total abundance was lower at intermediate levels of the C_3 megaphyll plant growth index and soil sand content. Abundance increased with canopy height, soil carbon content and weathering intensity index. Abundance decreased with the C_3 microphyll growth index. The two-way interactions included soil carbon content \times weathering intensity, temperature isothermality \times fire frequency and weathering intensity \times temperature isothermality. The first interaction indicated that abundance was weakly related to soil carbon in highly weathered locations, but positively related to soil carbon where weathering was low. For the second interaction, abundance was weakly related to temperature isothermality when fire frequency was low, but became negatively related to isothermality as fire frequency increased. Finally, relationships between weathering intensity and abundance shifted from positive to negative as temperature isothermality increased. As expected, there was substantial unexplained variation in the total abundance model, with a root mean square error (RMSE) of 299.03 individuals per 1000 m² [median proportional error (MPE)=0.71; Supplementary material Appendix 8].

The model of species richness did not include any two-way interactions. Unsurprisingly, species richness had a positive, saturating relationship with total abundance (Supplementary material Appendix 6, 7). Richness was negatively related to regolith depth, fire frequency and soil sand content, and positively related (linearly or nearly so) to mean annual radiation and canopy height. Richness was higher at intermediate levels of diurnal temperature range, cation exchange and topographic wetness. The richness model had a RMSE of 5.64 species per 1000 m² (MPE=0.24) and performed better than the abundance model (Supplementary material Appendix 8).

The model of relative abundance included both total abundance and richness as covariates, and they exhibited positive and negative log-linear relationships, respectively (Supplementary material Appendix 6, 7). After accounting for these conditional variables, the remaining selected environmental variables had very weak quadratic relationships with ln-transformed relative abundance. The relative abundance model also performed well, as indicated by a RMSE of 0.13 (Pielou's evenness; MPE=0.08). In addition, predictions of species abundances at the site level (n_{ij}) were relatively accurate, with a RMSE of 23.71 stems per species per 1000 m² (MPE=0.34; Supplementary material Appendix 8).

Cross-validation showed that random removal of 10% of the sites did not generally reduce the performance of the abundance (RMSE=360.51 stems per 1000 m², MPE=0.78), richness (RMSE=5.71 species per 1000 m², MPE=0.24) and relative abundance (Pielou's evenness RMSE=0.13,

MPE=0.09) models (Supplementary material Appendix 8). Plots of coefficients of variation for all three RAD components showed that there was variability in predictions of abundance and richness in eastern areas of SEQ, and for evenness there was some variability in the north of the region (Supplementary material Appendix 8).

Spatial prediction under current climate conditions

Total abundance predictions across SEQ under current climate conditions ranged from 34 to 23 585 stems per 1000 m² however high abundances (> 2000 stems per 1000 m²) were only predicted in 0.001% of the 3.4 M cells in our spatial grid. Higher total abundances were predicted in areas currently dominated by dense vegetation types, including subtropical rainforest and coastal heathland (Fig. 3a, 4a). Conversely, low total abundances were predicted in the central inland of the bioregion where sparser sclerophyll woodlands with grassy understories are widespread.

Predictions of species richness under current climate conditions ranged from 2 to 52 species per 1000 m² (Fig. 3c). Spatial predictions closely followed those of abundance, with high levels of diversity predicted in the south-eastern rainforests. High values were also predicted for rainforest areas in the north and areas of moist sclerophyll forest in central SEQ (Fig. 3c, 4a). Areas dominated by sparse, grassy sclerophyll woodlands were predicted to have low species richness, as were some coastal heathland areas. While many shrubby heathlands in SEQ can have high species richness (Specht 1981), most woody diversity is typically found in the low shrub layers that were not included in the present analysis.

Most of SEQ was predicted to have moderate levels of evenness under current climate conditions. Less even distributions were predicted for some southern and central regions, whereas more even communities were predicted further north where the climate is warmer and more seasonal (Fig. 3e, 4a).

Predicted future climate conditions

Under the CanESM2 RCP8.5 future scenario for the year 2090, all of the plant growth indices used in our models were predicted to change. C₃ mesophyll and C₃ microphyll growth indices were predicted to decrease, particularly at higher altitudes, whereas the C₃ megaphyll plant growth index was predicted to increase or not change (Supplementary material Appendix 2). Diurnal temperature range and minimum temperature of the coldest period were both predicted to increase substantially across the region. Mean annual radiation was predicted to decrease in western areas and increase in the east, whereas the opposite trend was predicted for temperature isothermality (Supplementary material Appendix 2). Maximum vegetation height was predicted to increase by up to 6 m across most of the region, except for the southern rainforests and in the far north of SEQ where height may decrease by up to 4 m (Supplementary material Appendix 4).

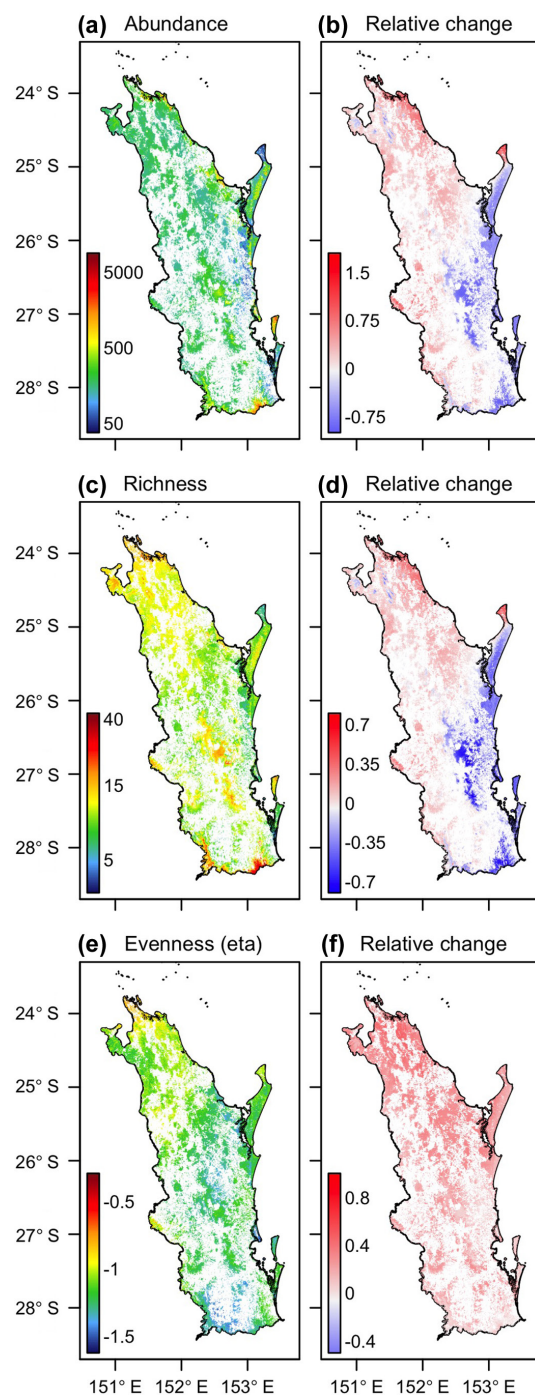


Figure 3. Mean predictions of the RAD components: (a) total abundance (N_j), (c) richness (S_j) and (e) evenness (η_j) across southeast Queensland under the current climate. Relative change plots (b, d, f) show the mean predicted relative proportion difference under climate change for each component. Values of abundance and richness indicate the number of stems/species in a 1000 m² plot and values of eta close to zero indicate more even communities. Note that abundance and richness are plotted on a log_e scale and the relative change values for evenness (f) were reversed so positive values indicate an increase in evenness, to aid interpretation.

Spatial prediction under future climate conditions

Given the predicted changes in climate and forest height, the RAD models predicted substantial changes for all three diversity components. Total abundance was predicted to increase in western and northern areas, with stem densities doubling in some areas, and to decline in the south-east of the bioregion (Fig. 3b, 4b). Increases in abundance were primarily driven by increases in maximum height and C_3 megaphyll plant growth index, and by reductions in the C_3 microphyll growth index across the region. This suggests that larger-leaved plants will contribute to the predicted increases in abundance at the expense of microphyll species, particularly at high altitudes. The declines in abundance predicted for the central part of the bioregion were partly driven by the interaction between fire frequency and temperature isothermality. Specifically, frequent fire is expected to reduce abundance more in southern areas that have higher isothermality (where temperature is less variable across the year) (Supplementary material Appendix 7). In terms of broad vegetation classifications, increases in abundance were predicted to occur primarily in areas currently dominated by sclerophyll forests, whereas decreases were predicted in rainforest and heathlands (Fig. 5a, b).

As with the spatial predictions under current climate conditions, richness closely followed changes in abundance under the future climate scenario. Richness was predicted to increase across the northern and western extents of the bioregion, and to decline mainly in the south-east (Fig. 3d, 4b). This apparent loss of species due to reduced abundance was

offset slightly by strong increases in mean annual radiation in the central coast and south-east (Supplementary material Appendix 2), which were positively associated with species richness (Supplementary material Appendix 7). As for abundance, richness was predicted to increase in areas currently dominated by sclerophyll forests and decrease in rainforest and heath (Fig. 5).

Unlike predictions for abundance and richness, evenness was predicted to almost-universally increase across the study region, irrespective vegetation type (Fig. 5), with greater increases generally occurring in the north (Fig. 3f, 4b). This was driven mainly by a universal increase in the minimum temperature of the coolest period and a widespread predicted reduction in the C_3 mesophyll growth index across much of SEQ (excluding the mountainous areas of the study region) (Supplementary material Appendix 7).

Discussion

Ecologists have long known that communities cannot be adequately characterised by a single number or metric (Purvis and Hector 2000). In particular, species richness alone does not provide a comprehensive understanding of community diversity (Wilsey et al. 2005), nor is it likely to inform effective conservation of ecosystems (Fleishman et al. 2006). Our extensive survey dataset of woody plant communities allowed us to sequentially model abundance, richness and evenness – attributes of the rank-abundance distribution (RAD) – and predict these under a future climate scenario for the first time in a terrestrial system. Consistent with some of our conceptual scenarios (Fig. 1), our models predicted reductions in abundance and richness in rainforest and shrubby heath communities, and increases in evenness across all vegetation types. Our results highlight the benefits in moving beyond the current reliance on occurrence data which limits our focus to richness alone. We have demonstrated that more holistic predictions of community diversity and abundance under climate change are possible (Smith et al. 2015), and given the increasing availability of large community-scale datasets (Hampton et al. 2013), it would be interesting to compare our findings with those from other regions and study taxa (Matthews et al. 2017).

Current spatial distributions of total abundance, richness and evenness

Predictions of abundance and richness under current climate conditions were highly correlated, however there was considerable unexplained variation in total abundance (Supplementary material Appendix 8). This is perhaps unsurprising given the importance of natural disturbances such as fire in driving vegetation structure in SEQ (Smith and Guyer 1983). Fire effects on stem densities can vary considerably through time and across space, even over tens of metres (Smith and Guyer 1983), making it difficult to explain density variation using a regional-scale, remote-sensed fire variable. Sporadic recruitment of

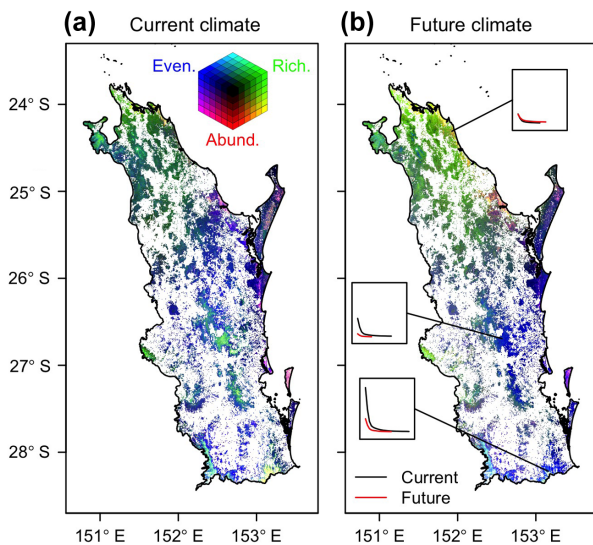


Figure 4. Composite view of (a) current and (b) future distributions of the three RAD components where each is assigned to one of the three RGB colour bands (red=abundance, green=richness, blue=evenness). Similar coloured cells indicate communities with similar RADs. Inset RADs (x-axis=ranked species, y-axis=abundance) under current and future climate conditions provide examples of a range of ecosystem types present in SEQ and how these are predicted to change into the future.

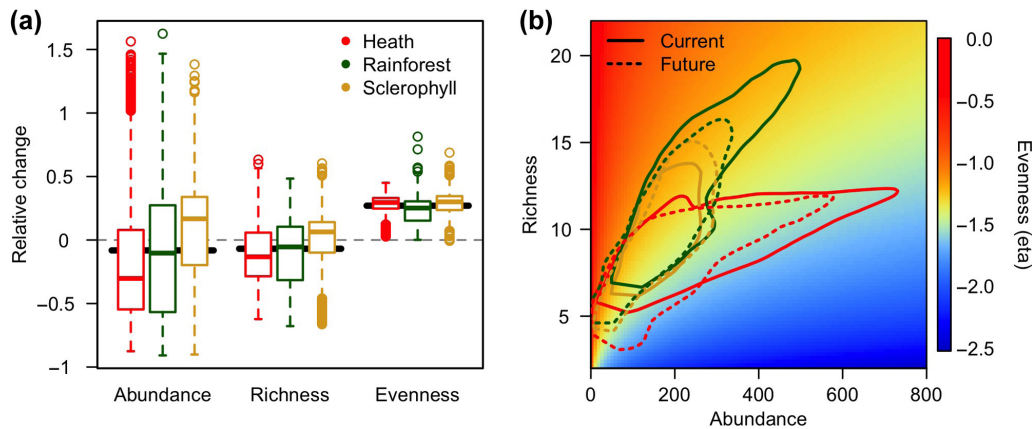


Figure 5. Predicted relative change of the three RAD components (abundance, richness and evenness) under climate change, from a random sample of 10 000 points for each of the three major woody vegetation types of southeast Queensland; heath (red), rainforest (green) and sclerophyll (yellow). (a) Boxplots comparing the relative change in RAD components across vegetation types (solid black lines represent the mean across all three vegetation types). (b) Predicted values of evenness (values close to zero indicate more even communities) in relation to total abundance and species richness. Polygons encompass 85% of the 10 000 sampled points from each vegetation type smoothed with a 10-point moving average. Separate polygons are shown for current and future predictions. Note that in (a) the relative change values for evenness were reversed so positive values indicate an increase in evenness, to aid interpretation.

species, regardless of fire regimes, can also increase variation in local stem densities (Connell et al. 1984). Regardless, the predictions from these models met our a priori expectations based on mapping of major vegetation types across SEQ (Fig. 2b). For example habitats classically defined as dense and species-rich, such as rainforest and heath (Specht 1970), were predicted as such across the region (Fig. 3a, c).

Predicted changes in total abundance, richness and evenness

Under climate change, reductions in abundance and richness, coupled with increases in evenness (as in Fig. 1b), were predicted for areas currently supporting subtropical rainforests and shrub-dominated heath (Fig. 5). For rainforests, this may represent a transition from complex mesic forms to drier, simpler forms of vine forest (Webb 1968), whereas heath systems may shift to more open forms (Specht 1981). However, our predictions for heath do not relate to shrubs under 1 m where much of the diversity exists (Specht 1981).

Broad-scale increases in abundance, richness and evenness (e.g. Fig. 1a) were predicted for extensive areas currently supporting sclerophyll forests and woodlands (Fig. 5). We anticipate that these increases will initially occur in forest understoreys, akin to woody thickening reported in savanna ecosystems world-wide. Specifically, the number of mesophyll and megaphyll rainforest species in understoreys is likely to increase, which is consistent with current trends of invasion by rainforest species into sclerophyll forests and open grasslands in Australia (Fensham and Fairfax 2003, Fensham et al. 2005) and abroad (Silva et al. 2001, Cabral et al. 2003, Wigley et al. 2010). However, woody thickening is not only contingent on climate, but also rising levels of atmospheric

CO₂ (not included in our models) which increase woody-plant growth rates and interrupt grass-fire cycles as woody stems outcompete flammable grasses (Brook and Bowman 2006, Tng et al. 2011). The broad-scale predicted increases in evenness also suggest that woody thickening in these forests and woodlands will result in reduced dominance. These results highlight the depth of information about vegetation change that is provided from RAD-based predictions compared to predicting richness alone.

Fire is also an important determinant of Australia's vegetation dynamics and is one of the primary factors maintaining boundaries between pyrophilic sclerophyll forests and pyrophobic rainforest (Webb 1968, Bowman 2000). Fire frequency was selected in all three components of the RAD model and was associated with reduced abundance, richness and evenness (Supplementary material Appendix 6). The transformative effects of fire under climate change will not only depend on climate, but also feedbacks with plant communities that vary in their flammability and requirements for fire disturbances (McFarland 1988, 1990, Bowman 2000, Watson and Wardell-Johnson 2004). Furthermore, although not directly considered here, extreme climate events such as droughts are predicted to become more severe and frequent in eastern Australia (Mpelasoka et al. 2008, Dowdy et al. 2015). Acute events such as droughts will almost certainly drive community changes and may also interact synergistically with fire to fundamentally transform ecosystems over relatively short time periods. For example, (Fensham et al. 2003) showed that drought-induced dieback is an important driver of tree densities in the savanna ecosystems in north-Queensland, and that subsequent fires suppress post-drought recruitment of a subset of fire-sensitive species.

As with all models, there are a range of important assumptions that underlie our approach. We modelled the RAD components of total abundance, richness and evenness as functions of environmental predictors without explicit consideration of ecological processes that generate and maintain diversity. Species-specific dispersal abilities, species interactions, priority effects and habitat connectivity may strongly influence how communities change as species disperse into new habitats (Meier et al. 2012). A failure to adapt or disperse at the velocity of climate change could lead to extinction (Loarie et al. 2009, Burrows et al. 2011, 2014). We modelled the maximal effect of climate change on RADs assuming that species will track their climate envelope instantly however, there is likely to be latency in species' responses to climate (Bertrand et al. 2011), especially for long-lived woody perennials. For example, at its northern limit in SEQ, *Nothofagus moorei* (Antarctic beech) maintains populations in mountain-top refugia by reproducing vegetatively rather than sexually (Howard 1981). Transient dynamics may also operate for extended periods (Fukami and Nakajima 2011), especially if climatic conditions continue to trend and not stabilise. In addition, we also predict changes to RADs under a single climate scenario. While we chose a relatively robust GCM for the region (Williams et al. 2014, Moise et al. 2015), considerable uncertainty surrounds the climate predicted for 2090. Ongoing research, especially studies informing specific management responses to climate change, should consider additional scenarios to better-account for this uncertainty.

Conclusions

We demonstrate the potential of modelling RADs across space and time and reveal that unabated climate change may have profound effects on woody plant species abundance, richness and evenness in SEQ; a region with extremely high species and ecosystem diversity. Areas of high density heath and rainforest are likely to experience altered structure and may contract in area (Fig. 5) and open forests and woodlands in the north and central regions may experience thickening and associated increases in richness. While predicted changes in abundance were usually associated with an equivalent directional change in richness, we predicted an almost universal increase in evenness across SEQ. This indicates an expected widespread reduction in dominance across SEQ under climate change, irrespective of changes in abundance and richness. As such, we show the benefits of harnessing existing survey data to concomitantly model multiple community attributes, providing more information than what is possible from models of richness alone.

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Supplementary material (Appendix ECOG-03552 at < www.ecogeography.org/appendix/ecog-03552 >). Appendix 1–8.