Defining plant functional groups to guide rare plant management

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Abstract To effectively manage plant populations for conservation, there is a need to provide reliable information on the conditions required for maintaining viable populations. This is particularly true for the management of populations of rare plant taxa. Western Australia contains over 45% of Australia's gazetted rare or threatened flora, 80% of which are found within the highly fragmented southwest region. Resources do not exist to undertake comprehensive studies on the population dynamics and demographics for every rare

Nomenclature Paczkowska and Chapman (2000).

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plant of this diverse region. Here, we describe a method of classifying rare plant taxa into functional groups as a basis for guiding rare flora conservation and management. Data on four floral and two life-history traits were collected for each of the 351 declared rare flora taxa of Western Australia. A hierarchical, agglomerative clustering method was applied to the resulting taxa by traits matrix to extract emergent groupings of plant taxa. The resulting polythetic groups were analysed to determine the variation in traits, including response to disturbance and recorded flower visitors, and how these may affect population persistence in a fragmented landscape. Multivariate methods were used to define emergent groups based on a combination of floral structure and life-history traits of the declared rare flora of Western Australia. Seven emergent functional groups were identified and were largely differentiated by flower shape and life form. These seven functional groupings varied significantly in their response to disturbance. By deriving these functional groups, we plan to develop models for each group on how rates of pollination, seed production and seed fitness are affected by population size and landscape context. The rationale would be to use these profiles to determine whether there are thresholds in population size or position in the landscape at which reproductive rates severely decline. General management guidelines could then be developed for each functional group.

Keywords Declared rare flora · Functional groups · Generalisation · Pollination · Western Australia

Abbreviations

DRF	Declared rare flora
SWAFR	Southwest Australian Floristic Region

Introduction

There are approximately 2,500 plant taxa listed as rare and poorly known occurring in the Southwest Australian Floristic Region (SWAFR) (Hopper and Gioia 2004), including 351 listed as threatened [declared rare flora (DRF)] under IUCN guidelines (Coates and Atkins 2001). A vast proportion of these occur in the highly fragmented intensive use zone or that area where extensive clearing has occurred, or is still occurring (such as in the wheatbelt area of the Transitional Rainfall Province). Inadequate levels of funding that preclude extensive biological research for every DRF taxa make the writing and implementation of interim recovery plans difficult. At present, the degree of threat and progress towards a recovery plan dictates the plant taxa for which research will be undertaken, with the majority of resources being focused on those taxa that are gazetted as critically endangered (Coates and Atkins 2001). This approach, however, should be regarded as triage as it may not yield the quantitative data required for declared endangered and vulnerable species and indeed other critically endangered taxa. How then can general insights be gained on the population dynamics of rare plant species that then can be applied across a broad range of taxa?

The relationship between form and function (or pattern and process) is one of the classical ecological paradigms (Smith et al. 1993). Form and function are intrinsically interwoven to such a degree that each can be thought of as causing the other. As Dafni (1992) states, "It is almost impossible to divorce the architecture of an organ from its function." For example, the morphology of a flower restricts the range of potential pollinators and increases the efficiency of allogamy. Hence, the interaction between pollinator and variation in flower trait is a potentially important feature driving the evolution of flower morphology (Thompson 2001). It is imperative to understand the relationship between form and function especially in the development of functional groups. There is a long history in ecology of developing functional group methodologies as a deductive system for the prediction of species and vegetation responses to a range of perturbations. In this study, we define a functional group as a nonphylogenetic classification leading to a grouping of organisms that respond in a common manner to a syndrome of environmental factors or have a common effect on ecosystem functioning (Gitay and Noble 1997; Díaz and Cabido 2001; Lavorel and Garnier 2002). The value in using functional groups is to provide a broad framework and to identify traits that may be used as a starting point in more explicitly targeted studies (Lavorel et al. 1997). The application of the functional group concept to plant ecology has been primarily used to identify groups containing taxa that respond in similar ways to chosen environmental factors (Lavorel et al. 1997). However, Noble and Gitay (1996) concluded that it is unlikely that an all encompassing unifying classification for all purposes will be found. Instead, they recommend context specific functional classifications (Noble and Gitay 1996). As such, it is vital that ecologists develop appropriate methodologies for identifying different functional groups, testing their applicability to the task for which they were developed and testing their robustness to application to other tasks.

Interest in the application of the functional group concept has increased in the past decade particularly as a framework for predicting species, plant community, and ecosystem responses to human-induced environmental change and the mechanisms underlying these responses. Functional group approaches have been used in the context of current concerns about the effects of global changes, especially biodiversity decline, CO2 increase, climate warming (Woodward and Cramer 1996 and others), and various ecosystem disturbances including grazing (McIntyre et al. 1999 and others), habitat fragmentation (Kolb and Diekmann 2005) and invasions on community dynamics and ecosystem functioning (Blondel 2003). Functional groups have also been well developed and used in fire ecology, particularly fire life-history traits that have been used to predict extinction risk (Noble and Slatyer 1980; Bradstock and Kenny 2003). By definition species within a functional group are ecologically equivalent and provide some degree of redundancy to the system (Blondel 2003).

The functional group concept will be of most value as a predictive tool in determining the response to identified threats such as landscape fragmentation. There is a general indication emerging from the literature that many plant species show a decline in seed production with increasing landscape fragmentation. Changes in the abundance and diversity of pollinators may be a critical factor in determining plant species persistence in a fragmented landscape. Furthermore, changes in mating systems and the disruption of pollination systems in fragmented landscapes are not as immediately obvious as other ecological processes at the community level.

Here, we suggest that we can focus our research efforts and define which rare plant taxa to study by assigning taxa into functional groups based on their floral morphology and life-history traits. Specifically, we focus on answering the following questions:

- 1. Can trait-based functional groups be determined among the DRF of Western Australia?
- 2. What are the attributes that serve to differentiate the functional groups and what are the associations among the attributes?
- 3. What is the ecological significance of such associations?

If the answers to the above questions were known, then it should emerge whether it is possible to form generalised models for rare plant population responses to a range of threats including those associated with landscape fragmentation.

Methods

Trait selection

Trait selection is critical in any study that uses functional traits to compartmentalise and generalise the variation in species ecological strategies. The 2003 Wildlife Conservation (Rare Flora) Notice was used to generate the list of vascular DRF taxa used in this study. For each DRF taxa included for analysis (see "Data analysis"), a core list of 26 specific traits that are known or suspected to be ecologically relevant for survival and reproduction were selected and were later used in the general description and interpretation of the derived functional groups. These traits, along with a complete list of DRF taxa used in this study, appear in Appendix S1 in Supplementary Material. From this initial dataset, a subset of six traits was retained for inclusion in the analysis to maximise the dissimilarity among the derived functional groups. The rationale for removing the other traits reflected the fact that many of the measured traits were closely related to each other or unsuitable for analysis. The trait subset included data on four floral and two lifehistory traits: flower shape, flower symmetry, petal morphology, floral display, life form and longevity (Table 1). These six traits represent important features of plant reproduction and were considered the most likely to be informative. Flower shapes were adapted from Faegri and van der Pijl (1979) and Endress (1994). Faegri and van der Pijl (1979) do not differentiate between flowers and inflorescences. Instead both are included in their description of anthium, this being defined as the fundamental functional unit in pollination (Faegri and van der Pijl 1979). Floral display was ranked into three categories, these being: solitary (true solitary flowers), grouped (flowers solitary but concentrated together on branches) or massed (flowers contained within an inflorescence). Life-form classifications follow those presented in Walker and Hopkins (1990).

The majority of trait information was gained from the measurement of herbarium specimens housed in the Western Australian Herbarium (PERTH). Data on morphological features that could not be reliably collected from herbarium specimens were gained by

Table 1Traits used todefine a functionalclassification of thedeclared rare flora ofWestern Australia

Trait	Trait state		
Flower shape	1: bell/funnel, 2: bowl/dish, 3: brush, 4: flag, 5: gullet, 6: trumpet, 7: tube		
Flower symmetry	1: actinomorphic, 2: zygomorphic		
Floral display	1: solitary, 2: grouped, 3: massed		
Petal morphology	0: reduced/absent, 1: free, 2: fused		
Longevity	1: perennial, 2: annual		
Life form	1: tree, 2: mallee tree, 3: shrub, 4: mallee shrub, 5: heath shrub, 6: chenopod shrub, 7: forb, 8: vine		

review of the published information, particularly Brown et al. (1998) and access to FloraBase (Western Australian Herbarium 1998). This included data on flower colour, flowering times, life form, maximum height gained, growth form and response to disturbance (i.e., resprouter or non-sprouter).

Data analysis

A multivariate clustering method was applied to the resulting species by traits matrix to determine what groupings of plant taxa would emerge. Clustering methods calculate similarity or association measures, based on the extent to which taxa have traits in common. Those taxa adapted to wind pollination, or those for which no data were obtained, were excluded from the final analysis (15 taxa) and will not be considered further. Obligate wind pollinated taxa were excluded as we believe that their reproduction and persistence in the landscape is less likely to be affected by fragmentation than those taxa that are largely dependent on faunal pollination vectors.

The dataset was analysed using a simple numerical hierarchical, agglomerative clustering method using Gower's General Similarity Coefficient (Gower 1971) in the PRIMER statistical package (Clarke and Gorley 2001). The Gower metric was chosen for this study as it can measure the association between mixed data types, whether these are a combination of

Fig. 1 Cluster analysis of declared rare flora of Western Australia based on flower shape, flower symmetry, petal morphology, floral display, life form and longevity. No level of clustering is shown above the 0.53 level of similarity as shown by the *dashed line*. Descriptions of the seven groups are given in Table 4 ordinal, continuous or binary data types. The clustering method used for the analysis was a fixed version of unweighted pair group method with arithmetic mean (UPGMA). The resulting groupings of taxa were analysed to determine which traits were commonly associated with each group. Similarity among taxa was further investigated via formal ordinations of the dataset using non-metric multidimensional scaling (nMDS) using the underlying similarity matrix as input. This allows a direct representation of the underlying classification in ordination space. A Principal Component Analysis (PCA) was performed on the similarity matrix to identify those attributes that accounted for the greatest amount of variation.

Results

Functional groups

The cluster analysis (Fig. 1) indicates seven groupings of DRF plant taxa at a 0.53 level of similarity. The seven groupings evident in Fig. 1 are very distinct, with similarity within each group considerably higher than the similarity among the groups. For example, similarities within Groups 1 and 2 were both greater than 0.95 while similarity between these two groups was 0.52. A major distinction is evident



Gower General Similarity Coefficient

between Groups 1 through 5 and Groups 6 and 7 with a similarity of only 0.209. This corresponds to a major division between the shrub-dominated groups (1–5) and the forb-dominated groups (6 and 7). This division is also evident in the nMDS plot (Fig. 2). An important sub-group of Group 6 contained members of the Orchidaceae, some of which may have very specialised pollination syndromes. This sub-group had a 0.65 similarity with other taxa in Group 6.

All traits used in the cluster analysis had significant associations with the resultant functional

Fig. 2 Non-metric multidimensional scaling (nMDS) ordination of the floral traits measured for the declared rare flora of Western Australia. The ordination is based on Gower's General Similarity Coefficient matrix generated for the cluster diagram. Stress = 0.06. Point labels follow the groupings and descriptions of each functional group





Deringer

Trait	Results
Flower shape	$\chi^2_{36} = 1187.14, P < 0.01$
Flower symmetry	$\chi_6^2 = 250.55, P < 0.01$
Floral display	$\chi^2_{12} = 395.19, P < 0.01$
Petal morphology	$\chi^2_{12} = 244.77, P < 0.01$
Longevity	$\chi_6^2 = 31.57, P < 0.01$
Life form	$\chi^2_{42} = 542.43, P < 0.01$
Flower colour	$\chi^2_{30} = 255.03, P < 0.01$
Flower to leaf position	$\chi^2_{12} = 99.57, P < 0.01$
Style length	$\chi^2_{12} = 58.16, P < 0.01$
Average flower width	$F_{6,336} = 21.63, P < 0.01$
Average flower length	$F_{6,336} = 21.95, P < 0.01$

 Table 2 Significant variation in measured traits for the declared rare flora of Western Australia

(>75% similarity) were longevity, petal morphology and flower symmetry. The complete list of DRF taxa including the functional group were listed in Appendix S1.

The nMDS ordination of DRF plant taxa based on the degree of similarity in their floral and life-history traits is presented in Fig. 2. Labels of the points in multidimensional space follow the clusters in which each taxa occurred (see Appendix S1). The majority of groups evident in the cluster diagram are supported by the ordination (Fig. 2). There is a major separation of plant taxa based on life form along Axis 1, with herbaceous taxa (Groups 6 and 7) separated from the woody taxa. The two members of Group 4 that occur with Groups 6 and 7 were recorded as vines. Axis 2 appears to be important in the discrimination of the groups, more so than Axis 3.

Based on the PCA, the major attributes differentiating the functional groups were life form, flower shape, floral display and petal morphology (Table 4). The first three principal components captured around 97% of the total information (Table 4). The first PCA axis, which accounted for 72.3% of the variance, had only one attribute with significant positive loading, that being life form. Both Group 6 and 7 were at one extreme with the shrub-dominated groups (1–5) occurring at the other end of the axis. The second axis also had a single attribute with significant positive loading (flower shape) and accounted for a further 20.9% of the variance. Axis 3 accounted for the other 3.8% and can be described as a contrast between floral display and petal morphology (Table 4).

Alternative reproductive strategies

There was a highly significant association between functional group and alternative reproductive strategies ($\chi_6^2 = 18.42$, P < 0.01) with each group varying in their response to disturbance. Group 1 recorded a higher than expected number of resprouters with all other functional groups recording higher than expected numbers of non-sprouters. Groups 1 and 2 are the only functional groups, where resprouting occurs as an alternative reproductive strategy for more than 25% of constituent taxa (50% and 26%, respectively: Fig. 3).

Table 3 Description of the major groupings derived from the cluster analysis presented in Fig. 1	Group number (n)	Description		
	Group 1 $(n = 64)$	Perennial mallee trees/shrubs with massed open-access actinomorphic brush-shaped flowers with reduced petals. Includes species of <i>Eucalyptus</i> and <i>Acacia</i>		
	Group 2 ($n = 86$)	Perennial shrubs with massed directed-access zygomorphic tube-shaped flowers with reduced petals. Includes species of <i>Banksia</i>		
	Group 3 ($n = 59$)	Perennial shrubs with grouped open-access actinomorphic mostly bowl/ dish-shaped flowers with free petals. Includes taxa from Sterculiaceae		
	Group 4 ($n = 29$)	Perennial shrubs with grouped closed-access zygomorphic flag-shaped flowers with free petals. Includes taxa from Papilionaceae		
	Group 5 ($n = 25$)	Perennial shrubs with solitary directed-access zygomorphic gullet-shaped flowers with fused petals. Includes species of <i>Eremophila</i>		
	Group 6 $(n = 44)$	Perennial forbs with solitary open-access zygomorphic mostly gullet- shaped flowers with free petals. Includes species of <i>Caladenia</i> and other Orchidaceae		
	Group 7 ($n = 29$)	Perennial forbs with massed directed-access actinomorphic mostly tube- shaped flowers with free petals. Includes species of <i>Conostylis</i>		

 Table 4
 Information captured and component loadings for the first three principal components based on the six variables analysed

	Principal components		
	Axis 1	Axis 2	Axis 3
Information captured	14.727	4.271	0.78
Percentage of total	72.31	20.968	3.829
Cumulative percentage	72.31	93.278	97.107
Component loadings			
Flower shape	0.023	0.991	-0.002
Flower symmetry	0.018	0.12	-0.092
Floral display	-0.066	0.039	0.829
Petal morphology	0.059	0.03	-0.543
Longevity	0.111	-0.012	0.032
Life form	0.989	-0.023	0.086

Values in bold type represent significant values



Fig. 3 Number of plant taxa that are resprouters or nonsprouters for each of the seven functional groups determined for the declared rare flora of Western Australia

This ability is relatively insignificant in the other functional groups (<15% constituent taxa) indicating that the majority of groups are dependent on seeds for population persistence.

Discussion

Multi-species classifications

The multi-species model presented here has classified the 351 vascular DRF into seven functional groups based primarily on floral traits. The clusters presented in Fig. 1 can be viewed as speculative functional groupings suggesting that groups derived from ecological traits relevant for survival and reproduction served well to distinguish groups from the vast array of floral characters displayed by the DRF of Western Australia. By its very nature, the cluster analysis process is inherently subjective. The researcher is often compelled to run various combinations of traits and clustering methods, as was the case with this study. In fact, some multivariate statistics textbooks encourage the researcher to explore several clustering methods and compare the results (Ludwig and Reynolds 1988). Final clusters can then be determined from one of the cluster analysis methods based on the "underlying ecological knowledge of the data" (Ludwig and Reynolds 1988). The classification presented here is potentially biased by our selection of "ecologically relevant" traits and by data availability, but is objective in its clustering of taxa within functional groups. However, a functional classification such as the one presented here allows a large number of taxa to be reduced to a small number of groups that may have similar interactions with the pollinator community. The groupings presented here have certain combinations of traits occurring together more often than others within the DRF flora of Western Australia, so that although members of a group may be identified by reference to only one or a few traits, they nevertheless have a collection of attributes in common.

A number of other multi-species approaches have been employed as tools to assist conservation management. For example, Lambeck (1997) proposed a focal species approach to guide conservation efforts. This species-based scheme is based on the concept of umbrella species, or those whose requirements are believed to encapsulate the needs of other species (Lambeck 1997). The rationale behind this methodology is that by selecting the most significant species, a landscape that is designed and managed to meet the minimum demands of this single species will also meet the requirements of all associated species (Lambeck 1997). However, there is general agreement that it is inherently difficult to determine which species within an ecosystem is the most significant and which can be used as an umbrella species. With regards to this study, the umbrella species concept may not be appropriate as the suitable focal species may not necessarily be found in the DRF list. We suggest that the multi-species model presented here is advantageous for a number of reasons, including its simplicity, flexibility, statistical interpretability and ability to be applied across a broad range of plant taxa for which little ecological information is available. Furthermore, it could assist in the revised prioritisation of taxa requiring further research and the responses to identified threats.

In general, the grouping of species by cluster analysis (Fig. 1) is similar to the subjective grouping of plant taxa via Faegri and van der Pijl's (1979) anthium classes. However, the major difference between our classification presented here and the subjective anthium classification of Faegri and van der Pijl's (1979) is that we include a life-form designator, which proved to be the major division between Groups 1 through 5 and Groups 6 and 7. If the functional group concept has any predictive value, then the inclusion of additional floral and life-history traits should improve first-level predictions based on anthium class alone. Hence, a functional group derived in our classification may include plant taxa that bear flowers of a different shape to the predominant shape of that group since life form proved to carry a higher weighting than the other traits measured. This is evident in functional Group 7, where herbaceous taxa bearing tube-shaped flowers were the predominant form, which also included herbaceous taxa that bear bell/funnel or bowl/dish flowers. In a subjective classification based on flower shape alone, these would have been grouped together with shrubs or trees that have similar flower shape. This may be an important factor as an annual herbaceous non-sprouting species (such as those in Group 7) may have a higher risk of extinction in fragmented landscapes than, say, a reprouting woody species due pollen limitation or increased competition with non-native herbaceous species. We would then hypothesise that taxa of a functional group respond to habitat fragmentation in a similar fashion despite their individual flower shape and that first-level predictions based on flower shape alone are strengthened by the inclusion of other floral and life-history traits.

Potential application of a functional group approach

The functional group approach presented here will have direct application to rare plant management including responses to a range of threats associated with landscape fragmentation. Landscape fragmentation reduces the size of plant populations and increases their isolation (Saunders et al. 1991; Hobbs 1993; Glanznig 1995). For rare and threatened plant taxa that occur in remnant vegetation of a fragmented landscape, such as the majority of the DRF of Western Australia, the disruption of pollination systems and resultant decrease in seed production may be a critical factor threatening their persistence in the landscape (Jennersten 1988; Aizen and Feinsinger 1994; Kearns et al. 1998; Spira 2001). For any plant taxa to persist in a fragmented landscape a number of important considerations need to be examined. First, the reproductive dependence of a plant species on pollinators needs to be determined. Aspects of the breeding system and finally, the importance of seeds in the demography of the plant taxa also need to be considered (Bond 1994).

The degree of specialization in the pollination system of plants will undoubtedly affect their risk of extinction, especially within a fragmented landscape (Yates and Ladd 2004). Those taxa with a single to a few pollinators (specialists) would be at the highest risk with those plant taxa with many pollinators (generalists) likely to be more resilient (Bond 1994; Waser et al. 1996; Kearns et al. 1998; Spira 2001). Plant species occupy virtually every point on the continuum from extreme specialization to extreme generalisation (Waser et al. 1996; Johnson and Steiner 2000). Functional Group 1, with their open-access brush-shaped flowers, represent the most generalised of all the functional groups. However, individual taxa within a given functional group may nonetheless be sensitive to fragmentation as even generalist species may be prone to pollen limitation, i.e., when populations are small or isolated and therefore less attractive.

Some plant species may display other compensatory mechanisms to buffer them against the lack of pollen limitation (Bond 1994). For example, some species may display self-pollination, apomixis, or show a reduced demographic dependence on seeds through vegetative reproduction such as resprouting (Bond 1994). The effects of fragmentation on population persistence may be important for the plant demographics of a large proportion of non-sprouting taxa in each functional group derived in this study. This is particularly true for those taxa that are solely dependent upon the production of viable seed to persist in the landscape, but which may also be susceptible to the disruption of the plant-pollinator interaction or the alteration of the regeneration niche. In Mediterranean climate shrublands, fire is a recurring disturbance and often an important cue for seed

germination and seedling establishment. If the prevailing fire regime is altered as a consequence of landscape fragmentation, non-sprouting plant taxa that rely on seeds for population persistence maybe more susceptible to local extinction than resprouting taxa. If fragmentation is leading to the loss of some pollinator species from the landscape, how does this affect the persistence of DRF and other plant taxa especially those with specialised pollination systems? Since it is apparent that the functional groups derived in this study are seemingly dependent on seeds for reproduction and population persistence, then it is vital to investigate how each group responds to habitat fragmentation especially since some species of pollinators may be more at risk from fragmentation than others. The predicted response of these functional groups and of individual species to specific threats such as landscape fragmentation constitute a set of hypotheses that need to be verified through targeted field studies for selected taxa. These taxa will provide informative and representative data that can be applied across all taxa within a functional group. This information will aid in the prediction of functional group responses to identified threats and will assist in the development of conservation management plans for DRF taxa.

Conclusion

Many different ecological classification systems for plants have been developed, which categorise taxa into groups based on various alternative attributes. Here, we have proposed and described a method of grouping together DRF taxa without regard to their taxonomic position. Such a method provides a powerful means for objectively assessing floral morphology in relation to pollination biology, phylogenetic relatedness and the characterisation of taxa into functional groups. We hypothesise that these functional groups act as natural ecological units and that they facilitate comparisons of pollination systems at the community level. These functional groups will assist in the development of management strategies for a large number of threatened taxa occurring in the mega-diverse SWAFR.

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