

Linking changes in community composition and function under climate change

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Abstract. Climate change is expected to directly alter the composition of communities and the functioning of ecosystems across the globe. Improving our understanding of links between biodiversity and ecosystem functioning across large spatial scales and rapid global change is a major priority to help identify management responses that will retain diverse, functioning systems. Here we address this challenge by linking projected changes in plant community composition and functional attributes (height, leaf area, seed mass) under climate change across Tasmania, Australia. Using correlative community-level modeling, we found that projected changes in plant community composition were not consistently related to projected changes in community mean trait values. In contrast, we identified specific mechanisms through which alternative combinations of projected functional and compositional change across Tasmania could be realized, including loss/replacement of functionally similar species (lowland grasslands/grassy woodlands) and loss of a small number of functionally unique species (lowland forests). Importantly, we demonstrate how these linked projections of change in community composition and functional attributes can be utilized to inform specific management actions that may assist in maintaining diverse, functioning ecosystems under climate change.

Key words: biodiversity; climate change; dissimilarity; ecosystem function; management actions; modeling; plant community composition; plant functional traits; plant species; Tasmania, Australia; vegetation structure.

INTRODUCTION

Climate change is likely to dramatically alter many ecosystems around the world, in terms of the composition of species occurring in each area, as well as the magnitude and variation of important ecosystem functions. Substantial research has focused on applying models to project outcomes for biodiversity under climate change across large regions, indicating potentially large shifts in the distributions of species and the composition of communities (McMahon et al. 2011, Bellard et al. 2012). Separate research has investigated the potential implications of altered community composition on ecosystem functioning, primarily through local-scale experimental and observational studies (Cardinale et al. 2012, Hooper et al. 2012). This work has shown that loss of compositional or functional diversity can directly alter ecosystem functioning, particularly when considering multiple functions over longer time periods (Isbell et al. 2011).

Local-scale research into the potential consequences for ecosystem functioning of biodiversity loss, brought about through drivers such as climate change, has been

valuable in clarifying the magnitude of these effects and the mechanisms by which they are expressed (Traill et al. 2010). However, an important challenge remains in understanding and predicting links between changes in biodiversity and ecosystem functioning across large regions under rapid climate change (Cardinale et al. 2012). Extending this science to larger scales is particularly important for it to be useful in informing policy and management decisions relevant to maintaining diverse functioning ecosystems into the future, such as where best to invest resources into conservation or management actions (Pressey et al. 2007).

There are a number of approaches that have begun to address this issue of linking changes in biodiversity and ecosystem functioning across large regions. For example, relationships between the current diversity of forest communities and primary productivity have been assessed using large numbers of forestry plots over national scales (Paquette and Messier 2011, Ruiz-Benito et al. 2014). A substantial body of research has also focused on understanding the relationships between functional traits and community compositional change along environmental gradients (Diaz et al. 1998, Weiher et al. 1998, Thuiller et al. 2004, Shipley et al. 2006, Suding et al. 2008, Cornwell and Ackerly 2009, Laughlin et al. 2012). These approaches have improved our understanding of links between biodiversity, functional

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traits, and ecosystem functioning across larger spatial scales, yet they have limited capacity to directly inform likely outcomes and appropriate management responses under a rapidly changing climate.

A relatively small number of studies have attempted to meet this challenge by predicting concomitant change in biodiversity outcomes and ecosystem functioning under climate change scenarios. A simple approach to achieving this objective has been to link projected changes in the distributions of individual species with information on the functional attributes of those species, to inform potential changes in the functional composition and diversity of the assemblages obtained when the species-level predictions are “stacked” (Thuiller et al. 2006, Buisson et al. 2013, Gallagher et al. 2013, Terrier et al. 2013). Alternatively, current community-level functional attributes have been modeled in response to key environmental variables and projected into the future (Dubuis et al. 2013). These studies highlight the potential utility in combining information on biodiversity composition and functional traits, yet they have provided limited assessment of the concordance between likely compositional and functional change in communities under climate change (Thuiller et al. 2006).

Here we apply a macroecological modeling perspective to assess the relationship between projected change in community composition and community-level functional attributes for all vascular plants across Tasmania, Australia, under predicted climate change. We highlight that the relationship between climate-induced change in community composition and functional attributes will depend on the representation of functional traits within each community and the functional attributes of species lost or gained from each community (Fig. 1). For plants in Tasmania, we apply fine-resolution spatial projections to demonstrate how differences in the magnitude of projected compositional and functional change can provide new insight into likely outcomes for natural communities under climate change and better inform management aimed at maintaining diverse functioning ecosystems.

METHODS

Study region

Our study region is the island state of Tasmania, Australia (42°01' S; 146°36' E) see Appendix A. This region comprises an area of ~68 000 km², of which 77% is natural vegetation (TASVEG 2009) and 45% is protected for conservation (CAPAD 2010). Our analyses were carried out on a 250-m resolution spatial grid over this region, as defined by the Australian GEO-DATA 9 Second Digital Elevation Model (GEODATA 2008).

Environmental data

To derive and project the models in this study, we utilized spatially complete environmental data across the study region. We applied the 250 m digital elevation

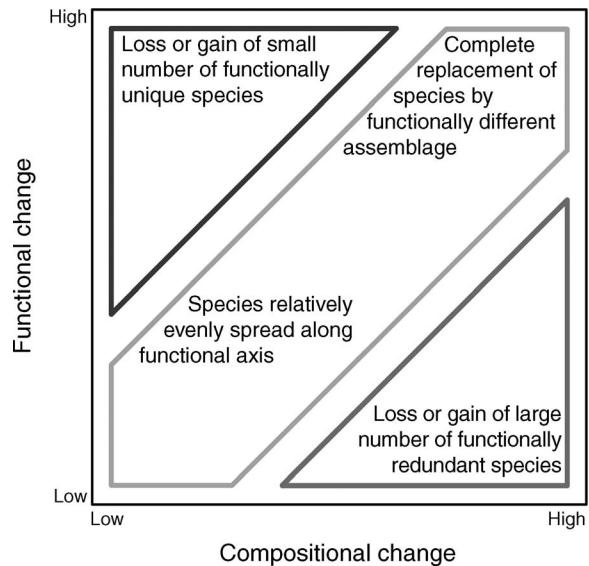


FIG. 1. Hypothesized implications of different combinations of community functional and compositional change.

model of the study region in ANUCLIM (Xu and Hutchinson 2010) to obtain climate data (precipitation, evaporation, temperature, radiation (adjusted for slope and aspect), and bioclimatic variables (plant growth indices) across the 1 157 587 grid cells of the spatial grid (averages for the period 1976–2005); see Appendix B. We also applied a range of spatial geological (mean geological age, weathering index) and soil (depth, nutrients, bulk density, water holding capacity) data layers, obtained from various sources (McKenzie et al. 2000, Western and McKenzie 2004, Raymond 2009, Wilford 2012, Williams et al. 2012).

Plant community composition data

To model plant community mean attributes, we utilized the same data on plant community composition in Tasmania as in Mokany et al. (2012). Specifically, the plant species composition of 175 grid cells across Tasmania (Appendix A) was obtained by aggregating 562 772 occurrence point records of native plant species (2051 species, from 1970 to 2010) (Tasmanian Natural Values Atlas) to 250-m grid cells, then a sampling function applied (Mokany et al. 2012) to select those grid cells with sufficient records to be deemed a “community sample.” The cells occur across all regions of Tasmania (Appendix A) and span the full range of major environmental characteristics in the region, including the full altitudinal and precipitation ranges as well as representative substrate in each region. Although there is a slight bias in the 175 grid cells being more commonly in lower elevation, drier, and warmer locations (Appendix A), this is not expected to influence our results, given the modeling approaches that we apply. In total, 1220 plant species were recorded in the 175 grid cells with community composition data.

Functional trait data collation

We collated functional trait data (maximum height, maximum leaf length, maximum leaf width, mean seed mass) for as many of the 1220 species occurring in the 175 focal grid cells as possible. These traits were chosen because they represent the three primary axes of plant functional trait variation (Westoby [1998]; with leaf size applied here instead of specific leaf area) and for which data are readily available for a large number of species. Data on leaf length and width were collated for the smallest lamina for compound leaves and ferns, with length and width for all species combined to calculate a single “leaf area” trait, by assuming elliptically shaped leaves for every species. Trait data were collated from a variety of published material (Reid et al. 1999, Harden 2000, Jordan 2001, Maslin and Tame 2001, McGlone et al. 2010), and field collection by the authors. We obtained height data for 1086 species (89%), leaf data for 924 species (76%), and seed data for 578 species (47%), which equates to having trait information for 95%, 81%, and 55% of occurrence records across the 175 grid cells for height, leaf size and seed mass, respectively.

Where trait information could not be obtained for recorded species, we estimated species traits by applying the mean value across all species in the nearest taxonomic group (i.e., genus, family). Community mean trait values calculated using only recorded trait data showed reasonably strong correlation to those calculated using the combined recorded and interpolated trait data (Appendix C). However, the potential bias in trait data being recorded more regularly for species that are taller, and that have larger leaves and larger seeds, warrants application of the interpolated traits in calculating community mean trait values, as seen in the tendency for community mean trait values including interpolated traits to be typically lower than those based only on the recorded traits (Appendix C).

Modeling community mean trait values

For each of the 175 focal grid cells containing compositional data, we calculated community mean values for each of the three traits (height, leaf area, seed mass) by combining the compositional and trait data for each species and then averaging the values across the species occurring in each grid cell. We then generated models of plant community mean traits using the generalized regression and spatial prediction package (GRASP; Lehmann et al. 2003) in R (R Development Core Team 2014). GRASP applies a generalized additive modeling (GAM) framework, and for the current implementation we used a Gaussian link function with three degrees of freedom for each independent variable. We developed models of community mean trait values using GAMs to account for nonlinearity in the relationships with environmental variables and a lack of existing knowledge on the likely nature of these relationships. We applied an interactive backward variable selection process, using a range of

environmental variables that we hypothesized could be important in influencing plant community mean traits in the study region (Appendix B). Candidate environmental variables were gradually omitted based on model Bayesian information criterion values, variable significance, variable contribution to deviance reduction, and a priori expectations of their relative importance. The predictive power of the final models was evaluated using a repeated ($n = 100$) random split-sample cross-validation procedure, with 70% of the data used for model training and the remaining 30% used to evaluate predictions, based on Spearman rank correlation between observed and predicted values (as in Dubuis et al. 2013). Plant community mean traits for each cell on the spatial grid of the region were predicted using the final model and the environmental variables for every grid cell.

Modeling compositional dissimilarity

We applied generalized dissimilarity modeling (Ferrier et al. 2007) to model pairwise plant community compositional dissimilarity (Sørensen's dissimilarity) as a function of environmental variables and the community mean trait values for the three functional traits (height, leaf area, seed mass). Incorporating community mean trait values as explanatory variables into the model accounts for the physiological drivers that may precipitate compositional turnover, which are not otherwise reflected in the environmental predictor variables. We applied the same five environmental variables as previously used to model plant community compositional dissimilarity in Tasmania (Mokany et al. 2012), as well as the three community mean trait values, with the significance of all variables assessed through a permutation test (1000 repetitions). We applied the same repeated split-sample approach to cross-validation for our model of compositional dissimilarity as was used for the models of community mean trait values, with data from 70% of sites used to train the GDMs, and the remaining 30% of sites used to evaluate the subsequent predictions of compositional dissimilarity. Spatial projections of the compositional dissimilarity model were generated by applying the spatially complete environmental layers and the model projections for community mean trait values.

Climate change projections

For the climate change analyses, we applied bias-adjusted, fine-scale (0.1°), dynamically down-scaled climate projections for 2100 from the Climate Futures for Tasmania project (Corney et al. 2010, Grose et al. 2010), using the CSIRO-Mk3.5 general circulation model and A2 emissions scenario. This projected climate future represents a worst-case scenario for plant biodiversity in Tasmania (greatest warming: $+3.2^\circ\text{C}$). The climate projections were further down-scaled statistically in the present analysis to 250-m grid resolution using ANUCLIM v6.1 (Xu and Hutchinson

TABLE 1. Variable contribution to the generalized additive models for plant community mean traits across Tasmania, Australia, and the significance of the smooth function for each variable.

Response variable and predictor variables	All-variable model deviance lost (%)	Single-variable model deviance explained (%)
Community mean plant height		
Minimum temperature coldest period	11.1***	15.8***
January solar radiation	4.6**	22.6***
C ₃ mesophyll plant growth index	13.7***	22.3***
Soil bulk density	4.4*	12.3***
Mean geological age	5.6*	11.7***
Community mean leaf area		
Precipitation :PET ratio	6.0**	14.6***
Temperature isothermality	4.5*	7.0**
Maximum temperature warmest period	12.1***	8.2**
C ₃ microphyll plant growth index	4.8**	6.8**
Elevation variation (SD)	4.2*	7.2**
Community mean seed mass		
Annual precipitation	4.6**	19.7***
Precipitation :PET ratio	8.7***	18.5***
January solar radiation	8.9***	9.5***
C ₃ mesophyll plant growth index	6.4***	10.0***
Substrate weathering index	5.0**	7.4**

Note: PET is potential evapotranspiration.
* $P < 0.05$ ** $P < 0.01$; *** $P < 0.001$.

2010), with radiation corrected for slope and aspect. We then projected the models of plant community mean traits and compositional dissimilarity under the projected future environmental conditions.

RESULTS

The final models of community mean plant height, leaf area, and seed mass all contained five explanatory variables, although these differed between the models (Table 1; see Appendix D). The model of community mean plant height explained 56.7% of the deviance, with the most important explanatory variable being C₃ mesophyll plant growth index (Table 1; see Appendix D). The model of community mean leaf area explained 36.7% of the deviance, with the most important explanatory variables being the maximum temperature of the warmest period, and the precipitation :potential evapotranspiration (PET) ratio (Table 1; Appendix D). The model of community mean seed mass explained 49.3% of the deviance, with the most important explanatory variable being the precipitation :PET ratio (Table 1; Appendix D). Spearman correlations (ρ) between observed and predicted community mean trait values from the cross-validation procedure indicated moderate to strong support for the models of community mean plant height ($\rho = 0.651$), leaf area ($\rho = 0.464$), and seed mass ($\rho = 0.575$).

Spatial projection of the community mean plant height model across current environments showed the largest values in moist lowland areas currently occupied by tall eucalypt forest (i.e., excluding the moist, but oligotrophic, regions of southwest Tasmania), and the smallest values in high-altitude alpine areas (Fig. 2a). A similar pattern was observed in the spatial projection of the model for community mean leaf area, with

communities having the largest leaves (on average) occurring in moist lowland areas (Fig. 2d). In contrast, spatial projection of the community mean seed mass model showed the largest values in high-rainfall lowland habitats of western Tasmania (Fig. 2g). When projecting the models of plant community mean traits to the year 2100 under climate change (Fig. 2b, e, h), there were relatively consistent changes from current projected patterns. Habitats at higher elevation in central Tasmania were projected to have the largest increases in community mean plant height (Fig. 2c), leaf area (Fig. 2f), and seed mass (Fig. 2i) under climate change, whereas habitats in lower elevation and coastal areas had the largest reductions in these mean trait values (Fig. 2c, f, i).

The final model of plant community compositional dissimilarity contained eight significant predictor variables, which together explained 59.2% of the deviance ($P < 0.001$) (Table 2; see Appendix E). The most important environmental variable explaining compositional dissimilarity was the precipitation :PET ratio, whereas the most important trait predictor was community mean seed mass (Table 2; Appendix E). Community compositional turnover was predicted to be greatest at low values of each of the community mean trait measures, with the slope of the response functions decreasing with increases in community mean trait values (Appendix E; Fig. E2). Spearman correlations (ρ) between observed and predicted compositional dissimilarity from the cross-validation analysis indicated strong support for the GDM model of compositional dissimilarity ($\rho = 0.763$). When the model of compositional dissimilarity was projected under climate change, the largest changes in plant community composition from now until 2100 were projected for the highest elevation habitats of

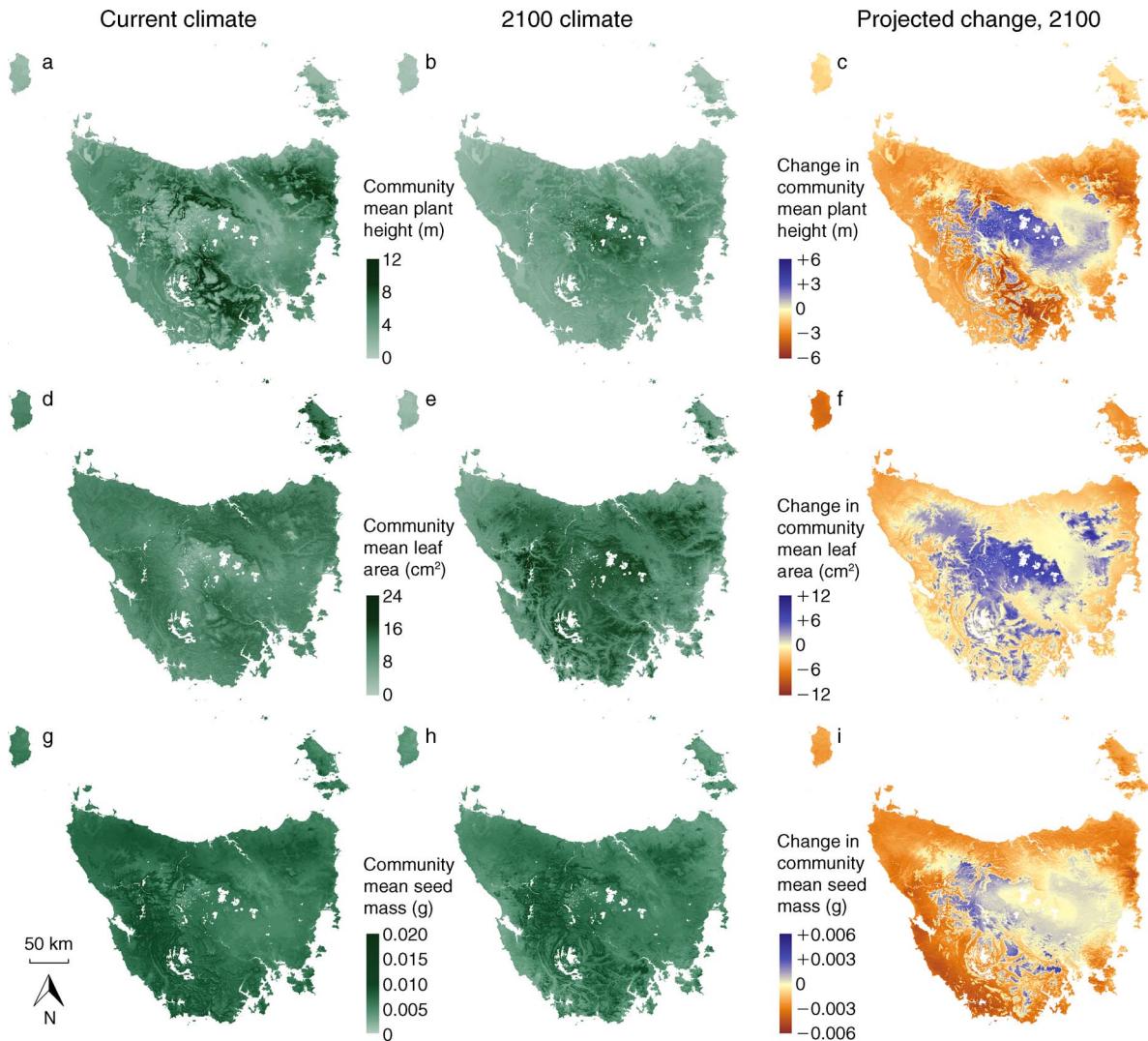


FIG. 2. Projections of plant community mean (a, b, c) height, (d, e, f) leaf area, and (g, h, i) seed mass across Tasmania under (a, d, g) current climate, (b, e, h) the climate in 2100 under climate change (CSIRO mk3.5, A2 emissions scenario), and (c, f, i) the projected resultant change in each community mean attribute under climate change.

TABLE 2. Variable contribution to the generalized dissimilarity model for plant community compositional dissimilarity across Tasmania, Australia.

Predictor variable	All-variable model deviance lost (%)	Single-variable model deviance explained (%)
Precipitation:PET ratio	4.8***	42.2***
Minimum temperature coldest period	1.8***	16.5***
Temperature isothermality	0.9***	22.5***
January solar radiation	0.4**	28.0***
Geographic distance	0.7***	16.0***
Community mean height	0.9***	14.6***
Community mean leaf area	0.7**	13.9***
Community mean seed mass	2.4***	14.1***

Note: The full model was fit to all 15 225 site pairs, with 59.2% deviance explained ($P < 0.001$) and an intercept of 0.556.

** $P < 0.01$; *** $P < 0.001$; PET is potential evapotranspiration.

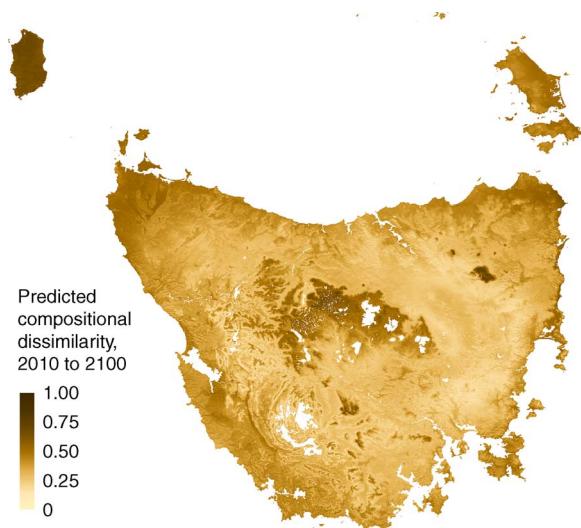


FIG. 3. The projected change in plant community composition (Sørensen's dissimilarity) across Tasmania from 2010 to 2100 under climate change (CSIRO mk3.5, A2 emissions scenario).

Tasmania, with moderate turnover in coastal areas and relatively small change in community composition projected for low-elevation inland areas (Fig. 3).

We examined the relationships between projected change in community mean trait values under climate change (Fig. 2c, f, i) and projected change in plant community composition (Fig. 3) by extracting values from these projections for 10 000 random grid cells. This analysis identified positive relationships between projected absolute change in all community mean traits and predicted community compositional dissimilarity to 2100 (Fig. 4). Relationships between projected change in community composition and community mean trait values under climate change were strongest for leaf area (Fig. 4b; $r^2 = 0.35$), moderate for seed mass (Fig. 4c; $r^2 = 0.20$), and weakest for plant height (Fig. 4a; $r^2 = 0.02$). Relationships between actual projected change in the values of community mean traits and composition are provided in Appendix F: Fig. F1.

To assess the relationship between multiple-trait community mean attributes and predicted compositional change to 2100, we combined the projected absolute change for each of the three community mean traits by weighting each equally and normalizing values to a range of no projected change (0) to the highest projected change (1). There was a strong positive relationship between predicted compositional dissimilarity and normalized predicted change in all community mean attributes (Fig. 5a; $r^2 = 0.40$). We projected the relative difference between normalized predicted change in all community mean attributes and predicted compositional dissimilarity to 2100 under climate change across Tasmania (Fig. 5b). This analysis indicated that lowland areas of central Tasmania (the Midlands) had moderate projected compositional change but low projected

functional change; lowland areas in the southwest and northeast had moderate projected compositional change but high projected functional change; while areas at higher elevation were projected to experience high levels

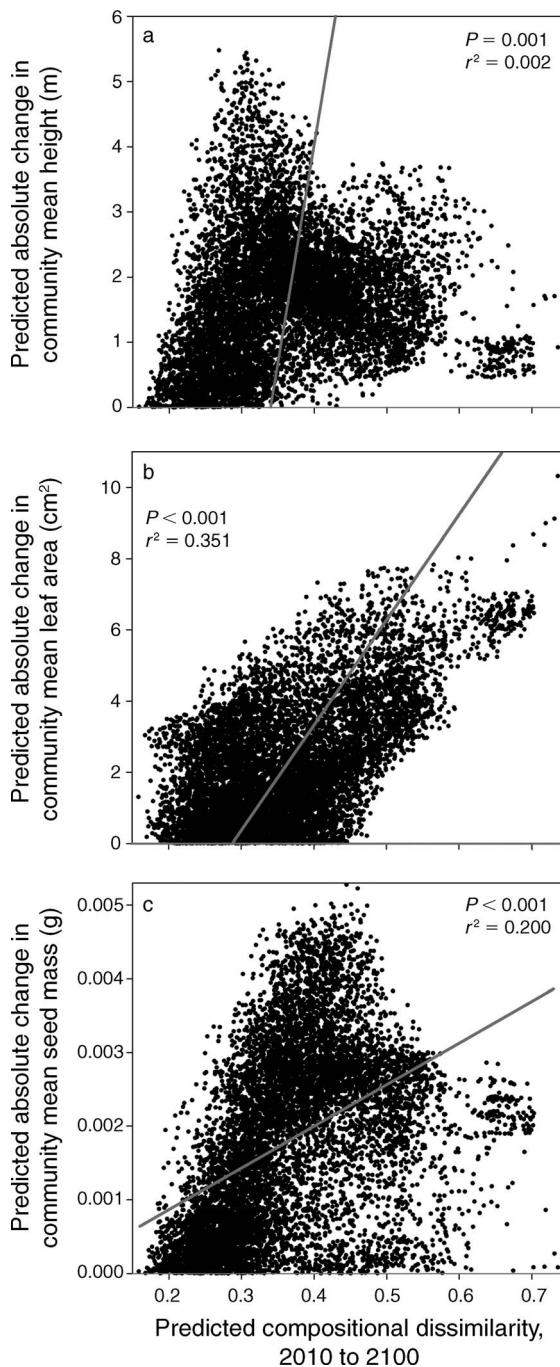


FIG. 4. The relationship between the predicted change in plant community composition (2010 to 2100) under climate change (CSIRO mk3.5, A2 emissions scenario) and the predicted absolute change (2010 to 2100) in plant community mean (a) height; (b) leaf area, and (c) seed mass for 10 000 randomly selected locations across Tasmania. Lines are for model II simple linear regression.

of both compositional and functional change under climate change (Fig. 5b).

DISCUSSION

Understanding changes in composition and function

Improving our capacity to identify management responses to climate change that achieve desired outcomes for both biodiversity and ecosystem functioning across large regions requires better linking of projected outcomes for these two aspects of natural systems (Cardinale et al. 2012). Here we have shown how combining compositional and functional projections under climate change can improve our understanding of how communities are likely to change into the future (Fig. 1). Importantly, our results for Tasmanian plant communities emphasize that the degrees of compositional and functional change projected for a given area under climate change are often not equivalent.

Our macroecological models indicate strong fundamental relationships between plant community mean trait properties and key environmental gradients in Tasmania (Table 1; Appendix D). The strong environmental dependence of plant community mean traits and relatively high explanatory power of the macroecological models provides some confidence in the projection of community mean trait values over space and over time under climate change (Dubuis et al. 2013) (Fig. 2). In addition, previous research suggests that these community-level trait properties are likely to be strongly related to important ecosystem functions, such as primary productivity (plant height and leaf area; Chapin 2003), carbon storage (plant height; de Bello et al. 2010), response to disturbance (seed mass; Tautenhahn et al. 2008), provision of habitat for animals (plant height; Tews et al. 2004), and herbivory (leaf area; Carmona et al. 2011).

Combining the projections of plant compositional and functional change under climate change provides new insight into how communities are likely to change into the future. For example, we project the largest reductions in community mean plant height (up to -5.8 m) for areas in southeastern Tasmania currently occupied by tall, wet eucalypt forests (Fig. 2a–c). Given the low compositional change projected in these areas (Fig. 3), substantial reductions in mean plant height could be expressed through loss or reduced extent of a small number of canopy or rain forest understorey tree species under warmer conditions and probably increased drought and fire frequency (Williamson et al. 2014). Concomitant projected increases in mean plant height (up to $+4.1$ m; see Fig. 2a–c) and high compositional turnover (Fig. 3) in alpine heath and herbaceous communities of high-altitude Tasmania (Fig. 2a–c) could be realized through replacement of many resident low-statured, cold-adapted species by invading tree and shrub species under less extreme low temperatures (Kirkpatrick 1997).

Combining functional and compositional projections to inform management

Although assessing likely changes in each community mean trait individually is informative, an overall understanding of community-level functional outcomes can be achieved by synthesizing across multiple traits or multiple ecosystem functions (de Bello et al. 2010, Isbell et al. 2011). Here we applied a relatively simple approach to calculating the overall level of projected change across community mean height, leaf area, and seed mass combined. Our index of overall community functional change has some limitations, given that the same magnitude of change could be achieved through different combinations of change in the individual traits. However, reducing this multidimensional issue to a single index enables us to compare overall projected functional and compositional change. This analysis indicated that for some areas, particularly high-elevation habitats, the levels of functional and compositional change expected under climate change are equivalent, and typically high (Fig. 5). Given this projected substantial replacement of alpine assemblages by functionally distinct lower-elevation species (Fig. 1), management could focus on ensuring the maintenance of some high-elevation refugia for alpine taxa, such as by actively suppressing fire and the spread of lower-elevation species into focal refugial areas (Keppel et al. 2015). The large projected compositional and functional changes may also have implications for water yields in regulated higher-elevation catchments relied upon for generation of hydroelectricity and provision of water for irrigated agriculture (Farley et al. 2005, Bennett et al. 2010).

Our analyses indicate that other areas may experience moderate levels of compositional change, but low levels of functional change under climate change, particularly the lowland Midlands of central Tasmania dominated by native grasslands and grassy woodlands (Fig. 5b). In these areas, we suggest that the species lost from local communities under climate change are more likely to be functionally redundant on a local scale (Rosenfeld 2002), or to be replaced by functionally equivalent species (Fig. 1). Climate-induced compositional change in these lowland grassy habitats is likely to be facilitated by the short generation times of much of the herbaceous-dominated flora. The consequences of our projections for management of these lowland areas may entail greater emphasis on the conservation of rare plant species through in situ protection and targeted management actions (e.g., grazing, burning) that promote the persistence of these rare species (Kirkpatrick et al. 2005).

In contrast, many lowland plant communities in Tasmania are projected to experience high levels of functional change under climate change, but relatively modest levels of compositional change (Fig. 5). Given that the community mean trait projections suggest large reductions in height, leaf area, and seed mass in these

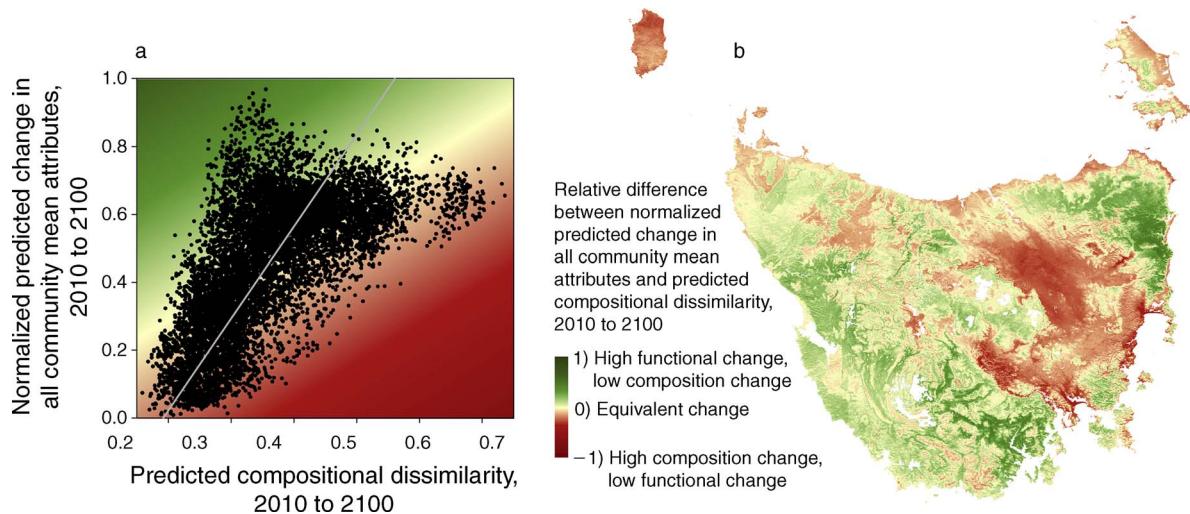


FIG. 5. (a) The relationship between the predicted change in plant community composition under climate change (CSIRO mk3.5, A2 emissions scenario) and the predicted change in community mean attribute normalized across all three traits (height, leaf area, seed mass), 2010 to 2100. (b) The relative difference between the normalized predicted change in all community mean attributes and the predicted compositional dissimilarity for Tasmanian plants under climate change, 2010 to 2100. The line in (a) shows model II simple linear regression ($P < 0.001$, $r^2 = 0.401$).

areas (Fig. 2), the projected levels of compositional and functional change could be realized through loss of a relatively small number of tree or shrub species (Fig. 1). Should it be deemed desirable to maintain some of the ecosystem functions currently provided by these systems into the future (e.g., carbon storage, supply of timber for forestry), possible management actions could include translocating native woody species adapted to warmer conditions from mainland Australia into these communities (Williamson et al. 2014).

Future research priorities

Here we have presented a relatively simple analysis combining compositional and functional projections for Tasmanian plant communities under climate change. Given the simplicity of our approach, we have inherently made a number of important assumptions that could be better addressed in future research. Although our models of compositional dissimilarity and mean trait values were based on strong relationships with key environmental drivers, they are correlative models in which the compositional and functional aspects interact through community mean trait values acting as predictors of compositional dissimilarity. There is a strong need for new generic modeling approaches that better integrate the processes involved in simultaneous compositional and functional change across large regions and diverse taxa under rapidly changing environments (Mokany et al. 2013). Our quantification of community mean trait values could be further improved if more detailed information became available on species abundances, rather than presence-only data (Garnier et al. 2004), traits for all species (to avoid the need for trait

interpolation), and intraspecific trait variation (Bolnick et al. 2011). Future research could also incorporate consideration of uncertainty in projections of community mean traits under climate change by considering a broad range of climate models and scenarios (Beaumont et al. 2008), as well as accounting for model projection into novel climate space (Williams and Jackson 2007), increasingly fire-modified environments, and temporal lags in community change.

Despite the obvious scope for improving projections of compositional and functional outcomes under climate change, our relatively simple analyses highlight the potential benefits to be gained in combining projections of these two aspects of natural systems. We have demonstrated how this combined assessment of likely compositional and functional change can illuminate likely outcomes for each of these components, and help inform management actions that may be appropriate in maintaining diverse functioning ecosystems into the future. We strongly advocate extending this and previous work to better account for the feedbacks between biodiversity composition and ecosystem function over large regions and rapidly changing environments.

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LITERATURE CITED

Beaumont, L. J., L. Hughes, and A. J. Pitman. 2008. Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters* 11:1135–1146.

- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15:365–377.
- Bennett, J., F. Ling, B. Graham, M. Grose, S. Corney, C. White, G. Holz, D. Post, S. Gaynor, and N. Bindoff. 2010. Climate Futures for Tasmania: water and catchments. Antarctic Climate and Ecosystems Cooperative Research Centre, Hobart, Australia.
- Bolnick, D. I., P. Amarasekare, M. Araujo, R. Burger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* 26:183–192.
- Buisson, L., G. Grenouillet, S. Villéger, J. Canal, and P. Laffaille. 2013. Toward a loss of functional diversity in stream fish assemblages under climate change. *Global Change Biology* 19:387–400.
- CAPAD. 2010. Collaborative Australian Protected Area Database. Australian Government Department of Sustainability, Environment, Water, Population and Communities, Parkes, ACT, Australia. <http://eatlas.org.au/data/uuid/25673a26-37b9-430f-8c20-34681e1d9060>
- Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. *Nature* 486:59–67.
- Carmona, D., M. J. Lajeunesse, and M. T. J. Johnson. 2011. Plant traits that predict resistance to herbivores. *Functional Ecology* 25:358–367.
- Chapin, F. S., III. 2003. Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Annals of Botany* 91:455–463.
- Corney, S., J. Katzfey, J. McGregor, M. Grose, J. Bennett, C. White, G. Holz, S. Gaynor, and N. Bindoff. 2010. Climate Futures for Tasmania: climate modelling technical report. Antarctic Climate and Ecosystems Cooperative Research Centre, Hobart, Australia.
- Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79:109–126.
- de Bello, F., et al. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation* 19:2873–2893.
- Diaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9:113–122.
- Dubuis, A., L. Rossier, J. Pottier, L. Pellissier, P. Vittoz, and A. Guisan. 2013. Predicting current and future spatial community patterns of plant functional traits. *Ecography* 36:1158–1168.
- Farley, K. A., E. G. Jobbágy, and R. B. Jackson. 2005. Effects of afforestation on water yield: a global synthesis with implications for policy. *Global Change Biology* 11:1565–1576.
- Ferrier, S., G. Manion, J. Elith, and K. Richardson. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions* 13:252–264.
- Gallagher, R. V., L. Hughes, and M. R. Leishman. 2013. Species loss and gain in communities under future climate change: consequences for functional diversity. *Ecography* 36:531–540.
- Garnier, E., et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85:2630–2637.
- GEODATA. 2008. GEODATA 9. Second Digital Elevation Model (DEM-9S) Version 3. Geoscience Australia.
- Grose, M., I. Barnes-Keoghan, S. Corney, C. White, G. Holz, J. Bennett, S. Gaynor, and N. Bindoff. 2010. Climate Futures for Tasmania: general climate impacts technical report. Antarctic Climate and Ecosystems Cooperative Research Centre, Hobart, Australia.
- Harden, G. J. 2000. Flora of New South Wales. University of New South Wales Press, Kensington, Australia.
- Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–108.
- Isbell, F., et al. 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477:199–202.
- Jordan, G. J. 2001. An investigation of long-distance dispersal based on species native to both Tasmania and New Zealand. *Australian Journal of Botany* 49:333–340.
- Keppel, G., K. Mokany, G. W. Wardell-Johnson, B. W. Phillips, J., and A. E. Reside. 2015. Quantifying refugia quality for conservation planning under climate change. *Frontiers in Ecology and the Environment* 13:106–112.
- Kirkpatrick, J. B. 1997. Alpine Tasmania: an illustrated guide to the flora and vegetation. Oxford University Press, Melbourne, Australia.
- Kirkpatrick, J. B., L. Gilfedder, K. Bridle, and A. Zacharek. 2005. The positive and negative conservation impacts of sheep grazing and other disturbances on the vascular plant species and vegetation of lowland subhumid Tasmania. *Ecological Management and Restoration* 6:51–60.
- Laughlin, D. C., C. Joshi, P. M. van Bodegom, Z. A. Bastow, and P. Z. Fulé. 2012. A predictive model of community assembly that incorporates intraspecific trait variation. *Ecology Letters* 15:1291–1299.
- Lehmann, A., J. M. Overton, and J. R. Leathwick. 2003. GRASP: generalized regression analysis and spatial prediction. *Ecological Modelling* 160:165–183.
- Maslin, B. R., and T. Tame. 2001. Wattle: acacias of Australia. CSIRO, Collingwood, Melbourne, Australia.
- McGlone, M., S. Richardson, and G. Jordan. 2010. Comparative biogeography of New Zealand trees: species richness, height, leaf traits and range sizes. *New Zealand Journal of Ecology* 34:137–151.
- McKenzie, N., D. Jacquier, and H. Cresswell. 2000. Estimation of soil properties using the atlas of Australian Soils. CSIRO, Canberra, Australia.
- McMahon, S. M., S. P. Harrison, W. S. Armbruster, P. J. Bartlein, C. M. Beale, M. E. Edwards, J. Kattge, G. Midgley, X. Morin, and I. C. Prentice. 2011. Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology and Evolution* 26:249–259.
- Mokany, K., H. M. Burley, and D. R. Paine. 2013. β diversity contributes to ecosystem processes more than by simply summing the parts. *Proceedings of the National Academy of Sciences USA* 110:E4057.
- Mokany, K., T. D. Harwood, K. J. Williams, and S. Ferrier. 2012. Dynamic macroecology and the future for biodiversity. *Global Change Biology* 18:3149–3159.
- Paquette, A., and C. Messier. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* 20:170–180.
- Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling, and K. A. Wilson. 2007. Conservation planning in a changing world. *Trends in Ecology and Evolution* 22:583–592.
- R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raymond, O. 2009. New digital geological map of Australia. *AusGeo News* 93:3.
- Reid, J., R. Hill, M. Brown, and M. Hovenden. 1999. Vegetation of Tasmania. Australian Biological Resources Study, Canberra, Australia.
- Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. *Oikos* 98:156–162.

- Ruiz-Benito, P., L. Gómez-Aparicio, A. Paquette, C. Messier, J. Kattge, and M. A. Zavala. 2014. Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and Biogeography* 23:311–322.
- Shipley, B., D. Vile, and E. Garnier. 2006. From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science* 314:812–814.
- Suding, K. N., S. Lavorel, F. S. Chapin, J. H. C. Cornelissen, S. Diaz, E. Garnier, D. Goldberg, D. U. Hooper, S. T. Jackson, and M. L. Navas. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14:1125–1140.
- Tasmanian Natural Values Atlas. 2015. State of Tasmania, Australia. <http://www.naturalvaluesatlas.tas.gov.au/>
- TASVEG. 2009. TASVEG version 2.0. Tasmanian vegetation monitoring and mapping program. Department of Primary Industries, Parks, Water and Environment, Tasmania, Australia.
- Tautenhahn, S., H. Heilmeyer, L. Götzenberger, S. Klotz, C. Wirth, and I. Kühn. 2008. On the biogeography of seed mass in Germany: distribution patterns and environmental correlates. *Ecography* 31:457–468.
- Terrier, A. I. M. P. Girardin, C. Périé, P. Legendre, and Y. Bergeron. 2013. Potential changes in forest composition could reduce impacts of climate change on boreal wildfires. *Ecological Applications* 23:21–35.
- Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31:79–92.
- Thuiller, W., S. Lavorel, G. Midgley, S. Lavergne, and T. Rebelo. 2004. Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. *Ecology* 85:1688–1699.
- Thuiller, W., S. Lavorel, M. T. Sykes, and M. B. Araújo. 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions* 12:49–60.
- Traill, L. W., M. L. M. Lim, N. S. Sodhi, and C. J. A. Bradshaw. 2010. Mechanisms driving change: altered species interactions and ecosystem function through global warming. *Journal of Animal Ecology* 79:937–947.
- Weihner, E., G. D. P. Clarke, and P. A. Keddy. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81:309–322.
- Western, A., and N. McKenzie. 2004. Soil hydrological properties of Australia. CRC for Catchment Hydrology, Melbourne, Australia.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- Wilford, J. 2012. A weathering intensity index for the Australian continent using airborne gamma-ray spectrometry and digital terrain analysis. *Geoderma* 183–184:124–142.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.
- Williams, K. J., L. Belbin, M. P. Austin, J. L. Stein, and S. Ferrier. 2012. Which environmental variables should I use in my biodiversity model? *International Journal of Geographical Information Science* 26:2009–2047.
- Williamson, G., L. Prior, M. Grose, R. B. Harris, and D. J. S. Bowman. 2014. Projecting canopy cover change in Tasmanian eucalypt forests using dynamically downscaled regional climate models. *Regional Environmental Change* 14:1373–1386.
- Xu, T., and M. Hutchinson. 2010. ANUclim Version 6.1 user guide. Fenner School of Environment and Society, Australian National University, Canberra, Australia.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–F are available online: <http://dx.doi.org/10.1890/14-2384.1.sm>

Data Availability

Data associated with this paper have been deposited in CSIRO's Data Access Portal: <http://dx.doi.org/10.4225/08/5542FE88058AF> (for Tasmanian plant functional traits) and <http://dx.doi.org/10.4225/08/5542FEA245D6F> (for Tasmanian plant community composition).