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Species loss and gain in communities under future climate change: consequences for functional diversity

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It is anticipated that anthropogenic climate change will lead to substantial reassembly within communities in coming decades as individual species shift their ranges to track optimal conditions for growth and survival. As species are lost and gained in communities, what are the consequences for functional trait diversity? Functional traits are the characteristics of species that affect individual performance and provide the vital link between biodiversity at the species level and ecosystem function. We investigated how projected changes in species richness in plant communities under climate change scenarios for the decade 2050 will affect the distribution and diversity of five functional traits. We aggregated range change projections made in Maxent for the decade 2050 across all species in the regional pool of littoral rainforest vines in eastern Australia ($n = 163$ species). The effect of richness changes on trait diversity was assessed in nine rainforest reserves along the east coast of Australia. Although richness was predicted to significantly decline across all communities, functional diversity remained stable, indicating a decoupling in response to climate change at these two different levels of biological organization. A high degree of redundancy in trait composition in communities may buffer against the loss of function in these plant communities. Scaling-up our understanding of the impact of climate change from the species level to communities is a critical step towards developing conservation strategies aimed at preserving ecosystem function.

The ranges of many plant species appear to be shifting in response to human-induced climate change (Kelly and Goulden 2008, Lenoir et al. 2008). By the end of this century, the geographic distribution of around two-thirds of California's endemic plant species is projected to contract by over 80% (Loarie et al. 2008). Similarly dire forecasts have been made for plants in Europe (Thuiller et al. 2005), and south-west Australia (Yates et al. 2010). However, many plant species are also projected to expand their range as climate warms (Dullinger et al. 2004, Hallinger and Wilmking 2011) and evidence is emerging that range expansions are already occurring, particularly towards higher altitudes in montane regions (Kelly and Goulden 2008, Harsch et al. 2009).

Species richness (the number of species present in a given community or area), will be determined by the balance between range 'expanders' and 'contracters' in communities in coming decades. Species will turnover within sites as a function of their ability to track optimal conditions for survival. Changes in richness resulting from species turnover and localised extinction are expected to affect the composition of functional traits in communities, with important consequences for ecosystem function (Wardle et al. 2011).

Functional traits are the characteristics of organisms that affect individual fitness by regulating growth, reproduction or survival (Hillebrand and Matthiessen 2009). Traits can

be morphological (e.g. leaf size, seed mass), physiological (e.g. photosynthetic rate, stomatal conductance) or phenological (e.g. timing of flowering or bud burst), and are increasingly being used to understand patterns of plant diversity. For instance, a range of functional diversity indices have been developed in recent years to measure the magnitude of functional differences among species in communities (reviewed by Petchey and Gaston 2006). These indices have been employed to investigate the response of plant communities to human activities (deforestation: Mayfield et al. 2005; land-use intensification: Laliberté et al. 2010; river regulation: Catford et al. 2011) and trait-based approaches for measuring diversity are emerging as critical tools for understanding vegetation response to rapid anthropogenic climate warming (Suding et al. 2008). Here, we investigate the relationship between projected species richness and functional diversity under current and future climate conditions using species distribution modeling and a multivariate index of trait diversity, known as functional dispersion (Laliberté and Legendre 2010). We define functional diversity as the range and value of species traits that influence ecosystem services sensu Tilman (2001) and illustrate our approach using data for climbing plant communities from critically endangered littoral rainforests in eastern Australia.

Community-level responses to climate change can be modeled using either a 'top-down' or 'bottom-up' approach

(Ferrier and Guisan 2006). We employed a bottom-up approach, also known as a ‘predict first, assemble later’ strategy, where individual predictions for each species in a community are aggregated into a single spatial projection. Although time-intensive, this approach allows the incorporation of individualistic species’ responses that, taken collectively, will drive the widespread reorganization of communities in coming decades. Individualistic responses may be poorly captured by top-down methods in which a single predictive relationship is modeled for all species in the community based on their physical environment. Bottom-up approaches have been widely applied to investigate changes in species richness under climate change (Thuiller et al. 2006, Buisson and Grenouillet 2009), but few studies have used the resulting richness projections to investigate potential changes in functional traits, particularly for plants.

One such study (Thuiller et al. 2006) explored compositional changes in plant functional groups – sets of species with similar ecosystem responses – under future climates using projected changes in tree species richness across Europe. Despite its long history, the use of plant functional groups to define differences in ecological strategies has a number of limitations when investigating patterns of functional diversity (reviewed by Hillebrand and Matthiessen 2009). Perhaps the most serious criticism is the inherent subjectivity involved in delineating groups, and the consequences this has for accurately summarizing the effect of trait variation on community and ecosystem processes. Newer methods circumvent this issue by measuring the distance between species in multivariate space defined by a set of *a priori* traits. In this context, we calculated the functional dispersion of communities – the average distance to the centroid across species in multivariate trait space – and used this index to compare potential trait diversity under current and future conditions (Anderson et al. 2006, Laliberté and Legendre 2010).

Functional traits provide a vital link between biodiversity and ecosystem function through their influence on key processes, such as nutrient cycling and carbon acquisition. Therefore, strong ecological justification is imperative when choosing which traits are the most appropriate for assessing functional diversity (Petchey and Gaston 2006). Each trait should be ecologically informative, capturing important information about how species acquire and

turnover nutrients in the constraints of their physical environment, and how they pass on fitness to subsequent generations. Traits are typically grouped into two categories: response and effect (Lavorel and Garnier 2002). Response traits, such as seed mass and dispersal mode, indicate which species will be most successful in response to some form of environmental perturbation. For example, small or wind dispersed seeds are most likely to colonise canopy gaps. By contrast, effect traits are those that directly influence ecosystem functions, such as carbon acquisition and biomass accumulation and include specific leaf area, leaf size and growth habit. Previous studies have identified a range of response traits that are expected to be advantageous for persistence under future climates, such as structures that promote long distance dispersal, and phenological plasticity (Hughes 2000). However, fewer studies have addressed how climate change may alter the diversity of effect traits in communities. Therefore, we have focused on a mixture of both response (seed mass, dispersal mode), and effect traits (leaf area, growth habit, climbing mechanism) in this study.

Our aims were to 1) illustrate the potential effects of projected changes in climate by the decade 2050 on species richness in communities using species distribution modeling, and 2) link the effect of changes in species richness to changes in functional diversity using data on five key traits and a multivariate measure of dispersion.

Material and methods

Study system

We focused on nine littoral rainforest climbing plant communities in eastern Australia (Fig. 1a). Littoral rainforests are closed canopy forests found within 2 km of the coast or saltwater intrusion. Salt-laden winds act as a strong environmental filter on plant composition in these systems, leading to lower floristic diversity than inland rainforest communities (Keith 2004). Canopy height varies with the degree of wind exposure and may reach up to 30 m in protected sites. Littoral rainforests occur on a range of soil types, including deep podsolc sands and volcanically derived silts, and have a naturally patchy distribution that reflects the occurrence of these substrates along the

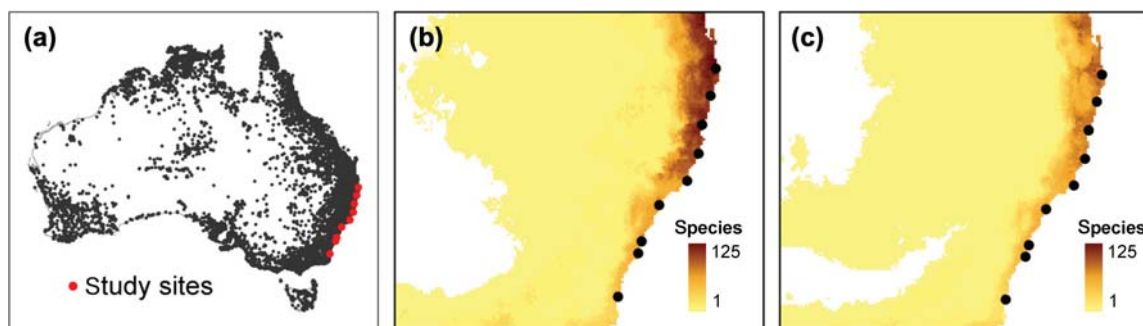


Figure 1. (a) Location of nine littoral rainforest communities used in this study (red dots) and the distribution of calibration points used in Maxent modeling (black dots), (b) maps of projected richness of climbing plant species under baseline climate conditions, (c) and climate conditions in 2050. Darker colours in (b–c) represent increases in the total number of species for which climatically suitable habitat is projected to be present at each time step in the study region.

Australian east coast. These forests have been extensively cleared for sand mining and coastal development and <1% of the original spatial extent remains. These remnants are protected under state and federal environmental laws and the effect of climate change is cited as a key threat to their continued persistence (<www.environment.gov.au/epbc/publications/pubs/littoral-rainforest.pdf>).

We focused solely on climbing plants in this study because they represent a diverse, but understudied, functional group in this vegetation community. Evidence is accumulating globally that climbers may be responding to climate warming and increased emissions of CO₂ at a faster rate than free-standing species (see Schnitzer and Bongers 2011 for a thorough review) making the need to understand the response of this growth form critical for adaptation planning.

A comprehensive list of climbing plant species occurring in littoral rainforests between Princess Charlotte Bay in Queensland (14°13'S, 143°58'E) and Gippsland Lakes in Victoria, Australia (38°08'S, 147°28'E) was compiled from field surveys, published sources and herbarium databases (see Supplementary material Appendix 1 for complete list of sources). These 163 species represent the regional species pool for littoral rainforest climbers in eastern Australia.

Projecting changes to species richness

Point occurrence records (latitudes and longitudes) for each species were collated from Australia's Virtual Herbarium (<http://chah.gov.au/avh/public_query.jsp>) and the Queensland Herbarium BRISMapper application. All sub-species and variety records were pooled at the species level because of the difficulty in resolving sub-specific taxa from online records. The average number of georeferenced locations compiled for each species was 285, and varied between 31 and 1580 across the 163 species (see Fig. 1 and Supplementary material Appendix 2 for further information on occurrence records used to calibrate models). Herbarium records of Australia plants have been accumulating in herbaria since European contact in 1770, and the accuracy of locality data associated with records has increased since the advent of global positioning systems. However, some records – particularly those from early periods of Australia's scientific history – may only be accurate within a 10 km radius as their latitudes and longitudes were retrospectively assigned during digitization using the location of the nearest town.

All distribution records were used to develop species distribution models for each species under baseline climate conditions (1950–2000 average) using Maxent (ver. 3.3.1). Maxent is a widely applied tool for distribution modeling with presence-only data that is ranked among the best performing modeling approaches (Elith et al. 2011). Species distribution models such as Maxent associate species occurrence points with environmental parameters (e.g. climate, soils) to build a spatial prediction of the location of suitable habitat. By projecting the resulting model onto climate futures – spatial surfaces that describe projected climate conditions under General Circulation Models (GCMs) – the expansion or contraction of suitable habitat in coming decades can be projected.

We used four climate variables to model the distribution of each species in Maxent: mean annual temperature, mean annual precipitation, temperature seasonality and precipitation seasonality. These variables were chosen because they are critical factors in determining the distributional limits of a wide range of plant species (Woodward 1987) and they were not highly correlated ($r < 0.65$ in all pairwise combinations). Baseline climate surfaces for each variable were downloaded from the Worldclim web application at 5 arc minute resolution (ver. 1.4, Hijmans et al. 2005) (<www.worldclim.org/download.htm>). This spatial resolution was chosen because it closely corresponds to the accuracy of species level observations in the Australian Virtual Herbarium (i.e. ~10 km). Maxent models were built using the optimized default settings outlined in Phillips and Dudík (2008) with two exceptions: 1) models were trained on ten cross-validated data partitions to reduce the likelihood of spatial bias in the occurrence records used in model training, and 2) the selection of background points (sometimes known as pseudo-absences) was constrained to areas within an 800 km radius of known occurrences for each species to improve model accuracy (Van Der Wal et al. 2009, Yates et al. 2010, Elith et al. 2011). Models run with background points selected within this radius had the greatest predictive accuracy in an exploratory modeling exercise performed on a subset of species in this study (results not shown). Model accuracy was measured using the area under the receiver operating curve (AUC) which assesses the rate of correct classification of presence points by the modeled function. AUC scores were calculated across background points using script developed in R ver. 2.12.1 (R Development Core Team). AUC scores greater than 0.75 were defined as providing a useful level of discrimination.

We projected distribution models built on baseline conditions onto climate scenarios for the decade centered around 2050 generated from four atmosphere-ocean GCMs under the A2 emission scenario (Nakicenovic and Swart 2000) (see Supplementary material Appendix 3 for interpolation methods for GCM surfaces). The GCMs chosen were the Bjerknes Centre for Climate Research Bergen Climate Model ver. 2, CSIRO Mk3.5, INMCM 3.0 Model, and the K-1 Coupled GCM (MIROC) ver. 3.2.2 medium resolution. These four GCMs were used in the Intergovernmental Panel on Climate Change Fourth Assessment Report and chosen for this study because they perform comparatively well at modeling Australian climate conditions (Suppiah et al. 2007).

Mapping and comparing projected species richness in communities

Maxent provides gridded output as continuous probability fields which we converted to a binary classification (0 = climatically unsuitable, 1 = climatically suitable) using a threshold value that maximized the test sensitivity and specificity on the receiver operating curve. This threshold value has been widely applied in distribution modeling and provided a suitable balance between commission (false positive) and omission (false negative) error rates. For each species, areas classified as climatically suitable across all

GCM projections were determined by summing the four binary raster maps and assigning grid cells with a value of 4 to a value of 1 (climatically suitable) using the package raster (ver. 1.8-12) in R (ver. 2.12.1).

Two maps of potential species richness (baseline, 2050) were created by summing the binary distribution maps produced for each of the 163 species in the study at each time step (Fig. 1b–c). Richness was calculated for each 5' × 5' grid cell across the study area by counting the number of species for which climatically suitable habitat was present in each cell. The ability of species to realise shifts in climatically suitable habitat in 2050 will be, in part, dependent on their dispersal capacity. Many previous studies have assumed one of two dispersal scenarios: full dispersal, or no dispersal (Thuiller et al. 2005, Loarie et al. 2008). We propose a new approach which uses seed dispersal mode as a surrogate for a species' dispersal capacity, and assumes that only those species dispersed by highly mobile vertebrates (e.g. birds, bats), wind or water will be capable of occupying suitable habitat outside the current range in 2050. Species with unassisted, invertebrate or ballistic dispersal were considered unlikely to substantially shift their distributions by 2050. Although long-distance dispersal can occur in species with these dispersal mode it is rare (Higgins et al. 2003), and the majority of seeds are expected to travel over short distances resulting in slow rates of migration.

Lists of species for which climatically suitable habitat was present were extracted for each of the nine littoral rainforest communities under baseline and 2050 conditions from richness maps using an R function that returned all species whose distribution fell within each reserve boundary containing the community. These species lists were used to examine how richness patterns in littoral rainforests may be affected by projected changes in climate by 2050 using a paired t-test ($\alpha = 0.05$) in R (ver. 2.12.1). Shapefiles of reserve boundaries for littoral rainforests were compiled from three digital mapping sources: 1) protected area boundaries accessed through the NSW Office of Environment and Heritage (OEH) spatial data download site (< <http://mapdata.environment.nsw.gov.au/DDWA/> >), 2) areas protected under the NSW State Environmental Planning Policy Number 26 – Littoral Rainforests, acquired

through the Community Access to Natural Resources Information website (< www.canri.nsw.gov.au/ >) using the ANZLIC unique identifier ANZNS0157000046, and 3) localised mapping of littoral rainforests in the south coast region of NSW performed by staff at the NSW OEH (M. Beukers pers. comm.).

Comparing functional traits between baseline and future conditions

We appended data on five functional traits – leaf area (cm²), seed mass (mg), climbing mechanism, dispersal mode, and growth habit – to all species projected to occur in the nine littoral rainforest communities. These traits were chosen because collectively they capture variation along key axes of strategy variation present among species. Seed mass – the dry mass of the endosperm – is a central component of the reproduction and establishment strategies of species (Leishman et al. 2000). Dispersal mode is a useful surrogate for the distance a seed can travel in the landscape (Leishman et al. 2000) and the size of leaves is important for water balance and energy budgets, as well as light interception and penetration to lower canopy layers (Parkhurst and Loucks 1972). Larger leaves require more evaporative cooling to remain at optimal temperature for photosynthesis and are selected against in dry or sunny environments. Species with woody and herbaceous growth habits differ in their relative growth rates, specific leaf area (leaf dry mass per unit area) and photosynthetic rates (Hunt and Cornelissen 1997), all of which are important for defining how species capture and deploy resources. Climbing species attach to their hosts using a range of mechanisms including tendrils, twining, adventitious roots or spines, and the type of mechanism employed has been associated with differences in leaf area, specific leaf mass and leaf nitrogen content (Castellanos et al. 1989). The mechanism used to climb also mediates interactions between climbers and their hosts (DeWalt et al. 2000).

Trait data for each species were collected in the field and compiled from published sources (Table 1; Supplementary material Appendix 4 and 5). The resulting datasets for

Table 1. Five functional traits used in this study, their units and methods used to compile data for each trait. Details of all sources used to compile trait data are provided in Supplementary material Appendix 3.

| Trait | Units | Source |
|--------------------|---|--|
| Seed mass | mg | For 63 species compiled from the Royal Botanic Gardens Kew Seed Information Database; for remaining 87 species calculated from seed volume using the equation: $\log_{10} \text{seed mass} = (1.104 \times \log_{10} \text{seed volume}) - 0.275$, $R^2 = 0.94$, $p < 0.01$ (see Supplementary material Appendix 5 for full details) |
| Leaf area | cm ² | For 113 species 25 mature, fully expanded leaves were collected in the field and scanned; for the remaining 37 species calculated from leaf dimensions in floras using the equation: $\text{leaf area} = \text{length} \times \text{width} \times 0.7$, $R^2 = 0.98$, $p < 0.001$ (Kraft et al. 2008) |
| Climbing mechanism | 5 categories: twiner; tendrils; scrambler; adventitious roots; spines/hooks | Published literature; floras; internet databases |
| Dispersal mode | 3 categories: abiotic (wind, water); biotic (animal); unassisted | Published literature; floras; internet databases |
| Growth habit | 3 categories: herbaceous; semi-woody; woody | Published literature; floras; internet databases |

each site and time-step were used to explore the effect of projected changes in richness on the distribution and the diversity of functional traits in each littoral rainforest community in two ways: 1) using univariate tests to compare each individual trait between time-steps, and 2) by combining all traits in a multivariate diversity index. We used two-sample Kolmogorov–Smirnov tests to compare the distribution of continuous traits (leaf area, seed mass) between time-steps in each of the nine communities. For categorical traits (climbing mechanism, dispersal mode, growth habit), chi-squared goodness-of-fit tests were used to compare the proportions of trait states between time-steps. Univariate tests were performed in R (ver. 2.12.1), ($\alpha = 0.05$) and leaf area and seed mass were \log_{10} transformed before analysis to reduce skew.

We used a measure of multivariate functional dispersion (FDis; Laliberté and Legendre 2010) to compare trait diversity between baseline and future conditions using data on all traits simultaneously. FDis calculates the average distance of individual species to their group centroid in multivariate trait space that has been defined by an appropriate distance measure. Tighter clustering of species in multivariate trait space corresponds to lower functional diversity and thus lower FDis values. Although a range of functional diversity indices exist we chose FDis because, unlike other techniques, it is largely unaffected by species richness (sample size). Our aim in combining response and effect traits in a single index was to complement univariate analyses of trait distributions, rather than to identify any potential effects of richness changes on specific ecosystem functions.

Correlations between traits may affect reported levels of functional redundancy (Petchey and Gaston 2002). Therefore, we also tested for associations between trait values using Pearson product-moment correlations for continuous traits, one-way ANOVA for continuous and categorical trait combinations and chi-squared tests for categorical traits. We found a significant relationship between seed mass and dispersal mode ($F = 4.2$; $DF = 134$; $p = 0.02$), but tests on all other pair-wise trait combinations were non-significant at the 0.05 alpha level. Although correlated, we included both dispersal mode and seed mass in FDis calculations because they capture different aspects of plant regeneration strategies.

For each combination of site and time-step ($n = 18$) we calculated FDis from a Gower's matrix of similarities between species based on the five functional traits selected. The Gower similarity coefficient was chosen because it accommodates both categorical and continuous variables (Gower 1971). All data matrices were normalized prior to analysis. We used values of FDis to test for differences in functional dispersion between baseline and 2050 communities using a paired sample t-test ($\alpha = 0.05$). Non-metric multidimensional scaling plots were used to visualise the multivariate data in two-dimensions. The distance between two observations in these plots is a measure of their similarity as computed by Gower's coefficient; species that are more similar in their traits appear closer together. We used 50 random restarts of the iteration to reach an optimal configuration of multivariate trait variation in two-dimensional space. Stress values indicating how reliably the higher-dimensional relationships were reduced to two-dimensions

were calculated for each plot. Stress values of < 0.20 were considered to provide useful reduction (Quinn and Keough 2002). All multivariate analyses were performed in R using the FD (ver. 1.0-11), and ecodist (ver. 1.2.3) packages.

Results

Accuracy of species distribution models

On average, Maxent models for the 163 species had a high level of accuracy (mean AUC = 0.92, $SD = +/ - 0.04$, range = 0.74–0.99). Therefore, we are confident that the species richness maps derived from aggregated model output across all species accurately captured individualistic relationships between species occurrences and climate.

Projected changes in species richness

Climbing plant species richness was projected to decline significantly across all nine littoral rainforest reserves by 2050 as a result of changing climatic conditions ($t = -3.09$; $DF = 8$; $p = 0.02$; Fig. 2a). Under baseline conditions the nine reserves provide climatically suitable habitat for 149 species. By 2050, assuming a dispersal scenario based on known dispersal structure, 46 of these species were no longer projected to have climatically suitable habitat in any of the nine reserves. Projected reductions in species richness were most pronounced in subtropical areas at lower latitudes in the north of the study region (Fig. 2a). For example, the community currently occurring at the lowest latitude was projected to lose climatically suitable habitat for around one-third of climbing plant species by 2050 (Table 2). Other communities showed more stable patterns

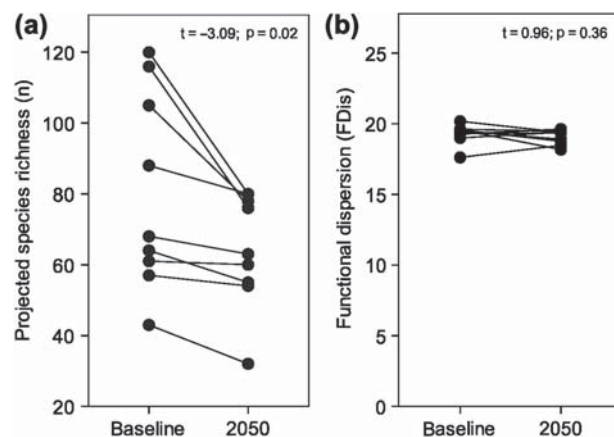


Figure 2. Projected changes in climbing plant species richness (a) and functional dispersion across five traits (b) in nine eastern Australian littoral rainforest communities. Richness changes are projected by species distribution models for baseline climate conditions (1950–2000 average) and 2050 climate conditions under the A2 emission scenarios (consensus across four future scenarios of climate in 2050 derived from different general circulation models). Functional dispersion was calculated across five traits using a multivariate index (FDis) computed from a Gower's matrix of similarities. Sites are ordered top to bottom by latitude. Results of paired t-tests between time steps are shown.

Table 2. Species richness and functional dispersion in nine littoral rainforest climbing plant communities under baseline (1950–2000) and 2050 climate conditions. The percentage of species lost and gained (% turnover) by 2050 relative to baseline conditions is provided. Functional dispersion was measured using distance to the centroid in multivariate trait space.

| Littoral rainforest community | Latitude | Predicted richness (baseline) | Predicted richness (2050) | % species turnover by 2050 | Functional dispersion (baseline) | Functional dispersion (2050) |
|-------------------------------|----------|-------------------------------|---------------------------|----------------------------|----------------------------------|------------------------------|
| Wooyung Nature Reserve | –28°26'S | 120 | 79 | 0 | 19.3 | 19.6 |
| Iluka Nature Reserve | –29°25'S | 105 | 70 | 8 | 19.0 | 19.4 |
| Bongil Bongil National Park | –30°26'S | 116 | 70 | 5 | 19.6 | 19.5 |
| Sea Acres Nature Reserve | –31°28'S | 88 | 72 | 9 | 19.3 | 19.4 |
| Myall Lakes National Park | –32°26'S | 61 | 52 | 13 | 19.6 | 18.2 |
| Wyrabalong National Park | –33°23'S | 64 | 49 | 9 | 19.6 | 18.8 |
| Bass Point Reserve | –34°04'S | 68 | 55 | 12 | 19.5 | 18.9 |
| Beecroft Peninsula | –35°01'S | 57 | 49 | 9 | 17.6 | 18.5 |
| Mimosa Rocks National Park | –36°35'S | 43 | 27 | 12 | 20.2 | 19.4 |

of species richness between time-steps, but this was the result of turnover in species rather than stasis in climatic suitability (Table 2). For example, in Myall Lakes National Park, nine species projected to lose suitable habitat by 2050 were replaced by eight species projected to undergo poleward range expansions (Table 2).

The effect of changes in species richness on individual traits

We found no evidence for differences in the distribution of continuous traits (leaf area, seed mass) between baseline and 2050 climate conditions in any of the nine communities examined (Fig. 3a–i; Supplementary material Appendix 5, Fig. A2a, Table A1). Similarly, the proportions of species exhibiting different dispersal mode, climbing mechanism, and growth habit did not differ between baseline and future communities (Supplementary material Appendix 5, Fig. A2b–d, Table A1).

The effect of changes in species richness on functional diversity

Despite significant reductions in species richness we found no significant differences in functional dispersion between time-steps across the nine littoral rainforest communities (Fig. 2b, Fig. 4). This finding was consistent across communities with little or no species turnover in 2050 (e.g. Wooyung Nature Reserve, Bongil Bongil National Park) and those with substantial turnover (e.g. Myall Lakes National Park) (Table 2). Therefore, the volume of trait space occupied by baseline and future communities remains relatively stable despite projections of significant reductions in species richness by 2050.

Discussion

The impact of climate change on vegetation is most commonly investigated at the species level (Thuiller et al. 2005, Lenoir et al. 2008, Loarie et al. 2008, Yates et al. 2010), but it can also be extended to explore how the distribution of physical traits may change in coming decades. The main objective of this study was to compare the effect of climate

change at the species and functional trait levels in communities and our results show clear differences in responses between these two levels of biological organisation. Species richness was projected to significantly decrease under future climates across the communities examined, whilst functional diversity remained stable. This finding has important implications for management of littoral rainforests and highlights that the impacts of climate change at the species and trait level may be decoupled. The decoupling of species richness and functional diversity has been identified in previous studies (Petchey and Gaston 2002) and will have significant consequences for conservation practice and management of plant communities as climate changes in coming decades.

Functional redundancy may buffer against the impact of climate change on trait diversity in communities

We found that the degree of projected species turnover did not influence changes in the functional dispersion of communities between baseline and future conditions and our results were consistent in univariate tests of individual response and effect traits. This finding indicates that trait values are highly similar amongst species in the regional species pool and that range shifts that lead to the introduction of novel species into a community may be able to compensate for range contraction in others, resulting in no net loss of functional trait diversity. Our results also suggest that functional redundancy – a high degree of similarity in functional traits amongst species (Walker 1992) – may provide a buffer against the effect of potential species losses on trait diversity in littoral rainforest climber communities as climate change progresses. Redundancy in the composition of traits may act as an insurance policy against the loss of functional diversity should species richness decrease and this may in turn increase the resilience of these communities to changing climate regimes, as suggested in other studies (Kahmen et al. 2005). The potentially high level of trait redundancy in littoral rainforests' species pool may be the result of strong abiotic filtering of traits related to salt-tolerance or physical disturbance, both of which have been shown to shape species composition in these forests (Keith 2004).

Filtering has been shown to restrict the range of viable trait strategies present in communities, leading to the

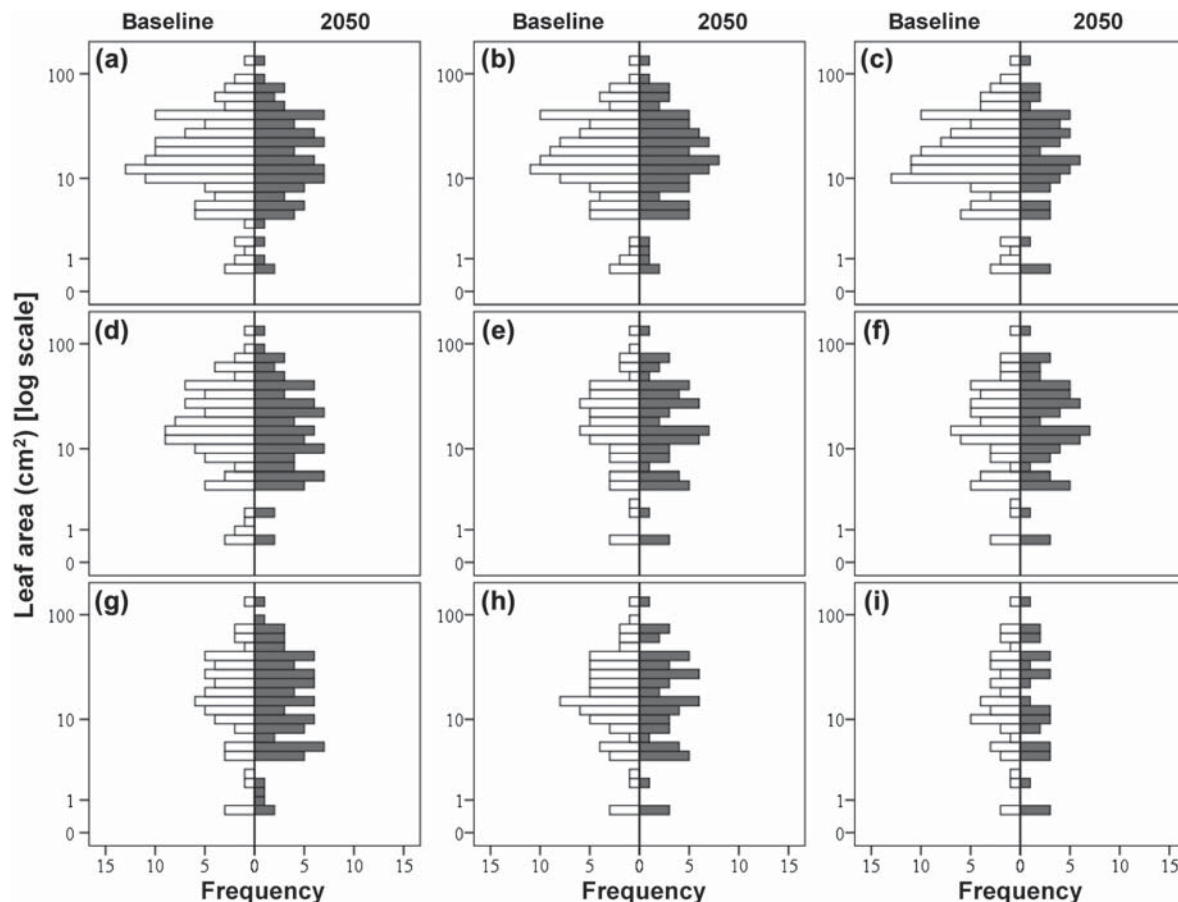


Figure 3. Comparative histograms of leaf area (cm^2) in climbing plant communities derived from baseline and 2050 climate conditions. Histograms indicate that the spread of trait values remains similar between time-steps whilst the number of species decreases in 2050 relative to baseline conditions. (a) Wooyung Nature Reserve, (b) Iluka Nature Reserve, (c) Bongil Bongil National Park, (d) Sea Acres Nature Reserve, (e) Myall Lakes National Park, (f) Wyrabalong National Park, (g) Bass Point Reserve, (h) Beecroft Peninsula, (i) Mimosa Rocks National Park.

under-dispersion of trait values amongst co-occurring species at a site (Mayfield et al. 2005, Kraft et al. 2008). Selection towards a restricted range of trait values through filtering creates a higher degree of overlap in the trait states within a community as unfavourable strategies are screened out.

Evidence is emerging that communities whose trait diversity is shaped by strong environmental filtering may be more resilient to climate warming, providing that a positive correlation exists between the traits that are favoured by filtering and the traits that confer resilience under climate

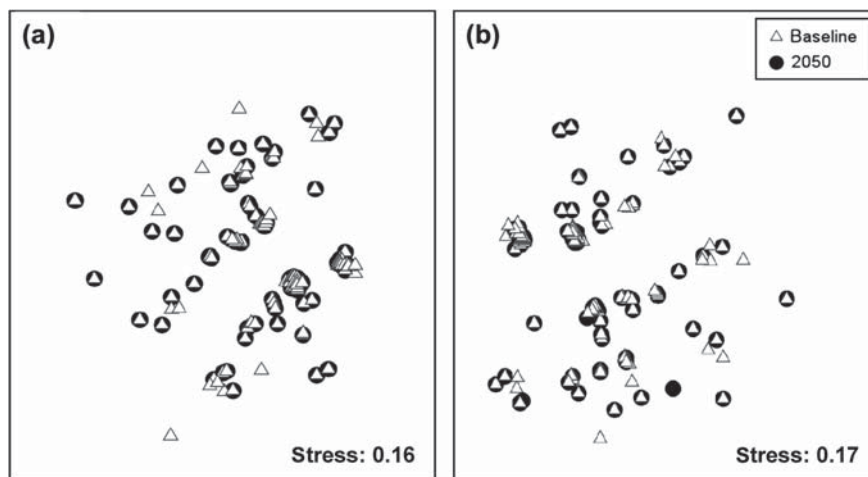


Figure 4. Non-metric multidimensional scaling plots of functional dispersion. Plots show the spread of species in multidimensional space defined by a set of five a priori traits in (a) Wooyung Nature Reserve, and (b) Bongil Bongil National Park.

change (Vinebrooke et al. 2004). However, if such 'positive co-tolerance' does not occur, communities subject to strong filtering may be under an increased threat due to diminished levels of response trait variation essential for climate change adaptation.

It is also important to note that the number and type of traits selected to summarise functional diversity is a key consideration when interpreting results of functional diversity indices. The more traits measured, the tighter the correspondence between species richness and functional diversity – the relationship between these two factors becomes linear as more of the inherent variation between species is quantified (Petchey and Gaston 2006). The justification for trait choice must therefore be done carefully to avoid 'over-fitting' of the index in trait space. The collection of trait data is time consuming and a balance needs to be struck between choosing ecologically relevant traits and the effort needed to collect data, which becomes particularly prohibitive in large-scale studies of this kind. Therefore, the selection of traits becomes a trade-off between ecological relevance and availability. With respect to the number and type of traits examined in this study, we have deliberately avoided interpreting our results in terms of changes to particular ecosystem functions. This is particularly important given we combined both response and effect traits in a single index (Laliberté et al. 2010).

Although our results indicate that a significant reduction in the number of species in communities does not lead to an appreciable loss in trait diversity we do not advocate abandoning species-based conservation approaches in these forests for several reasons. Firstly, despite the ability of functional redundancy to promote community persistence under climate change, all species losses reduce the potential for functional compensation to occur. A critical threshold of species richness may exist, beyond which communities begin to lose trait diversity and function (i.e. the rivet-popper hypothesis first proposed Ehrlich and Ehrlich 1981). Accelerating rates of extinction as a result of warming climate and land degradation makes understanding how many species can be lost from a system, before function is lost a challenging but essential task for community ecologists.

Secondly, our modeling approach has not assessed potential species abundance under climate change and this omission may limit our ability to understand the importance of highly abundant individual species in maintaining trait diversity. The ability to weight species and traits by their abundance in a community would clarify whether some species play a more critical role in preserving functional trait diversity than others (Laliberté and Legendre 2010). However, predicting the abundance of species and traits in future communities was beyond the scope of this study; progress towards this goal is being made despite significant methodological and theoretical challenges (Renwick et al. 2012).

Finally, species losses – whilst not being linked to losses in functional diversity in this study – may have important implications for the preservation of genetic integrity and phylogenetic diversity in communities. In light of this, we advocate an integrated approach to understanding the impact of climate change on communities that examines not only the effects on biodiversity at the species and trait level, but extends to investigations of population dynamics

and genetics as well as to below-ground microbial diversity. Conservation focused on preserving trait diversity in communities, at the expense of species-level conservation strategies, may be imprudent given our results which show species richness is at a higher risk of decline in comparison to functional trait diversity.

Caveats and future directions

Bioclimatic modeling is an imperfect tool for understanding the response of species to changing climatic conditions (reviewed by Guisan and Thuiller 2005). However, its widespread use reflects its utility as a current best-practice method for understanding the potential response of species to changing climate regimes. In the context of this study, we emphasize one particularly important limitation relating to the calibration of Maxent models which needs to be taken into account when considering our results. Namely, because we chose to model species distributions at a relatively coarse spatial scale (5') in order to match the positional accuracy of occurrence records, aggregated predictions of richness patterns should only be interpreted at this scale. Although fine-scale (e.g. <1 km) modeling of habitat suitability of littoral rainforest vines is theoretically possible, various limitations – such as the availability of appropriate calibration data (both presences and absences) – made it impractical for this study. More generally, another problematic limitation of most bioclimatic models is their inability to directly incorporate biotic factors (species interactions) into estimations of the realised niche of species (Godsoe and Harmon 2012). Although climate is a key driver of species' distributions (Woodward 1987), interactions between species also define where species occur and therefore the composition of communities. Therefore, models built on climatic factors alone may overestimate the extent of range shifts and the results of this study should be considered conservative assessments of potential changes to richness and functional diversity with climate change.

In this study we have treated species traits as static entities without the ability to respond adaptively to changes in climate. Although evolutionary processes and phenotypic plasticity may allow some species to persist within current range boundaries, incorporating these dynamic processes into modeling of community response to climate change is problematic. The main issue is that current understanding of the prevalence and magnitude of in situ adaptive capacity across species is limited (reviewed by Gienapp et al. 2008). This makes it impractical to examine the effect of trait changes on functional diversity and community trait composition. However, linking trait evolution, adaptive capacity of species and climate warming is a key future direction for understanding the ability of species to persist under rapid environmental change. These linkages may be achieved through better integration of manipulative experimental outcomes and ecological theories of species coexistence in communities.

Climate change may precipitate significant declines in species richness in littoral rainforest communities as illustrated by this study, however richness in this vegetation community may also be affected by other components of

global change in coming decades. In particular, projected increases the frequency and magnitude of storm surges and in sea levels in eastern Australia may further degrade coastal habitats (McInnes et al. 2003) and projected changes to fire regimes may alter vegetation composition (Clarke et al. 2011). We have shown that responses at the species level do not necessarily lead to similar consequences for trait diversity. These findings highlight the need to account for different responses at various levels of biological complexity when devising conservation strategies to confront the threat of climate change to life on Earth.

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Supplementary material (Appendix E7514 at <www.oikosoffice.lu.se/appendix>). Appendix 1–5.