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Relating species rarity to life history in plants of eastern Australia

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ABSTRACT

We examined species rarity in relation to life history in plants of eastern Australia. Correlated-divergence analysis (using phylogenetically independent contrasts) and cross-species analysis (exploring patterns across present-day species) were employed in a complementary fashion to test the hypothesis that rare and common species differed with respect to life history. Two measures of rarity, threat of extinction and geographical range size, were investigated for relationships with growth form, longevity, pollination mode, mating system, dispersal and seed mass. Species threatened with extinction had, on average, significantly smaller seed mass than non-threatened species. This emerged in both correlated-divergence and cross-species analyses, independently of the effects of the other life-history traits. In cross-species analysis, but not as phylogenetic contrasts, a significant number of species with short life spans were less likely to be threatened with extinction. This arose because most short-lived species not threatened with extinction diverged from long-lived species threatened with extinction at a major node deep in the phylogenetic tree (where monocotyledons diverged from dicotyledons). Mating system was significantly related to geographical range size in correlated-divergence analysis, but not across present-day species. There was evidence that evolutionary divergences for dioecy have been significantly correlated with the occupation of a wide geographical range, although this relationship has not been maintained across present-day species. Growth form, pollination mode and dispersal could not account significantly for variation in either threat of extinction or range size. Because relationships for plants of eastern Australia were found to differ considerably from those emerging for other species assemblages on other continents, support is provided for the notion that associations between species rarity and life history are highly dependent on geographical context and the species assemblage under scrutiny.

Keywords: evolutionary divergence correlation, geographical range size, phylogenetic regression, threat of extinction.

INTRODUCTION

Large numbers of plant species have become rare in Australia since European settlement as a result of human activities (Leigh and Briggs, 1992). Identifying life-history features that

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predispose some species and not others to rarity has considerable value for conservation (Gaston, 1994; Kunin and Gaston, 1997; Bevill and Louda, 1999). Unfortunately, given both financial and time constraints, long-term autecological studies cannot be implemented to document completely the biology of all rare species (Edwards, 1998). However, large comparative studies designed to elucidate differences in life history between rare and common species offer a practical and cost-effective alternative (Murray *et al.*, 2002).

Although a recent survey found that over 90 different plant attributes have been examined in comparative studies in relation to species rarity, it was also reported that most attributes have yet to be examined in more than one study at a given spatial scale (Murray *et al.*, 2002). Few studies have considered patterns among large numbers of species to determine whether evolutionary divergences in life-history traits have been consistently correlated with rarity throughout species' phylogenies (e.g. Kelly and Woodward, 1996; Eriksson and Jakobsson, 1998; Thompson *et al.*, 1999). These features of the literature have so far made it difficult to demonstrate whether robust generalizations across studies can be established regarding trait relationships with plant rarity. This needs to be resolved, since the identification of such relationships has considerable potential for guiding global strategies aimed at the long-term conservation and management of rare species.

We conducted a comparative study to test the hypothesis that rare and common species in eastern Australia differ with respect to life history. Both correlated-divergence and cross-species analyses were used. Cross-species analysis describes relationships that are ecologically relevant in the present day (Westoby *et al.*, 1995). Significant trait correlations across present-day species indicate consistent relationships among taxa that are currently maintaining populations. In contrast, correlated-divergence analysis (using phylogenetically independent contrasts) assesses whether evolutionary divergences in particular traits have been correlated consistently throughout the species' phylogenies (Westoby *et al.*, 1998). Thus, the two types of analyses ask different, but complementary, questions. Phylogenetic analyses are explicitly oriented towards evolutionary questions. However, the use of cross-species analysis is warranted in asking some evolutionary questions because evolutionary processes where niches are phylogenetically conservative may be quantified better across present-day species than by correlated-divergence analysis (Price, 1997; Harvey and Rambaut, 2000).

In the present study, two measures of rarity were adopted, a categorical variable separating species into those threatened with extinction and those considered not threatened, and a continuous variable that estimated the geographical range size of each species. We focused on six strategically important life-history traits, including two vegetative attributes, growth form and longevity, two reproductive attributes, mating system and pollination mode, and two regenerative attributes, namely dispersal and seed mass. Although only a small body of literature has investigated relationships between these six traits and rarity measured as extinction risk (e.g. Harper, 1979; Lahti *et al.*, 1991), several studies, primarily from the northern hemisphere, have centred on their relationships with geographical range size (e.g. Aizen and Patterson, 1990; Kelly and Woodward, 1996; Byers and Meagher, 1997; Thompson *et al.*, 1999). Australia's long-term geographical isolation in the southern hemisphere and its unique vegetation provide an opportunity both to expand the small body of data on the relationships between traits and extinction risk, and to evaluate the generality of relationships between life-history traits and plant rarity emerging on other continents.

METHODS

Study species

The Southern Tablelands and surrounding regions of eastern Australia are host to a wide diversity of plant species (Burbidge and Gray, 1970; Harden, 1990–93). The area has suffered immensely from land clearing for agriculture and urban development (Environment Protection Authority, 2000), resulting in increasing numbers of species becoming rare. A complete list of plant species from the Tablelands was obtained from the Australian National Herbarium in Canberra. From this list we compiled a data set of 254 species from 124 genera, spanning 48 families in 26 orders. The data set consisted of 151 non-threatened species and 103 species listed as threatened with extinction within Australia.

Rarity measures

The first assessment of rarity was made by reference to the threatened flora listing prepared by the Australian and New Zealand Environment and Conservation Council Endangered Flora Network (ANZECC, 1999). Species are listed if they are presumed extinct or threatened with extinction (endangered or vulnerable species). Endangered and vulnerable species were pooled into one threatened category for analyses. Species presumed to be extinct were not considered, as information on life history for many species is either not available or not completely reliable. Our threat-of-extinction classification was based on definitions used by the Threatened Plants Committee, Species Survival Commission, World Conservation Union (IUCN, 1994). Rare species may have a naturally restricted range within a widespread habitat, may be specialists in narrowly distributed habitats, or may have range sizes reduced by human activity (Leigh and Briggs, 1992; Edwards and Westoby, 2000). Categorizing species with respect to their type of rarity is not currently possible for the list considered here. Thus, we interpret cautiously patterns emerging in the present study with respect to the different types of rarity encapsulated within the threatened species list (e.g. McIntyre, 1992; Edwards, 1998; Edwards and Westoby, 2000).

The second measure of rarity used latitude × longitude records on the distribution of each species obtained from six major herbaria in the states or territories within which study species were located (Australian National Herbarium, Herbarium of the Northern Territory, National Herbarium of New South Wales, National Herbarium of Victoria, Queensland Herbarium and the Tasmanian Herbarium). Geographical distributions varied considerably among species, with very rare taxa occurring at one location only, and widespread species ranging from the northern tip of the continent to the southern regions of Tasmania. To estimate geographical range size, a two-dimensional grid sheet ($0.5° \times 0.5°$ grid cells) was superimposed on latitude × longitude distribution maps for each species, and the total number of occupied grid cells was counted (e.g. Murray *et al.*, 2002). Thus, species rarity and commonness were treated as a continuous variable (see Kelly and Woodward, 1996). We calculated an additional estimate of range size for each species by counting the number of biogeographical regions within which each species occurs (e.g. Oakwood *et al.*, 1993; Edwards and Westoby, 1996; Murray *et al.*, 1999), using the Census of Australian Vascular Plants (Hnatiuk, 1990). The Census records the presence of species within each of 97 regions of Australia, with regions delimited by biogeographical zones recognized by relevant herbaria in each state. The delineation of regions is defined as

capturing important ecological differences between regions (Oakwood *et al.*, 1993). Our analyses revealed that relationships between traits and range size were quantitatively similar for both latitude × longitude distribution records and Census estimates, hence we present results using latitude × longitude records only.

Life-history traits

The life-history characteristics of each species were described by placing each species into one of two categories for each of growth form, longevity, pollination mode, mating system and dispersal. Seed mass was a continuous variable measured as the average mass of embryo, endosperm and coat, estimated from five seed samples taken from separate herbarium specimens for each species. Where seed material was not available, we extracted seed mass estimates from the literature (sources listed below). Growth form categories were: (1) trees and (2) understorey plants (including forbs, graminoids, shrubs and climbers). Longevity categories were: (1) 1–10 years and (2) > 11 years life span. Pollination mode categories were: (1) wind- and (2) animal-pollinated plants (both invertebrates and vertebrates). Mating system included: (1) monoecious and hermaphroditic or (2) dioecious plants. The dispersal type of seeds was categorized as: (1) no investment in structural modifications for dispersal or (2) investment in extra features for dispersal of seeds (including seeds with wings or hairs, seeds contained within fleshy fruits, seeds with barbs or hooks, seeds with an ant-attracting food body, and seeds contained within a specialized pod which opens explosively). Data for traits were obtained from the following published sources: *Flora of Australia* (Australian Government Publishing Service, 1981), *Flora of New South Wales* (Harden, 1990–93), *Flora of ACT* (Burbidge and Gray, 1970), *Flora of Victoria* (Walsh and Entwisle, 1994–99), *Flora of the Sydney Region* (Carolin and Tindale, 1994), *Native Plants of the Sydney District* (Fairley and Moore, 1995), Brooker and Kleinig (1983–94), Westoby *et al.* (1990) and issues of *Cunninghamia* containing the Ecology of Sydney Plant Species (e.g. Benson and McDougall, 2000). For a number of the very rare species, unpublished Threatened Species Recovery Plans were obtained from Environment Australia (Canberra, Australia) to provide trait information not available in the literature.

Statistical analysis

Correlated-divergence analysis was performed by implementation of the phylogenetic regression (PHYLO.GLM version 1.03; Grafen, 1989). The construction and coding of a working phylogeny (see details below under 'The working phylogeny') were required for phylogenetic regression models. Each node in the constructed phylogenetic tree contributed one independent data point (contrast) in the analysis. Cross-species analysis was carried out by fitting general linear models to the data set where each species contributed one data point (GLIM version 3.77, Royal Statistical Society, London). Just as general linear models have underlying assumptions about the data (e.g. normality, homogeneity of variance), confidence in the results of phylogenetic analyses depends on the extent to which the tree of phylogenetic relationships is accurately known, and the extent to which evolutionary changes throughout history fit the assumed model (e.g. Brownian motion; Grafen, 1989; Price, 1997). In many cases, the findings of evolutionary-divergence and cross-species correlations are not significantly different (Ricklefs, 1996). When the

outcomes of correlated-divergence and cross-species analyses differ, the possibility must be considered that the assumptions of one or the other analysis have not been met. Nonetheless, different outcomes from correlated-divergence and cross-species analyses have provided important insights into the evolution and present-day competency of various species' trait combinations (e.g. Nee *et al.*, 1991).

Pairwise relationships between life-history traits were analysed first. Significant relationships emerged between many pairs of traits in both correlated-divergence and cross-species analyses (Table 1). This had the potential to obscure relationships between life-history traits and rarity, because significant associations might emerge through an indirect correlation with one or more other variables (Duncan and Young, 2000). Thus, we tested whether each trait was related to species rarity when the influence of all other traits had been removed, in addition to each trait being considered on its own in a model. We also considered it essential to control for the influence of other life-history traits, because 'correcting for phylogeny' does not automatically remove cross-correlations with all other variables (Westoby *et al.*, 1995). In particular, agreement between evolutionary-divergence and cross-species correlations does not preclude the need to consider potentially confounding traits (Price, 1997).

A binomial error structure with a logit link was employed in cross-species models with binary response variables. Changes in deviance were compared with chi-square tables. A normal error structure with an identity link was used for models with geographical range size and seed mass as the response variable. The 'default method' was used in phylogenetic regression models, and path segment lengths for the phylogenetic tree were calculated by assigning a height to each node that was one less than the number of species below or at that node in the tree (Grafen, 1989).

We plotted the ranked residuals of continuous response variables against a cumulative normal distribution to test assumptions for parametric tests that residuals were normally distributed, and plotted residuals against fitted values and all independent variables to assess whether the variance was constant (Crawley, 1993). Geographical range size and seed mass were log-transformed for analyses. Given multiple statistical testing of the same hypothesis, we used conservative Bonferroni corrections in all analyses to maintain an overall significance value of 5% (Norman and Streiner, 2000).

The working phylogeny

The large-scale structure of the tree for the 254 species studied here was based on phylogenetic interrelationships of angiosperm orders compiled from recent cladistic analyses by the Angiosperm Phylogeny Group (1998) (generic concepts followed Harden, 1990–93). The affinity of four families (Celastraceae, Dilleniaceae, Vitaceae and Winteraceae) was uncertain at the ordinal level, hence these families were treated as monofamilial clades and grafted onto the tree as basal polychotomies at the lowest node where affinity was certain. This is the most conservative manner of incorporating such groups into correlated-divergence analysis (Wright *et al.*, 2000). Phylogenetic relationships within orders that contained three or more families were structured using consensus cladistic trees (based on both molecular and morphological data) drawn from the most recent publications. Phylogenies were obtained for Asparagales (Fay *et al.*, 2000), Asterales (Gustaffson *et al.*, 1996), Gentianales (Struwe *et al.*, 1994) and Oxalidales (Nandi *et al.*, 1998). As there is no published phylogeny for the Poales *sensu* Angiosperm Phylogeny Group (1998), the four

Table 1. Correlated-divergence (above diagonal) and cross-species (below diagonal) analyses of pairwise relationships between life-history traits

	Growth form	Longevity	Pollination mode	Mating system	Dispersal	Seed mass
Growth form		−0.46***, −0.45**	−0.46*, −0.37*	0.64**, 0.33	0.44***, 0.47**	0.00, −0.01
Longevity	12.0**		0.62**, 0.46**	−0.67**, −0.23	0.44***, 0.51***	0.12, 0.18
Pollination mode	3.3	12.9**		−0.83***, −0.56**	0.27*, 0.41	0.06, 0.02
Mating system	4.6	1.5	14.0***		−0.14, −0.38	−0.01, 0.06
Dispersal	15.9***	18.3***	3.1	1.1		0.12, 0.30*
Seed mass	0.0	9.0**	0.0	0.3	65.1***	

Note: Correlation coefficients are presented for the correlated-divergence analysis. Changes in deviance values, presented for the cross-species analysis, were tested against a chi-squared distribution. For correlated-divergence analysis, the first and second values in each cell used traits heading the column and traits leading the row respectively as response variables in models (no differences emerged if the response and independent variables were switched in cross-species models). Bonferroni corrections were employed to maintain an overall significance value of 5% (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

families from that order in our data set (Cyperaceae, Poaceae, Restionaceae, Xyridaceae) were treated as an unresolved polytomy. Relationships within families containing three or more genera and within genera containing three or more species were structured using recent taxonomic treatments from the literature and by contacting taxonomists working on particular clades: *Acacia* (Maslin and Stirton, 1997; J. Miller, unpublished data), Asteraceae (Bremer, 1994), *Banksia* (Thiele and Ladiges, 1996), Cunoniaceae (Hufford and Dickison, 1992), *Eucalyptus* (Ladiges and Udovicic, 2000, and references therein), Fabaceae (Crisp and Doyle, 1995), Goodeniaceae (Carolin, 1978), Lamiaceae (Olmstead *et al.*, 1998) and Myrtaceae (L. Craven, unpublished data; P. Wilson, unpublished data). The working phylogeny can be obtained from the authors on request.

RESULTS

Small seed mass was found to be significantly related to threat of extinction after controlling for all other independent variables in correlated-divergence and cross-species analyses (Tables 2 and 3). The log seed mass of threatened species (0.48 ± 1.99; mean ± standard deviation) was lower than that of non-threatened species (1.12 ± 2.21). Longevity was significantly related to extinction threat in cross-species models when considered on its own, and after controlling for all other independent variables (Table 3). A significant proportion (78%) of species with short life spans were less likely to be threatened with extinction. Significant relationships observed here are weak, and consistent with the idea that coefficients of determination will not be high in such analyses (Kunin and Gaston, 1997). There were no significant differences in growth form, pollination mode, mating system or dispersal between threatened and non-threatened species.

Mating system was significantly related to geographical range size in correlated-divergence analysis, but not across present-day species (Tables 4 and 5). There is evidence that evolutionary divergences for dioecy have been significantly correlated with the occupation of a wide geographical range, although this relationship has not been maintained across present-day species. An example of where this is evident is the divergence between the genus *Phyllanthus* (dioecious, mean log range size 4.06 grid cells) and three other closely related genera within the same clade (all monoecious, mean log range size 3.47 grid cells). Longevity was significantly related to range size in cross-species analysis; however, this relationship was not upheld after controlling for the effects of all other traits (Table 5). Growth form, pollination mode, dispersal and seed mass could not account for significant variation among species in geographical range size.

DISCUSSION

We found that plant species threatened with extinction had, on average, significantly smaller seeds than non-threatened species. This occurred in both correlated-divergence and cross-species analyses. Importantly, this relationship emerged strongly after controlling for interrelatedness among explanatory variables. Not taking cross-correlation of explanatory variables into account might in part explain why some authors have observed no relationship between seed mass and extinction risk (Lahti *et al.*, 1991; Witkowski and Lamont, 1997). Our results suggest that some of the ecological correlates of small seed mass might play a significant role in defining extinction threat for plants of eastern Australia. Such correlates include reduced competitive ability in early seedling establishment (e.g. Turnbull

Table 2. Correlated-divergence analysis adding life-history traits in the left-hand column to phylogenetic regression models with threat of extinction as the response variable

Life-history traits	Control				Alone			
	F	d.f.	r^2	*P*	*F*	d.f.	r^2	*P*
Seed mass	10.9	1,103	0.10	**0.001**	5.9	1,97	0.06	0.02
Longevity	5.6	1,113	0.05	0.02	4.9	1,97	0.05	0.03
Dispersal	1.6	1,113	0.01	0.2	0.4	1,97	0.00	0.5
Pollination mode	0.3	1,113	0.00	0.6	0.4	1,97	0.00	0.5
Growth form	0.3	1,113	0.00	0.6	0.3	1,97	0.00	0.6
Mating system	0.1	1,113	0.00	0.8	0.1	1,97	0.00	0.8

Note: Each trait was considered in a model that controlled for the effects of all other independent variables (control) and in a model on its own (alone). Bonferroni corrections were employed to maintain an overall significance value of 5% (adjusted *P* for significance = 0.0125; significant *P*-values in **bold**).

Table 3. Cross-species analysis adding life-history traits in the left-hand column to general linear models with threat of extinction as the response variable

Life-history traits	Control			Alone		
	CD	d.f.	*P*	CD	d.f.	*P*
Longevity	8.1	1	**0.004**	8.6	1	**0.003**
Seed mass	7.3	1	**0.007**	3.2	1	0.07
Growth form	1.7	1	0.2	2.9	1	0.09
Mating system	1.6	1	0.2	1.3	1	0.3
Dispersal	1.2	1	0.3	0.06	1	0.8
Pollination mode	0.2	1	0.7	1.25	1	0.3

Note: Each trait was considered in a model that controlled for the effects of all other independent variables (control) and in a model on its own (alone). Change in deviance (CD) was tested against a chi-squared distribution. Bonferroni corrections were employed to maintain an overall significance value of 5% (adjusted *P* for significance = 0.0125; significant *P*-values in **bold**).

et al., 1999), and lower seedling tolerance of defoliation (Armstrong and Westoby, 1993). Field and glasshouse experiments will be required to determine the relative importance of these correlates for extinction vulnerability. Some species with small seeds, however, are not at risk of extinction (e.g. *Baeckea diosmifolia*, *Callistemon linearis*). In addition, some threatened species have large seeds (e.g. *Grevillea caleyi, Persoonia mollis*). This leads us to conclude, not unexpectedly, that seed mass is only one of many important factors that account for extinction vulnerability.

We also found that a significantly large proportion of species with short life spans were less likely to be threatened with extinction across present-day species. We suggest that since short life span is generally correlated with higher intrinsic rates of increase, the ability to reproduce rapidly would be an advantage in colonizing disturbed environments that continue to be opened up as a result of land clearance and habitat fragmentation. Our finding for longevity differs from published studies from the northern hemisphere,

Table 4. Correlated-divergence analysis adding life-history traits in the left-hand column to phylogenetic regression models with geographical range size as the response variable

Life-history traits	Control				Alone			
	F	d.f.	r^2	*P*	*F*	d.f.	r^2	*P*
Mating system	7.8	1,113	0.06	**0.006**	13.0	1,117	0.10	**0.0001**
Seed mass	2.0	1,113	0.0	0.2	2.8	1,117	0.02	0.1
Longevity	0.9	1,113	0.0	0.4	2.0	1,117	0.02	0.2
Dispersal	0.2	1,113	0.0	0.7	0.1	1,117	0.0	0.8
Pollination mode	0.2	1,113	0.0	0.7	5.8	1,117	0.05	0.02
Growth form	0.1	1,113	0.0	0.8	1.2	1,117	0.01	0.3

Note: Each trait was considered in a model that controlled for the effects of all other independent variables (control) and in a model on its own (alone). Bonferroni corrections were employed to maintain an overall significance value of 5% (adjusted *P* for significance = 0.0125; significant *P*-values in **bold**).

Table 5. Cross-species analysis adding life-history traits in the left-hand column to general linear models with geographical range size as the response variable

Life-history traits	Control				Alone			
	F	d.f.	r^2	*P*	*F*	d.f.	r^2	*P*
Longevity	5.3	1,247	0.02	0.02	7.7	1,252	0.03	**0.006**
Seed mass	4.7	1,247	0.02	0.03	1.9	1,252	0.01	0.2
Dispersal	0.9	1,247	0.0	0.3	0.6	1,252	0.0	0.4
Growth form	0.6	1,247	0.0	0.4	0.5	1,252	0.0	0.5
Pollination mode	0.1	1,247	0.0	0.8	1.9	1,252	0.01	0.2
Mating system	0.0	1,247	0.0	0.9	0.2	1,252	0.0	0.7

Note: Each trait was considered in a model that controlled for the effects of all other independent variables (control) and in a model on its own (alone). Bonferroni corrections were employed to maintain an overall significance value of 5% (adjusted *P* for significance = 0.0125; significant *P*-values in **bold**).

where threat of extinction was found to be unrelated to plant life span (Harper, 1979; Lahti *et al.*, 1991).

Although the relationship that emerged between longevity and extinction threat was significant across present-day species, it was not apparent in correlated-divergence analysis. This suggests that divergences for short life span have not been consistently correlated with reduced risk of extinction throughout the species' phylogenies. Inspection of our working phylogeny revealed a major node deep in the tree where most short-lived species not threatened with extinction diverged from long-lived species threatened with extinction. This occurred where monocotyledons diverged from dicotyledons, with most short-lived species not threatened with extinction placed in three monocotyledon orders (Asparagales, Poales and Commelinales). Such events, although involving many contemporary species, count as single data points in correlated-divergence analysis, explaining why a significant association did not emerge in evolutionary correlations.

Mating system was related significantly to geographical range size in correlated-divergence analysis, with dioecy associated with the occupation of a wide geographical range. Longton (1992) reported a higher proportion of monoecious species than of dioecious species was rare among British mosses. It was argued that some degree of self-fertilization may be expected among monoecious species, which would lead to lower genetic diversity. We extend this argument to monoecious and hermaphroditic plants of eastern Australia. Low diversity among constituent genotypes could limit both ecological tolerance and the capacity to adapt to environmental change, leading to rarity (Longton, 1992). It is worth noting that the contrasting patterns between correlated-divergence and cross-species analysis emerging here for mating system and range size, as well as for longevity and extinction risk, emphasize the need to complement one analysis with the other for a comprehensive understanding of how life-history variation relates to species rarity.

We found that growth form, pollination mode and dispersal were not related to either extinction risk or range size. Growth form and pollination mode in the flora of Crete were similarly unrelated to range size; however, in the flora of Britain, it emerged that tree species and species that were wind-pollinated tended to be common (Kelly and Woodward, 1996). Oakwood *et al.* (1993) reported that shrubs and trees, rather than herbs, were significantly more likely to have smaller ranges in the floras of central Australia and maritime Sydney. Harper (1979) found that growth form and pollination mode were significantly related to extinction risk in the vascular floras of three American States, with rare species tending to be herbaceous and animal-pollinated rather than woody and wind-pollinated. However, similar to the findings of the present study, Lahti *et al.* (1991) found growth form, pollination mode and dispersal to be unrelated to rarity in vascular plants of Finland. Relationships between dispersal and rarity have been investigated in numerous studies, with results varying quite considerably. While some studies have reported no relationship (e.g. Byers and Meagher, 1997; Eriksson and Jakobsson, 1998), others have found that adaptations for dispersal are correlated with rarity (Peat and Fitter, 1994). A comparison of our findings with those of the few studies which have controlled for the effects of other aspects of life history and which have examined patterns in a phylogenetic context (e.g. Oakwood *et al.*, 1993; Kelly and Woodward, 1996; Eriksson and Jakobsson, 1998), indicates that relationships between life-history traits and species rarity are idiosyncratic, varying from one geographical region and flora to another.

One possible explanation for variation among studies in relationships between life-history traits and extinction risk relates to differences in the criteria used to compile lists of threatened species. Burgman *et al.* (1999) evaluated the concordance between several methods for setting conservation priorities for a small set of Australian plant species, and found that consistency between the methods was very low. Thus, if lists of threatened species compiled for different geographical regions are based on different criteria, different outcomes from comparative studies relating extinction risk to life history might be expected. If it were possible to subdivide threatened species lists into different rarity types (e.g. artificially *vs* naturally rare), then it might be possible for global consistency to emerge in relationships between traits and extinction risk. However, at this stage, it is very difficult – and, in some cases, impossible – to subdivide such lists in this manner, especially since lists of threatened species and the information used to create them are isolated from one another and the data are not easy to come by (Burgman, 2002).

It has been emphasized previously that significant relationships between life-history traits and species rarity will be broad and have only moderate predictive ability (Kunin and

Gaston, 1997). At the same time, however, it has been stressed that the identification of such patterns has considerable value in conservation and management (Gaston, 1994; Kunin and Gaston, 1997; Thompson *et al.*, 1999; Murray *et al.*, 2002). Management can usefully employ the findings of studies exploring relationships between life history and species rarity to correct for biases arising from data that have been obtained only from better studied common species (Kunin and Gaston, 1997). For example, correcting such biases using the results of the present study might include incorporating into models of extinction risk the fact that threatened species tend to be smaller-seeded and that a large proportion of species with short life spans are not threatened with extinction. Similarly, biases could be corrected by application of our finding that dioecious species tend to have a greater capacity to extend their range in models of geographical range size. Biologically realistic simulation models could also be built to explore how critical life-history features such as seed mass interact in different spatially explicit scenarios (i.e. metapopulations) to influence spread, persistence and distribution across the landscape. The advantage of such models is that one can generate empirically testable hypotheses, thus guiding future experimental and comparative studies.

CONCLUSION

Relationships between species rarity and life-history traits are likely to be determined by complex interactions among environmental factors, local historical events and plant life history. Because of this, one can predict multiple equivalent states for many life-history traits in relation to species rarity. For example, dandelions and coconuts are both good dispersers and capable of establishing populations over a wide geographical range, but clearly do so by adopting entirely different seed dispersal and seed mass strategies. Our findings provide support for the notion that relationships between species rarity and variation in life history are highly dependent on geographical context and the assemblage of species under scrutiny (Edwards and Westoby, 2000; Murray *et al.*, 2002), given that patterns observed for plant species of eastern Australia are substantially different from patterns emerging elsewhere. An expectation of comparative studies of species rarity and commonness is that there will be clear-cut distinctions in life history between rare and common species, and that these distinctions will be consistent at a global scale. However, the general situation that is emerging seems to indicate that this will rarely be the case (Murray *et al.*, 2002). Separate studies, in different regions and for different floras, will be required to obtain a comprehensive understanding of how plant life history relates to species rarity.

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