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Underestimated effects of climate on plant species turnover in the south-west Australian floristic region

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Abstract

Aim Spatial turnover in species composition reflects the interplay between species' environmental requirements and their dispersal dynamics. However, its origins are also historical, arising from speciation, extinction and past range dynamics. Here, we test the effects of current environmental conditions vs. spatial separation on plant species turnover in the South-West Australian Floristic Region (SWAFR). Using a new approach we then interpret residual (unexplained) gradients in species turnover.

Location 650 inventory plots in remnant native vegetation in the 230,000 km² wheatbelt of the SWAFR.

Methods We fitted generalized dissimilarity models of species turnover across sites as a function of current climate, topography, soils and inter-site distances. We then decomposed the model errors into independent axes of residual variation, representing unexplained species turnover. We mapped the spatial patterns evident on the main residual axes, and interpreted these using ancillary data on the life form and geographical ranges of associated species, the distributions of some major habitat types, and predictions of last glacial maximum (LGM) climate.

Results Soil and climatic variables made sizeable independent contributions to explained deviance, whereas deviance explained by inter-site distances and climate co-varied strongly. Total explained deviance was 34%. The major soil and climatic predictors were phosphorus and wet quarter precipitation, respectively. Residual analysis highlighted unexplained floristic similarity among many southern sites. A secondary residual axis highlighted unexplained variation in a south-westerly to easterly direction. Consistent trends in the life form and broader geographical ranges of associated species suggest that these patterns are climate-related. LGM climatic variables were correlated with patterns on the second residual gradient.

Main conclusions Floristic turnover in this region is jointly structured by current climatic and edaphic gradients. However, residual analyses revealed unexplained broad-scale trends in floristic composition, linked to imperfect modelling of the effects of current and perhaps historical climate on species turnover.

Keywords

beta-diversity, environmental history, Mediterranean climate, model error, plant community, residual ordination, species range dynamics, unexplained variation, variation partitioning.

INTRODUCTION

Spatial turnover in species composition is a fundamental characteristic of all natural systems. At regional to global scales, turnover is partly attributable to environmental variation, partly to species' dispersal abilities, and is partly a response to geographical or landscape structural features that affect dispersal. However, the origins of species turnover are also historical, arising from speciation, extinction and species range dynamics under past environmental conditions and landscape connectivity (Normand *et al.*, 2011). The strength and type of historical imprints on species turnover will vary among regions (Cowling *et al.*, 2014).

The Southwest Australian Floristic Region (SWAFR, *sensu* Hopper & Gioia 2004) is a global hotspot of both plant diversity and endemism which is located far from the equator, and is hence anomalous in the context of latitudinal diversity gradients (Hopper & Gioia, 2004; Hopper, 2009; Cowling *et al.*, 2014). The precise reasons for high diversity are unknown but prolonged landscape and relative climate stability in the Cenozoic are likely to have contributed to species accumulation by enabling the persistence of many plant lineages (Hopper, 2009; Cowling *et al.*, 2014).

Plant species richness trends in the SWAFR are known to correlate with current climate and soil conditions (Gioia & Piggott, 2000; Gibson *et al.*, 2004; Lambers *et al.*, 2011; Prober & Wiehl, 2012). Species turnover both within particular subregions (Hnatiuk & Hopkins, 1981; Brown & Hopkins, 1983; Brown, 1989) and regionally (Gibson *et al.*, 2004; Fitzpatrick *et al.*, 2013) has also been linked to both edaphic and climatic gradients. The role of soil phosphorus as a driver of changes in plant species richness and composition, and of plant nutrient acquisition strategies and other traits, has been the focus of a particularly large body of work in the SWAFR (e.g. Lamont, 1982, 2003; Lambers *et al.*, 2006, 2011). However, recent work by Laliberté *et al.* (2014) on a chronosequence of coastal dunes highlighted the role of soil pH, which mediates nutrient availability, as an environmental filter driving

variation in species richness. Other soil factors have, however, received less attention, and the relative importance of current climatic and soil gradients as drivers of regional species turnover has not been examined.

The degree to which floristic turnover is predictable from current environmental conditions will depend partly on the extent to which species occupy suitable habitat. A major constraint on this is their dispersal ability, in conjunction with landscape structure (Réjou-Méchain & Hardy, 2011). If dispersal limitation is a major driver of species turnover, the general expectation is that there will be distance-decay in floristic similarity among sites, at least under relatively homogeneous environmental conditions (Hubbell, 2001). In the SWAFR, the combination of long-term environmental stability and nutrient deficient soils has been argued to have selected for plant persistence traits rather than traits for efficient dispersal, based on the low prevalence of morphological mechanisms for long distance dispersal (Hopper & Gioia, 2004).

Historical range dynamics are another explanation for spatial patterns of species turnover unrelated to current environmental conditions. Species with poor dispersal may, for example, have had insufficient time to expand to fully occupy their potential environmental ranges since speciation, arrival in a region, or past range contractions. Compared with those in other mid- and high-latitude regions, Pleistocene climate changes in the SWAFR were less severe and the region remained ice-free. Cooler and drier climates are likely to have prevailed during glacial maxima and warmer, wetter climates during inter-glacials (Petherick *et al.*, 2013; Reeves *et al.*, 2013). However, projections of past climate based on global circulation models are highly uncertain and continuous terrestrial records or marine cores correlated with climatic and environmental variability over these long timescales are largely lacking for this region (Reeves *et al.*, 2013). Phylogeography nonetheless reveals a complex and dynamic evolutionary response of SWAFR plant species to Pleistocene climatic fluctuations (Byrne *et*

al., 2003; Byrne, 2007, 2008). The most striking pattern is the presence of high levels of intra-specific diversity that is geographically structured, with lineages often showing highly localized structuring of haplotypes (Byrne, 2008). This is consistent with expectations from a hypothesis of divergence through repeated cycles of localized population contraction and expansion, combined with limited migration (Byrne 2008). Genetic signatures of large scale population contractions and expansions from major refugia, indicative of migration as a main response to climate fluctuations, are also emerging (Dalmaris, 2012; Nistelberger *et al.*, 2014). During periods of increased aridity associated with glacial maxima it is inferred that more water-demanding species either contracted to local mesic refugia or retreated coastwards to major refugia and subsequently expanded during mesic periods, albeit in rather an idiosyncratic fashion (Byrne, 2007, Dalmaris 2012; Nistelberger *et al.* 2014). Granite (bedrock?) rock outcrops, which collect moisture at their fringes (Laing & Hauck 1997), are proposed to have acted as important inland mesic refugia for some species (Abbott, 1984; Hopper *et al.*, 1997; Byrne *et al.*, 2001; Schut *et al.*, 2014). Furthermore, while the region is generally topographically subdued, several coastal hill ranges outside the wheatbelt are associated with high species richness and numbers of restricted range species, which is probably partly linked to a refugial role (Hopper & Gioia, 2004). It is nonetheless unknown whether historical imprints in present-day species composition, arising from congruence in past species range dynamics, are detectable across the region.

Generalized dissimilarity modelling (GDM) is a flexible method enabling plant species turnover among localities to be modelled as non-linear functions of environmental conditions and site spatial separation, with the latter intended to model the effects of current dispersal limitation (Ferrier *et al.*, 2007; Jones *et al.*, 2013; Fitzpatrick *et al.*, 2013). A potential way forward in assessing the role of historical processes, such as palaeoclimatic effects, is to then examine residual floristic variation, unexplained by present-day parameters, for evidence of

non-random spatial structure. Two reasons why this may be preferable to the direct inclusion of palaeoclimatic predictor variables in the GDM model are the fact that predictions of past climate are highly uncertain, and the fact that species distributions may since have evolved in multiple ways. Important caveats are that structure in the model residuals will also be detected if important current environmental drivers of floristic turnover are either missing or poorly captured in the model, and that priority is given to current environment relative to historical drivers.

Here, we model plant species turnover across hundreds of plots representing native terrestrial vegetation in the inland wheatbelt region of the SWAFR. We examine the relative contributions of present-day environmental conditions (climate, topography, soils) and inter-site spatial separation to floristic turnover. In a novel approach, we then decompose the model errors (or ‘noise fraction’) into independent axes of residual variation, representing unexplained species turnover. We interpret these axes by means of ancillary data and discuss the likelihood of the patterns reflecting historical processes vs. other missing effects.

MATERIALS AND METHODS

Study region

Within the SWAFR, our study targeted the 230,000 km² agricultural wheatbelt. Despite generally subdued topography (Fig. 1a) the region covers a semi-arid to mesic climatic transition and a complex soil mosaic. Total annual precipitation ranges from 300-800 mm and peaks in the south-western corner of the region (Fig. 1b). Half of all precipitation falls in the wettest quarter of the year, with the same geographical distribution as total annual rainfall (based on the Bioclim digital climate layers at worldclim.org/bioclim, Hijmans *et al.*, 2005). Dry quarter rainfall, in contrast, is more evenly distributed across the south. Temperature gradients across the region generally run approximately south to north (Fig. 1d). Bioclim

predictions for the Last Glacial Maximum (LGM, based on the Community Climate System Model of global climate) suggest that the region was cooler and also drier, at least inland, than at present. The anomaly between recent and last glacial maximum (LGM) mean annual temperature is predicted to be lowest on the present-day west coast and the precipitation anomaly is predicted to be lowest in the very south-west of the region. Hence these areas can be considered the most climatically buffered.

Duplex soils are typically found in the region's broad valleys and laterites and sandplains in the uplands, with occasional outcrops of granite bed rock [which vary in form from flat rock surfaces to small hills](#) (Mulcahy & Hingston, 1961; Gibson *et al.*, 2004). A major drainage divide (the Meckering line) runs in a roughly north-south direction across the study region, to the east of which there are poorly connected Tertiary salt lake systems, and to the west of which there is more active drainage (Gibson *et al.*, 2004; Hopper, 2009). While the wheatbelt landscape itself is rather flat, [the extensive Darling scarp runs along its western margin and several separate hill ranges are found on its southern margin](#).

Some 4000 native plant species occur in the wheatbelt, many of which are extremely rare (Gibson *et al.*, 2004). The native flora of the wheatbelt is furthermore highly fragmented by intensive agricultural land-use, and is subject to multiple threats and management challenges, including continued habitat modification, increasing secondary salinisation, competition from invasive species, and projected future climate change (Coates & Atkins, 2001; Bates *et al.*, 2008; Laurance *et al.*, 2011).

Plant inventories and soil sampling

Terrestrial vegetation inventory plots, excluding wetland habitats, were established at 682 sites representing native vegetation within the wheatbelt region between October 1997 and September 2000 (Gibson *et al.*, 2004). Sampling extends across parts of five IBRA

bioregions (Interim Biogeographic Regionalisation for Australia; Department of the Environment, 2012), covering much of the Avon wheatbelt region but also extending into the surrounding Geraldton Sandplains, Jarrah Forest, Mallee and Esperance Plains regions (Fig. 1a).

To gain a representative sample of the native vegetation, plots targeted high quality sites such as protected areas and sampling within subregions was partly stratified with respect to landscape position. Each plot comprised a 20 m × 20 m quadrat sampling the overstorey vegetation and a nested 10 m × 10 m quadrat sampling all other vascular plants for species presence/absence information. Site coordinates were recorded with a GPS, mostly to c. 10 m horizontal accuracy but to c. 100 m (due to global GPS signal scrambling) for some of the sites which were established early on and have not been revisited. Sampling took place in spring, when the detection probability of annual and herbaceous perennial plants was anticipated to be greatest. Most sites were visited twice, in different years.

Non-native plant species (130 species, 5% of the total) were excluded prior to analysis. Eleven sites missing environmental data, and 21 sites showing signs of secondary salinisation, were also excluded, leaving a total of 650 terrestrial flora inventory plots. Major habitat types sampled included shrublands on sandy substrates (sometimes referred to as [kwongan vegetation](#), n = 193 sites) and woodlands on more nutrient-rich fine-textured soils (n = 349 sites). Other habitats represented in the remaining 108 plots include mallee shrubland on duplex soils, and low herblands on granite rock aprons.

In each 10 m x 10 m vegetation subplot a stratified and bulked soil sample was collected from the top 10 cm of soil. Soil samples were analysed at the Chemistry Centre of Western Australia for electrical conductivity (ECCO, mS^m⁻¹), pH in water, organic C (%), total N and P (ppm), (HCO₃) available P and K (ppm), exchangeable Ca, Mg, Na and K (me%), and for texture (% sand, silt and clay), McArthur (1991).

GDMs of species turnover and variation partitioning

We fitted generalized dissimilarity models (GDMs, Ferrier *et al.*, 2007) of species turnover across the inventory plots. Species turnover was defined as the change in species composition among site pairs quantified by the Sørensen dissimilarity index (Legendre & Legendre, 2012).

Species turnover was modelled as non-linear functions of selected climatic and topographic variables, selected soil variables, and inter-site geographical distances. Six candidate climatic variables, six candidate topographic variables, and ten candidate soil variables were considered at the outset.

The ten candidate soil variables included 9 of the 14 available soil chemical and textural variables and a weathering intensity index based on airborne gamma-ray spectrometry imagery and elevation (Wilford, 2012). Total P was included, rather than available P, because differences among sites in the former correlated slightly better with plant species turnover (Mantel $R = 0.19$ vs. 0.14). Similarly, exchangeable K rather than available K was included, because these two variables were very highly correlated ($R = 0.96$). Na was excluded as it was highly correlated with ECCO ($R = 0.83$). Similarly, total N was excluded because it was highly correlated with organic C ($R = 0.87$). Finally, just two of the three soil textural variables (Silt and Sand) were included.

The six candidate climatic variables were pre-selected from a much larger set of bioclimatic predictors generated and downscaled to a 9 second resolution in ANUCLIM v. 6.1 (Xu & Hutchinson, 2011). Pre-selection of climatic variables was based on their hypothesized importance in driving species turnover. We assumed that the effects of both precipitation and temperature would be strongest when water was either abundant (wet quarter) or limiting (dry quarter). Wet quarter rainfall was very highly correlated with total

annual rainfall ($R = 0.93$), hence the latter was excluded. We also included measures of seasonality in temperature (mean annual temperature range, °C) and radiation (standard deviation of weekly solar radiation estimates relative to their mean, %). Precipitation seasonality was highly correlated with mean temperature in the dry quarter ($R = 0.80$) and hence was not included.

The six candidate topographic variables were similarly pre-selected from a larger set available at the CSIRO Soil and Landscape Grid of Australia (clw.csiro.au/aclep/soilandlandscapegrid/index.html), which were generated by John Gallant and co-workers based on Australia-wide analyses of 3 and 1 second resolution digital elevation models. These were clipped to the study region and aggregated to match the 9s resolution of the climate data. We focused on six topographic variables that we assumed might indirectly capture aspects of local climatic variation relevant to plants. These were slope (degrees), Elevation (m), Elevational range (m, within 1km), Eastness [$\sin(\text{aspect})$], Northness [$\cos(\text{aspect})$], and a topographic wetness index. The latter was calculated as $\ln(\text{specific catchment area/slope})$, following Gallant & Wilson (2000).

A final subset of environmental variables for predicting species turnover was selected from among the candidate variables by permutation-based backward elimination. At each step of the procedure, each variable included in the environmental model was permuted in turn and the change in explained deviance relative to the un-permuted model was calculated. Permutations were run 1000 times, and the variable with the least significant contribution to explained deviance at each step was excluded. This procedure was repeated until all variables retained in the model made significant unique contributions to explained deviance ($p < 0.05$). Variation partitioning was then used to calculate the unique and shared contributions of the climatic and topographic variables together, the soil variables, and the inter-site geographical distances to deviance explained (Borcard *et al.*, 1992). GDM fitting used a modified version

of the R language (R Core Team, 2013) functions available at sites.google.com/site/gdmsoftware/ and variable selection and variation partitioning were run using custom-written R code.

Analysis of residual deviance

We extracted the standardized Pearson residuals of the final GDMs including all selected climatic/topographic and soil variables, and inter-site distances. Each residual value (positive, negative or zero) represented the prediction error, i.e. the difference between observed and predicted dissimilarity in species composition, for a pair of sample plots. To identify the major patterns in residual floristic dissimilarity, we ran a principal coordinates analysis (PCoA) ordination of the residual matrix with Cailliez correction for negative eigenvalues (Legendre & Legendre, 2012). PCoA produces independent axes of variation in model residual values across site pairs, such that any two sites with similar predicted dissimilarity errors relative to all other sites will tend to be located close to each other in ordination space. While PCoA in principle takes any distance matrix as input data, it does not correctly handle negative values in the matrix because all values are squared during the computation. However, Cailliez correction solves this problem, in addition to correcting for negative eigenvalues, because it involves adding a constant to all pair-wise values in the matrix (except for those on the diagonal). This results in a transformation of all values in the matrix into values ≥ 0 , whilst maintaining the absolute differences in observed vs. predicted dissimilarity represented in the original matrix. It should be noted that Lingoes correction for negative eigenvalues does not do the same, because the Lingoes constant is only added to values in the input matrix after they have been squared. Hence Cailliez correction and not Lingoes correction should be applied in analyses of GDM residuals. We then examined the

major residual floristic dissimilarity patterns in the dataset, as represented on the first three residual PCoA axes.

We first tested how much added deviance in species turnover was captured by each of these residual PCoA axes, above that explained by present-day environmental variation and geographical distances between sites. This was done by entering each axis as an added variable in a GDM alongside the final set of selected environmental predictors and geographical distance. The aim was not to actually use the residual PCoA axes to gain new model predictions, which would be circular, but simply to gain some idea of the relative importance of the missing factor or factors represented by each axis in contributing to regional floristic turnover.

We then mapped the patterns represented on the major residual PCoA axes (i.e., those that captured a substantial amount of residual floristic turnover) to look for any visually interpretable trends. To aid our interpretation of these unexplained floristic gradients we examined correlations between site scores on each residual PCoA axis and several sets of ancillary data: 1) a binary variable indicating whether or not the site belonged to one of the two main habitat types surveyed (shrublands and woodlands), 2) a binary variable indicating whether or not the site was on a granite outcrop, since these sites are proposed mesic refugial areas, and 3) the anomalies between predictions of recent and LGM total annual rainfall and mean temperature extracted from the Worldclim database, with LGM values based on the CCSM (Community Climate System Model) global climate model (Fig 1c, e).

Furthermore, we identified the ten species that were most strongly positively and negatively correlated with each of the major residual PCoA axis. We examined 1) whether these tended to represent particular life forms, and 2) their broader geographical ranges using maps in the online Atlas of Living Australia portal (ala.org.au).

RESULTS

Plant species richness

In total, 2453 native plant taxa were encountered in the 650 terrestrial inventory plots. These were usually identified as either named species or morphospecies, with just a few taxa identified to subspecific level. All are henceforth referred to as species. Species richness per plot ranged from 3-79 (mean 37, sd 16). The plant life forms represented, in descending order of prevalence, were shrubs (55% of species), perennial herbs (19%), annual herbs (12%), geophytes (7%), trees and mallees (5%), perennial climbers (0.6%), perennial parasitic shrubs or climbers (0.4%) and arborescent monocots (0.3%).

GDM and variation partitioning

Five climatic, one topographic and six soil variables were retained as predictors of species turnover (Fig 2). Total deviance in species turnover explained by these variables and by inter-site geographical distances was 33.5%. The soil and climatic variables explained sizeable independent fractions of variation, whereas deviance explained by geographical distance entirely overlapped with that explained by climate. The unique contribution of the only selected topographic variable (elevation) to explained deviance was negligible (0.2%, Appendix S1).

The three soil predictors with the greatest unique contributions to explained deviance were total P, Mg and pH (Fig. 3). Species turnover with phosphorus was predicted to be extremely rapid with small increases in availability in low phosphorus soils, but much less pronounced after a threshold of c. 50 ppm. The corresponding climatic variables were precipitation in the wet quarter, radiation seasonality and precipitation in the dry quarter. ~

Residual spatial structure in the flora

Residual axes 1 and 2 made significant added contributions to explained deviance (10% and 5% respectively, as compared with the total of 33.5% explained by the selected environmental variables and geographical distance), suggesting the existence of one or more major drivers of species turnover that were not captured by our predictor variables. The added contribution of residual PCoA axis 3 to explained deviance was, however, negligible (0.9%). Unexplained patterns on the first two residual ordination axes were hence deemed to be those of primary interest.

Intriguingly, site scores on residual axes 1 and 2 were almost fully correlated with those of the first two axes of a PCoA ordination of the original Sørensen floristic dissimilarity matrix (not illustrated). This implies that the two principal floristic gradients detectable in the wheatbelt dataset were almost entirely unexplained by the available predictor variables. Patterns on the third axes of the residual and Sørensen PCoAs were, however, more different ($R = 0.46$) suggesting that floristic variation described by this axis in the original dataset was partly driven by (or at least statistically explained by) the available environmental data.

Residual axis 1 illustrates a broad-scale spatial pattern, where positive site scores are predominantly found in a band across the southern wheatbelt, whereas sites with negative scores are more widespread (Fig. 4a). Site scores on this axis were positively correlated with the presence of sandy shrublands ($R = 0.41$) and negatively with the presence of woodlands ($R = -0.33$). This residual pattern is not, however, simply explained by the shrubland-woodland habitat division, as equivalent analyses of the shrubland and woodland subsets of plots showed the same broad-scale spatial pattern of unexplained floristic similarity in the south (results not illustrated). Sites on granite outcrops tended to have negative scores on this axis ($R = -0.20$). However, axis scores were not at all correlated with the anomalies between

recent and LGM mean temperature or total annual precipitation ($R = -0.00$ and $R = 0.02$, respectively).

The ten species whose occurrences correlate most strongly and positively with residual axis 1 scores comprise a variety of perennial life forms, of which six are shrubs, three are herbs, and one is a geophyte (Appendix S2). The geographical ranges of these species are mostly limited to south-western Australia, but two species also occur in south-eastern Australia. In contrast, the species with the strongest negative correlations with this axis include just two shrub species, with the remainder being either annual or perennial herbs, all of which are broadly distributed across semi-arid and in some cases arid inland Australia.

Residual axis 2 broadly indicates unexplained species turnover from the south-west towards the east of the study region, with south-westerly sites tending to have negative axis scores and easterly sites positive scores (Fig. 4b). Site scores on this axis were not at all correlated with the presence of shrublands ($R = 0.00$) and only weakly with the presence of woodlands ($R = -0.11$). However, sites on granite outcrops tended to have negative scores on this axis ($R = -0.41$), i.e., to be floristically similar to south-westerly sites. Furthermore, site scores on this axis were negatively correlated with the anomalies between recent and LGM mean temperature and total annual precipitation ($R = -0.23$ and $R = -0.24$, respectively). This is because of the general trend whereby the east of the wheatbelt, in particular, is predicted to have had lower LGM temperature and rainfall values than at present, whereas westerly sites are predicted to have been more buffered. Furthermore, site scores were slightly better correlated with the predicted absolute values of LGM than recent total annual precipitation ($R = -0.24$ vs. -0.18). The same tendency was apparent for the absolute values of predicted LGM vs. recent mean annual temperature ($R = -0.08$ vs. -0.03).

The ten species whose occurrences were most strongly and positively correlated with residual axis 2 are all perennial life forms, principally shrubs, most of which are widely

distributed across semi-arid and in some cases arid inland Australia (Appendix S2). In contrast, the species with the strongest negative correlations with this axis are all annual herbs. The geographical ranges of all, but two of these species extend widely across south-temperate Australia.

DISCUSSION

Current environmental drivers of regional species turnover

Our results highlight the joint importance of rainfall and temperature gradients, and the largely independent effects of soil gradients, in structuring plant communities in the south-west Australian wheatbelt. The effects of inter-site distances, which can be considered a surrogate for those of dispersal limitation, were not however separable from those of climatic gradients because of broad-scale spatial structure in climatic conditions in this region.

Phosphorus limitation of plant growth is to be expected in old landscapes where soil phosphorous has been gradually lost during long-term soil and ecosystem development (Vitousek *et al.*, 2010). Nonetheless, in south-western Australia, as in some extremely weathered tropical regions, low phosphorus environments are associated with a very high diversity of plant species with a plethora of adaptations for phosphorus and other nutrient acquisition (Lamont, 2003; Lambers *et al.*, 2006, 2011; Laliberté *et al.*, 2012, 2014, 2015). Our models predicted changes in soil phosphorus to be the most important driver of changes in plant species composition. However, this was only true of the most phosphorous-limited soils (those with < 50 ppm total P). Thereafter, other factors were statistically more important, such as magnesium and pH among the soil chemical variables. This suggests that soil phosphorous is not the predominant determinant of species turnover once a threshold in its availability is exceeded. Low phosphorous environments, as defined by the 50 ppm total P threshold, are nonetheless a very prevalent feature of the non-cultivated part of the wheatbelt

landscape. They comprised almost half of the sample plots in this study. Laliberté *et al.* (2012) similarly found evidence for a transition from phosphorus-limitation of plant growth in the oldest soils represented on a coastal dune chronosequence elsewhere in the SWAFR to limitation by nitrogen, and perhaps potassium and other micronutrients, in the youngest calcareous soils. However, in subsequent work on the same dune system Laliberté *et al.* (2014) emphasized the role of variation in soil pH over that in soil P as the major environmental filter determining potential site colonists from the regional species pool. In our study system, however, soil total P and pH were much less strongly correlated ($R = 0.19$ vs. $R = 0.97$), and the two variables had sizeable independent effects on species turnover.

Non-uniform patterns of species turnover, including abrupt transitions, were predicted along several climatic gradients, such as precipitation in the dry quarter. This might imply that tipping points exist, where small changes in climate in the future may induce abrupt changes in floristic composition (Guerin *et al.*, 2013). However, such patterns should be interpreted with caution. Furthermore, turnover patterns on the two most important climatic gradients, wet quarter rainfall and radiation seasonality were more uniform.

Elevation was the only topographic variable linked to species turnover in our model, and it played a minor role relative to that of the soil and climatic predictors, which is unsurprising considering the subdued topography of the region. Furthermore, interactions between topography and climate were not captured in our models, but some earlier work from the wheatbelt region suggests that species responses to local topography may change along rainfall gradients and that such patterns translate to the plant community level (Dirnböck *et al.*, 2002).

Interpreting unexplained species turnover

When modelling species turnover among sites it is common practise to partition explained variation into several components, such as the fractions explained here by climate, soils vs. inter-site distances. However, the unexplained fraction of variation has been considered a ‘black box’ about whose origins we can only speculate. The usual candidates for unexplained variation in plant species composition that are discussed include missing abiotic or biotic drivers vs. true ‘noise’ arising from chance dynamics of species colonization and mortality, and from sampling constraints. If major drivers are either missing or poorly specified in the model, this is likely to result in significant unexplained structure in the model errors. Here, we present a new method for identifying such major axes of unexplained species turnover. As we show here, interpretation of these axes can be aided by mapping their spatial patterns and particularly by the use of various sources of ancillary information (e.g. additional environmental variables, and species traits, geographical distributions, and perhaps phylogenetic relatedness).

Intriguingly, although climatic and soil predictors explained about a third of deviance in species turnover across our study region, analyses of the model residuals indicate that the two principal gradients in floristic composition detectable were not well explained by these variables. The most prominent unexplained pattern was the floristic similarity of many sites in the southern wheatbelt. Species whose occurrences were most strongly correlated with this pattern were mainly perennial shrubs or herbs restricted to south-western Australia, whereas species associated with negative scores on the same axis were mainly annual or perennial herbs with wide distributions across semi-arid and in some cases arid inland Australia.

A second residual axis reflected unexplained species turnover running broadly from the south-west to the east of the study region. Furthermore, sites on granite outcrops across the region tended to have negative scores on this axis, meaning that they share species with the south-westerly end of this gradient. The ten species most strongly correlated with this end of

the residual gradient are all annual herbs, which are either restricted in range to south-west Australia alone, or in many cases range into temperate south-eastern Australia. Their geographical ranges and association with granite outcrops, which collect moisture at their fringes, suggest that these are species of relatively mesic environments. In contrast, the species associated with the easterly end of this residual gradient are largely perennials of various life forms, with broad distributions into semi-arid and even arid inland Australia.

The southern wheatbelt is cooler on average than the north, but is more seasonal in terms of temperature and radiation, and receives more summer rainfall. However, both overall and winter precipitation peak in the very south-west. The major residual patterns that we have detected could hence simply reflect imperfect modelling of the effects of current climate on species turnover. A climatic interpretation is supported by the fact that both the life form composition and the broader geographical ranges of species strongly associated with either end of these two residual gradients differed. The extent to which historical vs. recent climatic conditions are involved is not entirely clear. Evidence of a historical origin for patterns on the first residual axis is lacking in our analyses. However, anomalies between recent and LGM mean annual temperature and total annual rainfall were correlated with values on the second residual axis. Furthermore, the absolute LGM values for these variables correlated better with axis scores than did recent climate values. Hence it is plausible that species responses to the last ice age have left a detectable signal in current turnover patterns in this region. Moreover, species responses to earlier glacial cycles may have been more pronounced. There is growing evidence that mid-Pleistocene climatic instability considerably fragmented the flora in the SWAFR (Byrne, 2007, 2008; Dalmaris, 2012; Nistelberger *et al.*, 2014). A further important point to recognise is that strong gradients in species turnover will only be detected if there is congruence in species distributions arising from their responses to either measured or unmeasured drivers. Even if species range dynamics under past climatic

fluctuations have been strong, if they have also been highly idiosyncratic, their effects would not be detected in this type of analysis.

Granite rock outcrops are proposed to have acted as inland refugia for plant species requiring more mesic conditions during drier climatic periods in the past (Hopper *et al.*, 1997; Byrne & Hopper, 2008; Schut *et al.* 2014). Indeed, genetic studies suggest long-term isolation of populations of numerous plant species on granite outcrops (Sampson *et al.*, 1988; Bussell, 1999; Yates *et al.*, 2007; Byrne & Hopper, 2008; Tapper *et al.*, 2014a, b). At first glance, the unexplained floristic link we detected between granite outcrops throughout the wheatbelt and wetter south-westerly sites lends some support to this idea. However, the fact that the species most strongly linked to this residual pattern were all annual herbs – many of which have broad southerly distributional ranges – suggests that it may be better explained by ongoing metapopulation dynamics than by historical population fragmentation, maintained by dispersal limitation.

Overall, we suggest that the two main residual gradients detected, which furthermore closely correspond to the two main floristic gradients detectable in the raw data, arise from the effects of species responses to aspects of climate that were not captured by our climatic predictor variables. Hence, climate matters for plant species turnover in this region even more than is apparent from the variation partitioning results. It is certainly possible that the available digital climate surfaces do not adequately capture current climatic conditions near the ground that determine plant species distributions, even in the generally flat wheatbelt, which contains a relatively dense network of meteorological stations. In addition, particular local climatic characteristics, such as the moisture-gathering effects of granite outcrops, were certainly not well captured, despite the inclusion of some topographic variables in our study. Furthermore, our models did not include any information on deeper soil properties or on water-holding capacity, which are likely to significantly influence plant distributions.

Fire regimes, habitat fragmentation, weed invasions and other disturbance factors undoubtedly also impact on plant species composition in this region (REF?). Missing factors such as these are likely to account for finer-grained residual variation in floristic turnover. It does not, however, seem likely that they explain the broad-scale residual spatial trends we have identified.

Future directions

Climate change simulations predict drier and warmer conditions for south-west Australia over the coming decades (Bates *et al.*, 2008). Hence, a logical next step might be to use present-day modelling results as the basis for projections of the degree of expected species turnover under different future climate scenarios (Blois *et al.*, 2013; Guerin *et al.*, 2013). However, aside from the uncertainty inherent in future climate projections, our results show that a failure to account for soil variation, and for the broad-scale patterns in residual floristic dissimilarity that we have identified, would result in substantial prediction errors. Future analyses should test and include high resolution digital soil layers. Determining how to account for the residual patterns we have identified will, however, be more challenging.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Deviance in species turnover explained by selected sets of climatic-topographic vs. soil variables and geographical distances in the full terrestrial flora of the wheatbelt, in shrublands and in woodlands.

Appendix S2 Ten species with the strongest positive and negative correlations with site scores on residual PCoA axes 1 and 2, their life form, and geographical range in Australia

BIOSKETCH

Mirkka Jones's main research focus is on ecological modelling of plant communities in highly diverse ecosystems, ranging from tropical rainforests to the Mediterranean-climate South-West Australian Floristic Region. Her co-authors' combined expertise extends from macro-ecological modelling of biodiversity to an in-depth knowledge of the flora and ecology of south-west Australia.

Author contributions: M.M.J., N.G., C.Y., S.F. & J.C.S. conceived the ideas; N.G. was part of the team that collected the vegetation data; K.M. & K.J.W. generated the climatic and topographic data; G.M. and K.M. programmed the GDM and variable selection functions; M.M.J. analysed the data; M.M.J., N.G. & C.Y. led the writing.