POLLINATION ECOLOGY OF *TRACHYMENE INCISA* (APIACEAE):

UNDERSTANDING GENERALISED PLANT-POLLINATOR SYSTEMS

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DECLARATION

I hereby declare that the work contained in this thesis is my own and contains the results of an original investigation, except where otherwise referenced or acknowledged. This work was carried out while I was enrolled as a student for the degree of Doctor of Philosophy in the School of Biological Sciences, The University of Sydney. This thesis has not been previously submitted for examination at this, or any other, university.

Yvonne C. Davila

March 2006

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This doctoral research is dedicated to my parents,
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who always encouraged me to do my best and have given me the opportunity to achieve it.

ABSTRACT

A renewed focus on generalised pollinator systems has inspired a conceptual framework which highlights that spatial and temporal interactions among plants and their assemblage of pollinators can vary across the individual, population, regional and species levels. Pollination is clearly a dynamic interaction, varying in the number and interdependence of participants and the strength of the outcome of the interaction. Therefore, the role of variation in pollination is fundamental for understanding ecological dynamics of plant populations and is a major factor in the evolution and maintenance of generalised and specialised pollination systems. My study centred on these basic concepts by addressing the following questions: (1) How variable are pollinators in a generalised pollination system? To what degree do insect visitation rates and assemblage composition vary spatially among populations and temporally among flowering seasons? (2) How does variation in pollinators affect plant reproductive success? I chose to do this using a model system, *Trachymene incisa* subsp. *incisa* (Apiaceae), which is a widespread Australian herbaceous species with simple white flowers grouped into umbels that attract a high diversity of insect visitors. The Apiaceae are considered to be highly generalist in terms of pollination, due to their simple and uniform floral display and easily accessible floral rewards. Three populations of *T. incisa* located between 70 km and 210 km apart were studied over 2-3 years.

The few studies investigating spatial and temporal variation simultaneously over geographic and yearly/seasonal scales indicate that there is a trend for more spatial than temporal variation in pollinators of generalist-pollinated plants. My study showed both spatial and temporal variation in assemblage composition among all populations and variation in insect visitation rates, in the form of a significant population by year interaction. However, removing ants from the analyses to restrict the assemblage to flying insects and the most likely pollinators, resulted in a significant difference in overall visitation rate between years but no difference in assemblage composition between the Myall Lakes and Tomago populations. These results indicate more temporal than spatial variation in the flying insect visitor assemblage of *T. incisa*.

Foraging behaviour provides another source of variation in plant-pollinator interactions. *Trachymene incisa* exhibits umbels that function as either male or female at any one time and offer different floral rewards in each phase. For successful pollination, pollinators must visit both male and female umbels during a foraging trip. Insects showed both preferences and non-preferences for umbel phases in natural patches where the gender ratio was male biased. In contrast, insects showed no bias in visitation during a foraging trip or in time spent foraging on male and female umbels in experimental arrays where the gender ratio was equal.

Pollinator assemblages consisting of a mixture of different pollinator types coupled with temporal variation in the assemblages of populations among years maintains generalisation at the population/local level. In addition, spatial variation in assemblages among populations maintains generalisation at the species level. Fire alters pollination in *T. incisa* by shifting the flowering season and reducing the abundance of flying insects. Therefore, fire plays an important role in maintaining spatial and temporal variation in this fire-prone system.

Although insect pollinators are important in determining the mating opportunities of 90% of flowering plant species worldwide, few studies have looked at the effects of variation in pollinator assemblages on plant reproductive success and mating. In *T. incisa*, high insect visitation rates do not guarantee high plant reproductive success, indicating that the quality of visit is more important than the rate of visitation. This is shown by comparing the Agnes Banks and Myall Lakes populations in 2003: Agnes Banks received the highest visitation rate from an assemblage dominated by ants but produced the lowest reproductive output, and Myall Lakes received the lowest visitation rate by an assemblage dominated by a native bee and produced the highest seedling emergence.

Interestingly, populations with different assemblage composition can produce similar percentage seed set per umbel. However, similar percentage seed set did not result in similar percentage seedling emergence. Differences among years in reproductive output (total seed production) were due to differences in umbel production (reproductive effort) and proportion of umbels with seeds, and not seed set per umbel.

Trachymene incisa is self-compatible and suffers weak to intermediate levels of inbreeding depression through early stages of the life cycle when seeds are self-pollinated and biparentally inbred. Floral phenology, in the form of synchronous protandry, plays an important role in avoiding self-pollination within umbels and reducing the chance of geitonogamous pollination between umbels on the same plant. Although pollinators can increase the rate of inbreeding in *T. incisa* by foraging on both male and female phase umbels on the same plant or closely related plants, most consecutive insect movements were between plants not located adjacent to each other. This indicates that inbreeding is mostly avoided and that *T. incisa* is a predominantly outcrossing species, although further genetic analyses are required to confirm this hypothesis.

A new conceptual understanding has emerged from the key empirical results in the study of this model generalised pollination system. The large differences among populations and between years indicate that populations are not equally serviced by pollinators and are not equally generalist. Insect visitation rates varied significantly throughout the day, highlighting that sampling of pollinators at one time will result in an inaccurate estimate and usually underestimate the degree of generalisation. The visitor assemblage is not equivalent to the pollinator assemblage, although non-pollinating floral visitors are likely to influence the overall effectiveness of the pollinator assemblage.

Given the high degree of variation in both the number of pollinator species and number of pollinator types, I have constructed a model which includes the degree of ecological and functional specialisation of a plant species on pollinators and the variation encountered across different levels of plant organisation. This model describes the ecological or current state of plant species and their pollinators, as well as presenting the patterns of generalisation across a range of populations, which is critical for understanding the evolution and maintenance of the system.

In-depth examination of pollination systems is required in order to understand the range of strategies utilised by plants and their pollinators, and I advocate a complete floral visitor assemblage approach to future studies in pollination ecology. In particular, future studies should focus on the role of introduced pollinators in altering generalised plant-pollinator systems and the contribution of non-pollinating floral visitors to pollinator assemblage effectiveness. Comparative studies involving plants with highly conserved floral displays, such as those in the genus *Trachymene* and in the Apiaceae, will be useful for investigating the dynamics of generalised pollination systems across a range of widespread and restricted species.

PREFACE

This thesis is set out as a series of papers, an option available at The University of Sydney. The papers have either been submitted or will be submitted to appropriate peer-reviewed scientific journals in the form presented here or similar. As a consequence, there is some redundancy among chapters.

Chapters that have been submitted to peer-reviewed journals are indicated at the beginning of each chapter. My co-author on these papers is Dr Glenda M. Wardle. Glenda provided supervision of the project, including discussions on initial concepts, design and analyses of data, and improved earlier versions of the chapters.

CHAPTER 1

INTRODUCTION

Photograph: newly opened *Trachymene incisa* umbel

For each pollinator bee is in fact a little cupid

that creates hot romances between plants thought to be stupid.

Each bee can be considered a matchmaking agency

that arranges introductions for a nominal nectar fee.

From "Cupid" by Paul D. Haemig, http://www.ecology.info/cupid.html

POLLINATION ECOLOGY

Mutualistic interactions are among the most widespread interactions in nature, but also the least well understood compared to other interactions such as predation (Ollerton 2006). Mutualisms are relationships between species that result in reciprocal benefits. Biotic pollination, the transfer of pollen by animals from the anther to the stigma of flowers, is a mostly mutualistic interaction (see Renner 2006 for exceptions), with pollinators usually receiving pollen and/or nectar from plants in return for their pollinating service. Animal pollinators have been important since the angiosperms evolved, with evidence indicating that early members of the angiosperms were insect pollinated (Crane *et al.* 1995). Over 91% of the 240 000 angiosperm species worldwide are animal-pollinated (Buchmann and Nabhan 1996), distributed throughout approximately 93% of angiosperm genera (Renner and Ricklefs 1995). With vertebrates pollinating only 0.51% of species, insects are responsible for pollinating over 90% of angiosperm species (Buchmann and Nabhan 1996). The four largest orders of insects, Coleoptera, Hymenoptera, Lepidoptera and Diptera, include species that are known to pollinate flowering plants (Proctor *et al.* 1996). The total number of pollinator species is unknown, although estimates vary between 130 000 and

300 000 (Shepherd *et al.* 2003). Pollination is therefore a dominant interaction involving several hundred thousands of species, spanning most terrestrial habitats.

Pollination ecology addresses the mechanisms through which plants donate and receive pollen, including floral phenology, floral adaptation, pollinator behaviour and plant breeding (Wyatt 1983; Morgan and Schoen 1997). Pollination ecology provides examples of coevolution and evolutionary conflict, and was used by Charles Darwin and other early evolutionary biologists to test ideas of evolutionary theory (Pellmyr 2002). Pollination is a fundamental aspect of plant reproduction, and is therefore important for the disciplines of plant life history and demography, sustainable agriculture and horticulture. On larger scales, pollination is an essential ecosystem service and is central to understanding interaction networks and food webs, ecosystem function, conservation and restoration biology.

Many ecological interactions are dynamic, varying in the number and interdependence of participants and the strength of the outcome of the interaction. A fundamental aspect of any ecological interaction is the degree to which it is specialised or generalised (Waser 2006). Pollination is no exception and with so many species involved, there is a range of specialised (plants pollinated by one or very few pollinators) and generalised (plants pollinated by several pollinators) systems (although see Appendix 1 for other definitions). Variation in the interacting partners forms a major part of the origin, maintenance and stability of an interaction. In terms of pollination, variation in pollinators is critical for plant mating (ecological context) and long term dependence and adaptation of the plant to its pollinating partners (evolutionary context).

VARIATION IN POLLINATORS

Flowers can receive visits from one to many pollinators. Variation in pollinators can affect the number and quality of seed production by plants and thus have flow on effects for plant demography and population structure. Figure 1-1 is a flow diagram of these links between pollinators and plant reproduction. Firstly, pollinator assemblages can vary in several natural ways. Plants and their pollinators rarely completely overlap in range (Thompson 1994; Waser *et al.* 1996) which results in different assemblages across the range of a plant. Community composition varies among habitats, which support different assemblages of pollinators and relationships between a plant species and a pollinator species may change among communities (Kearns and Inouye 1997). Widespread plant species are likely to experience varying climatic conditions throughout their range, which may favour different assemblages of floral visitors. Similarly, plants with long or multiple flowering periods may overlap flowering with different plants and pollinators during the course of the flowering period (reviewed by Minckley and Roulston 2006).

Disturbance is another source of variation to pollinator assemblages. For example, fragmentation of subtropical dry forests caused declines in native flower visitors (Aizen and Feinsinger 1994). The introduction of non-native pollinators, such as honey bees (*Apis mellifera*) and bumble bees (*Bombus terrestris*) in Australia, is also a source of disturbance to pollinator assemblages. Several studies have shown that these introduced pollinators differ in foraging behaviour to native pollinators, can alter the foraging patterns of native pollinators, and can displace or compete with native floral visitors (Gross and Mackay 1998; Hingston and McQuillan 1998; Hingston and McQuillan 1999; Horskins and Turner 1999; Gross 2001). Therefore, the foraging behaviour of pollinators will be dependent on the presence of other competing pollinators (Hingston and McQuillan 1998).

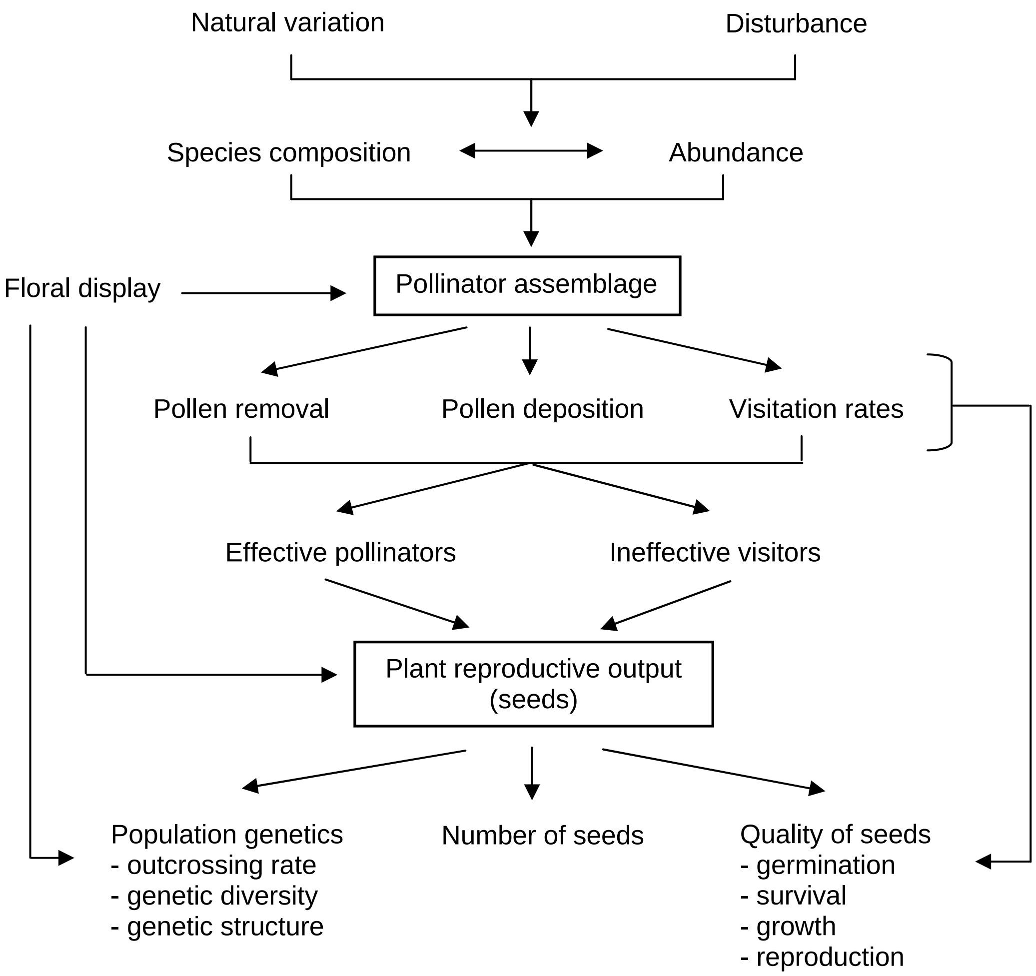

Fig. 1-1 Flow diagram of the links between variation in pollinators and plant reproduction.

Natural and induced variation in the pollinator assemblage leads to spatial and temporal variation in the species composition and abundance of each species. The pollinator assemblage also has properties that determine success at pollination. These are the ability of pollinators to collect pollen from anthers and deposit it onto conspecific stigmas, and the rate at which they do this. Not all floral visitors are effective pollinators and not all pollinators are equally effective at pollination (Herrera 1987; Wilson and Thomson 1991; Herrera 2000). The behaviour of pollinators individually and as a group will determine the reproductive output of the plant species they pollinate.

Plant reproductive output can be measured in terms of the quantity and quality of seeds. The number of seeds produced is related to the reproductive effort (number of ovules produced) and the floral display (number and arrangement of flowers). The floral display plays an important role in attracting pollinators. Pollinators determine the type of mating, self- and/or cross-pollination, that occurs between flowers and influence the quality of offspring in terms of germination, survival, growth and subsequent reproduction (Herrera 2000). At the population level, pollinator behaviour affects plant population genetics through the outcrossing rate and different patterns of pollen (gene) flow.

A greater understanding of pollination requires a clearer idea of the range of specialisation and generalisation of plants and pollinators, the temporal and spatial variation in these relationships, and the factors that promote and constrain the evolution of niche breadth (Waser *et al.* 1996; Waser 2006).

GENERAL AIMS OF THIS THESIS

The role of variation in pollination is fundamental for understanding ecological dynamics of plant populations and is a major factor in the evolution and maintenance of generalised and specialised pollination systems. My study centred on the role of variation in pollination by addressing the following questions:

1. How variable are pollinators in a generalist pollination system? Specifically, to what degree do insect visitation rates and assemblage composition vary spatially among populations and temporally among flowering seasons?

2. How does variation in pollinators affect plant reproductive success (seed production, seed mass and seedling emergence) and the potential for inbreeding?

In order to answer these questions, a study system which exhibits generalised plant-pollinator interactions, the ability to record this variation in floral visitors on relevant spatial and temporal scales, the ability to record differences in reproductive success and the ability to conduct experimental pollination treatments is needed. I chose to answer these questions with *Trachymene incisa* subsp. *incisa* (Apiaceae), which exhibits these and other features that make it ideal to study variation in a plant-pollinator system.

TRACHYMENE INCISA **SUBSP.** ***INCISA***

There are approximately 56 species of *Trachymene* Rudge, 39 occur in Australia and 38 are endemic (Hart and Henwood 2006). *Trachymene incisa* Rudge subsp. *incisa* is a common and widespread herbaceous species occurring on sandy soils and rock crevices from Fraser Island, Queensland, south to Ulladulla and inland to the Nandewar Range near Narrabri, NSW (Powell 1992; Hart and Henwood 2006). This large latitudinal range provides the potential for significant variation in pollinator assemblage composition among populations. This widespread species is distinguished from the restricted *T. incisa* subsp. *corrugata* L.A.S.Johnson using mericarp (seed) characteristics (Hart and Henwood 2006). *Trachymene incisa* subsp. *incisa* has been abbreviated to *T. incisa* throughout this thesis for brevity.

Trachymene incisa is an erect or ascending perennial herb 60-80 cm high (Wardle 2003; Hart and Henwood 2006; Fig. 1-2). It grows on infertile sandy soils and in rock crevices in dry eucalypt woodland or scrub (Benson and McDougall 1993). Population sizes range from less than 20 individuals to more than 10 000 (Wardle 2003). Plants have a thick rootstock with some lateral branching, although plants are not connected by underground branching and are not clonal (Watson 2000).

Fig. 1-2 *Trachymene incisa* subsp. *incisa* in flower, growing on sandy soils at the Tomago Sandbeds.

Plants flower between September and May, with a peak in flowering during summer between December and February (Powell 1992; Y. C. Davila, personal observation). There are approximately 72 flowers per inflorescence, arranged in simple umbels approximately 2 cm in diameter (Davila 1999; Davila and Wardle 2002). Umbels are borne in dichasial cymes (Hart and Henwood 2006), where the secondary umbels branch off the stalk of the terminal primary umbel and the tertiary umbels branch off the stalks of the secondary umbels and so forth, usually up to four orders. There are on average four inflorescence stalks per plant (Davila and Wardle 2002). The umbels attract a large suite of insect visitors, with morphospecies from 20 families from three orders (Hymenoptera, Diptera and Lepidoptera) observed visiting umbels at one population (Agnes Banks) in 1999 (Davila and Wardle 2002). With such a large visitor assemblage (Fig. 1-3), significant variation is possible and expected on both spatial and temporal scales.

Each flower has five stamens and two equally sized carpels (bilocular) each of which are connected to an elongated style at female anthesis (Hart and Henwood 2006). The flowers are protandrous and open centripetally within the umbel (Davila and Wardle 2002). During the male phase, the anthers dehisce sequentially within the flower while the styles remained curled and stigmas are non-receptive. Once the anthers are spent, the stamens fall off and the flower enters a quiescent phase. The female phase begins once all the flowers in the umbel have entered the quiescent phase (Davila and Wardle 2002). Therefore, whole umbels function as either male (pollen presenting, ~16 d) or female (pollen receptive, ~4 d) at any one time (Fig. 1-4). This phenological pattern, termed complete or synchronous protandry at the umbel level, prevents self-pollination within the umbel (Davila 1999; Davila and Wardle 2002).

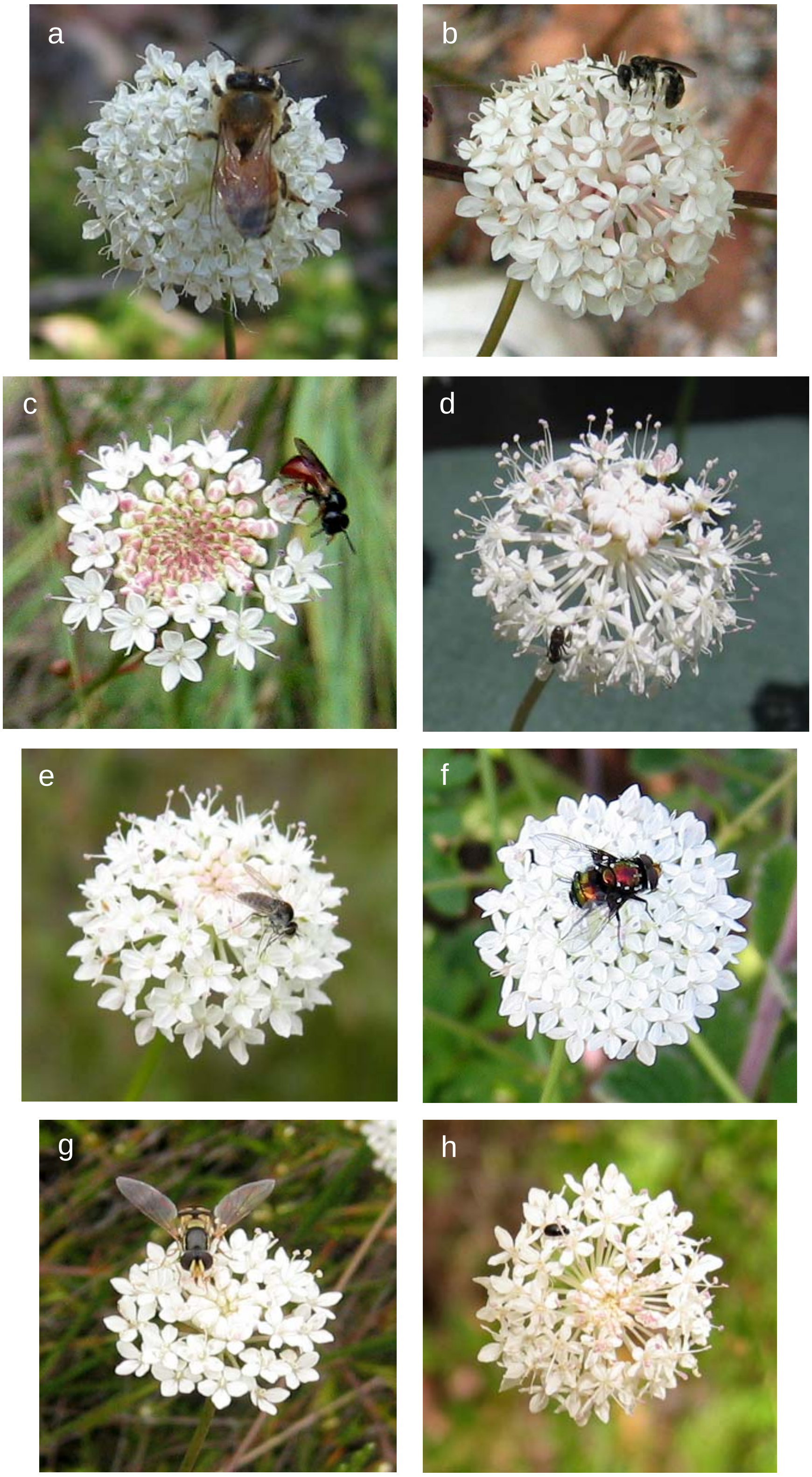

Fig. 1-3 Diversity of floral visitors to umbels of *Trachymene incisa*: (**a**) introduced honey bee *Apis mellifera* (Apidae); (**b**) native bee *Lasioglossum* sp. (Halictidae); (**c**) native bee *Lasioglossum* sp.; (**d**) ant (Formicidae); (**e**) bee fly (Bombyliidae); (**f**) fly (Muscidae); (**g**) hover fly (Syrphidae); (**h**) beetle (Coleoptera). Umbel diameter is approximately 2 cm.

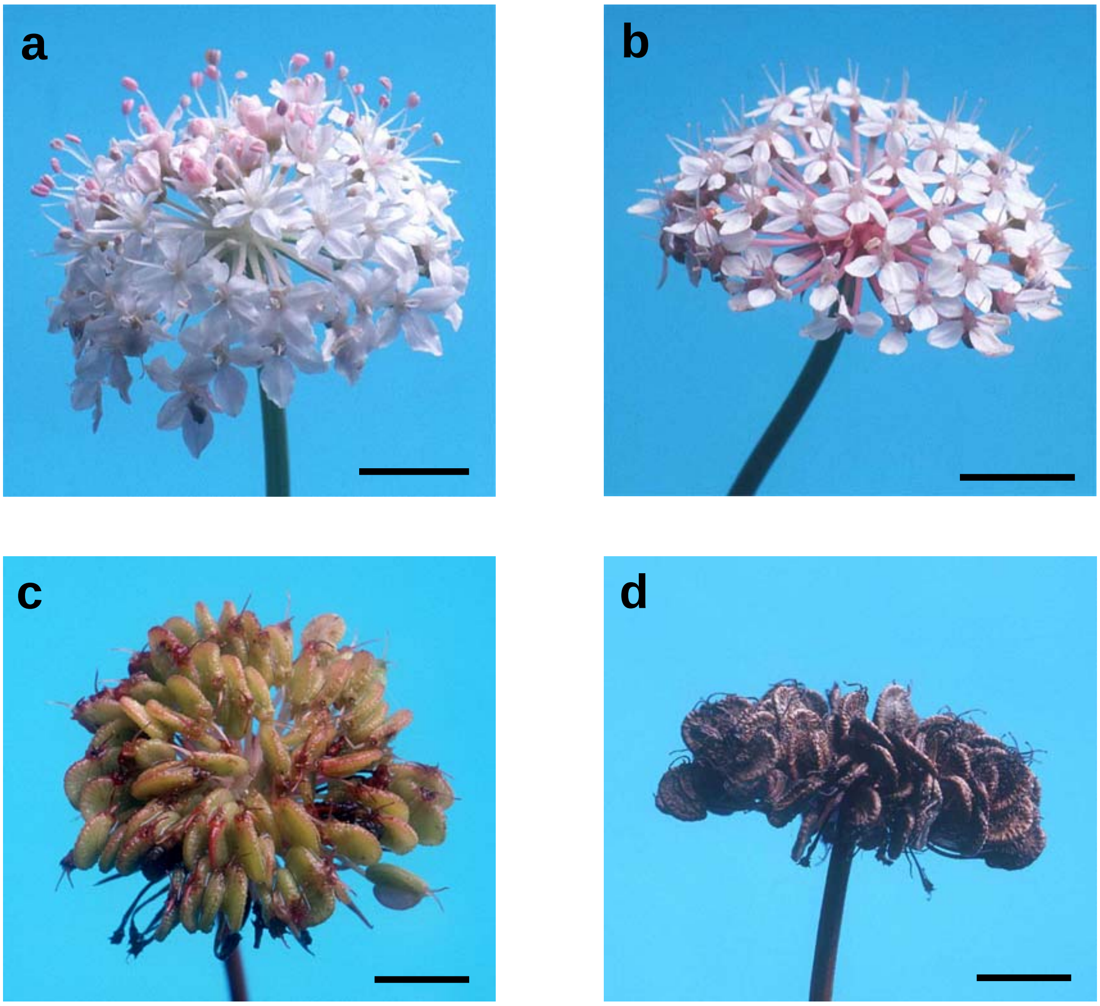

Fig. 1-4 *Trachymene incisa* subsp. *incisa* umbels from the Agnes Banks Woodland: (**a**) male phase umbel with outermost flowers in quiescent phase, intermediate flowers with dehiscing anthers and innermost flowers in bud; (**b**) female phase umbel with all flowers with elongated styles and receptive stigmas; (**c**) developing fruit (view from above); (**d**) mature seeds prior to dispersal (view from the side). Scale bar = 5 mm.

However, male and female phase umbels are usually present on the same plant at the same time, as each umbel order flowers, allowing the possibility for geitonogamous pollination. This multicycle protandry (Schlessman and Graceffa 2002) provides the possibility for a mixed mating system, where the degree of selfing is determined by the amount of pollinator movements between male and female umbels on the same plant. Nectar is produced during the male and female phases, but pollen is only available during the male phase (Davila and Wardle 2002). This fundamental difference in floral rewards between umbel phases may also affect pollinator visitation and effectiveness.

The mature fruit of *T. incisa* may consist of one or two mericarps (Hart and Henwood 2006; Fig. 1-4). The diaspore or seed is a single mericarp. *Trachymene incisa* is self compatible, although seed set resulting from self-pollination is less than seed set resulting from cross-pollination (Davila and Wardle 2002). Pollinators are needed for seed production, therefore, variation in pollinator visitation rates and behaviour will play a critical role in determining reproductive output and the amount of inbreeding experienced in *T. incisa*.

Trachymene has traditionally been placed within the Apiaceae, however, recent molecular studies have questioned this positioning (Chandler and Plunkett 2004). Since the phylogenetic relationships have not yet been resolved, I have followed Hart and Henwood's (2006) conservative placement of *Trachymene* within the Apiaceae.

The Apiaceae are characterised by a high degree of floral uniformity. The plants have been termed "promiscuous" because of their open and simple floral systems that present no restrictions to floral rewards and the large diversity of insect visitors that apparently pollinate them indiscriminately (Bell 1971). In a study examining generalisation across 962 plant species, Olesen (2000) found that *Anthriscus aemula* from the Apiaceae was the most generalised, being visited by 189 insect species.

Practically, experimental crosses in the field and glasshouse are easy to conduct on *T. incisa*, the seeds readily germinate in the field, glasshouse, growth cabinet and laboratory and plants can be kept in cultivation in the greenhouse (Davila and Wardle 2002; Wardle 2003; Appendix 2). These features, in addition to the widespread distribution and generalised pollination system, make *T. incisa* an ideal species to consider one of the central issues in pollination ecology, the spatial and temporal variation in plant-pollinator interactions.

SPECIFIC AIMS AND THESIS STRUCTURE

To investigate the degree and effects of spatial and temporal variation in pollinators in a generalist plant-pollinator system, I conducted mensurative and manipulative experiments using *Trachymene incisa* and its pollinator assemblage.

Chapter 2 explores spatial variation in insect visitation rates and assemblage composition of *T. incisa*, and the relationship with reproductive success. The objectives of this chapter were to:

- Quantify the variation in insect visitation rates, throughout the day and across three populations of *T. incisa* that occur in floristically similar habitats that are geographically separated
- Identify the main insect groups visiting umbels at different times of the day and at different populations, and their contribution to the overall assemblage in terms of visitation
- Determine how the pollinator assemblage relates to the floral display and reproductive output across the three populations

Chapter 3 investigates whether there is more spatial than temporal variation in the floral visitors of *T. incisa*, which is important in maintaining generalisation at different scales. Some data from the previous chapter and data collected in a subsequent year were used to:

- Determine the degree of variation in visitation rates of insects, taxonomic composition of the visitor assemblage, and resulting reproductive output of *T. incisa* across three populations and two years
- Examine whether there is a correlation between insect visitation rates and percentage seed set, considering the role of ants and the absence of honey bees in the system

Chapter 4 explores the pollination ecology and the role of fire in altering pollination of *T. incisa* in the Agnes Banks Woodland, a unique endangered ecological community which hosts one of the largest populations of *T. incisa*. Some data from Chapters 2 and 3, in addition to a third year of data collected in the Woodland, were used to:

- Investigate the variation in diurnal and nocturnal floral insect visitors and the resulting reproductive success of *T. incisa* in the Woodland over three flowering seasons after fire
- Report how fire affects the onset of flowering and pollination services to *T. incisa* in the Woodland

The expression of synchronous protandry at the umbel level in *T. incisa* provides a special case where pollinators must visit both male and female umbels during a foraging trip for successful pollination to occur. Chapter 5 addresses the potential for pollinator preferences in this generalist system given that male and female phase umbels offer different floral rewards. More specifically, I investigated the following questions:

- Do insects visit male and female inflorescences equally overall?
- Do insects visit male and female umbels equally during a foraging trip?
- Do insects spend equal amounts of time foraging on male and female umbels?

Chapter 6 addresses the effects of synchronous protandry on pollinator foraging behaviour, the potential for and effects of inbreeding in *T. incisa*. I used experimental hand-pollinations, analysis of inbreeding depression on seedling performance and observations of insect foraging within and between plants of *T. incisa* to:

- Determine whether geitonogamous self-pollination and biparental inbreeding (matings between relates) results in negative effects in terms of seedling emergence, short-term survival and growth
- Investigate the potential for geitonogamous pollination through insect visitation patterns

Chapter 7 is a discussion of two conceptual frameworks, defining generalisation in pollination systems and an assemblage approach to investigating the consequences of variation in pollinators on plant reproductive success, in light of the major results of this thesis and further directions in the study of generalised plant-pollinator systems.

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LITERATURE CITED

Aizen MA, Feinsinger P (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serrano". *Ecological Applications* 4, 378-392.

Bell CR (1971) Breeding systems and floral biology of the Umbelliferae or Evidence for specialization in unspecialized flowers. In 'The Biology and Chemistry of the Umbelliferae'. (Ed. VH Heywood) pp. 93-108. (The Linnean Society of London (by Academic Press): London)

Benson DH, McDougall L (1993) Ecology of Sydney Plant Species: Part 1 - Ferns, fern-allies, cycads, conifers and dicotyledon families Acanthaceae to Asclepiadaceae. *Cunninghamia* 3, 257-422.

Buchmann SL, Nabhan GP (1996) 'The Forgotten Pollinators.' (Island Press/Shearwater Books: Washington D.C.)

Chandler GT, Plunkett GM (2004) Evolution in Apiales: nuclear and chloroplast markers together in (almost) perfect harmony. *Botanical Journal of the Linnean Society* 144, 123-147.

Crane PR, Friis EM, Pedersen KR (1995) The origin and early diversification of angiosperms. *Nature* 342, 27-33.

Davila YC (1999) Reproductive ecology of *Trachymene incisa* (Apiaceae). BSc (Hons) thesis, The University of Sydney.

Davila YC, Wardle GM (2002) Reproductive ecology of the Australian herb *Trachymene incisa* subsp. *incisa* (Apiaceae). *Australian Journal of Botany* 50, 619-626.

Gross CL (2001) The effect of introduced honeybees on native bee visitation and fruit-set in *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. *Biological Conservation* 102, 89-95.

Gross CL, Mackay D (1998) Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). *Biological Conservation* 86, 169-178.

Hart JM, Henwood MJ (2006) A revision of Australian *Trachymene* (Apiaceae: Hydrocotyloideae). *Australian Systematic Botany* 19, 11-57.

Herrera CM (1987) Components of pollinator "quality": comparative analysis of a diverse insect assemblage. *Oikos* 50, 79-90.

Herrera CM (2000) Flower-to-seedling consequences of different pollination regimes in an insect-pollinated shrub. *Ecology* 81, 15-29.

Hingston AB, McQuillan PB (1998) Does the recently introduced bumblebee *Bombus terrestris* (Apidae) threaten Australian ecosystems? *Australian Journal of Ecology* 23, 539-549.

Hingston AB, McQuillan PB (1999) Displacement of Tasmanian native megachilid bees by the recently introduced bumblebee *Bombus terrestris* (Linnaeus, 1758) (Hymenoptera: Apidae). *Australian Journal of Zoology* 47, 59-65.

Horskins K, Turner VB (1999) Resource use and foraging patterns of honeybees, *Apis mellifera*, and native insects on flowers of *Eucalyptus costata*. *Australian Journal of Ecology* 24, 221-227.

Kearns CA, Inouye DW (1997) Pollinators, flowering plants, and conservation biology. *BioScience* 47, 297-307.

Minckley RL, Roulston TH (2006) Incidental mutualisms and pollen specialization among bees. In 'Plant-pollinator interactions: from specialization to generalization'. (Eds NM Waser and J Ollerton) pp. 69-98. (The University of Chicago Press: Chicago)

Morgan MT, Schoen DJ (1997) The role of theory in an emerging new plant reproductive biology. *Trends in Ecology and Evolution* 12, 231-231.

Olesen JM (2000) Exactly how generalised are pollination interactions? In 'The Scandinavian Association for Pollination Ecology honours Knut Fægri'. (Eds Ø Totland, WS Armbruster, C Fenster, U Molau, LA Nilsson, JM Olesen, J Ollerton, M Philipp and J Ågren) pp. 161-178. (The Norwegian Academy of Science and Letters: Oslo)

Ollerton J (2006) "Biological barter": patterns of specialization compared across different mutualisms. In 'Plant-pollinator interactions: from specialization to generalization'. (Eds NM Waser and J Ollerton) pp. 411-435. (The University of Chicago Press: Chicago)

Pellmyr O (2002) Pollination by animals. In 'Plant-animal interactions: an evolutionary approach'. (Eds CM Herrera and O Pellmyr) pp. 157-184. (Blackwell Science Ltd: Oxford)

Powell JM (1992) 110 Apiaceae. In 'Flora of New South Wales'. (Ed. GJ Harden) pp. 87-116. (New South Wales University Press: Kensington)

Proctor M, Yeo P, Lack A (1996) 'The Natural History of Pollination.' (Timber Press: Portland)

Renner SS (2006) Rewardless flowers in the angiosperms and the role of insect cognition in their evolution. In 'Plant-pollinator interactions: from specialization to generalization'. (Eds NM Waser and J Ollerton) pp. 123-144. (The University of Chicago Press: Chicago)

Renner SS, Ricklefs RE (1995) Dioecy and its correlates in the flowering plants. *American Journal of Botany* 82, 596-606.

Schlessman MA, Graceffa LM (2002) Protogyny, pollination, and sex expression of andromonoecious *Pseudocymopterus montanus* (Apiaceae, Apioideae). *International Journal of Plant Sciences* 163, 409-417.

Shepherd M, Buchmann SL, Vaughan M, Hoffman Black S (2003) 'Pollinator Conservation Handbook.' (The Xerces Society: Portland)

Thompson JN (1994) 'The Coevolutionary Process.' (The University of Chicago Press: Chicago)

Wardle GM (2003) Experimental determination of seed emergence and carry-over in the soil seed bank of the herbaceous perennial, *Trachymene incisa* (Apiaceae). *Austral Ecology* 28, 161-172.

Waser NM (2006) Specialization and generalization in plant-pollinator interactions: a historical perspective. In 'Plant-pollinator interactions: from specialization to generalization'. (Eds NM Waser and J Ollerton) pp. 3-17. (The University of Chicago Press: Chicago)

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. *Ecology* 77, 1043-1060.

Watson C (2000) Root demography of an Australian herb: *Trachymene incisa*. BSc (Env) (Hons) thesis, The University of Sydney.

Wilson P, Thomson JD (1991) Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. *Ecology* 72, 1503-1507.

Wyatt R (1983) Pollinator-plant interactions and the evolution of breeding systems. In 'Pollination Biology'. (Ed. L Real) pp. 51-95. (Academic Press: Orlando)