Nestedness patterns reveal impacts of reduced rainfall on seedling establishment in restored jarrah forest

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ABSTRACT

Directional climate change can potentially cause a nested pattern of species occurrences as species move or go extinct. That is, species-poor communities may become a nested subset of species-rich communities with climate change. There is a precedent for understanding these patterns in the context of historical climate change but few researchers have studied these patterns in the context of recent climate change. Here we show the value of nestedness analyses for understanding plant community responses to reduced annual rainfall using data on seedling establishment in restored jarrah forest between the years of 1992 and 2010. Specifically, we recorded the annual seedling establishment of species assemblages in plots 15 months after restoration. We tested to what extent jarrah-forest assemblages that established in low (< 1000 mm) rainfall years were nested within assemblages that established in years of moderate (1000–1200 mm) and high (> 1200 mm) rainfall, and whether assemblages established following lower standard restoration practice were nested subsets of those following higher standard practices. We also tested how both types of nestedness patterns varied among trait groups defined by status (i.e., native or non-native), life-form and seed size. We found high support for species and trait assemblages that established in dry years being a nested subset of assemblages that established in years of moderate rainfall, and consistently low support for nestedness of high in low, and moderate in low, rainfall years. Nestedness patterns associated with restoration practice were as we predicted. Recruitment failure in low rainfall years was the most parsimonious explanation for nestedness patterns associated with rainfall (i.e., selective environmental tolerance). Nestedness patterns associated with restoration practice were explained by differential seed dispersal of species via topsoil and their tolerance of inferior restoration practice. Taken together, we demonstrate the application of the nestedness approach for understanding community responses to climate change in a restoration context. Indeed, generalising species responses to climate change by linking these to ecological processes and traits will help to meet the current global demand for forest restoration. Therefore, we anticipate our findings will interest practitioners working to restore the world's forests under climate change.

Keywords

Beta diversity; climate change; ecological restoration; plant community dynamics; plant traits; species turnover.

1. Introduction

Current understanding of global climate change impacts highlights the potential for biotic responses to occur at all levels of biological diversity from genes through to biomes (Parmesan 2006, Bellard et al. 2012). Much attention has focused on predicting species responses to climate change and there have been calls to consider other levels of organisation such as communities (Devictor et al. 2010, IPCC 2014). Understanding community responses to climate change is of particular importance to conservation and restoration especially where goals are linked to ecosystem functions and services rather than conservation of particular species assemblages. A commonly used metric of community response to climate change is species richness which helps to detect net species loss and gain (e.g., Walther et al. 2005, Wilson et al. 2007). Species turnover describes differences in species composition of assemblages along spatial, temporal or environmental gradients (MacArthur and Wilson 1967, Anderson et al. 2011) and so provides another measure of community response to directional climate change. Species turnover can be seen as analogous to beta diversity, except that species turnover is specific to changes along a gradient, while beta diversity can also refer to non-directional variation in community structure (Anderson et al. 2011).

Traditional measures of species turnover (e.g., Peterson et al. 2002, Thuiller et al. 2005) tended to conflate the two distinct components of turnover, these being species replacement and nestedness (Baselga 2010). Nestedness is detected when the species in more species-poor communities are nested subsets of the species occurring in larger, more speciose communities (Patterson and Atmar 1986, Ulrich et al. 2009). The nestedness component of species turnover is due to systematic colonisations or extinctions along a gradient, such that communities at one end of the gradient

include only a subset of the species of those at the other end of the gradient (Ulrich et al. 2009). In contrast, species replacement describes the extent to which species are lost and replaced by new species, with perfect replacement thus implying that two communities have similar species richness, but no species in common. Recent developments of measures of species turnover differentiate between species replacement and nestedness, to understand better how they each contribute to species turnover (Baselga 2010, 2012; Albouy et al. 2012).

Several recent studies have measured species replacement and nestedness associated with spatial, temporal and climatic gradients to understand and project community responses to climate change. For example, a study of global freshwater fishes suggested a strong influence of Quaternary climate changes on modern-day patterns of beta diversity, with species replacement and nestedness being associated with climate stability and climate oscillations respectively (Leprieur et al. 2011). Selective extinction and colonisation of species associated with glaciation, and dispersal limitations owing to geographical isolation of drainage basins, were identified as likely mechanisms for the patterns of species turnover. For European mammals, species turnover has been largely driven by species replacement, with only a limited contribution of nestedness, a pattern which suggests significant influences of the steep latitudinal climate gradient at regional and continental scales and the existence of multiple climate refugia during the Pleistocene glaciations (Svenning et al. 2011). A steep climate gradient was again implicated in the assembly of non-native flora on mountains, where species assemblages at higher elevations were a nested subset of the assemblages at lower elevations likely due to progressive ecological filtering of species (Alexander et al. 2011). Unlike the previous two studies, the mechanisms responsible for species turnover could be isolated in this study because the arrival of the non-native species was recent and human mediated (Alexander et al. 2011). Lastly, in one of the few studies to compare the same assemblages before and after climate change, Patterson (1990) revealed the more recent assemblages of mammals, birds and herptiles in the Holocene to be nested in the historical assemblages, and that this pattern was mostly explained by extinction. Taken together, these studies support the prediction of nestedness

developing along climate gradients and identify local extinction and selective environmental tolerances as key causal mechanisms (Ulrich et al. 2009).

Studies linking patterns of species turnover to recent climate change are also emerging (e.g., Fox et al. 2014, Habel et al. 2015) and some studies have estimated the contribution of nestedness to these patterns (e.g., Benedetti et al. 2018). Here, we evaluate patterns of nestedness in species assemblages of restored jarrah forest to determine if these patterns are linked to rainfall amounts at seedling establishment. Annual rainfall varied 3-fold over the period of study (i.e., 469 mm to 1401 mm; Standish et al. 2015) in the context of regional wide reductions in mean annual rainfall that have occurred since the 1970s (Bates et al. 2008, CSIRO and Bureau of Meteorology 2014). Data describing seedling establishment of jarrah forest species were collected 15 months after each annual restoration effort between 1992 and 2010. A previous analysis of the same dataset revealed a significant effect of rainfall amounts on species richness of the assemblages (Standish et al. 2015). Specifically, species richness peaked with moderate amounts of rainfall at 30–60 days after the onset of the wet season (Standish et al. 2015). In this study, we investigated the contributions of nestedness to these variations in species richness. We categorized species assemblages according to the total wet-season rainfall at the time of their establishment: high (> 1200 mm), moderate (1000–1200 mm) and low (< 1000 mm), and tested pairwise combinations of these rainfall groups for nestedness. We also investigated the extent of nestedness between assemblages grouped according to a variable describing restoration practice (i.e., topsoil handling), which also affects species richness (Standish et al. 2015). Finally, we grouped species by traits that are ecologically meaningful in the context of seedling establishment, in order to determine if nestedness patterns varied with these traits.

Our ultimate aim was to infer the relative importance of selective environmental tolerance, local extinction and selective colonisation as community responses to restoration in a drying climate and to assess key plant traits underlying these responses. We predicted assemblages that established in

high rainfall years would be a nested subset of assemblages that established in moderate rainfall years, and assemblages that established in dry rainfall years would be a nested subset of assemblages that established under moderate rainfall. Such nestedness patterns would be consistent with selective tolerances of species to high and low rainfall amounts, respectively, and potentially, local extinction. A majority of jarrah forest species colonise restoration sites via the soil seedbank (Tacey and Glossop 1980). Thus, dispersal limitation is minimised when topsoil is stripped and applied, undiluted, to restoration sites less than six months after the forest at the donor site is cleared (Standish et al. 2015). We predicted that assemblages that established after inferior topsoil handling be a nested subset of assemblages that established after optimal topsoil handling. Such nestedness patterns would be consistent with selective colonisation of restoration sites.

2. Materials and methods

2.1. Study system

Jarrah forest grows on the nutrient-poor soils of the Darling Range in south-western Western Australia. Jarrah forest is dominated by jarrah (*Eucalyptus marginata* Donn ex Sm.) and marri (*Corymbia calophylla* Lindl.); bull banksia (*Banksia grandis* Willd.), sheoak (*Allocasuarina fraseriana* Miq.) and grasstree (*Xanthorrhoea preissii* Endl.) occur in the midstorey over a species-rich understorey of shrubs and herbaceous perennials (Bell and Heddle 1989). The region experiences a Mediterranean climate characterised by summer drought and winter wet seasons (Gentilli 1989). Seedling establishment generally occurs in the wet season (Abbott 1984, Bell et al. 1993, Grant 2006). The summer drought season occurs when monthly rainfall in mm is less than twice the mean temperature in °C and conversely, the winter wet season occurs when rainfall is more than twice the mean temperature (e.g., Bellairs and Bell 1990). We used this relationship and data from climate stations (i.e., running 30-day averages of both daily rainfall and maximum temperature) at the two study sites to define the wet seasons at each site between 1992 and 2010 (Standish et al. 2015).

Then we partitioned years into low, moderate and high wet-season rainfall using the trends in wet-season rainfall for the 19-year period (Fig. 1).

Fig. 1. Average species richness (Y) in plots (n = 40–86 plots per average) according to annual wet-season rainfall (X) at Huntly (HU) and Willowdale (WD) between 1992 and 2010; where $Y = 16.47 + 0.065X - 0.0202X^2$ at Huntly ($R^2 = 0.18$, d.f. = 16, $P = 0.21$), and $Y = 40.77 + 0.026X - 0.0067X^2$ at Willowdale ($R^2 = 0.03$, d.f. = 16, $P = 0.76$). Mod = moderate rainfall. The sequence of annual rainfall amounts in the 19-year period at Huntly was: high, moderate, low, moderate, high, low, moderate $\times$ 3, low, moderate, high, moderate $\times$ 2, low, high, moderate, high and low. The same sequence at Willowdale was: high, moderate, low, moderate, high, low, mod $\times$ 3, low, mod $\times$ 3, high, low, high, moderate $\times$ 2, low.

Alcoa of Australia Ltd (hereafter Alcoa) has mined bauxite in the jarrah forest since 1963; approximately 550 ha of forest has been cleared, mined and restored each year since then (Koch 2007). Restoration after mining includes landscaping, and deep and shallow soil ripping, as described by Koch (2007). A critical step of restoration practice is the application of fresh topsoil, stripped from sites recently cleared of forest, to increase plant species dispersal and recruitment from the soil seed

bank (Tacey and Glossop 1980, Standish et al. 2015). Thus, any delays between forest clearing and the topsoil stripping and between stripping and spreading of the topsoil onto the restoration site results in reduced richness of species that establish compared with sites where there were fewer (i.e., less than 6 months total) or no delays between these steps (Standish et al. 2015). Other topsoil-handling practices to optimise seedling establishment include topsoil screening to concentrate the seeds by removing the inert gravel fraction from the soil and minimal dilution of topsoil with sub-soil (Koch 2007). We derived a composite measure of topsoil handling by scoring these practices on a scale of 1 to 7 where a score of 1 was worst (i.e., delays, dilution) and a score of 7 was best (i.e., no delays, no dilution; Standish et al. 2015). These data were available for 1444 plots (i.e., 75% of the total number of plots). After the application of topsoil, the seeds of woody and herbaceous species are broadcast, and finally fertilisers are applied (Koch 2007). Unlike topsoil handling, the species richness and composition of the seed mix had no statistically significant effect on species richness and other measures of restoration success (Standish et al. 2015).

2.2. Sampling design

We monitored the establishment of seedlings in plots 15 months after each year's restoration effort at two sites within Alcoa's mining lease: Huntly 32°37'S 116° 03'E and Willowdale 32°55'S 116°05'E. Monitoring captured seedling establishment triggered by the first and second wet seasons after the onset of restoration. These data described the species composition of the newly restored jarrah forest within 40–86 plots at each site in each year between 1992 and 2010; there were data for $n = 1938$ plots in total (Fig. 1). Plot number increased with the number and size of the mine pits restored each year at Huntly and Willowdale. Despite being proximate in space, restoration practice and plant species composition and abundance can differ between Huntly and Willowdale (Standish et al. 2015), which warranted separate analyses for each site. Data were recorded as species frequencies based on their presence within five 4 m × 4 m quadrats nested within 20 m × 20 m plots. Scores were 0, 20, 40, 60, 80 or 100 whereby a score of 0 indicated absence and a score of 100 indicated

presence in all five quadrats. We excluded data for taxa that could not be identified to species level owing to their small size ($n = 15$ taxa) so that the assemblage and trait datasets were matched; there were data for 476 species in total. Plant traits included: status (native, $n = 367$ species; non-native, $n = 109$ species), life form for groups represented by more than 12 species, these were: annual forb, $n = 107$ species; perennial forb, $n = 129$ species; annual grass, $n = 17$ species; shrub, $n = 174$ species (of 11 life forms in total) and seed size (split into three groups according to order of magnitude: small 0.005–0.5 mg, $n = 162$ species; medium 0.5–5 mg, $n = 177$ species and large 5–1000 mg, $n = 137$ species). Status and life-form were ascribed with reference to the Western Australian Herbarium (2012) whereas seed size was measured or retrieved from the Seed Information Database (Royal Botanic Gardens Kew 2012).

2.3. Statistical analysis

Several metrics have been developed to quantify and test nestedness (Almeida-Neto et al. 2008) and several software packages are available to compute these metrics. We explored the use of BINMATNEST (Rodríguez-Gironés and Santamaría 2006), which calculates 'T', the matrix temperature measure (Atmar and Patterson 1993), as well as ANINHADO (Guimarães and Guimarães 2006) and NODF programs (Almeida-Neto and Ulrich 2011), which both calculate the NODF, *Nestedness based on Overlap and Decreasing Fill*, index. We opted to quantify nestedness using the NODF index because of its superior statistical properties (Almeida-Neto et al. 2008), and a recent modification of the original NODF-index permitted the use of quantitative data (rather than presence-absence data) to estimate nestedness (i.e., WNODF; Almeida-Neto and Ulrich 2011). The WNODF index is calculated using standard species abundance matrices, with columns for plots and rows for species. We recoded the WNODF calculation algorithms in R (R Core Team 2016; Appendix S1) so that it could handle plots assigned to unordered or ordered factor levels: in this case the three rainfall classes and seven topsoil handling classes. Perfect nestedness is rarely observed in nature; however, the degree of nestedness can be measured and compared with null models (Patterson and

Atmar 1986, Ulrich and Gotelli 2013). We first calculated and tested the pairwise nestedness between all pairs of the three rainfall categories (i.e., six comparisons using species and trait data for 1938 plots). Then we grouped plots according to topsoil handling and looked for evidence of sequential nestedness from worst practice to best practice and vice versa (i.e., two sequential comparisons using data for 1444 plots). We also calculated the mean topsoil handling scores for high, moderate and low rainfall years to check if restoration practice was related to rainfall because any relationship might influence nestedness patterns ascribed to rainfall.

Since our focus was the extent to which the species within one set of plots were nested subsets of the species within another set of plots, we calculated nestedness based only on column/plot comparison (i.e., we used the test statistic WNODFc; Almeida-Neto and Ulrich 2011). We did not include row/species comparisons because we were not concerned whether the plots occupied by certain species were a subset of the plots occupied by other species (and so we did not consider the test statistics WNODFr or WNODF, which combines WNODFc and WNODFr (Almeida-Neto and Ulrich 2011). To evaluate statistical significance, the observed WNODFc index was compared to the 1000 WNODFc values obtained from abundance matrices randomised by column. Using a null model algorithm randomised by column was the logical choice given our focus on calculating WNODFc, and ensured row and column totals were consistent (Gotelli 2000). We could have randomised the rows as well but it would not have made a difference to the WNODFc calculations. The WNODFc nestedness index thus indicates the extent to which species are less abundant within one group of sites than within a second group of sites, and a significant WNODFc index ($p < 0.05$) thus indicates that this nestedness is more than would be expected to be observed 95% of the time if those same sites were grouped at random. Finally, we constructed Venn diagrams to display the number of exclusive and shared species among low, moderate and high rainfall years at the two study sites. We used the diagrams to understand the contribution of species replacement to species turnover, as a complement to our nestedness analysis (Louzada et al. 2010).

Results

Species assemblages that established in low rainfall years were significantly nested within the assemblages that established in moderate rainfall years at Huntly (Table 1). Species assemblages were sequentially nested at Willowdale, with low nested within moderate rainfall years and moderate within high rainfall years (Table 2). Nestedness patterns for the assemblages grouped by traits followed a variety of patterns, with some trait-groups showing consistency with the nestedness pattern for the overall species assemblages at each site (Tables 1 and 2). Each dataset showed a degree of nestedness using WNODFc metrics (Tables 1 and 2). Overall, at both sites, there was high support for species and trait assemblages that established in low rainfall years being nested within assemblages that established in years of moderate rainfall, and consistently low support for nestedness of high in low, and moderate in low, rainfall years. The largest discrepancy between sites was for assemblages that established in moderate rainfall years being nested in high rainfall years, for which there was high support at Willowdale and no support at Huntly.

Table 1. Pairwise nestedness values for species and trait groups in assemblages of restored jarrah forest at Huntly according to wet-season rainfall at seedling establishment. High was > 1200 mm, mod is short for moderate and was 1000–1200 mm, and low was < 1000 mm; ‘in’ is short for ‘nested within’, for example, ‘high in mod’ tests whether assemblages that established in wet years were a nested sub-set of assemblages that established in moderate rainfall years. Asterisks denote statistical significance of nestedness calculated by randomisation tests: *P<0.05 and **P<0.01.

Response	High in mod	Low in mod	Low in high	High in low	Mod in high	Mod in low
All species	0.039	0.402**	0.376	0.326	0.326	0.301
Native species	0.373	0.407**	0.389*	0.318	0.337	0.302
Non-native species	0.387**	0.336	0.301	0.384**	0.289	0.326
Annual forbs	0.405*	0.402*	0.374	0.370	0.331	0.325
Perennial forbs	0.387	0.424**	0.413*	0.326	0.363	0.321
Annual grasses	0.255	0.240	0.249	0.299	0.268	0.302*
Shrubs	0.356*	0.369**	0.338	0.314	0.301	0.290
Small seeded	0.411*	0.401*	0.369	0.376	0.336	0.336
Medium seeded	0.384*	0.417**	0.388*	0.318	0.321	0.286
Large seeded	0.335	0.362*	0.354	0.311	0.326	0.310

Table 2. Pairwise nestedness values for species and trait groups in assemblages of restored jarrah forest at Willowdale according to wet-season rainfall at seedling establishment. High was > 1200 mm, mod was 1000–1200 mm and low was < 1000 mm, and ‘in’ is short for ‘nested within’. Asterisks denote statistical significance of nestedness calculated by randomisation tests: *P<0.05 and **P<0.01.

Response	High in mod	Low in mod	Low in high	High in low	Mod in high	Mod in low
All species	0.321	0.395*	0.425**	0.285	0.389*	0.320
Native species	0.307	0.387*	0.431**	0.285	0.404*	0.325
Non-native species	0.389	0.425**	0.389	0.316	0.327	0.318
Annual forbs	0.348	0.408	0.429*	0.331	0.410	0.370
Perennial forbs	0.330	0.352	0.391	0.354	0.417*	0.399*
Annual grasses	0.418**	0.436**	0.353	0.306	0.272	0.259
Shrubs	0.277	0.381**	0.427**	0.240	0.378**	0.276
Small seeded	0.362	0.421*	0.427*	0.320	0.392	0.348
Medium seeded	0.322*	0.367	0.398*	0.319	0.354	0.354
Large seeded	0.280	0.366**	0.409**	0.241	0.357*	0.262

264 Nestedness patterns associated with restoration practice were as predicted, whereby assemblages
265 that were restored under worst practice were sequentially nested within assemblages that were
266 restored under best practice (Table 3). There were exceptions to this rule at Willowdale due to the
267 higher frequency of establishment of non-native species under worst practice, which is also reflected
268 in the results for annual forbs and annual grasses (i.e., trait groups that non-native species
269 dominate) as well as for the non-native species trait group (Table 3). Lastly, topsoil handling scores
270 were greater in moderate and high rainfall years compared with topsoil handling scores in low
271 rainfall years (mean $\pm$ 95 % CI): high (4.12 ± 0.27), moderate (3.87 ± 0.19) and low (3.02 ± 0.24 ; $F_{2,1441}$
272 = 19.01, $P < 0.001$). In other words, best practice (low scores) occurred more often in low rainfall
273 years than in moderate and high rainfall years.

Table 3. Sequential nestedness values for species and trait groups in assemblages of restored jarrah forest at Huntly and Willowdale according to topsoil handling at seedling establishment. Topsoil handling was scored on a scale of 1 to 7 where 1= best (standard) and 7 = worst (inferior) practice. Again, 'in' is short for 'nested within'. Asterisks denote statistical significance of nestedness calculated by randomisation tests: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Response	<u>Huntly</u>		<u>Willowdale</u>	
	Inferior in standard	Standard in inferior	Inferior in standard	Standard in inferior
All species	0.488***	0.224	0.478**	0.229
Native species	0.500**	0.220	0.525**	0.191
Non-native species	0.354	0.319	0.287	0.462**
Annual forbs	0.417**	0.317	0.366	0.414*
Perennial forbs	0.533**	0.221	0.592**	0.170
Annual grasses	0.257	0.252	0.249	0.444**
Shrubs	0.422**	0.246	0.457**	0.202
Small seeded	0.449**	0.291	0.391	0.378
Medium seeded	0.491**	0.222	0.527**	0.199
Large seeded	0.429**	0.249	0.453**	0.202

The majority of species were shared among high, moderate and low rainfall years, at both sites (i.e., 60.4 % and 61.7 % of the respective species pools; Fig. 2). There were fewer species shared between low and high rainfall years, than between low and moderate, and high and moderate rainfall years. The sites were similar in terms of the relative percentage of both shared species and exclusive species between and among the rainfall groups (i.e., <4 % difference) with the exception of species that established exclusively in wet years (i.e., 9.2 % at Huntly versus 4.3 % at Willowdale; Fig. 2). The two canopy dominants, jarrah and marri, and the common mid-storey species, bull banksia, sheoak

and grasstree, established as frequently in low, moderate and high rainfall years (data not shown). Native perennial forbs, native shrubs and non-native annual forbs dominated the species pool at both sites (Table 4). Trait-groups were not strongly associated with rainfall; a few species were exclusive to low, moderate or high rainfall years but the majority of species representing the trait groups established in two or more of low, moderate and high rainfall years (Table 4 and Fig. 2).

Fig. 2. Venn diagrams representing the distribution of species according to wet-season rainfall at seedling establishment at the two study sites, Huntly and Willowdale; where high is > 1200 mm, mod is 1000–1200 mm and low is < 1000 mm. In each segment, data are species counts and the percentage of species relative to the total (γ).

Table 4. Traits of plant species exclusive to low, moderate or high rainfall years at Huntly and Willowdale, where n = number of species and pool = species pool. Trait groups with fewer than 12 representative species are not listed (n = 26 and 28 trait groups in total for Huntly and Willowdale respectively).

Trait groups	Huntly				Willowdale			
	HIGH	MOD	LOW	Pool	HIGH	MOD	LOW	Pool
Native annual forb, small seed	5	0	0	33	2	2	1	36
Native perennial forb, small seed	4	5	4	34	2	5	6	34
Native perennial forb, medium seed	1	0	1	40	0	5	2	39
Native perennial forb, large seed	2	0	1	24	0	1	2	24
Native shrub, small seed	4	2	0	16	1	1	1	15
Native shrub, medium seed	4	4	2	55	1	7	4	57
Native shrub, large seed	6	7	4	81	2	7	3	74
Non-native annual forb, small seed	6	0	3	34	3	5	3	39
Non-native annual forb, medium seed	0	4	3	14	0	0	1	13

3. Discussion

Nestedness analysis can inform the selection of sites for biodiversity conservation in landscapes altered by human-mediated processes including habitat fragmentation (Ficetola and De Bernardi 2004) and land-use change (Louzada et al. 2010). High nestedness suggests a strategy of conserving species-rich sites whereas low nestedness can indicate high species replacement (i.e., if coupled with a high number of species that are exclusive to sites), which suggests a strategy of conserving multiple sites, and not necessarily the species-rich sites (Patterson and Atmar 1986, Patterson 1990, Gibson et al. 2017). Additionally, nestedness analysis can be repeated for different taxa of the same community, or coupled with data on species characteristics, to help identify groups of species or

taxa at risk of extinction in response to human-mediated disturbance (Ficetola and De Bernardi 2004, Feeley et al. 2007, Louzada et al. 2010). A majority of studies have focused on the effects of habitat fragmentation on nestedness patterns. In this paper, we investigated nestedness patterns associated with rainfall for overall species assemblages and smaller trait-based species groups, and we compared these patterns to the strong indications of nestedness associated with restoration practice. Our analysis of nestedness and species exclusivity patterns helps to understand if nestedness or species replacement underlie small but significant changes in species richness associated with low rainfall amounts at seedling establishment (Standish et al. 2015).

We found evidence of strong nestedness among rainfall groups for both overall species assemblages and trait-based groups. Different patterns of nestedness at each site were consistent with patterns of species richness whereby species richness was maximised in years of moderate rainfall at Huntly but years of high rainfall at Willowdale. Nonetheless, assemblages that established in low rainfall years at both sites were a species-poor subset of the assemblages that established in moderate rainfall years at Huntly or moderate and high rainfall years at Willowdale. This trend was evident despite best practice having occurred more often in low rainfall years than in moderate or high rainfall years. Delays between vegetation clearing, topsoil stripping and spreading might be reduced in dry years owing to the greater opportunity for these earthworks compared with wet years when rain could limit opportunity for earthworks. Regardless, nestedness patterns associated with rainfall cannot be attributed to differential dispersal of species to plots via topsoil. In contrast, nestedness patterns associated with restoration practice are likely explained by differential dispersal of species to plots and their tolerance of inferior restoration practice. Non-native species with wind-dispersed seeds (e.g., Asteraceae, Poaceae) can colonise stock-piled soil (Koch and Ward 1994) and germinate rapidly following soil disturbance associated with additional topsoil handling (i.e., dilution) and the onset of the wet season (Ward et al. 1996). Taken together, these findings suggest that nestedness patterns associated with rainfall are driven primarily by the species' responses to the rainfall gradient.

While deducing process from nestedness patterns requires additional data (Ulrich et al. 2009), the low percentage of species and traits exclusive to low, moderate or high rainfall years suggests that local extinction of species from restored jarrah forest has not significantly contributed to nestedness patterns. The system is likely buffered from local extinction by three interacting factors. One relates to the temporal pattern of annual rainfall. Decline in annual rainfall, has occurred in the region over the past forty years (Bates et al. 2008), and yet in our 19-year dataset, low rainfall years were wedged between years of moderate and high rainfall amounts, and there was at least 3-years interlude between dry years. Thus, plant species that require moderate or high rainfall to establish may have the opportunity to do so having missed just one opportunity for recruitment. The missed opportunity is unlikely to be significant for the jarrah forest species that maintain a persistent soil seed bank (e.g., perennial forbs and shrubs; Ward et al. 1997), but could be significant for rare species with short-lived soil seed banks. For example, two of the five annual forbs (with small seeds) exclusive to high rainfall years at Huntly were rare at Huntly and not recorded at Willowdale, which could increase their susceptibility to local extinction. However, even these species may be buffered from extinction by their occurrence in nearby mature jarrah forest. Vegetation is cleared for mining in patches with unmined jarrah forest or restored jarrah forest at different stages of maturity occurring in the landscape matrix. Furthermore, fire is a common disturbance of mature forest in this landscape, which facilitates recruitment of many native shrubs and trees. Overall, the temporal respite from low rainfall years, the traits of jarrah forest species, and the patchy nature of restoration and fire, work together to prevent species being lost from the restored jarrah forest.

A likely explanation for the nestedness patterns for native species assemblages is selective tolerance of rainfall conditions by some species during seedling establishment. This interpretation is consistent with what is known about the germination requirements of native seeds (Bell et al. 1993). While germination syndromes reflect adaptation to environmental stresses more broadly, and especially fire, the onset of winter rainfall and temperatures cues seed germination and seedling establishment for many jarrah forest species. The available data suggest sensitivity of the two dominant canopy-

trees, jarrah and marri, to dry soils and the cold micro-climates that can affect some restoration sites (McChesney et al. 1995). We found no evidence for the establishment of these species being different among low, moderate and high rainfall years. Beyond this study, there are limited data for other jarrah forest species. We have identified five native annual forb species that appeared to show marked intolerance of low rainfall years but further study would be required to confirm this finding because all five species were rarely observed (i.e., recorded three times or less) and are therefore prone to the passive sampling effect. This effect often contributes to nestedness patterns because regionally abundant species are more likely to colonise a site compared with regionally rare species (Leibold et al. 2004, Ulrich et al. 2009). More generally, the majority of plant species (native and non-native) recruited regardless of rainfall at seedling establishment. Perhaps rainfall reliability is more critical for seedling establishment of these species rather than rainfall amount (Standish et al. 2015).

The nestedness patterns we identified have important implications for jarrah forest restoration and management under climate change. The prevalence of nestedness patterns whereby assemblages that established in low rainfall years were nested within assemblages that established in moderate or high rainfall years suggests that wet-season rainfall amounts greater than 1000 mm is optimal for establishment of most jarrah forest species. Future research on the impacts of projected rainfall decline (CSIRO and Bureau of Meteorology 2007) on jarrah forest restoration might use this rainfall amount to guide predictions for seedling establishment and re-plant the few at-risk species when necessary. For now, the key implication of this study is consistent with that of the previous study using the same dataset, which is that species richness of restored jarrah is maximised under best restoration practice (Standish et al. 2015). In that study we discovered that the negative impacts of low rainfall can be offset by best restoration practice that tends to coincide with low rainfall years. We also showed that establishment of non-native species can be reduced by following best practice. Beyond these implications there are some outstanding questions that could impact the restoration and conservation of jarrah forest into the future. A key outstanding question is the effect of

repeated, consecutive droughts (associated with low rainfall years) on the establishment and persistence of jarrah forest species. A recent study of nearby shrubland vegetation has highlighted the potential impact of sequential disturbances on similar Mediterranean-type ecosystems (Gower et al. 2015). Additionally, drought may interact with fire to influence vegetation dynamics of both restored and unmined jarrah forest. Indeed, a recent study has documented increased potential for wildfire in unmined jarrah forest following drought-induced tree death and drought creating more favourable microclimates for fire ignition and spread (Ruthrof et al. 2016). These topics are worthy of more research and the findings would likely inform future management of jarrah forest in this landscape.

4. Conclusions

Our findings suggest that temporary species 'loss', or more specifically recruitment failure, rather than species loss and replacement, are responsible for species turnover during seedling establishment under low rainfall years in restored jarrah forest. Species loss is temporary because while dry conditions may prevent recruitment in some plots in low rainfall years, these same species have opportunities for recruitment at different plots in subsequent, wetter rainfall years. Consequently, both at the species-level and the community-level there is evidence of seedling establishment being resistant to the drying climate, at least to the extent so far experienced (Standish et al. 2015, this study). However, if the projected changes to climate eventuate, then local extinction could become a significant component of species turnover as sequences of dry years become too long for some species to persist. Additionally, species replacement could increase in the future too as species 'move' with their preferred climate—where species movement via the soil seed bank is determined by the standard of restoration practice. Outside the restoration context, high species turnover is well documented for the region. Two recent studies of plant species turnover for forests, woodlands and shrublands growing along the steep rainfall gradient that extends from the wet coast to the arid interior identify rainfall, current and possibly historic, as being an important

driver of these patterns (Fitzpatrick et al. 2013, Jones et al. 2016). Furthermore, these studies and one other of species turnover in shrublands growing along the same rainfall gradient, consistently identify dispersal limitation as a factor contributing to high species turnover at varying spatial scales (Fitzpatrick et al. 2013, Jones et al. 2016, Gibson et al. 2017). Consequently, some plant species at the drier end of the regional rainfall gradient may be at risk of extinction due to climate change (Renton et al. 2012). Large-scale ecological restoration efforts within the region offer the opportunity to test the assisted migration of these species and to monitor community response. Such experimental data are critically needed to guide management interventions for biodiversity conservation under climate change.

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Appendix A. Supplementary material

Supplementary material A contains the R code written by Michael Renton that we used to calculate nestedness.

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