

1 **Coordinated shifts in allocation among reproductive tissues across 14**  
2 **coexisting plant species**

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11

## 16 **Abstract**

17 Plant species differ in the amounts of energy allocated to different reproductive tissues, driving  
18 differences in their ecology and energy flows within ecosystems. While it is widely agreed that  
19 energy allocation is key to reproductive outcomes, few studies have estimated how reproductive  
20 effort (RE) is partitioned among different pools, for multiple species in a community. In plants, RE  
21 can be partitioned in several meaningful ways: seed versus non-seed tissues; into flowers that form  
22 seeds and those that fail to develop; into pre- versus post-pollination tissues, and into successful  
23 versus aborted ovules. Evolutionary theory suggests several hypotheses about how these tissues  
24 should be coordinated across species. To quantify variation in allocation to different reproductive  
25 tissues, we collected detailed RE measurements for a year from 14 perennial species in a recurrent-  
26 fire coastal heath community in eastern Australia. Overall we found that total accessory costs – the  
27 proportion of RE not directly invested in provisioning the seed – were very large, varying from  
28 95.8% to 99.8% across the study species. These results suggest that studies using seed or fruit  
29 production as measures of RE may underestimate it by 10- to 500-fold. We propose a suitable  
30 alternative that well-approximates true RE. When comparing species, we found strong support for  
31 three evolutionary trade-offs that are predicted to arise when a given energy pool is divided into  
32 different tissue masses and counts across species: 1) between successful pollen-attraction costs and  
33 mature ovule count, 2) between total reproductive costs and seed count, and 3) between seedset and  
34 relative investment in pollen-attraction costs. As a result of these trade-offs, species were also  
35 predicted to show coordinated shifts in the amounts invested in floral construction, in seedset and  
36 seed size. These shifts in investment were indeed observed, with the amount allocated to discarded  
37 tissues increasing with seed size and the amount allocated to pollen-attraction decreasing with seed  
38 size. It is already well-established that the seed size axis aligns with the colonization-competition  
39 life history spectrum; here we show that relative construction costs of pollen-attraction versus  
40 provisioning tissues and seedset are also part of this trajectory, expanding our understanding of the  
41 relative sizes of floral and fruiting structures observed across angiosperms.

42

## 43 **Introduction**

44 Plants allocate a sizeable share of their photosynthetic energy to reproduction (Obeso 2004;  
45 Hirayama *et al.* 2008; Thomas 2011; Wenk & Falster 2015). This allocation takes the form of  
46 provisioned seeds and also of many other tissues associated with reproduction, termed accessory  
47 costs. Accessory costs include energy associated with forming a successful seed (e.g. flower petals,  
48 seed pod, and dispersal tissues) and energy lost via aborted and discarded buds, flowers and fruit.  
49 Previous studies show that for perennial species anywhere from 15% – 99% of total reproductive  
50 investment may go into accessory costs (Haig & Westoby 1988; Ashman 1994; Henery & Westoby  
51 2001; Lord & Westoby 2006; Chen, Felker & Sun 2010). Since fruit set and seed set are generally  
52 below 50% in perennial species (Stephenson 1981; Wiens 1984; Sutherland 1986; Knight *et al.*  
53 2005; Rosenheim *et al.* 2014), the cost of aborted and discarded tissues may be a substantial  
54 proportion of total accessory costs. Yet, despite being a significant energy sink in ecosystems, little  
55 is known about the allocation of energy among different reproductive tissues across the plant  
56 kingdom and how this links with plant reproductive strategies.

57 While plant species demonstrate an extraordinary diversity of reproductive structures and strategies,  
58 reproductive investment can be divided into broad functional categories that are consistent across  
59 species (Figure 1a). We define categories as follows. Total energy investment per seed matured is  
60 *reproductive costs*. This can be divided into investment in required parts, termed *success costs*, and  
61 energy expenditure on flowers, fruit, and seeds that never form mature propagules, called *discarded*  
62 *tissue costs*. All are calculated on a *per seed matured* basis. *Success costs* can be further divided  
63 into structures that form before pollination (*pollen-attraction costs*; i.e. the flower, including petals,  
64 calyx, pedicel) versus structures developed post-pollination (e.g. seed pod, seed), hereafter termed  
65 *provisioning costs*. The provisioning component is comprised of the seed itself (seed size) versus  
66 the dispersal and packaging tissues. Although in much of the literature seed mass is understandably

67 treated as including the seed coat, for purposes of this paper we treat embryo plus endosperm mass  
68 as seed mass and position the seed coat among the dispersal and packaging component of accessory  
69 costs. The *discarded tissue costs* can likewise be divided into energy invested prior to versus after  
70 pollination, here termed *discarded pollen-attraction costs* and *discarded provisioning costs*.  
71 *Accessory costs*, all tissues besides the seed mass itself, are the sum of *discarded tissue costs*,  
72 *pollen-attraction costs*, and *packaging and dispersal costs*, terms high-lighted in red in Figure 1a.  
73 Throughout the manuscript “costs” indicates dry mass investment per seed matured, while  
74 “investment” refers to total dry mass invested in a structure.

75 There are multiple reasons to expect that both success costs and discarded tissue costs will be  
76 substantially larger than the mass of the seed itself. The success cost components are undeniably  
77 beneficial for successful formation and dispersal of a seed. Without showy petals insects would not  
78 be attracted to the stamens and stigma, without sepals the developing bud would not be protected,  
79 without a seed coat a seed would not be protected during dispersal, and without an attractive fruit,  
80 many seeds would not be dispersed. High discarded tissue costs (due to low seedset both pre- and  
81 post-pollination) occur in perennial plants for a diversity of reasons, some the result of conditions  
82 beyond the plant’s control and others by evolutionary design to increase fitness. They include  
83 pollen-limitation, pollen-ovule incompatibility, parental embryo abortion, resource limitation and  
84 bet-hedging strategies to capitalize on stochastic variation in pollen availability, pollen quality, and  
85 resource availability to mature fertilized ovules (Bierzychudek 1981; Stephenson 1981; Sutherland  
86 1986; Burd 1994, 2008; Ramsey 1997; Obeso 2004; Ashman *et al.* 2004; Knight *et al.* 2005;  
87 Holland & Chamberlain 2007; Rosenheim, Schreiber & Williams 2015). Variation across species in  
88 the relative size of the reproductive tissue energy expenditures should indicate different  
89 reproductive energy allocation strategies underpinned by trade-offs (Figure 1a). Species may differ  
90 in how they divide their finite pool of reproductive energy into different tissue types, displaying  
91 variation in relative investment in pollen-attraction versus provisioning costs as well as variation in  
92 the number of ovules formed and the number of seeds matured.

93 The literature identifies two main reproductive strategy trade-offs relating reproductive energy  
94 pools and counts of reproductive parts to each other. Here we expand upon those hypotheses and  
95 show that they capture the same life history strategy spectrum from different perspectives. The first  
96 is the well-supported seed size-seed number trade-off, from the plant functional trait literature. The  
97 second is the seed set-pollen-attraction cost trade-off described in the parental optimist-parental  
98 pessimist literature. Each of these trade-offs is separate, for each considers different resources, yet  
99 together these yield hypotheses on how energy allocation to the energy pools illustrated in Figure 1a  
100 should differ systematically with respect to seed size through evolutionary linkages.

101 **Seed size – seed number trade-off:** Whatever pool of energy is available to a plant for seed  
102 production can be divided into many small seeds or fewer larger seeds (Smith & Fretwell 1974). A  
103 log-log plot of seed size versus seed count scaled to plant size should have a slope of -1 all else  
104 being equal. Indeed, a slope of -1 has been observed across species in the field (Henery & Westoby  
105 2001; Moles *et al.* 2004; Sadras 2007). Very small and very large seeds represent endpoints of a  
106 continuous spectrum of life history strategies (Rees & Westoby 1997; Leishman 2001; Turnbull *et*  
107 *al.* 2004; Moles & Westoby 2006). Small-seeded species have a greater chance of reaching any  
108 given colonization opportunity, while larger-seeded species have a greater likelihood of establishing  
109 and better competitive outcomes at any given location (Moles & Westoby 2006).

110 The seed size-seed number trade-off does not consider energy invested in accessory tissues, leading  
111 us to hypothesize two related trade-offs. First, within a given total expenditure on reproduction,  
112 there should be a trade-off between seed count and total reproductive costs per seed matured (trade-  
113 off 1 in Figure 1b). This trade-off is similar to the seed size-seed count trade-off, but includes all of  
114 a plant's reproductive energy expenditures to construct a seed, not just the seed mass itself. Second,  
115 within a given amount of energy spent to mature ovules to the point of pollination, there should be a  
116 trade-off between pollen-attraction costs per ovule and the number of ovules that are displayed to  
117 pollinators (trade-off 2 in Figure 1b). Species with higher pollen-attraction costs are expected to

118 produce fewer ovules. Both trade-offs are predicted to have a slope = -1, but the trade-off between  
119 pollen-attraction costs and ovules at point of pollination should have a higher intercept, since seed  
120 set per ovule is <1. These are two independent trade-offs, each simply showing there exists a fixed  
121 pool of energy to be divided among offspring. Species variation in seedset, the ratio of seed count to  
122 ovule count, provides the link between these two trade-offs, and is itself one of the axes in the trade-  
123 off described below.

124 **The pollen attraction-seed provisioning versus seed set trade-off:** Haig & Westoby (1988)

125 developed a conceptual model for the relative allocation of energy to different reproductive tissues,  
126 dividing the total energy investment per seed between the costs of acquiring pollen and the cost of  
127 provisioning pollinated ovules. Their simple model makes several predictions, including that plants  
128 1) produce excess ovules and flowers to optimize seed production across a population and across  
129 time, 2) face a trade-off between pollen attraction and embryo provisioning, and 3) allocate just  
130 enough to pollen-attracting tissues to ensure pollination of the number of ovules they are able to  
131 provision *on average*. This initial model has since been extended to use the proportion of energy  
132 invested in pollen attraction versus seed provisioning tissues to predict seed set across species  
133 (Rosenheim *et al.* 2014, 2016). The models, supported by empirical data, indicate that species with  
134 relatively low pollen-attraction costs should produce a greater excess of ovules relative to what they  
135 are able to provision; in other words they should have lower seedset.

136 This axis of variation aligns with the parental optimist-parental pessimist strategy continuum (Mock  
137 & Forbes 1995; Burd 2008; Rosenheim *et al.* 2014). A parental optimist is a species that  
138 overproduces ovules, relatively few of which mature in an average year due to limited resource  
139 supply. Such a species is “optimistic” in the sense that should environmental conditions be  
140 unusually favorable, it will be able to respond with high seed production. Since an optimist, in  
141 average years, discards so many ovules – both pollinated and unpollinated – it must reduce the cost  
142 of producing a single pollinator-ready ovule. The alternative, a species with proportionally higher

143 pollen-attraction costs, should display parental pessimism and produce relatively fewer ovules, with  
144 embryo number limiting seed production in many years.

145 Since parental optimists have lower seedset (seed to ovule ratio), logically they need to ensure that  
146 the seeds they mature are likely to germinate and establish. One mechanism to increase seed and  
147 seedling success is to invest more resources in embryo provisioning, manifested as higher  
148 packaging and dispersal costs and higher seed mass. High per seed resource investment in turn will  
149 favor provisioning embryos that are vigorous genotypes, in part accomplished by being selective  
150 about which pollen grains to use and which zygotes to provision, termed selective abortion. This  
151 has been shown to be an important mechanism to increase plant fitness (Willson & Burley 1983;  
152 Sutherland 1986; Kozlowski & Stearns 1989; Guittian 1993; Melser & Klinkhamer 2001; Harder &  
153 Barrett 2006). A parent plant can exert stronger zygote selection if a large pool of excess zygotes is  
154 brought into existence, exactly the strategy displayed by a parental optimist. In summary, we expect  
155 the ratio of ovules to seeds, defined here as *choosiness* (the inverse of *seedset*), to be highest in  
156 parental optimists, those species with relatively lower pollen-attraction costs (trade-off 3 in Figure  
157 1b). (Note that *choosiness* as defined here encompasses a number of processes that occur between  
158 ovule maturation and the onset of zygote provisioning, including pollen-limitation, pollen-ovule  
159 incompatibility, and selective embryo abortion. However among these processes, it is selective  
160 abortion that is expected to be stronger in species with a relatively higher ovule count, i.e. parental  
161 optimists.)

162 **The three trade-offs combine to form a single reproductive strategy continuum:** The count-size  
163 trade-offs and parental optimist-parental pessimist trade-off emerge from different bodies of  
164 literature, but by extending them to consider total reproductive investment and counts of parts at  
165 two key times in a plant's reproductive cycle, it becomes apparent that they represent the same  
166 reproductive strategy continuum and together predict a syndrome of traits associated with large-  
167 seeded (depicted in Figure 1c) versus small-seeded species. Consider a large-seeded species, one

168 lying at the low seed count-high reproductive costs end of trade-off 1 (Figure 1b). Such species will  
169 align with the high choosiness-low relative pollen attraction costs end of trade-off 3, for species  
170 with high reproductive costs will be most selective about which embryos to provision (connection 1  
171 in Figure 1c). A species with low seed count and high choosiness (low seedset) must as a matter of  
172 logic produce a relatively larger ovule count, aligning these species with the high ovule count-low  
173 pollen-attraction costs end of trade-off 2 (connection 2 in Figure 1c). Indeed, trade-off 3 is nearly a  
174 ratio of the two energy pool-count trade-offs: it reflects what decisions plants make after allocating  
175 energy to pollen-attraction (trade-off 2), but before beginning to allocate the provisioning  
176 component of total reproductive investment (part of trade-off 1).

177 In summary, at one end of the spectrum are species that produce relatively few, but large seeds, and  
178 have low seedset. These parental optimists display greater selectivity in which zygotes to provision,  
179 since they are investing more energy in each offspring and maturing fewer seeds. These species  
180 invest relatively more in seed provisioning and relatively less in pollen attraction per ovule (Figure  
181 1c). Parental pessimists, relative to the parental optimists, have the same energy to invest in ovules  
182 or seeds, but produce relatively fewer, more costly ovules and relatively more, less costly seeds.  
183 Two previous studies have indeed observed that big-seeded species have lower seedset, also  
184 attributed to greater choosiness (Lord & Westoby 2006, 2012).

185 Based on these trade-offs we predict that the proportion of reproductive energy going to the  
186 different outcomes in Figure 1a will shift with seed size: 1) In large-seeded species total pre-  
187 provisioning investment will be predominately into discarded tissues, as most of the ovules  
188 produced will be shed or aborted before the onset of provisioning. 2) Once large-seeded species  
189 begin provisioning a zygote they are more likely to successfully create a viable seed, such that the  
190 proportion of total provisioning investment allocated to successful tissues versus discarded tissues  
191 should be higher in large-seeded species. 3) With increased seed size, species spend a decreasing



192 proportion of their success costs on pollen-attraction costs, as they are expected to produce a large  
193 number of inexpensive ovules.

194 Overall, we ask the following questions:

- 195 1. How much do individual plants invest in different reproductive tissues and does the proportional  
196 investment differ among species?
- 197 2. Do the hypothesized trade-offs exist between pollen attraction costs and ovules available for  
198 pollination and between success costs and seed count?
- 199 3. Is there a trade-off between choosiness and pollen-attraction costs?
- 200 4. Does the proportion of energy allocated to different reproductive tissue types shift with seed  
201 size?
- 202 5. Within a species, do total accessory costs or particular accessory cost components shift with  
203 plant size, age, or reproductive investment?

204 The dataset we use to address these questions is, to our knowledge, the most complete dataset where  
205 plant size, vegetative investment, reproductive investment, seed investment, seed count, and seed  
206 mass were simultaneously measured across multiple species at different size and ages in a native  
207 community. In a recurrent-fire coastal heath community, we studied fourteen species differing in  
208 seed size, lifespan, and maximum height. Individuals were sampled at different ages across a fire-  
209 created chronosequence, from 3 months to 30 years. We assessed total reproductive investment  
210 every 3 weeks for a year, to determine total investment both in tissues that developed into mature  
211 seeds and in tissues that were aborted during the developmental trajectory. This detailed accounting  
212 allows us to investigate correlates of reproductive tissue pool investment across and within species.

213 Finally, given the complexity of measuring all the components of reproductive investment, we  
214 assess how well different surrogate measures potentially predict total reproductive investment. For

215 this purpose we consider variables including total seed mass, total fruit mass, and total investment  
216 to the point of pollination.

## 217 **Methods**

### 218 **Study system**

219 The study was carried out in Kuring'gai National Park, just to the northeast of Sydney, Australia.  
220 The sandstone surfaces throughout the park host a coast heath community, whose dynamics have  
221 been governed by fire for at least 6000 years (Kodala & Dodson 1988). Fire regimes under  
222 traditional aboriginal management are unknown, but current New South Wales National Parks and  
223 Wildlife Service (NSW NPWS) management practises seek to achieve an average interval between  
224 7-30 years to maintain the current floristic diversity (NSW Office of the Environment 2006). The  
225 community includes perennial species that re-sprout following fire and also obligate seeders,  
226 species that are killed by fire and re-establish from seed. The obligate seeders included in this study  
227 germinate within a year of the fire and often after the next rain. Since the fire history of the park is  
228 well documented, the age of obligate seeders at a site can be estimated. In total, we selected 14  
229 obligate-seeder, woody perennials that are common in the community, with asymptotic heights  
230 ranging from 0.5 m – 5 m. They were *Banksia ericifolia* (Proteaceae), *Boronia ledifolia* (Rutaceae),  
231 *Conospermum ericifolium* (Proteaceae), *Epacris microphylla* (Ericaceae), *Grevillea buxifolia*  
232 (Proteaceae), *Grevillea speciosa* (Proteaceae), *Hakea teretifolia* (Proteaceae), *Hemigenia purpurea*  
233 (Lamiaceae), *Leucopogon esquamatus* (Ericaceae), *Persoonia lanceolata* (Proteaceae), *Petrophile*  
234 *pulchella* (Proteaceae), *Phyllota phyllicoides* (Fabaceae), *Pimelea linifolia* (Thymelaeaceae),  
235 *Pultenaea tuberculata* (Fabaceae). The family Myrtaceae is well represented in the community, but  
236 absent from the study, as all locally common Myrtaceae re-sprout following fire. All sites were  
237 chosen to have minimal *Eucalyptus* cover, such that *Banksia ericifolia*, *Hakea teretifolia*, and  
238 *Allocasuarina distyla* (not included in our study because it is dioecious) would be the dominant  
239 canopy species late in succession, at heights of 3-5 m.

## 240 **Field measurements**

241 The study was conducted over a single year, with the initial plant measurements and subsequent  
242 harvest conducted during the late autumn and early winter, the period of minimal vegetative growth  
243 in this plant community. Repeat visits were made throughout the year to record reproductive  
244 activity. Individuals were sampled at different ages across a fire-created chronosequence, from 3  
245 months to 30 years. Site ages were estimated from fire records maintained by NSW National Parks  
246 and Wildlife Service. At the conclusion of the study, the approximate ages of the individuals on the  
247 six sites were: 1.4, 2.4, 5, 7, 9 and 31 years. Plants were tagged during May-June 2012 and  
248 harvested during May-June 2013, with a given individual tagged and harvested within 2 weeks of  
249 the same calendar date. Only one species, *Persoonia lanceolata*, displayed any shoot extension  
250 during these months. These months are similarly a period of minimal reproductive activity – only  
251 *Banksia ericifolia*, *Grevillea speciosa*, and (occasionally) *Hemigenia purpurea* flowered during this  
252 period – although a number of species had immature fruit from the previous year (*Persoonia*  
253 *lanceolata*) or small buds that would open in the subsequent year (*Boronia ledifolia*, *Conospermum*  
254 *ericifolium*, *Epacris microphylla*, *Grevillea buxifolia*, *Leucopogon esquamatus*).

255 Seven healthy individuals of each species were selected at each site (and thus age). At the beginning  
256 of the study year, basal diameter was recorded approximately 10 mm above the base to avoid the  
257 basal swelling. At the end of the study year, diameter was remeasured at the same location. Plants  
258 were then harvested at ground level and oven dried at 60°C for at least 1 week. Leaves and stems  
259 were separated and weighed.

260 Flowering parts on all individuals were recorded during repeat censuses, every four weeks during  
261 cooler months and every three weeks during spring and summer. At each census, all flowering parts  
262 were counted, including buds (by size class), flowers, young fruit (by size class), and mature fruit.  
263 For some species the size of immature and mature fruit and cones was also measured, as the final  
264 size of the structures was quite variable. The exact flowering parts considered varied considerably

265 by species due to their diverse floral structures. Flowcharts detailing what flower parts were  
266 included for each species are provided in the Supplementary Material Tables S5-S18 and Figures  
267 S1-S14. The Supplementary Material also includes a table that indicates how each flowering part  
268 was counted and/or measured for each species. Each of the flower parts was independently  
269 collected from multiple untagged individuals in the community to determine its dry mass.

## 270 **Calculating reproductive investment and cost components**

271 Total reproductive effort (RE) is the sum of investment in all the different flowering parts during  
272 the year, tabulated on a dry mass basis. For each species, reproductive parts were designated as  
273 either forming up to the point of pollination (pollen-attraction; i.e. the flower) or post-pollination  
274 and were summed into one of the two respective investment pools. For floral parts that were present  
275 at the time of pollination and continued to develop into either the seed or packaging and dispersal  
276 tissues post-pollination, the fraction of the final mass present at the time of pollination was  
277 designated part of the pollen-attraction investment and the remaining fraction as part of the  
278 packaging and dispersal investment. All calculations were made on an individual basis, although the  
279 average mass of many plant parts are based on species-level measurements. These calculations  
280 yielded total pollen-attraction tissue investment and total provisioning tissue investment. Total  
281 pollen-attraction costs and total provisioning costs are calculated by dividing the respective  
282 investment values by seed count.

283 To calculate the three success cost components, pollen-attraction costs, packaging and dispersal  
284 costs, and seed mass, the unit mass of reproductive parts required for the successful creation and  
285 provisioning of a single propagule were summed together. For pollen-attraction tissues, unit mass  
286 was determined by dividing the mass of the part at the time of pollination by the number of ovules it  
287 supported. All calculations make the assumption that each species produces a fixed (average)  
288 number of ovules per flower, but individual-level calculations are made for cones or inflorescence  
289 stalks which support variable numbers of flowers and hence ovules. For packaging and dispersal

290 tissues, the unit mass was calculated by dividing the mass of the part at seed maturity by the number  
291 of seeds it supported. For seed mass, we chose to designate the endosperm and embryo as the  
292 primary reproductive unit, for it provides a consistent comparison of tissue mass across species. It is  
293 hereafter referred to as *seed size*. In contrast, the propagule includes the seed coat, and additional  
294 dispersal tissues in some species, but not others. See the Supplementary Material for a depiction of  
295 the parts for each species and the number of ovules in each part.

296 Discarded pollen-attraction tissue costs were then determined as:

297 Total pollen-attraction costs – Successful pollen-attraction costs.

298 Discarded provisioning tissue costs were then determined by the following formula, where  
299 successful provisioning costs is the sum of seed size and successful packaging and dispersal costs:

300 Total provisioning costs – Successful provisioning costs.

301 Reproductive count values used in the manuscript are defined as follows: *Ovule count* indicates the  
302 count of all ovules initiated by the plant. *Reach flowering count* indicates the count of ovules that  
303 developed to maturity and were presented to pollinators. *Post-pollen count* indicates the count of  
304 ovules that experienced at least some provisioning and is divided into *seed count*, the count of  
305 mature seeds formed, and *post-pollen aborted count*, the count of zygotes that aborted after  
306 provisioning had commenced. All counts are for a one-year time period.

307 Further detailed information on the calculation of all reproductive tissues is provided in the  
308 supplementary information.

### 309 **Statistical methods**

310 Bivariate relationships among the variables were quantified using two methods. When testing for a  
311 significant correlation between two variables we report the  $r^2$  and p-value of an ordinary linear

312 regression. When testing whether the slope of a particular trade-off or relationship differs from a  
313 specified value, we report the slope of the Standardised Major Axis line fit to the data (Warton *et al.*  
314 2006). All analyses were conducted in R 3.2.4 (R Core Team 2015) using the package `smatr` for  
315 comparing slopes of SMA lines (Warton *et al.* 2012). In addition, the code replicating this analysis  
316 (and all figures) is available at [https://github.com/traitecoevo/reproductive\\_allocation\\_kuringgai](https://github.com/traitecoevo/reproductive_allocation_kuringgai)  
317 (doi: will be added at proof stage).

## 318 **Results**

### 319 **Accessory costs and accessory cost components**

320 Of the 599 plants included in this study, 223 individuals produced at least one seed during the year.  
321 Across these individuals, on average 97.5% of reproductive investment went to accessory tissues  
322 rather than to seeds, decreasing to 91.5% if the entire propagule mass was treated as direct  
323 investment in offspring instead of just the embryo and endosperm components. Hereafter, all results  
324 report results for the embryo and endosperm component, designating them as seed size. Across  
325 species, accessory costs ranged from a low of 95.8% for *Epacris microphylla* to a high of 99.8% for  
326 *Hakea teretifolia* (Table 1).

327 Total reproductive costs can be divided into discarded tissue costs (the mass of all aborted and  
328 discarded parts, including mature flowers that fail to set seed) versus reproductive success costs  
329 (seed mass plus the total per ovule cost of required floral parts, both before pollination and during  
330 seed provisioning). Only the two cone-bearing species – *Banksia ericifolia* and *Petrophile pulchella*  
331 – had success costs that were higher than discarded tissue costs (Table 1). Three species – *Hakea*  
332 *teretifolia*, *Phyllota phyllicoides*, and *Pultenaea tuberculata* – spent more than 90% of their  
333 reproductive investment on discarded tissues (Table 1). For most species, these discarded tissues  
334 were predominantly pre-provisioning, with aborted seeds and fruit a minor component of discarded  
335 tissue costs (Table 1). Note that fruit that abort after pollination but before the onset of visible  
336 provisioning were recorded as shed flowers, such that pollen-attraction costs (pre-provisioning)

337 included costs associated with ovules aborted both due to lack of pollination and due to early  
338 maternal selection.

339 Total success costs are divided into mass of parts formed up to the point of pollination (pollen-  
340 attraction costs) versus the mass of the seed, packaging, and dispersal structures (provisioning  
341 costs). The relative size of these cost components shifted markedly across species (Table 1). Four  
342 species – *Epacris microphylla*, *Hemigenia purpurea*, *Pimelea linifolia*, and *Pultenaea tuberculata* –  
343 had pollen-attraction costs that were greater than 50% of total success costs, while 5 species had  
344 pollen-attraction costs that were less than 10% of total success costs (Table 1). The percentage of  
345 success costs invested in provisioning tissues (including the seed itself) ranged from a low of 18%  
346 (for *Epacris microphylla*) to a high of 99% (*Banksia ericifolia*) (Table 1). The maximum  
347 percentages of reproductive investment any species invested directly in seeds were 4.2% for  
348 *Epacris microphylla* and 4.1% for *Hemigenia purpurea*.

#### 349 **Observed trade-offs**

350 Plants produce many inexpensive ovules or proportionally fewer more expensive ovules, such that  
351 the relationship between ovule count at the time of pollination, scaled to the plant's leaf area, versus  
352 pollen-attraction costs is highly significant and has a slope not significantly different from -1  
353 (Figure 2a;  $r^2=0.88$ , slope = -1.12, with 95% confidence interval [-0.90 – -1.41]). Similarly, plant  
354 produce a greater number of more expensive seeds or proportionally fewer less costly seeds, such  
355 that the relationship between seed count, scaled to the plant's leaf area, and reproductive costs also  
356 has a slope of -1 (Figure 2a;  $r^2=0.93$ , slope = -0.99, with 95% confidence interval [-0.84 – -1.17]).

357 There also exists a trade-off between choosiness (ovule to seed ratio, the inverse of seedset) and  
358 pollen-attraction costs, scaled to the plant's leaf area (Figure 2b;  $r^2=0.26$ , rising to  $r^2=0.77$  when  
359 *Epacris microphylla* with strangely high leaf area relative to all other metrics is removed; slope = -  
360 1.25, with 95% confidence interval [-0.91 – -1.71]). Plants which expend less of their energy budget

361 to produce a single mature ovule, abort and discard a greater proportion of the ovules displayed to  
362 pollinators.

363 The values for the plotted points are listed in either Table 1 or Supplementary Material Table S1.

#### 364 **Changes in relative energy investment with seed size**

365 The strong trade-offs between the cost to produce a specific reproductive tissue and the number of  
366 units produced by the plant is manifested as shifts in the proportion of reproductive energy invested  
367 in different reproductive tissue pools across the seed size spectrum. As seed size increases, there is  
368 also a trend toward increasing expenditure on discarded pollen-attraction tissues in comparison to  
369 successful pollen-attraction tissues (Figure 2c;  $r^2 = 0.60$ ,  $p = 0.0012$ ), reflecting the increased  
370 choosiness (decreased seed set) in larger-seeded species ( $r^2 = 0.59$  for the seed set-seed size  
371 regression;  $p = 0.0013$ ). Increased seed size was only marginally related to a shift in the proportion  
372 of provisioning energy invested in successful versus discarded tissues, with larger-seeded species  
373 showing a slight increase in proportional investment in successful tissues (Figure 2d;  $r^2 = 0.24$ ,  
374  $p = 0.0741$ ). Larger-seeded species expend a greater proportion of their *success costs* on provisioning  
375 tissues versus pollen-attraction tissues in comparison to smaller-seeded species (Figure 2e;  $r^2 = 0.80$ ,  
376  $p < 0.0001$ ).

377 These shifts are also reflected in the relative slopes of the regression between seed size and  
378 provisioning costs and between seed size and pollen-attraction costs: provisioning costs show a  
379 steeper than isometric increase with seed size, while pollen-attraction costs show a less than  
380 isometric increase with seed size (Figure 2f; Table 2). The per seed matured costs of most other  
381 reproductive tissue pools show slightly steeper than isometric increases with increasing seed size,  
382 indicating the costs are relatively higher for larger-seeded species (Table 2).

383 The values for the plotted points are listed in either Table 1 or Supplementary Material Table S1.



384 **Shifts in accessory costs with plant size, age, or reproductive effort**

385 None of the study species demonstrated a decrease in per seed accessory costs with increasing plant  
386 size or RE, and only one species showed a decrease in per seed accessory costs with age. With only  
387 1/42 tests significant (Supplementary Material Table S2), this likely represents little more than  
388 chance. There are also two regressions, where accessory costs increased with plant size or age  
389 (Supplementary Material Table S2).

390 **Correlates with total reproductive investment**

391 Of the 599 plants included in this study, 357 individuals produced buds and 223 individuals  
392 produced mature seeds. Even among the individuals that produced seeds, embryo and endosperm  
393 investment was only rather loosely correlated with total reproductive investment, both within and  
394 across species (Table 3, Figure 3, and Supplementary Material). All but one species showed a  
395 significant correlation between the two metrics, but only three species displayed an  $r^2$  above 0.80  
396 and only eight of the species had an  $r^2$  above 0.70. Furthermore, the slopes and intercepts of the  
397 relationship differed across species with the result that the correlation between reproductive  
398 investment and propagule investment across individuals of all species had an  $r^2$  of just 0.52 (Figure  
399 3a, Table 3). Combined these results indicate that measures of seed production alone provide poor  
400 predictors of total reproductive investment.

401 To assess what approximation of reproductive investment was the best alternative to measuring  
402 total reproductive investment, we regressed additional investment categories against total  
403 reproductive investment. Measures that included only investment in tissues associated with the  
404 production of mature seeds, were inferior predictors of total reproductive investment compared to  
405 measures that included investment in discarded tissues (Table 3). In particular, the correlation ( $r^2$ )  
406 between investment in all discarded tissues versus all reproductive tissues was 0.97, while the  
407 correlation between investment in all successful tissues (success costs\*seed count) versus all  
408 reproductive tissues was only 0.73. Investment in discarded tissues is a better predictor for two

409 reasons. First, discarded tissues accounted for 73% of total reproductive investment; and second,  
410 energy investment into buds and flowers was more predictable, while further filtering processes  
411 occurred before buds become mature seeds. A composite metric, the count of buds initiated \*  
412 average flower mass, when regressed against total reproductive investment, had an  $r^2$  of 0.92,  
413 making it nearly as strong a predictor of total reproductive investment as discarded tissue  
414 investment. Twelve of the species had the same slope for the relationship and eleven of the species  
415 had the same intercept for the relationship as the all-individuals regression (Supplementary Material  
416 S3).

## 417 **Discussion**

418 There were four key outcomes from this study. First, we observed that plants of the 14 long-lived  
419 perennial species studied expended a very large proportion of reproductive energy on accessory  
420 costs. Investment in seed dry mass represented a quite modest proportion of total reproductive  
421 investment (RE) for the 14 perennial species included in this study, with just 0.2-4% of RE going to  
422 seeds versus other reproductive tissues (Table 1). Even the individual with the lowest accessory  
423 costs invested just 9.5% of its RE into the seed itself. Second, we observed a trade-offs between  
424 ovule count and pollen-attraction costs and between seed count and total reproductive costs. The  
425 trade-offs indicate there exists a fixed pool of energy to invest and species differ in the relative cost  
426 of a part versus the number of parts they can produce. We also observed a trade-off between  
427 choosiness, the inverse of seedset, and pollen-attraction costs: species that expend less energy to  
428 produce an ovule produce a greater excess of ovules. These are species at the *parental optimist* end  
429 of the optimist-pessimist spectrum, which have proportionally costlier provisioning tissues relative  
430 to pollen attraction tissues (Rosenheim *et al.* 2014). In combination, these trade-offs lead to  
431 systematic differences in the way reproductive energy is allocated across species, resulting in a  
432 syndrome of reproductive traits values observed for large-seeded versus small-seeded species, our  
433 third outcome. The *parental optimists* were, as predicted, the large-seeded species: part of the big

434 seed-size, low seedset strategy is to invest proportionally less in flower construction to the point of  
435 pollination and proportionally more in provisioning tissues. The fourth major result was that for  
436 perennial species with low seedset, total reproductive investment was best predicted by energy  
437 expenditure in buds and flowers, not by investment in seeds or fruit.

#### 438 **Accessory costs are large**

439 All species in this study allocated an enormous proportion of RE to accessory costs, both accessory  
440 success costs and discarded tissues (Figure 1a, Table 1). Many estimates of plant energy investment  
441 in reproduction do not account for total accessory costs, leading to potentially misleading results  
442 (reviewed in Obeso 2002; Lord & Westoby 2006; Rosenheim et al. 2014; Wenk & Falster 2015).  
443 For example, studies seeking to estimate the cost of reproduction may reach erroneous conclusions  
444 if they record only shifts in seed production year upon year, ignoring investment in accessory  
445 tissues (Obeso 2002). Reproductive allocation, the proportion of energy spent on reproduction  
446 rather than on growing and replacing vegetative tissue (Ashman 1994; Bazzaz, Ackerly & Reekie  
447 2000; Wenk & Falster 2015), will also be substantially underestimated, leading to overestimates of  
448 the proportion of energy (and absolute amount of energy) available for vegetative growth. The  
449 current study indicates that fair assessment of RE needs to account for all pools of accessory tissues,  
450 since both discarded tissue costs and success cost components (see Figure 1a for definitions)  
451 contributed to the high accessory costs (Table 1).

452 Our study species have diverse floral and fruiting structures, such that disparate tissues comprise  
453 success cost expenditures in different species (Figure 1a, Table 1). For three species (*Epacris*  
454 *microphylla*, *Hemigenia purpurea*, and *Pimelea linifolia*), the costs of producing pollen-attraction  
455 tissues (on flowers that eventually produce mature seeds) was 21-27% of total RE, while for other  
456 species it was substantially less (Table 1). The two cone-producing species, *Banksia ericifolia* and  
457 *Petrophile pulchella*, had the costliest packaging and dispersal tissues, spending 71.0% and 60.5%  
458 of total RE, respectively. Other species also had high packaging and dispersal expenditure due to

459 structures including fleshy fruit (*Persoonia lanceolata*), woody seedpods (*Grevillea* species), and  
460 thick seedcoats (*Leucopogon esquamatus*). These are tissues that must be produced to mature each  
461 seed and their exact structures have presumably evolved to maximize seed production and survival.

462 Discarded tissues, those tissues associated with ovules that abort instead of developing into a  
463 mature seed, are the complement to success investment. For 12 of the 14 study species, discarded  
464 tissues accounted for more than 60% of total reproductive investment (Table 1). Only in *Banksia*  
465 *ericifolia* and *Petrophile pulchella*, the two species with very high energy investment in woody  
466 cones, was a smaller proportion of RE attributable to discarded tissues. The majority of discarded  
467 tissue costs was due to buds and flowers that were aborted before seed provisioning became  
468 substantial (Table 1). Indeed, a large energy investment in discarded tissues has been found for all  
469 species that display low seed or fruit sets (Stephenson 1981; Sutherland 1986; Ramirez & Berry  
470 1997; Knight *et al.* 2005).

471 These high accessory costs, and in particular high discarded costs, should presumably be considered  
472 a cost of sex. That is, the only reason for incurring them would be in order to create zygote genomes  
473 that conferred superior fitness, compared to zygotes created by selfing or apomixis. Having a  
474 surplus of ovules, relative to the number of offspring that can be provisioned to maturity, allows the  
475 plant to be selective about which zygotes to mature. Explanations for the abortion of a large number  
476 of mature ovules near the time of pollination include environmental stochasticity, pollen-limitation,  
477 poor pollen-tube growth, pollen incompatibility, selective abortion, and resource limitation  
478 (Ashman *et al.* 2004; Knight *et al.* 2005; Ruane, Rotzin & Congleton 2014). Additional zygotes will  
479 be lost during the provisioning period due to factors including insect attack and poor environmental  
480 conditions.

481 In the following sections we explore whether the three trade-offs that are observed predict how  
482 relative investment in different accessory cost pools shifts across species.

### 483 **Count-cost and choosiness-cost trade-offs exist**

484 The first two trade-offs identified in the introduction describe how a given pool of energy can be  
485 divided into many small units or proportionally fewer large units. Abundant theory and empirical  
486 evidence underpins the seed size-seed number trade-off (Smith & Fretwell 1974; Moles *et al.* 2004;  
487 Sadras 2007) and here we extend the theory to include two trade-offs that account for the significant  
488 accessory costs required for seed production. The first trade-off is between seed count and total  
489 reproductive costs, closely related to the well-established seed size-seed count trade-off,  
490 demonstrating that large-seeded species are those species with high overall per seed reproductive  
491 costs and low seed counts (Smith & Fretwell 1974; Rees & Westoby 1997; Moles & Westoby  
492 2006). The second is the ovule count-pollen-attraction costs trade-off, suggesting plants have a  
493 fixed pool of energy to allocate to construct flowers to the point of pollination and this energy may  
494 be divided into fewer showier flowers or into more numerous but cheaper flowers (Rosenheim *et al.*  
495 2014).

496 The third trade-off is between choosiness (inverse of seedset) and the relative cost of producing a  
497 single ovule to the point of pollination: species for whom producing an ovule is less costly tend to  
498 have lower seedset (Lord & Westoby 2006; Rosenheim *et al.* 2014). Species with low seed set are  
499 also termed parental optimists: they produce excess pollinated ovules, relative to the seeds they can  
500 provision in an average year, because they are always optimistic that the year will be better than  
501 average. Due to the large number of ovules they produce, they are selected to reduce their pollen-  
502 attraction costs (Haig & Westoby 1988; Schreiber *et al.* 2015; Rosenheim *et al.* 2015). Since these  
503 species have lower seed output, they are under stronger selection to produce seeds that will  
504 successfully establish (Lord & Westoby 2006). Simply being larger is part of their strategy (Moles  
505 & Westoby 2006), but ensuring their seeds have vigorous genotypes is another correlate of this  
506 same strategy dimension and one achieved through greater choosiness for the most vigorous  
507 embryos shortly after pollination (Westoby & Rice 1982; Willson & Burley 1983; Sutherland 1986;  
508 Guittian 1993). Having excess ovules pollinated means parental optimists can be more selective in

509 terms of pollen receipt (Zimmerman & Pyke 1988) and which zygotes to provision (Willson &  
510 Burley 1983; Sutherland 1986; Guittian 1993).

### 511 **Coordinated shifts in reproductive energy allocation across species**

512 Together, the three trade-offs predict a single axis of variation in reproductive strategies, showing  
513 how species exhibit coordinated shifts in resource allocation, leading to a syndrome of reproductive  
514 traits associated with large-seeded versus small-seeded species (Figure 1c). At one end of the  
515 spectrum are parental optimists, using their pool of pre-pollination energy to produce many,  
516 inexpensive ovules, but their total pool of reproductive energy to produce relatively few, costly  
517 seeds, resulting in low seedset. The parental pessimists fall on the opposite end of the spectrum. As  
518 a result, species are expected to be under strong selection to coordinate their relative investment in  
519 the different energy pools described in Figure 1a. The first and third of the predicted relative shifts  
520 in tissue investment with seed size were strongly borne out by our data, while support for the  
521 second was weaker. First, since large-seeded species had lower seedset – and in particular high  
522 ovule and embryo abortion near the point of pollination – they spent a larger proportion of their  
523 pool of energy for pollen-attraction tissues on tissues that are discarded, relative to smaller-seeded  
524 species (Figure 2c). Second, since these large-seeded species had a small proportion of ovules  
525 passing through the many filters to reach the point of provisioning and since these embryos had  
526 likely been carefully selected, the large-seeded species were expected to provision a larger  
527 proportion of the selected embryos to become mature seeds. There was only a weak trend in this  
528 direction, in part reflecting the overall high success rate of embryos once post-pollination  
529 provisioning commenced among species of all seed sizes (Figure 2d).

530 Third, given that large-seeded species were producing relatively many inexpensive ovules and  
531 relatively fewer expensive seeds, the proportion of *success costs* allocated to pollen-attraction  
532 materials was expected to decrease with seed size while the proportion of *success costs* allocated to  
533 provisioning materials should increase with seed size, a pattern strongly observed among the study

534 species (Figure 2e). This represents a fundamental shift in floral construction with seed size. In  
535 relative terms, larger-seeded species were producing larger packaging and dispersal tissues, but less  
536 costly pollen-attraction materials. This is being accomplished both through a reduction in floral size  
537 and, for some plant families, an increase in the number of ovules per flower or inflorescence (Lord  
538 & Westoby 2006, 2012). This trend can also be depicted by plotting pollen-attraction costs and  
539 provisioning costs against seed size: *Pollen-attraction costs* display a less than isometric increase  
540 with increasing seed size, while *provisioning costs* display a greater than isometric increase with  
541 increasing seed size (Table 2, Figure 2f). Identical patterns have been observed in other studies  
542 (Lord & Westoby 2006, 2012). They have been attributed in part to larger seeded-species tending to  
543 have biotic dispersal agents, with animal-dispersed species allocating a greater proportion of their  
544 reproductive energy to packaging and dispersal materials (Hughes *et al.* 1994; Moles *et al.* 2005;  
545 Eriksson 2008).

546 In this study, total reproductive costs and accessory costs both showed a steeper than isometric  
547 increase with seed size (Table 2), indicating the proportion of reproductive energy invested in  
548 accessory tissues is higher in larger-seeded species. Our result suggests that among our study  
549 species there are (slight) additional benefits to being large-seeded that have not been explored in  
550 this study, such as higher seedling germination and success (Moles & Westoby 2006). Previous  
551 studies have not found evidence for the increase in total reproductive costs and accessory costs with  
552 increasing seed size to be other than isometric in angiosperms (Henery & Westoby 2001; Moles,  
553 Warton & Westoby 2003; Lord & Westoby 2006; Chen *et al.* 2010; Lord & Westoby 2012). Note,  
554 that in these studies, seed size was defined as the mass of the entire propagule. When we recalculate  
555 the slopes of the relationships using total propagule size, we too observe an isometric relationship  
556 between total reproductive costs or total accessory costs and propagule size (Supplementary  
557 Material Table S4.)

558 **Shifts in accessory costs with plant size and age**

559 An additional motivation for this study was to determine if accessory costs shifted with plant age,  
560 size or RE. The theoretical literature suggests that for plants to increase their allocation to  
561 reproduction (versus growth) as they grow and age, plants must realize some compounding benefit  
562 (Myers & Doyle 1983; Sibly, Calow & Nichols 1985; Reekie & Bazzaz 1987a; Kozlowski 1992).  
563 Increasing mortality with age has the effect of decreasing future reproductive value and selecting  
564 for increased current RE in older plants. If accessory costs declined with RE, making seed  
565 production more efficient, then plants should be selected to have fewer, larger reproductive  
566 episodes (Kelly 1994; Kelly & Sork 2002) or to delay reproduction until they are larger and can  
567 invest more energy in reproduction (Cole 1954; Wenk & Falster 2015). Such a pattern was not  
568 observed in this dataset. Across individuals within a species, total accessory costs and accessory  
569 cost components barely shifted with plant size, age, or total reproductive investment  
570 (Supplementary Material S2). The consistent lack of shift in per seed accessory costs (or seedset,  
571 data not shown) with RE (or bud count, data not shown) surprised us. There is a large literature on  
572 expected and observed trends in pollination and seedset with the size of the floral display, showing  
573 varied patterns (e.g. Primack 1987; Klinkhamer, de Jong & de Bruyn 1989; Ohara & Higashi 1994;  
574 Goulson et al. 1998), but the literature had not led us to expect a flat relationship for all 14 species  
575 (Supplementary Material S2). For many of the species studied here sample sizes were large and we  
576 sampled across their entire age range. We believe that if a shift in accessory costs (or accessory cost  
577 components) existed with plant size, age, or RE for these species it should have been detected in  
578 this data.

579 **Estimating reproductive effort**

580 Realistic estimates of RE are essential for many research questions, for example plant functional  
581 growth models require estimates of the proportion of photosynthetic energy that is allocated to  
582 growth versus reproduction (Fisher *et al.* 2010; Falster *et al.* 2011; Scheiter, Langan & Higgins  
583 2013), while demographic models may need estimates of seed production for a given RE (Garcia &



584 Ehrlen 2002; Miller *et al.* 2012). The current study, along with others, has shown that plants are  
585 allocating energy to many different reproductive tissues, with a notably small proportion going to  
586 seeds. However, the detailed measurements required to account for all reproductive energy  
587 expenditure are not practical for many research projects and pointing researchers to the best rapidly-  
588 obtainable estimates of total RE would be beneficial to many.

589 At the individual level, embryo and endosperm investment, propagule investment, and fruit  
590 investment were relatively poor predictors of RE (Table 3). Even within species, knowing seed  
591 investment provided only a mediocre estimate for total RE, with only 8 of the 14 species having an  
592  $r^2 > 0.70$  and one species not even displaying a significant correlation across individuals  
593 (Supplementary Material S3). In contrast total investment in discarded tissues (primarily  
594 representing investment in aborted flowers and buds), and our artificial composite measure “total  
595 bud count \* average flower mass at the time of pollination”, provided strong estimates of total RE  
596 ( $r^2 = 0.96$  and  $r^2 = 0.92$  respectively for regressions across all individuals; Table 3). While total  
597 discarded tissue investment is not a “quick measure”, requiring repeat visits to the field and tedious  
598 accounting, the composite measure would work well for species where most of their buds and  
599 flowers are visible at a single point in time. Doing a single bud count and determining flower  
600 weight for the species would be a manageable prospect and give you a quite accurate estimate of  
601 total RE. This composite metric has the merits that it would be relatively easy to measure on large  
602 numbers of plants and that it effectively combines both the within and across species variation  
603 (Figure 3b, Table 3, Supplementary Material S3).

604 Conversely, these results demonstrate that if your research question requires seed investment or  
605 seed count as an output, estimates of RE will not accurately predict seed production. Instead, and in  
606 contrast to many herbaceous species (Shipley & Dion 1992), for perennial species with relatively  
607 low seedset, seed count or seed investment must be determined for each individual.

608 The explanation for the poor correlation between seed investment and RE is clear: most of these  
609 species have relatively low seedset (Table 1) and moreover, seed set is quite variable across  
610 individuals at a single site (Figure 3). The unpredictability of seedset and overall low seedset means  
611 that investment in seeds, at the individual level, cannot be predicted by any easy-to-measure  
612 metrics. Many stochastic processes, from pollinator activity to pollen compatibility to resource  
613 availability lie between bud production and seed production (Herrera *et al.* 1998; Wesselingh 2007;  
614 Gómez 2008). These processes lead to both individual and inter-annual variation in seed production  
615 (Copland & Whelan 1989; Mitchell 1997; Herrera *et al.* 1998).

### 616 **Methodological considerations**

617 To reach meaningful conclusions about trade-offs between reproductive costs, counts, and seedset,  
618 accurate measurements of total reproductive investment are essential. Our accounting scheme is  
619 very detailed, but of course imperfect. The largest source of error is that we have not measured  
620 nectar production. Some of these species are known to produce abundant nectar, particularly  
621 *Banksia ericifolia*, *Hakea teretifolia* and both *Grevillea* species (Pyke 1983; Pyke, O'Connor &  
622 Recher 1993; Lloyd, Ayre & Whelan 2002). Very rough back-of-the-envelope calculations, based  
623 on studies of closely related species in nearby communities, indicate nectar production increases  
624 total reproductive investment by ~20% for *Grevillea speciosa*, 10% for *Hakea teretifolia*, and well  
625 under 5% for *Grevillea buxifolia* and *Banksia ericifolia*. Accounting for nectar production in our  
626 study would have the effect of increasing pollen-attraction costs (both successful and discarded)  
627 relative to provisioning costs (Pyke 1983; Pyke *et al.* 1993; Lloyd *et al.* 2002).

628 Are dry masses the best measures of expenditure, especially in a community growing on soils  
629 known to be very low in P (Beadle 1968)? Previous studies indicate that using the concentration of  
630 a limiting mineral nutrient to calculate nutrient allocations may be a better measure of a plant's  
631 allocation choices (Reekie & Bazzaz 1987b; Ashman 1994; Rosenheim *et al.* 2014), but also that all  
632 currencies yield similar results. For example, nectar production, in comparison to reproductive

633 tissues such as seeds, might seem relatively less expensive, in units of P than in units of dry weight  
634 or energy, potentially relevant for a community growing on low P soils. This is a direction for  
635 future investigations.

636 A persistent issue in assessing reproductive costs is that some green reproductive tissues are known  
637 to photosynthesize (Cohen 1976; Reekie & Bazzaz 1987a; Wesselingh 2007). It can be argued that  
638 their dry mass is not a fair measure of cost, with some of it being paid back from their own  
639 photosynthesis. Against this, it can be argued that all the plant's photosynthesis should be  
640 considered a common pool of resource, and dry mass of different parts fairly reflects the relative  
641 allocation to different activities and tissue functions. We have adopted this second view.

642 This dataset does not address other known factors that may contribute to low seedset in this system,  
643 including pollen-limitation (Burd 2008, 2016) and environmental stochasticity. Insufficient pollen  
644 receipt may certainly be contributing to the patterns observed, but given recent theoretical  
645 treatments that suggest pollen-limitation should be more severe among parental-pessimists  
646 (Rosenheim *et al.* 2014, 2016), it is unlikely the observed trend of lower seedset among the  
647 parental-optimists is primarily attributable to pollen-limitation. Environmental stochasticity, both in  
648 terms of pollen receipt and resources to provision embryos, also selects for overproduction of  
649 embryos in parental optimists (Haig & Westoby 1988; Rosenheim *et al.* 2014). Parental optimists  
650 are so-named because they are optimistic about the number of ovules they will be able to mature  
651 and therefore produce additional ovules that can be matured when sufficient resources are available  
652 (Mock & Forbes 1995; Burd *et al.* 2009; Schreiber *et al.* 2015; Rosenheim *et al.* 2015).

## 653 **Conclusions**

654 In summary, the correlations observed in our study indicate that seed size, ovule production versus  
655 seed production, and the magnitude of specific reproductive tissue pools are coordinated across  
656 species. While a plant's accessory costs may be startlingly large at first glance, allocation of energy

657 to different tissues is expected to represent an evolved strategy to maximize fitness. Identifying  
658 trade-offs between specific energy allocation choices – and then determining that energy allocation  
659 within this community matches the predicted patterns – provides a framework for understanding  
660 coordinated responses for seed size, seedset, and allocation to pollen-attraction versus seed  
661 provisioning tissues. Just as species have long been shown to follow a seed size-seed number trade-  
662 off, so do all species have the same amount of energy (relative to their leaf area) to invest in ovules,  
663 leading to a trade-off between the cost of pollen-attraction tissues and ovule count. Large-seeded,  
664 low seedset species have proportionally less costly pollen-attraction tissues and on average produce  
665 a proportionally larger excess of ovules relative to the seeds they are able to provision.

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## Tables

species	Seed size (mg)	Seedset	Reproductive costs (mg)	Proportion reproductive costs (%)					Success costs (mg)	Proportion success costs (%)	
				Discarded		Success				Pollen attraction	Provisioning
				Pollen attraction	Packaging and dispersal	Pollen attraction	Packaging and dispersal	Seed			
 <i>Epacris microphylla</i>	0.014	0.317	0.525	54.6	12.3	27.0	1.9	4.2	0.112	81.6	18.4
 <i>Pimelea linifolia</i>	0.183	0.274	10.463	64.0	2.1	23.7	8.1	2.0	3.05	70.0	30.0
 <i>Hemigenia purpurea</i>	0.222	0.312	7.054	45.5	21.8	21.7	6.9	4.1	1.841	65.5	34.5
 <i>Leucopogon squamatus</i>	0.405	0.312	24.695	29.4	25.6	13.1	28.4	3.5	5.164	28.8	71.2
 <i>Conospermum ericifolium</i>	0.589	0.177	24.020	43.0	34.5	11.1	8.7	2.7	5.078	52.4	47.6
 <i>Pultenaea tuberculata</i>	0.867	0.067	121.561	85.1	5.5	5.9	2.4	1.2	6.951	62.8	37.2
 <i>Phyllota phyllicoides</i>	1.394	0.047	302.609	87.1	4.4	4.0	2.9	1.6	7.449	48.0	52.0
 <i>Boronia ledifolia</i>	2.158	0.036	151.481	68.8	11.9	4.2	12.3	2.8	14.802	21.8	78.2
 <i>Petrophile pulchella</i>	2.531	0.341	180.254	18.2	10.5	8.5	60.5	2.2	119.907	11.3	88.7
 <i>Persoonia lanceolata</i>	3.368	0.062	1140.445	50.6	12.2	2.3	34.4	0.4	283.475	6.4	93.6
 <i>Hakea teretifolia</i>	7.559	0.004	4348.682	80.0	14.0	0.3	5.5	0.2	205.875	5.6	94.4
 <i>Grevillea speciosa</i>	7.728	0.014	587.822	59.4	19.5	1.6	17.4	2.0	83.208	8.0	92.0
 <i>Banksia ericifolia</i>	18.511	0.032	3385.342	16.8	10.4	0.7	71.0	1.1	2218.899	0.8	99.2
 <i>Grevillea buxifolia</i>	22.408	0.015	844.298	68.7	9.5	1.4	17.1	3.3	149.768	6.2	93.8

**Table 1.** Reproductive investment data for each species. Seed size indicates the mass of the embryo and endosperm only (mg). Seedset is mature seeds per ovule initiated. Reproductive costs are the total reproductive investment per seed matured. The proportion of reproductive costs allocated to discarded tissues formed for pollen-attraction versus packaging and dispersal, successful pollen-attraction tissues, successful packaging and dispersal tissues and the seed itself are shown. Success costs are the components of total reproductive costs required for the formation of a successful seed, and are divided into two components, pollen attraction costs and provisioning costs. Note that for seed costs, the weight of the seed itself is considered part of provisioning costs. Colored dots indicate plotting colors used for each species in Figure 3.

Reproductive cost component	$r^2$	Slope ( <i>confidence interval</i> )
Total reproductive costs	0.91	1.27 (1.05 - 1.54)
Total accessory costs	0.90	1.27 (1.05 - 1.54)
Success costs	0.88	1.28 (1.02 - 1.59)
Pollen-attraction costs	0.82	0.67 (0.52 - 0.87)
Provisioning costs	0.89	1.51 (1.23 - 1.85)
Discarded tissue costs	0.87	1.26 (1.01 - 1.57)
Discarded pollen-attraction costs	0.85	1.28 (1.01 - 1.63)
Discarded provisioning costs	0.87	1.30 (1.03 - 1.63)

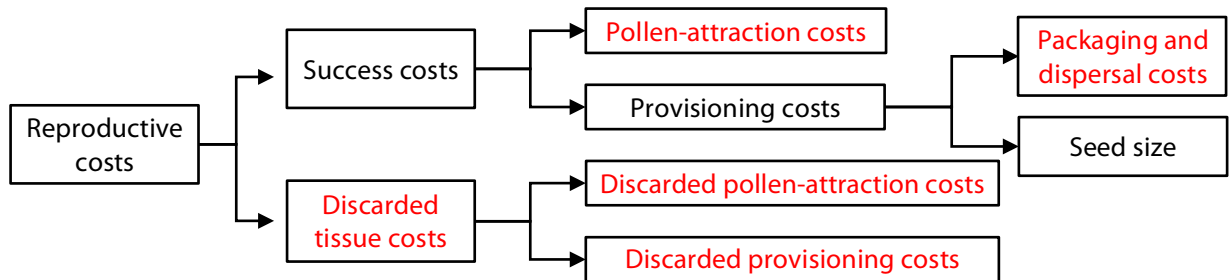
**Table 2.** Scaling of reproductive tissue costs with seed size. All variables were showed a strong correlation with seed size ( $p < 0.0001$ ). Tables show properties of SMA line fits, between different variables and seed size.

Estimate of reproductive investment	n	r <sup>2</sup>
Total plant weight (mg)	357	0.620
Embryo and endosperm investment (mg)	223	0.660
Propagule investment (mg)	223	0.525
Fruit investment (mg)	223	0.675
Flower investment (mg)		
(flower weight * bud count)	223	0.922
Successful investment (mg)		
(success costs * seed count)	223	0.728
Successful pollen-attraction investment (mg)	223	0.380
Successful provisioning investment (mg)	223	0.736
Discarded tissues (mg)	357	0.968

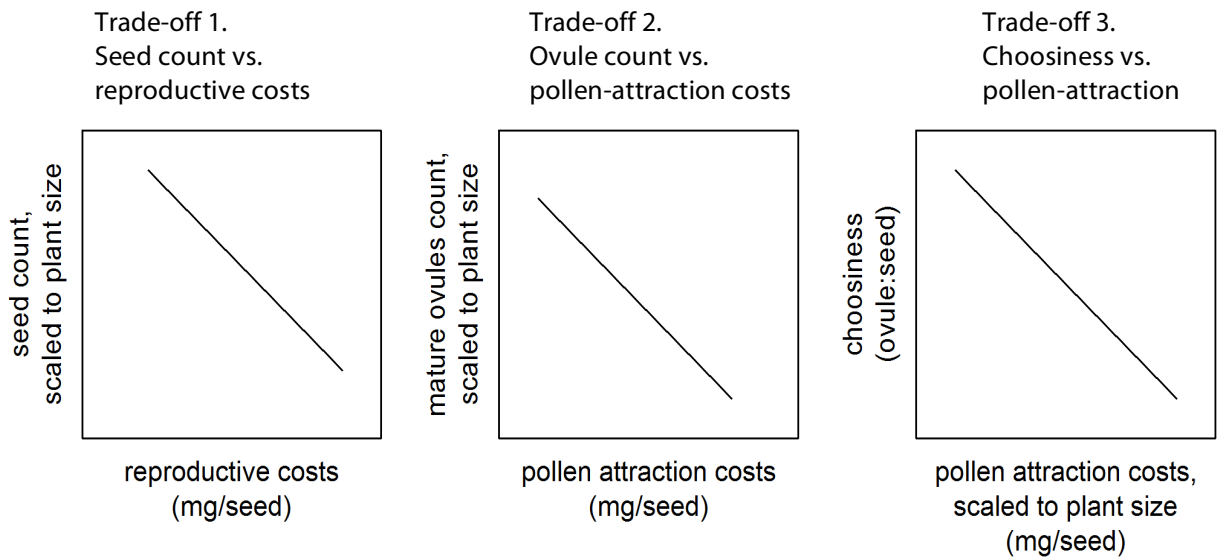
**Table 3. Correlation of different estimates of reproductive investment (and total plant weight) against total reproductive investment (mg).** Regressions are done across all individuals of all 14 study species for which both reproductive investment and the *estimate* variable are greater than zero. The total cost of failed tissues or simply the energy expenditure into flowers provides the best approximation of total reproductive investment. All fits were highly significant with  $p < 0.0001$ .

## Figures

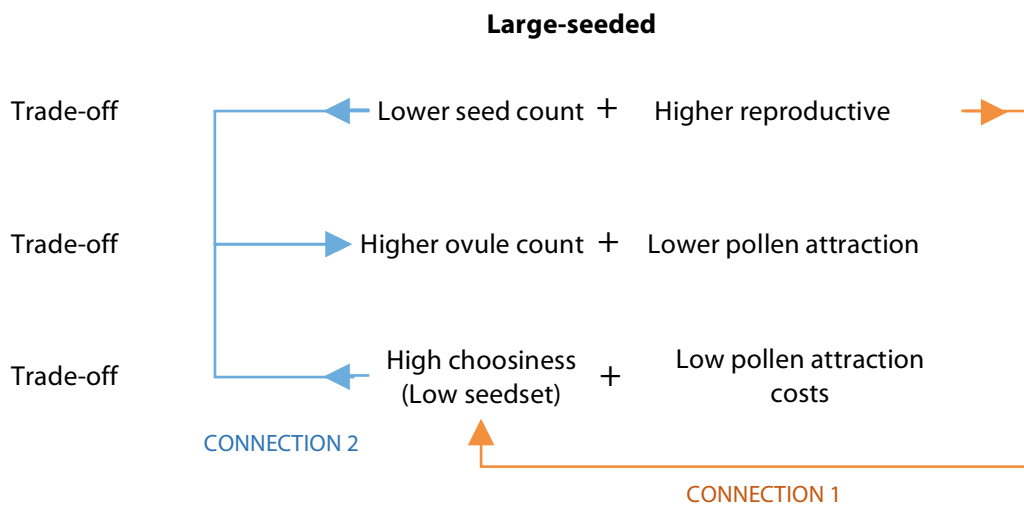
### a. Investment categories



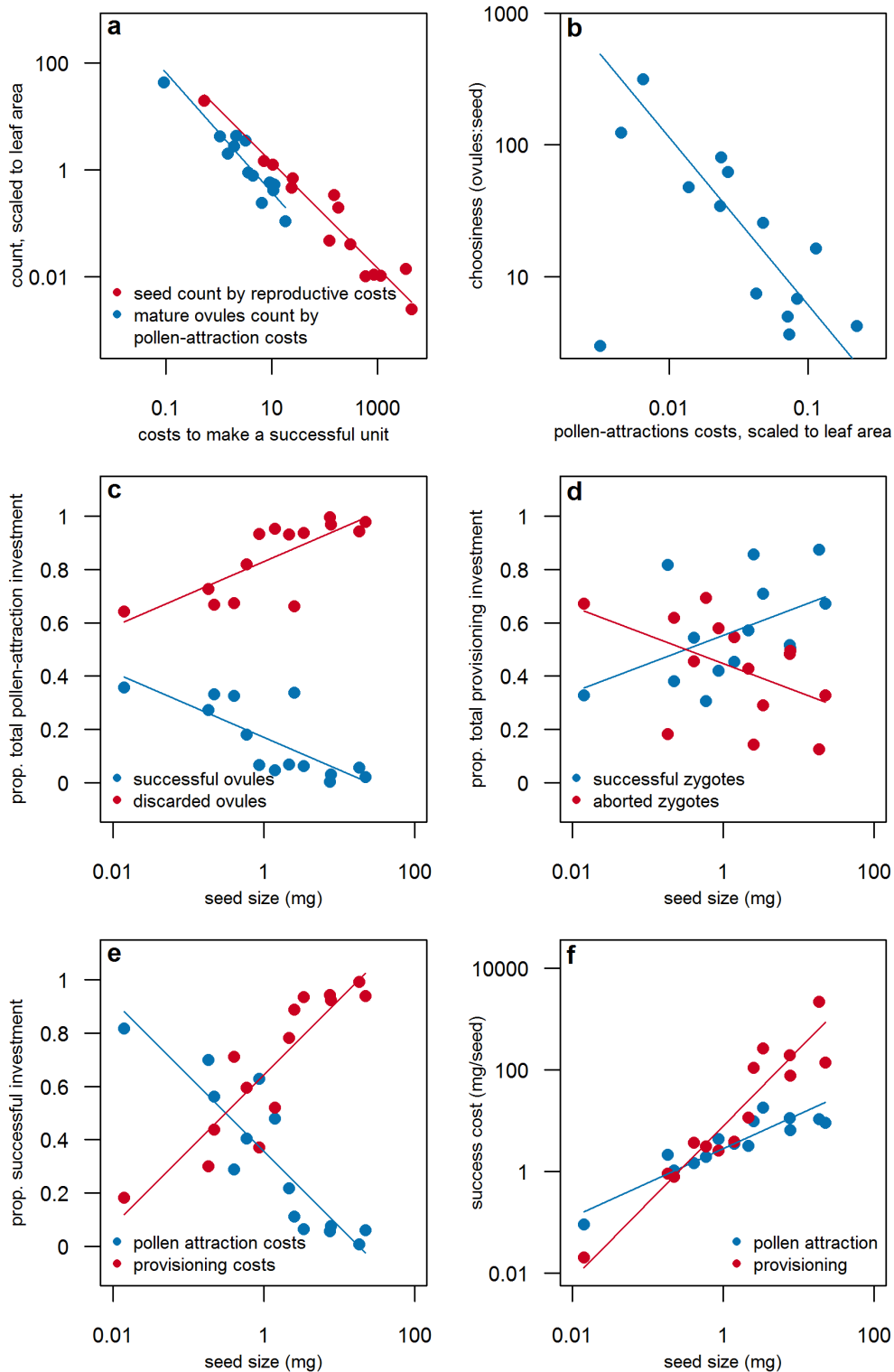
### b. Trade-offs



### c. Links between trade-offs

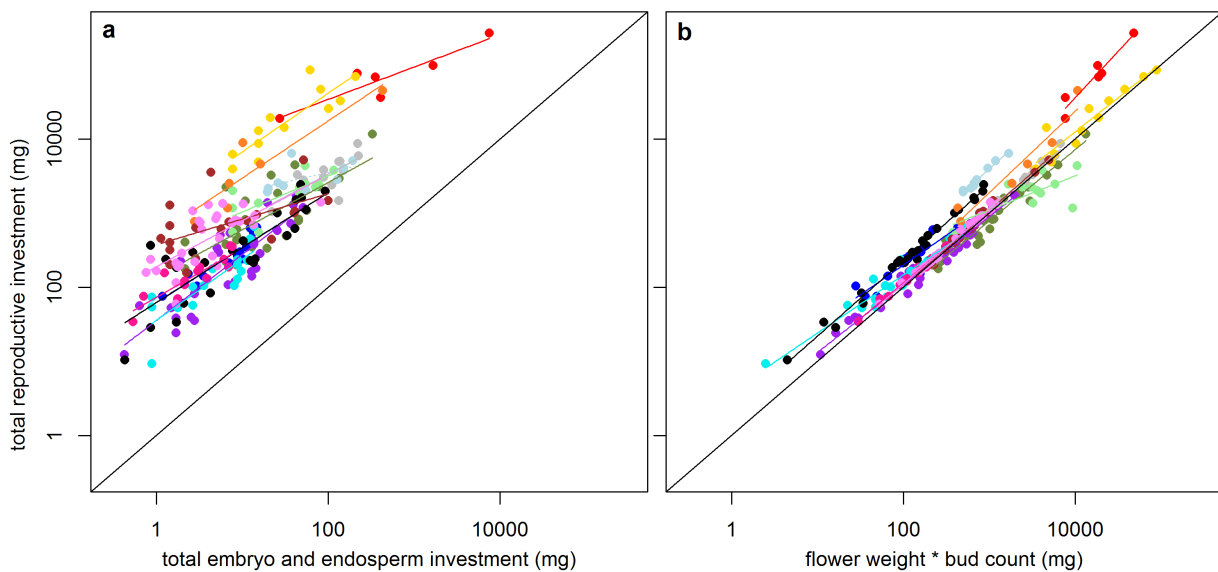


**Figure 1.** a) Categories of reproductive investment, expressed as “costs”, defined as investment divided by count of seeds matured. Categories in red are components of total accessory costs. b) Three trade-offs are predicted: Trade-off 1. For a given energy pool to be invested in total reproduction, there is a trade-off between total reproductive investment per seed produced and number of seeds produced; Trade-off 2. For a given energy pool to be invested to the point of pollination, there is a trade-off between pollen-attraction costs and the number of mature ovules produced; and Trade-off 3: A trade-off between “choosiness”, the ratio of mature ovules to mature seeds, and pollen-attraction costs, scaled to plant size, is also predicted, for a plant with more costly pollen-attraction tissues will be able to produce fewer excess ovules. c) Together, these trade-offs predict a syndrome of reproductive traits for large versus small-seeded species, for the three trade-offs are linked by natural selection and logic. Connection 1 indicates that species with high reproductive costs will also be highly selective about which ovules to mature. Connection 2 shows that a species on the low seed-count end of trade-off 1 and the high choosiness end of trade-off 3 will, by definition, have a relatively high ovule count. The figure depicts the end of each trade-off predicted for a large-seeded species. A small-seeded species is predicted to have cost and count values at the opposite end of each trade-off.





**Figure 2.** Species shift energy allocation patterns with seed size, reflecting different tissue construction costs and counts of ovules and seed produced. Each point shows average values for individuals of a species. a) The hypothesized trade-offs between pollen-attraction costs and ovule count ( $r^2=0.88$ ) and between total success costs and seed count ( $r^2=0.93$ ) both exist. b) There also exists a trade-off between pollen-attraction costs (scaled to total leaf area) and choosiness (the ratio of mature ovules to mature seeds) ( $r^2=0.76$ ). As a result of these trade-offs, the proportion of energy invested in discarded versus successful tissues and into pollen-attraction costs versus provisioning costs shifts with seed size: c) larger seeded species invest a greater proportion of their success costs into provisioning tissues; d) larger seed species invest a greater proportion of pollen-attraction investment into discarded tissues versus successful tissues; e) there is a weak trend toward larger seeded species investing a greater proportion of their provisioning investment into successful tissues versus discarded tissues. Together, these allocation differences mean that the slope of the successful pollen-attraction costs-seed size regression is significantly lower than the slope of the successful provisioning costs-seed size regression.



**Figure 3.** Embryo and endosperm investment is much more poorly correlated with total reproductive investment, than is a composite variable, the product of a count of the buds initiated multiplied by average flower weight. In each plot, different colored points represent the 14 study species; see Table 1 for the key. The colored lines are best fit lines through each species' points. There are more points in panel b, as some individuals produce buds, but no seeds. In plot b, some individual's flower weight \* bud count is higher than their total reproductive investment due to a large proportion of buds aborting prior to reaching their mature flower weight. In this plot, propagule weight, the weight of the dispersed unit, not embryo and endosperm weight are used, as the purpose is to plot the commonly used currency.