

2006

Are seed dispersal and predation in fire-sensitive *Persoonia* species (Proteaceae) associated with rarity?

Paul Rymer
University of Wollongong

Follow this and additional works at: <https://ro.uow.edu.au/scipapers>



Part of the [Life Sciences Commons](#), [Physical Sciences and Mathematics Commons](#), and the [Social and Behavioral Sciences Commons](#)

Recommended Citation

Rymer, Paul: Are seed dispersal and predation in fire-sensitive *Persoonia* species (Proteaceae) associated with rarity? 2006.
<https://ro.uow.edu.au/scipapers/4833>

Are seed dispersal and predation in fire-sensitive *Persoonia* species (Proteaceae) associated with rarity?

Abstract

Seed dispersal and predation are key processes affecting the colonization and extinction of populations in fire-prone environments. If these processes influence distribution and abundance, rare species may be expected to have less seed removal and/or greater seed predation than common congeners. I compared seed removal and predation under plants in two closely related pairs of fire-sensitive common and rare *Persoonia* species with fleshy fruits in two replicate populations of each species. Seed removal by macropods was significantly greater in the two common species (>50% seeds/plant) than in their rare congeners (<25%). There was no overall effect of rarity on seed predation by rodents, but there were significantly more seeds of the rare *Persoonia mollis* subspecies *maxima* eaten than of the other three species. Plant size was the only attribute measured that was significantly correlated with seed removal ($r = 0.50$). After including plant size as a covariate in the analysis, I still detected a significant effect of rarity on seed removal. High levels of seed removal were sustained in both small and large populations of the common *Persoonia lanceolata*, suggesting that population size may not be contributing to the differences between these common and rare species. The common-rare difference in the seed removal of *Persoonia* species seems robust across several plant and population attributes.

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

Publication Details

Rymer, P. (2006). Are seed dispersal and predation in fire-sensitive *Persoonia* species (Proteaceae) associated with rarity?. *International Journal of Plant Sciences*, 167 (6), 1151-1160.

ARE SEED DISPERSAL AND PREDATION IN FIRE-SENSITIVE *PERSOONIA* SPECIES (PROTEACEAE) ASSOCIATED WITH RARITY?

Paul D. Rymer¹

Institute for Conservation Biology, School of Biological Sciences, University of Wollongong,
Wollongong, New South Wales 2011, Australia

Seed dispersal and predation are key processes affecting the colonization and extinction of populations in fire-prone environments. If these processes influence distribution and abundance, rare species may be expected to have less seed removal and/or greater seed predation than common congeners. I compared seed removal and predation under plants in two closely related pairs of fire-sensitive common and rare *Persoonia* species with fleshy fruits in two replicate populations of each species. Seed removal by macropods was significantly greater in the two common species (>50% seeds/plant) than in their rare congeners (<25%). There was no overall effect of rarity on seed predation by rodents, but there were significantly more seeds of the rare *Persoonia mollis* subspecies *maxima* eaten than of the other three species. Plant size was the only attribute measured that was significantly correlated with seed removal ($r = 0.50$). After including plant size as a covariate in the analysis, I still detected a significant effect of rarity on seed removal. High levels of seed removal were sustained in both small and large populations of the common *Persoonia lanceolata*, suggesting that population size may not be contributing to the differences between these common and rare species. The common-rare difference in the seed removal of *Persoonia* species seems robust across several plant and population attributes.

Keywords: colonization, extinction, frugivory, plant rarity, seed dynamics.

Introduction

Processes operating on seeds (e.g., dispersal and predation) play important roles in population dynamics, particularly in landscapes dominated by disturbances (such as fire). In addition, seed dispersal is a central process in recolonization after disturbance events. Frequent fires may result in reduced populations sizes and plant densities, increased population fragmentation, and even localized extinctions in fire-sensitive plants (Bradstock et al. 1996; Keith and Tozer 1997). The persistence of populations in fire-prone habitats may be influenced by seed predation, which limits the availability of seeds for postfire recruitment (Auld and Denham 2001). The importance of seed dispersal and predation in affecting population dynamics and shaping the distribution and abundance of plants is well established (Loveless and Hamrick 1984; Cain et al. 1998; Rey and Alcántara 2000; Kameyama et al. 2001). However, few empirical studies have explored their potential role in plant rarity (Pirie et al. 2000; Simon and Hay 2003; Scott and Gross 2004).

The causes and consequences of rarity (based on geographic range size, local abundance, and degree of habitat specificity; Rabinowitz 1981) are almost certainly complex, and studies on rare taxa should be conducted at multiple spatial scales (Hartley and Kunin 2003). This is particularly important when exploring the extinction risk associated with plant rarity (IUCN 2001), given that the importance of factors influencing

colonization ability and population persistence may vary from local to regional scales (Froberg and Eriksson 1997). In interpreting impacts, it is essential to take account of both individual plant and site attributes to account for differences in animal foraging behavior (Alcántara et al. 2000). Many plant and microhabitat attributes may also affect animal foraging activity, including plant size (Alcántara et al. 2000), fruit quantity (Mittelbach and Gross 1984; Cummings and Alexander 2002), plant density (Notman et al. 1996), and vegetation cover (Manson and Stiles 1998). At a larger scale, population size is likely to affect animal foraging behavior, leading to variation in the levels of seed dispersal and predation found within and among populations (Garcia et al. 2001). The relative importance of such attributes for plant rarity must be addressed through comparative studies.

Comparisons of closely related congeners with widespread and restricted geographic distributions have been used to understand the potential causes of rarity (Kruckeberg and Rabinowitz 1985), minimizing the confounding effects of disparate phylogenetic histories (Silvertown and Dodd 1996). This study employs such a comparative approach to test whether seed removal and seed predation differ between common and rare perennial shrubs in the genus *Persoonia* (family Proteaceae). I used seed removal as a relative measure of dispersal, assuming that the majority of seeds that were removed were not destroyed and were deposited in favorable sites. To estimate seed predation, I used the number of seeds eaten (i.e., destroyed) *in situ*, which may underestimate seed predation levels. I selected two pairs of closely related taxa (hereafter referred to as species) with sharply contrasting geographic distributions, on the basis of morphological and genetic

¹ Telephone 44 (0)1865 275017; fax 44 (0)1865 275074; e-mail paul.rymer@plants.ox.ac.uk.

characters (Weston 1995, 2003) indicating that the two species in each pair are very closely related. One pair was *Persoonia mollis* R. Br. ssp. *nectens* S.L. Krauss & L.A.S. Johnson (common) and *P. mollis* ssp. *maxima* S.L. Krauss & L.A.S. Johnson (rare). The other pair was *Persoonia lanceolata* Andrews (common) and *Persoonia glaucescens* Sieber ex Spreng (rare). These species pairs have similar plant structures and gross fruit morphology (Weston 1995; Krauss 1998) and occur in comparable dry, open, sclerophyllous vegetation.

Many of the species in the plant genus *Persoonia* that are listed as threatened (Australasian Legal Information Institute 1995; Australian Government 1999) are obligate seeders occurring in fire-prone habitats, suggesting that their response to fire may have been an important influence on their current status. However, some obligate-seeding *Persoonia* species are common and widespread, so this character alone cannot explain rarity. Current geographic distributions (fig. 1) probably reflect differences between species in range contraction into refugia in the last glacial maximum and expansion thereafter (Krauss 1998). These processes are dependent on colonization and extinction events. Plants in the genus produce fleshy fruits capable of being dispersed over relatively long distances (a few kilometers) by large mammals and birds (Rose 1973; Buchanan 1980; Lane 1999; McGrath and Bass 1999). Given this, I proposed that a plausible explanation for differences in rarity among the obligate seeder species, which

rely on seed to reestablish after fire, is that they differ in the level of seed dispersal and predation.

The primary objective of this study was to explore the relationship between rarity and seed dispersal and predation and thereby test my prediction that rare species have less seed removal and/or greater seed predation than common species. Seeds removed and eaten were used as indicators of the processes of seed dispersal and seed predation, respectively. I aimed (1) to determine the proportion of seeds removed and eaten in two common and two rare *Persoonia* species and (2) to explore the association of seed dispersal and predation with plant size, fruit quantity, plant density, and vegetation cover. Population size is typically a confounding factor when comparing common and rare species; the latter often have smaller population sizes, and therefore I also used one common species (*P. lanceolata*, found in small and large populations) to investigate the potential effect of population size on seed dispersal and seed predation.

Material and Methods

Study Species

The four *Persoonia* species chosen for this study are all erect shrubs that occur in southeastern Australia (Weston 1995, 2003) and are obligate outcrossers (Rymer et al.

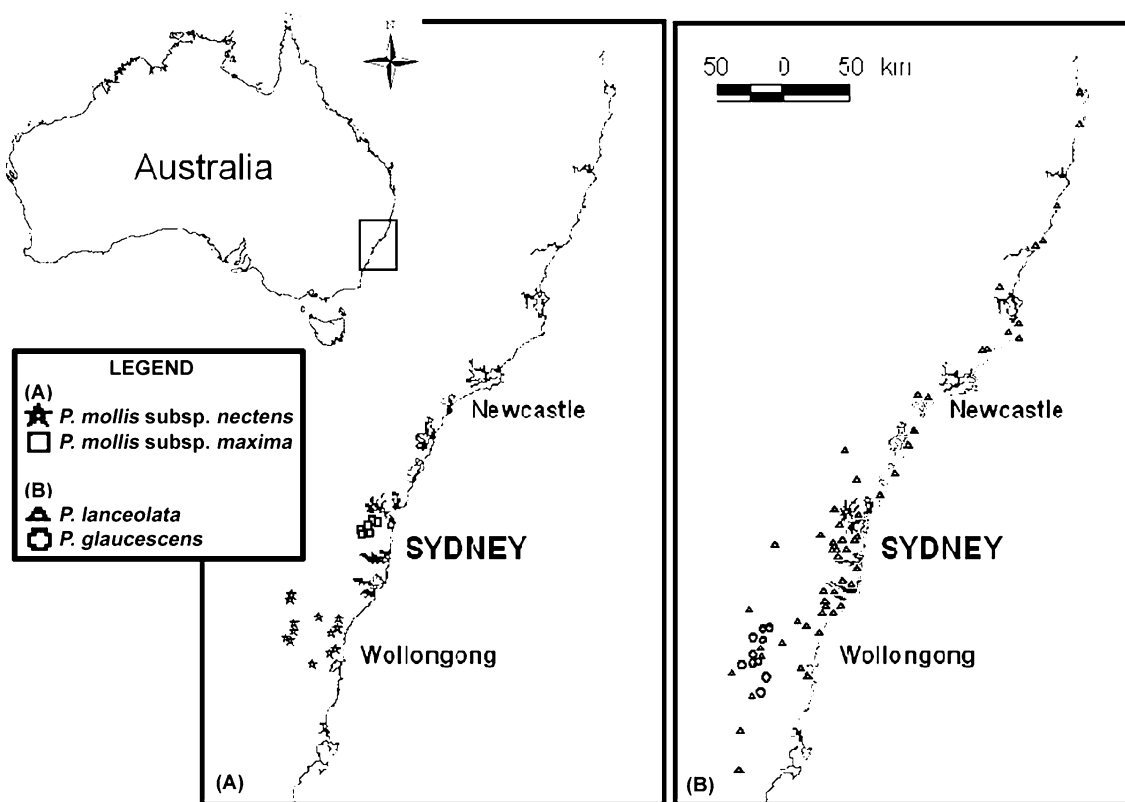


Fig. 1 Map of the Sydney region showing the geographic distributions of species pair 1 (A, *Persoonia mollis* subsp. *nectens*, *P. mollis* subsp. *maxima*) and species pair 2 (B, *Persoonia lanceolata* and *Persoonia glaucescens*). The records were compiled from the New South Wales National Herbarium.

2005). Effective pollination is provided by a solitary bee species, which provides more visits to flowers of the common species, resulting in greater reproductive success than their rare congeners (Rymer et al. 2005). *Persoonia* species produce fleshy fruits (drupes) that are variable in size and shape, maturing in late spring after a summer flowering the previous year (Weston 2003). All the *Persoonia* species investigated in this study drop their fleshy fruits to the ground after they have matured. Both species in pair 1 (*Persoonia mollis* ssp. *nectens* and ssp. *maxima*) drop fruits that are firm, round, and bright green in color. In pair 2, the fruits of *Persoonia lanceolata* are firm, elliptical, and bright green and partially red in color when they drop, while *Persoonia glaucescens* fruits are more narrow and pointed and deep red in color. The fruits of all species ripen while on the ground, becoming initially softer and darker red in color. After 2–3 wk, the flesh starts to dry and the epidermis turns black, and all fruits are dry and black after 4 wk.

I conducted a preliminary study in November 2000 to determine the timing of seed removal and predation and the potential agents responsible in sites of several *Persoonia* species (including all the study species except *P. mollis* subsp. *maxima*). Seed removal and predation are not mutually exclusive processes, and both occur predominantly between dusk and dawn. I found seed removal to be confined to the 4 wk following fruit drop before the flesh becoming dry and black. The majority of seed predation also occurred within these 4 wk, but I observed seeds to be eaten over a longer period of time (up to 11 mo or until the seeds are covered by litter/soil). Macropod marsupials (*Wallabia bicolor* and *Macropus*

rufogriseus) were the main agents of seed removal, while rodents (*Rattus fuscipes* and *Rattus rattus*) were the main seed predators (identified through fruit/seed remains, scats, and tracks). Both are common in the Sydney region (New South Wales National Parks and Wildlife Service Atlas database). Seed removal by large birds (currawongs) and seed predation by mammals (possums and wombats) cannot be excluded, but these agents left little evidence behind. Macropod scats collected within the study sites contained intact and viable *Persoonia* seeds (ranging from 0 to 8 seeds/scat during peak fruiting), confirming that they are potential seed dispersal agents rather than seed predators. The scats of rodents contain fragments of woody endocarp of *Persoonia* species, indicating that they are seed predators (Auld and Denham 1999, 2001).

Comparison of Common and Rare Species

For each of the two common and rare species, I selected two study sites in which seed removal and predation were estimated. Sites were chosen that contained relatively large populations (>100 plants) with no history of anthropogenic disturbance (>50 m from roads or any development) within the core of the distribution of each species. Because no locations were found where the study species co-occurred in large enough numbers to conduct this work, separate study sites were used for each species (table 1). Within each site, 20 fruiting plants were selected. Criteria for selection were that the canopy did not intersect with adjacent plants and that all mature fruits could be removed from the canopy, in order to control fruit numbers beneath the plant. Under each plant, five

Table 1

Location, Estimated Population Area, and Size of the Study Sites Selected for Common and Rare *Persoonia* Species

Species (rarity) and study site	Latitude, longitude ^a	Population area (ha) ^b	Population size ^c	Mean (SE)			
				Plant size (m) ^d	Fruit quantity ^e	Distance to plant (m) ^f	Vegetation cover (%) ^g
<i>Persoonia mollis</i> ssp. <i>nectens</i> (common):							
Hilltop	150°28'41"S, 34°19'48"E	40	300	2.3 (0.1) ^B	59.9 (18.1) ^{AB}	7.0 (1.1) ^{BC}	34.2 (4.0) ^{ABC}
Little River	150°30'54"S, 34°16'05"E	100	600	2.5 (0.1) ^B	107.9 (28.7) ^{AB}	3.9 (0.4) ^{AC}	30.9 (4.1) ^{ABC}
<i>Persoonia mollis</i> ssp. <i>maxima</i> (rare):							
Ku-ring-gai	151°8'02"S, 33°40'34"E	100	200	3.3 (0.2) ^C	156.1 (38.6) ^B	7.2 (1.5) ^B	14.5 (1.7) ^{AD}
Galston Creek	151°04'12"S, 33°39'21"E	30	100	2.5 (0.3) ^C	...	5.1 (0.3) ^{AC}	...
<i>Persoonia lanceolata</i> (common):							
Moore Track	151°03'34"S, 34°06'47"E	500	>1000	1.2 (0.0) ^A	50.0 (5.7) ^A	1.5 (0.2) ^A	25.9 (4.7) ^{AC}
Bundeena	151°05'60"S, 34°06'11"E	350	>1000	1.3 (0.0) ^A	57.2 (5.9) ^{AB}	1.1 (0.2) ^A	42.4 (4.4) ^{BC}
Bola Heights	151°01'41"S, 34°10'00"E	40	100	1.5 (0.0) ^A	11.0 (2.8) ^A	6.1 (1.4) ^{AC}	51.6 (5.9) ^{BC}
Ulloola Track	151°01'30"S, 34°07'28"E	35	50	1.5 (0.1) ^A	28.3 (2.9) ^A	5.3 (0.9) ^{AC}	39.1 (4.0) ^{BC}
<i>Persoonia glaucescens</i> (rare):							
Braemar	150°28'26"S, 34°25'05"E	80	400	2.4 (0.1) ^B	157.5 (34.0) ^B	2.6 (0.3) ^A	20.3 (2.7) ^{AC}
Buxton	150°30'54"S, 34°15'07"E	35	100	2.0 (0.3) ^B	...	3.1 (0.4) ^A	...

Note. Including the mean plant and microhabitat attributes ($n = 40$ plants) at each site. Ellipses indicate missing values. Sites statistically different from each other do not share the same letter (Tukey's test, $\alpha = 0.05$).

^a Based on GPS position using datum WGS1984.

^b Estimated area based on vegetation maps and field observations.

^c Estimated number of flowering individuals per population.

^d Plant height.

^e Number of fruits under the plant canopy.

^f Distance to nearest flowering plants.

^g Percentage ground cover under the plant canopy.

fruit caches of 10 mature fruits (confined within a 0.1-m diameter PVC ring partially pushed into the ground, with 1 cm protruding from the ground) were established in November 2001, representing fruit densities and patchy distributions similar to those naturally found under relatively large reproductive plants (ranging from 10 ± 6 seeds/0.31 m² for the common species to 6 ± 5 seeds/0.31 m² during peak fruiting).

I revisited individual caches of fruits every week for 4 wk. I searched the area within the ring and its immediate surroundings (~20-cm radius) for intact seeds, evidence of fruit/seed remains, and animal scats, tracks, and diggings. Seeds remaining intact were recorded as remaining, and seeds that were cracked or chewed open with the embryo missing were recorded as being eaten. Seeds that could not be relocated after 4 wk were recorded as being removed. Seed removal and predation were estimated as the number of seeds missing and eaten, expressed as a proportion of the number of seeds initially placed in each cache and a proportion of seeds remaining after removal, respectively (thereby making these factors independent and uncorrelated, $R = 0.09$).

I used a multifactor mixed-model ANOVA (performed in MINITAB, ver. 13.1) to test the hypothesis that seed removal and predation differed between common and rare species. The ANOVA was constructed with rarity (common and rare) and pair (species pairs 1 and 2) as fixed factors. The two sites were used as replicates for each pair \times rarity combination (two sites/combination \times four combinations = eight sites). Site and plant were nested factors, with site being nested within the pair \times rarity combination and plant being nested within site (within (pair, rarity)). Because the raw data were expressed as proportions, I transformed them using an angular transformation to conform to the distributional assumptions of the analysis (Zar 1999). Tukey's post hoc HSD test was used to determine which combinations were significantly different in seed removal and predation. The α level was corrected for multiple comparisons using a Bonferroni correction (Underwood 1997). The levels of seed removal and predation was compared between years for those sites that were used in the pilot study (*P. mollis* ssp. *nectens* site 1, *P. lanceolata* sites 5 and 6, *P. glaucescens* site 7) to determine the level of temporal variation using a two-way ANOVA (with site and year as factors).

Plant Size, Fruit Quantity, Plant Density, and Vegetation Cover

For the plants monitored for seed removal and predation in 2001, I recorded several plant and microhabitat attributes, except for plants at two sites (Galston Creek and Buxton; see table 1) where only plant size was measured because of time constraints. I made the following measurements: plant size (height, width at widest point, perpendicular width, and basal diameter at ground level), fruit quantity (the number of fruits under the plant canopy), local plant density (distance to nearest *Persoonia* plant and number of *Persoonia* plants <5 m away), and vegetation cover (percent ground cover under plant canopy, recorded as 12%, 25%, 37%, 50%, 62%, 75%, 87%, and 100%).

I used a multiple regression to test whether seed removal and predation were related to any of these variables (plant size, fruit quantity, plant density, and vegetation cover). For

variables that were highly correlated with each other, one was selected on the basis of biological interpretation (i.e., for plant size, volume was included and basal diameter was omitted to simplify the analysis; $r^2_{\text{adj}} = 0.643$). Variables that produced a relationship significant at $\alpha = 0.05$ were used in a regression model, and the linear relationship is reported. These variables were then used as covariates in further analyses. I performed separate regressions for common and rare species using the variables that were significant in the model that used all four rarity \times pair combinations.

I used an ANCOVA to test whether the covariates accounted for any potential differences in the main factors (rarity and pair). In addition, the number of seeds removed under a plant was significantly correlated with the number of seeds eaten ($n = 154$, $r = 0.35$, $P = 0.001$). Consequently, I also included the proportion of seeds eaten as a covariate in the ANCOVA on seed removal (and vice versa). An ANCOVA was performed with the covariate preceding the main factors in the model statement (covariate, pair, rarity, covariate \times pair, covariate \times rarity, pair \times rarity, covariate \times pair \times rarity, site) using a Type I (sequential) sum of squares. None of the interaction terms between the main factors and the eaten covariate were close to significant ($P > 0.45$), so to simplify the removal ANCOVA, I have removed them from the final analysis. Some plants could not be measured for all the covariates during the field season, resulting in unequal numbers of plants at the various sites in the ANCOVA, which complicates the analyses. In the F ratios, the denominator is a linear combination of several mean squares, and its degree of freedom is not an integer.

Effect of Population Size

To explore the potential effect of population size, which usually differs between the common and rare species (table 1), I tested whether levels of seed removal and predation varied between large and small populations in the common *P. lanceolata*. Using the experimental setup described above, I established two additional sites comprising small populations of plants (Bola Heights and Ulloola Track; equivalent in size to populations of the rare *P. glaucescens*) to compare with the large populations at Moore Track and Bundeena. I determined the size of populations on the basis of the size of the vegetation unit (Sandstone Heath) with which *P. lanceolata* is associated (D. A. Keith, unpublished data) and field observations. All four *P. lanceolata* sites are located within Royal National Park and are separated by areas of relatively undisturbed natural bushland.

I used an ANOVA to test for differences in seed removal and predation between small and large populations of *P. lanceolata*. Population size was fixed, and site was a nested random blocking factor. Plant (nested within site) was a random factor. Because the raw data were expressed as proportions, I transformed them using an angular transformation to conform to the distributional assumptions of the analysis (Zar 1999).

Results

Comparison of Common and Rare Species

More than 50% of the seeds were removed from all sites for the common species, while sites for the rare species had less than 25% removed. Seed removal varied between sites of

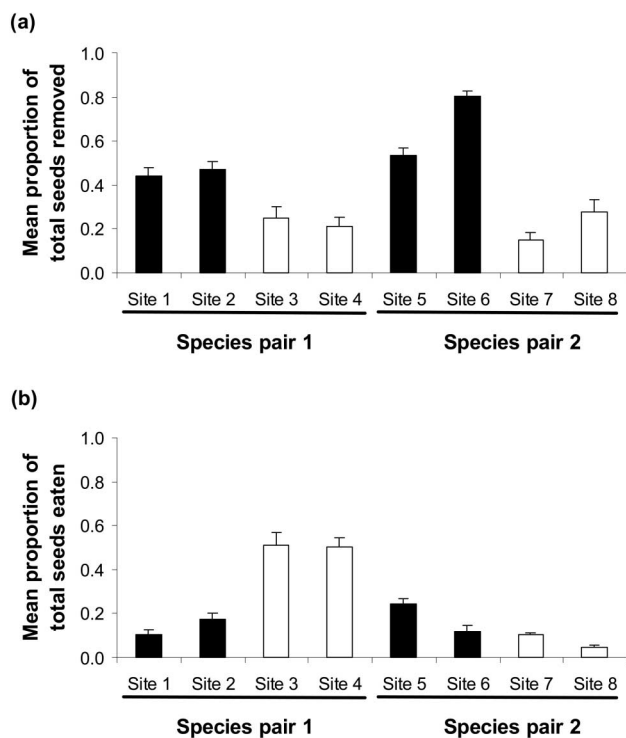


Fig. 2 Mean proportion of seeds removed (a) and eaten (b) in caches under adult plants after 4 wk, across replicate sites from two pairs of common and rare *Persoonia* species. *Persoonia mollis* ssp. *nectens* = sites 1 and 2, *Persoonia mollis* ssp. *maxima* = sites 3 and 4, *Persoonia lanceolata* = sites 5 and 6, and *Persoonia glaucescens* = sites 7 and 8. Filled bars represent the common species, and open bars represent the rare species.

both common and rare species (fig. 2a). The two common species had significantly more seeds removed from under plants after 4 wk than their rare congeners (rarity $F_{1,4} = 13.92$, $P = 0.020$; table 2). This pattern was consistent for both species pairs.

Pair and rarity effects on seed predation depended on each other, indicating that the rarity of the species did not consistently determine seed predation levels (pair \times rarity $F_{1,4} = 80.47$, $P = 0.001$; table 2). Overall, the percentage of seeds eaten after 4 wk was similar for common and rare

species (mean \pm SE = $38\% \pm 8\%$ and $38\% \pm 16\%$, respectively), but this varied within each pair and within each rarity category (fig. 2b). A post hoc comparison (at an overall level of significance of 0.001) of seed predation found that *Persoonia mollis* ssp. *maxima* (50%–51%) had more seeds eaten than the other three species. *Persoonia mollis* ssp. *nectens* (10%–17%) had levels of seed predation similar to those for *Persoonia lanceolata* and *Persoonia glaucescens*, but *P. glaucescens* (5%–10%) had significantly fewer seeds eaten than *P. lanceolata* (12%–24%).

These patterns of seed removal and predation were consistent between years, on the basis of a subset of sites explored in the pilot study (one site of *P. mollis* ssp. *nectens* and *P. glaucescens*, and two sites of *P. lanceolata*). Differences between species and sites were greater than those observed between consecutive years ($df = 1$, $P > 0.25$) (fig. 3).

Plant Size, Fruit Quantity, Plant Density, and Vegetation Cover

The multiple-regression analysis revealed that only plant size was correlated with seed removal, and none of the other attributes measured were significantly associated with either seed removal or predation (including fruit quantity, plant density, and vegetation cover). The proportion of seeds removed was significantly correlated with plant height ($n = 153$, $r = -0.38$, $P < 0.001$) (fig. 4), but the linear relationship only explained a small proportion of the total variation across all species ($r^2_{\text{adj}} = 0.189$). Slightly more variation was explained in the common species ($r^2_{\text{adj}} = 0.229$), but there was no relationship in the rare species ($r^2_{\text{adj}} = 0.004$) (fig. 4). The common species were on average shorter and had greater seed removal than their rare relatives (table 3).

Plant height had some value in predicting seed removal within a site and species (plant height was squared to account for nonlinearity) (ANCOVA $F_{1,4.9} = 9.27$, $P = 0.029$). However, even when plant height was accounted for in the ANCOVA, plant rarity remained a significant factor ($F_{1,4.5} = 28.40$, $P = 0.004$; table 4).

Seed predation was not associated with any of the site and plant variables measured (plant size, fruit quantity, plant density, and vegetation cover); however, it was significantly correlated with the number of seeds removed ($n = 154$, $r = 0.35$, $P = 0.001$). Including seed removal as a covariate in the analysis testing the effect of species pair and plant rarity on

Table 2

Mixed-Model ANOVA

Source	df	Seed removal			Seed predation		
		Adjusted MS	F	P	Adjusted MS	F	P
Pair	1	2307.2	1.76	0.255	3616.5	9.48	0.037
Rarity	1	18,263.7	13.92	0.020	0.1	0.00	0.988
Pair \times rarity	1	2908.8	2.22	0.211	30,695.3	80.47	0.001
Site (pair, rarity)	4	1313.1	9.33	0.001	381.6	1.77	0.138
Error	146	140.7			215.4		

Note. Data for a comparison of the proportion of seeds removed and eaten from experimental caches under adult plants after 4 wk in closely related (pair) common and rare species (rarity) across populations (site). Removal data = $\arcsin[(\text{seeds removed}/\text{total seeds})^{1/2}]$. Predation data = $\arcsin\{[\text{seeds eaten}/(\text{total seeds} - \text{seeds removed})]^{1/2}\}$. Site was a nested random factor. To calculate the F values, the adjusted MS for pair, rarity, and pair \times rarity was divided by MS(site), while site was divided by MS(error). Statistically significant P values are underlined.

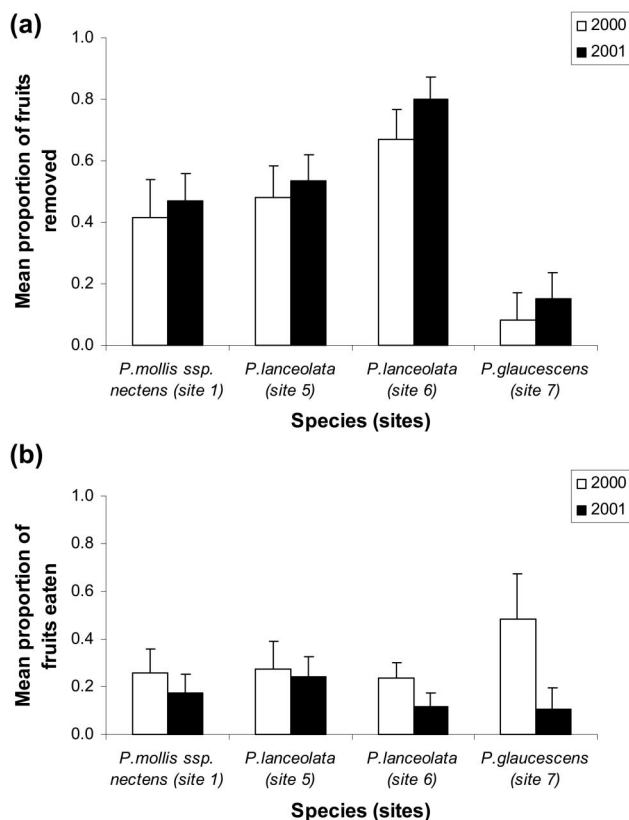


Fig. 3 Mean proportion of seeds removed (a) and eaten (b) in caches under adult plants after 4 wk, across years for sites of *Persoonia* species.

seed predation did not alter the original analysis (ANCOVA pair $F_{1,6.7} = 18.94$, $P = 0.013$; pair \times rarity $F_{1,6.7} = 129.04$, $P = 0.001$). However, when the interaction terms with removal were included in the analysis, species pair became marginally insignificant ($F_{1,3.6} = 7.88$, $P = 0.055$), and the pair \times removal term ($F_{1,7.7} = 32.25$, $P = 0.001$) and the site term ($F_{1,142} = 2.57$, $P = 0.041$) both became significant, along with pair \times rarity ($F_{1,4.7} = 38.67$, $P = 0.002$).

Effect of Population Size

The proportions of seeds removed under *P. lanceolata* plants were similar in large ($54\% \pm 8\%$, $80\% \pm 7\%$) and small populations ($66\% \pm 9\%$, $76\% \pm 8\%$) ($F_{1,4} = 21.29$, $P = 0.804$; table 5). Similar levels of seed predation were found in large ($24\% \pm 8\%$, $12\% \pm 8\%$) and small ($26\% \pm 9\%$, $16\% \pm 8\%$) populations ($F_{1,4} = 8.23$, $P = 0.103$; table 5). Seed removal showed variation between sites of both large and small populations (fig. 5).

Discussion

This comparative study explored the association between seed dispersal and predation in plant rarity using two pairs of closely related common and rare species. This allowed me to test my prediction that rare species have lower levels of seed dispersal and/or greater seed predation than common species, potentially explaining the different levels of rarity

(Gaston and Kunin 1997). I found that common *Persoonia* species had more than twice as many seeds removed (and therefore potentially dispersed) than their rare relatives in both species pairs (fig. 2a), supporting my prediction. These differences between sites were consistent between years, on the basis of a subset of sites explored in the pilot study (fig. 3a). In addition, this pattern of dispersal confirms the results of a genetic analysis indicating that common *Persoonia* species have greater levels of gene flow between populations (Rymer and Ayre, forthcoming). Plant size and population size differ between common and rare species, potentially confounding this comparison; nevertheless, rarity still had a significant effect on seed removal even when these attributes were accounted for in the analysis. Furthermore, the common *Persoonia* species studied here have been found to have greater reproductive success than their rare congeners (Rymer et al. 2005), indicating that the proportion of the total fruits produced being dispersed will be much greater for the common species. Seed predation, on the other hand, was not related to rarity or to any of the plant and microhabitat attributes measured, and it appeared to be unaffected by population size. There was, however, significantly more seed predation in the rare *Persoonia mollis* ssp. *maxima* than in its common relative (*Persoonia mollis* ssp. *nectens*) (fig. 2b), but the other species pair did not fit with my prediction. These findings have implications for plant rarity.

The Spatial Scale of Foraging Animals

Animal foraging behavior may vary at different spatial scales (Kollmann 2000), depending on a range of plant and site characteristics. I found that seed removal by large mammals (macropods) and seed predation by small mammals (rodents) varied significantly between sites. The plant-scale attributes measured here may not explain the variation between sites. Although plant size was associated with seed removal, it explained a relatively small proportion of the total variation. Plant size is often thought of as a surrogate for fecundity,

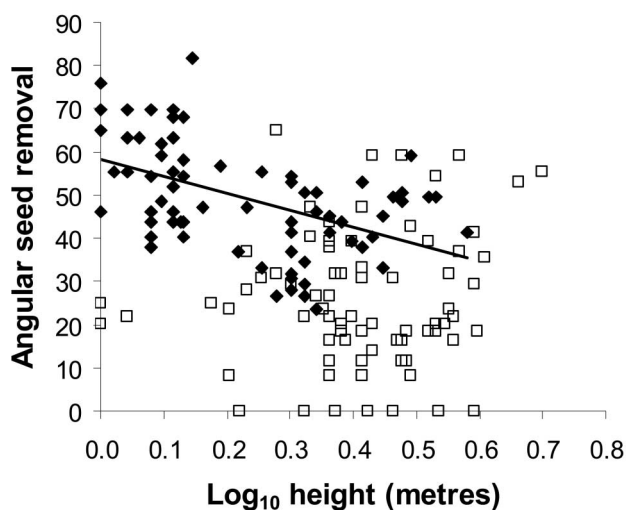


Fig. 4 Relationship between seed removal and plant height in common (diamonds) and rare (squares) *Persoonia* species. The solid line represents the line of best fit for the common species ($y = -39.181x + 58.181$; $r^2_{\text{adj}} = 0.229$).

Table 3

Mean (SE) Seed Removal and Plant Height of the Two Pairs of Closely Related Common and Rare *Persoonia* Species

Pair and rarity	<i>n</i>	Seed removal	Plant height (m)
1:			
Common	37	0.45 (0.03)	2.42 (0.04)
Rare	39	0.24 (0.03)	3.17 (0.01)
2:			
Common	40	0.67 (0.03)	1.25 (0.03)
Rare	38	0.22 (0.03)	2.23 (0.03)

Note. Seed removal indicates proportion of seeds removed.

which has been found to have a strong relationship with seed removal and predation (Casper 1988; Herrera et al. 1994; Delgado Garcia 2002), with an obvious link to animal foraging behavior. The weak relationship of increasing plant size associated with decreasing seed removal in common species (fig. 4) may reflect satiation of seed removal agents in larger plants, if such larger plants have larger fruit crops. In this study, individual plant fecundity and local plant density were not related to seed dispersal and predation, but mammals may be responding to these factors at a larger spatial scale (i.e., site or populations). I found no effect of population size on seed removal or predation in the common *Persoonia lanceolata* within a relatively continuous natural landscape. While the small populations selected were of equivalent size to those of the rare relative of this common species (*Persoonia glaucescens* found in fragmented agricultural landscapes), differences in habitat connectivity and the quality of the surrounding matrix may have consequences for seed dispersal and predation (Guariguata et al. 2000; Hewitt and Kellman 2002). Future research needs to link mammal foraging behavior to landscape and local-scale attributes to gain a better understanding of the underlying mechanisms influencing the variation in seed dispersal and predation.

Common-Rare Differences

Seed dispersal and predation are important factors influencing colonization and extinction events, thus potentially determining the distribution and abundance of species. Rela-

tively few studies have explored the role of seed dispersal and predation in plant rarity. A small number of well-replicated comparative studies using groups of unrelated species have failed to find any relationship between dispersal mode and geographic range (Kelly and Woodward 1996; Hegde and Ellstrand 1999; Murray et al. 2002), suggesting that dispersal mode alone cannot explain rarity. Studies looking at closely related species with similar dispersal modes have had mixed results. Pirie et al. (2000), for example, found that seed removal and predation by rodents did not differ between a congeneric widespread and endemic species pair (after accounting for differences in seed availability), whereas Scott and Gross (2004) found lower seed predation by ants (when mammals were excluded) in a common species than in its rare congener. While these studies may minimize potentially confounding differences by using related species (Silvertown and Dodd 1996), they lack spatial replication and only investigate a single species pair. A review of the literature was unsuccessful in finding other comparative studies exploring this relationship, and my study may be the first to use replicated common-rare comparisons (two pairs of closely related species), with some spatial replication (two populations) for each species. Clearly, more research with adequate replication is required to test the generality of the potential relationship found here between plant rarity and seed dispersal for fleshy-fruited plants.

Effect of Dispersal on Rarity

Where populations are prone to extinction through disturbance (e.g., frequent fire), species with a high capacity to recolonize areas would be expected to cover a greater proportion of the landscape (e.g., Froberg and Eriksson 1997). Fire is a major disturbance in many habitats throughout the world (Whelan 1995) and is particularly regular in the fire-prone sclerophyllous vegetation on the east coast of Australia. In this landscape, populations of fire-sensitive plants are vulnerable to extinction (Bradstock et al. 1996; Keith and Tozer 1997) and may contract into fire refuges (i.e., areas with more optimal fire frequencies) during periods of persistently frequent fires. These fire refuges may provide a source of seed

Table 4

Mixed-Model ANCOVA

Source	df	Adjusted MS	<i>F</i>	<i>P</i>	Sequential MS	<i>F</i>	<i>P</i>
Eaten	1	19.1	0.12	0.726	213.6	0.38	0.567
Height ²	1	0.2	0.00	0.968	5228.6	9.27	<u>0.029</u>
Pair	1	700.1	3.07	0.093	77.6	0.11	0.756
Rarity	1	4332.8	18.73	<u>0.001</u>	18,555.3	28.4	<u>0.004</u>
Pair × height ²	1	125.2	0.81	0.370	962.1	2.92	0.121
Rarity × height ²	1	201.7	1.30	0.255	253.0	1.00	0.332
Pair × rarity	1	774.2	3.40	0.078	380.3	1.11	0.320
Pair × rarity × height ²	1	218.8	1.42	0.236	938.3	3.69	0.072
Site (pair, rarity)	4	809.9	5.24	<u>0.001</u>	809.9	5.24	<u>0.001</u>
Error	141	154.6			154.6		

Note. Data for a comparison of the proportion of seeds removed from experimental caches under adult plants after 4 wk in closely related (pair) common and rare species (rarity) across populations (site), accounting for seed predation (eaten = $\arcsin \{[\text{seeds eaten}/(\text{total seeds} - \text{seeds removed})]^{1/2}\}$) and plant size (height²). Removal data = $\arcsin [(\text{seeds removed}/\text{total seeds})^{1/2}]$. Site was a nested random factor. The adjusted MS and the sequential MS were both used to estimate the effect of including the covariates in the analysis. Statistically significant *P* values are underlined.

Table 5
Mixed-Model ANOVA

Source	df	SS	Seed removal			Seed predation		
			Adjusted MS	F	P	Adjusted MS	F	P
Size	1	0.0316	0.0316	0.08	0.8041	0.6734	8.23	0.1031
Site (size)	2	0.7916	0.3958	21.29	<u>0.0001</u>	0.0819	1.18	0.3132
Error	76	1.4129	0.0186			0.6945		

Note. Data for a comparison of the proportion of seeds removed and eaten from experimental caches under adult plants after 4 wk between large and small populations (size), with replicate sites for *Persoonia lanceolata*. Removal data = $\arcsin[(\text{seeds removed}/\text{total seeds})^{1/2}]$. Predation data = $\arcsin\{[\text{seeds eaten}/(\text{total seeds} - \text{seeds removed})]^{1/2}\}$. The site factor was set as a random effect. To calculate the *F* values, the adjusted MS for size was divided by adjusted MS(site), while site was divided by adjusted MS(error). Statistically significant *P* value is underlined.

to recolonize areas during more optimal conditions, but refuge areas may move around the landscape over time (Keith and Tozer 1997). Thus, the persistence of populations in fire-prone landscapes may be dependent on the species colonization ability. Assuming that fruit removal is positively correlated with colonization ability (Valverde and Silvertown 1997), the higher levels of fruit removal found in common *Persoonia* species compared with rare *Persoonia* species (fig. 2) could explain the different geographic distributions and local abundances observed in these fire-sensitive species within this fire-prone landscape. To test this hypothesis, it would be necessary to determine whether increasing fruit removal increases the probability of reaching a suitable site.

Effect of Predation on Rarity

Seed predation limits the availability of seeds for postfire recruitment (Auld and Denham 2001) and therefore influences the persistence of populations in fire-prone landscapes (Regan et al. 2003). I found seed predation to vary between species, with no consistent pattern between common and rare species. The high level of seed predation I found in the rare *P. mollis* ssp. *maxima* may limit the number of seeds contributing to the soil-stored seed bank (<50% seeds). The other three species had a similar predicted contribution to the seed bank (75%–95% combining seeds removed and those remaining under plants) but different proportions of seeds found under (local) plant canopies and dispersed (away) from parents. In fact, the number of seeds available to contribute to the local seed bank was greater for the rare *P. glaucescens* than for the other three species (where *P. mollis* ssp. *nectens* > [*P. mollis* ssp. *maxima* ≈ *P. lanceolata*]). This has implications for the ability of species to persist under different fire regimes; however, the response of the soil seed bank to different fires is poorly understood (Edwards and Whelan 1995; Regan et al. 2003), and this complexity requires further investigation.

Conclusion

These results indicate that seed dispersal is limited in rare fire-sensitive *Persoonia* species, but without an understanding of the fate of seeds, it is difficult to quantify differences in the colonization ability between common and rare species. Documenting long-distance dispersal events is not easy through traditional ecological methods (tracking the movements of dispersal agents and collecting dispersed seeds in the landscape), but it may be possible through the combination of molecular markers with detailed field studies. For ob-

ligate seeders, there is a direct link between seed predation and the availability of seeds for postfire recruitment, but the complexity of persistent soil-stored seed banks (where residual seeds remain viable through consecutive fires) creates uncertainty in predictions for the persistence of populations. This is further complicated by the high degree of spatial and

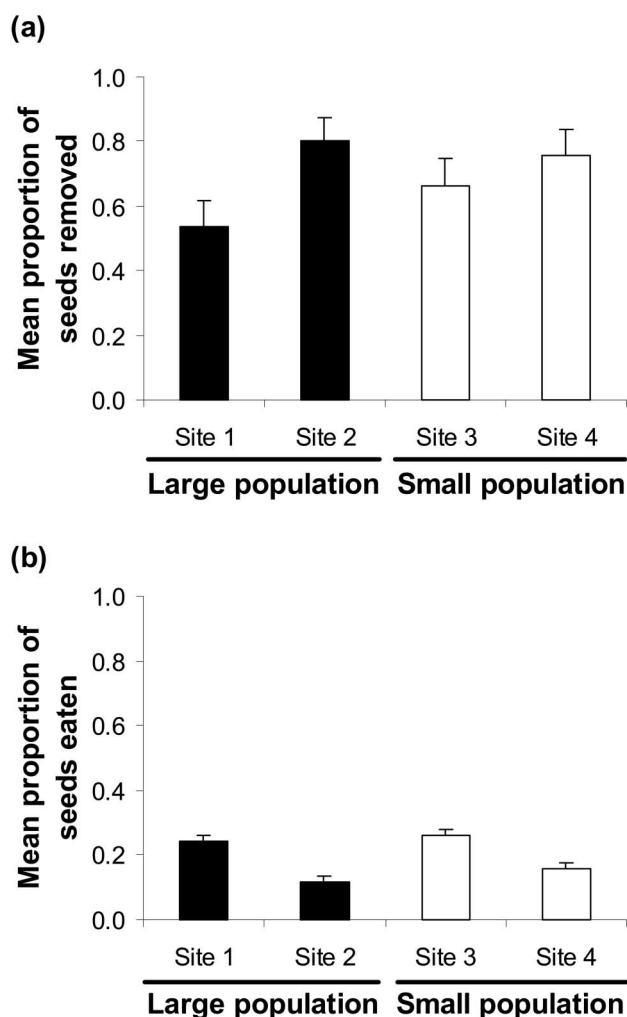


Fig. 5 Mean proportion of seeds removed (a) and eaten (b) in caches under adult plants after 4 wk, across replicate sites from large and small populations of *Persoonia lanceolata*. Filled bars show the large populations, and open bars show the small populations.

temporal variability in wildfires. Incorporating seed dispersal and predation into a metapopulation framework (through ecological modeling) may provide further insights into the relative importance of colonization and extinction events for plant rarity.

Acknowledgments

This project was supported by an Australian Research Council linkage grant to Robert J. Whelan and David J. Ayre (C00001913), with logistical and financial assistance

provided by the Department for Environment and Conservation (National Parks and Wildlife Service and Botanic Gardens Trust divisions). I thank members of the University of Wollongong for help with the field studies, especially David McKenna. Associate Professor Ken Russell (University of Wollongong, Statistical Consulting Service) provided assistance with the statistical analysis. This manuscript has been improved by the input of Tony D. Auld, Rob J. Whelan, and David J. Ayre. I conducted this work under the specifications of a section 91 license to pick/collect threatened species and a scientific license to work in National Parks (B2199).

Literature Cited

- Alcántara JM, PJ Rey, AM Sánchez-Lafuente, F Valera 2000 Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. *Oikos* 88:362–370.
- Auld TD, AJ Denham 1999 The role of ants and mammals in dispersal and post-dispersal seed predation of the shrubs *Grevillea* (Proteaceae). *Plant Ecol* 144:201–213.
- 2001 The impact of seed predation by mammals on post-fire seed accumulation in the endangered shrub *Grevillea caleyi* (Proteaceae). *Biol Conserv* 97:377–385.
- Australasian Legal Information Institute 1995 Threatened Species Conservation Act. Australasian Legal Information Institute, Sydney. http://www.austlii.edu.au/au/legis/nsw/consol_act/tsc1995323/.
- Australian Government 1999 Environment Protection and Biodiversity Conservation Act. Attorney-General's Department, Australian Government, Canberra. <http://www.comlaw.gov.au/ComLaw/Legislation/ActCompilation1.nsf/frameLodgmentAttachments/5991C484A23587F2CA2571540002B9A5?OpenDocument>.
- Bradstock RA, M Bedward, J Scott, DA Keith 1996 Simulation of the effect of spatial and temporal variation in fire regimes on the population viability of a *Banksia* species. *Conserv Biol* 10:776–784.
- Buchanan RA 1980 The Lambert Peninsula Ku-ring-gai Chase National Park Australia: physiography and the distribution of podzols shrublands and swamps with details of the swamp vegetation and sediments. *Proc Linn Soc N S W* 104:73–94.
- Cain ML, H Damman, H Muir 1998 Seed dispersal and the holocene migration of woodland herbs. *Ecol Monogr* 68:325–347.
- Casper BB 1988 Post-dispersal seed predation may select for wind dispersal but not seed number per dispersal unit in *Cryptantha flava*. *Oikos* 52:27–30.
- Cummings CL, HM Alexander 2002 Population ecology of wild sunflowers: effects of seed density and post-dispersal vertebrate seed predators. *Oecologia* 130:274–280.
- Delgado Garcia JD 2002 Interaction between introduced rats and a frugivore bird-plant system in a relict island forest. *J Nat Hist* 36: 1247–1258.
- Edwards W, R Whelan 1995 The size, distribution and germination requirements of the soil-stored seed-bank of *Grevillea barklyana* (Proteaceae). *Aust J Ecol* 20:548–555.
- Froberg H, O Eriksson 1997 Local colonization and extinction of field layer plants in a deciduous forest and their dependence upon life history features. *J Veg Sci* 8:395–400.
- Garcia D, R Zamora, JM Gomez, JA Hódar 2001 Frugivory at *Juniperus communis* depends more on population characteristics than on individual attributes. *J Ecol* 89:639–647.
- Gaston KJ, WE Kunin 1997 Rare-common differences: an overview. Pages 12–29 in WE Kunin, KJ Gaston, eds. *The biology of rarity: causes and consequences of rare-common differences*. Chapman & Hall, London.
- Guariguata MR, JJ Rosales Adame, B Finegan 2000 Seed removal and fate in two selectively logged lowland forests with contrasting protection levels. *Conserv Biol* 14:1046–1054.
- Hartley S, WE Kunin 2003 Scale dependency of rarity, extinction risk, and conservation priority. *Conserv Biol* 17:1559–1570.
- Hegde SG, NC Ellstrand 1999 Life history differences between rare and common flowering plant species of California and the British Isles. *Int J Plant Sci* 160:1083–1091.
- Herrera CM, P Jordano, L Lopez-Soria, JA Amat 1994 Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecol Monogr* 64:315–344.
- Hewitt N, M Kellman 2002 Tree seed dispersal among forest fragments. II. Dispersal abilities and biogeographical controls. *J Biogeogr* 29:351–363.
- IUCN 2001 IUCN Red List of Threatened Species. <http://www.iucnredlist.org>.
- Kameyama Y, Y Isagi, N Nakagoshi 2001 Patterns and levels of gene flow in *Rhododendron metternichii* var. *hondoense* revealed by microsatellite analysis. *Mol Ecol* 10:205–216.
- Keith DA, MG Tozer 1997 Experimental design and resource requirements for monitoring flora in relation to fire. Pages 274–279 in BJ McKaige, RJ Williams, WM Waggitt, eds. *Bushfire '97. Proceedings of the Australian Bushfire Conference*. CSIRO, Darwin.
- Kelly CK, FI Woodward 1996 Ecological correlates of plant range size: taxonomies and phylogenies in the study of plant commonness and rarity in Great Britain. *Philos Trans R Soc B Biol Sci* 351: 1261–1269.
- Kollmann J 2000 Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspect Plant Ecol Evol Syst* 3:29–51.
- Krauss SL 1998 A phylogeographic analysis of allozyme variation among populations of *Persoonia mollis* (Proteaceae). *Aust J Bot* 46: 571–582.
- Kruckeberg A, D Rabinowitz 1985 Biological aspects of endemism in higher plants. *Annu Rev Ecol Syst* 16:447–479.
- Lane GE 1999 Food of satin bowerbirds. *Corella* 23:17.
- Loveless M, J Hamrick 1984 Ecological determinants of genetic structure in plant populations. *Annu Rev Ecol Syst* 15:65–95.
- Manson RH, EW Stiles 1998 Links between microhabitat preferences and seed predation by small mammals in old fields. *Oikos* 82: 37–50.
- McGrath RJ, D Bass 1999 Seed dispersal by emus on the New South Wales north-east coast. *Emu* 99:248–252.
- Mittelbach GG, KL Gross 1984 Experimental studies of seed predation in old fields. *Oecologia* 65:7–13.
- Murray BR, PH Thrall, AM Gill, AB Nicotra 2002 How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecol* 27:291–310.

- Notman E, DL Gorchov, F Cornejo 1996 Effect of distance, aggregation, and habitat on levels of seed predation for two mammal-dispersed Neotropical rain forest tree species. *Oecologia* 106: 221–227.
- Pirie CD, S Walmsley, R Ingle, AP Jimenez, AS Magallanes, CK Kelly 2000 Investigations in plant commonness and rarity: a comparison of seed removal patterns in the widespread *Jatropha standleyi* and the endemic *J. chamelensis* (Euphorbiaceae). *Biol J Linn Soc* 71:501–512.
- Rabinowitz D 1981 Seven forms of rarity. Pages 205–217 in H Synge, ed. *The biological aspects of rare plant conservation*. Wiley, New York.
- Regan HM, TD Auld, DA Keith, MA Burgman 2003 The effects of fire and predators on the long-term persistence of an endangered shrub, *Grevillea caleyi*. *Biol Conserv* 109:73–83.
- Rey PJ, JM Alcántara 2000 Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *J Ecol* 88:622–633.
- Rose BA 1973 Food of some Australian birds. *Emu* 73:173–183.
- Rymer PD, DJ Ayre Forthcoming Does genetic variation and gene flow vary with rarity in obligate seeding *Persoonia* species (Proteaceae)? *Conserv Genet*, doi:10.1007/s1052-006-9135-8.
- Rymer PD, RJ Whelan, DJ Ayre, PH Weston, KG Russell 2005 Reproductive success and pollinator effectiveness differ in common and rare *Persoonia* species (Proteaceae). *Biol Conserv* 123:521–532.
- Scott B, CL Gross 2004 Recovery directions for monoecious and endangered *Bertya ingramii* using autecology and comparisons with common *B. rosmarinifolia* (Euphorbiaceae). *Biodivers Conserv* 13:885–899.
- Silvertown J, M Dodd 1996 Comparing plants and connecting traits. *Philos Trans R Soc B Biol Sci* 351:1233–1239.
- Simon MF, JD Hay 2003 Comparison of a common and rare species of *Mimosa* (Mimosaceae) in central Brazil. *Austral Ecol* 28: 315–326.
- Underwood AJ 1997 *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge.
- Valverde T, J Silvertown 1997 A metapopulation model for *Primula vulgaris*, a temperate forest understorey herb. *J Ecol* 85:193–210.
- Weston PH 1995 *Persoonia*. Pages 50–125 in *Flora of Australia*. Vol 16. CSIRO, Melbourne.
- 2003 Proteaceae subfamily Persoonioideae. *Aust Plants* 22: 62–91.
- Whelan R 1995 *The ecology of fire*. Cambridge University Press, Cambridge.
- Zar JH 1999 *Biostatistical analysis*. 4th ed. Prentice-Hall, Upper Saddle River, NJ.

Copyright of International Journal of Plant Sciences is the property of University of Chicago Press and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.