Plant functional types determine how close postfire seedlings are from their parents in a species-rich shrubland

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- **Background and Aims** Fine-scale spatial patterns of the seedlings of co-occurring species reveal the relative success of reproduction and dispersal and may help interpret coexistence patterns of adult plants. To understand whether postfire community dynamics are controlled by mathematical, biological or environmental factors, we documented seedling–adult (putative parent) distances for a range of co-occurring species. We hypothesized that nearest-seedling-to-adult distances should be a function of the distance between the closest conspecific seedlings, closest inter-adult distances and seedling-to-parent ratios, and also that these should scale up in a consistent way from all individuals, to within and between species and finally between functional types (FTs).
- **Methods** We assessed seedling–adult, seedling–seedling and adult–adult distances for 19 co-occurring shrub species 10 months after fire in a species-rich shrubland in south-western Australia. Species were categorized into 2 × 2 FTs: those that are killed by fire [non-(re)sprouters] vs. those that survive (resprouters) in nine taxonomically matched pairs, and those that disperse their seeds prefire (geosporous) vs. those that disperse their seeds postfire (serotinous).
- **Key Results** For the total data set and means for all species, seedling–adult distance was essentially a mathematical phenomenon, and correlated positively with seedling–seedling distance and adult–adult distance, and inversely with seedlings per adult. Among the four FTs, seedling–adult distance was shortest for geosporous non-sprouters and widest for serotinous resprouters. Why adults that produce few seedlings (resprouters) should be further away from them defies a simple mathematical or biological explanation at present. Ecologically, however, it is adaptive: the closest seedling was usually under the (now incinerated) parent crown of non-sprouters whereas those of resprouters were on average four times further away.
- **Conclusions** Our study highlights the value of recognizing four reproductive syndromes within fire-prone vegetation, and shows how these are characterized by marked differences in their seedling–adult spatial relations that serve to enhance biodiversity of the community.

Key words: Fire ecology, geosporous, sclerophyll shrubland, nearest neighbour, PFT, resprouter, seedling–parent relations, serotiny, spatial arrangement.

INTRODUCTION

Fire resets and synchronizes community dynamics in fire-prone ecosystems throughout the world (Marod *et al.*, 2002; Nathan and Ne'eman, 2004; He *et al.*, 2019). The postfire pathway depends on the fire-related traits possessed by each component species (Paula *et al.*, 2009; Keith, 2012). The most basic dichotomy is whether individuals are killed by fire [non-(re)sprouter, NR] or recover vegetatively (resprouter, R) and this usually operates at the population and species levels (Keeley and Zedler, 1978; Bell, 2001; Esther *et al.*, 2011; Clarke *et al.*, 2015; Treurnicht *et al.*, 2016). These two fire-response types are often correlated with a number of morphological traits in these systems: NR may be taller (Midgley, 1996), while R have extensive below-ground bud banks and spread widely from their base or are clonal (Pausas *et al.*, 2018); and reproductive traits: NR usually have higher viable seed/ovule ratios (Lamont and Wiens, 2003), while R have lower numbers of seedlings per

parent (Enright and Lamont, 1989; Moreno and Oechel, 1992). Despite their lower fecundity, the fitness benefits of seeds spreading beyond the crown of fire-surviving adults are clear. Nevertheless, pointing to the advantages of long-term ‘persistence’ (R) over ‘dispersal’ (NR) as a form of trade-off, Bond and Midgley (2001) and Levin *et al.* (2003) expect R to have poor dispersibility compared with NR. However, at least in terms of long-distance dispersal, Merwin *et al.* (2012) showed that life form among co-occurring banksia shrubs is not correlated with their dispersibility.

Another well-established dichotomy is between those species that store their seeds in the soil (geosporous) and thus germinate postfire, and those that lack dormancy and germinate continuously interfire (Pausas and Keeley, 2014). However, in Australia and southern Africa, and to a lesser extent in the Mediterranean Basin and North America, the dichotomy is more likely to be between geosporous and on-plant seed storage (serotiny) with postfire release and germination synchronized to fire as with

soil-stored seeds (Yeaton and Bond, 1991; Enright *et al.*, 2007; Lamont *et al.*, 2020). This yields four major fire-related functional types (FTs). These have received some attention in terms of differential germination requirements (Enright *et al.*, 2007; Ne'eman *et al.*, 2009) and ability to survive reduced rainfall due to climate change (Enright *et al.*, 2014). However, most postfire seedling research has concentrated on NR, either possessing geospory (Moreno *et al.*, 2011; Santana *et al.*, 2012; Wright *et al.*, 2016) or serotiny (Heelemann *et al.*, 2008; Calvo *et al.*, 2013), or R, either with geospory (Seligman and Henkin, 2000) or serotiny (Calviño-Cancela *et al.*, 2018). More comprehensive studies have compared co-occurring serotinous NR and R (Enright and Lamont, 1989; Hammill *et al.*, 1998;

Treurnicht *et al.*, 2016). At best, postfire recruitment studies follow one or two species that are taken to represent the FT groups, usually confamilial or congeneric to minimize taxonomically related differences not under study (Bond *et al.*, 1984; Cowling and Lamont, 1987; Lamont *et al.*, 1999).

A community can be viewed as a collection of FTs (each made up of different species), and/or species (each made up of different individuals) and/or individuals independent of their taxonomy (Fig. 1A). Scale has been ignored in fire-prone systems in the past other than the detailed work of Perry *et al.* (2013, 2014, 2017, 2020), who compared spatial patterns among individual adult plants, species and FTs; or the type of population dynamics is simply applied as a trait label

FIG. 1. (A) Scheme showing how individual responses to an independent variable, e.g. closest seedling–adult distance (S–A) as a function of closest inter-adult distance (A–A), can be scaled up to individual responses within species, then between species, then between functional types. Multiples of any number 1, 2, ..., 8 represent individual plants of species represented by 1, 2, ..., 8. The grey arrows represent increasing values of the dependent variable within the reference group. (B) Model of how S–A distances are affected by A–A and inter-seedling (S–S) distances and number of seedlings per parent (S/A). Note that closer S–A distances can be achieved either by increasing the density of adults (greater prefire population size but fixed postfire seedlings per parent), increasing the density of seedlings (unchanged prefire population size but more postfire seedlings per parent) or increasing prefire population density and maintaining postfire seedlings per parent.

to species or FTs (Keith and Bradstock, 1994; Tyler, 1995; Esther *et al.*, 2011; Moreno *et al.*, 2011). It is assumed that the patterns at one scale apply to the next. However, this should not be taken for granted: if there are inconsistencies, then an issue of ecological concern exists that needs to be explored. Consider scale aspects of the closest seedling (S) to adult (A) distance (S–A). There is particular interest in S–A as this indicates the potential for the new generation to replace the prefire parents spatially if they are killed or to compete with, or are likely to be displaced by, their parents if these survived (Yeaton and Bond, 1991). As a working hypothesis, we could propose that S–A is a function of the closest inter-adult distances, A–A (see Fig. 1B). Across a range of species, the total individuals independent of their species identity will span a wide range of [A–A, S–A] pairs (Scenario 1 in Fig. 1A) that can be correlated. We would then expect to show similar correlations of [A–A, S–A] when individuals within each species are regressed, provided the sample size is adequate (Scenario 2). Some species will have low mean values of [A–A, S–A] through to those with high values, spaced along the same gradient (Scenario 3). These species can then be grouped into FTs with short, or wide, [A–A, S–A], and those variously intermediate (Scenario 4).

Studies of spatial relationships among individuals in mature, postfire vegetation point to aggregation of species as indicative, especially among geosporous non-sprouters (Miller *et al.*, 2010; Perry *et al.*, 2013). This FT will correspond to the short [A–A, S–A] group. Clearly, such patterns must be instigated at the postfire seedling stage. That is, the relevant interactions are at the individual scale during the recruitment phase, Scenarios 1 and 2 in Fig. 1B. Two variables affect the distance a seedling is from an adult plant: S–A decreases when more A are added to a nominated area, expressed by shorter closest inter-adult distances (A–A), although this also decreases the seedling to parent ratio (S/A) (Fig. 1B). Additionally, more S can be added, expressed by shorter, closest inter-seedling distances (S–S), that also increases S/A. Where adults are isolated, then usually the density of S declines sharply with distance from the parent in a binomial/exponential/leptokurtic fashion, peaking at its base or displaced to the edge of the crown (Lamont, 1985a; Hammill *et al.*, 1998; Eshel *et al.*, 2000; Lambert, 2001; Daskalakou and Thanos, 2004; Vekemans and Hardy, 2004; Krauss *et al.*, 2009).

The distribution of seedlings should be a function of the number of seedlings per parent (S/A). Consider one plant with an S/A of 10 and another with 100: assuming a normal curve distribution centred on each plant, then about seven seedlings will occur around the smaller parent within a distance of 1 SD (x) and none beyond 3 SD ($3x$), and ~26 around the larger parent within the same distance and ~32 beyond $3x$ ($= 1$ SD of the latter). Thus, seedlings of both plants will be clustered close to the parent but the tail of the less fecund plant will be much shorter so that most seedlings will be much closer. As S/A and the density of A increase (Fig. 1B), seedling shadows about their parents increasingly overlap and merge. As a result, S–A will also be predicted by the closest distance a nominated seedling is from its nearest sibling, S–S (supported by empirical data in Gilbert *et al.*, 2001). Thus, S–A distances are mathematical functions of the local densities of S and A: S–A will increase as A–A and S–S increase, and S/A decreases (Fig. 1B).

At a fixed density of A, the density of S may not always be a simple diminishing function of distance from the centre of the parent plant. Dispersal agents can play a key role in the shape and size of the seed/seedling shadow. Prevailing winds displace winged seeds/fruits to one side of the plant (Lamont, 1985a). Ants transport hard, aril-bearing seeds to their nests so that seedlings are concentrated at nest sites (Yeaton and Bond, 1991). Since granivores and herbivores are most active where seed/seedling density is greatest, especially after fire, they can deplete the offspring beneath or near the parent crown (Zwolak *et al.*, 2010). The level of predation depends on the food preferences of the animals (Jones *et al.*, 2003; Rafferty and Lamont, 2007) and their abundance (Tasker *et al.*, 2011; Talluto and Benkman, 2014). The soil beneath plants that have been killed can be associated with either improved conditions for seedling establishment (Boyd and Davies, 2010) or worse conditions (Ne'eman *et al.*, 1992). At a finer scale, postfire-transported seeds and debris can accumulate in local depressions and around fallen branches independently of the location of prefire plants to give seedling-rich and seedling-impooverished microsites (Lamont *et al.*, 1993). Fluctuating levels of soil heating due to the patchiness of fuel distribution can lead to localized death of soil-stored seeds, especially where combustible prefire plants were previously located (Odion and Davis, 2000). Thus, the distribution of seedlings about their parents will be the net effects of their inherent dispersal curves plus the intensity and pattern of postfire environmental influences.

We sought to describe the range of postfire S–A distances that occur in species-rich shrublands and determine to what extent they are controlled by mathematical, biological or environmental factors. Our study was undertaken in heathland, centred on the Eneabba sandplain, 270 km north of Perth, Western Australia. The vegetation of the Eneabba Plain has been intensively studied over many years (Lamont *et al.*, 1977; Enright and Lamont, 1989; Perry *et al.*, 2013; Lamont and Keith, 2017, Lamont, 2019) so that we had an ideal background for undertaking a study on the novel topic of seedling–parent spatial relationships. Its postfire community dynamics compare favourably with those in the scrub-heath of Eastern Australia, the South African fynbos, the maquis/garrigue of the Mediterranean Basin and the chaparral of California (Letten *et al.*, 2014; Treurnicht *et al.*, 2016; Lamont and Keith, 2017; Esler *et al.*, 2018). Component species are readily allocated to four fire-related functional types (NR/R $\times$ geosporous/serotinous), with > 95 % of species either NR or R and storing their seeds until stimulated to germinate by fire (Enright *et al.*, 2007; Esther *et al.*, 2011). Studies of the spatial arrangements of individuals and species within the same mature vegetation as examined here have shown strong aggregation, especially among geosporous non-sprouters (Miller *et al.*, 2010; Perry *et al.*, 2013), although random and segregation effects have been shown to dominate when individual shrubs and species are considered collectively (Perry *et al.*, 2014, 2020). Research has concentrated on postfire community dynamics as expressed through NR and R, highlighting the universal death of NR species but survival of mature R in response to a wide range of fire types, the much greater fecundity of NR compared with R, the dynamics of serotinous seed release, and *en masse* germination and recruitment of soil- and plant-stored seeds of NR compared

with R (Enright and Lamont, 1989; Herath *et al.*, 2009). Past seedling studies have been done in the context of the role of postfire microsites (Lamont *et al.*, 1993) but none has been spatially explicit in terms of S–A relationships, in contrast to those on long unburnt vegetation (Perry *et al.*, 2013, 2020). However, S–A studies are essential if we are to understand the causes of spatial patterns in mature fire-prone vegetation.

The scale of our study covered S–A, S–S and A–A distances for 20 replicates within a given species, 19 species with their associated life-history, growth-form and diaspore attributes, and four reproductive functional types each represented by four to six species across two families equally represented in each. We hypothesized that:

- (a) Seedling to adult distance (S–A) is a direct function of inter-seedling distance (S–S) and inter-adult distance (A–A) and an inverse function of seedling to parent ratio (S/A) between all individuals independent of species, within and between species, and between functional types (consistent mathematical/ecological relationships across all scales). These basic patterns will be modified as follows:
- (b) Species that release their wind-dispersed diaspores prefire will have a shorter S–A than those that release their wind-dispersed diaspores postfire (as there are more obstacles to wind dispersal then).
- (c) S–A distance for species with ant-dispersed diaspores will be greater than prefire, wind-dispersed diaspores (as ant nests are more likely to be located in bare patches away from dense patches, our personal observations).
- (d) S–A will be shorter for NR than R (as their S/A is higher and they are more likely to be aggregated, and their ultimate fitness is not deterred by establishing beneath their dead parents, unlike R).
- (e) In conflict with (d), seedlings are more likely to occur under the crown of R than N (as they produce fewer seeds so that their dispersal curve is smaller, their crowns often cover a greater area, and fitness is enhanced by remaining associated with the ‘persistence niche’).
- (f) S–A distance of the geosporous N functional type will be the shortest compared with geosporous R, and serotinous N and R [as they will have both the highest S/A and aggregation (shortest A–A), and most obstacles to seed dispersal among the four functional types].
- (g) Overall, the inherent binomial dispersal curve dominates the patterns of seedling establishment over other possible modifying influences.

MATERIALS AND METHODS

Study site descriptions

The two study sites were located ~270 km north of Perth, Western Australia: the South Eneabba Nature Reserve (29°52.493'S, 115°15.078'E), 7 km south of Eneabba, was burnt in early May 2005 (an experimental fire of about 5 ha) at moderate fire intensity. The previous fire was in summer 1986, such that the prefire vegetation had experienced 19 winter-wet seasons. The specific site was on the crest of a gently sloping dune of deep siliceous sand (15 m depth to hardpan). The vegetation is a

species-rich, sclerophyll shrubland (scrub-heath) and has been well described in previous studies at this site (Perry *et al.*, 2013, 2014). A total of 110 evergreen species in a 40 × 40-m area has been recorded here (Lamont and Keith, 2017). The second site was in the same reserve (29°56.677'S, 115°16.179'E), 12 km south of Eneabba, and was burnt on 25 December 2004 (about 1000 ha; due to powerlines falling during a thunder-storm). The previous fire was not recorded but the vegetation was estimated to be 15–20 years old. The site was on shallow sand-over-laterite soil with low heath vegetation of the type described in detail previously (Perry, 2013, 2014). Only the two *Dryandra* species were studied at this site.

Fieldwork details

Fieldwork was undertaken through December, following a particularly wet and cool winter–spring. Six-month-old seedlings were abundant and there was no evidence of seedling death from early summer drought or herbivory. This is consistent with previous monitoring at matched deep-sand sites that showed less than 40 % of seedlings emerge by mid-June (early winter), seedling emergence peaks in September (early spring), seedlings transpire strongly in November (late spring), seedling mortality is negligible up to December (early summer) but may be substantial by February (late summer), and herbivory of seedlings and resprouts is restricted to graminoids (Lamont *et al.*, 1993; Lamont and Witkowski, 1995; Richards and Lamont, 1996; Herath *et al.*, 2009). It should also be noted that there is negligible seedling establishment in subsequent years but that summer death of recruits continues at a diminishing to zero rate over time (Enright *et al.*, 1998). The western corolla cockatoo (*Cacatua pastinator*) is a postfire granivore of serotinous diaspores in the area but the clumping of serotinous seedlings in litter microsites indicated that they had not frequented our study sites. Species pairs were selected based on whether they are killed by fire (non-sprouter, NR) or survive fire (resprouter, R), and within these, whether their seeds are released prefire (soil-stored, geosporous) or postfire (plant-stored, serotinous). [No R in this flora is ‘obligate’ (*sensu* Pausas and Keeley, 2014), i.e. seed production and germination are not delayed until many years after fire among R, with 95 % strictly geosporous or serotinous (Enright *et al.*, 2007)].

Selection criteria included that ‘skeletons’ of the fire-killed plants were still intact (this excluded Ericaceae as these small plants were incinerated), and that there were at least 20 burnt adults with evidence of bearing fruits prefire (therefore increasing the likelihood that they were parents of the closest seedlings) available (three species used had 15–19 plants that otherwise met the criteria). In addition, there was an attempt to match them by family and sub-family to minimize phylogenetic confounding. Several species were rejected as taxonomically matched pairs (all Fabaceae in the area were geosporous R) or sufficient plants could not be found for them. This procedure was successful for eight NR–R pairs. A ninth pair was chosen that was NR–R, both with ant-dispersed seeds but in unrelated families. An additional R that otherwise met the criteria was added. Only four geosporous–serotinous pairs in the same families were available. This yielded four geosporous NR

species, four geosporous R species, five serotinous NR species and six serotinous R species, 12 in the Proteaceae, six in the Myrtaceae and one in the Fabaceae (Table 1). Nomenclature followed the Western Australian Herbarium (florabase.dpaw.wa.gov.au) except that we retained *Dryandra* as a separate genus from *Banksia* as species pairs from each clade were used (George, 2014).

The first adult plant sighted meeting the criteria was selected as number 1 and then its nearest neighbour was chosen on a meandering walk, not repeating any plants, through the site until the required number of plants (20 fecund adults) was reached. This was equivalent to the ‘wandering quarter method’ of Catana (1963) except that the next plant did not have to be in a fixed quarter (which would veer sampling in a certain direction that would require constant resetting of the starting point). The data were not used for estimating density as the design was only intended to provide a practical field method for identifying the closest neighbour to a representative sample of adults in the study area. That the sampling points might have got locked into a cluster and thus provided an underestimate of closest adult distances is unlikely as Perry *et al.* (2013) showed for this particular study site that most species clustered at a width < 1 m whereas only two of our study species had a (mean $\pm$ SD) apart of < 1 m. The rule of excluding any plant already encountered meant that sampling was continually pushed away from clusters and served to increase A–A to counter any tendency to underestimate it. This method is also consistent with the theory developed in the Introduction for S–A and S–S. Thus, as the distance between two adults is reduced, their dispersal ‘shadows’ will increasingly overlap and their S–A will shorten. As S/A increases around any A, both S–A and S–S distance will decline. Independent of any potential bias in this method of sampling A and S distances, it was applied equally to all three pairs of measurements on the 20 individuals of the 4–6 species $\times$ 4 FTs assessed.

Although the above-ground parts of the NR species, *Conospermum incurvum*, were almost completely combusted, the 1–2-cm-wide protruding black stumps were clearly recognizable, especially when excavated. They have a deep taproot that descends vertically, with fibrous bark and wide medullary rays in transection (Purnell, 1960) that confirmed their identity.

To obtain estimates of prefire adult height and crown diameter, an adjacent unburnt patch with plants of the same cohort was inspected, and again using clearly reproductive adults, height, crown diameter and stem basal diameters were measured as before. The best-fit regression lines for rootstock diameter (independent variable) with (1) plant height and (2) crown diameter (dependent variables) were determined. The means and standard deviations of the basal areas of the two sets of plants were also indistinguishable. The regression equations were applied to the burnt adults to estimate prefire dimensions.

The following traits were measured on each selected adult: (1) stature (height to tallest twig with effect of its missing leaves estimated), (2) crown diameter in a north–south direction, (3) rootstock [base of stem(s) at ground level] diameters (longest and that at 90° to the longest), (4) distance to the closest conspecific adult to the nearest centimetre, (5) distance to the closest conspecific seedling, and (6) distance of that seedling to its closest conspecific seedling. The number of excluded prefire plants was also recorded as possibly of ecological significance.

Fruits were collected from each species at the study sites. Seeds were removed from the fruits if dehiscent but left intact if indehiscent (testa and pericarp fused), and at least 20 from each species were weighed to a precision of 0.1 mg. The terminal velocity of the diaspores was then determined by dropping them from a height of 4 m in a windless building void to estimate their air buoyancy (Enright and Lamont, 1989). Data for these two attributes was obtained for four species from Lamont *et al.* (1993) and B. Lamont (unpubl.).

Data analyses

For each plant, crown and rootstock areas were calculated as $\pi(\text{diameter}/2)^2$. Whether the closest seedling was at a distance less than the radius of the crown was noted. To determine the number of seedlings per parent, the density (ρ) of seedlings and adults can be estimated by a plotless method assuming that each adult/seedling pair are representative points in the landscape and using their distance from the closest adult (A–A) or seedling (S–S): $\rho = 100/(\text{distance})^2$ as number of adults or seedlings/100 m² (Mueller-Dombois

TABLE 1. Closely related non-sprouter and resprouter species pairs ($n = 9 \times 2$), grouped into pre- ($n = 8$) and postfire ($n = 11$) seed dispersers

Seed dispersal	Non-sprouter (NR)	Resprouter (R)	Plant family, subfamily
Soil-stored seeds (prefire dispersal)			
Wind	<i>Calytrix flavescens</i>	<i>Pileanthus filifolius</i>	Myrtaceae, Myrtoideae
Wind	<i>Conospermum incurvum</i>	<i>Conospermum wycheleyi</i>	Proteaceae, Proteoideae
Wind	<i>Verticordia aurea</i>	<i>Verticordia grandis</i>	Myrtaceae, Myrtoideae
Ant/passive	<i>Adenanthos cygnorum</i>	<i>Daviesia quadrilatera</i>	Proteaceae/Fabaceae*
Plant-stored seeds (postfire dispersal)			
Wind	<i>Banksia hookeriana</i>	<i>Banksia attenuata</i>	Proteaceae, Grevilleoideae
Wind	<i>Dryandra carlinoides</i>	<i>Dryandra shuttleworthiana</i>	Proteaceae, Grevilleoideae
Wind	<i>Hakea psilorrhyncha</i>	<i>Xylomelum angustifolium</i>	Proteaceae, Grevilleoideae
Passive	<i>Beaufortia elegans</i>	<i>Melaleuca leuropoma</i>	Myrtaceae, Leptospermoideae
Wind	<i>Petrophile drummondii</i>	<i>Isopogon tridens</i>	Proteaceae, Proteoideae
Passive/wind		<i>Lambertia multiflora</i>	Proteaceae, Grevilleoideae

**Adenanthos cygnorum* is not closely related to *Daviesia quadrilatera*, but they are paired as both are ant-dispersed and have opposing fire responses, in the absence of other suitable co-occurring candidates.

and Ellenberg, 1974; Krebs, 2017). The recommended point-centred quarter method for density uses the nearest plant in each of four quarters per point and takes their mean, $m = (X_1 + X_2 + X_3 + X_4)/4$. However, in our case, we only measured $X_1 = A-A$ or $S-S$, the shortest distance among four possible quarters. Hence, our method will overestimate density to the extent that $(X_2 + X_3 + X_4)/3 > X_1$ and thus we did not use these data to estimate density. Then, the true $m = (X_1 + aX_1)$ where a is approximately a constant for a given species and growth stage. For example, for X_1 , X_2 , X_3 and X_4 equal to 2, 4, 6 and 8 at one point (say, centre of a cluster) and 3, 6, 9 and 12 at another (edge of cluster), $m = 5$ and 12.5, but a remains constant at 1.5. In support of this, Cottam and Curtis (1956) showed for randomly distributed individuals that $a = 1$ when only X_1 is known. Since the distribution patterns, sampling method and actual locations for $S-S$ mirror their associated $A-A$ for any given species, mean a will remain approximately constant for ρ of both $S-S$ and $A-A$ [also supported by the principal components analysis (PCA) results given later]. Thus, the number of seedlings per putative parent becomes $[100/(1 + a_s)(S-S)^2] / [100/(1 + a_A)(A-A)^2]$, which simplifies to $(A-A)^2/(S-S)^2$, as $a_s \approx a_A$, thus minimizing bias in the estimation of seedlings per adult.

Means and standard deviations (SD) were calculated for all variables. For statistics, analyses were conducted at the scale of individuals within species, between the 19 species, and between the two fire-response types (nine matched pairs) and four functional types (four to six species per group) (Table 1). Phylogenetic corrections were not undertaken as all but one of the species belonged to just two families (Proteaceae, Myrtaceae) that were distributed almost equally across the FTs (and for the NR/R comparisons they were in taxonomically matched pairs). The results showed no clustering of traits at the family level but clustering of traits at the subfamily level, as the traits we assessed are used to separate the subfamilies (Table 1). Thus, the FTs we recognized were partly a reflection of taxonomic relationships but this is almost always the case as all diagnostic taxonomic traits have an adaptive basis.

For bivariate comparisons, regressions were undertaken selecting the curve (linear, logarithmic, exponential, power) that best accounted for the variance (highest R^2) and giving its P value. The nine NR–R pairs were compared by a paired t -test, and geosporous–serotinous species by a t -test. Data that did not meet equal variance requirements were logged or the unequal-variance form of the tests was used. Multiple regressions were undertaken on the whole data set (370 replicates) and means for the 19 species using $S-A$ as the dependent variable and $S-S$, $A-A$ and S/A as the independent variables. Multiple regression equations were then prepared, noting the contribution to total variance of each variable and the error term. The functional-type attributes were compared by 2×2 ANOVA with interaction effects. Some ordinal data were compared by the Fisher exact probability test as the expected value was not > 5 that prevented use of the Chi-square test.

To overcome differences in sample size, and to show the pattern of $S-A$ independently of S/A among FTs, the frequency of $S-A$ occurrences at 5-cm intervals from the putative parent was determined after ranking from closest to furthest. The percentage occurrence in each interval was then calculated and the

two values per FT were averaged. Thus, each fire response type comprises equal contributions from geosporous and serotinous species whose values were added and the sum halved. All these tests were undertaken using the online program Vassarstats.net (R. Lowry, 1998–2020). PCA and canonical variates analysis (CVA) of the mean data for the 19 species were undertaken using the six variables that showed significant correlations with $S-A$ distance. These were based on the partial correlation coefficient/covariance matrix between these six variables. The analyses were undertaken in R version 3.6.3. For the PCA, the R package FactoMineR was used on the correlation matrix, and Factoextra was used for visualization of the data (Kassambara, 2017). For the CVA, the package Morpho (Schlanger, 2013) was used and the biplots were created using the CVA function in the BiplotGUI package (la Grange, 2015, <http://biplotgui.r-forge.r-project.org/>). A dendrogram for the four functional-type groups based on the covariance matrix was performed using the Mahalanobis distance (Schlanger, 2013; Varmuza and Filzmoser, 2016).

RESULTS

Comparisons between all individuals

When all species and replicates were combined, to give 370 sets of values, $S-A$ was directly related linearly to $S-S$ and $A-A$, and inversely related linearly to $\log(S/A)$, all at $P < 0.00001$ (Fig. 2). Thus, independent of species identity or functional type, seedlings were closer to an adult when inter-seedling and inter-adult distances were shorter and seedlings per parent (the adults collectively, if not individually, can be considered parents of the seedlings present as all seeds were dispersed in the burnt area) were greater, as hypothesized. However, these curve fits accounted for only 41 % of the variance for $S-S$ down to 12 % for $\log(S/A)$. A partial correlation matrix was consistent with these trends, showing in addition significant correlations between $S-S$ and $A-A$ (positive) and $\log(S/A)$ (negative) (Fig. 3). An exception was the positive correlation between $A-A$ and $\log(S/A)$, i.e. as the closest adults became further apart (and their density declined) their seedling to parent ratios became higher. Although it only accounted for 4 % of the variance, P was < 0.0001 . A linear multiple regression showed that $S-S$ accounted for most variance with $S-A$, and $\log(S/A)$ the least, with > 50 % unaccounted for by this relationship (Fig. 3).

Within-species comparisons

Most relationships of $S-A$ with $S-S$, $A-A$ and S/A within species showed no pattern. The exceptions were seven species, where the shorter the $S-S$ (greater density of seedlings), the closer $S-A$ (Supplementary Data Fig. S1A), as hypothesized. The best-fit curve for six of these was linear, with a logarithmic fit for the seventh, and these accounted for 30–75 % of the variance. The Fisher exact probability test gave $P = 0.0080$ for the null hypothesis that no relationship was expected (i.e. these trends were ‘real’), and $P < 0.0001$ that all species would show a significant relationship (i.e. these trends were species-specific). There was no trend in functional attributes of these seven species that might be correlated with this relationship.

S–A was correlated with A–A for two species, and with S/A for one, which are no more than might be expected by chance alone.

FIG. 2. Relationship between shortest seedling to adult distances (S–A) and index of number of seedlings per adult [$\log(S/A)$], and shortest inter-adult (A–A) and inter-seedling (S–S) distances for all (370) replicates among 19 species.

FIG. 3. Partial correlation coefficients (R^2 and P) and resultant linear multiple regression for comparison between S–A distances as the dependent variable and S–S and A–A distances and $\log(S/A)$ as the independent variables for all replicates (370) among 19 species.

The only other relationship evident was $\log(S/A)$ vs. the independent variable, A–A, for which three species were positive linear, one positive logarithmic, and one negative exponential, and these individually accounted for 44–56 % of the variance (Supplementary Data Fig. S1B). The Fisher exact probability test gave $P = 0.0463$ for the null hypothesis that no relationship was expected, and $P < 0.0001$ that all species would show a significant relationship. There was no trend in functional attributes of the four species that might be correlated with their positive relationship. *Verticordia aurea*, the only species with a negative relationship, is a rare, localized species that forms small, dense populations (George, 1991; our pers. observ.).

Species comparisons

The species with the shortest S–A (mean of 15 cm for these five species) were *Verticordia aurea*, *Conospermum incurvum*, *Beaufortia elegans*, *Adenanthos cygnorum* and *Calytrix flavesces* (all NR with geospority) (Fig. 4; Supplementary Data Table S1). *Xylomelum angustifolium* had by far the greatest S–A followed by *Isopogon tridens* and *Dryandra shuttleworthiana* (mean of 204 cm for these three species, all R with serotiny). S–A for the ant-dispersed species was both short (*Adenanthos cygnorum*) and wide (*Daviesia quadrilatera*), while the passively dispersed species were short (*Beaufortia elegans*) and intermediate (*Melaleuca leuropoma*). The five species with shortest A–A were on average 68 cm apart, and the five with the longest A–A were

FIG. 4. PCA with biplot for six variables measured on 19 species to show their relationship with seedling to adult distances. 1 = *Calytrix flavesces* NR/G wind, 2 = *Verticordia aurea* R/G wind, 3 = *Adenanthos cygnorum* NR/G ant, 4 = *Conospermum incurvum* NR/G wind, 5 = *Verticordia grandis* R/G wind, 6 = *Daviesia quadrilatera* R/G ant, 7 = *Pileanthus filifolius* R/G wind, 8 = *Conospermum wycherleyi* NR/G wind, 9 = *Petrophile drummondii* NR/S wind, 10 = *Hakea psilorrhyncha* NR/S wind, 11 = *Banksia hookeriana* NR/S wind, 12 = *Dryandra carlinoides* NR/S wind, 13 = *Beaufortia elegans* NR/S passive, 14 = *Banksia attenuata* R/S wind, 15 = *Isopogon tridens* R/S wind, 16 = *Dryandra shuttleworthiana* R/S wind, 17 = *Xylomelum angustifolium* R/S wind, 18 = *Melaleuca leuropoma* R/S passive, 19 = *Lambertia multiflora* R/S wind. Traits: NR = non-sprouter, R = resprouter, G = geosporous, S = serotinous, followed by primary dispersal vector. The seedling to adult distance vector has been extrapolated to show how it relates to each species.

on average 447 cm apart (Table S1). The five species with shortest S–S were on average 21 cm apart and the five with the widest were on average 380 cm apart.

At the species level, the partial correlation coefficient matrix showed that S–A distance was a highly significant direct function of S–S and A–A distances and a less significant inverse function of $\log(S/A)$ (Fig. 5; Supplementary Data Table S2). Among morphological traits, S–A increased with greater rootstock size ($P = 0.0011$) and inversely with height/crown ($P = 0.0644$). Also of interest was S–S as a highly significant inverse function of $\log(S/A)$. A–A lacked any relationship with $\log(S/A)$ at the between-species level. The resultant multiple linear regression, excluding the morphological traits, showed that most (68 %) of the variation in S–A could be attributed to S–S, with decreasing contributions from $\log(S/A)$ and A–A, with an error term of only 9 % (Fig. 5).

Using A–A as the independent (prefire) variable, simple linear regressions showed that the dependent (postfire) variables, S–A and S–S, were strongly correlated, with ~60 % of their variance (R^2) accounted for by the relationship (Supplementary Data Fig. S2). At < 300 cm apart, the A–A relationships were controlled by NR, and at > 300 cm apart, the A–A relationships were controlled by R. There were two trends associated with fire-response type for S/A: among the NR, S/A increased as A–A increased, but S/A was extremely low among R, showing no relationship with A–A.

Comparisons between functional types

Non-sprouters vs. resprouters. More than twice as many prefire R were rejected from the study as NR, mainly because they appeared to be immature (slow to mature) or barren and could not have been parents of any of the seedlings (Supplementary Data Table S3). There was no significant difference in stature between the NR and R but the crowns of the R were four times larger on average. As a result, the height/crown diameter ratio of NR was twice that of R. Rootstocks (lignotubers) of R were

on average 80 times the area of the NR (no lignotuber). A–A of R tended to be much greater than that of NR (0.0639).

Diaspores of R were over four times heavier than NR on average and had 17 % faster terminal velocity (Supplementary Data Table S3). S–A was almost four times shorter on average for NR than for R, and their S–S was over four times shorter. Comparing species means, seedlings were located under the crown of seven of nine NR but none of ten R. The Fisher exact probability test gave $P = 0.0007$ that these patterns were the same, and $P = 0.2353$ that this pattern was different from an expectation that all NR would have seedlings under them. There was no exception to the expectation that none of the R would have seedlings beneath them. Although the coefficient of variation about the mean of NR exceeded that of R, they averaged 32 times more seedlings per parent.

Soil-stored-seed species vs. plant-stored-seed species. There was greater variation about the mean among these two groups than among NR and R. As a result, the only significant difference was S–A for species with soil-stored seeds, which was on average half the distance as for plant-stored seeds ($P = 0.0525$) (Supplementary Data Table S4). There was no significant difference in diaspore weight or terminal velocity between these two FTs.

Four functional-types compared. Of seven attributes assessed, only two separated NR from R solely: NR had twice the height/crown ratio of R, and R had over an order of magnitude greater rootstock area compared with NR (Table 2). All seedling–adult relationships could be separated according to one or more of the four FTs: S–A for geosporous NR was one-tenth the distance of serotinous R with the other two groups intermediate. Exactly the same pattern existed for S–S [linear relationship between them, $P = 0.0011$ (one-tailed) on 3 d.f.]. The closest seedlings were invariably under the crown of geosporous NR species but were typically outside the crown in the other three categories, with the two R groups at a mean distance four times greater than geosporous NR, with serotinous NR intermediate. A–A was much greater for serotinous R than for the other three categories. The order of magnitude greater S/A for NR over R was mainly due to the greater S/A for geosporous NR species.

On a percentage of total S–A distances per FT, almost 40 % among NR were located within 15 cm of the putative parent with few beyond 100 cm (Fig. 6). By contrast, almost no R was located within 15 cm and > 40 % were beyond 100 cm. Overall, N fitted a binomial-type curve but R showed no clear peak. Storage type was less extreme with almost 40 % of geosporous species located within 20 cm and < 10 % beyond 100 cm, and < 20 % of serotinous species located within 20 cm and almost 40 % beyond 100 cm. Both tended to have a broad peak closest to their parents and tapering off with distance away, less clearly with serotinous species. This means that geosporous NR were collectively closest to their parents and serotinous R were furthest.

CVA showed that the four groups were best described as a progressive increase from geosporous NR (group 1) to serotinous NR (2) to geosporous R (3) to serotinous R (4) in S–A, $\log(\text{rootstock area})$ and S–S, and a decrease in height/crown diameter (Fig. 7). $\log(\text{seedlings per parent})$ decreased in the order: group 1 > 2 > 3 = 4. A–A increased

(S: seedling, A: adult, S/A: seedlings per parent, χ : distance)

Regression: $S-A = -220 + 143(S-S) - 24.7\log(S/A) + 0.072(A-A) + E$

Contribution to variance: 68.3% 13.7% 8.9% 9.0%

FIG. 5. Partial correlation coefficients (R^2 and P) and resultant linear multiple regression for comparison between S–A distances as the dependent variable and S–S and A–A distances and $\log(S/A)$ as the independent variables for means of 19 species.

TABLE 2. Two-way ANOVA with interaction for fire-killed (non-sprouting, NR, nine species) vs. resprouting (R, ten species), and soil-stored (geosporous, eight) vs. plant-stored (serotinous, 11) species

Attribute	Fire response	Seeds soil-stored	Seeds plant-stored	<i>P</i> fire response	<i>P</i> storage response	<i>P</i> interaction
Height/crown (cm) [†]	NR	2.44 ± 1.49 ^a	1.98 ± 0.59 ^a	0.0072	0.3604	0.8894
	R	1.18 ± 0.18 ^b	1.06 ± 0.24 ^b			
Rootstock area (cm ²) [*]	NR	14 ± 21 ^b	8 ± 10 ^b	<0.0001	0.2337	0.2757
	R	138 ± 79 ^a	1433 ± 1576 ^a			
Closest seedling–adult distance (cm) (S–A) [†]	NR	15 ± 4 ^c	47 ± 44 ^{bc}	0.0010	0.0191	0.8648
	R	78 ± 48 ^b	155 ± 65 ^a			
(S–A)/crown radius (cm cm ^{–1}) [†]	NR	0.67 ± 0.13 ^c	1.72 ± 2.05 ^b	0.0092	0.1180	0.3263
	R	2.36 ± 2.50 ^a	3.23 ± 4.04 ^a			
Closest inter-adult distance (cm) (A–A) [†]	NR	189 ± 103 ^b	111 ± 43 ^b	0.0246	0.1962	0.0326
	R	166 ± 123 ^b	386 ± 189 ^a			
Closest inter-seedling distance (cm) (S–S) [*]	NR	17 ± 3 ^c	78 ± 86 ^b	0.0003	0.0247	1.0000
	R	156 ± 107 ^a	293 ± 213 ^a			
Seedlings per adult (S/A) ^{†‡}	NR	134 ± 90 ^a	15 ± 26 ^b	0.0044	0.0084	0.0112
	R	2 ± 2 ^b	3 ± 2 ^b			

Data are means ± SD. Different superscript letters per attribute indicate categories different by Tukey's HSD test ($P < 0.05$). Analyses for plant stature, crown area, seed terminal velocity and seed mass are omitted as there were no differences less than $P = 0.1000$ in any data set, essentially due to their high variances.

*Log₁₀-transformed (untransformed data given here).

[†]Unequal variances.

[‡]Based on inter-seedling² to inter-adult² distances.

FIG. 6. Frequency of closest seedlings in 5-cm distance classes from conspecific adults grouped into 2×2 functional types (FTs). (A) NR vs. R, (B) geosporous (prefire seed dispersal) vs. serotinous (postfire seed dispersal). Each group comprises equal representation of its two component FTs: thus, geosporous and serotinous species contribute equally to each NR and R category, and vice versa.

in the order: $2 < 1 < 3 = 4$. As a result, group 1 never overlapped with 3/4, and 1/2 never overlapped with 4. Thus, at least five of the six variables helped separate 1/2 (NR) from 3/4 (R) but none of the variables served to separate 1/3 (geosporous) from 2/4 (serotinous). A dendrogram based on the Mahalanobis distance, which takes covariance into account, confirmed the primary separation of the species was based on NR vs. R, followed by geosporous and serotiny within each of these (Fig. 8).

DISCUSSION

The closest seedling to adult distance (S–A, 370 records) on an individual pair basis varied by two orders of magnitude (2–800 cm), within each of 19 species by an order of magnitude (mean 26–220 cm), between species by an order of magnitude (mean 10–257 cm), and between four reproductive FTs by an order of magnitude (mean 15–155 cm). The challenge was to see if the spatial patterns were consistent across these four scales and to what extent they could be explained by species

FIG. 7. Canonical variates analysis for 19 species placed in 2×2 functional-type groups (1 to 4) based on two morphological traits, three spatial traits and one reproductive trait. Ellipses are the minimal circular areas encompassing the members of each group. Arrows indicate the direction of increase in each variable.

FIG. 8. Hierarchical relationship between the four FTs examined compared by the Mahalanobis distance from the partial correlation matrix among three seedling-related and three adult-related traits (Supplementary Data Table S2; Fig. 7). Note the fundamental separation between NR and R, and the similar dendrogram distances separating geosporous (soil-stored) and serotinous (plant-stored) species within each fire-response type. Values are the means within each group.

traits or *ad hoc* ecological processes or if inherent dispersal (mathematical) processes were sufficient. We expected S–A distance gradients among all individuals would also be mirrored at broader scales: within and between species, and between FTs. There was reasonable support for consistency in the trends (Table 3). Generally, a linear relationship existed across the scales for S–A vs. inter-seedling distances (S–S) and inter-adult distances (A–A), and inverse for seedling-to-parent ratios (S/A), decreasing in the fraction of variance accounted for. The only exception was between individuals within species where most of the species showed no relationship. This may have been because of small sample size (20 pairs per species), large

coefficient of variation, and/or limited range of values compared with those between all individuals, species or FTs. Any observational errors (possibly missing seedlings when they were rare, so overestimating S–A) will also have had the most impact on significance at the within-species scale that would be obscured by the averaging effect and order of magnitude difference between species and FTs.

That the weakest (inverse) relationship of seedling–adult distance was with seedlings per adult is surprising in view of its clear relevance. Part of the explanation is that S/A tends to have extreme values at all scales (Table 3), and thus is non-linear and vulnerable to exaggerating the effect of atypical situations. Thus, A–A may be large (which tends to ensure S–S is also large) but adjacent seedlings may sometimes occur in clumps within litter microsites (Lamont *et al.*, 1993) or arise from ant nests (Yeaton and Bond, 1991) so that sometimes S–S may only have been a few centimetres. Since the index of seedlings per adult is calculated as $(A-A)^2/(S-S)^2$, this compounds these oddities, giving occasional misleadingly large values for S/A. There is a weak exponential relationship between S/A and A–A when all records are compared collectively but it is strong for four within-species records and for N species only. This might be spurious because S/A is calculated from $(A-A)^2$ and thus they are not strictly independent (although this cannot explain the lack of an overall relationship between species and FTs). Alternatively, it might well be the case that, as adults become further apart, they are more fecund (less conspecific competition that is invariably greater than interspecific competition, Adler *et al.*, 2018), particularly for the larger species, so producing more seedlings, or more suitable microsites are available for their seeds. As S/A increases so S–S will become shorter (Fig. 1B), and this was confirmed across all scales. However, it was only evident among NR as S/A was so low among R that no relationship could be detected.

Our results highlight how fire-response type (NR vs. R) is a fundamental dichotomy in the morphology, fecundity and population dynamics of plants in fire-prone ecosystems

TABLE 3. Collation of trends for seedling–adult (S–A) distances and seedling to parent ratios (S/A) across the four scales examined in this study

	Between individuals	Within species	Between species	Between functional types
S–A vs. S–S	Strong linear	Strong linear (7 species only)	Extremely strong linear	Strong linear
S–A vs. A–A	Strong linear	Strong linear (2 species only)	Strong linear	Moderate linear
S–A vs. S/A	Moderate inverse exp	Strong inverse linear (1 species only)	Weak inverse exp	Weak inverse exp
S/A vs. A–A	Weak exp	Strong exp (4 species + 1 species inverse exp)	No overall relationship, linear (NR only)*	No relationship
S–S vs. S/A	Strong inverse exp	Strong inverse exp	Strong inverse power function (mainly due to NR)*	Moderate inverse linear

exp = exponential curve.

* No relationship with R.

(Supplementary Data Table S3; Fig. 8). As we used nine taxonomically matched, co-occurring pairs, the quality of this conclusion confirms the NR–R dichotomy as one of the best supported theories in fire ecology. The case for recognizing FTs based on the location of stored seeds (geosporous vs. serotinous) as basic within each of these categories is also convincing, with both about half as different as between the fire-response types based on the Mahalanobis distance (Fig. 8). This validates the earlier recognition of these four FTs that has been used for other purposes (Keith and Bradstock, 1994; Enright *et al.*, 2007, 2014; Ne’eman *et al.*, 2009) but our study now adds a novel spatial dimension to these FTs (Table 3). [In parallel, the case for recognizing soil-stored and non-stored seeds in other systems as part of four reproductive syndromes must also be considered strong; Pausas and Keeley, 2014.]

The mathematics of the relationships described above break down when S–A for NR and R are compared. Having shown that S/A for R is an order of magnitude less than for NR (Supplementary Data Table S3; Fig. 6), the few seedlings should have been clustered around their scattered parents. Instead, their mean S–A and S–S distances were four times further apart. Whereas seven of the nine NR species had seedlings beneath their prefire crown area, none of the ten R species did even though their crowns were on average four times wider. When the number of records was converted to a percentage basis, 40 % of S–A records for NR seedlings were within 15 cm of their putative parent but 99 % of R seedlings were beyond this distance (Fig. 6). Unlike clustering around the NR parents, R seedlings showed no clear aggregation and the nearest seedlings tended to be scattered at distances up to 800 cm away. The short S–A of NR was not due to their closer A–A (as one possibility, Fig. 1B), because the scale of the pattern was much finer than their distances apart, but it was due to their high S/A (Fig. 9). This clustering was most extreme for the geosporous NR FT and least for the serotinous R FT (Table 3; Figs 6 and 9). We now have an explanation for the strong aggregation of NR compared with R species as noted in mature sclerophyll shrublands (Miller *et al.*, 2010; Perry *et al.*, 2013) – it originates at the seedling establishment stage (shorter S–A and S–S as S/A is higher among NR) and its legacy continues with successive postfire generations (shorter A–A among NR).

The pattern is clearly adaptive: NR seedlings can take advantage of the ‘regeneration niche’ created by their parents (Grubb, 1977). Many are located near where their parents established, the parent has died and even left a legacy of microhabitat

FIG. 9. Stylized relationship, although numerically accurate, between adults and seedlings for the means of two extreme functional types drawn to the same scale: (A) non-sprouter, soil-stored (geosporous) seeds (prefire released), and (B) resprouter, plant-stored (serotinous) seeds (postfire released). A = adult, S = seedling, (outer) circle corresponds to the area of the plant crown, and (inner) circle corresponds to the area of the lignotuber. Broken line infers adult plant is dead. Panel (A) has on average 130 seedlings per adult (parent), and (B) has two seedlings per adult (parent) derived from $(S-S)^2/(A-A)^2$. The other two functional groups have patterns intermediate between these two.

conditions and symbiotic microbes conducive to growth (Boyd and Davies, 2010) and free of competitors arising from soil-stored seeds in some cases (Odion and Davis, 2000; Nathan and Ne’eman, 2004). Conversely, the parents of R survived the fire, and while they might have a role as a ‘nurse’ plant sometimes, eventually, if not immediately, they will compete with their offspring for resources (Lamont, 1985b). However, on average, the nearest seedlings were three times the radius of the putative parent crowns away (Supplementary Data Tables S1 and S2). The few seedlings that they produce are often considered poor competitors as much of their carbon is devoted to building bud-storing structures rather than photosynthetic capacity (Pate *et al.*, 1990; Pausas *et al.*, 2018). By spreading over a wide area

it increases their chances of arriving at microsites conducive to their recruitment (Lamont *et al.*, 1993). In addition, stabilizing processes associated with rarity (e.g. conspecific competition that exceeds interspecific competition is minimized) may even be invoked (Groenvelde *et al.*, 2013; B. Lamont, unpubl. data). This is consistent with ideas that R have a ‘high potential’ to disperse far from their parents (Keeley, 1986 – although this proposal referred to ‘obligate’ R that are absent from the system we studied). However, it is the antithesis of ‘persistence’ (R) vs. ‘dispersers’ (NR) as proposed by others (Bond and Midgley, 2001; Levin *et al.*, 2003). Interestingly, Merwin *et al.* (2012) showed both clonal and lignotuberos banksias displayed similar levels of long-distance dispersal as an NR banksia occurring in the same vegetation type that we studied.

While an ‘ultimate’ (adaptive) explanation for the great disparity in S–A between NR and R is clear, a satisfactory ‘proximate’ (mechanistic) explanation is much more difficult to identify. For example, contrary to the evidence of Midgley (1996) in South Africa, the stature of taxonomically matched R in our study was not less than NR, and the more striking feature was the great variability among both (shrubs and subshrubs). Data for sclerophyll vegetation on five substrates elsewhere in SW Australia also did not show any difference in height classes between R and NR (Cowling and Witkowski, 1994). Clarke and Knox (2002) also recorded no differences in the stature of R and NR in eastern Australia. Indeed, it may take a decade or more for NR to catch up to the dimensions of prefire mature R followed by a greater rate of decline (Gosper *et al.*, 2012; He *et al.*, 2019). Thus, differences in mean release height of seeds, especially among serotinous species that only release their seeds in response to fire, cannot explain why S–A and S–S of NR were much closer to their putative parents than R. Similarly, differences in terminal velocity were ecologically insignificant, despite the much greater average mass of R seeds, their greater inertia implying that their seedlings should have been closer. Both our relative stature and terminal velocity results for NR and R agree with those of Hammill *et al.* (1998) for scrub-heath in eastern Australia.

On average, seedlings from postfire-dispersed seeds were two to four times as far from the nearest adult and seedling as those from prefire-dispersed seeds (Table 2). This supports our hypothesis that diaspores released postfire should travel further and be more scattered than those released prefire, as gauged by the distribution of seedlings. To what extent morphological differences are responsible is unclear as there were no significant differences in release height, seed mass or terminal velocity between the four FTs, so that the greater obstacles to dispersal in the prefire vegetation must have played a role (Lamont, 1985b). Although this effect was largely due to the extremely high S/A of the geosporous N group, S–A distance was greater for each serotinous category within NR and R, so that R do not have greater dispersibility potential than NR. Although only two ant-dispersed species were examined, they did not show a clearly greater S–A than wind-dispersed species: they were ranked third (*Adenanthos cygnorum*, N) and eighth (*Daviesia quadrilobata*, R) widest S–A among the eight prefire-dispersed species (Supplementary Data Table S1). This shows that ants were either only doing an average job of dispersal or that the primary role of ants is not as dispersal agents (He *et al.*, 2009).

The absence of seedlings beneath the crowns of R could have been due to ‘classic’ granivory and herbivory effects associated with preferential predation of seeds and seedlings at high density around the parents (Tyler, 1995; Zwolak *et al.*, 2010). However, it should have been more evident among the highly fecund NR than R species. Serotinous seeds are more vulnerable to granivores than those already buried at the time of fire (Tasker *et al.*, 2011), but again serotinous species were equally distributed across both NR and R so differential effects could not apply. Besides, because all NR and R pairs were matched taxonomically, they would be equally vulnerable to predators. Thus, all Myrtaceae produce essential oils that deter herbivory by kangaroos (Jones *et al.*, 2003). The only large, ‘grass-like’ species, attractive to marsupials (Rafferty and Lamont, 2007), was *Hakea psilorrhyncha* that showed no evidence of herbivory.

The adults of R might have an autotoxic or competitive effect on their seeds or germinants. Any potentially toxic secondary metabolites in the foliage or litter would be volatilized by fire heat and distributed widely elsewhere (He and Lamont, 2018). Thick litter could suppress germination but this was burned away. It could be replaced by toxic levels of ash (Ne’eman *et al.*, 1992) but there is no reason to expect more litter associated with R than NR, and local deposits of ash in this system are associated with prolific seedling numbers of both NR and R (Lamont *et al.*, 1993). Many species retain their dead foliage in these shrublands, especially among NR. He *et al.* (2011) suggested that this either ensures seeds are released from their serotinous structures in response to fire or provides extra nutrients for self-seedlings establishing under the dead parent and gives them a competitive edge. Working on proteas in the Cape of South Africa, Connolly and Midgley (2020) recently showed that the seedlings beneath the crowns of fire-killed parents were no larger than those beyond them and so dismissed this idea.

Of course, exposed lignotubers physically prevent seedling establishment but they only form a minor fraction of the crown cover (Supplementary Data Table S1; Fig. 9). It is possible that the surviving surface root systems of R depleted soil water levels required by germinating seeds or germinants (Lamont, 1985b) and occurred at such an early stage that we did not detect dead seedlings. For three *Banksia* species at this very site (two of which comprised the *Banksia* pair used here), Lamont and Bergl (1991) noted that the lateral roots terminated in clusters of rootlets forming a 5- to 10-mm-thick mat beneath the litter layer. However, these laterals extended an average distance of seven to eight times the radius of the crowns and often ended up beneath other species. Thus, it is unlikely that root competition effects are confined to seeds and seedlings beneath the crowns of R species.

Since N are short-lived and aggregated, it is possible that, by the time of the fires, self-thinning had resulted in the accumulation of geosporous diaspores in the soil not associated with the surviving adults, so inflating seedlings/adult and reducing seedling–adult distances. While it is true that geosporous R had much wider S–A distances than geosporous N (consistent with the idea), so too were serotinous R wider than geosporous N (that negates the idea) (Table 3). Additionally, this would not explain why R do not show the expected binomial distribution around their parents. Finally, it is possible that, as seedlings

were so rare among R, we missed locating the closest seedlings, so exaggerating S–A. However, this would only have rarified the dispersal curve, not annulled it.

We conclude that R have the ability to disperse their diaspores well beyond the boundary of influence from their parents by mechanisms currently unclear and whose identity must await more focused research. Future work should examine if only self-seedlings are absent from beneath or near the crowns of adult R or whether it is a general phenomenon of deterrence of seedlings of all species. Experiments would involve the placement of seeds of various species inside and at various distances outside the crown of surviving plants (with NR as controls) to see if germination is inhibited or there is premature death of germinants or seedlings. Following the fate of diaspores released at plant height immediately postfire would also be instructive. Although traditionally reserved to describe the fire-tolerant adults of R species, use of the term ‘persistence niche’ does not apply so aptly to their seedlings as these disperse widely, but it is certainly appropriate for the many seedlings of NR species that cluster around their dead parent that is perpetuated with each fire.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. **Table S1.** Mean $\pm$ SD of 13 attributes for 19 species grouped by fire response and seed storage. **Table S2.** Partial correlation matrix for 19 species and six attributes as used in the principal components and canonical variates analyses. **Table S3.** Prefire adult dimensions, postfire closest seedling to adult distance, and pertinent seed and seedling traits between paired nonsprouter and resprouter species. **Table S4.** Prefire adult dimensions, postfire closest seedling to adult distance, and pertinent seed and seedling traits between species whose seeds are soil-stored or plant-stored. **Fig. S1.** Relationship between shortest inter-seedling distances and shortest seedling to adult distances within each of seven species, and log and shortest inter-adult distances within each of five species. **Fig. S2.** Relationship between shortest inter-adult distances and closest seedling to adult and inter-seedling distances and number of seedlings per parent for means of 19 species.

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DATA DEPOSITION

All means and standard deviations for data collected on all species are given in [Supplementary Data Table S1](#).

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