

Properties of species in the tail of rank-abundance curves: The potential for increase in abundance

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ABSTRACT

It has recently been shown that most low-abundance species at a location are substantially more abundant somewhere else within their geographical range (somewhere-abundant). Fewer than 10% are everywhere-sparse. Here, two everywhere-sparse species from dry sclerophyll woodland were compared with phylogenetically contrasted somewhere-abundant species, at sites where both were at low abundance. In each pair, everywhere-sparse species produced approximately ten-fold fewer seeds per area of canopy cover than the somewhere-abundant species, consistently across replicate sites. Around individuals, a significantly larger proportion of the immediately colonizable neighbourhood was already occupied by the same species, for the everywhere-sparse compared to the somewhere-abundant species, in each pair and across replicate sites. Together, these differences amount to a much lower potential rate of increase in everywhere-sparse species compared with somewhere-abundant species, and are consistent with their having low capacity for opportunistic increase to high abundance. Our findings suggest novel differences between species that differ in local abundance patterns across geographical ranges, and provide a basis for further exploration of life-history and demographic differences between everywhere-sparse and somewhere-abundant species.

Keywords: everywhere-sparse, geographical range, macroecology, neighbourhood structure, rank-abundance curve, seed output, somewhere-abundant.

INTRODUCTION

Consistently within local plant and animal communities there are few high-abundance species and many low-abundance species (Preston, 1948; Whittaker, 1965; May, 1975). Rank-abundance curves provide graphical representations of species abundance versus their respective ranks in a community. Low-abundance species are found in the tail of these rank-abundance curves. Recently, it has been shown that most low-abundance tail species at any given location could be found in much higher abundance at some other locations within their geographical range (somewhere-abundant species; Murray *et al.*, 1999) (see Fig. 1). This macroecological pattern was found for plant species of both dry sclerophyll woodland and temperate rainforest. Respectively, 91% and 95% of low-abundance species from

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one location could be found in high abundance at some other locations within their range. Only 9% and 5% of species were everywhere-sparse, found in low abundance everywhere throughout their geographical range (see Fig. 1).

The results of Murray *et al.* (1999) were obtained by listing low-abundance species at focal sites and then establishing whether they achieved high abundance at any other location throughout their geographical ranges. They agree well with the results of previous studies of species abundance across geographical ranges (Rapoport, 1982; Schoener, 1987; Brown *et al.*, 1995), which have consistently found that species achieve high abundance at relatively few sites and are at low abundance at most sites. A novel feature in the results of Murray *et al.* (1999) is the small category of everywhere-sparse species. The present paper focuses on the relatively few everywhere-sparse species.

Both everywhere-sparse and somewhere-abundant species are in low abundance at most locations; the difference is the ability of somewhere-abundant species to become abundant at a few locations. These particular few locations might favour high abundance on a continuing basis (e.g. remnant populations; Eriksson, 1996), or, alternatively, high abundance might be achieved opportunistically and temporarily at any of a range of locations, or a mixture of these two explanations might operate. Consequently, one possible expectation about the (relatively few) everywhere-sparse species is that they might have lower capacity to take advantage of temporary opportunities for increase in abundance.

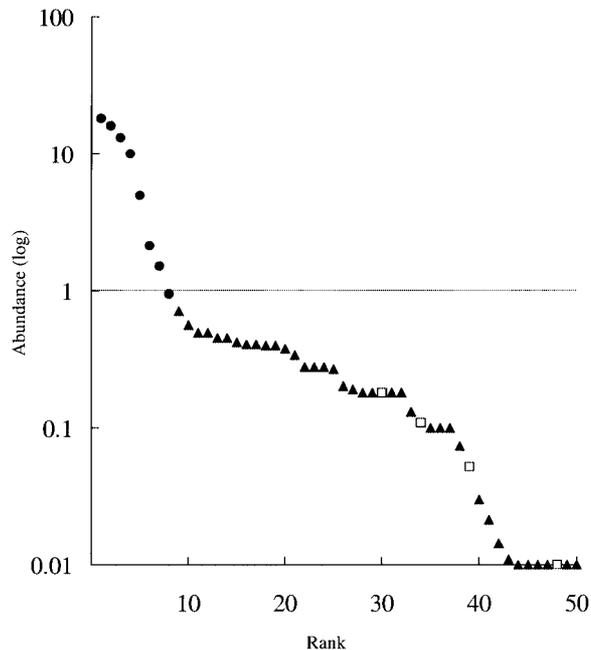


Fig. 1. Graphical representation of the abundance of 50 species versus their rank (rank-abundance curve) within a hypothetical community. ● = high-abundance species within the community, the dashed-line dividing these species from the long tail of low-abundance species. Of these low-abundance tail species, 91–95% can be found in high abundance somewhere else within their geographical range (▲ = somewhere-abundant species), whereas the remainder are everywhere in low abundance (□ = everywhere-sparse species).

Here we report investigations of two everywhere-sparse species (the only two that satisfied requirements for replication across sites), comparing aspects of their potential for increase with phylogenetically contrasted somewhere-abundant species. Although two species provide a restricted basis for generalization, the differences surprised us in their strength (approximately ten-fold effects) and consistency across sites, and deserve further investigation.

METHODS

Study species and sites

Working with a list of everywhere-sparse and somewhere-abundant species identified from dry sclerophyll woodland in a previous study (5 and 50 species, respectively; Murray *et al.*, 1999), we applied the following criteria for species selection in the present study: (1) species had to be of similar size and growth form (shrubs with maximum potential canopy cover between 0.04 and 4 m²; size-class 2 in Murray *et al.*, 1999); (2) they could be found in the same habitats at low abundance; (3) they recruited from seed after fire; (4) they flowered and set seed during the same period of the year; and (5) they constituted phylogenetically independent contrasts (Burt, 1989). Although our initial list included five everywhere-sparse species from dry sclerophyll woodland, we were unable to satisfy all of the above criteria for three of these species (*Bossiaea ensata*, *Dampiera purpurea* and *Logania albiflora*). Establishing phylogenetically contrasted somewhere-abundant species of similar size and growth form, that flowered and set seed during the same period of the year across replicate sites for each of these three everywhere-sparse species, was not possible. This resulted in two possible comparisons between everywhere-sparse and somewhere-abundant species. *Hovea linearis* and *Bossiaea scolopendria*, both everywhere-sparse species, were contrasted with the somewhere-abundant species *Boronia ledifolia* and *Dillwynia retorta*, respectively. All four species were studied at locations where their abundance was low, because the objective was not to compare abundant with less-abundant species, but to compare species at low abundance that had different potential for achieving high abundance. Sites were selected in dry sclerophyll woodland in Ku-ring-gai Chase National Park (~ 34°S, 151°E) in New South Wales. Each site measured 1 ha (100 × 100 m) in area, and was homogeneous to the extent that there was no evident trend in species composition from one side to the other. Sites were up to 10 km apart, with the minimum distance being 100 m between two of the sites (separated additionally by a road). Within each site, all four species were of equivalent low abundance (< 0.4% canopy cover over the whole hectare; Murray *et al.*, 1999).

Seed production

We located randomly between 5 and 15 individuals of each species at each of five sites using line transects. Several transects (between 5 and 10) were walked through each hectare for each species and mature individuals encountered were tagged carefully with fine cotton thread tied around the base of the stem. Forty-seven individuals of each species were followed in total across all sites. We monitored the progression from flowering to mature seed production in all tagged individuals beginning in early August 1996. The total number of flowers produced by each tagged individual was counted. An estimate was made of the

canopy cover of each plant by first finding the longest linear dimension from one end of the plant to the other and then the length of the perpendicular bisector, again from one tip to the other. Using these as the two dimensions (a and b) of an ellipse, the formula ($\pi ab/4$) was used to estimate canopy area. All measurements were then expressed as units per area of canopy cover. Each species was monitored once each week from the beginning of September to observe the development of fruit and seed. Individuals of each species adjacent to the study sites were used to decide when seeds had fully matured. When fruits on these were fully hardened and seeds had developed a hard coat, we began counting fruit and seed production within the study areas. This occurred between October and December. Seeds were counted and assigned to one of three categories: aborted, destroyed by predators, or matured. Aborted seeds were those that showed signs of having been initiated, but had ceased development without external signs of damage. Destroyed seeds had been partially eaten or completely removed (the latter determined from visible signs of predation on fruit) by invertebrate or vertebrate predators. Mature seeds were those that showed no signs of abortion or predation. Between 6 and 20 mature seeds from each species were tested for viability using Tetrazolium chloride solution (5%; Grabe, 1970) to provide general information on the percentage of mature seeds with the potential to recruit. Both *H. linearis* and *B. scolopendria* had 100% viability (6 of 6 and 15 of 15, respectively), whereas *B. ledifolia* and *D. retorta* had 86% (12 of 14) and 95% (19 of 20) viability, respectively.

Neighbourhood structure

Neighbourhoods were characterized for individuals of each species within four of the sites described previously. A neighbourhood was defined as the circular area around a focal plant, of a size such that another plant of the same species rooted within the circle would (on average) have overlapping canopy with the focal plant and thus be a neighbour. The size of the circle around the focal plant was determined as follows. Average canopy cover (m^2) for each of the four species was calculated using individuals measured for flower production. This area was then considered to be circular, and the average radius (r) of the circle was determined. The value of r was then doubled, and a new circular area calculated with this doubled radius. The new areas with their doubled radii were then considered to be the local neighbourhoods for each of the species (*H. linearis* $2r = 0.22$ m, *B. ledifolia* $2r = 0.26$ m; *B. scolopendria* $2r = 0.62$ m, *D. retorta* $2r = 0.40$ m). In total, the neighbourhoods of 30 randomly chosen focal plants of each species were assessed from the four sites. When a focal plant was encountered, the amount of conspecific and hetero-specific canopy cover that fell within its neighbourhood was measured. For heterospecific cover, two measurements were taken. One included only species of the same general growth form as the study species (intermediate-sized shrubs); the other embraced all species including graminoids and other ground cover beneath, and tree canopy cover overhead. The following comparisons were made between everywhere-sparse and somewhere-abundant species: (1) conspecific canopy cover (excluding the focal plant itself) as a proportion of the total area in an individual's neighbourhood; (2) conspecific canopy cover (excluding the focal plant itself) as a proportion of total canopy cover for species of the same general growth form; and (3) conspecific canopy cover (excluding the focal plant itself) as a proportion of total canopy cover for species of all growth forms.

Data analyses

Data for mature seed production per square metre of canopy cover, flower production per square metre of canopy cover, seeds aborted, seeds destroyed by predation, fruits per flower, and for each of the three measures of neighbourhood structure, were not distributed normally. All variables except fruits per flower and flower production per square metre of canopy cover were $(\log[x + 1])$ transformed prior to analysis. Data for flower production per square metre of canopy cover were log transformed. The number of fruits per flower was determined for each site by dividing the total number of fruits by the total number of flowers across all individuals per site. Hence, it was not possible to determine within-site variation in fruits produced per flower. In this case, Mann-Whitney U -tests were used to detect significant differences between everywhere-sparse and somewhere-abundant species after combining data across all sites. For all analysis of variance tests, the error mean square was used to calculate F -ratios, except where there were significant species \times site interactions, in which case the interaction mean square was used as the denominator for F -ratios.

RESULTS

Mature seed production per area of canopy cover was significantly lower in *H. linearis* and *B. scolopendria* than in contrasted somewhere-abundant species by approximately a factor of 10 (*H. linearis*, *B. ledifolia*: $F_{\text{species}} = 124.6$, $P < 0.01$; $F_{\text{site}} = 2.6$, $P < 0.05$; *B. scolopendria*, *D. retorta*: $F_{\text{species}} = 76.5$, $P < 0.01$; $F_{\text{site}} = 0.9$, $P > 0.05$; Table 1, Fig. 2). There were no significant species \times site interactions for mature seed production. The number of flowers produced per square metre of canopy cover (Table 1, Fig. 3) was significantly lower in the everywhere-sparse species of both contrasts (*H. linearis*, *B. ledifolia*: $F_{\text{species}} = 13.2$, $P < 0.05$; $F_{\text{site}} = 3.1$, $P < 0.05$; $F_{\text{species} \times \text{site}} = 6.3$, $P < 0.01$; *B. scolopendria*, *D. retorta*: $F_{\text{species}} = 40.7$, $P < 0.01$; $F_{\text{site}} = 3.6$, $P < 0.01$; $F_{\text{species} \times \text{site}} = 1.2$, $P > 0.05$). At one site for the *H. linearis* and *B. ledifolia* contrast, flower production was similar between everywhere-sparse and somewhere-abundant species (Fig. 3a). The number of fruits produced per flower (*H. linearis*, *B. ledifolia*: $U = 1.0$, $P < 0.05$; *B. scolopendria*, *D. retorta*: $U = 0.0$,

Table 1. Mature seed production and all measured components (mean \pm standard error) calculated across five sites^a

Reproductive components	<i>Hovea linearis</i> (ES)	<i>Boronia ledifolia</i> (SA)	<i>Bossiaea scolopendria</i> (ES)	<i>Dillwynia retorta</i> (SA)
Mature seed production per m ²	112 \pm 14**	1402 \pm 170	167 \pm 22**	1383 \pm 36
Flowers per m ²	1271 \pm 250*	2465 \pm 213	882 \pm 79**	1743 \pm 55
Fruits per flower	0.13 \pm 0.03*	0.28 \pm 0.02	0.10 \pm 0.01*	0.71 \pm 0.07
Proportion of seeds aborted	0.07 \pm 0.02**	0.43 \pm 0.02	0.09 \pm 0.01	0.17 \pm 0.01
Proportion of seeds destroyed by predation (of those not aborted)	0.03 \pm 0.01	0.02 \pm 0.01	0.45 \pm 0.04**	0.05 \pm 0.01

^a *Hovea linearis* (everywhere-sparse, ES) was contrasted with *Boronia ledifolia* (somewhere-abundant, SA), and *Bossiaea scolopendria* (ES) was contrasted with *Dillwynia retorta* (SA).

* $P < 0.05$ and ** $P < 0.01$ indicate a significant difference between everywhere-sparse and somewhere-abundant species.

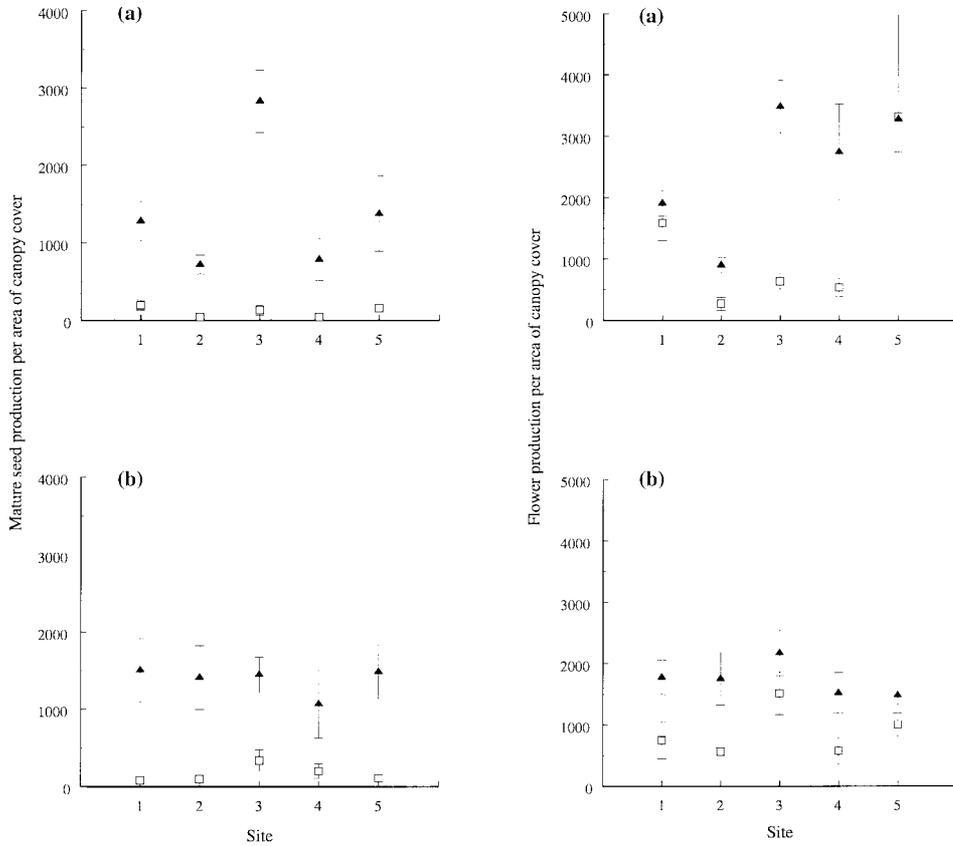


Fig. 2. (Left) Mature seed production per m² of canopy cover for (a) *H. linearis* (□) everywhere-sparse, *B. ledifolia* (▲) somewhere-abundant and (b) *B. scolopendria* (□) everywhere-sparse, *D. retorta* (▲) somewhere-abundant, at each of five sites. Values presented are the means for each site with standard errors.

Fig. 3. (Right) Flower production per m² of canopy cover for (a) *H. linearis* (□) everywhere-sparse, *B. ledifolia* (▲) somewhere-abundant and (b) *B. scolopendria* (□) everywhere-sparse, *D. retorta* (▲) somewhere-abundant, at each of five sites. Values presented are the means for each site with standard errors.

$P < 0.05$; Table 1, Fig. 4) was significantly lower in everywhere-sparse species than in contrasted somewhere-abundant species. Assessment of the fruits produced per flower within each of the five sites revealed apparently higher production by somewhere-abundant species within all five sites for both contrasts (Fig. 4), although this could not be tested formally. The proportion of seeds aborted was significantly lower in *H. linearis* than *B. ledifolia* ($F_{\text{species}} = 31.6$, $P < 0.01$; $F_{\text{site}} = 0.5$, $P > 0.05$; $F_{\text{species} \times \text{site}} = 4.0$, $P < 0.01$). Thus, the proportion of seeds aborted could not be responsible for lower mature seed output in *H. linearis*, as the lower abortion counters the lower mature seed output. A significant difference in the proportion of seeds destroyed by predation was only found between *B. scolopendria* and *D. retorta* ($F_{\text{species}} = 23.8$, $P < 0.01$; $F_{\text{site}} = 1.2$, $P > 0.05$; $F_{\text{species} \times \text{site}} = 5.3$, $P < 0.01$; Table 1);

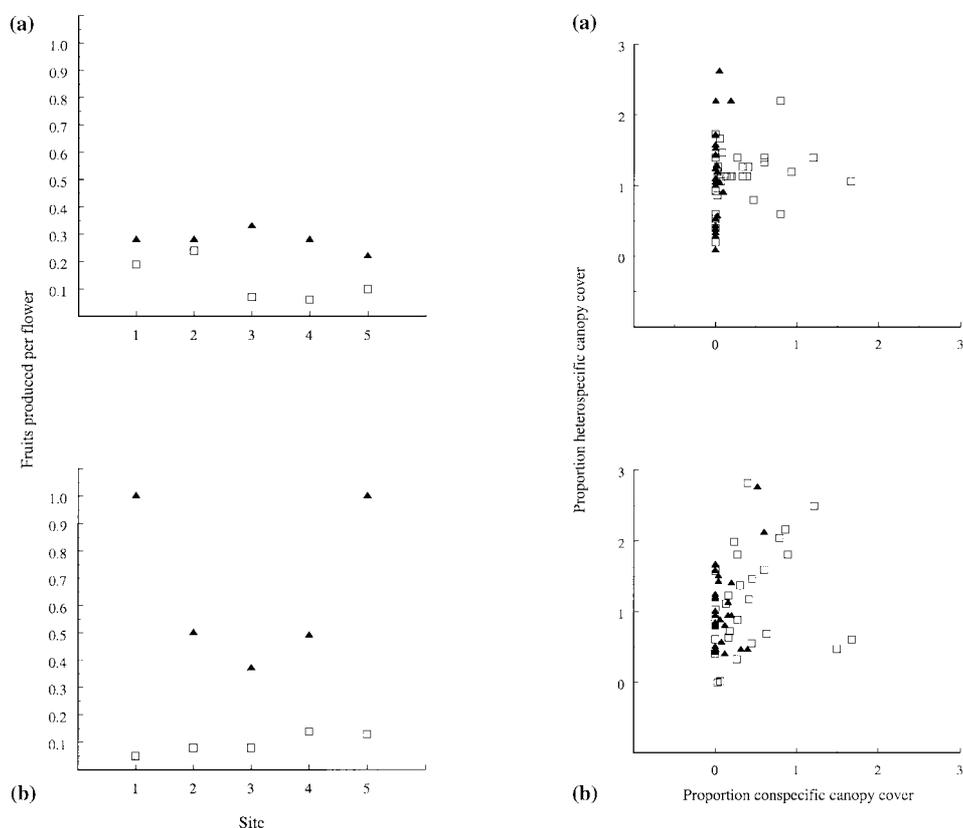


Fig. 4. (Left) Fruits produced per flower for (a) *H. linearis* (□) everywhere-sparse, *B. ledifolia* (▲) somewhere-abundant and (b) *B. scolopendria* (□) everywhere-sparse, *D. retorta* (▲) somewhere-abundant, at each of five sites. Values were determined by dividing the total number of fruits produced by the total number of flowers produced across all individuals within each site, hence no error bars are presented.

Fig. 5. (Right) Scatter-plots of conspecific versus heterospecific canopy cover (all growth forms) measured as proportions of total neighbourhood area (2 canopy-radii) for (a) *H. linearis* (□) everywhere-sparse, *B. ledifolia* (▲) somewhere-abundant and (b) *B. scolopendria* (□) everywhere-sparse, *D. retorta* (▲) somewhere-abundant across all sites. Note that proportions can be greater than 1 given canopy overlap among species within neighbourhoods.

thus, this component of mature seed output (as for the proportion of seeds aborted) could not contribute consistently to lower mature seed output in everywhere-sparse species.

Around individuals, a significantly larger proportion of the immediately colonizable neighbourhood was already occupied by the same species for everywhere-sparse compared with the somewhere-abundant species (Table 2, Fig. 5). This was true for the three different measures of neighbourhood structure we used (see Methods): (1) *H. linearis*, *B. ledifolia*: $F_{\text{species}} = 22.2$, $P < 0.01$; *B. scolopendria*, *D. retorta*: $F_{\text{species}} = 17.3$, $P < 0.01$; $F_{\text{site}} = 10.2$, $P < 0.01$; (2) *H. linearis*, *B. ledifolia*: $F_{\text{species}} = 22.8$, $P < 0.01$; *B. scolopendria*, *D. retorta*: $F_{\text{species}} = 15.3$, $P < 0.01$; (3) *H. linearis*, *B. ledifolia*: $F_{\text{species}} = 24.0$, $P < 0.01$; *B. scolopendria*,

Table 2. Conspecific canopy cover (mean \pm standard error) within the immediate neighbourhood (2 canopy-radii) of everywhere-sparse (ES) versus somewhere-abundant (SA) species calculated across four sites^a

Neighbourhood structure	Mean \pm standard error
1. Conspecific canopy cover as a percentage of total neighbourhood area	
<i>H. linearis</i> (ES) vs <i>B. ledifolia</i> (SA)	32 \pm 1 vs 2 \pm 0.1**
<i>B. scolopendria</i> (ES) vs <i>D. retorta</i> (SA)	40 \pm 2 vs 10 \pm 0.5**
2. Conspecific canopy cover as a percentage of cover of all species in same general growth form	
<i>H. linearis</i> (ES) vs <i>B. ledifolia</i> (SA)	35 \pm 1 vs 6 \pm 0.5**
<i>B. scolopendria</i> (ES) vs <i>D. retorta</i> (SA)	41 \pm 1 vs 15 \pm 0.8**
3. Conspecific canopy cover as a percentage of cover of all species in all growth forms	
<i>H. linearis</i> (ES) vs <i>B. ledifolia</i> (SA)	17 \pm 0.6 vs 2 \pm 0.1**
<i>B. scolopendria</i> (ES) vs <i>D. retorta</i> (SA)	27 \pm 0.8 vs 8 \pm 0.4**

^a Each of the three different measures of neighbourhood structure are presented (1, 2, 3).

** Significant difference ($P < 0.01$) between everywhere-sparse and somewhere-abundant species.

D. retorta: $F_{\text{species}} = 13.7$, $P < 0.01$. There were no species \times site interactions for these neighbourhood measure statistics, and only one site effect was found in the first measure for the *B. scolopendria*–*D. retorta* contrast.

DISCUSSION

Previous work on species in the tail of rank-abundance curves identified a small but novel category of everywhere-sparse species (Murray *et al.*, 1999). In the present study, we found markedly strong differences in seed production and neighbourhood structure for two everywhere-sparse species relative to somewhere-abundant species. The number of mature seeds produced per area of canopy cover by everywhere-sparse species was significantly lower, by approximately a factor of 10, than for contrasted somewhere-abundant species. In addition, a significantly larger proportion of the immediate neighbourhood was occupied by conspecifics in everywhere-sparse species.

Higher mature seed production in somewhere-abundant compared with everywhere-sparse species was consistent across all five study sites for each comparison. However, the factors contributing to the difference were not quite so consistent. Increased flower production per area of canopy cover and the higher proportion of flowers that gave rise to fruits were important contributors. Flower production was not consistently higher in somewhere-abundant species across all five sites for one of the contrasts. At one site flower production was similar in *B. ledifolia* and *H. linearis*, but at all other sites somewhere-abundant species produced more flowers per area of canopy cover than everywhere-sparse species in both contrasts. The five- to ten-fold higher proportion of flowers that produced fruits in somewhere-abundant compared with everywhere-sparse species appeared to be a more consistent contributor across sites to higher mature seed production. The difference in the proportion of flowers producing fruits might have been due to less effective pollination

in everywhere-sparse species, as ineffective pollination can play a critical role in determining fruit production and subsequent seed-set (e.g. Bierzychudek, 1981; Cunningham, 1996). Possible causes of ineffective pollination could include self-incompatibility together with lower receipt of out-cross pollen (Whelan and Goldingay, 1989) due to a shortage of effective pollinators or lower pollen loading (Mitchell, 1997) by the relevant pollinators. Both everywhere-sparse species produce heavier seeds on average, by a factor of 2–3, than their contrasted somewhere-abundant species (Murray, 1997). Theory predicts that these heavier-seeded species must produce fewer seeds per gram of reproductive effort than lighter-seeded species (Smith and Fretwell, 1974). Thus, seed weight differences between everywhere-sparse and somewhere-abundant species may also be partly responsible for the observed differences in seed production in the present study. It is also possible that there are above-ground biomass differences between everywhere-sparse and somewhere-abundant species. That is, species might have different biomasses within similar canopy areas. Such biomass differences might exaggerate patterns of seed production per area of canopy cover.

To summarize these results, although the demographic components contributing to seed production – flowers per area, fruits produced per flower, seed weight – were not wholly consistent in the nature of the differences between everywhere-sparse and somewhere-abundant species, the net outcome – seeds produced per square metre of canopy cover – was consistently different. This makes sense: it should be low seed production per square metre that restricts the potential for increase of everywhere-sparse species, irrespective of the cause of the low seed production.

For both everywhere-sparse species, a larger proportion of the immediate neighbourhood was occupied by conspecifics (for example, 32–40% vs 2–10% for contrasted somewhere-abundant species by the first measure of neighbourhood structure; see Table 2). Consequently, for everywhere-sparse species, a larger proportion of canopy expansion by growth, or of colonization into adjacent space by seedlings, will not have the effect of increasing overall cover of the species at the site, because that growth or colonization would be at the expense of other members of the same species. Equivalently, it could be said that individuals of these everywhere-sparse species experience more intense effects of within-species competition at smaller scales than individuals of the compared somewhere-abundant species. Modulation of within-species competition by spatial pattern has been shown to be very important in spatially explicit models (e.g. Pacala and Silander, 1990). This neighbourhood structure would weaken the capacity of the everywhere-sparse species to increase rapidly in response to temporary opportunities. There might be different causes for the observed neighbourhood structure – more local seed dispersal, greater aggregation of favourable microsites – but in either event the effect would be the same in weakening the capacity for rapid increase.

There might be two explanations for somewhere-abundant species: particular locations might favour high abundance on a continuing basis, or, alternatively, high abundance might be achieved opportunistically and temporarily at any of a range of locations. That these two everywhere-sparse species appear to be characterized by lower potential for opportunistic increase, suggests indirectly that opportunistic increase may be a cause of local abundance, at least for some species that are somewhere-abundant. Our findings should hopefully stimulate further exploration of fundamental life-history and demographic differences between everywhere-sparse and somewhere-abundant species, focusing on their capacity to take advantage of temporary opportunities for increase in abundance.

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