



# Population demography and fecundity do not decline with habitat fragmentation in the rainforest tree *Macadamia integrifolia* (Proteaceae)

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## ABSTRACT

Habitat fragmentation is often associated with reduced levels of fitness and local extinction of plant species, and consequently poses a major threat to the persistence of species worldwide. The majority of demography-based fragmentation studies to date have focussed primarily on fragmentation impacts on individual plant fecundity. Here we investigate the impact of habitat fragmentation on the demography (plant height classes and density) and key population dynamic processes for the rainforest tree species *Macadamia integrifolia* (Proteaceae). Raceme and fruit production and seedling emergence across fragmented sites exceeded that in more intact sites with no apparent difference in short-term mortality rates. Fecundity of flowering trees did not appear to be affected by fragmentation. Instead, overall reproductive output in fragmented sites was enhanced relative to undisturbed sites due to a higher proportion of reproductively active individuals. The probability of flowering and fruiting was negatively correlated with the projected foliage cover (PFC) surrounding individual trees, and average PFC was significantly lower in small and medium fragments, suggesting light availability as a potential contributor to the trends observed here.

This study demonstrates that the short-term effects of habitat fragmentation on population viability may not necessarily be detrimental for some species, and highlights the importance of assessing not only the fecundity of flowering individuals but also the proportion of individuals reproducing within fragments.

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## 1. Introduction

A well-developed body of population biology literature exists to suggest that habitat fragmentation, the conversion of relatively continuous ecosystems into smaller, more isolated parcels (Li and Reynolds, 1993), can lead to the local extinction of plant species through the disruption of vital demographic processes (reviewed in Hobbs and Yates, 2003; Bruna et al., 2009). This may occur as post-fragmentation habitat conditions become unsuitable for species or via a decline in fecundity and fitness due to reduced effective population size and/or increased isolation from other patches (Young et al., 1996; Benítez-Malvido and Martínez-Ramos, 2003). In particular, fragmentation may affect the population demographic processes of recruitment, mortality, immigration and emigration (Rathcke and Jules, 1993; Turner et al., 1996; Laurance and Bierregaard, 1997; Nason and Hamrick, 1997; Laurance et al., 1998a; Jules and Rathcke, 1999), the consequences of which can

include a shift in the age structure of a population (Harper, 1977), the number of individuals (Cordeiro and Howe, 2003), plant density and spatial structure (Bleher et al., 2002). These changes may subsequently affect reproductive output by altering pollinator visitation rates and foraging behaviour (Kunin, 1993, 1997; Young et al., 1993; Nason and Hamrick, 1997; Bosch and Waser, 1999; Ghazoul, 2005). A reduction in fecundity can ultimately increase the susceptibility of fragmented populations to local extinction from stochastic events or population decline (e.g. Lande, 1988; Barrett and Kohn, 1991; Ellstrand and Elam, 1993; Schemske et al., 1994; Lienert and Fischer, 2003).

In general, tropical trees are predicted to be particularly susceptible to habitat fragmentation due to their low densities, self-incompatibility systems, and typically high rates of outcrossing (Cascante et al., 2002). Widespread clearing of vegetation in the subtropics has resulted in extensive fragmentation of remnant forest (Catterall and Kingston, 1993; Coiacetto, 1995), and a large proportion of remnant Australian rainforest currently exists as small patches surrounded by agricultural land, or restricted to steep, inaccessible areas (Fox et al., 1997). Relatively few studies have been undertaken, however, that investigate the suite of demographic processes that contribute to population growth or decline

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in tropical or subtropical plant communities (Aguilar et al., 2006; Bruna et al., 2009).

*Macadamia integrifolia* (Proteaceae) is a medium sized endemic tree of the notophyll vine forests of subtropical South-Eastern Queensland, Australia (Gross, 1995a,b; Hardner et al., 2009), as well as a major contributor to the horticultural nut industry. As a result of extensive clearing within its natural range, the majority of known populations of *M. integrifolia* in the wild are present as small, isolated remnants, predominantly located on private property (Hardner, 2004; Powell et al., 2010). The species is listed as vulnerable under the Environment Protection and Biodiversity Conservation Act, 1999 (Cth), categorising it as likely to become extinct within the next 20–50 years.

The viability of the fragmented *M. integrifolia* populations may impact on the long term conservation of the species. The major threats to remnant populations are clearing, trampling by livestock, introduction of exotic plant species, and fires originating in nearby eucalypt forest or grassy woodland (Gross, 1995b). Many of these threats are associated with or exacerbated by habitat fragmentation (Laurance and Bierregaard, 1997; Benítez-Malvido and Martínez-Ramos, 2003). The viability of fragmented *M. integrifolia* populations may also be affected by decline in the fitness of individuals within these populations due to genetic bottlenecks at the time of clearing (Frankham et al., 2002) and subsequent genetic drift (Barrett and Kohn, 1991; Ellstrand and Elam, 1993) although these effects may not be immediately apparent (Lande and Orzack, 1988; Sherwin and Moritz, 2000). Conservation of *M. integrifolia* diversity is of particular concern as it is both an iconic Australian species and the only major food crop to be domesticated from the Australian flora (Hardner et al., 2009). Wild populations may also be valuable to the Australian macadamia nut industry as a germplasm resource for the development of new cultivars.

This study aimed to examine the impact of habitat fragmentation on the demography and critical population dynamic processes of *M. integrifolia*. We examined the hypothesis that fragmentation adversely impacts the key population parameters of demography and fecundity, specifically height class distribution, plant density, flowering, fruiting, seedling emergence and mortality.

## 2. Methods

### 2.1. Study species and study areas

*M. integrifolia* Maiden & Betche (Proteaceae) is an endemic tree of South-East Queensland, Australia (Gross, 1995a; Hardner et al., 2009; Powell et al., 2010). The distribution of the species prior to anthropogenic disturbance is unknown (but see Powell et al., 2010), however it currently occurs in scattered populations extending approximately 200 km north from the Queensland/New South Wales Border and 60 km west of the Queensland coastline (Hardner et al., 2009; Powell et al., 2010). Populations are located on high nutrient volcanic (mostly basalt and diorite) and alluvial soils of pH 5.5–6.5, with a texture that ranges from clayey sand through various loams to silty clay (Hardner et al., 2009; Table 1). All sites are well drained, many with exposed rock fragments or substrate on the surface. Average annual rainfall is between 1100 and 1300 mm across the range of the species and has a summer maximum (Commonwealth Bureau of Meteorology, 2003).

Mature *M. integrifolia* trees range in height from 6 to 18 m (Gross, 1995a). Individuals are generally multi-stemmed, most likely as a response to damage and/or stress (J. Neal pers. obs.). The pale cream florets are bisexual and borne on racemes 8.5–25 cm long in numbers of 100–300 (Gross, 1995a). Fruit are globose follicles 3–4 cm long and 2–4.5 cm wide (Strohschen,

1986; Gross, 1995a) that mature approximately 30 weeks after fertilisation (Nagao and Hirae, 1992; Boyton and Hardner, 2002; Stephenson, 2005). As the fruit dries, the husk generally splits along a single suture to release the seed, consisting of a rigid seed coat enclosing the embryo and cotyledons (Strohschen, 1986).

Studies in commercial orchards indicate that in these environments *M. integrifolia* flowers are primarily pollinated by stingless native bees (*Trigona carbonaria*) and introduced honey bees (*Apis mellifera*) (Vithanage and Ironside, 1986; Heard and Exley, 1994). The species is partially self-incompatible under orchard conditions (Sedgley et al., 1990), with lower final fruit set observed from selfing compared with cross-pollination (Trueman and Turnbull, 1994; Wallace et al., 1996; Hardner et al., 2009). Little is known of the mating system of the species in the wild. It is speculated that seeds are dispersed by gravity, water and animals (Pisanu, 2001; Peace et al., 2005).

### 2.2. Demographic plots

To study the impact of fragmentation on the demography of *M. integrifolia*, ten study sites were chosen from two regions, Amamoor (26.35°S, 152.64°E) and Samford (27.37°S, 152.82°E) (Fig. 1). Sites were selected within three area classes (referred to as fragment size classes herein): small (less than one hectare), medium (1–10 ha), and continuous habitat (greater than 100 ha), with three to four sites per class. Small and medium fragments were represented in both regions while continuous habitats were only available at Amamoor. Fragments size classes were used in preference to treating size as a continuous variable as the available experimental units fitted naturally into size classes, and fragments between 10 and 100 ha in size were not available.

Study sites varied from 0.24 ha to 361 ha (Table 1), with total number of individuals within sites ranging from 94 to approximately 10,500. The majority of small and medium fragments were located within a pasture matrix. All continuous sites were surrounded by sclerophyll forest with *Araucaria cunninghamii* (Araucariaceae) plantations on some borders. Fragmentation of the study sites likely took place between 1850 and 1940 at Amamoor, and between 1855 and 1955 at Samford (Long, 1998; Johnson and Saunders, 2007; aerial photographic records, Queensland Department of Natural Resources and Mines). Aerial photographs indicate that there has been little change in the area or connectivity of the study sites since 1940 (Amamoor) or 1955 (Samford), with the exception of site 8, which was completely cleared prior to 1940 and regenerated between 1940 and 1958.

Census was undertaken over the entire area of small and medium fragments, with the exception of site number 8 (small fragment size class), where approximately only two thirds of the patch was surveyed due to the large number of individuals in this fragment. In the continuous habitats (site numbers 128, 129 and 131), two randomly located, four-hectare square plots per site were established. All *M. integrifolia* individuals within the study areas were located and labelled.

### 2.3. Demographic assessment

Isolation distance and disturbance index were assessed for each study plot. Isolation was defined as the distance from the edge of the study fragment/habitat to the closest habitat known to contain *M. integrifolia*, and ranged from 150 m to 3 km. Disturbance index was estimated after Ross et al. (2002):

$$D_k = E_k \times S_k$$

where  $k$  = the type of disturbance,  $E_k$  = estimated extent (percentage of site area) affected by disturbance  $k$ , and  $S_k$  = estimated severity (score of intensity on a scale of one, no disturbance, to five, entirely

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