

How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales

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Abstract Comparative studies investigating relationships between plant traits and species rarity and commonness were surveyed to establish whether global patterns have emerged that would be of practical use in management strategies aimed at the long-term conservation of species. Across 54 studies, 94 traits have been examined in relation to abundance, distribution and threatened status at local, regional and geographical spatial scales. Most traits (63) have yet to be the focus of more than one study. Half of the studies involved less than 10 species, and one-quarter did not replicate rare–common contrasts. Although these features of the literature make it difficult to demonstrate robust generalizations regarding trait relationships with species rarity, some important findings surfaced in relation to traits that have been examined in two or more studies. Species with narrow geographical distributions were found to produce significantly fewer seeds (per unit measurement) than common species (in four of six studies), but did not differ with respect to breeding system (five of five studies). The majority of traits (including seed size, competitive ability, growth form and dispersal mode) were related to rarity in different ways from one study to the next. The highly context-dependent nature of most trait relationships with rarity implies that application of knowledge concerning rare–common differences and similarities to management plans will vary substantially for different vegetation types and on different continents.

A comparative analysis of distribution patterns in relation to several life-history and ecological traits among 700 Australian eucalypt species was then performed. A significantly disproportionate number of tall species and species with long flowering durations had wide geographical ranges. Trait relationships with distribution were explored further through the development of a methodology incorporating multiple spatial scales. Eight theoretical categories were described illustrating variation in distribution patterns (and hence rarity and commonness) across small, intermediate and large spatial scales, based on the spatial structure of species occurrence across the Australian landscape. Each eucalypt species was placed into a category, and trait variation was explored across all species in relation to distribution patterns across multiple spatial scales. This approach yielded important information about trait relationships with distribution among the eucalypts, linking the spatial structure of points-of-occurrence with patterns of rarity and commonness. With the pressing need to protect increasing numbers of threatened species and slow rates of extinction, the development and refinement of a broadly usable methodology for rarity studies that encompasses multiple spatial scales, which can be used for any geographical location, will be useful in both conservation and management.

Key words: abundance, commonness, distribution, geographical range, phenotypic plasticity, rarity, spatial scale, threatened species.

INTRODUCTION

We are currently witnessing a staggering increase in the number of species whose abundance and distribution have declined because of human activities. In this context, a thorough understanding of how life-history

and ecological traits vary among species in relation to rarity and commonness is central to providing a scientific basis for the development of strategies aimed at conserving species in the long term (Kunin & Gaston 1997). Of critical importance is determining whether there are traits that permit species to escape rarity and become abundant and widespread (Aizen & Patterson 1990; Edwards & Westoby 1996; Murray & Westoby 2000), or traits associated with persistence at low abundance or within restricted ranges (Rabinowitz *et al.* 1989; Kunin & Shmida 1997; Walck *et al.* 1999). Of equal importance is the identification of traits

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associated with species that have become endangered or vulnerable because of human activities causing habitat fragmentation and destruction, and the introduction of exotic species (Harper 1979; Lahti *et al.* 1991; Pavlik *et al.* 1993).

Comparing life-history and ecological traits between rare and common species has the potential to provide useful biological information for the conservation and management of rare species. Although autecological studies reveal important aspects of the biology of particular rare species, it is simply not feasible to perform such studies for every rare species. In fact, Edwards (1996) calculated that more than 8000 study years would be required to conduct thorough autecological studies for each species currently listed as threatened in the Australian flora. Considering the pressing need to understand and manage rare species, comparative studies of species rarity and commonness provide a rapid alternative for assessing whether there are traits that are characteristic of low-abundance, narrowly distributed or threatened species. Such knowledge can be used effectively in management strategies for rare species, thus potentially reducing the need for large numbers of expensive and time-consuming autecological studies.

Patterns of species rarity and commonness vary substantially from small through to large spatial scales (Rabinowitz 1981). Although some species are found at low abundance or are distributed narrowly at small spatial scales, the same species may be considerably more abundant or widespread at much larger scales. For example, the understory shrub *Hovea linearis* is widespread across Australia but sparse within local sites throughout its range. In contrast, *Persoonia pinifolia* is locally abundant, yet distributed narrowly across the continent (Murray *et al.* 1999). If different plant traits are related consistently to rarity at different spatial scales, it may be necessary to consider and to implement alternative strategies for conservation with respect to spatial scale. Another option is the development of a comparative framework that incorporates how species rarity and commonness change as a function of spatial scale, which could then be analysed with respect to important life-history and ecological features.

Our first aim in the present study was to assess critically those studies that have compared rare and common plant species for differences and similarities in life-history and ecological traits. We asked the questions, do consistent patterns emerge across studies, and to what extent do these patterns vary at different spatial scales for alternative measures of rarity? The answers allowed us to evaluate whether current knowledge is sufficient for application to management strategies for rare species in a global context. We then investigated rarity and commonness in relation to trait variation for 700 Australian eucalypt species. In the first instance,

trait variation was related to geographical range size in keeping with much of the comparative literature (Peat & Fitter 1994; Kelly & Woodward 1996; Thompson *et al.* 1999). Last, we developed a framework to relate trait variation among the eucalypts to patterns of rarity and commonness across multiple spatial scales.

TRAIT RELATIONSHIPS WITH SPECIES RARITY AND COMMONNESS

Introduction

We surveyed the ecological literature for research that compared traits of rare and common plant species. The focus of the present study was on traits related to growth (e.g. growth form, longevity), reproduction (e.g. breeding system, seed size), and both biotic and abiotic interactions (e.g. competitive ability, habitat specialization). Our objective was to identify traits involved in two or more studies at a particular spatial scale for a given rarity measure, and to determine whether they (i) distinguished between rare and common species consistently; (ii) were not significantly different for rare and common species consistently; or (iii) were related differently to rarity in each study, suggesting context-dependent relationships. Here, context refers to features such as geographical location, present-day environmental conditions and biogeographical history.

Methods

In total, 54 published research papers were identified and five features of each of these studies were initially noted, which included rarity measure, spatial scale, sample size, species taxonomy and whether phylogenetic relatedness among species was considered in analyses.

Studies were classified based on whether rarity was measured as abundance (density, percentage canopy cover, biomass, number of individuals, area of occupancy), distribution (extent of occurrence, number of populations, area of occupancy), or threatened status (rare species listed as endangered or vulnerable by relevant authorities particular to each study). Although correlations are often found between these measures of rarity, there is no reason to expect (either as cause or consequence) that traits related directly to low abundance are the same traits that are related directly to narrow distribution. Additionally, traits related directly to a higher risk of extinction (threatened status) may differ from traits associated with other forms of rarity. For example, vulnerability to human-induced habitat fragmentation may be due to possession of traits that

are not associated with low abundance or narrow distribution among species in the absence of human activities.

To address the issue of spatial scale, we classified studies based on whether research was conducted (i) within local assemblages (e.g. within 5 m × 0.2 m transects; Rees 1995); (ii) was carried out at a regional level (e.g. within tallgrass prairie in Missouri; Rabinowitz *et al.* 1984); or (iii) encompassed geographical ranges (e.g. across the entire Australian continent; Murray *et al.* 1999). The total number of taxa (including species, subspecies and varieties) that were examined in each study was noted. We additionally noted whether each study focused explicitly on angiosperms, gymnosperms, cryptogams or a selection of species across two or more vascular plant groups.

We then documented whether the analysis was performed with or without considering phylogenetic relatedness among the study species. Cross-species analysis, where phylogenetic relationships among the study species are not considered explicitly, is particularly relevant where relationships among contemporary species are of interest, and suggests something about what trait associations with rarity and commonness are ecologically relevant in the present day (Westoby *et al.* 1995, 1998). In contrast, an approach that employs phylogenetically independent contrasts (correlated-divergence analysis) provides information on whether divergence for a particular trait has been consistently correlated with rarity or commonness across independent evolutionary radiations (Westoby *et al.* 1998). It is commonly perceived in studies of species rarity and commonness that methods designed to detect correlated evolution supersede correlations across a set of present-day species, and that phylogeny is a source of confounding or error that requires controlling for. This view is incorrect, as phylogeny is part of the evolutionary process that may connect traits to rarity or commonness, not a competing explanation for any pattern. Evolutionary processes where niches are phylogenetically conservative may be quantified better by cross-species correlation than by evolutionary divergence correlation (Price 1997; Harvey & Rambaut 2000). Generally, cross-species and correlated-divergence approaches should be viewed as complementary.

Results

Four of the 54 studies investigated species rarity with respect to both abundance and distribution (Rees 1995; Kunin & Shmida 1997; Eriksson & Jakobsson 1998; Guo *et al.* 2000). Across a total of 58 separate investigations, rarity was most frequently measured as abundance (25 studies, 43%), followed by distribution (21 studies, 36%) and then threatened status (12 studies, 21%). For threatened status, rare species were

those with a higher risk of extinction (endangered or vulnerable species), whereas non-threatened species were considered common. Where rarity was measured as abundance or distribution, some studies made it apparent what constituted rare versus common species through the use of cut-offs or thresholds (Edwards & Westoby 1996; Murray *et al.* 1999). In other studies, rarity and commonness were treated as a continuous variable with no absolute threshold (Kelly & Woodward 1996).

In three studies, trait relationships were considered with rarity separately at more than one spatial scale (Kunin & Shmida (1997) at local, regional, and geographical scales; Eriksson & Jakobsson (1998) at regional and geographical scales; Thompson *et al.* (1999) at regional and geographical scales). Most frequently, relationships were explored at the largest scale encompassing geographical ranges (31 studies, 54%). Smaller numbers of studies were carried out at a local scale (14 studies, 24%), or at a regional scale (13 studies, 22%). With respect to sample size, 27 studies (50%) involved fewer than 10 species. In particular, 24% (13 studies) involved the contrast of one rare or one common species, which effectively presents no replication for reported trait patterns. Sixteen studies (30%) involved more than 100 species, whereas the remaining 20% (11 studies) involved between 10 and 100 species. There was a distinct bias in the taxa examined across the 54 studies, with the majority focused solely on angiosperms (47 studies, 87%) or angiosperms and other vascular plant groups (5 studies, 9%). There were only two studies (4%) that examined cryptogams (in this case bryophytes, Hedderon 1992; Longton 1992), and we found no studies involving gymnosperms exclusively. Thus, patterns discussed in the present study are centred on trends in angiosperm plant clades.

Cross-species analysis alone was used in 26 studies (48%). Seventeen studies (31%) contrasted rare and common species by establishing congeneric contrasts (not necessarily phylogenetically independent where more than two species were compared within a genus), and five studies (9%) used correlated-divergence analysis alone. Three studies (6%) used both cross-species and correlated-divergence analyses. Two studies explored patterns within major taxonomic groups (within-taxa method, Jensen 1992; Oakwood *et al.* 1993), whereas one study used hierarchical analysis of covariance (and analysis at a conservative taxonomic level) to examine relationships with respect to taxonomic variation (Peat & Fitter 1994).

A surprisingly large number of plant traits (94 in total) have been investigated in relation to species rarity (Tables 1–4). However, most traits (63) have yet to be the focus of more than one study. Of the traits that have been explored more than once for a particular rarity measure at a given spatial scale, 55% have been exam-

ined in two studies only, whereas other traits ranged from being investigated in three studies (flowering start in relation to threatened status at geographical scales)

to seven studies (seed size in relation to distribution at geographical scales). All 94 traits are listed here in four separate tables, based on whether they relate to plant

Table 1. Growth traits examined in comparative studies of species rarity and commonness; rarity measured as abundance, distribution or threatened status at local, regional, or geographical (range) spatial scales

Trait	Scale	<i>n</i>	Taxa	Analysis	Outcome
Abundance					
Capacity for immediate germination	Regional	723	A	C	Rare species had lesser capacity for immediate germination ¹
Capacity for lateral vegetative spread	Regional	723	A	C	No difference ¹
Establishment success	Local	25	A	C	No difference ²
Fire response	Range	171	A	C & PIC	No difference (in either analysis) ³
Growth rate	Regional	723	A	C	Rare species grew more slowly ⁴
Height	Local	38	A	C	Rare species were shorter in stature ⁵
	Range	171	A	C & PIC	No difference ³
Longevity	Regional	81	A	C & PIC	C: Rare species were annuals/biennials rather than perennials ⁶ PIC: No difference ⁶
Plant size	Regional	81	A	C & PIC	No difference (in either analysis) ⁶
Distribution					
Clonality	Range	>2000	A	PIC	Britain: Rare species were cloning rather than non-cloning ⁷ Crete: No difference ⁷
Germination numbers	Range	4	A	Con	No difference ⁸
Germination temperature	Regional	263	A	PIC	Rare species had a higher minimum temperature for 50% germination ⁹
	Range	263	A	PIC	No difference ⁹
Growth form	Range	>2000	A	PIC	Britain: Rare species were shrubs rather than trees ⁷ Crete: No difference ⁷
	Range	792	V	W	Rare species were shrubs and trees rather than herbs ¹⁰
Growth rate	Range	4	A	Con	No difference ⁸
Longevity	Range	81	A	C & PIC	No difference (in either analysis) ⁶
Plant size	Range	81	A	C & PIC	No difference (in either analysis) ⁶
Ramet production	Range	2	A	Con	Rare species produced fewer ramets per extant ramet ¹¹
Threatened status					
Germination numbers	Range	2	A	Con	No difference ¹²
	Range	2	A	Con	Rare species had less germinants ¹³
Germination rate	Range	2	A	Con	No difference ¹³
Growth form	Regional	>10 000	V	C	Rare species were herbaceous rather than woody ¹⁴
	Range	166	V	Con	No difference ¹⁵
Leaf area ratio	Range	3	A	Con	No difference ¹⁶
Leaf emergence	Range	2	A	Con	Rare species had leaves emerging later ¹²
Leaf length	Range	2	A	Con	Rare species had shorter leaves ¹²
	Range	2	A	Con	Rare species had shorter leaves ¹⁷
Leaf length/width ratio	Range	2	A	Con	Rare species had lower leaf length/width ratio ¹²
Leaf width	Range	2	A	Con	Rare species had narrower leaves ¹⁷
Leaf/peduncle ratio	Range	2	A	Con	Rare species had higher leaf/peduncle ratio ¹⁷
Life form	Range	166	V	Con	No difference ¹⁵
Longevity	Regional	>10 000	V	C	No difference ¹⁴
	Range	166	V	Con	No difference ¹⁵
Net assimilation rate	Range	3	A	Con	No difference ¹⁶
Post-fire survival	Range	2	A	Con	No difference ¹³
Resprouting vigour	Range	2	A	Con	No difference ¹³
Relative growth rate	Range	3	A	Con	No difference ¹⁶
Seedling growth	Range	2	A	Con	No difference ¹³
Shoot size	Range	166	V	Con	No difference ¹⁵
Specific leaf weight	Range	3	A	Con	No difference ¹⁶

Table 1. continued

Trait	Scale	<i>n</i>	Taxa	Analysis	Outcome
Vegetative dispersal (efficiency)	Range	166	V	Con	No difference ¹⁵
Vegetative dispersal (method)	Range	166	V	Con	No difference ¹⁵
Vegetative growth	Range	2	A	Con	Rare species facilitated vegetative growth well ¹⁷
	Range	2	A	Con	Rare species facilitated vegetative growth poorly ¹⁸

n, total number of species, subspecies and varieties. Taxa: A, angiosperms; V, vascular plants. Analysis: C, cross-species analysis; Con, congeneric contrasts; PIC, correlated-divergence analysis; W, within-taxa analysis. References: ¹Hodgson (1986b), ²Rabinowitz and Rapp (1985), ³Murray *et al.* (1999), ⁴Hodgson (1986c), ⁵Mitchley (1988), ⁶Eriksson and Jakobsson (1998), ⁷Kelly and Woodward (1996), ⁸Fiedler (1987), ⁹Thompson *et al.* (1999), ¹⁰Oakwood *et al.* (1993), ¹¹Byers and Meagher (1997), ¹²Anderson (1980), ¹³Witkowski and Lamont (1997), ¹⁴Harper (1979), ¹⁵Lahti *et al.* (1991), ¹⁶Snyder *et al.* (1994), ¹⁷Banks (1980), ¹⁸Morley (1982).

growth (Table 1), reproduction (Table 2), biotic interactions (Table 3), or abiotic interactions (Table 4). In these tables, differences or similarities in traits between rare and common species are reported where there were absolute and clear-cut differences (for example, where all rare species possessed one form of a given trait and all common species possessed a completely different form), and where a significantly disproportionate number of rare species possessed a particular trait that distinguished them on average from common species.

A meta-analysis in which the results of the different studies were weighted based on sample size (and hence replication of rare–common contrasts) would have been an ideal approach for the examination of trait relationships with rarity. However, a meta-analysis of this sort was precluded because of the generally small number of studies focusing on each trait (similar difficulties arose in Beville & Louda (1999)). In an attempt to overcome this problem, our discussion of the weight of evidence for each trait relationship with rarity takes into account not only the number of studies investigating each trait, but also the differences in sample size between studies.

Trait relationships with abundance

Of the 38 traits that have been examined for their relationship with rarity measured as abundance (Tables 1–4), seed size and competitive ability have by far received the most attention. The relationship between seed size and abundance within local plant communities was explored in four studies (Table 2); in two of these it was reported that rare species had larger seeds than common species (Rees 1995; Guo *et al.* 2000), and in another it was reported that four rare species had smaller seeds than three common species in tall grass prairie in North America (Rabinowitz 1978). Although the pattern was found by Rees (1995) across 16 species of British dune annual systems, the

pattern reported by Guo *et al.* (2000) was found across 43 species in a Chihuahuan desert community in North America (Arizona) only, and not in species data ($n = 70$) compiled from a variety of habitats in Northern England (Thompson & Grime 1979). Leishman and Murray (2001) explored the relationship in 10 different vegetation types (n ranged from nine to 157 species, vegetation ranged from North American chaparral to Australian tall open forest) and concluded that there was no consistent positive or negative relationship between seed size and abundance. In seven of the 10 communities, there was no significant seed size–abundance correlation. At a regional scale, Hodgson (1986b) reported that rare species had larger seeds than common species in cross-species analysis involving 723 species of the Sheffield region of Central England, whereas both Eriksson and Jakobsson (1998) and Bruun (2001) found no difference in seed size between rare and common species among 81 species of Swedish grasslands and 194 species in Danish grasslands, respectively (in both cross-species and correlated-divergence analyses). In the studies of both Eriksson and Jakobsson (1998) and Bruun (2001), seed size deviation (the absolute difference in log seed weight between each species and the community median value) was examined in relation to regional abundance (Table 2). Although Eriksson and Jakobsson (1998) found that the most common species had seeds of an intermediate size in correlated-divergence analysis (but not in cross-species analysis), Bruun (2001) found no such pattern. Considering the wide range of communities and geographical locations sampled across these studies, and for the most part the relatively large sample sizes involved, it can be concluded that the relationship between seed size and abundance is highly dependent on context.

The relationship between local abundance and competitive ability has been examined in six studies (Table 3), with no difference between rare and common species reported in three of these (Aarssen 1988;

Taylor & Aarssen 1990; Duralia & Reader 1993). In the other three studies it was reported that rare species were poor competitors relative to common species (Grubb 1986; Mitchley & Grubb 1986; Miller &

Werner 1987). In general, the sample sizes involved in these six studies were small ($n = 3, 3, 4, 5, 6, 14$) and only cross-species analysis has been used. There is considerable scope for further examination of the

Table 2. Reproductive traits examined in comparative studies of species rarity and commonness; rarity measured as abundance, distribution or threatened status at local, regional, or geographical (range) spatial scales

Trait	Scale	<i>n</i>	Taxa	Analysis	Outcome
Abundance					
Breeding system	Local	52	A	PIC	Rare species self-compatible ¹
	Regional	52	A	PIC	No difference ¹
Dispersal ability	Regional	7	A	C	Under constant conditions, seeds of rare species travelled further; not in field conditions ²
Dispersal mode	Regional	81	A	C & PIC	No difference (in either analysis) ³
	Range	171	A	C & PIC	No difference ⁴
Flower depth	Regional	52	A	PIC	If self-compatible, rare species had smaller and shallower flowers; if self-incompatible, rare species had larger and deeper flowers ¹
Flower longevity	Regional	52	A	PIC	Rare species had longer-lived flowers, especially among self-incompatible taxa ¹
Flower production	Range	4	A	PIC	Rare species produced fewer flowers per area of canopy cover ⁵
Flowering season	Range	171	A	C & PIC	No difference ⁴
Flowering season duration	Range	171	A	C & PIC	No difference ⁴
Flowering start	Regional	8	A	C	Rare species flowered earlier ⁶
Fruit production	Range	4	A	PIC	Rare species produced fewer fruits per flower ⁵
Fruiting season	Range	171	A	C & PIC	No difference ⁴
Fruiting season duration	Range	171	A	C & PIC	No difference ⁴
Petal length	Regional	52	A	PIC	If self-compatible, rare species had smaller petals; if self-incompatible, rare species had larger petals ¹
Reproductive failure	Regional	8	A	C	Rare species less likely to show reproductive failure ⁶
Reproductive performance	Regional	8	A	C	Flower and seed production considered together, rare species had less year-to-year variation ⁶
Seed abortion	Range	4	A	PIC	No difference ⁵
Seed production	Regional	81	A	C & PIC	No difference (in either analysis) ³
	Range	4	A	PIC	Rare species produced fewer seeds per area of canopy cover ⁵
Seed size	Local	113	A	C	Northern England: No difference ⁷
	Local	674	A	C	Arizona: Rare species had larger seeds ⁷
	Local	7	A	C	No difference (consistently across 10 different communities) ⁸
	Local	16	A	No	Rare species had smaller seeds ⁹
	Regional	194	A	C & PIC	Rare species had larger seeds ¹⁰
	Regional	81	A	C & PIC	No difference (in either analysis) ¹¹
	Regional	81	A	C & PIC	No difference (in either analysis) ³
	Regional	723	A	C	Rare species had larger seeds ¹²
	Range	171	A	C & PIC	No difference ⁴
	Regional	194	A	C & PIC	No difference ¹¹
Seed size deviation	Regional	194	A	C & PIC	No difference ¹¹
	Regional	81	A	C & PIC	C: No difference ³ PIC: Rare species did not have intermediate-sized seeds ³
Distribution					
Breeding system	Range	2	A	Con	No difference ¹³
	Range	4	A	Con	No difference ¹⁴
	Range	48	V	Con	No difference ¹⁵
	Range	52	A	PIC	No difference ¹
	Range	2	A	Con	No difference ¹⁶
	Range	4	A	Con	Rare species produced fewer bulbils ¹⁴
Bulbil production	Range	4	A	Con	Rare species produced fewer bulbils ¹⁴
Dispersal investment	Range	54	A	PIC	No difference in congeneric PICs with same dispersal mode; however, rare species invested less in dispersal in <i>Acacia</i> and <i>Eucalyptus</i> congeneric PIC's with different dispersal modes ¹⁷

Table 2. continued

Trait	Scale	<i>n</i>	Taxa	Analysis	Outcome
Dispersal mode	Regional	37	C	C	Most rare species reproduced by fragments (asexual), fewer produced spores ¹⁸
	Range	2	A	Con	No difference ¹³
	Range	81	A	C & PIC	No difference (in either analysis) ³
	Range	219	V	C	Rare species had succulent fruits rather than wind-dispersed fruits ¹⁹
	Range	792	V	W	Rare species were vertebrate-dispersed ²⁰
	Range	1777	A	T	Rare species were wind-dispersed rather than unspecialized for dispersal ²¹
Flowering percentage	Range	2	A	Con	Rare species had a smaller percentage of plants in flower ¹³
Flowering start	Range	2	A	Con	Rare species started flowering later ¹³
Mating system	Range	692	C	C	Rare species were monoecious rather than dioecious ²²
Pollination mode	Range	>2000	A	PIC	Britain: Rare species were non-wind-pollinated rather than wind-pollinated ²³ Crete: No difference ²³
Pollinator visitation	Range	4	A	Con	Rare species visited less frequently by insect pollinators ²⁴
Seed production	Range	2	A	Con	Rare species produced fewer seeds per flowering head ¹³
	Range	81	A	C & PIC	C: Rare species produced fewer seeds per individual ³ PIC: No difference ³
	Range	4	A	Con	No difference ¹⁴
	Range	1777	A	T	Rare species produce fewer seeds per plant ²¹
	Range	2	A	Con	Rare species produced fewer seeds per unit of canopy area ²⁵
Seed size	Range	2	A	Con	No difference ¹⁶
	Local	113	A	C	Northern England: No difference ⁷ Arizona: Rare species had larger seeds ⁷
	Local	16	A	C	Rare species had larger seeds ¹⁰
	Regional	263	A	PIC	Rare species had larger seeds ²⁶
	Range	27	A	C	Rare species had smaller seeds ²⁷
	Range	81	A	C & PIC	No difference (in either analysis) ³
	Range	54	A	PIC	No difference in congeneric PICs with same dispersal mode; however, rare species had smaller seeds in among-genera PICs with different dispersal modes ¹⁷
	Range	4	A	Con	No difference ¹⁴
	Range	39	A	W	No difference ²⁸
	Range	792	V	W	Rare species had larger seeds ²⁰
Seed size deviation	Range	263	A	PIC	No difference ²⁶
	Range	81	A	C & PIC	C: Rare species did not have intermediate-sized seeds ³ PIC: No difference ³
	Regional	263	A	PIC	Rare had lower velocities ²⁶
	Range	263	A	PIC	No difference ²⁶
Sexual reproduction	Range	4	A	Con	No difference ¹⁴
Sporophyte production	Range	692	C	C	Rare species did not produce sporophytes ²²
Threatened status					
Breeding system	Range	2	A	Con	No difference ²⁹
	Range	2	A	Con	Rare species self-incompatible ³⁰
	Range	2	A	Con	No difference ³¹
	Range	2	A	Con	No difference ³²
Canopy seed storage	Range	2	A	Con	No difference ³³
Dispersal mode	Range	166	V	Con	No difference ³⁴
Dormancy	Range	6	A	Con	Rare species had lower levels of dormancy ³⁵

relationship between competitive ability and abundance. A significant advance would be to investigate how competitive ability relates to abundance patterns across multiple spatial scales through the use of a large number of phylogenetically independent contrasts.

Trait relationships with distribution

Twenty-seven traits in total have been examined for

their relationship with rarity and commonness measured as distribution (Tables 1–4), but only six have been the focus of more than one study. Three of these (growth form, dispersal mode and seed size) have highly context-dependent relationships with rarity at a geographical scale.

The relationship between growth form and range size has been examined in two studies (Table 1). Although Oakwood *et al.* (1993) reported that rare

Table 2. continued

Trait	Scale	<i>n</i>	Taxa	Analysis	Outcome
Floral structure	Regional	>10 000	V	C	No difference ³⁶
Flower colour	Range	2	A	Con	Rare species had less colourful flowers ³²
Flower length	Range	2	A	Con	Rare species had shorter flowers ³⁰
Flower morphology	Range	2	A	Con	No difference ²⁹
Flower production	Range	2	A	Con	Rare species produced fewer flowers per genet ³²
Flower scent	Range	2	A	Con	Rare species had unscented flowers ³²
Flower size	Range	2	A	Con	No difference ²⁹
	Range	2	A	Con	Rare species had smaller flowers ³²
Flowering end	Range	166	V	Con	No difference ³⁴
Flowering percentage	Range	2	A	Con	Rare species had more plants flowering ³⁷
Flowering season duration	Range	166	V	Con	Rare species had a shorter flowering season ³⁴
Flowering start	Range	2	A	Con	Rare species started flowering later ²⁹
	Range	166	V	Con	No difference ³⁴
	Range	2	A	Con	Rare species flowered later ³²
Fruit production	Range	2	A	Con	Rare species produced fewer fruits per flower ²⁹
	Range	2	A	Con	Rare species produced more fruits per flower ³²
Ovules per flower	Range	2	A	Con	Rare species produced fewer ovules per flower ³²
Peduncle length	Range	2	A	Con	Rare species had shorter peduncles ³⁰
Pollen production	Range	2	A	Con	Rare species produced fewer pollen grains per flower ³²
Pollen viability	Range	2	A	Con	No difference ²⁹
	Range	2	A	Con	Rare species had lower pollen viability ³⁰
Pollination guides	Range	2	A	Con	Rare species lacked pollination guides ³²
Pollination mode	Regional	>10 000	V	C	Rare species were insect-pollinated rather than wind-pollinated ³⁶
	Range	166	V	Con	No difference ³⁴
Pollinator visitation	Range	2	A	Con	Rare species preferred less by insect pollinator ³⁰
Presence of nectaries	Range	2	A	Con	No difference ³²
Seed production	Range	2	A	Con	Rare species produced fewer seeds per fruit ³⁰
	Range	6	A	Con	Rare species produced fewer seeds per unit leaf area ³⁵
	Range	2	A	Con	Rare species produced fewer seeds per capsule ³²
	Range	4	A	Con	No difference ³⁸
	Range	2	A	Con	No difference ³³
Seed size	Range	2	A	Con	Rare species had smaller seeds ²⁹
	Range	166	V	Con	No difference ³⁴
	Range	2	A	Con	No difference ³³
Seed type	Range	166	V	Con	No difference ³⁴
Style length	Range	2	A	Con	Rare species had shorter styles ²⁹

n, total number of species, subspecies, and varieties. Taxa: A, angiosperms; C, cryptogams; V, vascular plants. Analysis: C, cross-species analysis; Con, congeneric contrasts; PIC, correlated-divergence analysis; T, hierarchical analysis of covariance (or analysis at a conservative taxonomic level); W, within-taxa analysis. References: ¹Kunin & Shmida (1997), ²Rabinowitz & Rapp (1981), ³Eriksson and Jakobsson (1998), ⁴Murray *et al.* (1999), ⁵Murray and Westoby (2000), ⁶Rabinowitz *et al.* (1989), ⁷Guo *et al.* (2000), ⁸Leishman and Murray (2001), ⁹Rabinowitz (1978), ¹⁰Rees (1995), ¹¹Bruun (2001), ¹²Hodgson (1986b), ¹³Byers and Meagher (1997), ¹⁴Fiedler (1987), ¹⁵Karron (1987a), ¹⁶Young and Brown (1998), ¹⁷Edwards and Westoby (1996), ¹⁸Hedderon (1992), ¹⁹Kelly *et al.* (1994), ²⁰Oakwood *et al.* (1993), ²¹Peat and Fitter (1994), ²²Longton (1992), ²³Kelly and Woodward (1996), ²⁴Karron (1987b), ²⁵Pirie *et al.* (2000), ²⁶Thompson *et al.* (1999), ²⁷Aizen and Patterson (1990), ²⁸Jensen (1992), ²⁹Anderson (1980), ³⁰Banks (1980), ³¹Bosch *et al.* (1998), ³²Mehrhoff (1983), ³³Witkowski and Lamont (1997), ³⁴Lahti *et al.* (1991), ³⁵Meagher *et al.* (1978), ³⁶Harper (1979), ³⁷Morley (1982), ³⁸Pavlik *et al.* (1993).

species were significantly more likely to be shrubs and trees (rather than herbs) in two of three floras, including central Australia ($n = 219$ species) and maritime Sydney ($n = 325$ species), Kelly and Woodward (1996) found no difference in growth form between rare and common species in the island flora of Crete ($n = 1084$ species). However, Kelly and Woodward (1996) did find that rare species were more likely to be shrubs (rather than trees) in the British flora ($n = 1196$ species).

Dispersal mode did not relate significantly to range size in two studies (Byers & Meagher 1997; Eriksson & Jakobsson 1998). However, both Oakwood *et al.* (1993) and Kelly *et al.* (1994) noted that rare species were more likely to have seeds dispersed by vertebrates than by other means (Table 2). Peat and Fitter (1994) found that rare species among 1777 British angiosperms were more likely to have seeds with modifications for wind dispersal rather than being unspecialized for dispersal.

No consistent rare–common relationship has emerged between seed size and range size (Table 2). Aizen and Patterson (1990) reported that rare species had smaller seeds than common species among approximately 27 North American oak species. For Australian plant species, Edwards and Westoby (1996) reported that rare species had smaller seeds in phylogenetically independent contrasts established among

genera ($n = 44$, where rare and common species differed in their dispersal modes), but they found no consistent rare–common differences in congeneric phylogenetically independent contrasts (where rare and common species had the same dispersal modes). Oakwood *et al.* (1993) reported generally weak correlations between seed size and range size, with rare species tending to have larger seeds. No relationship between seed size and range size has been found in other studies (Fiedler 1987; Jensen 1992; Eriksson & Jakobsson 1998; Thompson *et al.* 1999).

With respect to breeding system, in five studies it was consistently found that differences in geographical range size among species were unrelated to whether or not species were self-compatible or self-incompatible (Fiedler 1987; Karron 1987a; Byers & Meagher 1997; Kunin & Schmida 1997; Young & Brown 1998). These studies covered a wide range of geographical locations, including Australia (Young & Brown 1998), Israel (Kunin & Schmida 1997), and North America (Fiedler 1987; Byers & Meagher 1997). However, sample size remains an issue, with three of these studies only exploring one rare–common contrast (Fiedler 1987; Byers & Meagher 1997; Young & Brown 1998).

There is growing evidence (Table 2) that rare species produce fewer seeds (per unit measurement, e.g. seeds per m² of canopy cover) than common species (Peat &

Table 3. Biotic interaction traits examined in comparative studies of species rarity and commonness; rarity measured as abundance, distribution or threatened status at local, regional, or geographical (range) spatial scales

Trait	Scale	<i>n</i>	Taxa	Analysis	Outcome
Abundance					
Competitive ability	Local	4	A	C	No difference ¹
	Local	3	A	C	No difference ²
	Local	6	A	C	Rare species competitively poor ³
	Local	5	A	C	Rare species competitively poor ⁴
	Local	14	A	C	Rare species competitively poor ⁵
	Local	3	A	C	No difference ⁶
	Regional	7	A	C	Rare species competitively superior ⁷
Neighbourhood structure	Range	4	A	PIC	Around individuals of rare species there were more conspecifics ⁸
Palatability	Regional	7	A	C	Rare species were preferred by a herbivore ⁹
Predispersal seed predation	Range	4	A	PIC	No difference ⁸
Distribution					
Herbivory	Range	4	A	Con	Rare species more prone to leaf grazing ¹⁰
Rhizobial host specificity	Range	6	A	C	No difference ¹¹
Seed removal	Range	2	A	Con	No difference ¹²
Threatened status					
Competitive ability	Range	3	A	Con	No difference ¹³
	Range	2	A	Con	Rare species competitively poor ¹⁴
Seedling predation	Range	2	A	Con	No difference ¹⁵
Pre-dispersal seed predation	Range	2	A	Con	No difference ¹⁵

n, total number of species, subspecies, and varieties. Taxa: A, angiosperms. Analysis: C, cross-species analysis; Con, congeneric contrasts; PIC, correlated-divergence analysis. References: ¹Aarssen (1988), ²Duralia and Reader (1993), ³Grubb (1986), ⁴Miller and Werner (1987), ⁵Mitchley and Grubb (1986), ⁶Taylor and Aarssen (1990), ⁷Rabinowitz *et al.* (1984), ⁸Murray and Westoby (2000), ⁹Landa and Rabinowitz (1983), ¹⁰Fiedler (1987), ¹¹Murray *et al.* (2001), ¹²Pirie *et al.* (2000), ¹³Snyder *et al.* (1994), ¹⁴Walck *et al.* (1999), ¹⁵Witkowski and Lamont (1997).

Fitter 1994; Byers & Meagher 1997; Eriksson & Jakobsson 1998; Pirie *et al.* 2000). Some studies, however, have reported that there is no difference between rare and common species in seed production (Fiedler 1987; Young & Brown 1998). It is worth noting here that these studies that found no difference in seed production involved only one rare–common contrast, and despite non-significant results, there was a trend for the rare species to be less fecund.

In two studies (Table 4), it has been found that at a regional scale, those species that occupied a narrower range or a lower diversity of habitats (a high degree of habitat specialization) tended to be rare (Hedderon 1992; Thompson *et al.* 1999). At a local scale, rare (narrowly distributed) species were found to have larger seeds than common species (Rees 1995; Guo *et al.* 2000).

Trait relationships with threatened status

A total of 55 traits have been examined in relation to the threatened status of species (Tables 1–4). Small leaf length appears to characterize rare species (Anderson 1980; Banks 1980), whereas numbers of seeds germinating at a given germination event (Anderson 1980; Witkowski & Lamont 1997), the ability to grow vegetatively (Banks 1980; Morley 1982), flower size (Mehrhoff 1983), flowering start (Anderson 1980; Mehrhoff 1983; Lahti *et al.* 1991), fruit production (Anderson 1980; Mehrhoff 1983), pollen viability (Anderson 1980; Banks 1980), seed size (Anderson

1980; Lahti *et al.* 1991; Witkowski & Lamont 1997) and competitive ability (Snyder *et al.* 1994; Walck *et al.* 1999) do not appear to distinguish between rare and common species consistently among studies. It is important to note, however, that apart from the study of Lahti *et al.* (1991), in which 166 species were used, all of the other seven studies cited in this paragraph involved only one rare–common species contrast. Thus, the patterns emerging here are far from concrete.

In some studies, it has been found that breeding system is unrelated to an increased risk of extinction (Anderson 1980; Mehrhoff 1983; Bosch *et al.* 1998; but see Banks 1980). In several studies it has also been found that rare species produced fewer seeds (per unit measurement) than common species (Meagher *et al.* 1978; Banks 1980; Mehrhoff 1983); however, in two studies no difference between rare and common species was found in relation to seed production (Pavlik *et al.* 1993; Witkowski & Lamont 1997). In the case of Pavlik *et al.* (1993), although their findings were non-significant, both rare–common species contrasts showed that there was a trend for the rare species to be less fecund than the common species.

Discussion

Three important points emerged from our survey of comparative studies of plant species rarity and commonness. First, a wide range of traits have been compared between rare and common plant species.

Table 4. Abiotic interaction traits examined in comparative studies of species rarity and commonness; rarity measured as abundance, distribution or threatened status at local, regional, or geographical (range) spatial scales

Trait	Scale	<i>n</i>	Taxa	Analysis	Outcome
Abundance					
Geological strata	Regional	723	A	C	Rare species occurred on fewer strata ¹
Habitat disturbance	Regional	723	A	C	Rare species found less frequently on disturbed sites ¹
Habitat productivity	Regional	723	A	C	Rare species found less frequently at sites of high fertility ¹
Habitat range	Regional	723	A	C	Rare species occupied a narrower range of habitats ¹
Habitat specialization	Local	303	A	C	Rare species had more specialized habitat and regeneration niches ²
Land use	Regional	723	A	C	Rare species occurred in habitats most vulnerable to modern land use ³
Vegetation types	Regional	723	A	C	Rare species occurred in less common vegetation types ¹
Distribution					
Habitat specialization	Regional	37	C	C	Rare species occupied a narrower range of habitats ⁴
	Regional	263	A	PIC	Rare species exploited a lower diversity of habitats ⁵
	Range	263	A	PIC	Rare species exploited a lower diversity of habitats ⁵
Threatened status					
Climatic range	Range	2	A	Con	Rare species spanned a narrower range of climates ⁶
Drought tolerance	Range	2	A	Con	Rare species more tolerant of drought ⁷
Edaphic requirements	Range	166	V	C	Rare species more specialized in their requirements ⁸

n, total number of species, subspecies, and varieties. Taxa: A, angiosperms; C, cryptogams; V, vascular plants. Analysis: C, cross-species analysis; Con, congeneric contrasts; PIC, correlated-divergence analysis. References: ¹Hodgson (1986a), ²Hubbell and Foster (1986), ³Hodgson (1986b), ⁴Hedderon (1992), ⁵Thompson *et al.* (1999), ⁶Witkowski and Lamont (1997), ⁷Walck *et al.* (1999), ⁸Lahti *et al.* (1991).

Second, the majority of traits have yet to be investigated in more than one study at a particular spatial scale for a given rarity measure. Additionally, a large proportion of studies are characterized by small sample size, and there is often very little replication at the level of rare–common species contrasts. Third, where rare–common trait relationships have been explored in more than one study, the outcome is overwhelmingly for the studies to differ from one another in their findings. Thus, with few exceptions, we must view cautiously any general emergent rare–common patterns at this stage. Clearly, there is a pressing need for more comparative studies of species rarity and commonness designed to examine both cross-species and correlated-divergence patterns incorporating a large number of rare–common contrasts, if robust generalizations in relation to rare–common differences or similarities are to emerge.

Only one plant trait, seed production, distinguished between rare and common species fairly consistently. It emerged that species with narrow geographical distributions were less fecund than more common species. Higher seed output translates into greater colonization ability, providing the potential for a species to become widespread given suitable opportunity. Increased seed production was also found to distinguish between species capable of becoming abundant at locations throughout their ranges and species that were sparse everywhere (Murray & Westoby 2000). The generality of the latter pattern remains to be tested; nevertheless, the possibility exists for the emergence of a broadly general rare–common difference with respect to seed production regardless of whether rarity is measured as abundance, distribution, or threatened status.

Breeding system was revealed to be a trait that did not differ significantly between rare and common species consistently. A relatively large number of studies have found that the condition of being self-compatible (or self-incompatible) is not associated with narrow geographical ranges. This finding is somewhat unexpected, based on the prediction that self-fertilization would be favoured via natural selection in geographically restricted species that receive little or unreliable pollinator visitation (Karron 1987a). Clearly, it appears that self-incompatibility mechanisms can be, and are, maintained in rare (narrowly distributed) plant species (Young & Brown 1998).

Several other traits may potentially yield consistent rare–common patterns, but it is still too soon to state with certainty whether these patterns are broadly general. For example, consistent rare–common patterns have emerged in traits such as leaf length and habitat specialization, but only in two studies that involved few rare–common contrasts. In addition, although a number of traits have been explored in one study only, they have been investigated quite comprehensively. These include (among others) dispersal investment (Edwards & Westoby 1996), mating system (Longton

1992) and pollination mode (Kelly & Woodward 1996). Further exploration of these traits for rare–common patterns in different vegetation types and on other continents will prove invaluable.

All other traits including seed size, competitive ability, growth form, dispersal mode, and a suite of reproductive attributes that have been explored in two or more studies were related very differently to rarity in each study. This suggests that the nature of relationships between rarity and life-history and ecological traits will be highly context-dependent, perhaps reflecting the biogeographical history of particular regions, or differences in present-day ecology, or phylogeny. Indeed, it has recently been shown that families with the highest proportions of rare species are not consistent among the floras of Australia, New Zealand and North America (Edwards & Westoby 2000). It has been argued that such taxonomic variation in the incidence of rarity will preclude the emergence of traits that are consistently related to rarity on different continents (Edwards & Westoby 2000). However, such an argument may not apply to all life-history and ecological traits (e.g. seed production and breeding system).

An alternative explanation for contradictory findings between studies is that there may have been important differences in the way in which response variables (rarity measures) and explanatory variables (traits) were measured from one study to the next. For example, the seed size–local abundance patterns reported by Rees (1995) and Guo *et al.* (2000) were obtained by measuring abundance as number of individuals. In contrast, abundance was measured as percentage canopy cover or biomass in Rabinowitz (1978) and Leishman and Murray (2001). It would be interesting to re-examine the patterns in each of these latter studies by using the alternative method of obtaining abundance estimates to determine whether sampling technique can explain differences among studies. Along the same lines, the sampling method used in many studies to obtain mean values of continuous traits was not always clear. This may be important if differences in range size among species are being compared. Ideally, mean values should be obtained by sampling for the trait of interest from sites across the complete ranges of species, and not just from one or two localities. Not only can the mean value of traits be explored for rare–common patterns, but also the comparison of within-species variation in trait values between rare and common species may yield potentially valuable information.

In compiling studies for the present review, it was apparent that strikingly little work has explored how phenotypic plasticity of traits relates to interspecific variation in rarity and commonness. Capacity for plasticity in ecological and life-history traits is a feature we might expect to be important in facilitating wide distribution or high abundance. The failure to embrace

plasticity thus far in comparative studies of species rarity may additionally undermine our ability to identify consistent rare–common trait patterns. Plasticity is not simply another trait that should be added to the list of traits compiled here, but rather a phenomenon that demands we think about how we measure the traits we wish to compare between rare and common species.

In some recent studies, the physiological responses of related species with narrow and broad habitat specificity/ecological breadth have been contrasted (Walters & Field 1987; Field 1988; Chazdon 1992; Mulkey *et al.* 1993; Strauss-Debenedetti & Berlyn 1994; Sultan *et al.* 1998a,b; Bell & Sultan 1999; Greer & McCarthy 1999; Sultan 2001). In these studies it is suggested that species with narrow habitat specificity/ecological breadth may have a more uniform phenotype (in many cases suggestive of a specialist strategy), whereas species with broad specificity and breadth tend to be more plastic or generalist. Thus, the basic principles of these studies can be extended to formulate predictions about trait plasticity distinguishing rare from common species. Simply, we might expect that common species would demonstrate greater phenotypic plasticity than rare species. Potential for phenotypic plasticity can be described by examining norms of reaction (Schlichting 1986; Sultan 1987; Schlichting & Pigliucci 1998). Differences between rare and common species in the plasticity of a particular trait (e.g. specific leaf area, root length) can be assessed by comparing the extent of response (i.e. slope of reaction norms) under different environmental conditions (e.g. low and high moisture, nutrient or temperature conditions). If common species have greater plasticity, we would expect the slope of the relationship between the measured trait and the imposed condition to be greater than for rare species. By assessing plasticity in a range

of populations for a given species one can distinguish between genetic variability (likely to increase with range size) and plasticity. By developing and applying this method in studies covering a broad range of plant functional types, we can potentially advance our understanding of life-history and ecological differences between rare and common species considerably.

Finally, it was apparent that conflicting results for rare–common differences could emerge when different spatial scales were considered. As an example, rare species within chalk grasslands of southern England were shorter than common species (Mitchley 1988), but this pattern was not repeated across larger spatial scales for species of either dry sclerophyll woodland or temperate rainforest vegetation in Australia (Murray *et al.* 1999; Table 1). This may simply be a context-driven phenomenon given the very different floras of the two regions. Nevertheless, we can not ignore the possibility that scale may be an important consideration. Indeed, scale-of-study differences have been implicated previously where a lack of empirical consistency has emerged among studies addressing similar questions (Wiens 1989; Underwood & Petraitis 1993). The example of plant height (and others such as breeding system, germination temperature, seed production and competitive ability; Tables 1–3) clearly illustrates that rare–common trait patterns vary as a function of spatial scale. Such contradictory outcomes across studies are a major impetus for developing a framework for comparative studies of species rarity and commonness that incorporates multiple spatial scales.

Conclusion

One of the main goals of comparative studies of species rarity and commonness is to provide useful biological information for management strategies aimed at the

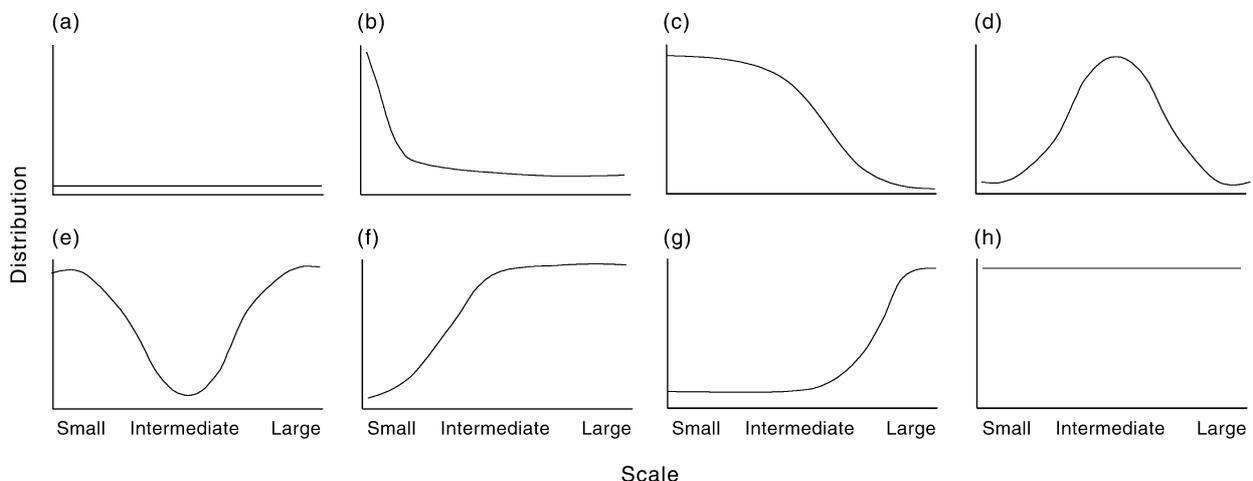


Fig. 1. The eight theoretical categories of distribution, (a)–(h) A to H, encompassing multiple spatial scales. The vertical axis represents increasing distribution, and the horizontal axis represents an increase in spatial scale from small, through intermediate, to large.

long-term conservation of species. To achieve this goal, life-history and ecological traits need to be identified that can or cannot distinguish consistently between rare and common species. A driving force behind our survey was to assess whether current knowledge is of sufficient quality for application to management strategies for rare species. Apart from the emerging patterns for narrowly distributed species to produce fewer seeds (per unit measurement), and for breeding system not to differ between narrowly and widely distributed

species, it appears that practical recommendations for applied use in a global context cannot be made from the data currently available. It is apparent that separate recommendations will need to be made for rare plants in different vegetation types and on different continents given the disparity in findings among studies for most traits.

RELATING LIFE-HISTORY AND ECOLOGICAL TRAITS TO DISTRIBUTION AT MULTIPLE SPATIAL SCALES IN THE GENUS *EUCALYPTUS*

Introduction

We performed a comparative analysis of distribution patterns in relation to several life-history and ecological traits for Australian eucalypts to address two issues. In the first instance, we examined the relationship between geographical range size and five traits (including growth form, fruit (seed) size, leaf size, flower size and flowering duration). Our aim was to relate observed rare–common patterns to the findings of previous studies of species rarity and commonness for growth form and seed size. We then described for the first time relationships between species rarity and leaf and flower size, as well as flowering duration, in relation to geographical distribution. These five traits were examined for their diagnostic value in identifying rarity with respect to distribution patterns in the eucalypts.

Because range size provides only one measure of distribution (at a geographical scale), and because distribution patterns vary considerably across a range of spatial scales (Erickson 1945; Brown 1995), we then developed a framework for relating plant traits to eucalypt distribution patterns across the Australian continent at multiple spatial scales. We initially described eight theoretical categories illustrating distribution patterns at multiple spatial scales, based on species occurring as rare at small, intermediate and large scales. Then, we classified each eucalypt species into one of the theoretical distribution categories, and explored trait variation in relation to the categories.

Methods

Data collection

We used an extensive and comprehensive herbarium database recording the occurrence (as latitude \times longitude points-of-occurrence) of 700 eucalypt species across the entire Australian continent and surrounding islands (more than 44 000 records). These locality records were obtained from the Australian

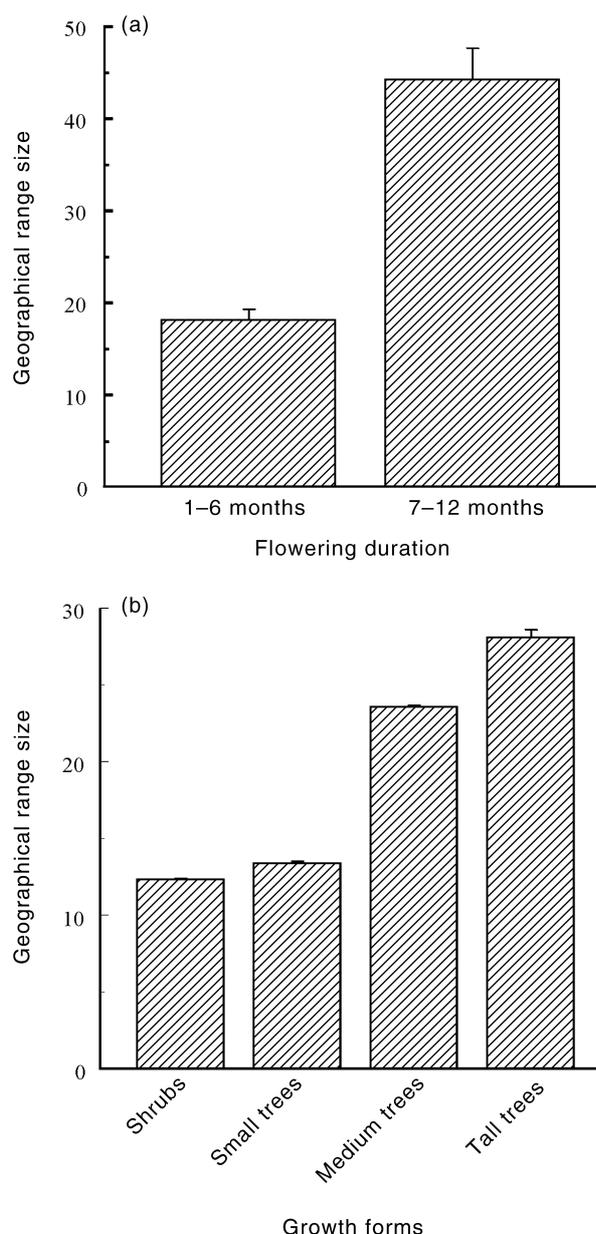


Fig. 2. (a) Mean (\pm SE) range size of species with flowering durations of 1–6 and 7–12 months inclusive, and (b) mean (\pm SE) range size of species in each of the four growth form categories. Range size was measured as the number of occupied $0.5^\circ \times 0.5^\circ$ grid cells.

National Herbarium, Canberra. Herbarium records of this type suffer from several weaknesses (Austin 1998). Nevertheless, they are the best data currently available for estimating geographical range size. Their value is further emphasized by their vital contribution to prioritizing species for conservation effort (Keith 1998; Keith *et al.* 2000). Indeed, the eucalypt database used here is among the most complete and up-to-date sources of such information available in Australia. We did not include hybrids or cultivated species, and for the purposes of the present study, both subspecies and

varieties were amalgamated into species (following Hughes *et al.* 1996). The data were screened for obvious location errors by mapping all points-of-occurrence for each species, and comparing them to published distribution maps (Brooker & Kleinig 1983, 1990, 1994). The maps were then verified by staff of the Australian National Herbarium (M. I. H. Brooker, J. Connors, B. J. Lepschi and A. Slee).

Data on growth form, fruit (seed) size, leaf size, flower size and flowering duration were extracted from Brooker and Kleinig (1983, 1990, 1994). Plant growth

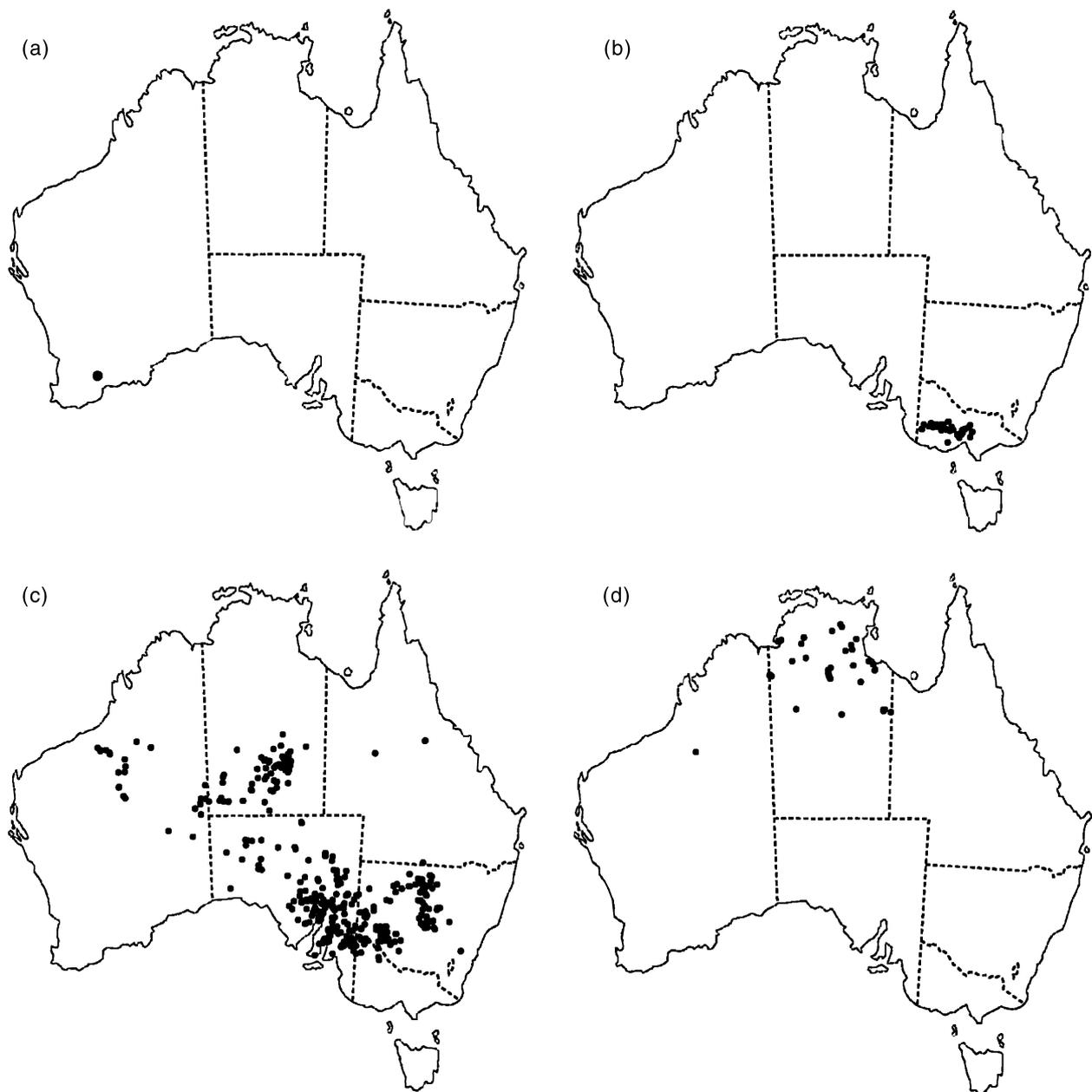


Fig. 3. Examples of the spatial structure of points-of-occurrence for eucalypt species across the Australian landscape: (a) *Eucalyptus desmondensis* (category B); (b) *Eucalyptus aromaphloia* (category D); (c) *Eucalyptus socialis* (category F); (d) *Eucalyptus aspera* (category G). The spatial structure of categories A and C (see Fig. 1 and text) were generally similar to category B, just with fewer (A) or more (C) points. No species was classified as either category E or H.

form was measured as one of four categories: shrubs, small trees (<10 m in height), medium trees (10–30 m), and tall trees (>30 m). Seed size estimates were available from the literature for only a small number of eucalypts, whereas fruit size has been recorded for a considerably larger number of species. Therefore, we used fruit size measurements as a surrogate for seed size for all species, based on the very tight positive allometric relationship between fruit and seed size in the genus (Gill *et al.* 1992; Murray & Gill 2001). Fruit, leaf and flower size were measured as maximum length (cm). Flower size estimates were maximum lengths of flower buds. Flowering duration was measured as the number of months over the course of a year in which a given species flowers.

Distribution measurements

To estimate range size for each species, a grid with cells of $0.5^\circ \times 0.5^\circ$ was superimposed on each species map and the total number of occupied cells was counted. These values provide an estimate of area of occupancy at a geographical scale (Gaston 1994).

We then identified theoretical curves predicting distribution patterns spanning small to large spatial scales, which resulted in eight categories (categories are hereafter referred to as A to H, as illustrated in Fig. 1). To classify each species into one of the distribution categories, a 4×4 grid of equal-sized cells was superimposed on points-of-occurrence maps for each species separately, starting at the level of the whole of Australia. Grid cells where at least one point-of-occurrence was found were divided further in a smaller 4×4 grid. Unoccupied grid cells were not considered further. This procedure was carried out a total of six times. The number of occupied grid cells was measured at each of the six spatial scales as a proportion of the total number of available grid cells (i.e. noting that

empty cells from the previous spatial scale had already been discarded). We considered that counts from the first two grid sizes provided an estimate of distribution at a large spatial scale, whereas counts from the next two provided distribution estimates at an intermediate scale. The final two counts represented distribution patterns at a small scale.

The number of occupied cells was plotted as a function of spatial scale, resulting in empirical curves that could be matched to the theoretical curves of distribution patterns at multiple spatial scales. We categorized a species as rare at a particular scale if ≤ 2 of the 16 grid squares were occupied. We then assessed the spatial structure of points-of-occurrence for species in each distribution category. The spatial arrangement of each species was scored qualitatively along two axes: (i) geographical extent (narrow-ranging, intermediate-ranging or wide-ranging points); and (ii) the proximity of points-of-occurrence to one another (tightly aggregated, loosely aggregated or non-aggregated points).

Data analysis

For the analysis of trait relationships with geographical range size, all parametric analyses were carried out using general linear models and a stepwise multiple regression procedure (GLIM 3.77 statistical package, Royal Statistical Society, London, UK). First, we fitted the maximal model that included all explanatory variables to the response variable (range size). Then, each of the explanatory variables was removed from the maximal model in a sequence as judged by their *t*-values (the least significant parameters were removed first; Crawley (1993)). Where the removal of a variable caused an insignificant change in deviance in the model, the term was left out of the minimum adequate model. We then carried out a further analysis where we included taxonomic membership within eucalypt subgenera in the general linear model. The modelling

Table 5. Stepwise multiple regression analysis relating life-history and ecological traits to rarity and commonness among Australian eucalypt species

	r^2	d.f.	<i>F</i>	<i>P</i>
Analysis without including taxonomic membership				
Flowering duration	0.09	1, 556	58.66	<0.001
Growth form	0.09	1, 557	51.71	<0.001
Leaf size	0.02	1, 555	12.87	<0.001
Fruit size	0.01	1, 554	4.85	<0.05
Analysis including taxonomic membership				
Flowering duration	0.08	1, 552	53.95	<0.001
Growth form	0.10	1, 553	57.97	<0.001
Leaf size	0.02	1, 551	13.72	<0.001
Fruit size	0.00	1, 550	1.28	NS

Data are analysed with and without incorporating taxonomic membership within eucalypt subgenera. Range size was treated as the response variable and explanatory variables included growth form, fruit (seed) size, leaf size, flower size and flowering duration. Flower size was not included in minimum adequate models as its removal from the maximal model caused an insignificant change in deviance. NS, non-significant.

procedure described previously was carried out with taxonomic membership being retained in the model at all stages (see Murray & Gill 2001). All range size, fruit size, flower and leaf length data were log-transformed prior to analysis.

To identify which traits discriminated most strongly among the distribution categories at multiple spatial scales, we used discriminant function analysis (SPSS for Windows, version 7.5). Discriminant analysis was carried out across all species, and separately within each eucalypt subgenus to determine whether trait relationships with distribution patterns occurred repeatedly in independent taxonomic lineages (see Murray & Gill (2001) for detail concerning eucalypt subgeneric classification used in analysis). Analyses within each of the subgenera revealed one marginally significant finding, thus no significantly consistent patterns emerged in the within-subgenus analysis.

Results

We found that four of the five traits were significantly associated with variation in geographical range size among eucalypts (Table 5). In analyses with and without the inclusion of taxonomy, flowering duration, growth form and leaf size consistently explained between 2 and 10% of the variation in eucalypt range size. However, although fruit size was able to explain a significant but small proportion of variation in range size in analysis where taxonomy was not included, no significant relationship was found in the analysis that included taxonomy (Table 5). Species with wide ranges tended to have longer flowering durations (Fig. 2a) and tended to be taller in stature (larger growth forms) (Fig. 2b). Although leaf size emerged as a significant associate of range size, its contribution was minor (Table 5).

Eucalypt species could be classified into six of the theoretical distribution categories. Most species (42%) were found to be rare at small spatial scales but common at intermediate and large scales (category F; Fig. 1f). These were species characterized by multiple populations of loosely aggregated and intermediate to wide-ranging points-of-occurrence (Fig. 3c). Twenty-eight per cent of species were rare at small and large scales, but common at intermediate scales (category D; Fig. 1d). Points-of-occurrence for these species generally occurred as one loosely aggregated and intermediate-ranging population (Fig. 3b). A considerable percentage (18%) of species were rare at every spatial scale (category A; Fig. 1a), being represented by one point-of-occurrence only, or a few non-aggregated and narrow-ranging points. Smaller percentages of species were rare at small and intermediate scales peaking at large scales (6%, category G; Fig. 1g), repre-

sented by non-aggregated and wide-ranging points-of-occurrence (Fig. 3d); rare at intermediate and large scales while common at small scales (3%, category B; Fig. 1b), with a small number of tightly aggregated and narrow-ranging points (Fig. 3a); and rare at large scales but common at small and intermediate scales (3%, category C; Fig. 1c), represented by a larger number (than category B species) of tightly aggregated and narrow- to intermediate-ranging points-of-occurrence. No species was found to be rare at intermediate scales but common at small and large scales (category E; Fig. 1e), or common at all spatial scales (category H; Fig. 1h).

Trait analyses revealed that both flowering duration and plant growth form were able to distinguish significantly among some of the distribution categories across all species. Flowering duration was the best discriminator ($F_{5,472} = 6.47$, $P < 0.001$), with category A (2.9 ± 0.1 , mean months per year \pm SE) differing significantly from categories D (3.6 ± 0.1) and F (4.0 ± 0.1 ; Tukey's test $P < 0.05$). After flowering duration was entered into the discriminant function, growth form was found to discriminate significantly among some of the categories ($F_{2,471} = 7.53$, $P < 0.001$). Here, category F differed from categories A, B, D, G (Tukey's test $P < 0.05$).

Discussion

Several traits were found to be significantly related to geographical range size among Australian eucalypts. Growth form and flowering duration explained significant but only moderate proportions of range size variation in analyses with and without the inclusion of taxonomic membership. The explanatory power of both leaf and fruit (seed) size for range size variation was consistently low and generally uninterpretable. Growth forms including medium to tall trees were disproportionately associated with wide ranges (although species with such growth forms could be found occupying narrow ranges), whereas species that were shrubs were found over comparatively narrow ranges. Given that tall eucalypts produce seeds of a smaller size than do eucalypt species of shorter stature (Murray & Gill 2001), the combination of increased height and small seed size could result in tall species being able to disperse their seeds further than could short species. This would provide tall species with a better chance of becoming widespread through improved dispersal to new areas. Appropriate circumstances to allow range expansion through dispersal would not necessarily occur for all tall species, explaining why some tall species occur within narrow ranges.

Our findings for the relationship between growth

form and range size are consistent with the pattern observed in the British flora, where trees were less likely to be rare (Kelly & Woodward 1996). However, our results differ from patterns reported for the floras of central Australia and maritime Sydney (Oakwood *et al.* 1993), and for the island flora of Crete (Kelly & Woodward 1996). Oakwood *et al.* (1993) found that tree (and shrub) species tended to have narrower ranges than herbaceous species, and Kelly and Woodward (1996) found no relationship between growth form and range size. Our study provides further evidence that the relationship between growth form and species rarity and commonness is highly dependent on context.

Flowering duration also emerged as a significant explanatory variable in relation to range size in the eucalypts. However, the measure of flowering is fairly broad: it is the months of the year within which the species is known to flower. It could be that the phenology of common species is similar to that of rare species, but we see overall longer times in common species because of gradients in environmental conditions experienced by widespread species. Flowering may thus be staggered geographically, with the outcome that common species appeared to flower throughout a greater proportion of the year. More comprehensive evidence for longer flowering times in widespread species will be obtained by closer examination of the phenology of rare and common species occurring in the same locations.

Considering trait relationships with distribution patterns at multiple spatial scales, both growth form and flowering duration discriminated significantly among some of the categories when analysed across all species. Category F had a greater representation of tall growth forms than did categories A, B, D and G. Considered in relation to our finding for a significant positive growth form–range size relationship, it appears that of the widespread species (categories F and G), those with multiple populations of loosely aggregated points (category F) are driving the relationship. Considering flowering duration, species in category A had significantly shorter flowering times than did species in categories D and F. It appears that the narrow ranges (arising from one or at most a few points-of-occurrence) of category A species are responsible for the overall significant positive flowering duration–range size correlation. Thus, analysing trait relationships with distribution patterns at multiple spatial scales has shed light on our previous findings in relation to growth form, flowering duration and range size.

Because of their extremely localized nature, species in categories A, B, C and to some extent category D will be under varying degrees of extinction risk from localized catastrophic events (e.g. large fires or a disease epidemic). Many species within the Australian

flora are at risk from such events (Leigh & Briggs 1992). Other threats such as habitat loss and degradation, grazing, and the introduction of exotic species will vary in their impact on species in different categories. Although species with populations dispersed across the landscape (e.g. categories F and G) may not be under immediate threat of extinction from localized catastrophic events, the gradual loss of habitat through grazing or competition with exotic weeds poses an important threat. It is worth considering that whereas species that fall in categories A, B, or C may have evolved mechanisms to counter the genetic consequences (e.g. inbreeding) of existing in small and/or isolated populations (e.g. naturally rare species), species with dispersed populations that have become fragmented recently as a result of human activities might be at risk of genetic erosion if dispersal and gene-flow among populations is not maintained. Metapopulation dynamics may play a central role in conservation strategies based on the framework presented here (Thrall *et al.* 2000).

The large amount of fragmentation of landscapes occurring through normal human economic activities in recent times, particularly since European settlement in Australia, will be reflected in the distribution patterns of species. Gill and Bradstock (1995) documented some examples of local angiosperm extinctions because of inappropriate fire regimes (Gill 1975), but lichens, mosses and liverworts can also be vulnerable (Scott *et al.* 1997). Species that were once widespread (e.g. categories F and G) might now be found in other categories (e.g. A or B). The result is an underestimate of the number of contemporary species formerly with wide ranges, and a subsequent overestimate of species with narrow ranges. This may have a major impact on the results of life-history analyses, indicating that it will be profitable to attempt to reconstruct the pre-European distributions of species for comparative analyses (see Murray & Dickman 2000). However, for many Australian plant species this will not be possible, as very little is known about their former distribution patterns.

Conclusion

A basic method for examining the distribution patterns of Australian eucalypts at multiple spatial scales in relation to life-history and ecological trait variation is presented here. This approach revealed important information about trait relationships with distribution patterns among Australian eucalypt species, linking the spatial structure of points-of-occurrence on the landscape with patterns of rarity and commonness. With the pressing need to protect an increasing number of rare species, the development and refinement of a broadly usable methodology for rarity studies that encompasses multiple spatial scales, which can be used for any

geographical location, will be useful for conservation and management.

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