



## 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. 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 changes to climate. 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.

### 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).

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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 (Leprieux 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). While species replacement can also develop along climate gradients, nestedness becomes more likely as assemblages decay to a set of tolerant species under extreme conditions (Patterson and Atmar, 1986, Worthen et al., 1998).

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., 469–1401 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. Using the findings of Standish et al. (2015) as a guide, 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 low rainfall years would be a nested subset of assemblages that established under moderate rainfall. Thus, we predicted that most species would establish in moderate rainfall years, 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 (0–15 cm depth) is stripped and applied at the same depth 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 (Gentili, 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. 1A).

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

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