

## Investigating the impact of plant traits on community structure in fire-prone woody vegetation using a model of 288 plant functional types

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### Introduction

A number of models provide potential explanations for the persistence of high plant species diversity of fire-prone Mediterranean-type ecosystems (e.g. Groeneveld et al. 2002). However, these models often deal with only a few species or are rather abstract and do not allow the investigation of detailed questions of community structure. We developed a spatially explicit, individual- and rule-based model for theoretically-possible plant functional types (PFTs) based on seven traits thought to be important for the persistence of woody perennials in fire-prone environments. In this paper we present the importance of seed input from a regional seed pool for the structure and diversity of a local plant community. We compare our simulation results with field data for a study site in the northern sandplains of the Mid-West region of Western Australia near the town of Eneabba, 270 km north of Perth, where 38 Plant functional types co-occur. We focus particularly on the following three questions: 1) Does seed input from a species-rich regional PFT pool increase local PFT richness and diversity? How do potential effects depend on 2) the mode (equal seed input number vs. equal seed input mass from all PFTs of the regional pool) and 3) the intensity (from low to high) of seed input?

### Materials and Methods

We conducted two simulation experiments: (i) Experiments with all 288 PFTs to determine a competitive hierarchy and (ii) experiments with the subset of 38 PFTs found for a field site on the Eneabba sandplain in Western Australia, to investigate the importance of regional and local processes for diversity maintenance. Each PFT is characterised by seven traits: *regeneration mode* (fire killed or resprouter), *seed production* (low, moderate and high), *seed size* (small, medium, large), *maximum crown diameter* (4m for shrubs and 1.2m for subshrubs), *seedling drought tolerance* (less, more), *dispersal mode* (short-range or long range) and *seed bank type* (canopy or soil). The ranges for all trait values are discrete and resulted in 288 possible PFTs. The simulation model is individual based and spatially explicit following the field of neighbourhood approach, i.e. the crowns or root systems of neighbouring adult plants can overlap and compete for space. After initialization, ecological processes are iteratively simulated for annual time steps. At the beginning of each time step we determine stochastically (based on a Weibull distribution) whether a fire occurs in the local community or not. If a fire occurs, fire survival, dispersal of canopy-stored seeds, and germination are simulated. If the local community is not burned, inter-fire survival of plants, competition, growth, establishment, seed production and dispersal of soil-stored seeds are simulated. How these processes are simulated in detail is described in Esther et al. (subm.). All simulations were conducted for at least 1,800 annual time steps and for 20 replications. At the end of each simulation, PFT richness, diversity and the distribution of traits among all coexisting individuals were recorded as model output. For the immigration experiments, seed immigration occurs at each time step for all PFTs regardless of their storage mode as a simplifying assumption since recruitment is mostly cued to fire in any case. We used two seed input scenarios; while the overall seed input mass was the same for the two scenarios, the first used equal seed number for all 38 PFTs (at input densities 0.161 and 1.61 seeds/m<sup>2</sup>, respectively), and the second, equal seed mass. In the latter case, seed input mass was divided between PFTs based on 11 PFTs with large seeds (50.00 mg/seed), 14 PFTs with medium seeds (8.58 mg), and 13 PFTs with small seeds (0.77mg), resulting in lower seed immigration numbers for the 11 large seeded PFTs (0.634 and 6.34 seeds/m<sup>2</sup>) and higher numbers for the 14 moderate sized seeds (4.707 and 47.07 seeds/m<sup>2</sup>) and 13 small seeded PFTs (48.648 and 486.48 seeds/m<sup>2</sup>), respectively.

### Results

The main result of the first simulation experiment is that virtual "super types" (e.g. resprouters with high seed production and large seeds) dominate the modelled local shrub community. The exclusion of 'super types' increases the number of co-existing PFTs and thus PFT diversity. In the second simulation experiment only 13 (median) of the 38 PFTs were able to coexist without seed immigration at the end of the simulations. However, the number of coexisting PFTs increases if seed immigration is included (Figure 1a). The equal seed mass scenario produces higher PFT richness at low seed immigration levels than does the equal seed number scenario: For the equal seed input mass scenario all 38 PFTs coexist for all levels of seed immigration, apart from a few outlier simulations (Figure 1). Without seed immigration, the median Shannon Diversity Index (SDI) is 1.67 after 1800 simulated years (Figure 1b) compared to a SDI of 2.88 calculated from the field data. The SDI increases to more realistic values with increasing immigration rates (Figure 1b). The level of diversity is associated with a significant interaction between immigration

intensity and seed input scenarios (LM,  $F(1,156)=13.6$ ,  $P<0.05$ ). The SDI increases significantly with increasing immigration intensity, with significant differences also between the equal seed input number and equal seed input mass scenarios. For the same immigration level, the SDI is always higher for the equal seed input mass per PFT scenario (Figure 1b).

### Discussion

In our first experiment, we could identify PFT “super types”, which reduced species richness and diversity. However, no species with these sets of attributes occur in reality, suggesting that they represent unrealistic sets of life history attributes that cannot arise due to trade-offs and constraints in resource allocation. Elimination of these types increased diversity substantially. In our second simulation experiment we investigated the impact of seed immigration intensity on plant functional type (PFT) richness and diversity in a simulated species-rich plant community based on field data for a Mediterranean-type, fire prone shrubland from Western Australia (with 38 PFTs). Our simulation results show that moderate levels of seed input can explain the species richness and diversity measured at the study site.

For PFT richness and SDI, the results show that immigration of seeds is a potential explanation for co-existence and diversity patterns. Without seed immigration the simulated community represents an isolated vegetation patch. Under these conditions the model predicts that the initially species rich community would decline towards a community which is dominated by only a few PFTs. These findings agree with the neutral theory, where isolated local communities drift towards the monodominant state (Hubbell 2001), although the PFTs are not neutral in our case. The model suggests that diversity is a function of dispersal as a regional process and local competitive processes associated with differences in demographic parameters and responses to fire. The importance of seed immigration also has been shown in empirical sowing experiments (Turnbull et al. 2000). The composition of seed rain is most often dominated by small seeded species, and since seed mass is generally considered to correlate with competitive ability, the dominance of small seeds in seed rain supports the colonization-competition trade off. Our simulation results are in accordance with these findings. The seed mass scenario, which considers a size-biased seed rain composition, produced much better results than the equal seed number scenario. However, it is difficult to determine empirically the density of seeds needed to maintain the current species diversity and community structure of a given ecosystem. Models allow the quantification of parameters that are difficult to measure in the field.

Our approach allows us to investigate not only patterns of species richness and species diversity, but also patterns of the frequency distribution of plant functional type traits, such as regeneration mode and seed size, among individuals in a community (not shown here). Seed immigration has been shown, as in our study, to positively contribute to species coexistence and diversity. However, consideration of detailed trait abundance patterns shows that seed immigration is not yet able to describe all important community level patterns and that further explorations of this approach are needed.

### References

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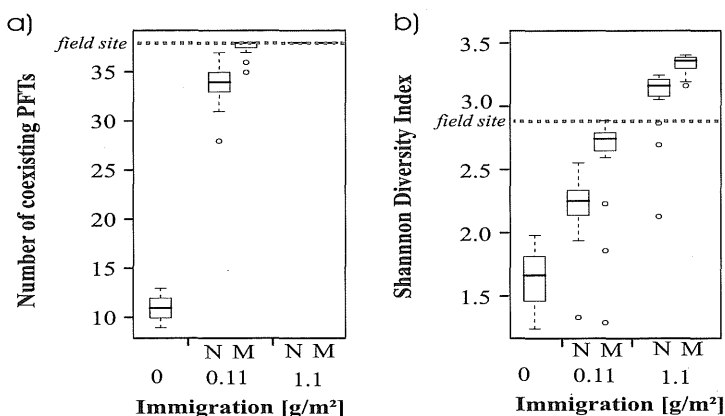


Figure 1. Box and whisker plots of a) Number of coexisting PFTs and b) Shannon Diversity Index, in relation to immigration intensity levels and seed input scenarios: equal seed input numbers (N) and equal seed input masses (M) for all PFTs. Centre, bottom and top lines of the box plots are the median, 25<sup>th</sup> and 75<sup>th</sup> percentiles respectively. Whiskers are 1.5 times the interquartile range; outliers are data points which lie beyond the extremes of the whiskers.