Reproductive success and pollinator effectiveness differ in common and rare *Persoonia* species (Proteaceae)

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Abstract

In plants, understanding the interactions between breeding systems and pollination ecology may enable us to predict the impacts of rarity. We used a comparative approach to test whether rarity is associated with reproductive biology in two closely-related species pairs. This system has been recently altered by changes in fire regimes and the introduction of European honeybees. More than 35% of flowers matured fruits in the common species after natural-pollination compared to <20% of flowers in the rare species. All species were obligate outcrossers in each of the study populations, but only the two rare species were pollen-limited, having significantly lower fruit-set on open-pollinated flowers than those cross-pollinated by hand (mean ± SE; 0.18 ± 0.02 vs. 0.42 ± 0.05; $p < 0.001$). Native bees (*Leioproctus* species) and introduced honeybees (*Apis mellifera*) visited all species. The native bees visited fewer flowers within a plant and moved greater distances between plants while foraging than honeybees, so the native bees are expected to be more effective in promoting outcrossing. While honeybees were the most frequent visitors to flowers of all species, native bees made more visits to common than rare species (0.65 ± 0.20 vs. 0.20 ± 0.09). Our results suggest that the poorer reproductive success in rare *Persoonia* species is associated with lower pollinator effectiveness, which is exacerbated by frequent fires and introduced honeybees. If this is a causal relationship, this may increase the probability of extinction in populations of these species.
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1. Introduction

The reproductive success of plants and hence their abundance must be at least partially dependent on their breeding systems (e.g. level of self-compatibility) and the activity of pollinators. Variation in plant breeding systems and the attractiveness of plants to pollinators may therefore be a determinant of rarity. However, empirical investigations of the causes of rarity have to date typically looked at these attributes in isolation and have so far yielded equivocal results (Murray et al., 2002). The small number of relevant studies also seldom includes comparisons of closely related taxa with similar suites of pollinators and floral characters (but see Banks, 1980). This kind of comparative approach has been strongly advocated as a tool with which to investigate the causes of rarity (Bevill and Louda, 1999).

Pollinators play an important role in the movement of pollen from flowers within and among flowering plants, thereby determining the availability of potential mates and influencing the reproductive success of plants (Talavera et al., 2001). Some animals are

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specialist-pollinators, being well adapted to forage for the floral resources of a particular species (or group of related species), which in turn receives compatible pollen for sexual reproduction. In contrast, generalist-pollinators utilise resources from a wide range of flowering plants, and often have characteristics that enable them to forage extensively on different species without being well suited to pollinate any particular species (Thostesen and Olesen, 1996; Waser et al., 1996). The European honeybee (*Apis mellifera*) is a generalist pollinator that harvests floral resources from numerous flowering plants in many cases without pollinating them (Paton, 1997). Honeybees have been introduced to many countries, including Australia in the 1820s, and have the potential to disrupt native plant/pollinator relationships (Butz Huryn, 1997).

The impact of pollinators on the mating system of plants (i.e. level of outcrossing) and their reproductive success is dependent, in part, on the level of self-compatibility exhibited by the plant. Indeed levels of self-compatibility can vary dramatically within (Young and Brown, 1998; McIntosh, 2002) and among plant populations (e.g. Vaughton, 1989; Medrano et al., 1999; Eckert, 2002). So, in order to predict the impacts of habitat fragmentation and plant rarity, we need to have an understanding of the interactions between the levels of self-compatibility and patterns of pollinator activity. The interaction between the quantity and quality of pollen a plant receives and the level of self-compatibility determines the degree to which reproductive success is affected by fragmentation (Aizen et al., 2002). For example, obligate-outcrossers are dependent on reliable pollinators transferring pollen between compatible mates to ensure fruit production (Richardson et al., 2000; Goodwillie, 2001). In such a case, we predict the impacts of rarity will be greatest for species with only a single specialist-pollinator, because as a population becomes smaller and more isolated the visitation rates will decrease as a result of stochastic processes (Steffan-Dewenter and Tscharntke, 1999). At the other extreme, autogamous species do not require pollinators to produce fruit and therefore reproductive success is likely to be less affected by fragmentation. Plants that are unable to set fruit via autogamy but are self-compatible still require pollinators to transfer pollen to the stigma. In this case, we predict that the impact of fragmentation will be least severe for plant species with a suite of generalist-pollinators (Johnson et al., 2004). However, there are a wide range of cases between these extremes that offer no simple predictions, including plants with partial self-compatibility and a mix of specialist and generalist-pollinators. The impacts of fragmentation and rarity are best explored in closely related species that have similar floral biology and share pollinators, whilst differing in local abundance and geographic distribution, which is the case for several *Persoonia* species (Bernhardt and Weston, 1996).

Persoonia are Proteaceous woody shrubs and small trees that produce fleshy, drupaceous fruits capable of being dispersed over long-distances by large mammals and birds (Rose, 1973; Lane, 1999; McGrath and Bass, 1999; P.D.R. pers. obs.). In fire-prone habitats, some species resprout after fire while others are obligate-seeders (i.e. adult plants are killed by fire and depend on a seed-bank for their regeneration). Frequent fires may result in reduced population sizes and reduced plant densities, increased population fragmentation and even localised extinctions, especially for obligate seeders (Bradstock et al., 1996). Many of the *Persoonia* species that are listed as threatened (*Environment Protection and Biodiversity Conservation Act, 1999*) are obligate seeders, which suggests that their response to fire may have led to their current status. However, some obligate-seeding *Persoonia* species are common and widespread, so this characteristic alone cannot explain rarity. A plausible explanation for differences in rarity among the obligate seeder species, given their reliance on seed production, is that they differ in their reproductive biology.

In this study, we used a comparative approach to test for differences in reproductive success, breeding system, and pollination ecology between common and rare *Persoonia* species. Two pairs of closely related taxa (hereafter referred to as species) were selected with sharply contrasting geographic distributions, which is probably a result of range contraction into refugia in the last glacial maximum and expansion thereafter (Krauss, 1998). Pair 1 consists of *Persoonia mollis* R. Br. subspecies *nectens* S.L. Krauss & L.A.S. Johnson (common) versus *Persoonia mollis* subsp. *maxima* S.L. Krauss & L.A.S. Johnson (rare). Pair 2 is *P. lanceolata* Andrews (common) versus *P. glaucescens* Sieber ex Spreng (rare). All these plants have a superficially similar habit, floral morphology, seed size (Weston, 1995; Krauss, 1998), and share the same suite of insect pollinators (Bernhardt and Weston, 1996), offering an opportunity to test the causes and consequences of rarity.

We hypothesised that the common species would have greater fecundity than rare species, due to differences in the breeding system and/or pollination. We predicted that fruit production in the rare species would be limited by pollination, being self-incompatible and receiving fewer visits from effective pollinators. The objectives of this study were first to determine the reproductive success in common and rare *Persoonia* species, and then to test for differences in the breeding system and pollination. Specifically, we aimed to (1) assess the level of self-compatibility, (2) determine if pollination is limiting reproductive success, and (3) investigate the behaviour and the visitation rates of pollinators.

2. Methods

2.1. Study species and sites

Persoonia species display a range of breeding systems, from self-compatible to obligate-outcrossing (Krauss, 1994; Goldingay and Carthew, 1998; Trueman and Wallace, 1999; Cadzow and Carthew, 2000). Flowers are small (6–14 mm long) and hermaphroditic. The peak flowering period is summer to autumn (November to April), and fruits mature into fleshy drupes in late spring (Weston, 2003).

All *Persoonia* species for which pollinators are known are pollinated by native bees, the most important of which appear to be species of *Leioproctus* subgenus *Cladocerapis* (Bernhardt and Weston, 1996). These are solitary bees that appear to be specialist foragers on and pollinators of *Persoonia* (Wallace et al., 2002). The European honeybee (*Apis mellifera*) also visits the flowers of *Persoonia*. Since its introduction in Australia *Apis mellifera* has become the dominant floral visitor in many species (Paton, 1997). *P. mollis* is a species complex that has been divided into nine subspecies based on morphological, genetic and geographic variation (Krauss and Johnson, 1991; Krauss, 1996, 1998). *P. mollis* subsp. *maxima* has been classified as endangered in New South Wales, under the *Threatened Species Conser-vation Act 1995*, and nationally, under the *Environment Protection and Biodiversity Conservation Act 1999*. It has a restricted geographic distribution (40 km^2 extent of occurrence) (Fig. 1). *P. mollis* subsp. *maxima* is allopatric to and sister lineage of the rest of the *P. mollis* complex and so could justifiably be recognised at species rank (Krauss, 1998). It is separated by more than 75 km from subspecies *nectens*, which is common and relatively widespread (1110 km^2 extent of occurrence) (Fig. 1). Both subspecies grow in dry to wet sclerophyll forests on sedimentary substrates (usually sandstone).

Persoonia glaucescens has been classified as endangered in New South Wales (*Threatened Species Conserva-tion Act 1995*) and nationally (*Environment Protection and Biodiversity Conservation Act 1999*). It has a restricted geographic distribution (460 km^2 extent of occurrence) (Fig. 1), which overlaps that of its closely related congener, *P. lanceolata*, which is common and widespread (13,340 km^2 extent of occurrence) (Fig. 1). Both species grow in dry sclerophyll forests on sandstone, where they sometimes co-occur, but *P. lanceolata* is also found in coastal heath (Weston, 1995).

For each of these four species, we selected two sites to compare reproductive success, breeding systems and pollinator behaviour. Sites (approximately 100×100 m) were chosen that contained relatively large populations (>100 plants). As no locations were found
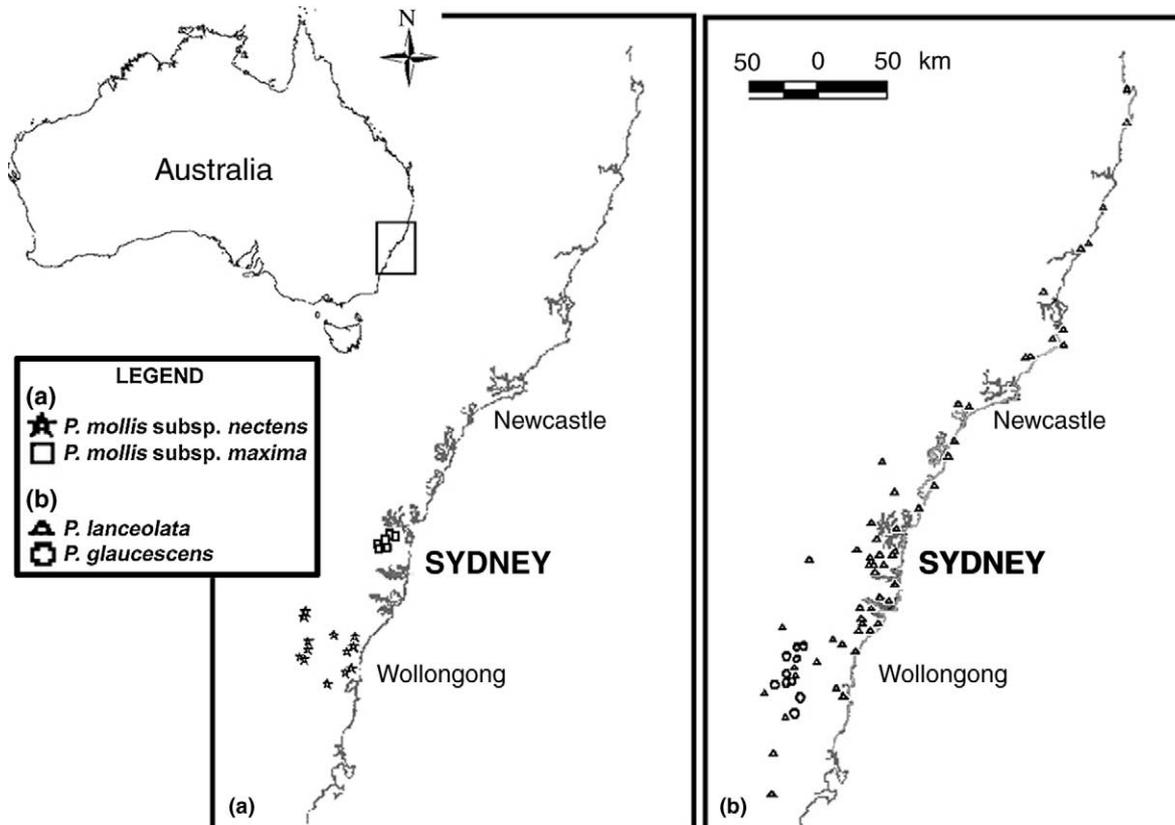

Fig. 1. Map of the greater Sydney district (Australia) showing the geographic distribution of *P. mollis* subsp. *nectens*, *P. mollis* subsp. *maxima*, *P. lanceolata* and *P. glaucescens*. The records were compiled from the New South Wales National Herbarium.

Table 1
The estimated population size, plant density, plant height and number of open flowers per plant for common and rare *Persoonia* species at the study sites

Species (Rarity) Study site	Latitude, longitude[a]	Population size[b]	Mean (SE)		
			Plants density[c]	Plant size[d]	Floral display[e]
P. mollis subsp. *nectens* (common)					
1. Hilltop	34°19′48″E, 150°28′41″S	300	0.5 (0.10)	1.8 (0.30)	260 (2.4)
2. Little River	34°16′05″E, 150°30′54″S	600	1.0 (0.15)	3.2 (0.40)	392 (2.5)
P. mollis subsp. *maxima* (rare)					
1. Ku-ring-gai	33°40′34″E, 151°8′02″S	200	0.3 (0.05)	3.5 (0.35)	253 (2.6)
2. Galston Creek	33°39′21″E, 151°04′12″S	100	0.2 (0.05)	2.5 (0.30)	170 (2.3)
P. lanceolata (common)					
1. Wise's Track	34°06′47″E, 151°03′34″S	500	1.5 (0.20)	1.3 (0.10)	79 (1.9)
2. Bundeena	34°06′11″E, 151°05′60″S	>1000	2.8 (0.20)	1.2 (0.10)	90 (2.0)
P. glaucescens (rare)					
1. Braemar	34°25′05″E, 150°28′26″S	400	1.3 (0.20)	2.5 (0.30)	54 (1.8)
2. Buxton	34°15′07″E, 150°30′54″S	100	0.4 (0.10)	2.0 (0.25)	71 (2.0)

[a] Based on GPS position using datum WGS1984.
[b] Estimated number of flowering individuals per population.
[c] Number of flowering plants per 10 m^2 ($n = 20$ random focal points).
[d] Plant height (m) ($n = 20$ plants).
[e] Number of open flowers per plant ($n = 20$ plants).

where the study species co-occurred in large enough numbers to conduct this work, separate study sites were used for each species (Table 1).

2.2. Reproductive success

At each site, we randomly selected (using random number) five large reproductive plants (along haphazard transects across the population) that were representative of the population. On each floral buds were tagged immediately prior to opening (January–April 2001). These flowers were left open to pollinator visits, and were monitored monthly until the fruit matured (October–November 2001). On each occasion, flowers were scored as 'aborted' if the gynoecium dropped off, and 'fertilised' if the ovary was swollen, indicating fruit initiation. The proportion of flowers that developed into mature fruits was used as an estimate of reproductive success in common and rare species after natural pollination.

We used an ANOVA (performed in SAS version 8.2) to test for differences in the reproductive success between the common and rare species. The ANOVA was constructed with Pair (two pairs of closely related species) and Rarity (common vs. rare) as factors in a 2×2 factorial design, with Site and Plant (within Site) as random block factors. The raw data in the analyses were the proportion of flowers to mature into fruits. To satisfy the assumptions of normality and homogeneity of variances we used angular transformation.

2.3. Experimental pollination

We carried out experimental pollinations to characterise the breeding systems and to determine whether pollination was limiting reproductive success. At each site (Table 1), we selected five large reproductive plants to undertake the hand-pollinations. From the available branches (20–40 cm in length) that were producing floral buds, we randomly selected four and assigned each to one of the following treatments: (1) Open: Floral buds tagged immediately prior to opening and left to allow pollinators to visit freely. (2) Closed: Floral buds tagged immediately prior to opening and the branch was bagged to exclude all flower visitors. (3) Self: Anthers removed from 1 to 2 day-old flowers (which appeared receptive and anthers had not yet dehisced) that opened within the bagged branch, self-pollen was applied to the stigma, the treated flowers were tagged and the branch re-bagged. (4) Cross: Anthers removed from 1 to 2 day-old flowers that opened within the bag, cross-pollen was applied to the stigma, the treated flowers were tagged and the branch re-bagged.

We compared the level of fruit-set after open-pollination on plants with and without additional treatments (including flowers that received high quality pollen from the cross-pollination treatment), which yielded no evidence for competition among branches for resources ($\chi^2_7 = 6.95$, $p > 0.25$). The allocation of plant resources for fruit development in *Persoonia* species is more likely to be confined to within branches (Trueman and Wallace, 1999), so the pollination treatments carried out on the same plant should be independent of each other.

In every treatment, we removed all insect-damaged floral buds; open flowers and senesced flowers were removed from the selected branches. We tagged the treated flowers with 2 mm clear plastic bands placed on the branch immediately below the flower. We used plastic coated wire to attach 30 by 60 cm black netting bags

(0.5 mm pore-size) to individual branches. We achieved pollination by application of either self-pollen (collected from other flowers on the same plant as the flowers to be treated) or cross-pollination (collected from three plants that were more than 10 m away from the treated plant). Pollen was collected by removing the anthers from bagged (1–2 day-old) flowers, placing them in a 1.5 mL centrifuge tube and flicking the tube until the pollen adhered to the sides. We applied pollen to the receptive stigmas with a toothpick within 2 h of collection.

We performed the pollination treatments to flowers between January and March 2001. Branches were checked two days after initial bagging, and we pollinated "receptive" flowers (i.e. with sticky stigmatic surfaces). We pollinated additional flowers on the following days until 10–40 flowers had been treated per branch. Bags removed after all the treated flowers had senesced, about two to three weeks after being pollinated.

We monitored the treated flowers monthly until the fruit matured in October–December 2001. On each occasion, flowers were scored as 'aborted' if the gynoecium dropped off, and 'fertilised' if the ovary was swollen, indicating fruit initiation. Prior to fruit drop, branches were re-bagged (at the end of September). Fruit set was recorded when the fruits matured (at the beginning of fruit drop).

Seed viability could not be tested at all the study sites due to extensive wildfires in December 2001. Four of the study sites were burned prior to fruit collection: *P. mollis* subsp. *nectens* at Hill Top and Little River, *P. glaucescens* at Buxton and *P. lanceolata* at Wise's Track. As a result, a statistically valid comparison of seed-viability in common and rare species was not possible.

We used an ANOVA, to test the hypothesis that common and rare species differ in their responses to the pollination treatments. The ANOVA was constructed with Treatment (four pollination treatments, open, closed, self and cross), and Rarity (common vs. rare) as fixed factors. Pair (two pairs of closely related species) was a random factor. These three factors (Treatment, Rarity and Pair) were combined in a full factorial design. Site and Plant (within Site) were random block factors. The two sites per species were used as replicates for each Pair by Rarity combination (2 sites/species × 4 species = 8 sites). The raw data were the proportion of flowers that matured fruits for each plant ($n = 5$). We transformed the raw data using an angular transformation to overcome heterogeneity of variances. After transformation a plot of the residuals versus the fitted values showed a relatively random scatter of points. A histogram of the residuals suggested a normal distribution (Kolmogorov–Smirnov test for normality $p > 0.15$). Where significant differences occurred, multiple comparisons were performed using Tukey's Studentised Range Test. Analyses of the raw data and the transformed data yielded the same significant results,

so we used the raw data to construct the tables and figures for ease of interpretation.

2.4. Pollinator observations

To determine the effectiveness of the insect visitors as pollinators, we made observations of the behaviour and movement of individual insects as they foraged on *Persoonia* plants within the study sites. We observed the foraging behaviour of pollinators for a period of 60 min for two days at each site. Observations were made during the middle of the day 1100–1500 h during the period of maximum insect activity (Richardson et al., 2000). We recorded the time that each insect spent on each flower, the number of flowers visited per plant, the total time foraging on the plant, whether the stigma and/or anthers were contacted and whether the insects were collecting pollen and/or nectar. In addition, the distance insects moved to the next plant was recorded, where possible. Insects were followed from plant to plant, to get an indication of the movement of pollen within the study sites. We also noted whether the floral visitor had pollen when they arrived at the plant. The ratio of the number of within versus between-plant movements was used as an indication of the quality of pollen received by flowers visited by insect visitors.

We also observed pollinators in order to estimate the visitation rates (pollen quantity). For each of the study sites (Table 1), we observed five large reproductive plants for 10 min during the middle of the day 1100–1500 h and the number of introduced honeybees (*Apis mellifera*); native bees (*Leioproctus* subgenus *Cladocerapis* spp.) and other floral visitors (including *Exoneura* species) were recorded to quantify the number of insects visits received by common and rare species.

We attempted an ANOVA (design as for reproductive success) to examine the hypothesis that common species receive more frequent insect visitor compared to rare species. However some of the data sets (the native bee, proportion of native bee, and the rate of native bee visits) showed skewed distributions that could not be improved through transformation. We therefore used a randomisation analysis (Edgington, 1995) that was constructed with Pair (random) and Rarity (fixed) factors in a full factorial design using the mean values for number of visits for each Pair by Rarity combination (4 species) as the raw data. To test for a Pair by Rarity interaction all possible randomisations (2520 in total) of pairs of raw data values to the four treatment combinations were carried out, and the *F*-value for the interaction calculated for each within a 2-way factorial ANOVA. The original *F*-value calculated from the raw data was then compared with the distribution of *F*-values after randomisation to obtain the probability of achieving a value as extreme as this by chance (*p*-value).

To test for differences between the two species pairs (Pair 1 and 2) the four mean values within each Rarity class (common and rare) were randomly allocated to the two Pairs without altering their Rarity, resulting in 36 allocations. Similarly, differences between the common and rare species (Rarity) were tested by randomly allocating the four mean values within each species pair (1 or 2) to the two Rarity classes without altering their species pair (36 allocations). *F*-values were calculated from each allocation. The *F*-value from the raw data was compared with this distribution of 36 values to obtain the probability value. The minimum possible *p*-value (2/36 or 0.056) for the test of each of the main effects (Pair and Rarity) was interpreted as a significant result.

3. Results

3.1. Reproductive success

Common and rare species showed a similar pattern of fruit initiation and development. Fruits initiated after 70–100 days following flowering in all species except *P. glaucescens*, which retained flowers much longer and initiated fruits after about 210 days. There was very little fruit abortion (<15% after initiation) and fruit matured into a fleshy drupe (8–14 mm diameter) in all species about 250 days after flowering. All species had high levels of seed viability, *P. mollis* subsp. *nectens* (91%), *P. mollis* subsp. *maxima* (89%), *P. lanceolata* (97%) and *P. glaucescens* (86%) in fruit matured after natural pollination.

The common species (*P. mollis* subsp. *nectens* and *P. lanceolata*) had significantly higher levels of fruit-set than the rare species (*P. mollis* subsp. *maxima* and *P. glaucescens*) (ANOVA; Rarity, $F_{1,4} = 15.08$, $p = 0.018$). On average, more than one third of flowers matured fruits in the common species after natural pollination compared to less than one fifth in the rare species (Fig. 2).

3.2. Breeding system

All species showed a similar response to the pollination treatments (Table 2). There were highly significant effects of pollination treatments on fruit-set (Treatment, $p < 0.0001$) (Table 2). Very few (<1% of treated flowers) fruits matured from the closed or self-pollination treatments (Fig. 3), indicating that both the common and rare species are self-incompatible. On the other hand, a relatively high proportion (range 17–54%) of fruits matured in both the open and cross-treatments consistently among sites and species (Table 3). This indicates that species are outcrossers and cannot produce seeds by selfing.

3.3. Pollen limitation

There was a significant interaction between the pollination treatments and plant rarity (Treatment × Rarity, $p < 0.001$) (Table 2). The two common species, *P. mollis* subsp. *nectens* and *P. lanceolata*, had similar levels of fruit-set in the open (mean ± SE; 0.35 ± 0.10, 0.41 ± 0.10, respectively) and cross-treatments (0.25 ± 0.18, 0.31 ± 0.16). In contrast, in the two rare species, *P. mollis* subsp. *maxima* and *P. glaucescens*, the levels of fruit-set in the open-treatment (0.18 ± 0.05, 0.18 ± 0.03) were significantly lower than the cross-treatment (0.43 ± 0.11, 0.40 ± 0.08) suggesting that pollination (quantity or quality) was limiting fruit-set in these taxa (Table 3).

3.4. Pollination behaviour and movement

The behaviour and movements of floral visitors were similar on all four *Persoonia* species. During the 16 h of direct observations, 241 honeybees (*Apis mellifera*) and 40 native bees (including 34 *Leioprotus* species and 6 *Exoneura* species) were recorded foraging on *Persoonia* flowers. Although honeybees and native bees displayed very different foraging behaviours, these were consistent across all the study species.

Honeybees contacted the stigmatic surface with their abdomens while foraging for pollen (and nectar), usually remaining on the flower for less than five seconds before moving to another flower. Honeybees visited an average of 8.0 ± 1.8 (±SE) flowers on a plant before moving to another *Persoonia* plant (of the same species), which was predominantly the plant's nearest neighbour (distance moved between plants ranged from 0.5 to 2 m). The majority of pollen collected by honeybees was transferred from their front collecting legs to the corbiculae on their hind legs. Additional pollen was frequently groomed from their abdomen and thorax to be stored on their hind legs. Honeybees collecting pollen consistently arrived at plants with large pollen loads, in the form of a smooth pellet found in the corbiculae.

Native bees (predominantly *Leioprotus* species) contacted the stigma frequently with their thorax and abdomen while collecting nectar and pollen. Fewer flowers were visited within plants (2.1 ± 0.8) by native bees than honeybees. In addition, native bees moved greater distances between *Persoonia* plants (range 1–5 m, usually out of sight) than honeybees. Native bees collecting pollen arrived with a large pollen load on the hairs of the dorsal surface of the thorax, abdomen and legs.

3.5. Pollinator abundance

There was a significant difference in native bee visitation between common and rare species (Table 4; Rarity, randomised $p = 0.056$). The common species (*P. mollis*
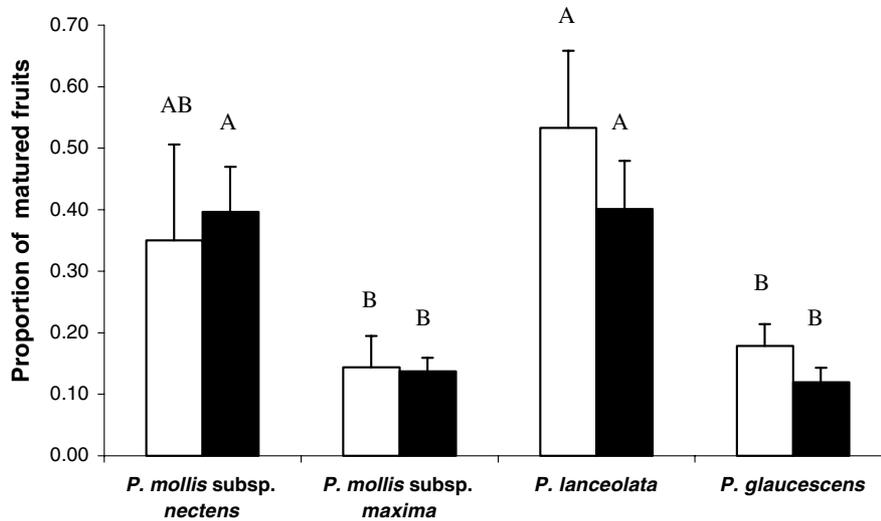
Fig. 2. The mean reproductive success (proportion of flowers that matured fruit) in plants (*n* = 5 plants with 21 to 48 flowers) open to natural pollination for common and rare *Persoonia* species in the eight study sites (as in Table 1). For each species site 1 and 2 are the clear and filled bars, respectively. Letters show the results of the Tukey's test, where two mean values that share the same letter are not statistically different (α = 0.05).

subsp. *nectens* and *P. lanceolata*) had three times more native bee (primarily *Leioprotus* species) visits than the rare species (*P. mollis* subsp. *maxima* and *P. glaucescens*) (0.65 ± 0.20 vs. 0.20 ± 0.09) (Fig. 4).

Overall, the introduced European honeybee (*Apis mellifera*) was the most common floral visitor to *Persoonia* flowers, being observed 3 to 10 times more frequently than native bees. The total number of insect visits (mean ± SE; 5.25 ± 0.71, 4.25 ± 0.69) and the number of honeybee visits (4.60 ± 0.70, 4.05 ± 0.65)

were similar for both pairs of common and rare species (Fig. 4).

There was a significant difference in the number of honeybee visits between the two pairs of closely related species (randomised *P* = 0.056) (Table 4). Species pair 1 (*P. mollis* subsp. *nectens* and *P. mollis* subsp. *maxima*) had more honeybees than pair 2 (*P. lanceolata* and *P. glaucescens*), which may be due to plant size (Table 1).

4. Discussion

This comparative study links reproductive success, breeding system and pollination ecology to plant rarity in two pairs of closely related common and rare species with replicate populations. It found that both common and rare *Persoonia* species are obligate-outcrossers and are dependent on insect-pollinators for sexual reproduction. Pollination was limited in the rare species, which was associated with fewer native bee visits, resulting in reduced reproductive success. Here we compare the associations between rarity and reproductive success, breeding system, and pollination found in this study with other findings in the published literature. Then we discuss the implications for the management of these historically rare species and consider the effects of recent habitat fragmentation and altered suites of pollinators.

4.1. Rarity and reproductive success

Greater seed production may enable plants to regenerate in greater abundance after disturbances (e.g. fire) and establish new populations more readily through

Table 2

Mixed model ANOVA for a comparison of the pollination treatments (Treatment) in closely related (Pair) common and rare species (Rarity) across populations (Site)

Source of variance	d.f.	MS	*F* value	*P*
Pair	1	21.53	0.77	0.57
Rarity	1	78.19	2.69	0.35
Pair × Rarity	1	29.02	0.34	0.64
Treatment	3	143.00	933.89	**0.0001**
Pair × Treatment	3	15.26	0.94	0.52
Rarity × Treatment	3	741.17	45.53	**0.005**
Pair × Rarity × Treatment	3	16.28	0.21	0.89
Site	4	145.36	1.71	0.17
Site × Plant	32	84.85	1.10	0.34
Error	108	76.85		

Data = arcsin($\sqrt{\text{mature fruits/number of treated flowers}}$). To calculate the *F* values the mean square (MS) for Pair was divided by MS(Pair × Rarity) + MS(Pair × Treatment) − MS(Pair × Rarity × Treatment) + 11E − 17 × MS(Error). Rarity was divided by MS(Pair × Rarity), and Pair × Rarity, Pair × Treatment, and Rarity × Treatment were divided by MS(Pair × Rarity × Treatment). Treatment was divided by MS(Pair × Treatment), while Pair × Rarity × Treatment and Site × Plant were divided by MS(Error), and Site was divided by MS(Site × Plant).
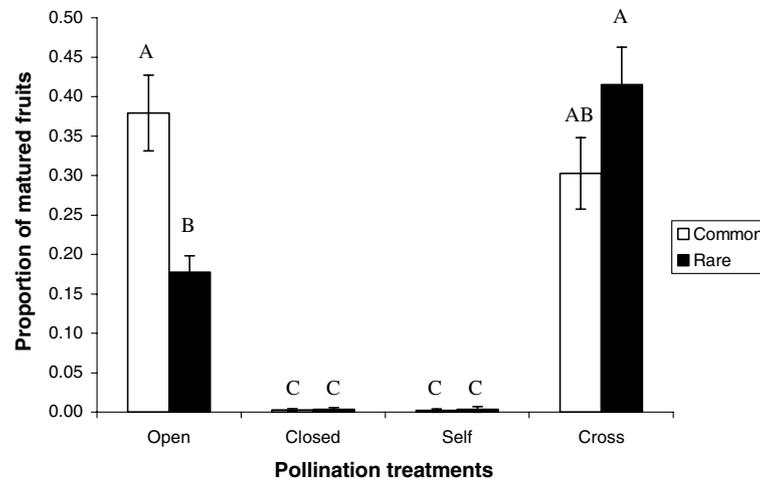
Fig. 3. The mean (±SE bars) proportion of flowers that matured into fruits from the pollination treatments (Open, Closed, Self and Cross) in the common and rare *Persoonia* species (*n* = 2 sites × 5 plants = 10). Letters show the results of the Tukey's test; where a Treatment × Rarity combination shares the same letter as another, they are not statistically different ($\alpha = 0.05$).

Table 3
The mean (SE) proportion of treated flowers that matured into fruits from the pollination experiment (Open, Closed, Self and Cross) for common and rare *Persoonia* species at the study sites (*n* = 10–40)

Species (Rarity)	Site	Pollination treatments			
		Open	Closed	Self	Cross
P. mollis subsp. *nectens* (common)	Hilltop	0.34 (0.13)	0.01 (0.01)	0.00 (0.00)	0.35 (0.09)
	Little River	0.35 (0.07)	0.00 (0.00)	0.00 (0.00)	0.22 (0.03)
	mean	*0.35 (0.10)*	*0.00 (0.00)*	*0.00 (0.00)*	*0.28 (0.08)*
P. mollis subsp. *maxima* (rare)	Ku-ring-gai	0.18 (0.06)	0.00 (0.00)	0.01 (0.01)	0.54 (0.09)
	Galston Creek	0.18 (0.05)	0.00 (0.00)	0.00 (0.00)	0.33 (0.12)
	mean	*0.18 (0.05)*	*0.00 (0.00)*	*0.01 (0.01)*	*0.43 (0.11)*
P. lanceolata (common)	Wise's Track	0.52 (0.11)	0.00 (0.00)	0.01 (0.01)	0.41 (0.13)
	Bundeena	0.31 (0.06)	0.01 (0.01)	0.00 (0.00)	0.23 (0.07)
	mean	*0.41 (0.10)*	*0.00 (0.00)*	*0.00 (0.01)*	*0.32 (0.11)*
P. glaucescens (rare)	Braemar	0.18 (0.04)	0.01 (0.01)	0.00 (0.00)	0.47 (0.08)
	Buxton	0.17 (0.02)	0.01 (0.01)	0.00 (0.00)	0.32 (0.08)
	mean	*0.18 (0.03)*	*0.01 (0.01)*	*0.00 (0.00)*	*0.40 (0.08)*

dispersal. There is growing evidence that common species are more fecund than rare species, with the majority of studies reviewed by Murray et al. (2002) supporting this trend (9 from 13 cited). In fact the studies that found no difference in fruit production involved only one common-rare comparison, and despite non-significant results (except for Witkowski and Lamont, 1997 where no difference was found) the rare species tended to produce few fruits (Fiedler, 1987; Pavlik et al., 1993; Young and Brown, 1998). We found both pairs of rare species to have a lower reproductive success than their common congeners across replicate populations (see Fig. 2). If this is a general trend, the variation in reproductive success may partially explain the marked differences in geographic distribution and local abundance observed between common and rare species.

4.2. Rarity and breeding system

Selfing has been suggested as an evolutionary consequence of rarity, providing reproductive assurance when compatible mates and/or pollinators become limited (Baker, 1955; Carpenter and Recher, 1979; but see Herlihy and Eckert, 2002). However, highly developed self-incompatibility mechanisms have been found across numerous plant families and habitats in both common and rare species (Kunin and Shmida, 1997; Murray et al., 2002). Our results (see Fig. 3) are consistent with the majority of published studies, in which the breeding systems of common and rare congeners are similar (Fitz-Sheridan, 1988; Sydes and Calder, 1993; Premoli, 1996; Bosch et al., 1998; Affre and Thompson, 1999). In those studies that have found inter-specific differences in breeding system, there is no consistent association be-

Table 4
Mixed model ANOVA for a comparison of honeybee (A) and native bee (B) visitation rates in closely related (Pair) common and rare species (Rarity)

Source of variance	d.f.	MS	*F* value	*p*	Randomized *p*
(A) Honeybee					
Pair	1	235.225	177.53	**<0.001**	**0.056**
Rarity	1	3.025	2.28	0.21	0.222
Pair × Rarity	1	1.225	0.92	0.39	0.495
Site	4	1.325	0.39		
Error	32	3.375			
(B) Native bee					
Pair	1	0.225	1.80	0.25	0.667
Rarity	1	2.025	16.20	**0.01**	**0.056**
Pair × Rarity	1	0.225	1.80	0.25	0.257
Site	4	0.500	0.24		
Error	32	16.800			

(A) Honey bee data = number of visits/plant/10 min. (B) Native bee data = number of visits/plant/10 min. To calculate the *F* values the mean square (MS) for Pair, Rarity and Pair × Rarity was divided by MS(Site). The *p* value was calculated based on standard *F*-tables, while the Randomized *p* value was based on output of the randomisation analysis (see Section 2).
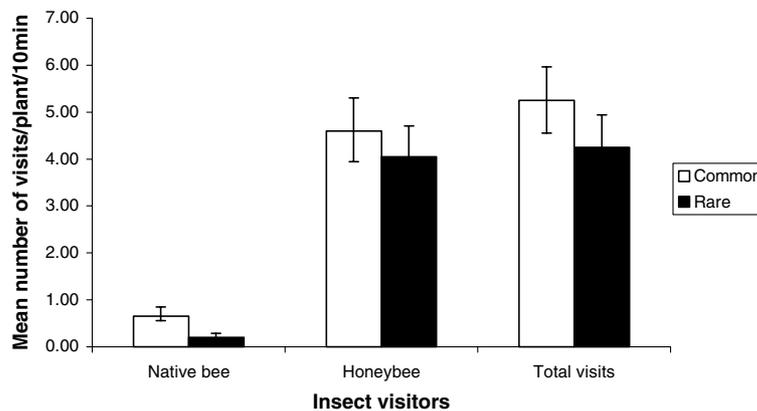

Fig. 4. The mean (±SE) number of native bee, honeybee and total insect visits per plant (per 10 min observation) in common and rare *Persoonia* species (*n* = 2 species × 2 sites × 5 plants = 20).

tween the level of self-compatibility and rarity, with both the common and rare species displaying selfing or outcrossing (Karron, 1989; Purdy et al., 1994; Herma-nutz et al., 1998; Mateu and Figueres, 1998; Ng and Corlett, 2000). We conclude, therefore, that plant breeding systems are not directly related to rarity and other factors, including population characteristics, may be more important in determining the level of self-compatibility.

4.3. Rarity and pollination

Pollination is required for seed production in species not capable of autogamy, even when self-pollination is possible. The effectiveness of different floral visitors as pollinators is dependent on their behaviour and movement (Wallace et al., 2002). Despite this, few studies have compared the association between pollination and plant rarity. Where this has been done for insect pollinated plants, rare species tend to receive fewer visits than their common relatives (Banks, 1980; Karron, 1987; Fitz-Sheridan, 1988; Sydes and Calder, 1993). The *Persoonia* species in our study are all obligate outcrossers and native bees (*Leioproctus* species) were observed moving between plants, carrying pollen and contacting anthers and stigmas, therefore promoting outcrossing. *Leioproctus* species forage primarily on *Persoonia* flowers (Bernhardt and Weston, 1996), suggesting that it may be a specialist-pollinator (Wallace et al., 2002). The frequency of visits to the rare species was significantly lower than to the common species (see Fig. 4). If this is a general pattern limited pollination may be a cause or consequence of rarity, however the exact mechanisms require further investigation.

4.4. Future effects of fragmentation

Recent habitat destruction has fragmented the landscape and led to populations becoming progressively more isolated and reduced in size, greatly increasing

the probability of extinction (Barrett and Kohn, 1991; Ellstrand and Elam, 1993; Young and Brown, 1996). Small isolated populations are expected to have altered pollinator behaviour and movement, as well as decreased pollinator visitation rates (Aizen and Feinsinger, 1994; Mustajarvi et al., 2001). As all the study species were obligate outcrossers with a single effective pollinator, the impacts of habitat fragmentation are likely to be severe, increasing the likelihood of inbreeding depression and reproductive failure (Severns, 2003), despite the fact that these species were probably historically restricted in range.

Populations of the four study species are affected by fragmentation to varying degrees, through natural and anthropogenic disturbances. Even though these obligate seeders possess adaptations, including a persistent soil-stored seed-bank and animal dispersed fleshy fruits (Auld et al., 2000; P.D.R. pers. obs.) that enable them to persist in these unpredictable (fire-prone) environments, continual frequent fires have the potential to reduce population sizes and ultimately force them to extinction (Bradstock et al., 1996). The encroachment of urban areas on natural bushland has led to subdivision of the available habitat and increased fire frequencies (through hazard reduction burning and arson). Populations of both common and rare *P. mollis* subspecies have patchy distributions within relatively continuous habitats, and are generally restricted to drainage lines and creeks (fire shadows; P.D.R. pers. obs.). *Persoonia lanceolata* and *P. glaucescens* populations are found in fragmented landscapes, subdividing populations by areas of urban and/or agricultural development. Population sizes differ between the species, with the common species locally abundant (ca. >500 plants) and the rare species generally consisting of fewer than 100 plants at a site. This is likely to alter pollinator visitation, depending on the nature of the matrix within the landscape.

4.5. Pollinator disruption

The introduction of the European honeybee may have disrupted the existing plant–pollinator interaction (Goulson, 2003). In Australia, honeybees have been recorded visiting a wide range of native flowering plants (Paton, 1993, 1997). In many of these species, their role as pollinators is questionable. In our study, honeybees were observed collecting and contacting stigmas of *Persoonia* flowers, and they are therefore potential pollinators. However, honeybees frequently groom pollen from their body, storing it in the corbiculae making it inaccessible for transfer onto the stigmatic surface (Bernhardt and Weston, 1996; Paton, 1997; Wallace et al., 2002). Combined with the high proportion of movements within plants (Gross, 2001; Dupont et al., 2004) and restricted movements between plants (Michaelson-Yeates et al., 1997), encouraging selfing and bi-parental inbreeding, respectively, the honeybee may be inefficient as a pollinator to these obligately outcrossing species. The results of other studies are mixed as to whether honeybees are effective as pollinators (Butz Huryn, 1997). It is clear, however, that the honeybee is now the dominant floral visitor to many native plants, which co-evolved with a range of vertebrates and solitary insect species (Paton, 2000; Spira, 2001). This shift in the composition of floral visitors has been shown to have a direct effect on reproductive success (Spira, 2001), to alter the genetic structure of populations (England et al., 2001) and to encourage (bi-parental) inbreeding depression (Spira, 2001). While honeybees appear to visit *Persoonia* species equally, their impact may be much greater in rare species and may merit a greater focus in future studies.

5. Conclusion

Both the common and rare *Persoonia* species are obligate outcrossers and the most effective pollination is likely to be provided by a native specialist pollinator. The rare species of *Persoonia* that we investigated are less fecund than their common relatives, and are visited less frequently by native bees. Despite these consistent differences between common and rare species, it is premature to conclude that differences in pollinator activities are the cause of rarity. Modified fire regimes and habitat fragmentation are important processes that have altered the distribution and abundance of plants, and pollinator activity may be responding to these changes. Further, the introduced honeybee is likely to be disrupting the existing plant–pollinator interactions in the genus *Persoonia*, and this relationship warrants further investigation. Whatever the ultimate cause of rarity, the reduced fecundity of the rare obligate-seeders may increase the likelihood of localised extinction in fire-prone environments.

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