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Habitat fragmentation leads to reduced pollinator visitation, fruit production and recruitment in urban mangrove forests

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Abstract

Mangrove forests worldwide undergo anthropogenic fragmentation that may threaten their existence, and yet there have been few tests of the effects of fragmentation on demographic processes critical for mangrove regeneration. Predicting the effects of habitat fragmentation on mangroves is problematic as pollinators may move more freely across water than terrestrial habitat, and propagules can be widely dispersed by water. Here, within each of two estuaries, we compared pollinator diversity and activity, reproductive effort and output, and rates of recruitment for sets of three large (> 1500 trees), medium (300-500) and small (< 50) stands. As predicted, most measures of reproductive activity and success were inversely related to stand size with large stands typically producing significantly more and larger fruit, and significantly more seedlings. Most strikingly, we found the effect of fragmentation on the abundance of pollinators (honeybees), the production and quality of fruit and the survival rate of seedlings to be similar, showing significant reduction of recruitment in small stands. This study provides the first rigorous evidence that recruitment of mangroves, like for many terrestrial plants, is negatively impacted by habitat fragmentation. From a management perspective, we argue that in the short term our data imply the importance of conserving the largest possible stands. However, additional work is needed to determine (1) the proportion of recruits within small stands that originate within large stands, (2) how seedling performance varies with fruit size and genotype, and (3) how seedling size and performance vary with the abundance and diversity of pollen.

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Habitat fragmentation leads to reduced pollinator visitation, fruit production and recruitment in urban mangrove forests

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Abstract Mangrove forests worldwide undergo anthropogenic fragmentation that may threaten their existence, and yet there have been few tests of the effects of fragmentation on demographic processes critical for mangrove regeneration. Predicting the effects of habitat fragmentation on mangroves is problematic as pollinators may move more freely across water than terrestrial habitat and propagules can be widely dispersed by water. Here, within each of two estuaries, we compared pollinator diversity and activity, reproductive effort and output, and rates of recruitment for sets of three large (>1500 trees), medium (300-500) and small (<50) stands. As predicted, most measures of reproductive activity and success were inversely related to stand size with large stands typically producing significantly more and larger fruit, and significantly more seedlings. Most strikingly, we found the effect of fragmentation on the abundance of pollinators (honeybees), the production and quality of fruit and the survival rate of seedlings to be similar, showing significant reduction of recruitment in small stands. This study provides the first rigorous evidence that recruitment of mangroves, like for many terrestrial plants, is negatively impacted by habitat fragmentation. From a management perspective we argue that in the short term our data imply the importance of conserving the largest possible stands. However, additional work is needed to determine (i) the proportion of recruits within small stands that originate within large stands, (ii) how seedling performance varies with fruit size and genotype, and (iii) how seedling size and performance varies with the abundance and diversity of pollen.

Keywords *Apis mellifera*; Australia; invasive species; mating system; population ecology

Introduction

Although the impacts of habitat fragmentation on reproductive success and regeneration of terrestrial plant species have been well documented (e.g. reviewed by Aizen et al. 2002; Ghazoul 2005; Aguilar et al. 2006), the demographic effects of fragmentation in mangrove forests have been largely ignored. This is surprising because, although mangroves have naturally fragmented distributions (Tomlinson 1986; Duke 2006; West et al. 1985), urbanisation and coastal development have increased the fragmentation of mangrove forests (reviewed by Rogers 2004), producing stands ranging from thousands of trees to isolated individuals (West et al. 1985). Urban mangrove populations may therefore experience demographic impacts of reduced stand size similar to those of terrestrial plant species (Collinge 2009; Nayak and Davidar 2010; Newman et al. 2013), affecting their capacity for regeneration and persistence. Nevertheless, in some regions mangroves have expanded their distributions, sometimes due to anthropogenic development that has increased sedimentation into estuaries (e.g. New Zealand: Stokes 2010; North America: Cavanaugh et al. 2013: Australia: Adam 2002; Duke 2006). Newly created stands, in combination with remaining fragments, provide a setting for rigorous tests of the effect of stand size on reproductive and demographic processes that would mirror changes seen if a large forests underwent fragmentation (e.g. Hermansen et al. 2014a).

In terrestrial forests, pollinator abundance is proportional to fragment size (Ghazoul 2005; Nayak and Davidar 2010), and can influence the success of reproduction and recruitment (Aguilar et al. 2006), with smaller fragments being the least resilient (e.g. Collinge 2009). Such effects may also be expected in mangroves, although predicting the influence of fragmentation in mangrove forests is made difficult by lack of knowledge of the capacity of pollinators to move among stands that are typically separated by water, and the extent to which waterborne dispersal of mangrove propagules reduces the isolation of stands (e.g. Minchinton 2006). In our preliminary investigations of the temperate estuaries of Sydney in Australia, we found the exotic honeybee *Apis mellifera* was the only effective pollinator of the mangrove *Avicennia marina* and was numerically dominant among the insects visiting flowers (Hermansen et al. 2014a), but it is not known whether this situation is consistent within estuaries. We also found reduced fruit set (but only significant for fruit produced per floral shoot: see Hermansen, 2013), and it is not known whether this effect is consistent or influences fruit performance and seedling recruitment. Our preliminary results suggest that stand size might influence the abundance of flower visitors and pollinators, the production of fruit, and the recruitment of seedlings, and thus influence the stand persistence.

The impacts of fragmentation on mating systems of terrestrial plants typically vary with the identity and behaviour of their pollinators, and pollinator disruptions can impact negatively on reproductive success (Aizen et al. 2002). The honeybee *A. mellifera* often forages on terrestrial plants, as well as temperate *A. marina*, in a manner promoting the transfer of pollen between flowers on a single tree or a set of trees in close proximity (Paton 1993; Whelan et al. 2009; Gilpin et al. 2014; Hermansen et al. 2014b). Because pollinator abundance is typically inversely related to stand size, such behaviour can reduce the level of outcrossing if pollen supply is limiting seed set (in small as compared to large stands), and individual pollinators carry only a small proportion of outcross pollen (Moeller et al. 2012). Indeed, in our study using genetic data from populations of temperate *A. marina* in Sydney estuaries, we demonstrated significantly reduced outcrossing rates in small stands as compared to large stands (Hermansen et al. 2015), suggesting potential impacts of fragmentation on reproductive performance and recruitment. We believe the effects of fragmentation as revealed by our results may reflect a more general picture of how fragmentation affects mangroves because they are surprisingly consistent with effects of fragmentation reported for a range of terrestrial plants.

Here we investigate the influence of stand size on visitation by the pollinator *Apis mellifera* and by other flower visitors, and on key demographic processes in the mangrove *Avicennia marina*. We use a spatially replicated design and compare these processes in small, medium and large stands within two urbanised estuaries with fragmented populations of the mangrove *A. marina* in Sydney, Australia. Specifically we test the hypotheses that (1) the abundance of *A. mellifera,* (2) the production and quality of fruit, and (3) the recruitment of seedlings, is inversely related to stand size of the mangrove *A. marina*.

Materials and methods

The mangrove *Avicennia marina*

Avicennia marina is a hermaphroditic mangrove species with yellow flowers each carrying four anthers and four ovules (Tomlinson 1986; Clarke and Myerscough 1991), and it is believed to be dependent on animals for pollination (Tomlinson 1986; Clarke and Myerscough 1991; Hermansen et al. 2014a). Flowers are developed from flower clusters extending from floral shoots (Clarke and Myerscough 1991), and organized as a compound cyme (a branched inflorescence: Simpson 2006; hereafter referred to as a floral shoot). In the present study *A. marina* flowered from mid January to mid March (Duke 2006; Clarke and Myerscough 1991), and mature fruit developed during several months and fell from trees from October to December (Duke 2006; Clarke and Myerscough 1991), after which they established and developed into seedlings (Minchinton and Dalby-Ball 2001). Fruit of *A. marina* are single seeded, sexually generated (Hermansen et al. 2015), cryptoviviparous (Kathiresan and Bingham 2001), and covered by a pericarp which provides buoyancy and dispersal by water (Saenger 2003; Minchinton 2006).

Study region and sampling design

This study was performed within the temperate, highly urban estuaries of the Parramatta River and Georges River (including the Woronora River tributary) in Sydney, Australia (Fig. 1). These estuaries are separated by ca. 20 km over land and by water at their mouths and contain numerous stands of *A. marina* of various sizes. The landscape matrix of these estuaries (excluding the extensive residential, commercial and industrial developments) includes stretches of water, patches of coastal saltmarsh and terrestrial habitats, and urban gardens, and all contain species of plants that flower simultaneously with *A. marina*. However, there were some differences between the mangrove stands within the two estuaries. Stands on the Parramatta River were more often surrounded by urban areas than those on the Georges River. Paramatta River was also generally more industrialized. On the Parramatta River the distance to the nearest large terrestrial forest area dominated by Eucalypt trees (Garigal National Park) was ca. 10 km, while the stands on the Georges River were located only ca. 5 km from the nearest large terrestrial forest area also dominated by Eucalypt (Royal National Park).

Within each estuary, nine stands of mangrove forest were selected: three large (>1500 trees), three medium (300-500 trees) and three small (< 50 trees) (Fig. 1). Stands were chosen so there was interspersion of the various stand sizes along each of the estuaries (Fig. 1). Large adult stands of >1500 trees were distributed over 15000 – 40000 m^2, intermediate stands of 300-500 trees were distributed over 5500 – 9000 m^2 and small stands of < 50 trees were distributed over

600 – 1600 m^2. Stands were separated by minimum Euclidian distances of 240 and 100 m and watercourse distances of 265 and 100 m, and by maximum Euclidean distances of 3.08 and 3.78 km and watercourse distances of 3.92 and 7.36 km, within the Parramatta River and Georges River estuaries, respectively.

Due to their locations along rivers bordered by urbanised land, all stands were roughly rectangular, and in most cases, lengths were at least twice their widths. Along the Parramatta River the mangrove stands were exclusively *A. marina*, whereas along the Georges River only two small stands were exclusively *A. marina*. In one small stand two trees of the smaller mangrove *Aegiceras corniculatum* were found, while in all the large and medium stands of the Georges River, *A. marina* were flanked by *A. corniculatum*, either on the landward or the seaward sides. Tree height varied little with stand size and investigated trees were 5-10 m tall. All stands investigated in this study may have originated within the last 100 years and developed either on areas that were cleared of mangroves since the early 19th century or on mudflats formed by sediment from runoff of the cleared forest areas (Thorogood 1985; Dunstan 1990; McLoughlin 2000; Adam 2002). Indeed all stands within the Parramatta River and seven within the Georges River (Fig. 1) can be confirmed to be of new origin using aerial photos (Hermansen et al., 2015), although individual tress may be older.

Abundance of honeybees and other insects

We used video cameras (JVC Evario HD; Sony Handycam HDR; Sony Handycam) to investigate the effect of stand size on the number of honeybees and other insects foraging on *A. marina*. Recordings were made on each of six, randomly selected replicate trees in each of nine mangrove stands (three large, three medium, three small) from each of the two estuaries (Parramatta and

Georges Rivers). Only trees bearing floral shoots were chosen, and the visitation of honeybees and other insects to 1 m^2 areas (0.75 m x 1.35 m) of canopy was recorded. Because the location of flowers varied among trees, recordings were done in a band one to three meters above the ground. Visitors to each tree were recorded on one occasion for 30 minutes on different days during the flowering season of 2010. Videos were recorded between 11 am and 3 pm because this is the time of maximal abundance of honeybees (Hermansen et al. 2014b). For each recording the number of honeybees and other insects visiting the targeted area of canopy during the 30 min interval was counted. Every time a honeybee or another insect was entering the recorded area it was counted as a new arrival (so it is possible that in a few cases individual insects were counted more than once). All recordings were done in sunshine with temperatures ranging between 19.3°C and 28.7°C.

Production of fruit

We tested the hypothesis that the number of fruit produced (expressed per floral shoot and per tree) was inversely related to stand size following flowering in 2010. The same sampling design (replicate trees within three stands of each size in each of two estuaries) was used as described above (see Abundance of honeybees), but here the number of fruit per tree and per floral shoot was quantified across the whole canopy of each tree. This was done for 20 randomly selected, replicate trees in all large and medium stands and, due to availability, for only eight, 14 and 17 trees from small stands along the Parramatta River and nine, 10 and 20 trees from small stands along the Georges River. Within each stand, the number of fruit present at the beginning of October, immediately before first fruit-fall, was counted. In some cases branches from other trees obscured part of the canopy and, therefore, fruit could only be counted on half of the canopy, and in these cases numbers were multiplied by two.

To test for the effect of stand size on the biomass of fruit (which are mainly composed of nutrient rich cotyledons for the early growth of seedlings: e.g. Tomlinson 1986; Minchinton 2001) we sampled undamaged mature fruit on the forest floor immediately after they fell from the trees during November and December 2010. From each of the nine stands in the two estuaries, 25 fruit (with pericarp) were collected beneath each of ten randomly selected trees. Fruit were then weighed fresh after blotting dry with a paper towel (pericarps could hold a tiny amount of water that would not entirely be removed by blotting dry), and the average fruit biomass per tree was calculated for each stand and used as the unit of replication for analysis.

Density of fruit and the resultant seedlings

To determine the effect of stand size on the density of mature fruit that had fallen onto the forest floor and the resultant successfully established seedlings, we quantified within each stand both the number of fruit per m^2 immediately after the period where the abscission of fruit from trees had peaked (and thus the density of fruit on the forest floor was greatest), the number of newly established seedlings per m^2, and the number of seedlings per m^2 surviving for three months, a time when most cotyledonary reserves would have been exhausted (Minchinton 2001). These surveys of fruit and seedling recruitment were performed during the season of 2010, and fruit were counted at the end of November 2010, the number of new established seedlings at the end of December 2010, and the number of surviving seedlings at the end of March 2011. For each of the three surveys, fifty 1 m^2 quadrats were randomly sampled in each of the nine stands in each estuary.

Statistical analyses

Three factor, nested analysis of variance (ANOVA) was performed to test for significant effects of Location (random factor: Parramatta River and Georges River), Size (fixed factor: Large, Medium or Small), and Stands (random factor nested within Location and Size) on eight response variables (i.e. density of honeybees or other insects; number of fruit per floral shoot or per tree; fruit biomass; and density of fruit, newly settled seedlings, or surviving seedlings). Because in small stands there were fewer than 20 trees upon which to estimate numbers of fruit per tree and numbers of fruit per floral shoot, this resulted in an unbalanced design. Therefore we performed two separate analyses for each of these variables. In the first, we balanced the design by randomly removing data until there were eight replicate trees (the lowest number sampled in a stand) for each of the stand sizes in each estuary and performed the three factor, nested ANOVA as outlined above. In the second we used all of the data: we calculated average values for each of the two variables for each stand, and used stands as replicates in a two factor ANOVA (Location as a random factor, Size as a fixed factor). Outcomes were identical and for consistency we present the results of the three factor, nested ANOVA. For all analyses, data were transformed to Sqrt(X+1) or Ln(X+1) as necessary, and Cochran's test subsequently failed to detect significant heterogeneity of variances. Student–Newman–Keuls (SNK) multiple comparisons tests were used to resolve differences among means following ANOVA. All designs were balanced and they were analysed using the statistical software WinGmav5.

Results

Although there was variation between stands of *A. marina*, there was a remarkably consistent inverse relationship between stand size and the abundance of pollinators and other flower visitors, the production and size of fruit and the density of fruit and seedlings (Fig. 2 to 4).

Abundance of honeybees and other insects

Honeybees were by far the most abundant flower visitors but visitation rates for both honeybees and all other insect visitors displayed a significant inverse relationship with stand size (Fig. 2, Table 1).

We observed a strong and significant inverse relationship between the numbers of honeybees visiting *A. marina* flowers and stand size. For both estuaries the average abundance of honeybees detected within large stands was almost double that detected within medium stands and more than three times that detected within small stands and this effect was significant and consistent across estuaries (Fig. 2a, Table 1a). Further, the abundance of honeybees was always almost twice as great for stands of all sizes on Parramatta River (overall mean = 17) than on Georges River (overall mean = 8) (Fig. 2a, Table 1a).

The visitation rates of insects other than honeybees also varied significantly with stand size and estuary (Fig. 2b, Table 1b), although their abundances did not vary between small and medium sized stands (Fig. 2b, Table 1b). Insects observed to visit flowers in the present study included flies, moths, wasps, beetles and bees, with flies and wasps the most common visitors (Table 1b).

Production of fruit

Similar to the abundance of honeybees and other insects, there was a trend for the production and biomass of fruit to be inversely related to stand size and to be greater at Parramatta than Georges River.

Our results revealed a significant effect of stand size on the production of fruit per floral shoot. In both estuaries small stands produced fewer fruit per shoot as compared with the medium and large stands that produced similar numbers of fruits per shoot (Figure 3a, Table 2a). On Parramatta River fruit production in medium and large stands was ca. one third greater, and on Georges River it was ca. twice that of small stands and this effect was significant (Figure 3a, Table 2a). Further, for fruit produced per tree, small stands also produced significantly fewer fruit than medium and large stands. However, the production of fruit per tree was significantly greater on Parramatta River than Georges River (Fig. 3b, Table 2b). The production of fruit per tree in medium and large stands was ca. three times that in small stands, on both estuaries (Fig. 3b, Table 2b).

In general there was an inverse relationship between fruit biomass and stand size, but biomass in medium stands was similar to small stands on both rivers (Fig 3c). Within both estuaries the weight of fruit from medium and small stands was significantly lower than the weight of fruit from large stands, and the effects of size and location were significant (Fig. 3c, Table 2c).

Density of fruit and the resultant seedlings

Our investigation of the effect of stand size on the density of fruit and seedlings per m^2 of the forest floor revealed consistently lower numbers of fruit and seedling establishment in small than in medium and large stands (Fig. 4a, Table 3a). There was, however, substantially greater variation among stands for fruit (propagules) measured on the forest floor (reflecting processes of dispersal and establishment) than for fruit measured on the trees.

On Parramatta River and Georges River, the number of fruit per m^2 in small stands was less than a third that in medium stands and in medium stands it was less than a third that in large stands, and this effect was significant (Fig 4a, Table 3a).

For newly established seedlings we detected the lowest number of seedlings per m^2 in small stands as compared to medium and large stands of both estuaries. On both estuaries the number of seedlings per m^2 was ca. two third and one third in medium and small stands as compared to large stands, but this difference was not significant (Fig. 4b, Table 3b).

The number of seedlings per m^2 surviving for three months in small stands was less than the half, and significantly lower than in medium stands, and two third and three forth respectively, in medium stands as compared to large stands which was also significant, on both Parramatta and Georges Rivers. Further, for stands nested within location and size, both for fruit, established seedlings and seedlings surviving for three months per m^2, there was substantial variation among stands (Fig. 4c, Table 3c).

Discussion

Although there have been few rigorous investigations of the effect of fragmentation on the reproductive and early life history processes of mangroves (though see Hermansen et al. 2014a, b, 2015), deforestation and anthropogenic fragmentation are thought to threaten the existence of mangroves worldwide (Duke et al. 2007). Our results for two urban estuaries matched our predictions that, despite their aquatic setting, pollinator activity and reproductive success would be inversely related to stand size. Our study therefore provides the first evidence that, with respect to pollinator activity and reproductive success, mangrove populations experience similar effects of fragmentation to those commonly reported for terrestrial forests, where such effects can reflect lower genetic diversity and consequently reduced fitness in small populations as well as changes in pollinator abundance and behaviour (Aizen et al. 2002; Ghazoul 2005; Aguilar et al. 2006; Collinge 2009; Nayak and Davidar 2010; Barbeta et al. 2011; Newman et al. 2013). Here the primary driver of reduced reproductive success in small stands appears to be variation in the abundance and changed foraging behaviour of the only effective pollinator, *Apis mellifera* (Hermansen et al. 2014a). In these estuaries genetic diversity does not vary with stand size (Hermansen et al. 2015). Reduced reproductive success in small stands therefore, most probably reflects pollen limitation because the deposition of pollen on the stigma of flowers is significantly reduced in small stands as compared to large stands (Hermansen et al. 2014b). Other studies will be needed to determine whether our results can be extrapolated to other species of mangroves. It would be particularly interesting to compare species or populations that are not heavily dependent on pollination by *A. mellifera*, but worldwide the pollinators of mangroves have been poorly investigated (Hermansen et al. 2014b).

Our study revealed a highly consistent difference between estuaries in abundance of both *Apis mellifera* and other flower visitors. Stands of *A. marina* within Parramatta River attracted far higher numbers of honeybees and other insects regardless of stand size and displayed significantly greater reproductive success. These findings suggest that, although the effects of fragmentation are consistent across estuaries, these effects may be ameliorated in estuaries such as that of the Parramatta River, which exists within a more urban matrix.

Pollination by *Apis mellifera*

Among the diverse assemblage of insects visiting flowers of *A. marina* in the investigated stands *A. mellifera* was numerically dominant (see Hermansen et al. 2014a for a list of flower visitors that includes ants, flies, moths, butterflies, wasps, beetles, bees and *A. mellifera*). Moreover, in earlier work we have shown that *A. mellifera* is currently the only effective pollinator in these estuaries. This is perhaps unsurprising as *A. mellifera* is the most important exotic pollinator of many Australian plants (Paton 1993). The consequences of the invasion by honeybees include a decline in the number and abundance of native pollinators due to aggressive foraging behaviour of honeybees (e.g. Steffan-Dewenter and Tscharntke 2000; Hermansen et al. 2014b). Honeybees have even been shown to remove competing pollinators from flowers (e.g. Kato et al. 1999; Steffan-Dewenter and Tscharntke 2000). It is likely our findings are not typical of *A. marina* populations outside the reach of *A. mellifera*, or perhaps of stands that are more isolated from major urban developments. However, the only other detailed assessment of visitation to *A. marina* flowers, carried out ca. 450 km north of Sydney in a more rural environment also revealed that *A. marina* was the dominant flower visitor (Homer 2009).

In our previous work we found individual honeybees most often forage on one or a small number of neighbouring plants (Hermansen et al. 2014a) and are therefore likely to promote self-pollination or inbreeding. Indeed this pattern of foraging has been argued to produce self-pollination or inbreeding in many studies with terrestrial plants (Paton 1993; Whelan et al. 2009; Gilpin et al. 2014). Such foraging behaviour may mean that even if large amounts of pollen are transferred (Hermansen et al. 2014b), this pollen may be arguably of lower quality than pollen that may have been transferred by native pollinators with a different foraging pattern. This may lead to negative consequences of plant populations due to production and dispersal of inbred seed and seedlings, resulting in reduced reproductive success (Westerkamp 1991; Vaughton 1996; Gross and Mackay 1998). For example, studies by Roubik (1996) and Gross and Mackay (1998) revealed reduced fruit production when honeybees dominated the pollination of *Mimosa pudica* and *Melastoma affine* respectively.

In the absence of other pollinators, reduced numbers of honeybees in small stands of the mangrove *A. marina* may lead to reduced pollen transfer, and pollen limitation may reduce the opportunity for mate choice (Hermansen et al. 2014b), resulting in reduced production and quality of fruit as shown in the present study and many terrestrial studies (Aizen et al. 2002; Ghazoul et al. 2005; Aguilar et al. 2006). Together with our former results showing reduced levels of outbreeding in siblings of small stands (Hermansen et al. 2015), results here indicate that small stands of temperate *A. marina* may display lower fitness, and this effect may increase with time. In some terrestrial studies such effects have resulted in the need for management to counter increased risk of population extinction (Murcia 1995; Jules and Rathcke 1999; Jacquemyn et al. 2002). Further, our genetic survey showed there was no difference in the genetic diversity of adult plants among stands regardless of size (Hermansen et al. 2015). Therefore, the finding of lower outcrossing rates in progeny off small stands supports the idea that despite moving similarly diverse pollen in small and large stands (Hermansen et al. 2014a), honeybees (pollinators) reduce the rates of outcrossing in small stands as compared to large stands due to reduced abundance and altered pollination behaviour.

Fruit production and seedling recruitment

Our finding that pollinator abundance and fruit production, quality and recruitment are all inversely related to stand size, mirrors findings for many terrestrial forests where fragmented populations showing reduced abundance and altered foraging patterns of pollinators, have been found to reduce fruit set and quality as a result of increased inbreeding (Cunningham 2000; Ghazoul 2005; Aguilar et al. 2006; Nayak and Davidar 2010; Newman et al. 2013). In mangroves small fruit typically provide seedlings with lower levels of nutrition resulting in reduced growth and increased mortality (Minchinton 2006), which makes them less fit for competition compared to those of large stands (Tomlinson 1986; Baskin and Baskin 2001).

Future research should be focused on revealing the cause of reduced recruitment within small stands, and importance of local recruitment into small stands. The genetic structure of *A. marina* populations within the investigated estuaries is relatively homogeneous, implying considerable gene flow among stands which could result either from long distance pollination (not expected if pollination is by *A. mellifera*) or the rafted dispersal of propagules (Hermansen et al. 2015). Lower levels of recruitment in small stands may however be a simple physical effect of size. If the density of trees is comparable in small and large stands, waves and currents caused by tide may remove a higher proportion of the fruit produced in small stands than in large stands because the tree barrier is more comprehensive in large stands, and therefore will hamper the effects of waves and tide related water currents.

Mangrove stands, recruitment and expansion

We think newer stands have been established both from propagules migrated from other stands, and propagules produced within the stands, but this needs further research to be confirmed. However, some data indicates this is the case. Propagules disperse via water currents and some of these may migrate to other stands of the same or other estuaries. Clarke (1993) found *A. marina* propagules disperse more than 10 km from a Sydney estuary and Minchinton (2006) found propagules disperse up to 20 km along the coastline south of Sydney. Moreover, the documented history of Parramatta River indicates propagules have the capability to disperse, establish and expand mangrove stands (e.g. Thorogood 1985; Dunstan 1990; McLoughlin 2000). Considering this and the number of established seedlings of the present study, mangrove stands of Parramatta and Georges River catchments may not be limited by propagule production because propagules are able to establish new stands and these are able to recruit sufficient saplings for expansion.

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References

Adam P (2002) Saltmarshes in a time of change. *Environ Conserv* 29:39-61. doi: 10.1017/S0376892902000048

Aguilar R, Ashworth L, Galetto L, Aizen MA (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecol Lett 9:968–980 doi: 10.1111/j.1461-0248.2006.00927.x

Aizen MA, Ashworth L, Leonardo G (2002) Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? J Veg Sci 13:885–892 doi: 10.1111/j.1654-1103.2002.tb02118.x

Barbeta A, Penuelas J, Ogaya R, Jump AS (2011) Reduced tree health and seedling production in fragmented *Fagus sylvatica* forest patches in the Montseny Mountains (NE Spain). Forest Ecol Manag 261:2029–2037 doi: 10.1016/j.foreco.2011.02.029

Baskin CC, Baskin JM (2001) Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California isbn-10: 0124166776

Cavanaugh KC, Kellner JR, Forde AJ, Gruner DS, Parker JD, Rodriguez W, Feller IC (2013) Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. P Natl Acad Sci USA 111:723–727 doi: 10.1073/pnas.1315800111

Clarke PJ (1993) Dispersal of gray mangrove (*Avicennia marina*) propagules in southeastern Australia. Aquat Bot 45:195–204 doi: 10.1016/0304-3770(93)90021-N

Clarke PJ, Myerscough PJ (1991) Floral biology and reproductive phenology of *Avicennia marina* in Southeastern Australia. Aus J Bot 39:283–293 doi: 0067-1921/91/030283505.00

Collinge SK (2009) Ecology of fragmented landscapes. Johns Hopkins University Press, Boltimore isbn: 9780801891380

Cunningham SA (2000) Depressed pollination in habitat fragments causes low fruit set. P Roy Soc B-Biol Sci 267:1149–1152 doi: 10.1098/rspb.2000.1121

Duke NC, Meynecke J-O, Dittmann S, Ellison MA, Anger K, Berger U, Cannicci S, Diele K, Ewel KC, Field CD, Koedam N, Lee SY, Marchand C, Nordhaus I, Dahdouh-Guebas F (2007) A World Without Mangroves? Science 317:41–42 doi: 10.1126/science.317.5834.41b

Duke NC (2006) Australia's mangroves. The authoritative guide to Australia's mangrove plants. University of Queensland, Brisbane isbn: 9780646461960

Dunstan DJ (1990) Some early environmental problems and guidelines in New South Wales estuaries. Wetlands (Australia) 9:1-6

Ghazoul J (2005) Pollen and seed dispersal among dispersed plants. Biol Rev 80:413–443 doi: 10.1017/S1464793105006731

Gilpin A-M, Ayre DJ, Denham AJ (2014) Can the pollination biology and floral ontogeny of the threatened *Acacia carneorum* explain its lack of reproductive success? Ecol Res 29:225–235 doi: 10.1007/s11284-013-1117-y

Gross CL, Mackay D (1998) Honeybees reduce fitness in the pioneer shrub *Melostoma affine* (Melostomataceae). Biol Conserv 86:169–178 doi: 10.1016/S0006-3207(98)00010-X

Hermansen TD (2013) Reproductive biology and genetic structure in fragmented population of the temperate mangrove *Avicennia marina*. PhD dissertation, School of Biological Sciences, University of Wollongong, North Wollongong, New South Wales, Australia http://ro.uow.edu.au/theses/4014/

Hermansen TD, Britton DR, Ayre DJ, Minchinton TE (2014a) Identifying the real pollinators? Exotic honeybees are the dominant flower visitors and only effective pollinators of

Avicennia marina in Australian temperate mangroves. Estuar Coast 37:621–635 doi: 10.1007/s12237-013-9711-3

Hermansen TD, Ayre DJ, Minchinton TE (2014b) Reduced pollinator density leads to reduced fruit set and quality in small stands of temperate *Avicennia marina*. Plant Ecol 215:1153–1162 doi: 10.1007/s11258-014-0374-3

Hermansen TD, Roberts DG, Toben M, Ayre DJ, Minchinton TE (2015) Small urban stands of the mangrove *Avicennia marina* are genetically diverse but experience elevated inbreeding. Estuar Coast 38:1898–1907 doi: 10.1007/s12237-015-9955-1

Homer L (2009) Population structure and distance of gene flow in *Avicennia marina* (Forsk.) Vierh. (Avicenniaceae) on a local/regional scale in the Northern Rivers of New South Wales, Australia. PhD dissertation, School of Environmental Science and Management, Southern Cross University, New South Wales, Australia http://epubs.scu.edu.au/theses/191/

Jacquemyn H, Brys R, Hermy M (2002) Patch occupancy, population size and reproductive success of a forest herb (*Primula elatior*) in a fragmented landscape. Oecologia 130:617–625 doi: 10.1007/s00442-001-0833-0

Jules ES, Rathcke BJ (1999) Mechanisms of reduced *Trillium* recruitment along edges of old-growth forest fragments. Conserv Biol 13:784–793 doi: 10.1046/j.1523-1739.1999.97435.x

Kathiresan K, Bingham BL (2001) Biology of mangroves and mangrove ecosystems. Advances Mar Biol 40:81–251 doi: 10.1016/S0065-2881(01)40003-4

Kato M, Shibata A, Yasui T, Nagamasu H (1999) Impact of introduced honeybees, *Apis mellifera*, uponnative bee communities in the Bonin (Ogasawara) Islands. Res Popul Ecol 41:217–228 doi: 10.1007/s101440050025

McLoughlin LC (2000) Estuarine wetlands distribution along the Parramatta River, Sydney, 1788–1940: implications for planning and conservation. Cunninghamia 6:579–610

Minchinton TE (2001) Canopy and substratum heterogeneity influence recruitment of the mangrove *Avicennia marina*. J Ecol 89:888–902 doi: 10.1046/j.0022-0477.2001.00599.x

Minchinton TE (2006) Consequences of pre-dispersal damage by insects for the dispersal and recruitment of mangroves. Oecologia 148:70–80 doi: 10.1007/s00442-005-0351-6

Minchinton TE, Dalby-Ball M (2001) Frugivory by insects on mangrove propagules: effects on the early life history of *Avicennia marina*. Oecologia 129:243–252 doi: 10.1007/s004420100715

Moeller DA, Geber MA, Eckhart VM, Tiffin P (2012) Reduced pollinator service and elevated pollen limitation at the geographic range limit of an annual plant. Ecology 93:1036–1048 doi: 10.1890/11-1462.1

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends Ecol Evol 10:58–62 doi: 10.1016/S0169-5347(00)88977-6

Nayak KG, Davidar P (2010) Pollinator limitation and the effect of breeding systems on plant reproduction in forest fragments. Acta Oecol 36:191–196 doi: 10.1016/j.actao.2009.12.004

Newman BJ, Ladd P, Brundrett M, Dixon KW (2013) Effects of habitat fragmentation on plant reproductive success and population viability at the landscape and habitat scale. Biol Conserv 159:16–23 doi: 10.1016/j.biocon.2012.10.009

Paton DC (1993) Honeybees in the Australian environment: Does *Apis mellifera* disrupt or benefit the native biota? BioScience 43:95–103 doi: 10.2307/1311970

Rogers K (2004) Mangrove and saltmarsh surface elevation dynamics in relation to environmental variables in Southeastern Australia. PhD dissertation, School of Earth and Environmental Sciences, University of Wollongong, North Wollongong, New South Wales, Australia http://ro.uow.edu.au/theses/653/

Roubik DW (1996) African honey bees as exotic pollinators in French Guiana. In: Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH (eds) The Conservation of Bees. Linnean Society Symposium Series, Academic Press, London 18:173-182 isbn: 0124797407

Saenger P (2003) Mangrove ecology, silviculture and conservation. Kluver Academic Publishers, Dordrecht, Netherlands isbn: 978-94-015-9962-7

Simpson MG (2006) Plant systematics. Elsevier Academic Press isbn: 9780080922089

Steffan-Dewenter I, Tscharntke T (2000) Resource overlap and possible competition between honey bees and wild bees in central Europe. Oecologia 122:288–296 doi: 10.1007/s004420050034

Stokes D (2010) The physical and ecological impacts of mangrove expansion and mangrove removal: Tauranga Harbour, New Zealand. PhD dissertation, University of Waikato, Hamilton, New Zealand http://researchcommons.waikato.ac.nz/handle/10289/4902

Thorogood CA (1985) Changes in the distribution of mangroves in the Port Jackson–Parramatta River estuary from 1930 to 1985. Wetlands (Australia) 5:91–96

Tomlinson PB (1986) The botany of mangroves. Cambridge University Press isbn: 0521255678

Vaughton G (1996) Pollination disruption by European honeybees in the Australian bird-pollinated shrub *Grevillea barklyana* (Proteaceae). Plant Syst Evol 200:89–100 doi: 10.1007/BF00984750

West RJ, Thorogood CA, Walford TR, Williams RJ (1985) An Estuarine Inventory for New South Wales, Australia. Fisheries Bulletin 2, Department of Agriculture, New South Wales

Westerkamp C (1991) Honeybees are poor pollinators – why? Plant Syst Evol 177:71 –75 doi: 10.1007/BF00937827

Whelan RJ, Ayre DJ, Beynon FM (2009) The birds and the bees: pollinator behaviour and variation in the mating system of the rare shrub *Grevillea macleayana*. Ann Bot 103:1395–1401 doi: 10.1093/aob/mcp091

Figure legends

FIG. 1 Map of the Parramatta and Georges River catchments in Sydney, Australia (Fig. 1 is reused from Hermansen et al. 2015, p. 1900) showing the location and size of the investigated stands

FIG. 2 Mean (+ SE) density of a) honeybees and b) other insects, measured as the number visiting 1 m^2 of canopy during six 30 min video recordings on individual trees in each stand (each bar in the figure represents one stand). Data are from large, medium and small stands (3 of each) located on the Parramatta River (P) and Georges River (G), during the flowering season of 2010. Indication of significance: Lo = location, Sz = stand size, P = Parramatta River, G = Georges River, L = large, M = medium, S = small

FIG. 3 Mean (+ SE) number of a) fruit per floral shoot, and b) fruit per tree, for 20 trees (if available), and c) fruit weight of 25 fruit from each of 10 trees, in all cases per stand (each stand are represented by a bar in the figure). Data are from large, medium and small stands (3 of each) located on the Parramatta River (P) and Georges River (G), during the flowering season of 2010. Indication of significance: Lo = location, Sz = stand size, P = Parramatta River, G = Georges River, L = large, M = medium, S = small

FIG. 4 Mean (+ SE) of a) the number of fallen fruit per m^2, b) the number of newly settled seedlings per m^2, and c) the number of seedlings surviving for three months per m^2, in all cases 50 quadrats of 1 m^2 per stand, and stands are represented by bars in the figure. Data are from large, medium and small stands (3 of each) located on the Parramatta River (P) and Georges

River (G), during the flowering season of 2010. Lo = location, Sz = stand size, P = Parramatta River, G = Georges River, L = large, M = medium, S = small

Tables

Table 1 Effects of location (Lo), size (Sz), stand (St) and interactions of location and size on abundance of a) honeybees and b) other insects per m^2 of canopy. Data are from large, medium and small stands (3 of each) located on the Parramatta River and Georges River, during the flowering season of 2010. Lo was treated as a random factor and Sz as a fixed factor; with St as a random factor nested within Lo and Sz. In a) data were Sqrt(x+1) transformed to meet assumptions of ANOVA, in b) data were not transformed; significant differences among Lo and Sz are described in text. In a) and b) Cochran's test was not significant. In a) and b) SNK for Lo was Parramatta>Georges and SNK for Sz in a) was Large>Medium>Small and in b) was Large>Medium=Small

a) Abundance of honeybees

Source	*d.f.*	*MS*	*F*	*P*
Lo	1	16.457	17.85	0.001
Sz	2	21.289	62.25	0.016
St(Lo×Sz)	12	0.922	0.42	0.951
Lo×Sz	2	0.342	0.37	0.698
Res	90	2.181		

b) Abundance of other insects

Source	*d.f.*	*MS*	*F*	*P*
Lo	1	8.333	30.00	0.000
Sz	2	6.787	34.90	0.028

St(Lo×Sz)	12	0.278	0.30	0.989
Lo×Sz	2	0.194	0.70	0.516
Res	90	0.937		

Table 2 Effects of location (Lo), size (Sz), stand (St) and interactions of location and size on abundance of a) fruit per floral shoot and b) fruit per tree counted on 20 trees (if available), and c) fruit weight of 25 fruit of each of 10 trees. Data are from large, medium and small stands (3 of each) located on the Parramatta River and Georges River, during the flowering season of 2010. Lo was treated as a random factor and Sz as a fixed factor; with St as a random factor nested within Lo and Sz. In a) and c) data were not transformed and in b) data were Sqrt(x+1) transformed to meet assumptions of ANOVA; significant differences among Lo and Sz are described in text. Cochran's test was not significant in any case. In b) and c) SNK for Lo was Parramatta>Georges. In a) and b) Sz was Large=Medium>Small and in c) it was Large>Medium=Small

a) Fruit per floral shoot

Source	*d.f.*	*MS*	*F*	*P*
Lo	1	0.396	2.51	0.136
Sz	2	12.520	7.93	0.005
St(Lo×Sz)	12	0.169	1.07	0.388
Lo×Sz	2	0.094	0.59	0.566
Res	126	0.157		

b) Fruit per tree

Source	*d.f.*	*MS*	*F*	*P*
Lo	1	1796.689	15.83	0.001
Sz	2	1081.671	9.53	0.002
St(Lo×Sz)	12	131.034	1.26	0.252
Lo×Sz	2	8.352	0.07	0.929

Res	126	104.205		

c) Fruit weight

Source	*d.f.*	*MS*	*F*	*P*
Lo	1	58.716	200.16	0.005
Sz	2	31.673	107.97	0.009
St(Lo×Sz)	12	1.469	0.33	0.983
Lo×Sz	2	0.293	0.20	0.822
Res	162	4.475		

Table 3 Effects of location (Lo), size (Sz), stand (St) and interactions of location and size on abundance of a) fruit per m^2, b) established seedlings per m^2 and c) surviving seedlings per m^2 (50 quadrats of 1 m^2). Data are from large, medium and small stands (3 of each) located on the Parramatta River and Georges River, during the flowering season of 2010. Lo was treated as a random factor and Sz as a fixed factor; with St as a random factor nested within Lo and Sz. In a) and c) data were Ln(x+1) transformed and in b) they were Sqrt(x+1) transformed to meet assumptions of ANOVA; significant differences among Lo and Sz are described in text. Cochran's test was not significant in any case. In b) SNK for Lo was Parramatta>Georges and in a) and c) Sz was Large>Medium>Small

a) Fruit per m^2

Source	*d.f.*	*MS*	*F*	*P*
Lo	1	23.570	2.78	0.122
Sz	2	91.727	34.37	0.028
St(Lo×Sz)	12	8.486	4.74	0.000
Lo×Sz	2	2.669	0.31	0.736
Res	882	1.789		

b) Newly settled seedlings per m^2

Source	*d.f.*	*MS*	*F*	*P*
Lo	1	44.674	31.23	0.000
Sz	2	46.743	15.98	0.059
St(Lo×Sz)	12	1.430	2.93	0.001
Lo×Sz	2	2.925	2.04	0.172
Res	882	0.489		

c) Surviving seedlings per m^2

Source	*d.f.*	*MS*	*F*	*P*
Lo	1	6.204	2.55	0.136
Sz	2	11.233	55.43	0.018
St(Lo×Sz)	12	2.433	6.79	0.000
Lo×Sz	2	0.203	0.08	0.921
Res	882	0.358		

Fig. 1

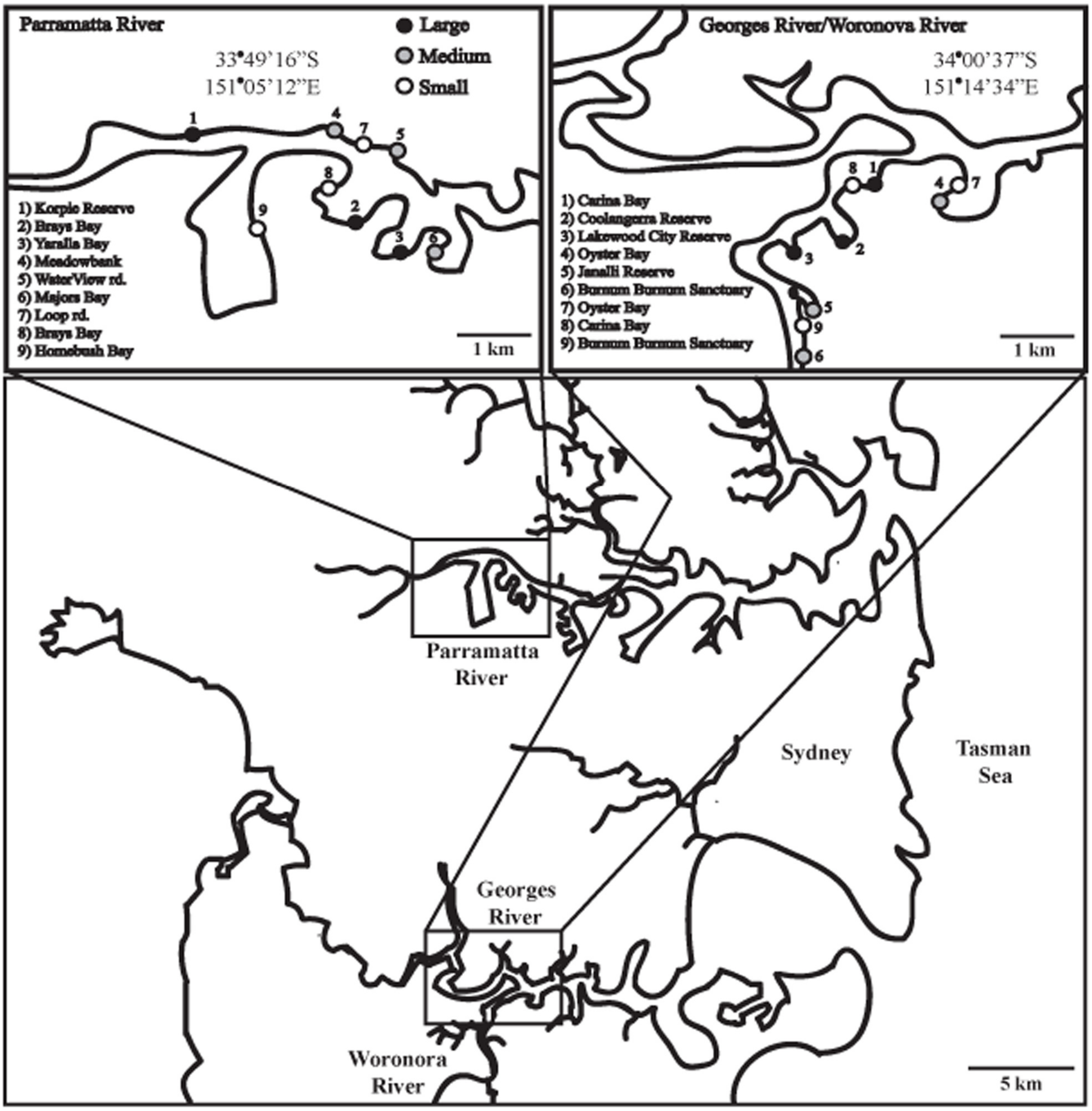

Parramatta River
● Large
● Medium
○ Small
33°49'16"S
151°05'12"E
1) Korpie Reserve
2) Brays Bay
3) Yaralla Bay
4) Meadowbank
5) WaterView rd.
6) Majors Bay
7) Loop rd.
8) Brays Bay
9) Homebush Bay
1 km
Georges River/Woronova River
34°00'37"S
151°14'34"E
1) Carina Bay
2) Coolangarra Reserve
3) Lakewood City Reserve
4) Oyster Bay
5) Janalli Reserve
6) Burnum Burnum Sanctuary
7) Oyster Bay
8) Carina Bay
9) Burnum Burnum Sanctuary
1 km
Parramatta River
Sydney
Tasman Sea
Georges River
Woronora River
5 km

Fig. 2

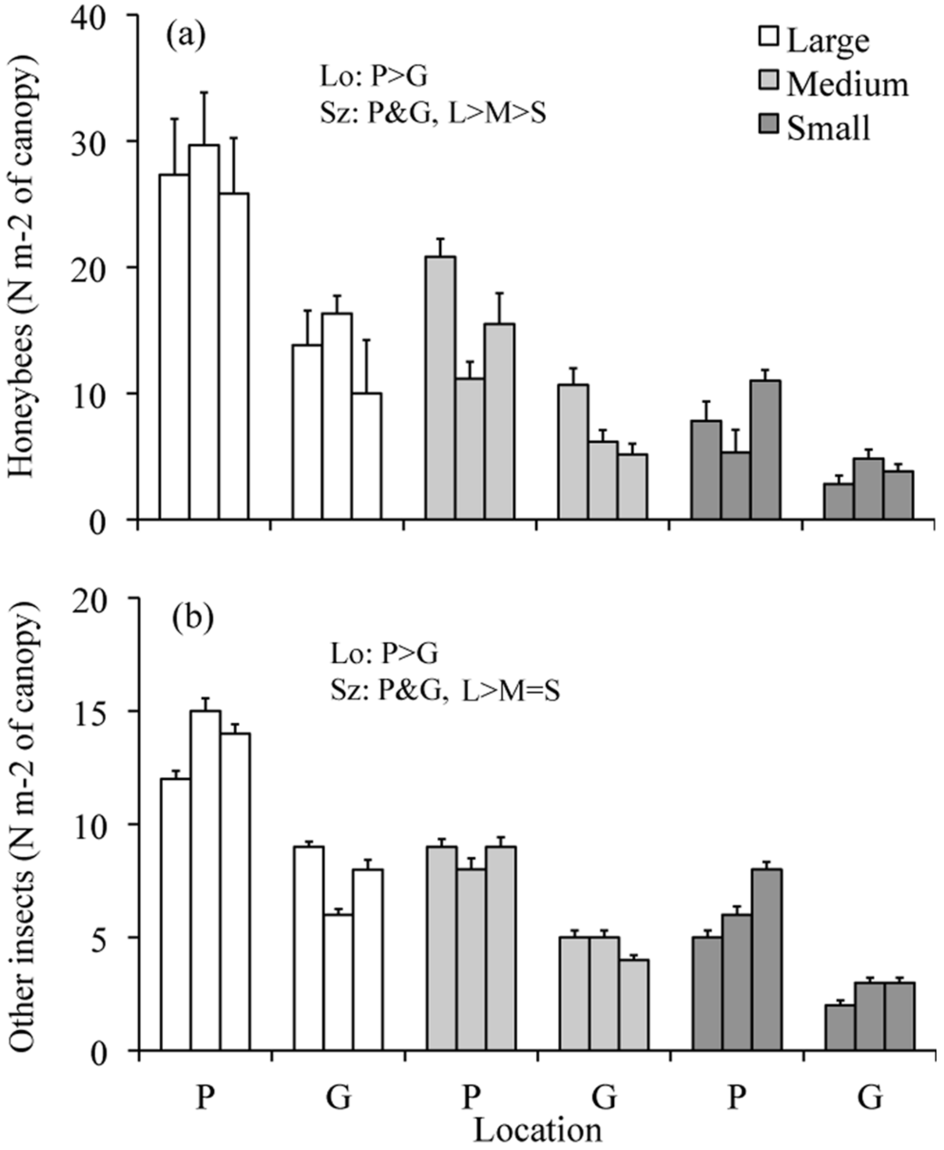

(a)
Lo: P>G
Sz: P&G, L>M>S
Large
Medium
Small
Honeybees (N m-2 of canopy)
0
10
20
30
40
(b)
Lo: P>G
Sz: P&G, L>M=S
Other insects (N m-2 of canopy)
0
5
10
15
20
P
G
P
G
P
G
Location

Fig. 3

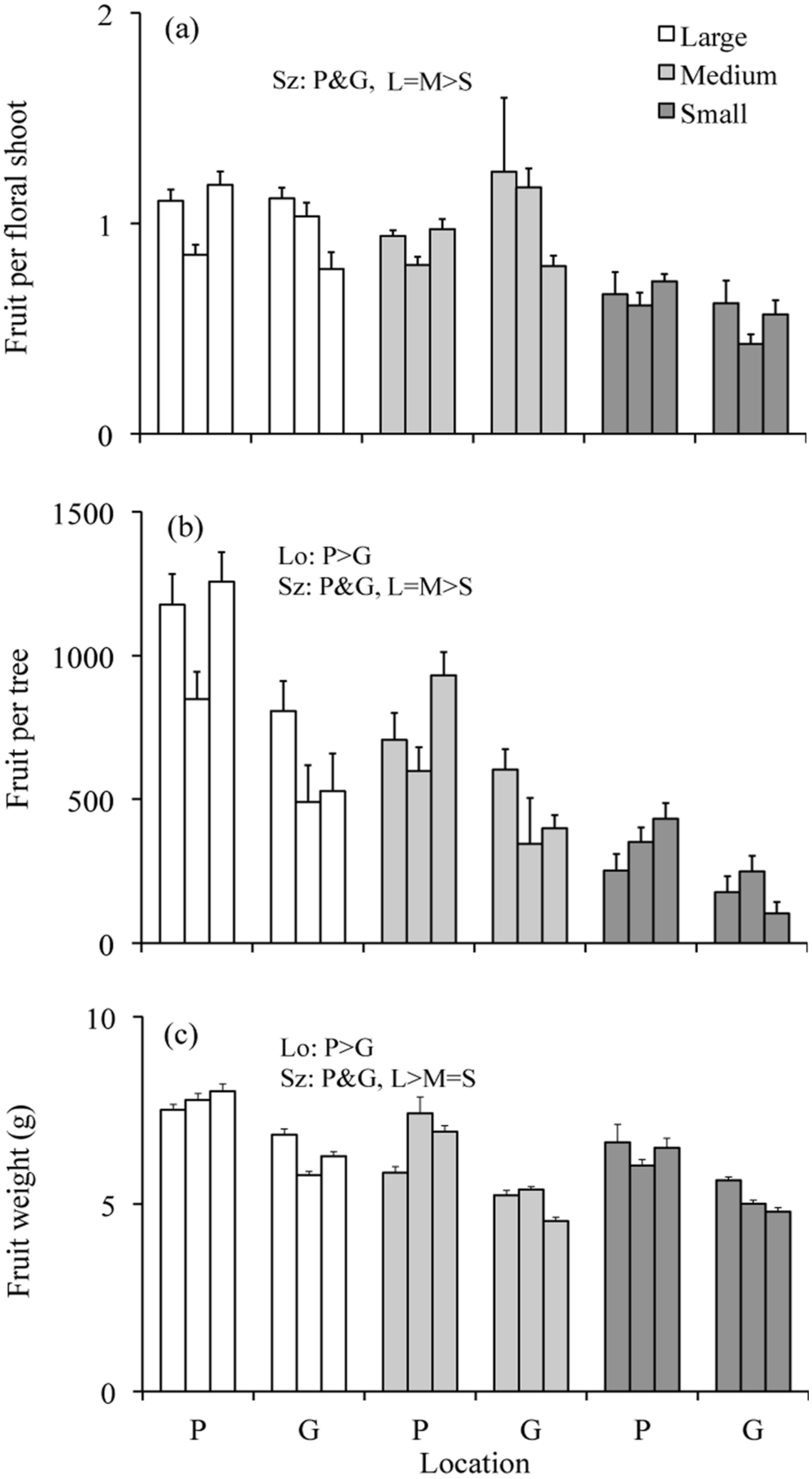
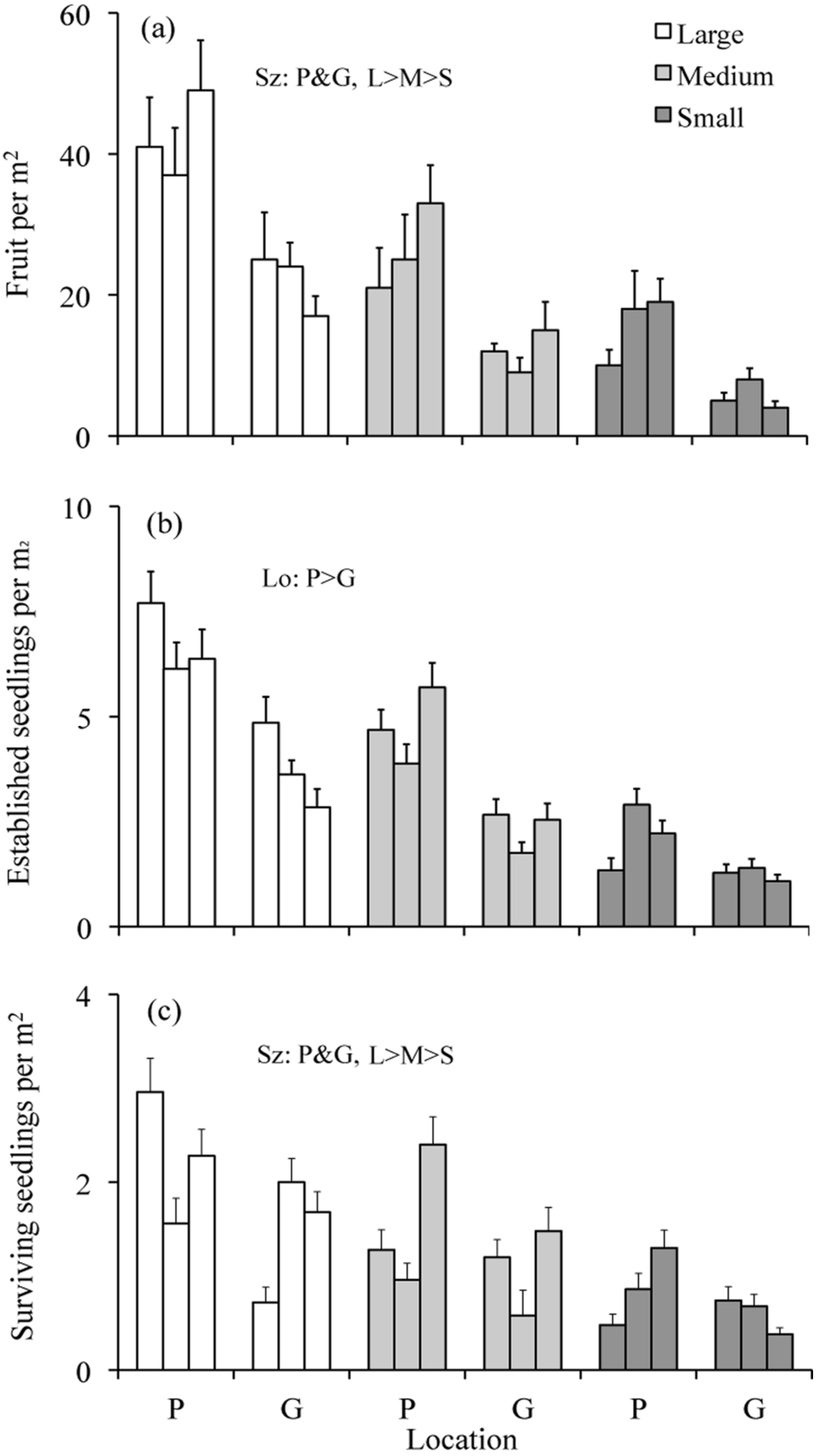

(a)
Sz: P&G, L=M>S
Large
Medium
Small
Fruit per floral shoot
2
1
0
(b)
Lo: P>G
Sz: P&G, L=M>S
Fruit per tree
1500
1000
500
0
(c)
Lo: P>G
Sz: P&G, L>M=S
Fruit weight (g)
10
5
0
P
G
P
G
P
G
Location

Fig 4


(a)
Sz: P&G, L>M>S
Large
Medium
Small
Fruit per m²
60
40
20
0
(b)
Lo: P>G
Established seedlings per m₂
10
5
0
(c)
Sz: P&G, L>M>S
Surviving seedlings per m²
4
2
0
P
G
P
G
P
G
Location