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Abstract

Populations of the mangrove *Avicennia marina* in the Sydney region exist as stands of varying size, reflecting both natural and anthropogenic fragmentation. We hypothesised that, as observed in many terrestrial forests, small stands (plants) would experience lower pollinator densities and altered pollinator behaviour and visitation and, in consequence, would display reduced pollen deposition as compared with large stands (>10,000 plants). Nevertheless, we recognise that such predictions may be overly simplistic because within this region *A. marina* attracts a diversity of flower visitors, but its only significant pollinator is the exotic honeybee *Apis mellifera*. Moreover, it is unclear how readily *A. mellifera* moves among groups of plants within different mangrove stands of varying sizes separated either by water or urban habitat matrix. Our detailed surveys within pairs of large and small stands in two locations support the predictions that pollinator density and pollen deposition are reduced or altered within small stands. Within small stands honeybee abundance and pollen deposition were on average reduced significantly by 84 and 61 %, respectively. Moreover, within small stands there was a non-significant 12 % increase in the mean time that honeybees spent foraging on individual plants and hence potentially depositing self pollen. Taken together, our data indicate that fragmentation affects the performance of *A. mellifera* as a pollinator of *A. marina* and reduce pollinator abundance, leading to pollen limitation in small as compared to large stands, which may negatively affect reproductive output.

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Effects of stand size on pollination in temperate populations of the mangrove

Avicennia marina

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Abstract Populations of the mangrove *Avicennia marina* in the Sydney region exist as stands of varying size, reflecting both natural and anthropogenic fragmentation. We hypothesised that, as observed in many terrestrial forests, small stands (<100 plants) would experience lower pollinator densities and altered pollinator behaviour and visitation and, in consequence, would display reduced pollen deposition as compared with large stands (>10000 plants). Nevertheless, we recognise that such predictions may be overly simplistic because within this region *A. marina* attracts a diversity of flower visitors, but its only significant pollinator is the exotic honeybee *Apis mellifera*. Moreover, it is unclear how readily *A. mellifera* moves among groups of plants within different mangrove stands of varying sizes separated either by water or urban habitat matrix. Our detailed surveys within pairs of large and small stands in two locations support the predictions that pollinator density and pollen deposition are reduced or altered within small stands. Within small stands honeybee abundance and pollen deposition were on average reduced significantly by 84% and 61% respectively. Moreover, within small stands there was a non-significant 12% increase in the mean time that honeybees spent foraging on individual plants and hence potentially depositing self pollen. Taken together, our data indicate that fragmentation affects the performance of *A. mellifera* as a pollinator of *A. marina* and reduce pollinator abundance, leading to pollen limitation in small as compared to large stands, which may negatively affect reproductive output.

Keywords Foraging behaviour, Fragmentation, Mating system, Pollination biology, Southeast Australia

Introduction

In terrestrial forests anthropogenic fragmentation can have profound effects on the abundance of pollinators, or on floral density (that may influence negatively on the abundance of pollinators) (Ghazoul 2005). This again may influence negatively on pollinator behaviour, rates of visitation and pollen deposition because pollinator visitation rates and rates of pollen transfer are reduced, important pollinators are lost and the patterns of pollen transfer are altered (Jennersten 1988; Aizen and Feinsinger 1994; Ghazoul 2005; Collinge 2009). These effects can result in negative consequences for plant reproduction (Murcia 1996; Aizen 1998; Aguilar 2006; Nayak and Davidar 2010). For example, pollen supply, quality or diversity can be limited by reduced flower visitation (Aizen and Feinsinger 1994; Sih and Baltus 1987; Cascante et al. 2002; Newman et al. 2013), the resultant mating system can be altered by changed foraging patterns of pollinators (Steffan-Dewenter and Tschardt 1999), or numbers and genetic diversity of mates can be reduced (Young and Pickup 2010). Separately or together these changes can lead to higher levels of self-pollination and inbreeding in plant populations (Aizen et al. 2002; Ghazoul 2005).

Although the effects of fragmentation on the reproduction of mangroves are unknown, despite their presence within an aquatic matrix, evidence from terrestrial forests suggest that the effects of fragmentation on the mangrove *Avicennia marina* may parallel those observed in terrestrial forests (Aizen et al. 2002; Ghazoul 2005; Aguilar et al. 2006; Collinge 2009). Specifically we expected that temperate *A. marina* forests display altered pollinator abundance and behaviour leading to reduced pollen deposition within small stands (Aizen et al. 2002; Ghazoul 2005; Ward and Johnson 2005; Aguilar et al. 2006; Nayak and Davidar 2010; Chanyenga et al. 2011; Newman et al. 2013). Importantly our own earlier work has shown that in the Sydney region *A. marina* is visited by a broad range of flower visitors, including ants, flies, moths, wasps, beetles, bugs and bees, but the exotic honeybee *A. mellifera*, a major pollinator of terrestrial plants in Australia and worldwide (Butz Huryn 1995; Paton 1993, 1996), always dominated as flower visitor and is currently the only

effective pollinator of temperate *A. marina* (Hermansen et al. 2014). However, not much is known about the effects of fragmentation on bees, including the social honeybees. A review of the effects of fragmentation on bees (Cane 2001) revealed that some authors found increased abundance of bees at flowers in small stands, while other authors found that habitat fragmentation is broadly deleterious for bees. Cane (2001) concluded that we only are beginning to understand the effects of fragmentation on bees. However, a study in Sydney, New South Wales, Australia revealed that the abundance of flowers and the main pollinator *A. mellifera* were significantly reduced in small remnant stands as compared to large re-vegetated stands of the shrub *Dillwynia sieberi* (Lomov et al. 2010). Further, while work with terrestrial plants has shown that *A. mellifera* is capable of travelling distances of up to 11 km to forage (e.g. Pahl et al. 2011), it is also known that when foraging on large terrestrial plants individual *A. mellifera* typically transfer pollen within plants or among near neighbours (Paton 1993; Whelan et al. 2009). For self-compatible plants, *A. mellifera* is therefore likely to produce high rates of self-pollination or biparental inbreeding within stands. Moreover, in temperate *A. marina*, as in fragmented terrestrial forests, it would be expected that, if the number of pollinators in small stands were reduced, more within plant foraging would occur and the level of outcrossing would be lower in small stands (Aizen et al. 2002; Aguilar et al 2006; Hermansen et al. [in review](#)). This seems likely for *A. marina* as a preliminary pollinator exclusion study by Clarke and Myerscough (1991) found that temperate *A. marina* is at least partially self-pollinating, suggesting that reduced pollinator movement or visitation will decrease outcrossing rates. Moreover, using a population genetic approach, we have shown that small stands display significantly lower levels of multilocus outcrossing (Hermansen et al. [in review](#)).

Typically *A. mellifera* is present in urban and bushland areas on the landward margins of our study sites where it is a dominant pollinator (see Homer 2009; Lomov et al. 2010; Hermansen et al. 2014). Little is known about the tendency of *A. mellifera* to fly across estuarine waters on foraging bouts (a foraging bout defined as starting when a honeybee leaves the hive and ending when

returning to the hive; e.g. Lihoreau et al. 2012). The habitat matrix, which is a combination of open water, wetland and terrestrial vegetation, and urban and suburban development, surrounding *A. marina* populations could either intensify or reduce any effects of stand size. Nevertheless, social bees such as honeybees seem to be less sensitive to changes in matrix within urban areas than other bees (Steffan-Dewenter et al. 2002), indicating that it is likely easier for honeybees to adapt to new environments.

Here we investigate the effects of stand size, on the abundance of pollinators and pollinator visitation and the resultant deposition of pollen on floral stigmas, and on the density of floral shoots, by comparing two large and two small stands of *Avicennia marina* from estuaries at Sydney and Minnamurra in southeast Australia. Based on the predictions that small stands would experience reduced pollinator abundance and altered foraging behaviour, resulting in reduced pollen deposition, and these effects would be boosted by reduced floral density in small stands, we specifically ask whether within small *A. marina* stands: (1) the production of floral shoots is reduced? And whether *A. mellifera*: (2) is less abundant? (3) displays altered patterns of foraging within and among floral shoots and trees? (4) effects lower levels of pollen deposition?

Materials and Methods

Study sites

The study was carried out in mangrove forests dominated by *A. marina* at two locations within the Sydney and Minnamurra regions, New South Wales, Australia. We selected one large (> 10000 trees) and one small (ca. 100 trees) stand within each of the Sydney and Minnamurra regions (Fig. 1). The large and the small stands, respectively, occupied approximately the same area at each location (large ca. 300000 m² and small ca. 1500 m²), yielding similar densities of trees in all stands. All stands were roughly rectangular with lengths at least twice their width. In Sydney the

large stand was located at Salt Pan Creek (33°56'47" S; 151°2'26" E), which forms a branch on the northern side of the Georges River, and the small stand was located at Five Dock Bay (33°51'8" S; 151°8'39" E) on the southern bank of the Parramatta River. In Minnamurra, the large stand was selected at Kiama Downs (34°38'15" S; 150°50'49" E) and the small stand near the Minnamurra River entrance (34°37'24" S; 150°51'13" E).

The large stand in Sydney is within an urbanized landscape with both a highway and public pedestrian pathways dissecting it, whereas the large stand in Minnamurra is within an agricultural landscape and surrounded by houses on its landward edge. Houses and open grassland border the small stand at Sydney and Minnamurra. The large stands are dominated by *A. marina*, with the smaller mangrove *Aegiceras corniculatum* occurring on their landward edge. Both large stands extend landward into salt marshes and are bordered by the dominant salt marsh chenopod *Sarcocornia quinqueflora*. Flowering plants from urban and suburban gardens (0-400 m from the stands), grassy areas (0-200 m from the stands), and small patches of terrestrial forest (0-250 m from the stands) flower simultaneously with *A. marina* at this latitude. The small stands are exclusively *A. marina* (not bordered by saltmarsh) and adjacent habitat includes various flowering plants from gardens and grassy areas (lawns and parks), situated 0-21 m from the stands, that flower simultaneously with *A. marina*.

Investigations of the large stands were confined to the landward edge of the stands, whereas for small stands we used both the landward edges and sides of stands in order to obtain a larger number of observation sites. The sides of the small stands were flanked by mudflat, which were exposed during low tide. Observations were done on *A. marina* trees of intermediate height (5-10 m), with approximately 200 floral shoots per m² (a density near maximum during the investigated flowering seasons). Investigations were conducted from mid to late summer (mid January to mid March) of the flowering seasons of 2009 and 2010 and on sunny days with temperatures in the shade between 16.4 and 33.8°C in Sydney and between 13.9 and 28.2°C in Minnamurra. The study

was confined to days of sunny weather because preliminary observations on cloudy days revealed substantially lower and highly variable abundances of honeybees (Hermansen unpublished data).

Flowering and pollination of *A. marina*

Avicennia marina is a hermaphroditic species with yellow flowers organized in clusters, and these clusters are further organized into a branched inflorescence (or a compound syeme: Simpson 2006) where the flowers are arranged in clusters of three to 14 flower buds, and two to seven clusters of flowers develop from a floral shoot (see Clarke & Myerscough 1991) (hereafter the term floral shoot will be used throughout the text). Flowers are small (≈ 5 mm tall and ≈ 5 mm wide), each with a stigma of 1.5-2.0 mm in length, and four anthers are anchored on the petals at a height approximately level with the stigmatic surface (Duke 1990, 2006; Clarke and Myerscough 1991). In the Sydney and Minnamurra regions, *A. marina* typically flowers from January to April (e.g. Duke 2006). Individual flowers are open for 2-5 days and a flower cluster has open flowers for 2-4 weeks. A flower can produce up to 16000 pollen grains and four ovules (Duke 1990; Clarke and Myerscough 1991).

The abundance of flower visiting honeybees

The effect of stand size on the abundance of honeybees visiting flowers of *A. marina* was tested at each of two sites in Sydney and Minnamurra, respectively, during the flowering season of 2009. To measure the abundance of honeybees during the day, the numbers of honeybees visiting 10 m² areas of canopy (4.0 m wide by 2.5 m high, and measured from the lowest point of the canopy, approximately 0.25 m above the ground, to a height of 2.75 m) were counted during each of seven, 2 h intervals (with each interval done on different days) covering the period from sunrise to sunset

(6 am-8 pm). In total counting was done during 56 hours scattered over 28 days. Counts were made at two different sites within each stand during either the first or the second hour of each 2 h interval. In each case bees were counted every 10 minutes, giving 6 counts per hour and in total 336 counts. Within the large stands the two sites were separated by 100-150 m and in the small stands they were separated by 20-30 m (a distance proportional to stand size). As the canopies of trees often overlap, each 10 m² area of canopy covered at least two trees and the honeybees could move freely between these trees. Finally, all honeybees observed in the 10 m² areas on which abundance was measured were also observed to be flower visitors.

Foraging of honeybees within floral shoots and trees

To compare the duration of foraging by honeybees within individual floral shoots and trees in the large and small stands during the flowering season of 2009, we quantified the foraging behaviour of (i) 200 honeybees on individual floral shoots within each stand (i.e. 200 independent observations per stand), and (ii) 55 honeybees on individual trees within each stand (i.e. 55 independent observations per stand). The duration of foraging within individual floral shoots or trees was measured using a stopwatch and observations were spread evenly across the seven, 2 h sampling intervals as described above (see *The abundance of flower visiting honeybees* subsection). Further, to determine the number of movements between floral shoots we observed 280 honeybees that were foraging on floral shoots of a single tree or a pair of neighbouring trees with overlapping canopies within small and large stands, respectively.

Pollen deposition on stigmas of *A. marina* flowers

To test the effect of stand size on pollen deposition during the flowering seasons of 2009 and 2010, a total of 150 flowers per year were harvested from each of the two large and two small stands (i.e. a total of 1200 flowers). In each year for each stand, fifty randomly chosen flowers (10 from each of five randomly chosen trees) were harvested, on each of three days, at three weeks intervals across the flowering season. The number of pollen grains per stigma was counted under a stereomicroscope (60x magnification) where it was possible to count them directly on the stigma (*in situ*). Pollen grains from the stigma of 50 flowers from each stand were captured on the tip of a needle and added to a drop of water prior to identification and photographed using an Olympus BHA 1.2 X dissection microscope at 120x magnification and a Nikon D300 camera.

Production of floral shoots of *A. marina*

We tested if pollinator abundance was influenced by the effect of stand size on the production of floral shoots. To estimate the density of floral shoots we counted all shoots on 50 haphazardly chosen trees within the two large stands and 17 and 19 trees (all available trees) within the two small stands during the flowering season of 2009. Trees were chosen because their canopies were distinct allowing thorough counts. However, because branches from other trees visually covered a part of the canopy in some cases, only a third of the floral shoots of a canopy were counted, and the result was multiplied by three. In each case the number of floral shoots was counted in the beginning of February when all shoots had been formed

Statistical analysis

To assess the effect of stand size on the number of honeybees visiting the floral shoots of *A. marina* a three factor analysis was used, where factors were location (Sydney or Minnamurra; L - random), stand size (Large or Small; S - fixed) and time interval (6-8 am, 8-10 am, 10-12 am, 12-2 pm, 2-4 pm, 4-6 pm or 6-8 pm, T - fixed). To assess the effect of stand size on the foraging duration of individual floral shoots or trees, the pollen deposition and the production of floral shoots, a two-factor analysis was used, where factors were location (Sydney or Minnamurra; L - random) and stand size (Large or Small; S - fixed). Data were appropriately pooled and transformed with $\text{Sqrt}(X+1)$ or $\text{Ln}(X+1)$ to normalise data and reduce variance heterogeneity. All ANOVA analyses were based on balanced designs and analysed using the statistical software WinGmav5. A two-tailed paired t-test was used to determine differences in the number of insect species (i.e. species richness) visiting large versus small stands.

Results

The abundance of flower visiting honeybees

The number of honeybees (*A. mellifera*) visiting *A. marina* flowers varied throughout the day in a similar manner within both large stands and small stand at Minnamurra and within the large stand at Sydney, with their abundance increasing steadily from six am to a peak at approximately noon (12-2 pm), followed by a steady decline until eight pm (Fig. 2a, b). In contrast there was no discernable peak of honeybee abundance within the small stand in Sydney where the plants of *A. marina* received fewer overall visits. Indeed these results are reflected in a strong three-factor interaction for the effect of location, stand size and time interval on honeybee abundance (ANOVA, $F=5.31$; $P<0.001$, $df_{6, 308}$) (Fig. 2).

The greatest abundance of honeybees was observed within the large stand in Sydney at midday (12-2 pm), where the numbers were almost 20 orders of magnitude greater than in the small stand in Sydney (on average 78 honeybees in the large and 4 in the small stand during midday) (Fig. 2a). At Minnamurra the corresponding difference was 43% (on average 21 honeybees in the large and 12 in the small stand during midday) (Fig. 2b). Overall we detected an average of 49.5 ± 0.8 (mean \pm SE) honeybees at the large and 8.0 ± 0.2 at the small stands (on average ca. 6x higher abundance in large stands).

The duration of foraging and number of movements

Comparisons of foraging behaviour designed to assess the potential of pollinators to increase the level of selfing revealed slight but not significant effects of stand size on the duration of foraging on individual floral shoots ($F=3.65$; $P=0.057$, $df_1, 797$) and trees ($F=2.05$; $P=0.388$, $df_1, 216$), with honeybees on average foraging for 10% and 12% longer in small as compared to large stands on shoots and trees, respectively. There was significant variation in foraging time among locations for both floral shoots ($F=70.60$; $P<0.001$, $df_1, 797$) and trees ($F=4.49$; $P=0.035$, $df_1, 797$), but no significant interaction effects ($P>0.05$) (Fig. 3).

Of 280 honeybees observed foraging on floral shoots, 88 foraged within individual trees and 192 moved between immediately neighbouring trees. Among the 88 honeybees foraging on individual trees we recorded almost identical numbers of movements between floral shoots, with 30 ± 2 movements (mean \pm SE) in the large and 33 ± 2 movements in the small stands, a difference of 9% between large and small stands. Of the 192 honeybees observed to move between immediately neighbouring trees with overlapping canopies, the number of movements between floral shoots was also almost identical, with 52 ± 2 movements (mean \pm SE) in the large and 54 ± 2 movements in the small stands. Nevertheless, at the end of these foraging events, honeybees within small stands were

more likely to continue their foraging bout by visiting other more distant trees within the stand (92 of 140 observations in small stands as compared to 57 of 140 observations in large stands) ($\chi^2 = 5.8$; df_1 ; $P < 0.05$).

Pollen deposition on stigma of *A. marina* flowers

The average number of pollen grains (mean \pm SE) deposited on the stigmas of *A. marina* flowers was substantially greater in the large (11.8 ± 0.7 pollen grains and 9.9 ± 0.6 pollen grains) than in the small stands (2.9 ± 0.4 pollen grains and 5.5 ± 0.6 pollen grains) in Sydney and Minnamurra, respectively, giving a difference of 75% between large and small stands in Sydney and 44% in Minnamurra (Fig. 4). These results are reflected in a strong two-factor interaction for the effect of stand size and location on pollen deposition (ANOVA, $F=31.91$; $P < 0.001$, $df_{1, 1196}$). Within the large stands only 7% of 600 (300 from each stand) stigmas examined did not carry any pollen grains, as compared to an average of 19% of 600 stigmas in small stands. Nevertheless pollinator fidelity did not vary with stand size, with on average 47 of the sets of 50 flowers examined per stand displaying only *A. marina* pollen grains and on average only 6% of all pollen grains examined was from other species, which was significantly lower compared to the number of *A. marina* pollen grains ($\chi^2 = 19.1$; df_1 ; $P < 0.001$).

Production of floral shoots of *A. marina*

The effect of stand size on the number of floral shoots produced per tree (Fig. 5) was not significant ($F=2.28$; $P=0.372$, $df_{1, 1196}$). On average 35% and 8% fewer floral shoots was produced per tree in small stands as compared to large stands in Sydney and Minnamurra respectively. Also the effect of location was not significant ($F=0.01$; $P=0.938$, $df_{1, 1196}$), with mean values of 1015 ± 109 and $983 \pm$

118 in Sydney and Minnamurra respectively. The interaction between the effect of stand size and location was not significant ($F=1.45$; $P=0.233$, $df_{1, 1196}$).

Discussion

We predicted that the abundance, visitation and levels of pollen deposition of the exotic honeybee *Apis mellifera* would be significantly reduced in small as compared to large stands, and that these effects would be boosted by reduced floral density in small stands. To our knowledge such effects of fragmentation have never been investigated in mangroves but comparisons can be made with results for fragmented terrestrial plant populations. Indeed, our findings closely match results from terrestrial forests where a frequent effect of fragmentation and reduced stand size is reduced pollinator abundance and pollen transfer (Jennersten 1988; Aizen and Feinsinger 1994, Aguirre and Dirzo 2008; Nayak and Davidar 2010). Overall our study revealed that, as for terrestrial forest plants, small stands receive fewer pollinators and display reduced pollen deposition when compared to large stands (Bierzychudek 1981; Burd 1994; Aizen et al. 2002; Ghazoul 2005; Aguilar et al. 2006, Newman et al. 2013). Our observations suggest that this reflects a combination of changed foraging behaviour and significantly reduced pollen deposition by *A. mellifera* within small stands. Our data also suggest that variation in floral density did affect the abundance of *A. mellifera*, but reduced pollen deposition reflected a significant effect of stand size on the abundance of *A. mellifera*.

Reduced pollinator abundance and pollen deposition

The matrix surrounding the investigated stands of *A. marina* includes a range of different types of vegetation including small patches of terrestrial forest, urban gardens, saltmarsh and grassland, which could potentially influence the suite of species visiting the flowers of *A. marina* (see

Hermansen et al. 2014). However, the only effective pollinator in this and our earlier study was the exotic honeybee *A. mellifera*, which was always the most abundant visitor (Hermansen et al. 2014). Small stands displayed correspondingly lower levels of pollen deposition and greater numbers of stigmas that lacked pollen. On average 9-11 pollen grains were deposited on stigmas of flowers taken from the two large stands (and on average 3-6 pollen grains on stigmas of flowers from the two small stands), which is similar to values reported from stands of temperate *A. marina* in the area of Sydney by Clarke and Myerscough (1991), who found on average nine pollen grains per stigma. These results are supported by observations for many terrestrial plants, which show evidence of reduced pollinator abundance and pollen limitation in small stands, resulting in disruption of reproductive output (Bradshaw and Marquet 2003; Ward and Johnson 2005; Aguilar et al. 2006; Nayak and Davidar 2010; Newman et al. 2013).

Altered foraging behaviour may lead to increased inbreeding

The present study suggests that within both large and small stands honeybees typically disperse *A. marina* pollen grains within individual trees and between immediately neighbouring trees which is congruent to results from terrestrial plants (Paton 1993; Whelan et al. 2009), although our data suggest that within small stands honeybees may effect slightly higher proportions of self-pollen transfer (i.e. the duration of foraging within floral shoots and trees were approximately 10% and 12% higher in small stands than large stands). In an earlier genetic survey we found that a high level of biparental inbreeding occurs within all stands (Hermansen et al. in review), which is supported by results from terrestrial studies where honeybees forage within small groups of trees for longer periods (Paton 1993; Whelan et al. 2009). Finally, when honeybees left a tree or pair of immediately neighbouring trees, on average 41% of these honeybees in the large and 66% in the small stands (a difference of 38%) flew to a nearby site of the same stand and started foraging

again. In this case the difference between large and small stands was statistically significant although the effect this would have on mating patterns or fitness is unclear. Honeybees not observed to visit another tree within the same stand might either visit another stand or return to their hive. If they visit another stand it may increase the possibility of outcrossing while returning to the hive may increase the possibility of inbreeding. Nevertheless, our genetic survey revealed a significant reduction of outcrossing in small temperate stands of *A. marina* on Georges and Parramatta River's in Sydney (Hermansen et al. in review).

Conclusion

Our data imply that, although small *A. marina* stands are currently serviced by the same pollinator as large stands, altered patterns of foraging in combination with reduced pollinator visitation results in pollen limitation and potentially reduced availability of outcross pollen within small stands. This reduction in the quality of pollinators foraging and rates of visitation in small stands would be predicted to result in both lower levels of outcrossing in small stands (which may reduce the fitness of progeny) and lower levels of fertilization (which may result in lower seed production). Within all stands the fact that among plant pollinator movements were typically between pairs of plants with overlapping canopies implies that the majority of outcross events will result from biparental inbreeding. These predictions are supported by the outcomes of recent genetic surveys of the progeny arrays of *A. marina* plants within Sydney estuaries which confirmed that all stands display high levels of biparental inbreeding but that multilocus outcrossing rates are significantly higher in large stands (Hermansen et al. in review).

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Figure legends

Fig. 1 Map of Australia highlighting the locations of the two large and small stands on Parramatta River, Georges River and Minnamurra River.

Fig. 2 Mean (\pm SE) number of honeybees visiting *A. marina* within large and small stands of *A. marina* in (a) Sydney and (b) Minnamurra. Visitation to eight flower clusters was measured by 12 counts of honeybees, during each of seven 2 h intervals spread across the daylight hours of the 2009 flowering season.

Fig. 3 Mean (\pm SE) duration of honeybee foraging within (a) floral shoots and (b) trees, from large and small stands at each of two locations (Sydney and Minnamurra) during the 2009 flowering season.

Fig. 4 Mean (\pm SE) number of deposited pollen grains on stigmas of *A. marina* flowers within large and small stands in Sydney and Minnamurra. A total of the 150 stigmas were harvested from each of the four stands during the flowering seasons of 2009 and 2010.

Fig. 5 Mean (\pm SE) number of floral shoots produced per tree by *A. marina* from 50 trees of each of the two large stands and 17 and 19 trees from the small stands in Sydney and Minnamurra, respectively.

Fig. 1

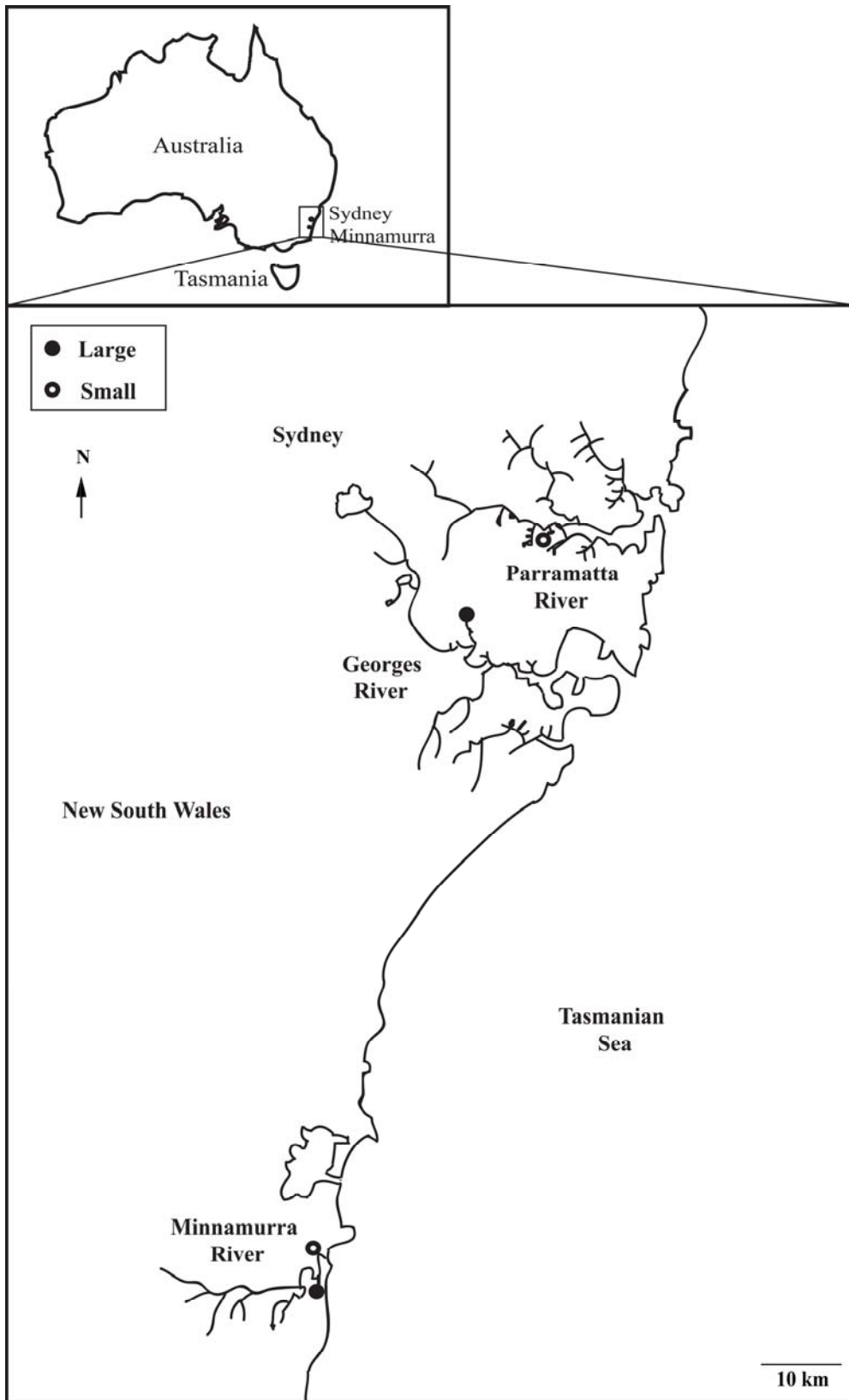


Fig. 2

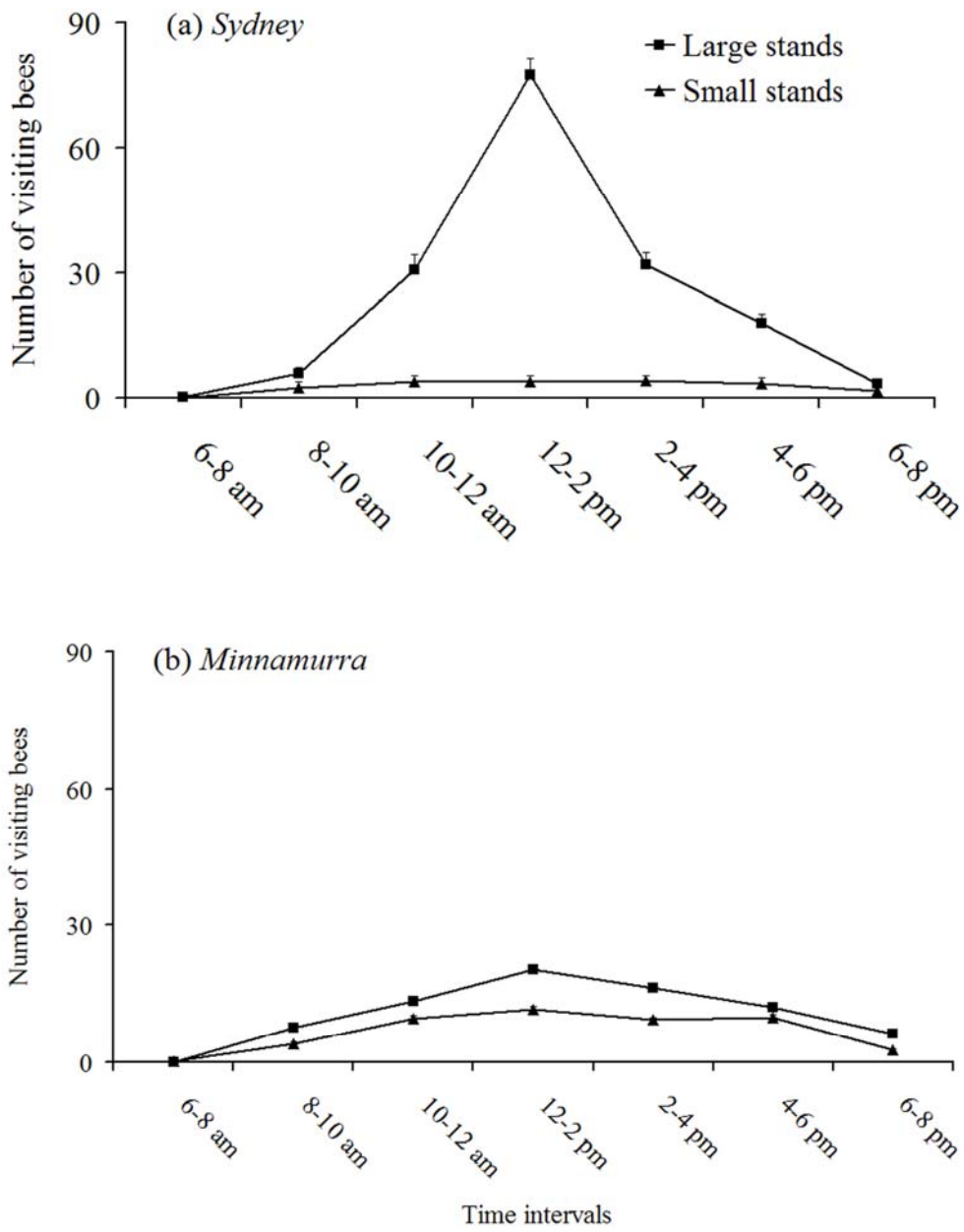


Fig. 3

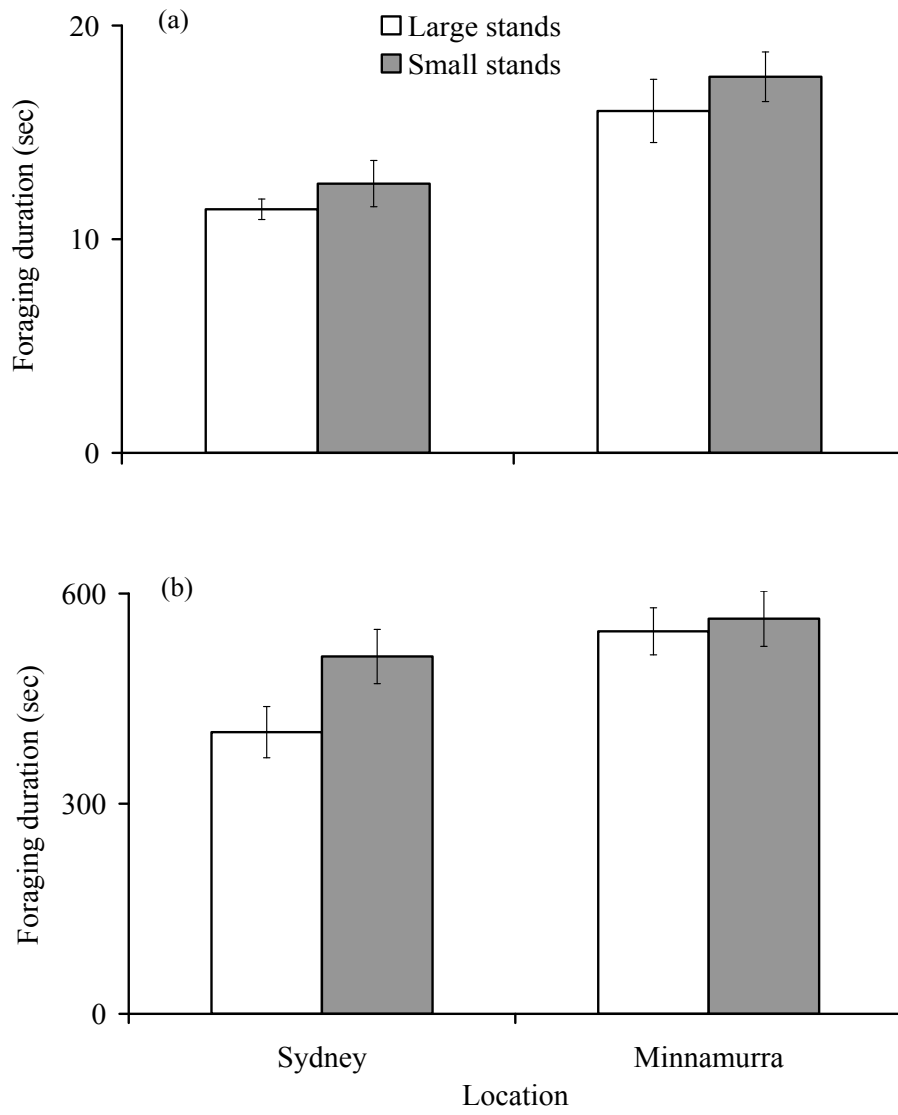


Fig. 4

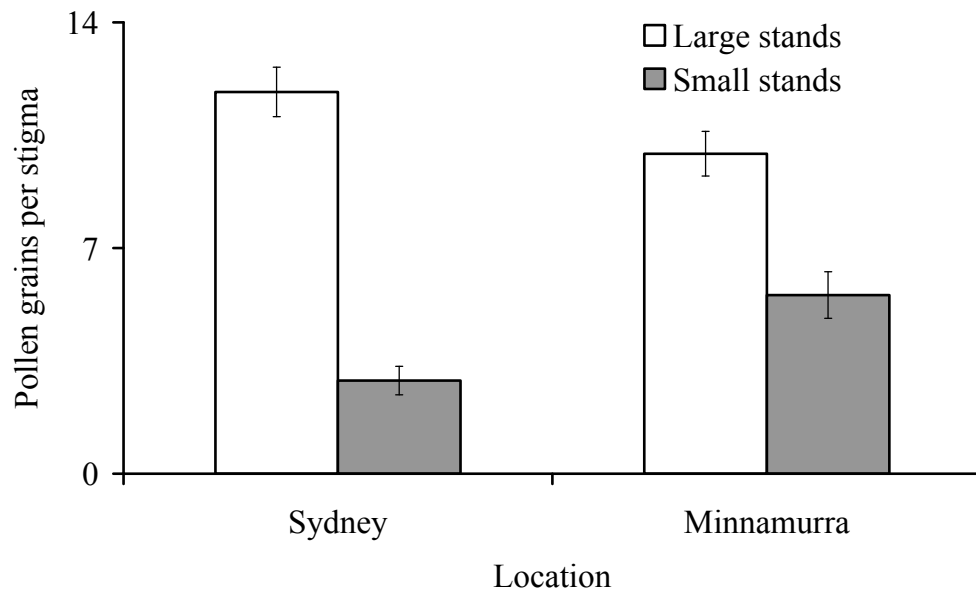


Fig. 5

