Impacts of landscape resource diversity and availability on bee foraging and fitness

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Image (next page): the Australian eusocial stingless bee *Tetragonula carbonaria.*
Image by Tobias Smith

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This thesis is based on the following manuscripts:

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ABSTRACT

Loss of natural and semi-natural habitat due to increasing human land use for agriculture and housing has led to widespread declines in bee pollinator diversity and abundance, which raised global concerns about the stability of pollination services. Bee population dynamics depend on floral resource diversity and availability in the surrounding landscape, and loss of plant biodiversity may thus directly impair the fitness of individual bee species. However, whether and how plant and resource diversity and availability affect foraging patterns, resource intake, resource quantity and nutrient quality and ultimately fitness of generalist social bees remains unclear.

In this thesis, we placed hives of the Australian eusocial stingless bee *Tetragonula carbonaria* (Apidae, Meliponini) in natural habitat (subtropical forests) and two landscapes differently altered by humans (suburban gardens and macadamia plantations), varying in plant species richness, resource abundance and respective habitat patch size. Foraging patterns and resource intake were compared between landscapes in different seasons and colony growth and fitness were monitored over two and a half years.

Bee foraging activity, pollen and sugar intake, diversity of collected pollen and resin resources, resource quantity (colony food stores), colony fitness (brood volume, queen- and worker reproduction) and colony growth overwhelmingly increased with plant species richness in the surrounding habitat. However, plant species richness and thus bee fitness was highest in gardens, not in natural forests, as bees in gardens benefited from the continuous floral resource availability of both natural and exotic plants across seasons. In contrast, foraging rates and success, forager orientation and consequently colony fitness was largely reduced in plantations. While bees maximized diversity of collected resources, collecting more diverse resources did however not increase resource functionality and nutritional quality, which appeared to be primarily driven by the surrounding plant community in our study. Conversely, individual worker fitness (body fat and size) was not affected by available resource diversity and abundance, showing that colonies seem not to increase the nutritional investment in single workers, but in overall worker population size.

This thesis consequently revealed the outstanding role of plant biodiversity as a key driver of (social) bee fitness by providing more foraging resources, even when only small but florally diverse patches are available.

ZUSAMMENFASSUNG

Der Verlust von natürlichem oder naturnahem Habitat durch fortschreitende menschliche Landnutzung für Landwirtschaft oder Besiedlung hat vielerorts zu Einbrüchen der Bienenvorkommen und -vielfalt geführt, so dass die Stabilität globaler Bestäubungsleistungen als gefährdet gilt. Da Populationsdynamiken der Bienen stark von Vielfalt und Verfügbarkeit der Blütenressourcen in Landschaften abhängen, nimmt die Fitness einzelner Bienenarten vermutlich mit dem Rückgang der Pflanzen-Biodiversität ebenfalls ab. Es ist bislang aber unbekannt, inwiefern Vielfalt und Verfügbarkeit von Pflanzenressourcen das Sammelverhalten, den Ressourceneintrag, die Menge und den Nährwert der Ressourcen und schließlich die Fitness sozialer Bienen beeinflusst.

Für diese Doktorarbeit wurden Bienenstöcke der eusozialen, stachellosen Bienenart *Tetragonula carbonaria* (Apidae, Meliponini) in ihrem natürlichen Habitat in Australien (subtropische Wälder) und zwei weiteren, menschengeformten Landschaften platziert (Gärten in Vorstädten und Macadamia-Plantagen), wobei sich Pflanzenreichtum, Ressourcenangebot und Fläche der jeweiligen Landschaftstypen zwischen den Standorten unterschieden. Das Sammelverhalten der Bienen und ihr Ressourceneintrag wurde zwischen den Landschaften verglichen und Koloniewachstum und -fitness über zweieinhalb Jahre beobachtet.

Mit ansteigendem Pflanzenreichtum in der Umgebung stiegen Sammelaktivität, Pollen- und Zuckereintrag, die Vielfalt von Pollen und Harztypen, Ressourcenvorräte im Nest, die Koloniefitness (Brutvolumen, Königinnen- und Arbeiterinnen-Zucht) und somit Kolonie-wachstum der Bienen drastisch an. Der höchste Pflanzenreichtum wurde allerdings in Gärten festgestellt und nicht im natürlichen Habitat (Wälder), und Bienen in Gärten konnten somit durch alle Jahreszeiten kontinuierlich Blütenressourcen von heimischen und exotischen Pflanzen nutzen. Im Gegensatz dazu waren in Plantagen Ressourceneintrag, Orientierungsvermögen und letztlich Koloniefitness deutlich geringer. Während die Bienen jeweils eine größtmögliche Diversität verschiedener Ressourcen gesammelt haben, stieg die Ressourcenqualität aber nicht direkt mit der Ressourcendiversität an, sondern wurde stattdessen vermutlich mehr von der Zusammensetzung der umgebenden Pflanzengemeinschaft beeinflusst. Die Fitness einzelner Arbeiterinnen (Körperfettanteil und Größe) hing darüber hinaus auch nicht von dem Ressourcenspektrum ab, was nahe legt, dass einzelne Kolonien nicht die Futterqualität und –menge bei der Larvenaufzucht reduzieren, sondern stattdessen die Anzahl der produzierten Arbeiterinnen.

Diese Doktorarbeit belegt damit die herausragende Rolle, die die Pflanzenvielfalt für die Bienenfitness einnimmt. Höhere Pflanzenvielfalt und somit bessere Ressourcenverfügbarkeit kann damit das Überleben von Bienen absichern, selbst wenn nur kleine Vegetationsflecken mit hoher Pflanzendiversität zur Verfügung stehen.

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I. GENERAL INTRODUCTION
Bee resource foraging and its consequences for bee fitness and bee declines

1.1. Introduction to pollination

Plant-pollinator interactions are among the most ecologically important plant-animal relationships (Kearns et al. 1998). Many plants could not set seed and reproduce without pollinators, pollinators in return would decline without floral rewards, and further destabilize other species (Kearns et al. 1998; Memmott et al. 2007; Ollerton et al. 2011). Globally, about 85 % of flowering plant species are pollinated by animals, with the proportion increasing from temperate zones (78 %) to the tropical regions, where up to 94 % of the plants are animal pollinated (Ollerton et al. 2011).

Pollination by animals is a key ecosystem service. The term 'ecosystem service', popularized in the Millennium Ecosystem Assessment (2005), refers hereby to the multitude of (free) benefits people obtain from ecosystems (Fisher et al. 2008). Pollination is important to the sexual reproduction of many crops and thus for food production, as 87 of the 124 leading global food crops depend or benefit from animal pollination, and pollination accounts for 35 % of global food production volume (Klein et al. 2007). Animal pollination further improves quantity and commercial quality of many crops compared to wind or self-pollination (Bommarco et al. 2012b; Garratt et al. 2014; Klatt et al. 2014). The resulting global economic value of pollination was estimated to be € 153 billion in 2005 (Gallai et al. 2009). Specifically production of fruits, vegetables and stimulants (such as coffee) are vulnerable to pollinator decline and global production could not meet current demand without pollinators. Moreover, global reliance on pollination (based on pollination dependencies and economic factors, like producer prices and purchasing power parities) show an increasing trend between 1993-2009 (Lautenbach et al. 2012). This increased dependence on pollinators is predicted to increase consumer prices and fuel potential conflicts between pollination services and other land uses (Aizen et al. 2008; Lautenbach et al. 2012).

Biodiversity is a critical driver of ecosystem functions (e.g. pollination), as it maintains the stability of ecosystem services and provides insurance against changing environmental conditions (Loreau et al. 2001). In theory, higher biodiversity can support pollinator populations, as higher biodiversity provides a greater variety of

resources to be exploited by consumers (Duffy et al. 2007). Increasing species richness of primary producers (e.g. flowering plants) could thus enhance biomass and richness of consumers (Gamfeldt et al. 2005). Multiple species or functional groups in diverse ecosystems may support the same ecosystem function, thereby increasing the resilience of the whole system (Yachi and Loreau 1999; Blüthgen and Klein 2011). Moreover, a greater number of producers and consumers in biodiverse ecosystems results in more interactions within or across trophic levels which can further stabilize ecosystem services (Ives et al. 2005; Balvanera et al. 2006). However, the mechanisms by which biodiversity as central driver affects pollinators in real ecosystems are not fully understood to date.

1.2. Bees as pollinators

1.2.1. *Honey bees*

Bees, specifically honey bees (*Apis mellifera*), are the most economically valuable pollinators of crops worldwide, and contribute significantly to human food production (Klein et al. 2007). Honey bees are kept and propagated in managed hives and are the most widely used pollinators in agriculture (Watanabe 1994). They increase yield in some animal-pollinated crops by up to 96 % and are often the only commercial solution to ensure crop pollination (Klein et al. 2007). Furthermore, honey bees also provide pollination services to many wild plants, although the amount they contribute is disputed (Potts et al. 2010b; Garibaldi et al. 2013). While honey bees are versatile, cheap and convenient to keep compared to wild bees, they are not the most effective pollinators for some crops, such as almond (Bosch and Blas 1994; Brittain et al. 2013b), watermelon (Kremen et al. 2004) or coffee (Klein et al. 2003; Jha and Vandermeer 2009).

HONEY BEE DECLINE. Today, there is clear evidence for severe regional declines in domestic honey bee stocks in the USA (59 % loss of colonies between 1947 and 2005) and Europe (25 % in central Europe between 1985 and 2005), raising substantial concerns about the future availability of honey bee pollination services (Potts et al. 2010b; vanEngelsdorp and Meixner 2010).

Modern pollination industries are under threat by multiple stressors, some specific to honey bees. Global trade has accelerated the spread of honey bee pests like parasitic mites (*Varroa jacobsoni*, *V. destructor* and *Acarapis woodi*; (Watanabe 1994)), the

small hive beetle (*Aethina tumida*) and the microsporidian parasite *Nosema ceranae* (Klein et al. 2007), that have eliminated wild and feral honey bee colonies in many regions in Europe and the USA, leaving only those kept by beekeepers (Potts et al. 2010a). Furthermore, beekeeping is an industry in decline, with aging beekeepers in Europe and North America (Klein et al. 2007; Potts et al. 2010b). Honey bees have suffered severe losses particularly since 2006-2007 in the USA when a syndrome called colony collapse disorder (CCD) was first described, with bees simply mysteriously vanishing from their hives (Oldroyd 2007; vanEngelsdorp et al. 2009). At the same time, many beekeepers and researchers also documented serious losses of honey bee colonies in Europe (Decourtye et al. 2010; Genersch et al. 2010). After years of intense research, there is now a general consensus that pests and pathogens are the single most important cause of otherwise inexplicable colony losses (Johnson et al. 2009; Genersch 2010; Nazzi and Pennacchio 2014).

Despite the described regional losses and pressing threats in Europe and North America, the *global* number of honey bee hives has increased by about 45 % in 1961-2007. However, the proportion of agricultural crops depending on pollinators is increasing much more rapidly (>300 %) so that demand for pollination services could outstrip the increase in hive numbers, leaving the dependence of agricultural crop pollination on a single pollinator species even more worrisome (Aizen and Harder 2009; Potts et al. 2010a).

1.2.2. *Wild bees*

Social and solitary bees, wasps, flies, beetles, butterflies and moths comprise the vast majority of the world's pollinators (Vanbergen and the Insect Pollinators Initiative 2013). Many wild pollinators are crucial for the pollination of fruit, vegetable, oil, seed and nut crops (Vanbergen and the Insect Pollinators Initiative 2013; Gill et al. 2016). Globally, wild insects pollinate crops more effectively than honey bees and thus enhance crop fruit set independently of honey bee visitation (Garibaldi et al. 2013). Yet in contrast to managed honey bees, wild pollinators provide crop pollination as a free ecosystem service.

Bees are the most effective pollinators of many crops and are the most numerous flower visitors worldwide (Klein et al. 2007; Winfree 2010). Bees are obligate florivores throughout their life cycle, with both adults and larvae dependent on floral products, primarily pollen and nectar (Winfree 2010; Nicolson 2011). Wild bees alone, in this context defined as native social or solitary bees not managed for pollination, can

fully pollinate crops in some agricultural contexts (Klein et al. 2003; Winfree et al. 2007b).

WILD BEE POLLINATION BENEFIT. Wild bees can further improve crop pollination when (managed) honey bees are already present: Brittain et al. (2013a) describe within-tree specialisation of native pollinators in almonds, as well as continued pollination by native pollinators at high wind speeds, when honey bee foraging ceased. In apple orchards, honey bees were found to prefer only densely flowering trees, whereas wild bees visited and pollinated trees more evenly throughout the orchard (Mallinger and Gratton 2015). More importantly, wild bees can enhance honey bee pollination effectiveness by directly re-depositing pollen or altering the behaviour of honey bees to switch between flowers more frequently, providing synergistic pollination effects (sunflowers: Greenleaf and Kremen 2006; almonds: Brittain et al. 2013b). Wild bees thus help stabilize pollination services, and visitation and fruit set consequently decrease when crops are at greater distances from natural habitat of wild bees (Garibaldi et al. 2011).

Aside from crop pollination, wild bees are of critical importance in natural ecosystems (Winfree 2010). The importance of wild pollinators dramatically increases in subtropical and tropical ecosystems, yet most tropical pollination systems remain poorly studied and management techniques only exist for a small number of non-*Apis* taxa (Winfree 2010; Winfree et al. 2011; Garibaldi et al. 2013). It is thus imperative to include other wild bee taxa in research to secure pollination in subtropical and tropical environments.

1.2.3. *Stingless bees*

Stingless bees (Hymenoptera: Meliponini) are considered particularly important pollinators in paleo- and neotropical ecosystems, but knowledge about stingless bees in pollination is still very patchy (Corlett 2004; Giannini et al. 2014). They are a monophyletic group of at least 600 described species in 61 genera and inhabit tropical regions worldwide (Rasmussen and Cameron 2010). At least twelve species of two genera (*Austroplebeia* and *Tetragonula*) are found on the Australian continent (Dollin et al. 1997; Dollin et al. 2015). Meliponini are highly eusocial bees, i.e. they form colonies with cooperative brood care, overlapping generations, and colonies are divided into reproductive (queens, drones) and non-reproductive castes (workers) (Roubik 1989; Michener 2007).

Figure I.1. **Stingless bees and meliponiculture**. Size comparison between honey bee (*Apis mellifera*) and stingless bee (*Tetragonula sp.*; **A**). Meliponiculture of *Tetragonula carbonaria* in Australia: stingless bee hive with two boxes housing the brood (bottom and centre box), additional honey super (top box) and protective roof (OATH hive design; **B**). For hive propagation, brood is cut horizontally between the bottom and centre box and both hive parts are then equipped with new empty boxes for both brood nuclei to rebuild two separate colonies (**C**). Nest and brood structure of *T. carbonaria*: construction of honey/pollen storage pots (**D**). Typical brood spiral of *T. carbonaria*, featuring open worker cells (on spiral rim) and one queen pupae (enlarged light yellow cell on left side; **E**).
Images: *Tobias Smith* (**A**), *Rhys Smith* (**B**), *Tim Heard* (**C**) *and Glenbo Craig* (**D, E**).

Nests are dug into soil, build in cavities of tree trunks, animal holes or artificial structures and contain from a few dozen up to several thousand workers (Roubik 1989; Roubik 2006). Inside the nest, the central brood area is typically surrounded by pots with stored food resources (honey and pollen, Figure I.1) and is insulated by a layer of propolis-structure, called batumen (Roubik 2006). Unlike honey bees, bumble bees and solitary bees of temperate zones, stingless bees form perennial colonies and can potentially forage in all seasons (Heard 1999; Slaa 2006).

Stingless bees are generalist flower visitors and visit a broad range of plant species (Ramalho et al. 1990; Biesmeijer et al. 2005; Slaa et al. 2006). Individual foragers tend to specialize on a single floral species for a certain amount of time, a behavioural trait commonly referred to as flower constancy, making them valuable pollinators for many plants (Ramalho et al. 1994; Slaa et al. 2003). As meliponines generally have no sting, they have been frequently domesticated for honey production and pollination (known as meliponiculture, Cortopassi-Laurino et al. 2006; Figure I.1). Furthermore, stingless bees are effective pollinators for at least 18 crops and are a promising option for managed commercial pollination of field crops and in greenhouses (Heard 1999; Slaa et al. 2006; Greco et al. 2011). Despite their importance for pollination in natural ecosystems, their broad distribution and potential use in managed crop pollination, stingless bees and their role as wild pollinators remain generally under-studied.

1.3.   Declines in wild bees

Disturbing reports of bee declines in Europe and North America in recent years received much attention in the media as well as the academic literature, fuelling environmental and economic concerns that global food security is at risk (Winfree 2010; Gill et al. 2016). Honey bee population shifts are poorly documented, but even less is known about recent changes in wild pollinator populations and communities (Potts et al. 2010a). Due to the lack of coordinated monitoring programmes, little is known about the extent of wild pollinator declines, but studies of bumblebees revealed wide-scale reductions in range and abundance of several species in North America (Cameron et al. 2011) and shifts from natural bee communities to few dominant bumble bee species in Sweden (Bommarco et al. 2012a). Curiously, declines of wild bee diversity in Britain and the Netherlands go hand in hand with declines in plant diversity, highlighting the importance of plant biodiversity for bees (Biesmeijer et al. 2006). However, most available data on pollinator declines is from the EU and the USA, but data is scarce for other parts of the world. It is therefore still debated, whether we face a global pollinator

decline and thus a global pollination crisis (Ghazoul 2005; Steffan-Dewenter et al. 2005; Ghazoul 2015; Goulson et al. 2015).

Indirect evidence for pollinator declines comes however from studies linking global anthropogenic landscape changes and bee declines. Winfree et al. (2009) suggests that agricultural intensification and habitat loss causes widespread declines of pollinator richness and abundance, which consequently reduces pollination services by wild bees (Kremen et al. 2002). As most natural landscapes around the world have been anthropogenically modified, it is likely that pollinator abundance and richness has declined in many parts of the world (Potts et al. 2010a).

1.3.1. *Drivers of wild bee decline*

Several reviews focused on single or combined stressors of wild pollinators, presenting a catalogue of potential drivers of pollinator declines. Potts et al. (2010a); Winfree (2010); and Vanbergen and the Insect Pollinators Initiative (2013) identified the key drivers of bee decline, which are summed up below. These effects are likely to interact in ecosystems, and interactions may greatly increase the pressure on pollinators (González-Varo et al. 2013; Goulson et al. 2015).

CLIMATE CHANGE. Plant and pollinator ranges are shifting, causing changes to pollinator populations that inhabit the edges of their species' climatic range, so they become more susceptible to population declines and even extinction as a result of climate change (Williams and Osborne 2009; Vanbergen and the Insect Pollinators Initiative 2013). Climate change may affect plants and pollinators differently, leading to mismatches between mutualistic partners. Differential migration rates of bees and co-occurring plants can lead to a **spatial** dislocation of the pollination process (Schweiger et al. 2008). Climate driven changes in some bees' phenology have been already observed (Bartomeus et al. 2011) and can lead to a **temporal** mismatch between bee emergence and flowering of preferred food plants. Depending on model assumptions, Memmott et al. (2007) predict phenological changes may lead to up to 17-50 % reduced floral resources available to all pollinator species.

INTRODUCTION OF ALIEN SPECIES: PLANTS, POLLINATORS. There is empirical evidence that **alien plants** are readily integrated into native plant-pollinator networks, and can act as additional pollen and nectar sources (Tepedino et al. 2008; Stout and Morales 2009; Potts et al. 2010a; Williams et al. 2011). In Europe, plants introduced as ornamentals with long flowering seasons, appealing scent or showy flowers may attract native bees (Potts et al. 2010a; Garbuzov and Ratnieks 2014) or even ensure survival of native bees

when native nectar resources are scarce (Kleijn and Raemakers 2008). However, several studies suggest that positive effects might be limited to generalist pollinators (Traveset and Richardson 2006; Tepedino et al. 2008; Gotlieb et al. 2011), thereby adding to the list of risk factors for specialists when alien plants replace or outcompete native plants. **Alien pollinators** introduced and managed for crop pollination, mainly *Apis mellifera*, may impact on native pollinators through competition for resources. Resource overlap in plant use (up to 90 %) between *Apis mellifera* and a native *Bombus* species was reported from the USA (Thomson 2006), and up to 70 % between one alien and a native *Bombus* species in Japan (Matsumura et al. 2004). Aggressive invasive Africanised honey bees outcompete native stingless bees in Mexico and dominate bee communities, especially in disturbed habitats (Cairns et al. 2005). However, it remains controversial whether and to what degree competition actually occurs and impacts native pollinator communities (Potts et al. 2010a; Winfree 2010).

PESTS AND PATHOGENS. A variety of **pathogens** affect honey bees, with *Varroa destructor* and other parasitic mites being the primary vector for many viruses (Sammataro et al. 2000; Vanbergen and the Insect Pollinators Initiative 2013). Translocated managed honey bees may increase the risk of pathogen spread (Stout and Morales 2009). Although little is known about the inter-specific transfer of pathogens in bee communities (Woolhouse et al. 2005), there is evidence that the extent and role of host shifts and shared pathogens has been underestimated, as several studies identified pathogen transfer within and between populations of managed and wild bee species (Singh et al. 2010; Cameron et al. 2011). The introduction of **pest** species (e.g. *Varroa destructor*) caused colony declines in wild and managed honey bees in all countries it has reached (Rosenkranz et al. 2010), but whether and how *V. destructor* will affect native wild bee populations in Australia, which is currently free of the parasitic mite, remains largely unknown (Iwasaki et al. 2015). Other pests (e.g. small hive beetle, *Aethina tumida*) posing significant threats to feral and managed honey bees (Neumann and Elzen 2004) are known to be effectively contained by native bees (Greco et al. 2010).

PESTICIDES. *Apis mellifera* is used as model in most toxicity studies of pesticides (Thompson and Maus 2007; Henry et al. 2012), and while growers may avoid spraying during times of honey bee activity, native bees are often not considered (Winfree 2010). Pesticides used in agriculture can cause mortality by direct ingestion (Alston et al. 2007), but pesticide exposure may also have sub-lethal effects on honey bees or bumble bees with implications for foraging, worker mortality, brood development and long term colony performance (Morandin et al. 2005; Thompson and Maus 2007; Gill et al. 2012).

Winfree (2010) expects wild bees to experience less pesticide exposure relative to honey bees since they do not forage exclusively on agricultural crops. Recent studies however have shown that wild social bees with smaller colonies are less resilient to pesticide contamination and that exposure to a combination of pesticides in landscapes can have dramatic effects on wild bees (Gill et al. 2012).

HABITAT LOSS AND FRAGMENTATION. Habitat loss is considered the leading cause of species decline (Winfree 2010) and landscape-related declines in wild bees received much attention in both case studies and reviews (Potts et al. 2010a; Winfree 2010; Roulston and Goodell 2011; Vanbergen and the Insect Pollinators Initiative 2013) and shall be discussed in detail in section 1.4.

1.4.   Impacts of landscape change on bees

Loss of natural habitat is generally thought to be the most important factor driving bee declines (Potts et al. 2010a; Garibaldi et al. 2014; Vanbergen 2014; Goulson et al. 2015; Gill et al. 2016). A meta-analysis of anthropogenic disturbance in wild bee communities found overall negative effects of habitat loss and fragmentation, specifically in systems with very little natural habitat remaining (Winfree et al. 2009; also see: Winfree et al. 2011). Another meta-analysis of 23 studies of 17 crops in agricultural landscapes from around the globe found a strongly significant negative effect of distance from natural habitat (due to habitat loss and/or conversion) on the richness and abundance of wild bees (Ricketts et al. 2008). Foraging distance and duration increased with isolation from natural habitat, decreasing breeding success in solitary bees, specifically impairing smaller species (Greenleaf et al. 2007; Zurbuchen et al. 2010).

FRAGMENTATION. Natural landscapes are often partially converted to other land uses, resulting in isolated natural habitat and fragmented landscapes. Access to natural and biodiverse habitat is critical for wild bees and corridors between patches can improve habitat quality in homogenous habitats (Williams and Kremen 2007; Winfree et al. 2007a; Viana et al. 2012; Kennedy et al. 2013). Many studies indicate that landscape fragmentation often leads to declines in diversity and abundance of insect pollinators (Steffan-Dewenter et al. 2002; Ricketts 2004), but some studies have recorded exceptions (Donaldson et al. 2002). This variability suggests that response may depend on life history (e.g solitary, parasitic and/or oligolectic bees; Roulston and Goodell

I. General introduction

2011), bee size (Brosi 2009; Jauker et al. 2013), or on specific characteristics of the studied landscape (Williams and Kremen 2007). Potts et al. (2010a) however point out that few studies could show an effect of fragmentation per se, thus addressing habitat isolation effects independently of habitat area effects. A surprising finding by Winfree et al. (2007a) was that bee abundance and species richness decreased within continuous patches of natural forest, but increased in disturbed landscapes.

LOSS OF PLANT BIODIVERSITY. Only very few studies linked loss of plant biodiversity to bee declines directly (Biesmeijer et al. 2006; Nicholls and Altieri 2013), but observed parallel declines of pollinators and the diversity of their food plants and highlighted the role of plant biodiversity in agro-ecosystems for bees. Yet it has been frequently observed that larger areas of natural or semi-natural habitat support a higher bee diversity and abundance compared to anthropogenically disturbed landscapes with lower biodiversity (Söderström et al. 2001; Steffan-Dewenter 2003; Jauker et al. 2012; Rollin et al. 2013; Woodcock et al. 2013). For example, Woodcock et al. (2013) show that solitary bee species richness increases with the percentage of semi-natural grassland and thus a more diverse plant community plant in agricultural dominated landscapes. Likewise, Rollin et al. (2013) highlight that specifically wild bee abundance depends on patches of wild flowers (e.g. as weeds in crops or at field margins) or flowering shrubs in hedgerows around fields. However, many of these studies defined landscape and habitat categories prior to the study, but did not investigate whether plant diversity directly influences wild bee richness or abundance. It thus remains unclear, whether bees can directly benefit from overall greater plant diversity in any landscape type, which could explain high bee species richness and abundance even in disturbed landscapes, as observed e.g. by Winfree et al. (2007a).

AGRICULTURE. Anthropogenic agricultural intensification and urbanization are considered major causes of habitat loss for wild bees, yet they might affect bees differently (Winfree 2010; Goulson et al. 2015; Gill et al. 2016). Intensified agriculture generally decreases bee richness and abundance, and negative effects on bees intensified from organic to conventional farms and from complex to simplified landscape contexts (Kennedy et al. 2013). While perennial cropping systems may create favourable landscapes (e.g. orchards with fruit trees), agricultural monocultures with annual cropping systems (e.g. oilseed rape fields) may only provide a narrow window of abundant bloom and thus food for bees (Decourtye et al. 2010).

URBANIZATION. The effect of urbanization on bees is however more controversial. A global review Hernandez et al. (2009) found bee species richness overall to be negatively affected by urbanization, but cavity-nesters and generalists to benefit in

urban habitats. Increasing urbanization, i.e. greater housing density from suburban areas to city centres, generally decreases bee diversity and abundance (McKinney 2008; Bates et al. 2011). Moreover, Ahrné et al. (2009) shows that bumble bee species composition may change along an urbanization gradient in Sweden, with some bee guilds disappearing in highly urbanized areas. In contrast, there is some evidence that urban or suburban gardens can add beneficial landscape elements and provide food resources or nesting space, which increases bee abundance and density in social and solitary bees (Gotlieb et al. 2011; Samnegård et al. 2011; Hinners et al. 2012). Only one study so far demonstrated that bumble bee colony growth is increased in suburbia by greater density and diversity of floral resources in gardens compared to adjacent farmland (Goulson et al. 2002).

Most studies investigating urban bees to date are correlative, and Hernandez et al. (2009) thus point out the need for manipulative studies and incorporation of landscape-scale assessments in those. There is growing evidence that bee populations are primarily regulated by food resources in landscapes (Hines and Hendrix 2005; Roulston and Goodell 2011; Jha and Kremen 2013), but it remains unknown how floral resources affect foraging patterns and resource intake of bees in urban and agricultural landscapes compared to natural habitats.

1.5. Foraging for resources

While many of the studies mentioned above focus on the overall *indirect* effect of the landscape and habitat context, Roulston and Goodell (2011) argue that improving the knowledge of *direct* effects will greatly enhance our ability to augment wild bee population abundance and diversity. Roulston and Goodell (2011) propose that wild bee populations are regulated by both (a) indirect factors, such as landscape context or abiotic factors (e.g. see Faria and Gonçalves 2013; Figueiredo-Mecca et al. 2013; Polatto et al. 2014), and (b) direct factors, like food resources (i.e. pollen and nectar; Hines and Hendrix 2005; Jha and Kremen 2013), nesting resources (e.g. Ricketts 2004) and incidental risks. Indirect evidence supporting food resource regulation of bee populations comes from studies assessing the effect of food resource availability and diversity on whole bee populations as discussed in sections 1.5.1 and 1.5.2.

1.5.1. *Food resource availability*

A variety of studies address temporal and spatial availability of floral resources, reviewed in Decourtye et al. (2010) for agricultural farmland and natural or semi-natural landscapes. Bumble bee abundance was limited by typical peaks of resource availability parallel to mass flowering of crops, followed by periods of food limitation in simplified agricultural landscapes in Sweden (Persson and Smith 2013). A comparable study from the UK could not identify abundance or diversity effects on bumble bees in field margins, despite differences in flower resource availability between study sites (Pywell et al. 2005). On the other hand, solitary bees can benefit from abundant nectar resources of mass-flowering oilseed rape crops, when this flowering is synchronized with the bees life-cycle (Jauker et al. 2012). Both bumble bee abundance and diversity were best predicted by resource availability in grasslands patches in Iowa, USA (Hines and Hendrix 2005). In an extensive comparison of historical land use change in the UK, Baude et al. (2016) show that past changes of vegetation and thus nectar resources concur with trends in pollinator diversity, which explains declines in both in the mid-twentieth century.

Continuous resource availability over the whole active season is a central driver for bee populations in temperate forests that provide good springtime floral resources for bees, but few resources in summertime (Winfree et al. 2007a; Roulston and Goodell 2011). Seasonal gaps in resource supply in late spring to early summer (specifically in landscapes dominated by intensive agriculture) can strongly disrupt resource foraging of honey bees and bumble bees and thus impair colony development and reproduction, as they typically have to build up colonies in this time (Mattila and Otis 2006; Williams et al. 2012; Requier et al. 2015). Managed honey bees thus use a combination of landscape elements, ranging from natural or semi-natural forests to artificial crop land and urban gardens, to forage for a diverse and continuous supply of pollen resources Odoux et al. (2012). While most studies of food limitations to social bees investigate annual bee colonies in temperate zones, perennial bee species in the tropics remain less studied, but Ferreira et al. (2010) showed how seasonally improved food availability in spring and summer shapes foraging and increases flight activity in perennial bee colonies in the tropics.

1.5.2. *Food resource diversity*

Bees must find and forage for specific resources in their environment to meet their nutritional needs, stressing the importance of resource diversity (Jha and Kremen 2013;

Jha et al. 2013). A higher diversity of nectar resources (i.e. a wider range of nectar volume / concentrations) in landscapes allows more foraging strategies and thus structures **bee pollinator communities** (Potts et al. 2003; Potts et al. 2004; Carvalho et al. 2014). Carvell et al. (2004) found that diverse field margins with a grass and wildflower mixture attracted the highest bumble bee abundances in the UK. Similarly, Torne-Noguera et al. (2014) found (for the majority of their study sites) that bee species richness was linked to flower species richness in Mediterranean scrubland. In general, enhancing flowering plant richness within crop fields can benefit pollinator richness (as reviewed by Garibaldi et al. 2014).

Foraging of **single bee species** can directly depend on resource diversity, as shown for bumble bees, which collected higher resource diversity (i.e. more pollen types) when floral species richness in the surrounding habitat was high (Jha et al. 2013). Jha and Kremen (2013) consequently found that resource diversity, not density, drives behavioural traits like foraging distance in bumble bees. Honey bees rely on a very wide diversity of plants as well to meet their pollen needs, even when mass flowering crops are abundantly available (Requier et al. 2015). Differences in nutrient composition in the pollen spectrum can shape individual foraging strategies of bee species to meet their specific needs, as demonstrated for honey bees and bumble bees (Leonhardt and Blüthgen 2012). Generalist bee foragers often have to deal with suboptimal food and switch consequently between food sources to reach a balanced diet (Williams and Tepedino 2003; Eckhardt et al. 2014). Solitary bees even incur greater energetic foraging costs to select pollen from a variety of plants instead of only exploiting a single plant species closer to the nest (Williams and Tepedino 2003), and bees raised on a mixed diet had higher body weight and thus fitness (Eckhardt et al. 2014). As generalist foragers most bees are exposed to a great diversity of secondary (often unfavourable) compounds in plants (Irwin et al. 2014). Thus mixing the products of many plants could dilute the negative effects of single compounds, which allows generalists to exploit food resources that contains secondary compounds, as described by Williams (2003) for solitary bees. Bees forage for and combine a variety of pollen and nectar regardless of the source, which may include weeds, garden and/or alien plants (Levy 2011). Alien plants add floral resources to the diet of generalist bee species, potentially not only bridging seasonal shortages, but also adding resource diversity to the nutritional mix (Tepedino et al. 2008; Stout and Morales 2009; Williams et al. 2011). Plant diversity may also indirectly benefit bees, as landscapes with higher plant diversity offer a wider range of flowering phenologies. Complementary flowering of different plant species is thus predicted to provide floral resources across seasons and bridging periods with

otherwise low resource availability (Blüthgen and Klein 2011). Experimental studies on honey bees confirmed that resource diversity of nearby woodland patches provided continuous resource availability in periods when flowering of field crops ceased (Odoux et al. 2012; Requier et al. 2015). Thus, bees benefit from a diverse pollen diet, as for example honey bees reared on a polyfloral diet reared more brood and lived longer (Höcherl et al. 2012), or lived longer when infected with the microsporidian parasite *Nosema ceranae* (Di Pasquale et al. 2013). Polyfloral diets enhance social immunity of honey bees by increasing glucose oxidase activity, which enables bees to sterilize their colony and brood food (Alaux et al. 2010). Artificial feeding of bumble bees with pollen mixtures showed that larval protein efficiency (weight of larvae/protein consumption) increased (Tasei and Aupinel 2008).

1.5.3. *Foraging regulation*

Besides resource availability and diversity, bee resource foraging is further influenced and regulated by a multitude of factors, but foraging regulation strongly depends on the bees' specialisation on plant species and life history (Roulston and Goodell 2011). Here, we focus on eusocial bees (forming colonies with castes of queens and workers and overlapping adult generations) which are plant generalist (i.e. polylectic bees foraging and consuming resources from multiple plant species and families), reviewed in detail in Waser (2006) and Jarau and Hrncir (2009). Resource collection of bee colonies is not centrally controlled, but foraging decisions of workers are influenced by internal factors (i.e. on individual level: memory and response threshold of bees) and external factors, such as colony conditions (i.e. on social level: colony food storage levels and recruitment) and environmental factors (resource availability/distribution and abiotic factors. Biesmeijer and de Vries 2001; Slaa et al. 2003; Nieh 2004; Hofstede and Sommeijer 2006; Kitaoka and Nieh 2009; Figueiredo-Mecca et al. 2013).

FORAGING OF BEE INDIVIDUALS. Individual bees, e.g. novice foragers or scouts, use a variety of cues during foraging, but predominantly combine visual information (Dyer et al. 2011; Morawetz and Spaethe 2012) with olfactory cues (Sommerlandt et al. 2014) to locate resources in environments. Rewarding food sources can trigger associative learning, and the stimuli experienced before the reward are memorized. Depending on stimuli combinations, specific regions in the bees' brain are activated, which are associated with short-term or long-term memory (Menzel 1993; Eisenhardt 2014). Foraging behaviour of individual bees is further modulated by a variety of

neurologically active chemical compounds (Erber et al. 1993), which can increase learning performance (i.e. octopamine: Scheiner et al. 2006) or impair memory formation, orientation skills and thus foraging success, as found for neonicotinoid pesticides (i.e. imidacloprid: Eiri and Nieh 2012; and thiamethoxam: Henry et al. 2012).

SOCIAL REGULATION OF FORAGING. Workers of social bee colonies forage communally to build up the food reserves of the colony and foragers or scouts are able to recruit other nest mates to rewarding food patches (von Frisch 1967; Nieh 2004; Lichtenberg et al. 2010). Bees use scents (e.g. cuticular compounds, trail pheromones), airborne sounds, mechanical signals (e.g. thoracic vibrations, jostling, waggle dances), trophallaxis (i.e. food transfer between bees) or a combination of those signals to recruit nest mates and to generally ensure information flow within the colony (von Frisch 1967; Crailsheim 1998; Barth et al. 2008; Ayasse and Jarau 2014). Bee colonies can thus increase recruitment and the total foraging activity as response to low storage levels or temporary overabundance of resources in the environment (Hofstede and Sommeijer 2006), but often directly enforce specific forager groups, i.e. nectar (Fewell and Winston 1996) or pollen foragers (Biesmeijer et al. 1999a; Dreller et al. 1999; Fewell and Bertram 1999).

RESOURCE LOCATION AND HOMING IN LANDSCAPES. Landscape patches differ in resource quality and quantity, and bees consequently need to locate the most rewarding food patches. Bees increase foraging rates when encountering high quality resources and memorize the most profitable resource patches (Cartar 2004; Kitaoka and Nieh 2009). Likewise, finding landscape patches with high resource quantities reduces the search radius for subsequent foraging trips, thus reducing foraging distances and duration of foraging trips (Westphal et al. 2006; Danner et al. 2016). To return to the nest after foraging, bees combine an egocentric and geocentric navigation system, i.e. they integrate all distances and angles travelled into a home vector and further memorize landmarks to infer their position in relation to the environment (Menzel et al. 1996; Wehner et al. 1996; Menzel and Greggers 2015). Though the navigational system of bees is not completely understood, they appear to rely mostly on celestial (i.e. polarized light in the sky) and terrestrial cues (i.e. landmarks) as navigational vectors to infer long-range directions and distances (Menzel et al. 1996; Collett and Graham 2015; Najera et al. 2015). It is therefore still unknown, if landscape structure as such (e.g. absence of landmarks in uniform agricultural areas) can impair the homing ability of foragers and thus reduce resource intake of colonies.

ABIOTIC FACTORS. Foraging activity of social bee colonies is strongly influenced by abiotic factors (e.g. weather conditions) and thus changes depending on daytime (Inoue

et al. 1985; Heard and Hendrikz 1993; Ferreira et al. 2010; Hilário et al. 2012) or season (Ferreira et al. 2010; Hilário et al. 2012; Figueiredo-Mecca et al. 2013). Weather conditions (i.e. temperature, humidity, solar radiation, atmospheric pressure, wind speed and rainfall) can further influence foraging patterns of bee colonies, thus certain weather conditions may hinder or facilitate the collection of specific plant resources (Inoue et al. 1985; Oliveira et al. 2012). Response to abiotic variations is often species specific in tropical bees and thus used to characterize bee communities and ecological niches of species (Faria and Gonçalves 2013; Polatto et al. 2014). It is however unknown, how abiotic factors (e.g. temperature, humidity, wind) interact with resource availability in landscapes in which factor predominantly shapes foraging activity and patterns.

To summarize, multiple studies show how bee populations are negatively affected by decreasing resource availability and diversity in landscapes. Studies investigating whole bee populations are however typically correlative and provide only indirect evidence. While foraging of individual bee species can be affected by a variety of factors (individual forager performance, social foraging regulation, navigation and abiotic factors) few studies have highlighted the direct influence of resource availability and diversity on single bee species (e.g. Jha and Kremen 2013; Requier et al. 2015). It has rarely been shown if individual bee species, under natural conditions, in fact forage on broader resource diversity and if the collected resource diversity depends on the landscape type, plant richness or overall resource abundance. Despite known beneficial effects of polyfloral diets, it is further still unknown if higher resource diversity collected by bees also leads to higher overall resource quality as well.

1.6. Resource quantity and quality

Floral nectar and pollen are the primary food source for most bee species, comprising both larval and adult diets (Figure I.2). Foraged pollen and nectar are processed (e.g. into fermented pollen and honey) and stored in the nest by social bees (Brodschneider and Crailsheim 2010). While nectar is the main energy source for larvae and adult bees, pollen provides crucial proteins, lipids, vitamins and minerals for brood rearing, but is scarcely consumed by adult eusocial bees (Brodschneider and Crailsheim 2010; Nicolson 2011). Resin, although not part of their diet, is collected by honey bees and tropical stingless bees from tree wounds (Howard 1985; Roubik 1989; Leonhardt and Blüthgen 2009; Simone-Finstrom and Spivak 2010). Tree resins processed into propolis

is used for nest construction and to protect colonies against predators and microbes (Leonhardt and Blüthgen 2009; Simone-Finstrom and Spivak 2010; Simone-Finstrom and Spivak 2012; Drescher et al. 2014).

Single consumers often face a trade-off between resource quantity (i.e. amount of resource) and quality (i.e. functional composition of resource), e.g. nutritional value of food (grazers: van Beest et al. 2010; nectar foragers: Kim et al. 2011). This is to say, that consumers need to decide to either forage on larger quantities of poor quality food resources or pursue higher quality resources, even when their availability is limited. Bees in particular may have a very specific nutritional target and need to balance protein and carbohydrate intake to establish a balanced diet (Altaye et al. 2010). In this context, Höcherl et al. (2012) found that honey bees compensate for the poor quality of a pure maize diet by consuming a greater quantity of maize pollen. In contrast, solitary bees opt to improve the quality of their offspring's diet and thus their fitness by seeking out and combining pollen from different plants (Williams 2003; Williams and Tepedino 2003).

1.6.1. *Resource quality*

While resource quantity is usually straightforward to measure, resource quality is more complex to assess, because bee foraging and fitness can be influenced by a multitude of quality factors in resources. However, bees often select for specific resource characteristics, which have been since used by a number of studies to define quality of pollen, nectar and resin.

POLLEN QUALITY. Bees preferentially forage on pollen with high protein content (Rasheed and Harder 1997; Robertson et al. 1999; Leonhardt and Blüthgen 2012), and high amino acid content (Cook et al. 2003; Somme et al. 2015), as shown for honey bees and multiple bumble bee species. Protein and lipid levels in pollen can vary greatly between forage plants (Roulston and Cane 2000b; Somerville and Nicol 2006; Somme et al. 2015), because they depend more on the reproductive traits of a plant species rather than the plant's dependency on animal pollination (Roulston et al. 2000). Pollen quality of bee collected pollen is thus typically measured as protein content (Génissel et al. 2002; Tasei and Aupinel 2008; Kitaoka and Nieh 2009), and is overall a good indicator, as protein content can furthermore positively correlate with contents of other nutrients (e.g. antioxidants: Di Pasquale et al. 2013; e.g. sterols: Vanderplanck et al. 2014).
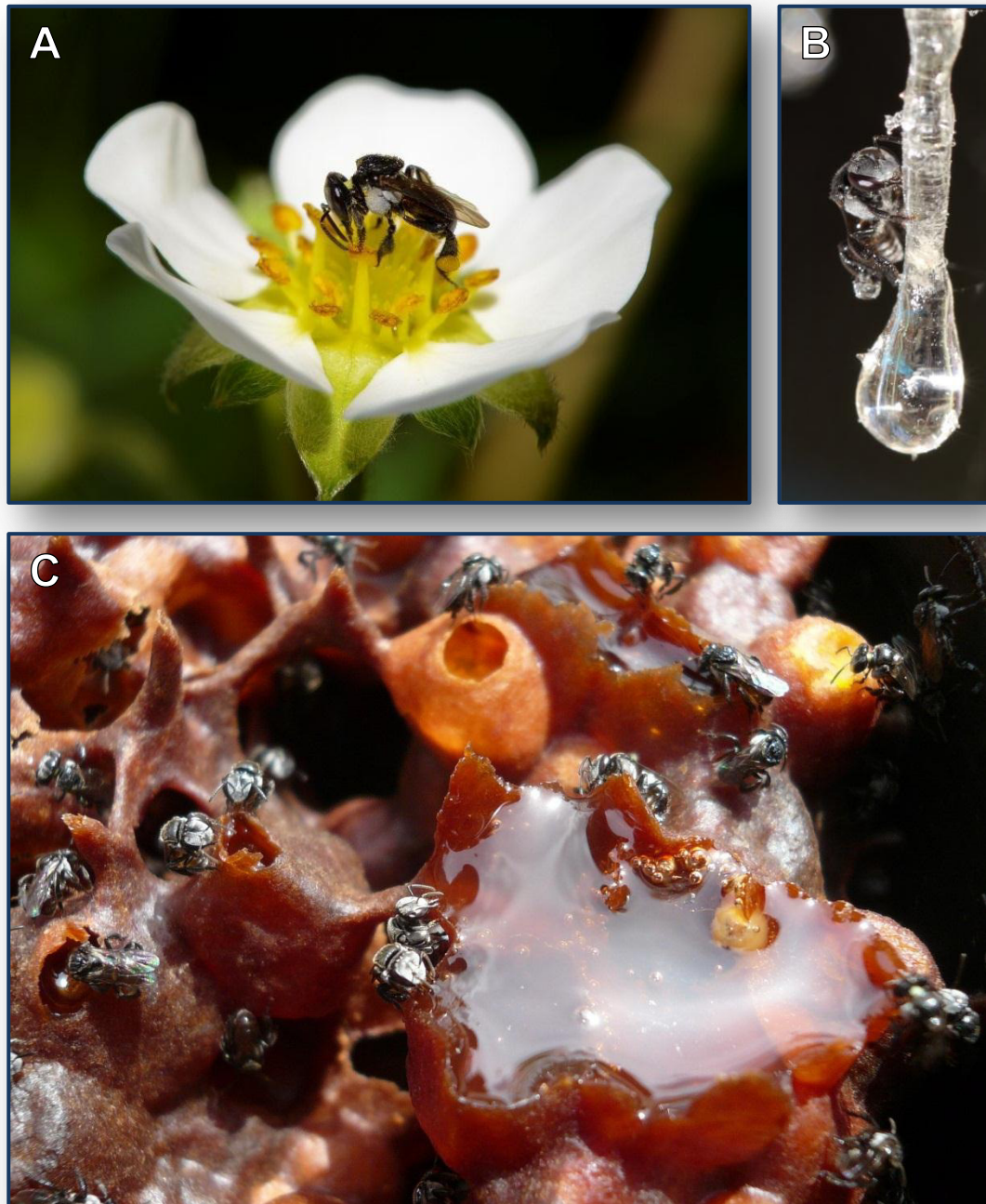
Figure I.2. **Resource foraging and storage** by the stingless bee *Tetragonula carbonaria*. Pollen and nectar foraging on strawberry flower (**A**) and collection of resin exuding from pine tree (**B**). Stingless bees store foraged resources in storage pots in the nest: nectar is processed and stored as honey (large pots in the front) and pollen is stored in pollen pots for fermentation (yellow pot, in the background right; **C**).
Images: *Tobias Smith* (**A**), *Jan Anderson* (**B**) *and Sara Leonhardt* (**C**).

NECTAR QUALITY. Bees can make use of a wide range of nectar concentrations (Biesmeijer et al. 1999b), but often target a species-specific optimal nectar concentration, as foraging strategies and handling efficiencies of higher concentrated nectar differ (Roubik et al. 1995; Kim and Smith 2000). However, highly concentrated nectar contains more energy and therefore allows bees to maximize energy intake. Consequently, nectar quality can be evaluated by measuring sugar composition and concentration (Somme et al. 2015).

RESIN QUALITY. Several bee species collect plant resins, typically from a wide variety of tree species (Roubik 1989; Bankova et al. 2006; Leonhardt and Blüthgen 2009). However, stingless bees often show preferences for specific tree species and resin from these preferred species efficiently repel predators and microbes (Leonhardt and Blüthgen 2009; Wallace and Lee 2010; Drescher et al. 2014; Massaro et al. 2014). Though bees use resin for a variety of tasks, the antimicrobial properties of resins are considered the most important function of resin in bee nests, and measurements of antimicrobial properties have been consequently used to assess resin quality (Simone-Finstrom and Spivak 2010; Drescher et al. 2014).

However, of the few studies focusing on the effect of resource quantity and quality of foraged resources, extremely few linked resource quantity and quality effects to fitness of single bee species in real ecosystems.

1.7. Bee fitness

Like all insects with holometabolic life cycles, the fitness of solitary bees or individual workers and reproductives of social bees is directly determined by the quality and quantity of the food resources available during larval development. **Solitary bees** complete multiple foraging trips per day and use the resources collected to directly provision their brood (e.g. Franzen and Larsson 2007). Offspring size (i.e. larval mass) of solitary bees raised on experimental diets was thus found to directly increase with protein content in pollen and available sugar in nectar (Roulston and Cane 2000a; Burkle and Irwin 2009). **Social bees** however collectively forage and provision brood and thus exhibit two forms of fitness: first, larvae and workers are affected by the nutritional quality of food resources (individual fitness), but, in addition, food resources affect the survival and reproduction of the whole colony as well (colony fitness; Brodschneider and Crailsheim 2010).

1.7.1. *Individual fitness*

Very few studies so far have investigated the effect of food resource quality on fitness of social bee workers, but there is evidence that food resources affect body fat and size of individual workers. Higher protein content of larval food and, only to a lesser degree, quantity of provisions increased body weight and size of stingless bees (Quezada-Euan et al. 2011). Worker size (mass) of social bees is linked to their body fat (i.e. amount of lipids), as found for bumble bees where smaller bees possess proportionally more lipids (Couvillon et al. 2011).

Limitations in body fat and size have consequences for foraging and thus the resource intake of the whole colony. Body size affects flight range in bees, and the foraging radius of larger bees may be greater, allowing them to exploit resources at wider ranges (Greenleaf et al. 2007). The relationship between body size and flight range exists for tropical stingless bees as well (Nagamitsu and Inoue 1998; Araújo et al. 2004). This effect was further observed within single species, where larger individuals of a colony forage longer distances than their smaller nest mates (Kuhn-Neto et al. 2009). Moreover, variations in body size in stingless bee colonies could be related to seasonal resource availability and shortages, highlighting that the bees' size, and therefore foraging ability, may be affected by their success in maintaining a consistent diet (Quezada-Euan et al. 2011). Males reared during food shortages have further smaller bodies and lower sperm counts, directly affecting the colony's reproductive capability (Pech-May et al. 2012).

It is however completely unknown, which mechanisms regulate individual fitness of workers, i.e. resource quantity or resource quality, and if individual fitness of bees is reduced when the colony faces low resource diversity or abundance conditions.

1.7.2. *Colony fitness*

Studies examining the colony fitness response of bees to resource diversity and abundance are extremely scarce and all existing knowledge comes from studies of bumble bees. Wild bumble bee colonies in subalpine meadows in the USA benefited from greater nectar quantity and produced over twice as many queens when fed with supplementary nectar (Elliott 2009). In contrast, bumble bee colonies with access to large amounts of oilseed rape and thus higher resource availability in Germany did not produce more males or queens (Westphal et al. 2009). In a comparison of bumble bee nests (placed in conventional farmland, farms with conservation measures and suburban gardens in the UK), Goulson et al. (2002) found similar numbers of queens and males in

nests across landscapes, but greater colony growth rates in gardens due to greater density and diversity of floral resources. In a large-scale experiment, Williams et al. (2012) placed bumble bee colonies along a gradient of natural and agricultural landscapes in the USA and quantified flower densities thus floral resource availability across seasons. The study showed a positive effect of floral resource availability on the number of workers and males produced, highlighting the importance of seasonal resource consistency (Williams et al. 2012). A mechanistic model based on the same study revealed that queen production increased with floral resources and was higher in semi-natural areas than in conventional farms (Crone and Williams 2016).

However, all presented studies linking bee fitness to resource availability used bumble bees as model organisms, which show a specific strongly seasonal life cycle. At the beginning of spring, new colonies of bumble bees grow by producing cohorts of workers and accumulate food reserves, until the colonies switch to invest food storages into the production of males and queens towards the end of the year (Duchateau and Velthuis 1988; Crone and Williams 2016). This strictly seasonal life cycle makes direct comparisons between bumble bees and other (tropical) social bees with perennial life cycles difficult. In contrast, most stingless bee colonies produce gynes (unmated queens) continuously throughout the year (Roubik 1989; van Veen and Sommeijer 2000; Sommeijer et al. 2003), and mechanisms which trigger or increase queen rearing in stingless bees are still largely unclear (Tarpy and Gilley 2004). In contrast to bees with annual life cycles, no study has as yet examined how floral resource diversity and abundance affect bees with perennial life cycles

Despite the number of studies correlating landscape and bee diversity and abundance, no study so far has related bee fitness to plant resources available in the bees' habitats and to the quality and quantity of resources collected. Social bees forage widely for resources, and bee abundance surveys can consequently reflect either true abundance (population size) or otherwise just forager concentration at rewarding resource patches (behavioural response; Crone and Williams 2016). Thus, to distinguish whether higher bee abundances in landscapes actually support stronger populations and not simply habitat preferences of foraging individuals, we need studies measuring and comparing the bees' fitness response to resource availability and diversity across landscapes. This will allow us to determine driving elements of the pollination crisis, be it landscape types, plant richness or availability and resource quality or quantity, and help set a focus for future conservation efforts.

1.8.   Research scope

Declines of wild bee populations due to ongoing global habitat loss are raising concerns about the stability of the free pollination service wild bees provide. Wild bee populations are known to be strongly regulated by resource availability and diversity in landscapes. But while wild bee populations thrive in natural and biodiverse landscapes, it remains largely unclear if positive effects can be attributed to habitat type, plant and resource diversity, overall resource abundance or constant seasonal resource availability. Furthermore, it is unknown how resources change (a) foraging patterns and foraging success of bees, (b) affect foraged resource quantity and quality and (c) ultimately influence fitness of bee species. It is thus imperative to gain a better understanding how plant biodiversity, and thus resource diversity and availability, may affect each single bee species and their fitness.

1.8.1.   *Model species and study design*

The eusocial stingless bee *Tetragonula carbonaria* is a generalist forager and naturally occurs in North-East Australia. *Tetragonula carbonaria* is a known seed disperser of the rainforest tree *Corymbia torelliana* (Myrtaceae) (Wallace and Trueman 1995; Wallace and Lee 2010) but also an efficient pollinator for macadamia (*Macadamia integrifolia*, Proteaceae) (Heard 1994). Since *T. carbonaria* is (a) present as native wild bee in the study region, but can (b) also be kept and propagated as a managed pollinator (Heard and Hendrikz 1993; Heard 2016), it represents an excellent model species to experimentally test landscape and resource effects on a single native pollinator.

In this thesis I experimentally placed hives of *T. carbonaria* in different landscapes, in their natural habitat (subtropical forests) and two landscapes differently altered by humans (suburban gardens and macadamia plantations; for detailed description of the setup see chapter II: sections 2.3.1 & 2.3.2). I monitored foraging patterns and colony growth across seasons over three years, to understand how resource availability and diversity in interaction with resource quality and quantity impact on bee fitness.

1.8.2.   *Research questions*

Plant diversity, resource diversity and resource availability in landscapes can affect bee foraging and fitness on many levels. To analyse the complex interactions between resources, bee foraging and fitness response, I developed a theoretical framework to

predict and test how single factors (e.g. bee foraging patterns) are interlinked, affect other elements (e.g. quantity and quality of bee collected resources) and ultimately drive bee fitness. The proposed theoretical framework relates biodiversity variables on (A) landscape level to (B) foraging patterns of *T. carbonaria*, to (C) the quality and quantity of their collected resources and (D) ultimately to colony and individual fitness (Figure I.3). To step-wise develop a better understanding of the study system, I investigated different sections of the framework in separate studies (chapter II, IV & V).

In particular I will answer the following research questions:

1. How do different landscapes, anthropogenically altered and natural, influence foraging patterns, i.e. foraging activity, forager numbers and overall sugar/pollen resource intake in a generalist social bee?

2. How is bee navigation and homing success (i.e. the proportion of bees returning to their hive) affected by landscape homogeneity in undisturbed and disturbed habitats?

3. How does plant richness in different landscapes impact on diversity of collected resources and does increasing resource diversity positively affect the quality of collected resources (i.e. pollen and resin)?

4. How do biodiversity factors (landscape patch size, plant resource diversity and abundance) and quantity or quality of foraged resources affect colony reproduction and (individual or colony) fitness factors?

(A) Landscape

(B) Foraging

(C) Res. quantity & quality

(D) Fitness

Plant biodiversity
- Plant species richness

Resource diversity

Resource availability
- Continuous seasonal availability

Number of foraging options

Resin diversity

Pollen diversity

Forager proportion (pollen, nectar, resin)

Forager numbers (pollen, nectar, resin)

Total sugar intake

Total pollen intake

Foraging activity

Weather:
- Wind
- Temperature
- Humidity
Homing ability

Quality of honey:
- Sucrose / water content
- pH of honey

Quality nest pollen:
- Amino acids
- Total protein
- Minerals

Individual foraging choice

Quality nest resin:
- Antimicrobial activity

Larval food composition

Quantity of stored resources (pollen, nectar, resin; ≙ overall weight)

Colony fitness:
- Brood circumference / volume
- Worker reproduction (open worker cells)
- Queen reproduction (queen pupae)

Individual fitness:
- body fat content
- body size (biometric values)

1.9. Thesis outline

Chapter II: Urban gardens promote bee foraging over natural habitats and plantations

In this chapter the overall study design and experimental setup in different landscapes (plantations, forests and gardens) are described. Foraging patterns of *T. carbonaria* colonies were monitored in different seasons over two years. Foraging activity, the allocation of foragers to different resources (pollen, nectar and resin) and overall resource intake are compared between landscapes to investigate how landscape and its interaction with season and weather drive foraging.

Chapter III: Resources or landmarks: which factors drive homing success in *Tetragonula carbonaria* foraging in natural and disturbed landscapes?

This chapter investigates how landscape structure and habitat homogeneity can affect navigation and thus homing success in bees. Bees were marked, released and re-captured in different landscapes to test whether foraging success is affected by visual

Figure I.3 (*previous page*). Proposed theoretical framework describing resource use of stingless bees and its effects. Shown are the relationship of landscape, foraging, resource quantity/quality and fitness variables. Elements in squares show variables measured in the experiment, while elements in circles represent theoretical factors, which are assumed to connect measured elements. On landscape level (**A**), higher plant diversity increases plant resource diversity and provides continuous seasonal resource availability (Blüthgen and Klein 2011; Jha and Kremen 2013). Bee foragers are proposed to collect higher pollen and resin diversity when presented with a higher number of foraging options (**B**). Foraging activity of colonies is expected to increase with greater resource availability but depend on weather conditions (Ferreira et al. 2010). Foragers respond to both resource availability and the colonies' resource needs by targeting pollen, nectar or resin collection, which is reflected in a greater proportion of foragers returning with this resource (Leonhardt et al. 2014). Higher foraging activity, in interaction with forager proportions, results in higher pollen, nectar or resin forager numbers respectively and consequently influences sugar and pollen intake of colonies. Nutritional quality or functionality of resources stored in the hive (pollen, honey and resin) is proposed to increase with the number of available foraging choices or collected pollen/resin diversity (**C**). Quantity of resources stored in the nest increases with higher resource intake and in turn influences foraging choices (Hofstede and Sommeijer 2006). Higher quality of stored honey, resin and pollen is expected to influence larval food composition and ultimately colony and individual fitness (**D**). In addition, overall resource quantity is proposed to influence fitness measures of colony and individual fitness.

landmarks. The proportion of bees and nectar foragers returning to their hives as well as the earliest time bees and foragers returned are compared between natural forests with few landmarks but large proportions of vegetation cover, and gardens and plantations as disturbed landscapes with many landmarks but fragmented vegetation cover.

Chapter IV: Generalist social bees maximize diversity intake in plant species rich and resource abundant environments

This chapter aims to investigate in a general sense whether and how biodiverse environments can benefit individual ecosystem members by providing a higher diversity of resources to choose from. To test whether bee consumers (actively or passively) maximize resource diversity intake, the diversity of bee collected resources of *T. carbonaria* (pollen and resin) was measured in different habitats varying in plant species richness and associated resource abundance (plantations, forests and gardens). Secondly, plant species richness, resource abundance and diversity of collected resources are related to nutritional quality and antimicrobial activity of resources to learn whether decreased resource diversity impairs resource quality.

Chapter V: Biodiversity drives social bee fitness

This chapter studies how plant resource diversity and abundance can affect fitness of generalist social bees. Colony growth and fitness of *T. carbonaria* in relation to plant species richness and resource abundance as well as to patch sizes of various landscape types (plantation forests and gardens) was monitored over two years. To elucidate the mechanisms underlying biodiversity effects on bee fitness, the influence of quantity and quality of food collected by colonies on colony reproduction, colony fitness (brood volume, queen- and worker reproduction) and individual fitness (worker fat content and size) is investigated.

1.10. References

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II. URBAN GARDENS PROMOTE BEE FORAGING OVER NATURAL HABITATS AND PLANTATIONS

2.1. Abstract

Increasing human land use for agriculture and housing leads to the loss of natural habitat and to widespread declines in wild bees. Bee foraging dynamics and fitness depend on the availability of resources in the surrounding landscape, but how precisely landscape related resource differences affect bee foraging patterns remains unclear. To investigate how landscape and its interaction with season and weather drive foraging and resource intake in social bees, we experimentally compared foraging activity, the allocation of foragers to different resources (pollen, nectar and resin) and overall resource intake in the Australian stingless bee *Tetragonula carbonaria* (Apidae, Meliponini). Bee colonies were monitored in different seasons over two years. We compared foraging patterns and resource intake between the bees' natural habitat (forests) and two landscapes differently altered by humans (suburban gardens and agricultural macadamia plantations). We found foraging activity as well as pollen and nectar forager numbers to be highest in suburban gardens, intermediate in forests and low in plantations. Foraging patterns further differed between seasons, but seasonal variations strongly differed between landscapes. Sugar and pollen intake was low in plantations, but contrary to our predictions, it was even higher in gardens than in forests. In contrast, resin intake was similar across landscapes. Consequently, differences in resource availability between natural and altered landscapes strongly affect foraging patterns and thus resource intake in social bees. While agricultural monocultures largely reduce foraging success, suburban gardens can increase resource intake well above rates found in natural habitats of bees, indicating that human activities can both decrease and increase the availability of resources in a landscape and thus reduce or enhance bee fitness.

2.2.   Introduction

Animal pollination is a key ecosystem function, and modern agriculture benefits from pollinators, particularly bees, for the production of many crops (Klein et al. 2007; Garibaldi et al. 2013). Reports of declines in managed and wild bees thus raise concerns about a global pollination crisis (Allen-Wardell et al. 1998; Winfree 2010). Bee pollinators are under pressure from human activities (Winfree 2010), and bee decline is often linked to habitat change and loss (Winfree et al. 2009; Potts et al. 2010; Vanbergen and the Insect Pollinators Initiative 2013). Many natural habitats have been destroyed or fragmented by urbanization and agricultural intensification with parallel declines observed in the diversity and abundance of insect pollinators (Aizen and Feinsinger 1994; Steffan-Dewenter et al. 2002; Ricketts 2004; Vanbergen and the Insect Pollinators Initiative 2013). Anthropogenic changes to habitat may confound underlying and interacting effects that regulate bee populations, such as food resource availability (Roulston and Goodell 2011). How landscape related differences in resource availability affect foraging patterns and resource intake of bees has however received little attention.

Bees typically find a constant supply of floral resources in (semi-)natural habitats, which provide a high diversity of plants (Cairns et al. 2005; Rundlöf et al. 2008; Roulston and Goodell 2011; Kennedy et al. 2013). In contrast, in intensively managed agricultural monocultures, food resources are only abundant during the short flowering seasons of crops (Decourtye et al. 2010). Subsequent shortages in food resources throughout the rest of the year have been linked to honey bee colony collapses in degraded habitats (Naug 2009). Urban areas may, on the other hand, also provide steady food resources throughout the year due to the presence of many native and exotic plant species in gardens (Loram et al. 2008; Roulston and Goodell 2011). However, foraging patterns and resource intake of bees in urban landscapes such as gardens have, to our knowledge, not yet been studied.

Highly social bees form long-lived colonies and thus need floral resources throughout the entire season. Foraging activity on the colony level is regulated by (a) the amount of resources stored within the nest and (b) the availability of resources in the environment (Biesmeijer et al. 1999; Hofstede and Sommeijer 2006; Altaye et al. 2010). Foraging activity and patterns of colonies with similar food storages, but located in different environments, should therefore be mainly determined by the availability of resources in the respective landscapes.

Bees collect a variety of plant resources, primarily floral nectar and pollen (Michener

2007; Brodschneider and Crailsheim 2010). Nectar is the main energy source for bees and pollen provides the proteins, lipids, vitamins and minerals crucial for brood rearing, but is also consumed by adult bees (Nicolson 2011). Highly social bees, such as tropical stingless bees (Apidae: Meliponini) and honey bees, collect resin as additional plant resource, predominantly from wounded trees (Roubik 1989). Resin is used for nest construction and defence against predators or parasites (Leonhardt and Blüthgen 2009; Greco et al. 2010) and is essential for colony survival. Bees therefore need to divide their foraging efforts between these different plant resources.

Foraging behaviour and daily flight activity of bees is further influenced by abiotic factors, such as temperature, humidity, solar radiation and wind (Heard and Hendrikz 1993; Hilário et al. 2012; Oliveira et al. 2012; Polatto et al. 2014). Variations in weather and resource availability can therefore differentially affect foraging activity depending on the season (Ferreira et al. 2010; Figueiredo-Mecca et al. 2013). Whether weather factors or resource availability in a landscape predominately shape the foraging behaviour of bees is however still unclear.

We compared foraging patterns, i.e. forager allocation and foraging activity, and resource intake of a common Australian stingless bee species, *Tetragonula carbonaria* Smith, between plantations, forests and suburban gardens. Our aim was to better understand how differently altered human landscapes, i.e. agricultural areas and gardens, affect resource foraging in highly social bees compared with patterns observed in their natural habitat.

We specifically addressed the following questions:

1. How do different landscapes, altered and natural, influence foraging patterns, i.e. foraging activity, forager numbers and proportions of bees collecting different floral resources, in a generalist social bee?

We predict foraging patterns to be influenced by long periods of food shortages in agricultural landscapes (Decourtye et al. 2010), resulting in low activity and forager numbers throughout most of the year except for the short macadamia flowering period. We further predict foraging activity and numbers to be intermediate in gardens due to a constant but patchy distribution of resources, and to be highest in natural landscapes due to year-long availability of abundant resources. Allocation of foragers to different resources (i.e. forager proportions) is expected to be similar across landscapes and seasons for pollen and nectar, while the number of unsuccesful foragers should be high in plantations and low in forests. Due to the higher abundance of trees in forests, we

expect our colonies to allocate more foragers to resin collection in forests than in gardens and plantations.

2. How does sugar and pollen intake by social bees differ between different landscapes?

Overall resource intake is predicted to increase in landscapes comparatively richer in plant resources, such as forests and gardens, and be highest in their natural habitat (forests).

3. How do abiotic factors (e.g. temperature, humidity, wind) interact with landscape in determining foraging activity and patterns?

We predict that abiotic factors contribute to foraging patterns, but that foraging patterns are mainly determined by landscape.

2.3. Methods

2.3.1. *Study species and landscapes*

The study was conducted in Queensland, Australia. We chose the Australian stingless bee *Tetragonula carbonaria* as a model species to address our research questions (Dollin et al. 1997; genus change: Rasmussen and Cameron 2007). *Tetragonula carbonaria* occurs as a wild bee and native pollinator in the study region, and can also be kept and propagated in boxes and thus be managed for crop pollination (Heard and Hendrikz 1993; Heard 2016). This allows colonies to be placed in specific landscapes and to experimentally test for the effect of habitat and landscape on a perennial bee species.

Observations were conducted within the native range of the species in Queensland. The East coast of Queensland is characterized by a subtropical climate with wet summer and dry winter seasons. To test how colonies of *T. carbonaria* were influenced by resource diversity and availability in different landscapes, we selected three landscape types characteristic of the region to experimentally place hives of *T. carbonaria*: forests, plantations and gardens.

Forests ranged from relatively open *Banksia* heathland to more dense forests with closed canopy, but were all dominated by an overstory of *Eucalyptus* and *Corymbia* species and thus reflected the variety of habitats commonly used by *T. carbonaria* (Dollin et al. 1997). Australian forests have been historically shaped by dynamic

processes like anthropogenic fire regimes and are continuously exposed to moderate disturbance (Bird et al. 2008). Thus, uncleared forests, as selected in this study, can be considered a natural environment. Before we started our study, we confirmed that wild colonies of *T. carbonaria* were present at all forest study sites to ensure that the forest sites represent valid natural control sites.

Our plantation sites were represented by commercial macadamia plantations (*Macadamia integrifolia* Maiden and Betche × *M. tetraphylla* Johnson). Macadamia are indigenous rainforest trees grown for their edible nuts, and are known to be pollinated by *T. carbonaria* (Vithanage and Ironside 1986; Heard 1994; Heard and Exley 1994). All plantations were monocultures with at most ten different genotypes as commercial macadamia varieties are genetic clones.

We additionally placed bee hives in another human altered landscape, suburban gardens, a habitat which has been successfully used to breed stingless bees by private bee enthusiasts in Australia (Klumpp 2007). Suburban gardens in the study region typically include houses, surrounded by gardens of 300-1000 m² with native and exotic plants. Exotic plants, i.e. introduced alien plant species as well as ornamental cultivars, commonly made up more than 50 % of all garden plant species in our study (data not shown). Gardens were mostly situated in suburbs with remnants of uncleared bush vegetation or small parks with mature *Eucalyptus* or other native trees.

2.3.2. *Experimental setup*

A total of twelve study sites were established in 2011 in two regions in South East Queensland, ranging from the Bundaberg region in the north to the Sunshine Coast area and Brisbane region in the south (Figure II.1, SM II.1; 24°38'-27°30' S, 152°6'-153°7' E). For each landscape type (plantation, forest and garden) we chose four study sites as replicates, with replicates of each landscape in the northern and southern region to avoid spatial autocorrelation. At each study site, we placed four wooden bee hives containing *T. carbonaria*. Consequently, a total of 48 *T. carbonaria* bee hives were set up at all study sites in 2011.

In gardens, space was limited and hives needed to be distributed among two suitable private garden locations in close proximity (mean ± SD distance: 706 ± 129 m, except for one garden site with 16 km between garden locations, Figure II.1). Two hives were placed on each location and both garden locations together were considered one garden site. We allowed for a 500 m flight radius of the bees around the hives which is considered the typical foraging range of bees of this size (Greenleaf et al. 2007,

equivalent to 0.78 km² flight range). We further made sure that flight ranges of different study sites did not overlap (sites separated by >1.1 km in plantations, >14.3 km in forests and >1.4 km in gardens). To ensure that more than 75 % of the flight range was covered by the target landscape (plantation, forest or garden) we evaluated the vegetation cover by aerial photographs from Google Earth. We outlined all vegetation patches to calculate their area with the software KML Toolbox. All vegetation patches were additionally validated by ground surveys.

Bee hives were mounted on metal posts 1 m above ground (in forests and
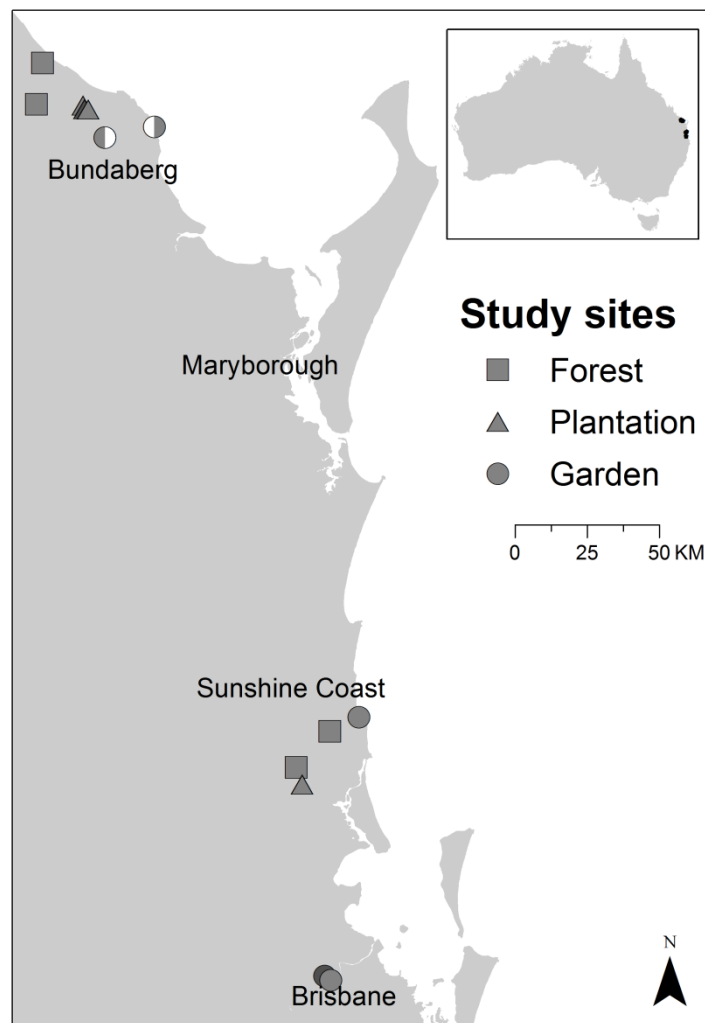
Figure II.1. Location of study sites in South East Queensland, Australia. Study sites of each landscape category (plantation, forest, garden) were established at three different regions, ranging from Bundaberg (north) to the Sunshine Coast area (centre) and to Brisbane (south). Half-filled circles represent the two locations (each with two hives) of one garden site in Bundaberg.

plantations), orientated with the entrance facing NE, or placed on bricks low above ground where sealed surfaces did not allow the use of posts (in gardens). All hives were placed with a minimum distance of 5 m in between and in shaded or semi-shaded locations and protected by a metal roof where no other cover was available. Our study hives were all provided by T. Heard. They had not been disturbed for at least three months prior to the setup and had comparable starting weights of 7.2 ± 0.7 kg (= combined weight of colonies and hive boxes). In plantations, hives were closed and covered for at least 24 hours when insecticides were applied to macadamia trees to prevent contamination of hives.

Nest densities in the experiment were similar to those found in Australian forests and suburban areas, i.e. typically 1 up to 3 colonies/ha (Heard 2016), and comparable to nest densities found for other stingless bee species in Australia and Borneo (Eltz et al. 2002; Halcroft 2012). The foraging behaviour of our hives should thus not be influenced by increased competition for food resources.

2.3.3. *Observations of foraging patterns*

To study how the three landscape types affected foraging patterns, activity and resource intake of hives, we observed foraging bees from September 2011 to September 2013. To account for seasonal differences in foraging behaviour, foraging observations were carried out in three seasons per year over two years: in the dry season (September-December), wet season (January-April) and cold season (May-August). In each season, observations of each hive were repeated on 3 different days to account for changing weather conditions. Each hive was revisited within 12 ± 9 days and all hives of targeted study sites were visited at least once within 31 ± 9 days. For each landscape type, two sites were selected for the foraging observations (one in the northern and one in the central region of the study area). At each site, 3-4 hives were observed per season (summing up to a total of 18-24 hives at overall six study sites). Overall, we assembled a data set with 9950 recorded foraging trips for 512 hive observations.

Observations were conducted between 7:30 and 15:30 on rain-free days (see SM II.2). The following weather conditions were recorded for each observation period: ambient temperature, humidity (PCE-555 Digital Psychrometer; PCE Instruments, Meschede, Germany) and cloud cover (estimated in 12.5 % steps of covered sky). In the second year, we also recorded wind conditions (average and maximum in m/s and gustiness: number of wind peaks /3 min; PCE-MAM 1 anemometer, PCE Instruments, Meschede, Germany).

The overall foraging activity of each hive was recorded first by counting the number of returning foragers for 3 minutes. Then 20 returning foragers were captured and their pollen, nectar or resin load visually inspected and counted to assess the total number and proportion of respective foragers as well as unsuccessful foragers (Leonhardt et al. 2014). To calculate forager numbers per minute for each resource, respective proportions were multiplied by activity. All foragers captured were held until the end of the observation period to avoid recapturing the same individual.

2.3.4. *Resource intake*

Nectar foragers were identified by their swollen abdomen. To collect the nectar, their abdomen was carefully squeezed to provoke regurgitation of the crop content. Nectar volume was quantified in 5 µL microcapillary tubes (Camag, Muttenz, Switzerland) and nectar concentration was measured to the nearest 0.5 g/g sucrose equivalent by hand-held refractometers (Eclipse Refractometer, Bellingham + Stanley Ltd., Lawrenceville, USA). The sugar concentration in nectar (c in %) was converted into x (in µg/µL) following (Kearns and Inouye 1993) with the values adjusted by Blüthgen, N. (personal communication) according to the equation:

$x = -0.0928 + 10.0131 * c + 0.0363 * c^2 + 0.0002 * c^3$.

With x and the measured nectar volume (V) we calculated the sugar load of each individual nectar forager (in mg). To calculate the average sugar intake (in mg/min) for each hive observation the following equation was applied:

$$\frac{\sum_{1}^{n}(x*V)*A*P_N}{n}$$

where n is the overall number of nectar foragers for a given hive and observation, A the hive activity, and P_N the corresponding proportion of nectar foragers.

Pollen loads of foragers were removed from each hind leg with forceps and collected in previously weighed Eppendorf tubes. The two pollen loads of each leg of a forager were collected in two separate Eppendorf tubes. Eppendorf tubes were reweighed after inserting pollen to calculate the average net pollen weight carried by all foragers. The total pollen intake per minute of each hive (in mg/min) was then calculated as follows:

$$\frac{(E_1 + E_2)*A*P_P}{n}$$

with E_1 and E_2 as the net pollen weights in each Eppendorf tube, n the number of captured pollen foragers, A the activity of the hive per minute and P_P the proportion of pollen foragers for this observation period.

2.3.5. *Statistical analysis*

We used generalized linear mixed effect models (GLMM) to analyse the effects of landscape type, season and weather variables (explanatory variables) on foraging activity, pollen, nectar, resin and unsuccessful forager proportions and numbers, as well as nectar concentration, sugar and pollen intake (response variables; R Development Core Team 2009; library lme4: Bates et al. 2011). As we collected data from several hives located at several study sites for each landscape, hive nested within site was entered as a random effect in all models. Landscape (plantation, forest, garden) and season (dry, wet and cold season) were entered as fixed categorical variables.

To test effects of landscape and season on the proportion of pollen, nectar and resin foragers, forager numbers were entered as a binomial vector, i.e. a two-column matrix with the columns giving the numbers of successes (e.g. number of pollen foragers) and failures (e.g. number of non-pollen foragers) using GLMMs with a binomial error distribution. Pollen, nectar, resin or unsuccessful foragers per minute as well as total sugar intake did not show a Gaussian distribution, even when response variables were transformed, and we therefore applied GLMMs with a Poisson distribution. Total pollen intake per minute showed over-dispersion and was thus square-root transformed and analysed with GLMMs with a Poisson distribution. Nectar concentration was arcsine square-root transformed.

For each response variable, different models were composed, starting with the most complex model (including all explanatory variables and interactions between them). Next, we stepwise dropped interactions between explanatory variables and then variables (wind, temperature, season and landscape type). The quality of all models was compared using Akaike's Information Criterion (AIC) and the model with the lowest AIC value was considered the model with the highest explanatory value. To test whether individual explanatory variables in the model with the lowest AIC value actually explained a significant proportion of the overall variance, we compared the model with a given variable to the same model without this variable using the anova command in the lme4 package which compares two nested models based on likelihood-ratio tests and chi-square statistics. For models with landscape as significant explanatory variable, differences between landscape types were further evaluated using

Tukey's post hoc test (package multcomp: Hothorn et al. 2008).

To test how weather affected foraging patterns and interacts with landscape, we performed a second set of models with the weather variables (i.e. temperature, humidity, wind, cloud cover) included. To account for collinearity of weather variables, we created a Spearman rank correlation matrix, which revealed two clusters of variables (a: temperature, humidity and cloud cover; b: wind gusts, average and maximum wind speed, see SM II.3). From those we selected temperature and average wind speed to test their influence on our response variables in the models. Note that comprehensive weather variables were only available for a smaller subset of the data and therefore analysed for this data set only to avoid the loss of degrees of freedom (compare Table II.1 and SM II.4), which in combination with the reduction of the data sets limits the explanatory power of the analysis.

2.4. Results

2.4.1. *Foraging patterns*

Differences in bee foraging activity were best explained by landscape, without any other explanatory factors contributing significantly (Table II.1). Across seasons, foraging activity was highest in gardens, lower in forests and lowest in macadamia plantations (mean activity $\pm$ SD in plantations: 17 ± 17; forests: 27 ± 19; gardens: 38 ± 26 foragers/min), with a significant difference between gardens and plantations (Tukey test, $P = 0.004$).

Differences in the number of foragers for all resources (pollen, nectar and resin) were best explained by the interaction between landscape and season (Table II.1, SM II.5: Figure II.5). That is to say, resource foraging showed different seasonal patterns in different landscapes, e.g. pollen, nectar and resin forager numbers were significantly highest in gardens in the wet but not in the cold or dry season (SM II.5: Figure II.5). Across seasons, significantly more pollen foragers returned to the hive per minute in gardens than in both forests and plantations (Figure II.2a), while nectar foragers were high in both forests and gardens (Figure II.2b). However, nectar foragers differed between forests and gardens in their seasonal patterns, as nectar foragers tended to be highest in forests in the cold season, but tended to be highest in gardens in the dry season (SM II.5: Figure II.5). Numbers of resin and unsuccessful foragers did not differ

Table II.1. Results of generalized linear mixed effect models (GLMMs) for each response variable. Given are χ^2-values and degrees of freedom (*df*) obtained for comparing the best model with the respective explanatory variable to a model with this variable dropped (landscape, season) and the interaction of both factors. Significance levels as follows: * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001, ns not significant.

Response variable	Landscape			Season			Interaction		
	χ^2	*df*	*P*	χ^2	*df*	*P*	χ^2	*df*	*P*
Foraging activity	8.88	2	*			ns			ns
Pollen foragers / min	171.54	6	***	259.67	6	***	160.94	4	***
Nectar foragers / min	150.27	6	***	164.81	6	***	139.74	4	***
Resin foragers / min	86.89	6	***	86.01	6	***	83.08	4	***
Unsuccessful foragers /min	122.43	6	***	192.89	6	***	119.95	4	***
Proportion pollen foragers	54.83	6	***	114.57	6	***	50.44	4	***
Proportion nectar foragers	101.77	6	***	196.27	6	***	100.19	4	***
Proportion resin foragers	37.04	6	***	53.10	6	***	34.65	4	***
Proportion unsuccessful foragers	56.81	6	***	101.25	6	***	48.45	4	***
Sucrose concentration in nectar	23.01	6	***	205.42	6	***	18.95	4	***
Total sugar intake / min	187699	6	***	316369	6	***	187685	4	***
Pollen load size			ns	43.17	2	***			ns
Total pollen intake / min	9.45	2	**	10.05	2	**			ns

between landscapes (Figure II.2c-d).

The interaction between landscape and season also best explained differences in forager proportions for all foraging resources (Table II.1, SM II.5: Figure II.6). Across seasons, hives located at different landscapes allocated similar proportions of bees to pollen foraging (Figure II.3a), but pollen foraging patterns strongly differed between landscapes for different seasons. For instance, in the wet season, pollen forager proportions were significantly highest in gardens and lowest in plantations, whereas the pattern tended to be reversed in the dry season (SM II.5: Figure II.6).

The proportion of nectar foragers was generally high in gardens and forests (plantations: 33 ± 23 %; forests: 40 ± 23 %; gardens: 37 ± 23 %; Figure II.3b), but showed the same inversed seasonal trends in forests and gardens as nectar forager numbers (SM II.5: Figure II.6). Proportions of resin foragers were overall low in gardens compared to forests and plantations (Figure II.3c), but did not differ between landscapes in the cold season (SM II.5: Figure II.6). Plantations had the significantly highest proportion of unsuccessful foragers in all seasons (Figure II.3d), but while the proportion of unsuccessful foragers was by trend lowest in gardens in the dry season, it tended to be lowest in forests in the cold season (SM II.5: Figure II.6).
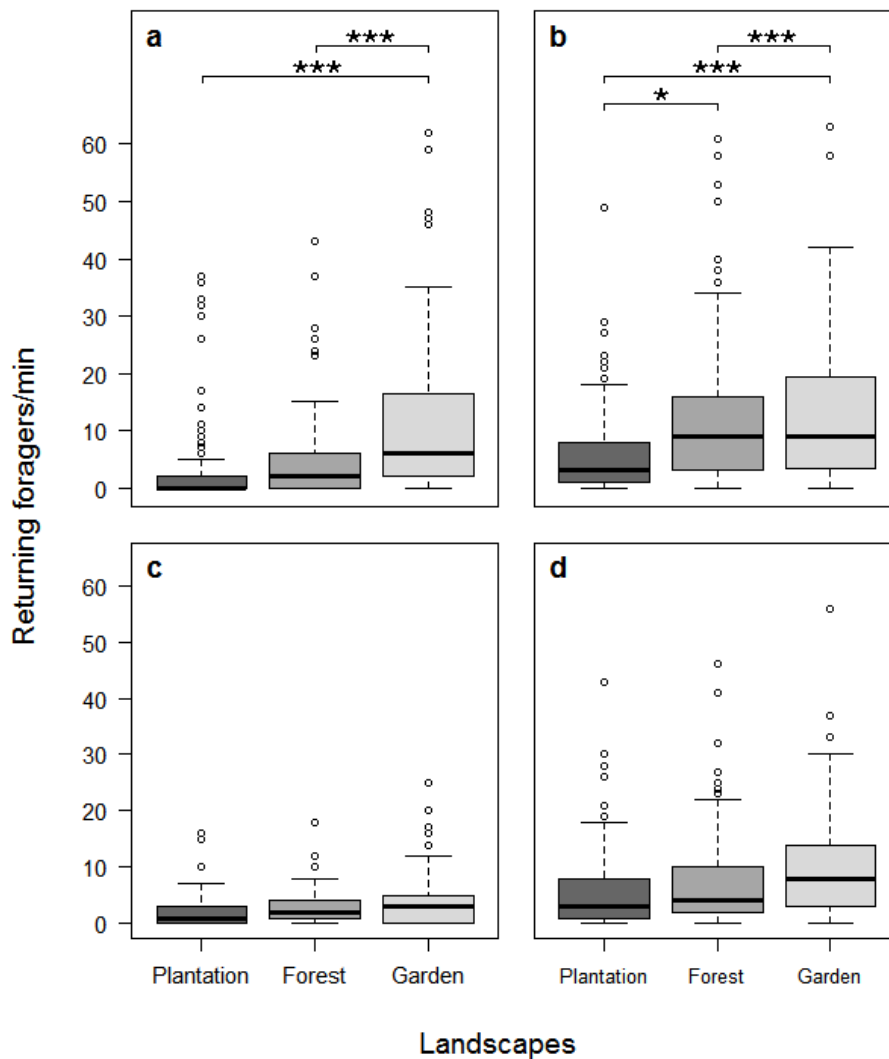
Figure II.2. Number of foragers per minute returning with (**a**) pollen, (**b**) nectar, (**c**) resin and (**d**) unsuccessful foragers in plantations (dark grey bars), forests (grey) and gardens (light grey). Boxplots display the median (thick bar), lower (0.25) and upper (0.75) quartile (grey box), minimum and maximum values (whiskers) and outliers of each dataset. Asterisks indicate significant differences between landscapes according to Tukey's posthoc test, significance levels as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

2.4.2. *Resource intake*

Differences in sugar concentration were best explained by the interaction of landscape and season (Table II.1). For more than half of our observations, sucrose concentration in nectar collected by foragers ranged between 60 and 75 % (total $N = 2647$) and did not significantly differ between landscapes (mean sucrose
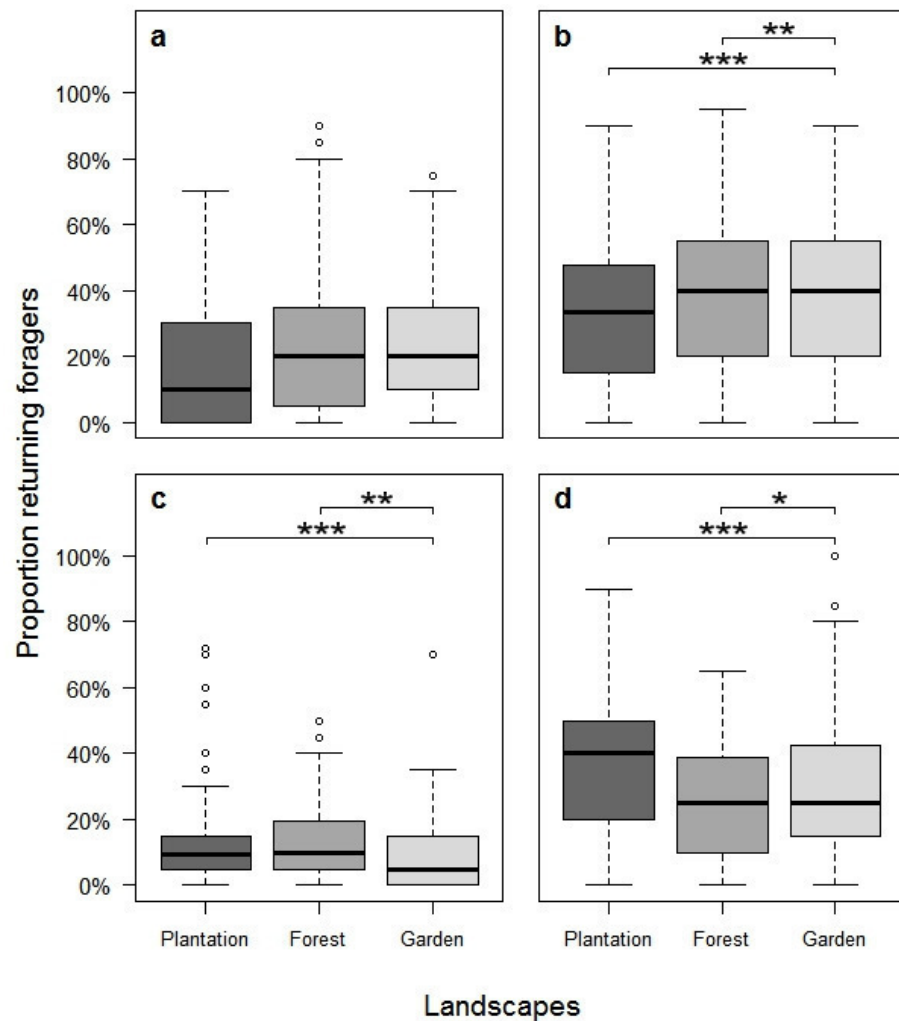
Figure II.3. Proportional resource intake in plantations (dark grey bars), forests (grey) and gardens (light grey). Shown are per cent of foragers returning with (**a**) pollen, (**b**) nectar, (**c**) resin and (**d**) unsuccessful foragers. Boxplots display the median (thick bar), lower (0.25) and upper (0.75) quartile (gray box), minimum and maximum values (whiskers) and outliers of each dataset. Asterisks indicate significant differences between landscapes according to Tukey's posthoc test, significance levels as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

concentration in plantations: 57.85 ± 13.61 %; forests: 52.56 ± 14.22 %; gardens: 55.83 ± 14.84 %). However, nectar sugar concentration varied over the year (SM II.5: Figure II.7) and was higher in the dry than in the wet and cold season (Tukey test, $P < 0.001$; dry season: 65.32 ± 13.63 %; wet season: 52.60 ± 18.81 %; cold season: 55.13 ± 14.69 %).

Whereas pollen load size of individual workers did not differ between landscapes (plantations: 1.13 ± 0.56 mg; forests: 1.15 ± 0.33 mg; gardens: 1.26 ± 0.47 mg), it did differ between seasons (SM II.5: Figure II.7; GLMM: $\chi^2 = 43.17$, $P < 0.001$) and was
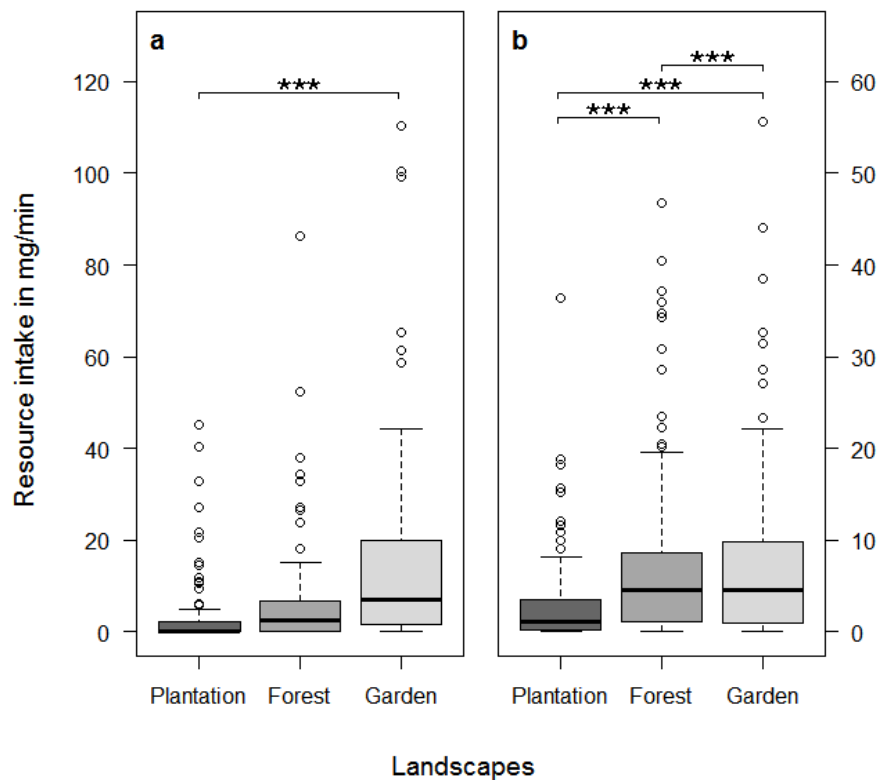
Figure II.4. Pollen (**a**) and sucrose (**b**) intake in plantations (dark grey bars), forests (grey) and gardens (light grey). Boxplots display the median (thick bar), lower (0.25) and upper (0.75) quartile (gray box), minimum and maximum values (whiskers) and outliers of each dataset. Asterisks indicate significant differences between landscapes according to Tukey's posthoc test, significance levels as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

overall highest in the wet season (1.32 ± 0.46 mg) and lowest in the cold season (0.91 ± 0.29 mg) and intermediate in the dry season (1.01 ± 0.44 mg). Landscape and season also best described differences in the total pollen intake per minute (Table II.1, SM II.5: Figure II.8). Total pollen intake per minute of the whole colony was overall lowest in plantations and significantly higher in forests and gardens (Figure II.4a).

Differences in the total sugar intake per minute were also best described by the interaction between landscape and season (Table II.1, SM II.5: Figure II.8). Sucrose intake per minute was generally high in gardens and forests and significantly lower in plantations (Figure II.4b), like the seasonal patterns of nectar foragers (Figure II.2b, SM II.5: Figure II.5).

2.4.3. *Influence of weather*

Weather variables, i.e. temperature and average wind speed, significantly affected our foraging response variables (SM II.4). However, variation in foraging activity and forager numbers was largely explained by interactions between landscape, season, temperature and average wind speed (SM II.4). The same was true for proportions of pollen, nectar and unsuccessful foragers as well as total pollen and sugar intake (SM II.4). The proportion of resin foragers was not influenced by temperature, and resin foragers per minute were not influenced by average wind speed (SM II.4). Consequently, landscape had a strong influence in all models even when weather variables were included, and the explanatory values of all models significantly decreased when landscape was dropped (GLMM: $P < 0.001$ in all cases, SM II.4).

2.5. Discussion

Wild bee populations are declining in human altered landscapes likely due to reduced availability of food resources (Decourtye et al. 2010; Winfree 2010; Roulston and Goodell 2011). Because plant resource availability and diversity in landscapes drive foraging dynamics in bees (Decourtye et al. 2010; Jha and Kremen 2013), we investigated how foraging patterns and resource intake in a highly social bee species are affected by landscape-related differences in resource availability. Our results clearly show that foraging patterns strongly differed between different human altered landscapes and the bees' natural habitat depending on season. Contrary to our expectations, pollen and nectar foraging, nectar forager numbers and sugar and pollen intake were highest in gardens, not in natural forests.

2.5.1. *Foraging patterns*

Foraging activities were highest in gardens across all seasons in both years, indicating that gardens provide abundant floral resources to forage on compared with other landscapes. All key resources needed for provison and rearing brood were abundant and fully utilized by bee hives in gardens. The steady food availability was most likely due to a mix of native and exotic plants in gardens which produce a continuous supply of floral resources (Head et al. 2004), known to benefit generalist bee species (Winfree 2010; Levy 2011). This result agrees with previous findings showing that urban or suburban gardens represent beneficial landscape elements by providing plentiful food resources and foraging opportunites for bees which increases bee

abundance and density in social and solitary bees (Gotlieb et al. 2011; Samnegård et al. 2011; Hinners et al. 2012). Moreover, access to anthropogenically disturbed patches with additionally planted (flowering) plant species in a homogenous natural landscape can improve habitat quality, as connected patches of high plant diversity in a mosaic landscape provide additional foraging opportunities (Williams and Kremen 2007; Winfree et al. 2007). Human altered, highly heterogenous habitats, such as gardens, can consequently be of high foraging value. While Hernandez et al. (2009) suggest that this positive effect of urbanization may be limited to eusocial or generalist bees, Baldock et al. (2015) found bee richness across taxa to be higher in urban areas than on farms and to be marginally higher in urban areas than in nature reserves.

Social bee colonies further respond to the spatio-temporal changes of resource availability in a landscape by adjusting the number of foragers for any target resource according to their colony needs. We found high proportions of nectar foragers and lower proportions of resin and unsuccessful foragers in gardens than in other landscapes, whereas the proportion of pollen foragers did not differ between landscapes. Pollen is a limited plant resource and is, unlike nectar, not constantly replenished by the plant and can thus be depleted over the course of a day (Roubik 1989). Bees should thus primarily collect pollen when available. Periods of high pollen availability occurred at all of our study sites. Consequently and as predicted, we found a similar proportion of pollen foragers when comparing landscapes across seasons.

The generally higher proportion of successful foragers in gardens is most likely due to the very small-scaled and patchy resource landscape with steady flowering across all seasons, including a variety of bird pollinated native plants with a continuous supply of nectar (Ford et al. 1979). Contrary to our predictions, resin foraging was not higher in forests than plantations, even though resin availability was predicted to largely increase with tree availability (Leonhardt and Blüthgen 2009). In gardens with limited numbers of resiniferous trees, hives allocated a smaller proportion of foragers, but similar overall forager numbers to collect resin. Stingless bee workers are known to rarely switch from or to resin foraging behaviour during the day, which keeps resin forager numbers fairly steady (Inoue et al. 1985; Wallace and Lee 2010). An overall higher foraging activity in gardens therefore allows hives to collect more pollen and nectar, while gathering similar total amounts of resin, compared to hives with lower foraging activities in forests or plantations. Contrary to our expectations, *T. carbonaria* thus seemed to have a specific intake target for resin as we observed similar numbers of returning resin foragers in all landscapes, which contradicts our prediction and suggests that resin is sufficiently available in all landscapes.

In contrast to gardens with their continuous pollen supply, pollen collection as well as overall foraging activity in forests seemed to be largely driven by the main mass flowering of eucalypts in the dry and cold season (Beardsell et al. 1993). The effect of mass flowering on a colony's pollen intake has also been shown for stingless bee colonies in Borneo which strongly responded to the mass flowering of dipterocarp trees (Eltz et al. 2001). Mass flowering crops also increase foraging and reproductive success in honey bees and solitary bees (Jauker et al. 2012; Odoux et al. 2012).

In accordance with our expectations, the number of unsuccessful foragers was high in plantations and foraging activity generally weak and only peaked during the 5-8 week period of macadamia mass flowering in the dry season (Heard 1993; Wallace et al. 1996). But even then, it rarely reached as high activity levels as observed in gardens. Plantation hives may have struggled to build up sufficient numbers of foragers to make use of the macadamia mass flowering after a long dormant state in the cold season. Foraging nevertheless continued all year long in plantations, but limited availability of flowering plants besides macadamia strongly constrained foraging activity of hives. This finding agrees with previous studies showing that seasonal resource limitation impacts on bee foraging in landscapes with mass flowering crops dominating (Decourtye et al. 2010; Williams et al. 2012).

2.5.2. *Resource intake*

Sucrose concentrations between 60-75 %, as often observed in our study, are unusually high compared to other ecosystems with maximum concentrations of 60 % or often less than 35 % sugar content of nectar collected by bees (Roubik 1989). Australia and specifically its arid areas have been proposed to offer plentiful carbohydrate resources, which in turn favour opportunistic social insects (Morton et al. 2011). We found highest nectar concentrations in the dry season across landscapes which further points to the importance of short flowering events of specific nectar plants, e.g. macadamia or eucalypts, as a driver of nectar foraging dynamics. Although the nectar collected likely originated from different foraging plant sources in the different landscapes, nectar of high quality seemed to be available in all landscape types and does not explain resource related shortcomings.

Sugar intake rates were nevertheless two to three times higher in gardens and forests than in plantations, with greatest differences between landscapes in the dry season. As nectar concentration varied little between landscapes and season, sugar intake rates were predominantly determined by the overall proportion of nectar foragers and hive foraging

activity.

Pollen intake rates of hives in forests were twice as high as in plantations and five times higher in gardens than in plantations. Yet the size of pollen loads of single workers, which corresponds to the efficiency of single foraging trips, did not vary between landscapes across seasons. Pollen foragers were thus likely able to maximize their load in all landscapes. Consequently, the higher pollen foraging success in forests and gardens was again due to higher foraging activity. This finding highlights the role of hive foraging activity as a response to landscape resource availability in determining the overall foraging success of social bees.

Unlike social bees, generalist solitary bees cannot equivalently increase their resource intake in response to increasing resource availability, because they cannot recruit additional bees to foraging when resources are plentiful. Thus, even if they could use all plant sources available to social bees, their abundance and fitness would most likely be more strongly affected by other parameters, such as foraging distances (Zurbuchen et al. 2010) or climate (Vicens and Bosch 2000), provided they have access to sufficient nesting opportunities (Zanette et al. 2005; Cane et al. 2006; Hernandez et al. 2009).

Abiotic factors, like temperature, humidity, wind speed and luminosity, are known to further strongly influence bee foraging behaviour, especially in tropical stingless bees (Ferreira et al. 2010; Figueiredo-Mecca et al. 2013) and other bees (Brittain et al. 2013; Kühsel and Blüthgen 2015). These weather factors also contributed to the activity patterns observed in our study, but their influence was minor compared to landscape related patterns of resource foraging.

To summarize, we found that landscape strongly affected foraging patterns and resource intake in a social bee. Moreover, bees responded differently to different anthropogenic habitat alterations compared to natural forest habitats, with foraging activity and thus resource intake being strongly impaired in agricultural monocultures, but largely improved in flower-rich gardens. While previous studies focused on the negative effects of plant resource impoverishment in agricultural landscapes on bees (Decourtye et al. 2010; Lentini et al. 2012; Williams et al. 2012), few studies have hitherto investigated how gardens affect bee foraging and resource intake (Hennig and Ghazoul 2012; Wojcik and McBride 2012). Cities worldwide differ in the extent of remaining green areas, flower resources and nesting space and may thus differentially

affect bees (Hernandez et al. 2009; Matteson et al. 2013; Lowenstein et al. 2014), but our study shows that gardens can increase resource intake and thus foraging success in social bees even beyond natural habitats.

2.6. Acknowledgments

2.7. References

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II. Urban gardens promote bee foraging

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Table II.2. **Location of study sites and geographic information.** Due to limited space in gardens, garden sites were split into two locations. Landscape cover is given for the main landscape types studied (i.e. forest, plantation, garden). Latitude and longitude were rounded to the nearest minute to safeguard data privacy of land owners. Original data is available upon request.

Landscape	Study site	Region	Altitude (a.s.l.)	Forest cover [%]	Plantation cover [%]	Garden cover [%]	Latitude	Longitude
Forest	F1	Bundaberg	23 m	96.36			24°38' S	152° 8' E
Forest	F2	Bundaberg	27 m	89.79			24°46' S	152° 6' E
Forest	F3	Sunshine Coast / Brisbane	51 m	97.52			26°43' S	153° 1' E
Forest	F4	Sunshine Coast / Brisbane	83 m	75.06			26°50' S	152°55' E
Plantation	P1	Bundaberg	25 m		94.73		24°46' S	152°15' E
Plantation	P2	Bundaberg	27 m		92.04		24°47' S	152°15' E
Plantation	P3	Bundaberg	26 m		93.21		24°47' S	152°16' E
Plantation	P4	Sunshine Coast / Brisbane	55 m		80.08		26°53' S	152°56' E
Garden	G1 - location A	Bundaberg	7 m			88.20	24°50' S	152°28' E
Garden	G1 - location B	Bundaberg	19 m			87.70	24°52' S	152°19' E
Garden	G2 - location A	Sunshine Coast / Brisbane	15 m			98.46	26°41' S	153° 7' E
Garden	G2 - location B	Sunshine Coast / Brisbane	3 m			76.99	26°41' S	153° 7' E
Garden	G3 - location A	Sunshine Coast / Brisbane	18 m			98.21	27°29' S	153° 0' E
Garden	G3 - location B	Sunshine Coast / Brisbane	17 m			82.23	27°29' S	153° 0' E
Garden	G4 - location A	Sunshine Coast / Brisbane	31 m			82.06	27°30' S	153° 1' E
Garden	G4 - location B	Sunshine Coast / Brisbane	45 m			78.23	27°29' S	153° 1' E

SM II.2. Influence of daytime

To test whether foraging patterns changed during the day, foraging observations were performed in the morning (9:30 – 12:50) and in the afternoon (13:55 – 16:40) from September to October 2011. We found that the proportion of pollen and nectar foragers significantly decreased from morning to afternoon (GLMM: pollen: $\chi^2 = 26.60$, $P < 0.001$, nectar: $\chi^2 = 5.01$, $P = 0.03$), whereas the proportion of foragers returning without any load increased over the course of the day ($\chi^2 = 31.56$, $P < 0.001$). Decreasing pollen foraging from morning to afternoon is consistent with findings in other stingless bees (Inoue et al. 1985; Wallace and Lee 2010). No differences were observed for the proportion of returning resin foragers over the day ($\chi^2 = 2.82$, $P = 0.09$). We therefore chose to perform our foraging observations at the earliest possible time for each observation day, when bee colonies reached sufficient activity levels. As a temperature sensitive species, workers of *T. carbonaria* need an ambient temperature of at least 18°C to start foraging (Heard and Hendrikz 1993). Observations in the cold season therefore started as late as 11:30 when temperature peaked at midday. Consequently, overall observation times ranged from 7:30 - 15:30 across seasons.

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SM II.3. Correlation matrix of forager numbers and weather variables

Table II.3. **Spearman correlation matrix** with correlation coefficients (r_S) for forager numbers and weather variables; significance levels as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Abbreviations: **Act**: foraging activity; P_P: proportion of pollen foragers; P_N: proportion of nectar foragers; P_R: proportion of resin foragers; P_n: proportion of foragers with no load; **Temp**: temperature; **Hum**: humidity; **Cloud**: cloud cover; W_{max}: maximum wind speed; W_{avg}: average wind speed; W_{gusts}: number of wind gusts; F_N: nectar foragers per minute; F_P: pollen foragers per minute; F_R: resin foragers per minute; F_n: foragers with no load per minute.

	Act	P_P	P_N	P_R	P_n	Temp	Hum	Cloud	W_{max}	W_{avg}	W_{gusts}	F_N	F_P	F_R
P_P	0.12 *													
P_N	0.15 **	-0.42 ***												
P_R	-0.13 *	-0.05	-0.41 ***											
P_n	-0.19 ***	-0.41 ***	-0.42 ***	0.05										
Temp	0.05	0	0.35 ***	-0.05	-0.39 ***									
Hum	0.16 **	-0.10	0.02	0.04	0.06	-0.22 ***								
Cloud	0.11 *	-0.05	0.07	0.07	-0.08	0.13 *	0.42 ***							
W_{max}	-0.27 ***	-0.08	-0.04	-0.12	0.09	0.20 **	-0.16 *	0.08						
W_{avg}	-0.25 ***	-0.12	-0.01	-0.09	0.11	0.19 *	-0.06	0.09	0.92 ***					
W_{gusts}	-0.22 **	-0.01	-0.12	-0.10	0.10	0.09	-0.02	0.11	0.82 ***	0.90 ***				
F_N	0.75 ***	-0.15 **	0.70 ***	-0.35 ***	-0.36 ***	0.23 ***	0.13 *	0.15 **	-0.22 **	-0.20 **	-0.23 **			
F_P	0.52 ***	0.85 ***	-0.29 ***	0	-0.38 ***	0.06	-0.04	-0.03	-0.17 *	-0.20 **	-0.12	0.19 ***		
F_R	0.45 ***	0.06	-0.28 ***	0.72 ***	-0.06	-0.01	0.14 *	0.09	-0.30 ***	-0.30 ***	-0.30 ***	0.12 **	0.30 ***	
F_n	0.72 ***	-0.14 **	-0.14 **	-0.07	0.46 ***	-0.17 **	0.18 **	0.06	-0.22 **	-0.20 **	-0.18 *	0.41 ***	0.21 ***	0.37 ***

Table II.4. **Results of generalized linear mixed effect models** (GLMMs) for each response variable, for the second year with all weather factors included as additional explanatory variables. Given are χ^2-values obtained for comparing the best model with the respective explanatory variable to a model with this variable dropped (landscape, season, temperature or wind). Significance levels as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns: not significant. NA indicates missing data.

For detailed model outputs see Appendix I, section 7.1

Response variable	Landscape			Season			Temperature			Wind		
	χ^2	df	P	χ^2	df	P	χ^2	df	P	χ^2	df	P
Foraging activity	55.04	24	***	54.18	24	***	41.48	18	***	35.43	18	**
Pollen foragers / min	375.87	24	***	460.25	24	***	276.53	18	***	159.37	18	***
Nectar foragers / min	255.96	24	***	293.72	24	***	119.67	18	***	241.74	18	***
Resin foragers / min	47.19	12	***	66.34	12	***	49.74	9	**			ns
Unsuccessful foragers /min	165.00	24	***	168.76	24	***	87.53	18	***	105.45	18	***
Proportion pollen foragers	133.02	24	***	153.90	24	***	91.81	18	***	43.51	18	***
Proportion nectar foragers	88.67	24	***	138.16	24	***	97.14	18	***	62.72	18	***
Proportion resin foragers	42.90	12	***	70.95	12	***			ns	40.48	9	***
Proportion unsuccessful foragers	125.64	24	***	138.28	24	***	95.84	18	***	74.71	18	***
Total sugar intake / min	189374	12	***	259112	12	***	251930	9	***	NA		
Total pollen intake / min	59.47	12	***	71.42	12	***	59.03	9	***	NA		

SM II.5. Foraging patterns and resource intake per season
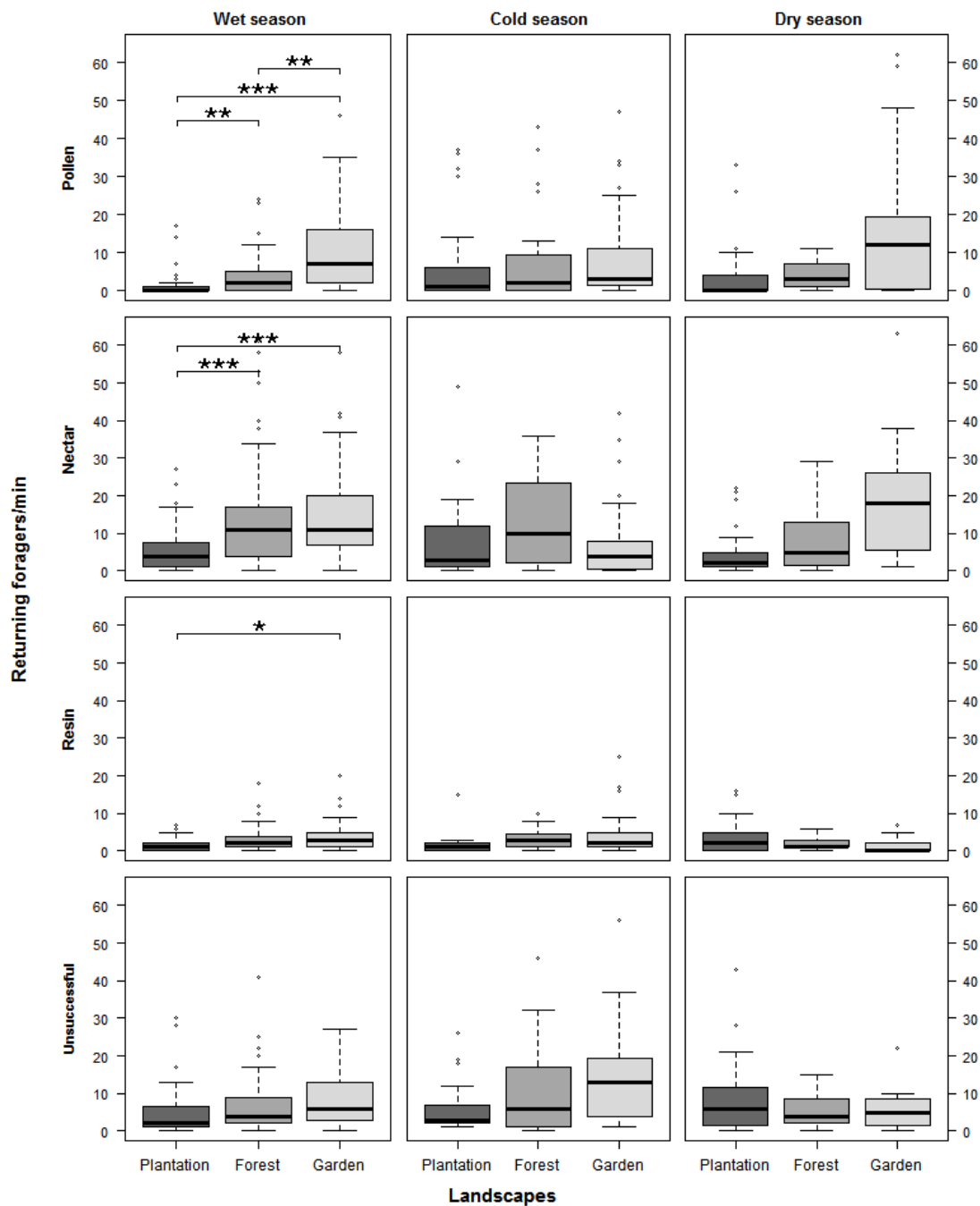
Figure II.5. **Number of foragers returning per minute** with pollen, nectar, resin or unsuccessful foragers in plantations (dark grey bars), forests (grey) and gardens (light grey) in the wet, cold and dry season. Boxplots display the median (thick bar), lower (0.25) and upper (0.75) quartile (grey box), minimum and maximum values (whiskers) and outliers of each dataset. Asterisks indicate significant differences between landscapes according to Tukey's posthoc test, significance levels as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
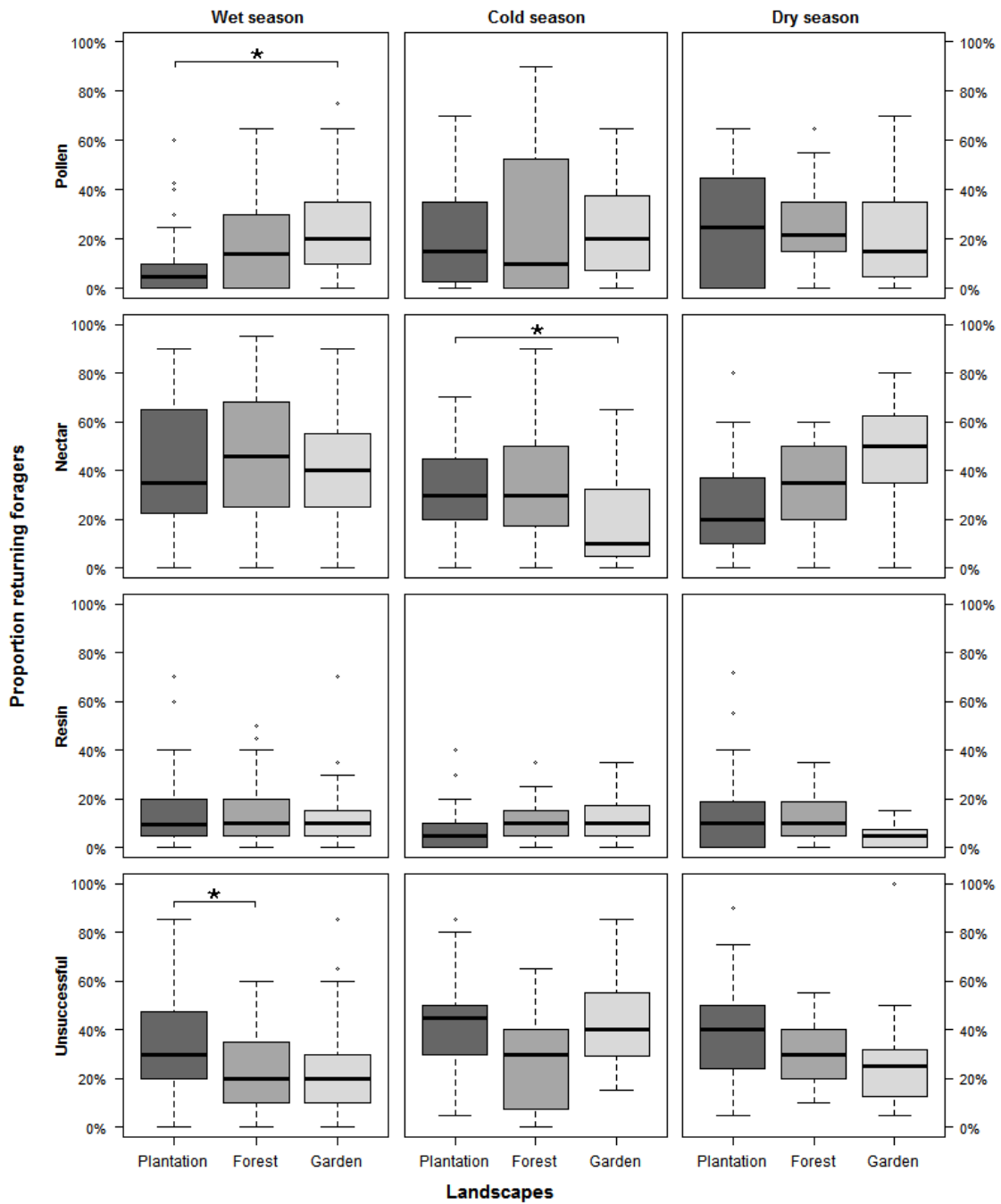
Figure II.6. **Proportional resource intake** in plantations (dark grey bars), forests (grey) and gardens (light grey). Shown are per cent of foragers returning with pollen, nectar, resin and unsuccessful foragers in the wet, cold and dry season. Boxplots display the median (thick bar), lower (0.25) and upper (0.75) quartile (grey box), minimum and maximum values (whiskers) and outliers of each dataset. Asterisks indicate significant differences between landscapes according to Tukey's posthoc test, significance levels as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
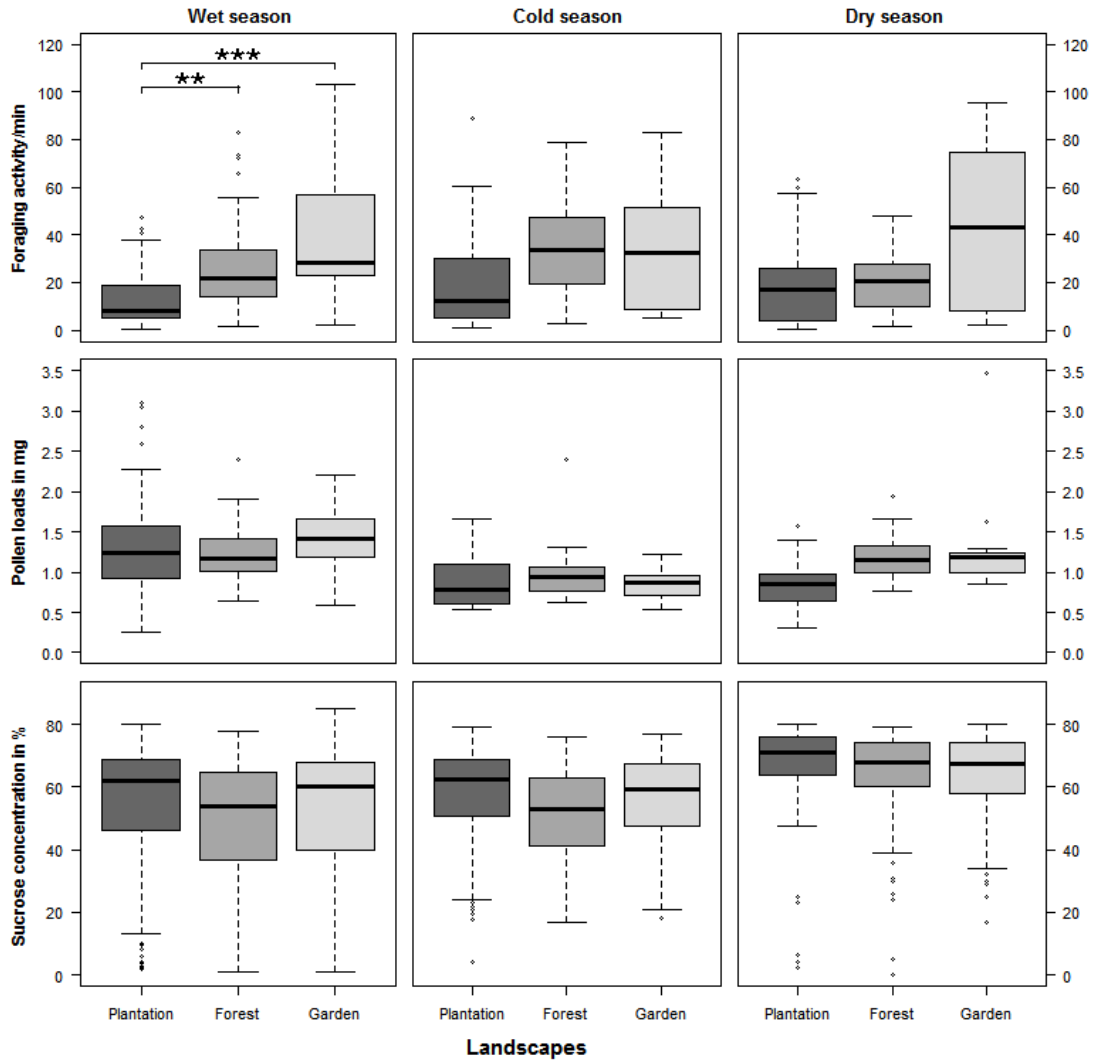
Figure II.7. **Hive foraging activity, pollen loads and sucrose concentration** of nectar in plantations (dark grey bars), forests (grey) and gardens (light grey) in the wet, cold and dry season. Boxplots display the median (thick bar), lower (0.25) and upper (0.75) quartile (grey box), minimum and maximum values (whiskers) and outliers of each dataset. Asterisks indicate significant differences between landscapes according to Tukey's posthoc test, significance levels as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
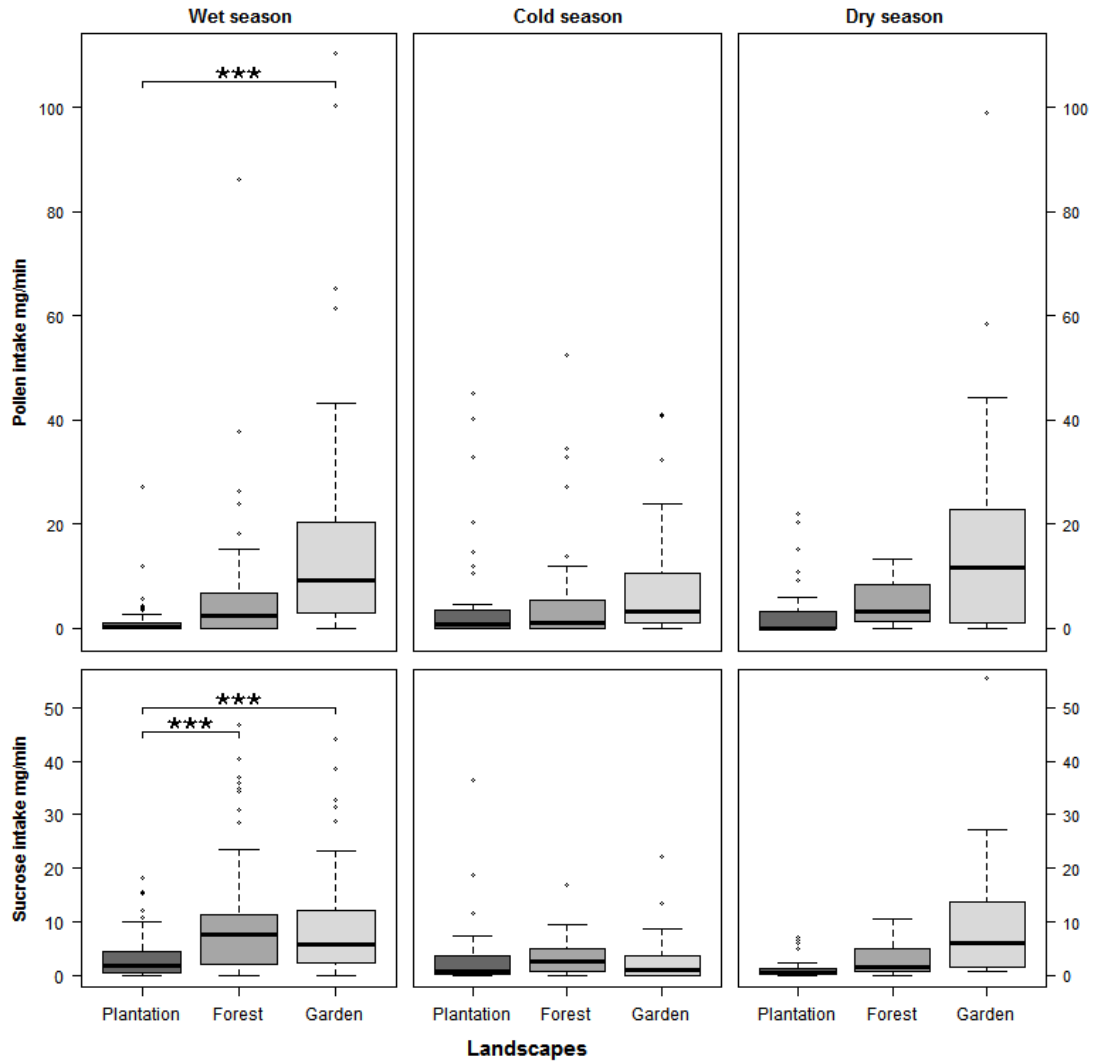
Figure II.8. **Pollen and sucrose intake** in plantations (dark grey bars), forests (grey) and gardens (light grey) in the wet, cold and dry season. Boxplots display the median (thick bar), lower (0.25) and upper (0.75) quartile (grey box), minimum and maximum values (whiskers) and outliers of each dataset. Asterisks indicate significant differences between landscapes according to Tukey's posthoc test, significance levels as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

III. RESOURCES OR LANDMARKS WHICH FACTORS DRIVE HOMING SUCCESS IN *TETRAGONULA CARBONARIA* FORAGING IN NATURAL AND DISTURBED LANDSCAPES?

3.1. Abstract

To date, no study has investigated how landscape structural (visual) alterations affect navigation and thus homing success in stingless bees. We addressed this question in the Australian stingless bee *Tetragonula carbonaria* by performing marking, release and re-capture experiments in landscapes differing in habitat homogeneity (i.e. the proportion of elongated ground features typically considered prominent visual landmarks). We investigated how landscape affected the proportion of bees and nectar foragers returning to their hives as well as the earliest time bees and foragers returned. Undisturbed landscapes with few landmarks (that are conspicuous to the human eye) and large proportions of vegetation cover (natural forests) were classified visually/structurally homogeneous, and disturbed landscapes with many landmarks and fragmented or no extensive vegetation cover (gardens and plantations) visually/structurally heterogeneous. We found that proportions of successfully returning nectar foragers and earliest times first bees and foragers returned did not differ between landscapes. However, most bees returned in the visually/structurally most (forest) and least (garden) homogeneous landscape, suggesting that they use other than elongated ground features for navigation and that return speed is primarily driven by resource availability in a landscape.

3.2. Introduction

Anthropogenic activities can severely affect and alter bee communities by converting natural habitats into landscapes with reduced resource availability and diversity, and by increasing exposure to pesticides and non-native pathogens (Winfree et al. 2009; Potts et al. 2010; Roulston and Goodell 2011; Vanbergen and the Insect Pollinators Initiative 2013; Goulson et al. 2015). Anthropogenic activities can further alter the structure of the bees' foraging landscape with severe consequences for foraging patterns and success

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(Steffan-Dewenter and Kuhn 2003; Westphal et al. 2006; Williams and Kremen 2007; Osborne et al. 2008; Kaluza et al. 2016).

While bee foraging success and thus fitness are predominantly affected by habitat related changes in resource availability and diversity (Roulston and Goodell 2011), the mere change of landscape (visual) structure, e.g. from spatially complex forests to uniform fields, may additionally affect foragers, e.g. by interfering with their navigation system, and therefore either benefit or impede foraging. This aspect has, to the best of our knowledge, not yet been examined.

Most studies on the navigation system of bees have focused on honeybees (*Apis mellifera*, Apidae: Apini) with their sophisticated recruitment system (von Frisch 1967). However, findings for honeybees most likely apply to most bee species, as orientation systems appear to be similar across invertebrates and even vertebrates (Dyer and Could 1983). Like other insects, bees combine a geocentric and egocentric navigation system, i.e. they integrate all distances and angles travelled into a home vector and further memorize landmarks to infer their position in relation to the environment, with visual information ('view-based matching') typically dominating over path integration in experienced foragers (Menzel et al. 1996; Wehner et al. 1996; Wystrach and Graham 2012; Menzel and Greggers 2015). They further use optical flow (i.e. integrate images moving in the eye) to assess travel distance between prominent landmarks while flying from nests to resource patches (Srinivasan 2014). Thus bees appear to rely mostly on visual cues provided by the sky (i.e. polarized light) and the terrestrial environment to infer long-range directions and distances towards resource patches and their nest (Najera et al. 2015) with landmarks likely playing an important role (Menzel et al. 1996; Collett and Graham 2015).

The precise nature of visual landmarks used and memorized by bees is still subject to debate (Dyer et al. 2008; Wystrach and Graham 2012). Honeybees and stingless bees have trichromatic colour vision peaking in the UV, blue and green region of the spectrum (Avarguès-Weber et al. 2012; Sánchez and Vandame 2012; Spaethe et al. 2014). They can thus perceive and memorize colours as well as visual shapes and patterns (Giurfa et al. 1999; Avarguès-Weber et al. 2012; Sánchez and Vandame 2012; Spaethe et al. 2014) and typically prefer global (i.e. the forest) over local (i.e. trees) patterns (Avarguès-Weber et al. 2015). Visual landmarks used in behavioural studies on navigation were often represented by shapes that are conspicuous to the human eye, including cars, tents, field margins (in field studies focusing on larger scales) and various paper shapes (in laboratory studies focusing on small scales;(Menzel et al. 1996; Fry and Wehner 2005). Radar tracking of inexperienced honeybee and bumblebee

foragers suggested that they preferentially navigate along visual landmarks, i.e. elongated ground features, such as hedge-rows, field margins or highways (Osborne et al. 2013; Collett and Graham 2015; Degen et al. 2015). Notably, such features conform with a very anthropogenic notion of landmarks (Wystrach and Graham 2012) and are most likely not found in the bees' original habitat, which consisted of non-fragmented forest- or shrub-land. It may thus be more likely that bees, like ants and birds, rely on panoramic views for navigation, which would allow them to better cope with the complexity of natural landscapes given their poor visual resolution (Wystrach and Graham 2012).

Comparing navigation of bees foraging in differently structured landscapes may shed some more light on the sort of landmarks used. However, to our knowledge, it has not yet been investigated whether landscapes differing in their visual/spatial structure differently affect bee navigation, e.g. whether modern (disturbed) landscapes facilitate bee navigation compared with more natural (undisturbed) closed forest or shrub-land habitats.

We addressed this question by investigating how (visual) habitat structure affected homing success in a highly social bee species, the stingless bee *Tetragonula carbonaria* (Apidae, Meliponini), which occurs in the tropical and subtropical forests of Australia, but also thrives in human dominated landscapes, such as cities (Dollin et al. 2009; Leonhardt et al. 2014b; Heard 2016).

We assumed that navigation in *T. carbonaria* was similar to honeybees and therefore facilitated in landscapes with landmarks that were conspicuous/prominent to the human eye. Based on this rather anthropogenic view, we consequently hypothesized that homing success (i.e. the proportion of bees returning to their hive within an hour and the earliest time first bees returned to their hives) increased with decreasing landscape homogeneity, i.e. from undisturbed forests (as visually homogenous landscapes with few, if any, prominent landmarks) to suburban areas (as visually heterogeneous landscapes with multiple prominent landmarks).

3.3. Methods

3.3.1. *Study species and landscapes*

The study was conducted in Queensland, Australia, between January and November 2013. Homing success was tested in the Australian stingless bee *Tetragonula*

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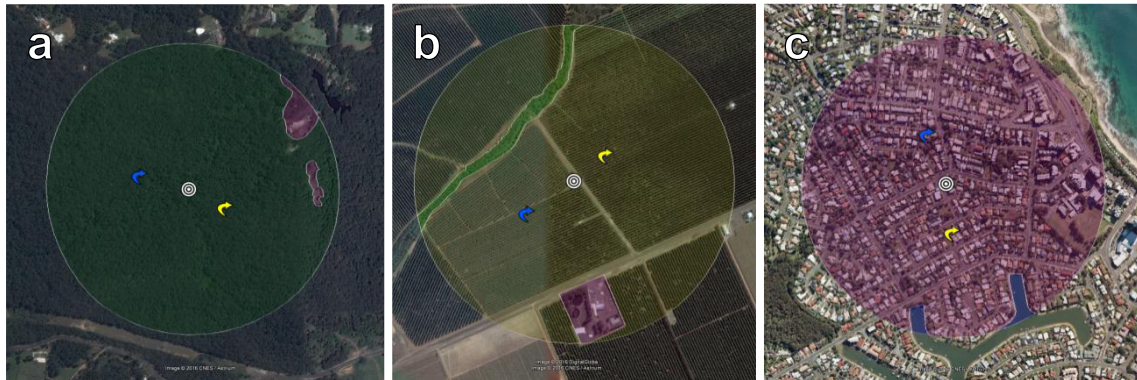
Figure III.1. Examples for each of the three landscape types in which homing success was studied: (**a**) forest, (**b**) plantation and (**c**) garden. *Circles* give 500 m foraging radii around experimental hives. Habitat patches are *outlined in color*, i.e. *green*: forest; *purple*: garden; *yellow*: plantation and *blue*: water. Circles indicate hive locations and *blue* and *yellow* arrows mark respective release points.

carbonaria (Apidae, Meliponini: Dollin et al. 1997; genus change: Rasmussen and Cameron 2007), which is native to the study region, but can also be kept and propagated in boxes (Heard 2016).

To test whether and how habitat alterations impact on homing success of *T. carbonaria*, we studied eleven colonies overall which had been experimentally placed in natural forests (four colonies) as well as two landscape types severely altered by humans, i.e. agricultural plantations (four colonies) and urban gardens (three colonies) (see Kaluza et al. 2016 for a detailed description of the study area, sites and landscape types) Table III.1, Figure III.1. Forests comprised relatively open *Banksia* heathland as well as denser sclerophyll forests with a closed canopy dominated by eucalypt species. Plantation sites comprised commercial macadamia plantations (*Macadamia integrifolia* Maiden and Betche × *M. tetraphylla* Johnson). Urban gardens in the study region typically included houses, surrounded by gardens of 300-1000 m² with both native and exotic plants.

3.3.2. *Experimental setup*

Overall twelve study sites had been established in 2011 (Kaluza et al. 2016), of which we used seven for this experiment (Table III.1). For each landscape type (plantation, forest and garden) we tested colonies at 2-3 study sites (Table III.1). Hives with colonies had been mounted on metal posts roughly 1 m above ground (in forests and plantations) with the entrance facing NE. When posts could not be used due to

Table III.1. Description of the different landscape types used in this study as well as of the parameters recorded to compare homing success in bees between different landscapes. The table shows the numbers of hives (**Hives**) and sites (**Sites**) used per landscape type (**Landscape**), the mean [± standard deviation] richness of tree and shrub (i.e. woody plant species richness WP_{Ric}), percentage of area covered by closed vegetation (forest or plantation; VC_A) and number of landmarks (**LM**) for each landscape, the mean [± standard deviation] of marked bees that were successfully released (N_{Bee}), the proportion of bees that returned within an hour ($Prop_{Bee}$), the proportion of bees that returned within an hour with nectar in their crop ($Prop_{Forager}$) as well as the earliest time (i.e. five minute interval) the first bee and forager returned ($1._{Bee}$ and $1._{Forager}$).

Landscape	Hives	Sites	WP_{Ric}	VC_A	LM	N_{Bee}	$Prop_{Bee}$	$Prop_{Forager}$	$1._{Bee}$	$1._{Forager}$
Forest	4	2	111 ± 10	76 ± 1	7 ± 1	56 ± 1	0.73 ± 0.06	0.28 ± 0.16	5 ± 0	13 ± 60
Garden	3	3	186 ± 42	0	30 ± 7	56 ± 6	0.51 ± 0.12	0.34 ± 0.23	5 ± 0	13 ± 80
Plantation	4	2	54 ± 24	76 ± 0	8 ± 0	52 ± 3	0.25 ± 0.21	0.31 ± 0.12	9 ± 5	26 ± 16

sealed surfaces (in gardens), hives were placed on bricks close to the ground. All hives were located in shaded or semi-shaded locations and protected by a metal roof when not covered by house roofs. By the time the homing experiment started, all colonies were habituated to the location and surrounding foraging environment.

We anticipated a flight radius of 500 m around hives which is the typical foraging range of bees of this size (equivalent to 0.78 km² flight range; Greenleaf et al. 2007; Smith et al. 2016). Flight ranges of different study sites did not overlap and more than 75 % of the flight range at each site was covered by the target landscape (plantation, forest or garden; Kaluza et al. 2016).

3.3.3. *Assessing habitat homogeneity*

Honeybees can navigate along visual landmarks that are easily perceived by humans, i.e. elongated ground features (Osborne et al. 2013; Collett and Graham 2015; Degen et al. 2015). Such landmarks are more likely to occur in heterogeneous landscapes with changing habitat types, such as urban areas or extensively used agricultural landscapes with small fields intermixed with semi-natural habitat and forest patches.

We therefore considered undisturbed natural landscapes with few prominent landmarks and large proportions of area covered by vegetation (i.e. forests) visually/structurally homogeneous, and disturbed landscapes with many prominent landmarks and fragmented or no extensive vegetation cover (i.e. gardens and plantations) visually/structurally heterogeneous (Table III.1, Figure III.1), which certainly represents a very anthropogenic classification. Landmarks that are conspicuous

to the human eye (i.e. water (ponds/ creeks/ rivers), roads/ bridges, tall buildings and small patches of natural habitats) were counted and vegetation cover (i.e. area covered by forest and/or plantations) assessed within the 500 m radius around hives using aerial photographs from Google Earth (Figure III.1). We outlined all vegetation patches to calculate their area with the software KML Toolbox and additionally validated our classifications by ground surveys (Kaluza et al. 2016). To further test whether homing success depended on the type of vegetation cover (i.e. uniform plantations with only one tree species vs. diverse forests with many different tree species), we also assessed shrub and tree (i.e. woody plant) species richness by performing transect walks at each site (Kaluza et al., submitted).

3.3.4. *Recording homing and foraging success*

We caught 60 individuals from each study colony by placing a clean clear plastic bag over the entrance thereby capturing bees leaving the hive. In particular stingless bee pollen foragers are known to carry small amounts of highly concentrated nectar in their crops, used as either 'fuel' or 'pollen glue'' (Leonhardt et al. 2007). To discourage bees from foraging, we therefore gently squeezed the bees' abdomen forcing them to regurgitate all nectar stored in their crop. Foragers were then separated into two groups (each consisting of 30 individuals) and marked with two different colours (acrylic paint) by carefully holding them between two fingers, placing a small droplet of paint on their thorax using brushes or small twigs and waiting for the paint to dry. Because painted bees were observed foraging for resources even up to 10 days after the experiment, we are confident that handling and marking did not significantly impact on bees. All marked bees of one group were kept in clear plastic insect containers prior to release.

Two people then simultaneously walked 150 m into opposite directions (up- and down-wind) from the hive using geographic information system devices (GPS, Garmin, Germany) for orientation. We consider 150 m a typical foraging distance for *T. carbonaria* as this species was found to have a maximum flight range of 500 m (Smith et al. 2016). In preliminary trials, we had also tested other distances and found distances >100 m sufficient for detecting obvious differences in homing behaviour while restricting the overall experiment duration.

Bees of both groups were released simultaneously by both experimenters by opening plastic containers and placing all bees on bare ground. We then waited for ten minutes to ensure that all marked bees took flight. Bees which did not leave within this time period were re-collected and kept in plastic tubes until the end of the experiment.

A third observer at the hive entrance re-captured all bees returning in five minute intervals for one hour. All returning bees were again placed in plastic containers and visually inspected for either pollen or resin on their corbiculae or nectar in their crops (see above) to determine whether the bees had gone foraging. We noted the number of bees returning within each five minute interval, the thorax colour and whether or not bees carried any resources. Note that none of the returning bees carried any pollen or resin, but several had nectar in their crops, which is why we decided to account for nectar foraging and thus indirectly the availability of resources (which differs between landscapes, Kaluza et al. 2016) as a potential major factor determining return speed in our study. Homing success was calculated as the proportion of bees returning to their hives within one hour (bees returned/ bees released) and the earliest time (i.e. five minute interval) the first bee returned to its hive. Nectar foraging was assessed as the proportion of returning nectar foragers (bees returned with nectar in crop/ bees returned) and the earliest time (i.e. five minute interval) the first nectar forager returned to its hive. We repeated the experiment for a total of eleven hives/ performed a total of eleven trials (4 trials/hives in plantations, 3 trials/hives in gardens and 4 trials/hives in forests, Table III.1).

3.3.5. *Statistical analysis*

To test whether releasing direction and thus wind influenced homing success and/or nectar foraging, we compared the proportion of bees returning within an hour, the earliest time (i.e. five minute interval) the first bee returned and the first nectar forager returned as well as the proportion of nectar foragers using Wilcoxon matched pair tests. Data for both directions was pooled if releasing did not affect our response variables (which was the case for all variables but the proportion of foragers), while we included releasing direction as a random factor in a generalized linear mixed effect model (GLMM, lmer function in the lme4 package) if it did. Pooled data was compared between landscapes (forest, garden, plantation) by analyses of variances (ANOVA) followed by Tukey posthoc-tests. All data were assessed for normality and homogeneity of variances using Shapiro and Bartlett test, respectively, and log10- or arcsine square-root-transformed if these assumptions were not met. The earliest time the first bee returned did not pass tests for normality and homogeneity and was thus analysed with a Kruskal Wallis rank sum test.
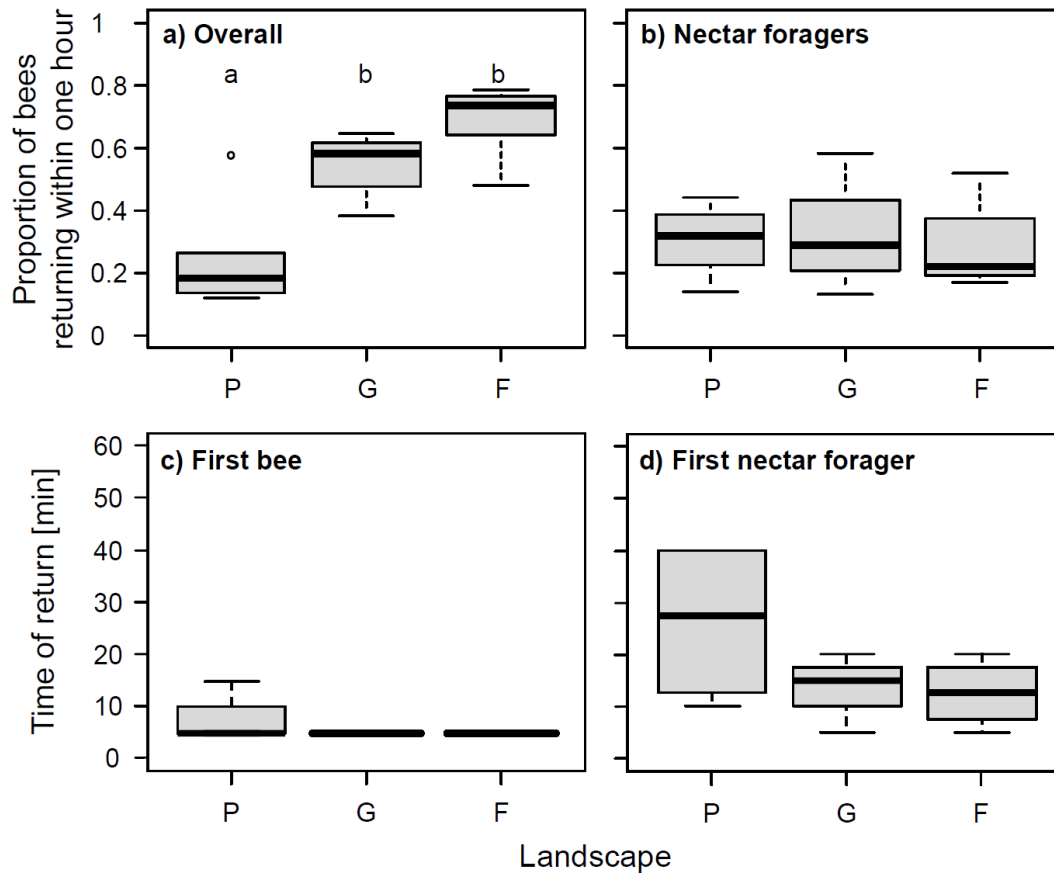
Figure III.2. Proportion of all released bees (**a**) and nectar foragers (**b**) returning within an hour as well as the earliest time (5 minute interval) the first bee (**c**) and nectar forager (**d**) returned in plantations (*P*), gardens (*G*) and forests (*F*). Boxplots display the median (*thick bar*), lower (0.25) and upper (0.75) quartiles (*grey box*), minimum and maximum values (*whiskers*) and outliers (*dots*) of each dataset. *Different letters* indicate significant differences between landscapes (*P* < 0.05) according to Tukey posthoc-tests. Overall, we performed 4 trials in plantations, 3 trials in gardens and 4 trials in forests.

To test whether single variables recorded for each site (i.e. area covered by vegetation, the richness of woody plant species, and the number of landmarks) better explained homing success and nectar foraging, we additionally composed generalized linear (mixed effect) models (GLMs, GLMMs) for each response variable. Because the area covered by vegetation and woody plant species richness were negatively correlated (Spearman correlation: $r = -056$, $p = 0.035$), we composed separate models for each explanatory variable. We finally used R^2-values to compare models comprising different explanatory variables (MuMIn package for R2-values from GLMMs: Bartoń 2013; Nakagawa and Schielzeth 2013) except for models with the earliest time the first bee returned which could not be modelled with an appropriate distribution.

Table III.2. Variance explained (R^2) for all response variables (except for the earliest time the first bee returned) by models including different explanatory variables. For mixed effect models, R^2 represents the marginal R^2-value.

Response variable	Explanatory variable(s)	R^2
Overall proportion of bees	landscape	0.67
	area covered + landmarks	0.02
	woody plant richness + landmarks	0.31
Proportion of nectar foragers	landscape	0.33
	area covered + landmarks	0.28
	woody plant richness + landmarks	0.19
Time first forager returned	landscape	0.25
	area covered + landmarks	0.34
	woody plant richness + landmarks	0.46

All statistical analyses were performed in R (R Development Core Team 2015).

3.4. Results

Homing success (i.e. the proportion of bees returning within one hour) differed between landscapes (ANOVA: $F = 10.99$, $P = 0.002$). More bees returned within an hour in forests and gardens than in plantations (Table III.1, Figure III.2a). The proportion of nectar foragers did not differ between landscapes (GLMM: $\chi^2 = 0.70$, $P = 0.855$; Figure III.2b), neither did the arrival time of the earliest bee (Kruskal Wallis test: $\chi^2 = 3.88$, $P = 0.144$; Figure III.2c) or nectar forager (ANOVA: $F = 1.32$, $P = 0.391$; Figure III.2d).

Models including only landscape as explanatory variables explained more variance in homing success and nectar foraging than models including the area covered by closed vegetation, number of landmarks, or woody plant species richness (Table III.2). Arrival time of the earliest nectar forager was however best described by the model including woody plant species richness and landmarks (Table III.2).

3.5. Discussion

In contrast to our expectations, homing was most successful, i.e. most bees returned, in undisturbed natural forest habitats as well as in heavily disturbed gardens. While gardens comprised a variety of elongated ground features which humans would easily

use as landmarks for orientation and thus navigation, forests represented a visually homogenous structure to the human eye which had few, if any, conspicuous landmarks. This finding confirms that bees perceive landscapes very differently from humans (Wystrach and Graham 2012) and shows that they do not need seemingly conspicuous landmarks (such as elongated ground features) for navigation. In fact, like honeybees, stingless bees may be able to differentiate complex combinations of visual objects (typically existing in natural landscapes) and thus easily navigate in seemingly homogeneous forests (Dyer et al. 2008). However, because closed forests represent more than a choice between two similar complex landmarks (as tested by Dyer et al. 2008) and light conditions change over time (potentially affecting visual landmark features), stingless bees may additionally integrate knowledge on the current position of celestial cues (e.g. polarized light or the position of the sun) with a panoramic memory of the entire landscape to reliably infer their position at any time, as has been shown for honeybees (Towne and Moscrip 2008).

Alternatively (or additionally), they may rely on other than visual cues for navigation, e.g. olfactory cues emanating from environmental sources such as different tree species. In fact, olfactory navigation is widely found across the animal kingdom (Jacobs 2012); and honeybees are known to use olfactory cues (i.e. floral scents) when communicating resource quality and location within hives (Farina et al. 2005) and when locating communicated food sources at close range in the field (Reynolds et al. 2009; Menzel and Greggers 2013). Stingless bees further use complex volatile blends to locate preferred resin sources (Leonhardt et al. 2010; 2014a; Wallace and Leonhardt 2015). Whether (stingless) bees can also use olfactory landmarks, e.g. the scent of flowering tree species or a rotting log, instead or in addition to visual landmarks for path integration and map memorizing, has, to our knowledge, not yet been investigated. Such olfactory mapping has however been demonstrated for desert ants (*Cataglyphis fortis*: Buehlmann et al. 2015) and should be subject to further study in bees.

Given that bees returned equally well in the most (forest) and least (garden) homogeneous landscape, their returning speed and thus the proportion of bees returning within an hour may have been mainly driven by the availability of nectar resources within the surrounding landscape, despite the handling procedure and removal of crop content. Although we did not expect bees to go foraging after having been squeezed, painted and kept in a plastic container for up to 30 minutes, we found bees returning with nectar in their crops, indicating that they nevertheless visited flowers for nectar collection. In contrast, designated pollen or resin foragers may have returned directly (without any nectar in their crops). Moreover, mean and variance recorded for the

earliest time the first nectar forager returned were highest in plantations (albeit not significantly different from other landscapes). Plantations provide the least woody plant species richness (Table III.1) and thus likely the least nectar resources across seasons (Kaluza et al. 2016). Searching for scattered resources likely increases foraging durations, as has also been shown for bumblebees in agricultural landscapes (Westphal et al. 2006). We therefore cannot rule out that reduced homing success in plantations was not (also) driven by limited resource availability. Moreover, variance in the time the first forager returned was better captured by a model including woody plant species richness and landmarks than by the model which included only landscape as explanatory variable, further stressing the importance of resource availability (i.e. plant species richness) in determining homing speed of nectar foragers. In contrast, variance in all other response variables was best described by landscape.

To conclude, our study demonstrates that homing success in bees can be strongly affected by the surrounding foraging landscape. However, landscape structural/visual alteration (by disturbance) does not seem to provide more or less visual information used for navigation than undisturbed natural habitats, as bees returned equally fast and successfully in natural forests and human altered urban garden areas. This finding indicates that return speed is primarily driven by resource availability in a landscape and suggests that elongated ground features are not necessary (as visual landmarks conspicuous to the human eye) for orientation, at least not for stingless bees. In fact, we found only few, if any, such landmarks in forests, suggesting that stingless bees visually assess landscape differently from humans, or use complex combinations of visual objects or olfactory landmarks in more natural, seemingly homogeneous habitats. Future studies should thus quantify respective differences between landscapes as seen from the (stingless) bees' perspective.

3.6. Acknowledgments

3.7. References

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IV. GENERALIST SOCIAL BEES MAXIMIZE DIVERSITY INTAKE IN PLANT SPECIES RICH AND RESOURCE ABUNDANT ENVIRONMENTS

4.1. Abstract

Numerous studies revealed a positive relationship between biodiversity and ecosystem functioning, suggesting that biodiverse environments may not only enhance ecosystem processes, but also benefit individual ecosystem members by e.g. providing a higher diversity of resources. Whether and how the number of available resources affects resource collection and subsequently consumers (e.g. through impacting functions associated with resources) has however been little investigated, although a better understanding of this relationship may help explain why the abundance and richness of species typically declines with decreasing plant (resource) diversity.

Using a social bee species as model, we investigated how plant species richness - recorded for study sites located in different habitats - and associated resource abundance affected the diversity and functional role (here defined as nutritional quality and antimicrobial activity) of resources (i.e. pollen, nectar and resin) collected by a generalist herbivorous consumer. The diversity of both pollen and resin collected strongly increased with increasing plant/tree species richness, while resource abundance was only positively correlated with resin diversity. These findings suggest that bees maximize resource diversity intake in (resource) diverse habitats. Collecting more diverse resources did however not increase resource functionality, which appeared to be primarily driven by the surrounding (plant) source community in our study. In generalist herbivores, maximizing resource diversity intake may therefore primarily secure collection of sufficient amounts of resources across the entire foraging season, but it also ensures that the allocated resources meet all functional needs. Decreasing available resource diversity may thus impact consumers primarily by reduced resource abundance, but also by reduced resource functionality particularly when resources of high functional quality (e.g. specific forest tree species) become scarce.

4.2. Introduction

Biodiversity is a critical driver of ecosystem functioning, as it maintains the stability of ecosystem processes and provides insurance against changing environmental conditions (Loreau et al. 2001). Diverse ecosystems typically contain more producers and consumers than less diverse ecosystems (Gamfeldt et al. 2005; Hines and Hendrix 2005), resulting in more interactions within or across trophic levels which can further stabilize ecosystem services (Ives et al. 2005; Balvanera et al. 2006). The same ecosystem process can be supported by multiple species or functional groups in diverse ecosystems which are functionally redundant, thus increasing resilience of the whole system (Blüthgen and Klein 2011). This increased resilience in ecosystem functioning due to biodiversity has frequently been demonstrated (Brittain et al. 2013; Garibaldi et al. 2013). However, whether single organisms in ecosystems also benefit from increasing biodiversity has received little attention.

Biodiverse systems provide a variety of resources to be exploited by consumers (Duffy et al. 2007). Higher resource diversity can in theory either benefit consumers by providing a constant supply of various resources to choose from and to compose ideal (e.g. nutritionally well balanced) resource mixtures, or negatively affect consumers by diluting preferred resources (as shown for several specialist insect herbivores: Yamamura 2002; Otway et al. 2005). Yet we still do not fully understand whether and, if so, how increased resource diversity affects resource collection in generalist consumers. They could, in theory, respond to increased available resource diversity in two ways: (a) by maximizing collected resource diversity (henceforth referred to as 'diversity maximization') or (b) by targeting a specific number of collected resources sufficient to cover all functional needs, leading to a saturation in collected resource diversity (henceforth referred to as 'diversity restriction'). While 'diversity restriction' will always require the time-consuming active selection of preferred resources in a resource diverse environment, 'diversity maximization' may be either passive (through foraging on any resource encountered next in diverse habitats) or active (through seeking for a maximum of different resources). Active maximization should consequently result in a constantly more even distribution of different resources, while passive maximization should lead to a more uneven resource distribution (as some plant sources are typically more abundant in environments than others).

Increasing resource diversity positively correlates with higher health and performance of (herbivorous) consumers (Alaux et al. 2010; Di Pasquale et al. 2013; Drescher et al. 2014), e.g. through improving nutritional balance or toxin dilution (in

mammals: Freeland and Janzen 1974; Glander 1982; and insect herbivores: Bernays et al. 1994; Singer et al. 2002; Simpson and Raubenheimer 2012; Irwin et al. 2014). These positive effects of resource diversity may render diversity maximization a reasonable strategy, although it may increase resource handling and search time and thus impair maximization of short-term energy gain as predicted by optimal foraging theory (Pyke et al. 1977).

To explore how resource diversity affects resource foraging in a generalist herbivore, we monitored resource diversity intake and its effect on resource functionality (here comprising nutritional quality and antimicrobial activity) in relation to plant richness (and thus resource diversity) using a generalist social stingless bee species (i.e. the tropical stingless bee *Tetragonula carbonaria* Smith) as a model consumer.

The diversity of plant resources is usually closely linked to habitat quality and composition and thus foraging landscapes (Williams and Kremen 2007). Natural or semi-natural habitats are typically richest in plant species and thus resources collected by bees, while landscapes altered by humans for agriculture or intense urbanization have reduced plant diversity and thus provide only limited resources (McIntyre and Hostetler 2001; McKinney 2008; Decourtye et al. 2010; Williams et al. 2012). Thus, the type of habitat investigated strongly determines the availability and composition of plant resources, which in turn directly influence the foraging patterns of consumers, e.g. bees (Roulston and Goodell 2011).

Herbivore foraging patterns are regulated by both plant resource diversity and (seasonal) plant resource abundance (here defined the overall amount of resources currently available to a forager; in bees: Williams et al. 2012; Jha and Kremen 2013; Jha et al. 2013), but resource diversity and abundance have hitherto rarely been considered separately, as they are mostly strongly correlated.

In our study, we attempted to investigate how the resource intake of a generalist consumer responds to changes in plant resource diversity and abundance, and whether and how resource diversity and abundance affect the functionality of the allocated resources. To address this question, we placed colonies of *T. carbonaria* in different habitats with varying plant species richness and thus varying resource diversity and abundance (Kaluza et al. 2016). We chose different habitats (here: landscapes differing in land-use intensity and anthropogenic influence) ranging from undisturbed natural habitats to anthropogenically altered habitats (agricultural plantation and urban gardens), and monitored foraging patterns and the diversity and functionality of resources (here defined as nutritional quality of pollen and nectar and antimicrobial

activity of resin) collected by colonies over two consecutive years.

Social bees typically collect a variety of plant resources, i.e. pollen, nectar and resin. Pollen is primarily fed to larvae as protein source, while nectar is consumed as an energy source by both larvae and adults (Nicolson 2011). Resin is collected mainly from tree wounds and used as nest material and to protect colonies against predators and microbes by many social species (Roubik 1989; Leonhardt and Blüthgen 2009; Simone-Finstrom and Spivak 2010; Drescher et al. 2014). Bees are known to benefit from both a more diverse pollen diet and a higher diversity of resin. For example, a polyfloral diet increases larvae weight of bumble bees, improves immuno-competence in honey bees and prolongs honey bees lives when parasitized (Tasei and Aupinel 2008; Alaux et al. 2010; Höcherl et al. 2012; Di Pasquale et al. 2013), while increased resin diversity provides better protection against multiple stressors (Drescher et al. 2014).

Pollen nutritional quality is typically measured as protein content (Génissel et al. 2002; Tasei and Aupinel 2008), which can positively correlate with contents of other nutrients (e.g. antioxidants: Di Pasquale et al. 2013; e.g. sterols: Vanderplanck et al. 2014). Protein content in pollen largely depends on the plant species' reproductive traits rather than the plant's need to attract pollinators (Roulston et al. 2000), but bees seem to forage preferentially on pollen with high protein content (Rasheed and Harder 1997; Robertson et al. 1999; Leonhardt and Blüthgen 2012) and high amino acid content (Cook et al. 2003; Somme et al. 2015). Moreover, higher protein content in larval food is known to increase body size and weight in bees (Roulston and Cane 2002; Quezada-Euan et al. 2011), and therefore represents a valid (albeit not the only) measure for assessing pollen nutritional quality.

Regarding nectar nutritional quality, bees are known to target a species-specific optimal nectar concentration, as foraging strategies and handling efficiencies differ (Roubik et al. 1995; Kim and Smith 2000), but can make use of a wide range of nectar concentrations (Biesmeijer et al. 1999; Tatsuno and Osawa 2016). However, Somme et al. (2015) used sugar composition and concentration to evaluate nectar quality, which we consider a valid quality measure, as more highly concentrated nectar represents more energy and would therefore allow bees to maximize energy intake.

Social bees typically collect plant resins from a wide variety of tree species (Roubik 1989; Leonhardt and Blüthgen 2009; Simone et al. 2009), but prefer some tree species over others (Leonhardt and Blüthgen 2009; Wallace and Lee 2010; Wilson et al. 2013; Drescher et al. 2014). Resin from preferred species efficiently repelled predators and microbes (Wallace and Lee 2010; Drescher et al. 2014; Massaro et al. 2014). As its

antimicrobial properties are considered the most important function of resin in bee nests (Simone-Finstrom and Spivak 2010), we here use the antimicrobial effect of resin collected by bees as a measure for resin functionality.

In our experimental field study, we consequently related plant richness as well as the diversity of pollen and nectar collected by colonies (at sites with varying plant richness and abundance) to resource functionality by determining the overall protein content of pollen loads, overall sugar content of nectar loads and the antimicrobial activity of resin stored within nests. We further compared whether resource foraging patterns were better explained by plant source richness and/or abundance or by landscape *per se*.

We generally assumed (a) plant richness to be highest in undisturbed habitats (i.e. subtropical forests), intermediate in urban areas and low in intensively managed agricultural areas (i.e. plantations). Given the benefits of resource diversity previously observed and the expected costs of active 'diversity restriction' (see above), we expected stingless bees to follow a (passive) resource 'diversity maximization' strategy. Thus we assumed that (b) pollen resource diversity collected by bees would increase with the overall surrounding plant richness in the landscape, while the resin diversity collected by bees was expected to increase with tree diversity as the main source of resin (Roubik 1989). On landscape level, resource diversity foraged by bees was predicted to be highest in forests, intermediate in gardens and lowest in plantations. Moreover, as plantations are usually dominated by few plant species, resource evenness was predicted to be lowest in plantations and highest in forests. As bee foraging patterns in these landscapes were found to be significantly affected by seasonal flowering events which differed between landscapes (Kaluza et al. 2016), we always considered resource intake in relation to season.

We further proposed that (c) increasing resource diversity in a landscape positively affected the functionality of resources (i.e. pollen, nectar and resin) collected, as higher resource diversity increases the number of different sources to select from. In other words, the chance of finding highly functional resources should be higher in diverse landscapes. In contrast, landscapes with low resource diversity are expected to provide limited choices and the chances of encountering any or larger numbers of highly functional sources are reduced. We therefore expected the protein content of pollen and sugar content of nectar collected to increase with increasing plant richness and pollen diversity. We further expected higher sugar intake in landscapes with higher plant diversity, and we predicted the antimicrobial efficiency of resin to increase with increasing tree richness and thus resin diversity collected.

4.3. Methods

4.3.1. *Experimental setup*

We investigated how plant resource richness and abundance affect the diversity and quality of resources collected by bees in different landscapes using the common Australian stingless bee *Tetragonula carbonaria* (Apidae, Meliponini). *Tetragonula carbonaria* is native to the study region in South East Queensland, Australia (24°38'-27°29' S, 152°6'-153°6' E), but is also commonly kept in hive boxes and used for managed crop pollination (Heard 2016). We established hives of *T. carbonaria* in three landscape types with varying resource diversity: forests, plantations and urban gardens (Kaluza et al. 2016). Forests were dominated by an overstory of *Eucalyptus* and *Corymbia* species and represented the natural habitats of *T. carbonaria* (Dollin et al. 1997). Plantations were commercial macadamia monocultures (*Macadamia integrifolia* Maiden and Betche × *M. tetraphylla* Johnson) and thus represented anthropogenically disturbed, agricultural landscapes. Australian urban gardens (i.e. in low density residential areas), another anthropogenically disturbed landscape, typically provide a mix of native and exotic ornamental garden plants (Head et al. 2004).

Four replicates were selected per landscape type (plantation, forest and garden) and each was divided into two sites with a minimum distance of 55 m in between, creating a nested design of 24 paired sites. In gardens, distances between paired sites were greater (706 ± 129 m) due to limited suitable sites. At each study site, we placed two bee hives with *T. carbonaria*, resulting in a total of 48 original bee hives in 2011 (Kaluza et al. 2016).

4.3.2. *Plant richness and resource abundance in landscapes*

We conducted botanical surveys at each study site to assess plant richness in the landscapes and to categorize each site according to the available resource diversity and abundance (Appendix II: plant species list). Plants were recorded along four 500 m transects, starting at the bee hives and extending south, east, north and west. All plant species within a 5 m wide corridor along these transects were identified and their abundance estimated according to the following categories: (a) rare: 1-5 individuals per plant species; (b) uncommon: 6-16 individuals and (c) common: >16 individuals. For each plant species, typical life form and size were determined according to the literature and each species was categorized as herb, shrub or tree (SM IV.1). We excluded grasses and ferns from the data analysis as these were unlikely to provide resources for bees. In

plantations and forests, paired study sites were in close proximity and had identical plant assemblages. We thus used the same survey data for plant richness and abundance for both respective paired sites, but performed separate transect walks for all (paired) garden sites.

We then estimated plant resource abundance available to bees using a maximum likelihood search to determine the most appropriate numerical values to replace our abundance categories (rare, uncommon and common) and life form categories (herb, shrub and tree) as described below. We used mean foraging activity as a response variable to estimate these values, as foraging activity is strongly related to resource abundance in landscapes (see Kaluza et al. 2016). Values were optimized for a generalized linear model (GLM) consisting of the interacting explanatory variables plant abundance and log of plant richness. In this model, randomly created values were repeatedly tested until a set of values was determined which best explained the model variance for foraging activity (optimized for R^2, see Nakagawa and Schielzeth 2013; R Development Core Team 2013). This optimization process was restricted by fixing herb < shrub < tree, and rare < uncommon < common, which resulted in a factor matrix for rare, uncommon, common × herb, shrub and tree (SM IV.1). In a corresponding frequency matrix for each study site, the relative frequency of each category (e.g. rare herb) was calculated by dividing the number of plant species in this category by the total number of plant species at this study site (SM IV.1). The obtained factor matrix was then multiplied with the frequency matrix for each study site, and the sum of all values in the resulting matrix was used as plant resource abundance value for the respective study site (SM IV.1).

Resin diversity and quality was expected to be influenced by tree richness and abundance. Tree resource abundance was therefore calculated using the same process and the same values obtained from the likelihood optimization, but restricted to tree abundances in the factor and frequency matrix, thereby emphasizing differences between tree resource abundance categories (rare, uncommon and common).

4.3.3. *Resource diversity collected by bees*

Observations of bee foraging and resource intake were conducted from September 2011 to September 2013, for three seasons per year, i.e. the dry season (September-December), wet season (January-April) and cold season (May-August). In each season, selected bee hives were visited on three rain-free days within 31 ± 9 days (see Kaluza et al. 2016). For the wet season 2012, hive observations were conducted for all hives at all

sites. Observations were then restricted to a subsample of 6-8 bee hives located at 3-4 sites for each landscape type in the remaining seasons to enable a reasonable sampling effort and were re-visited in all following seasons.

Observations were performed when hives had sufficient activity, i.e. from 7:30-15:30 in the dry season and 10:00-15:00 in the cold season. During each observation, 20 returning foragers were caught at the hive entrance and their load (nectar, pollen or resin) identified. Individuals were removed for the duration of the experiment to avoid recapturing.

Pollen and resin types were categorized by colour (pollen) or colour, texture and smell (resins). Colour diversity of pollen or resin loads can be used as a proxy for the diversity of plant species visited by bees (resin: Leonhardt et al. 2011; pollen: Leonhardt and Blüthgen 2012; Leonhardt et al. 2014). Moreover, different eucalypt (i.e. Myrtaceae) species typically have pollen that cannot be distinguished with palynological methods because of their parasyncolpate and tricolpate shape and similar size (Thornhill et al. 2012), rendering assessment by colour or costly DNA meta-barcoding a more appropriate approach for comparative analyses. We additionally assessed pollen diversity by (a) palynological analysis via pollen microscopy (see SM IV.2) and (b) pollen DNA meta-barcoding (SM 4, Keller et al. 2015; Sickel et al. 2015) for a subset of our samples (SM IV.3). These additional analyses revealed that the diversity of pollen colours (exponent of Shannon diversity, $e^{H'}$) was positively correlated with the diversity of pollen morphospecies types (as assessed by palynological analysis: $r = 0.81$, $P < 0.001$, SM IV.2), but that assessment by pollen colours generally underestimated actual taxon diversity (i.e. pollen colour diversity was 0.7 times lower than diversity of DNA meta-barcoding, SM IV.3) and therefore provides a valid, but rather conservative diversity estimate. Pollen microscopy was further used to check the purity of pollen loads and confirmed that bees rarely mixed pollen types on single foraging trips (overall 4 % polyfloral samples). Categorization of resin loads was validated by comparing the chemical profiles of samples obtained by gas chromatography mass spectrometry (GCMS) analysis as described in Leonhardt et al. (2011).

Pollen loads of each pollen forager were removed from hind legs, weighed and stored in Eppendorf tubes for subsequent analyses. Likewise, resin loads were removed and stored in hexane for control analyses. The numbers of pollen and resin categories were then pooled per site and day to assess pollen and resin diversity per site. Note that we only used pollen and resin samples which were collected by different hives at the same site on one observation day to estimate diversity, to avoid overestimating resource

diversity due to mismatching pollen and resin types across days.

We focused on pollen and resin diversity for observations, as nectar diversity cannot easily be assessed in the field, because sugar composition or sucrose concentration vary greatly within single plant species depending on flower age or time of day (Nicolson and Van Wyk 1998; Torres and Galetto 1998) and do therefore not allow for assessing nectar diversity based on foraged loads.

4.3.4. *Resource functionality*

PROTEIN CONTENT OF POLLEN. The amino acid content of pollen collected from all pollen foragers at each observation was analysed by ion exchange chromatography (IEC: Biotronik, amino acid analyser LC 3000) as described in Leonhardt and Blüthgen (2012). Pollen was first weighed, then mixed with 200 μL of 6 N HCl, heated for 4 h at 100 °C, cooled down to room temperature and centrifuged (10 min). The supernatant was transferred into a fresh Eppendorf tube and water content reduced at 100 °C. The sample was re-dissolved in 200 μL of purified water and centrifuged again for 10 min. Then, 100 μL of the supernatant was mixed with 20 μL of 12.5 % sulphosalicylic acid, extracted in the refrigerator (30 min), mixed and centrifuged (10 min). Finally, 100 μL of the supernatant was mixed with 100 μL sample rarefaction buffer in a fresh micro centrifuge tube, filtered and centrifuged (5 min), before the sample was transferred into a fresh micro centrifuge tube for further rarefaction with buffer (1:5) and analysis by IEC.

The resulting amino acid concentration (c in μMol/g) was used to calculate the average protein intake (F_P in μg) per foraging trip for (a) all amino acids and (b) only the essential amino acids for each hive observation:

$$F_P = \frac{2 * m_P * \sum_1^n c * M}{N_P}$$

where m_P (in g) is the pollen weight (pooled for all pollen foragers caught) * 2 (as we chemically analysed pollen from only one hind leg), M is the molar mass of the respective amino acid (n) and N_P the number of foragers whose pollen loads were analysed. We considered methionine, arginine, tryptophan, lysine, isoleucine, leucine, phenylalanine, histidine, valine and threonine essential for bees and included proline due to its importance in the flight muscle metabolism in adult bees (de Groot 1953; Micheu et al. 2000).

SUGAR CONTENT OF NECTAR. Nectar foragers were carefully squeezed to provoke regurgitation of the crop content. Nectar quantity was measured in 5 µL microcapillary tubes (Camag, Muttenz, Switzerland) and nectar concentration determined with hand-held refractometers (Eclipse Refractometer, Bellingham + Stanley Ltd., Lawrenceville, USA). To obtain a measure for the quality of overall sugar intake we calculated sucrose loads of individual nectar foragers by converting sugar concentration (c in %) into x (in µg/µL) following Kearns and Inouye (1993); (see Leonhardt et al. 2014; Kaluza et al. 2016) according to the equation:

$$x = -0.0928 + 10.0131 * c + 0.0363 * c^2 + 0.0002 * c^3.$$

ANTIMICROBIAL ACTIVITY OF RESIN. Resin samples were collected in 2012 from resin stores of 2-3 hives for 6 sites in each landscape. Resin stores typically contain soft, reusable resin collected by foragers across all seasons and provide resin in sufficient quantities for microbial assays. Resin samples of all hives on both paired sites were mixed (resulting in 3 samples per landscape type) and microbial assays were repeated 5 times per resin mix to determine the antimicrobial activity of the overall resin diversity available at landscape level (N = 45 per microorganism).

Microbial assays were performed following Drescher et al. (2014). For each mixed resin sample, 0.6 g resin was extracted in 20 mL of 70 % ethanol (3 % w/v) and filtered twice. Microbial growth inhibition was determined using the agar well diffusion technique on a 64-well plate (27.9*27.9*1 cm). Three type-culture strains of microorganisms were tested: *Bacillus cereus* (ATCC 11788, Gram-positive bacterium), *Salmonella* Typhimurium (ATCC 13311, Gram-negative bacterium) and *Candida albicans* (laboratory strain of unicellular fungus). Mueller-Hinton agar (growth media) was liquefied and inoculated with microbial suspension to a final concentration of $3*10^7$ CFU/ml. Agar with bacteria was poured onto plates to solidify before punching in holes as test wells. Wells were filled with 150 µL of resin extracts (effective resin amount: 4.5 mg/well) and plates then incubated at 36.5 °C for 20 h. Antimicrobial activity was quantified as the mean zone of growth inhibition.

For each microorganism, the growth inhibition of each sample was divided by the mean growth inhibition. The standardized results were then pooled across microorganisms as relative growth inhibition.

4.3.5. *Statistical analysis*

Generalized linear mixed effect models (GLMM) were used to analyse the effect of landscape or plant richness and resource abundance, and season (fixed explanatory

variables) on the response variables: pollen and resin diversity and evenness, as well as pollen, nectar and resin quality (i.e. sugar, total protein or essential amino acid loads of foragers and antimicrobial activity of resin).

For each response variable, we generated different models, starting with the most complex model which included all explanatory variables and their interactions. We then simplified models step-wise by excluding interactions and variables and evaluated model quality using Akaike's Information Criterion (AIC). The model with the lowest AIC value was considered the model with the highest explanatory value. To test whether individual explanatory variables explained a significant proportion of the overall variance, we compared the model with a given variable to the same model without this variable using the anova command in the lme4 package which compares two nested models using REML scores (library lme4: Bates et al. 2011). Differences between landscape types were evaluated using Tukey's HSD post hoc test (package multcomp: Hothorn et al. 2008), and effects of plant richness and abundance were assessed using Spearman-rank correlation tests. Note that plant species richness and resource abundance were independent variables ($r = -0.21$, $P = 0.44$).

To test whether landscape or plant resource richness and/or abundance better explained our findings regarding resource diversity intake and evenness, we always constructed two separate models, one including landscape and season, one including plant richness and abundance and season. Models were compared using variance explained (R^2) by the best models (library MuMIn: Bartoń 2013; Nakagawa and Schielzeth 2013) following AIC selection.

For the analysis of pollen and resin diversity or evenness and antimicrobial activity, paired site was included as random effect in all models, to account for the nested study design. Pollen and resin diversity were expressed as the exponent of Shannon diversity ($e^{H'}$) which is considered effective diversity (Jost 2006). When analysing sugar and protein loads, we compared data from several hives located at several study sites for each landscape, thus hive nested within site was entered as a random effect in all models. Variables were log transformed (i.e. pollen and resin diversity, protein and essential amino acid loads) or square root transformed (sugar loads) where necessary to achieve normality and analysed by GLMMs with Gaussian distribution. We additionally tested for a correlation between pollen/resin diversity and pollen/resin quality using Spearman-rank correlation tests. All analyses were performed in R (R Development Core Team 2013).

4.4. Results

4.4.1. *Plant richness and resource abundance in landscapes*

A total of 1128 plant species was recorded for all study sites, ranging from 40 species at the site of lowest and 411 species at the site of highest plant species richness. Plant species richness strongly varied with landscape type and was on average lowest in plantations, intermediate in forests and highest in urban gardens (Table IV.1). Likewise, tree species richness was lowest in plantations and highest in gardens (Table IV.1). Plant and tree resource abundance estimates were highest in forests, but, while plant resource abundance was similar in gardens and plantations, tree resource abundance was lower in plantations and intermediate in gardens (Table IV.1).

4.4.2. *Resource diversity collected by bees*

In total, we assembled a data set with 8297 recorded foraging trips for 414 hive observations. Bees collected a total of 47 different pollen and 88 different resin types on 4332 pollen and 2894 resin foraging trips. Average [± standard deviation] diversity collected per site and day was 2 ± 2 pollen and 4 ± 3 resin types in plantations, 5 ± 2 pollen and 5 ± 3 resin types in forests and 6 ± 3 pollen and 4 ± 3 resin types in gardens.

Diversity of pollen types was better explained by the landscape model than by the corresponding plant richness/abundance model (Table IV.2). Pollen diversity was highest in gardens and lowest in plantations, and showed the same seasonal variations in all landscapes (i.e. landscape did not interact with season, Figure IV.1A; Table IV.2). Pollen diversity significantly increased with surrounding plant richness ($r = 0.44$, $P < 0.001$; Figure IV.1B), while plant resource abundance had no influence ($r = -0.02$, $P = 0.79$; Figure IV.1C). Pollen diversity intake was further high across seasons and did not drop during resource pulses of single extremely abundant plant species (e.g. mass flowering of macadamia, SM IV.4).

Table IV.1. Mean [± standard deviation] plant/tree richness and plant/tree resource abundance for plantation, garden and forest study sites.

Landscape	Plant richness	Tree richness	Plant resource abundance	Tree resource abundance
Plantation	74 ± 42	20 ± 23	0.28 ± 0.06	0.14 ± 0.11
Forest	130 ± 53	48 ± 29	0.35 ± 0.03	0.24 ± 0.07
Garden	328 ± 71	97 ± 31	0.28 ± 0.01	0.17 ± 0.03
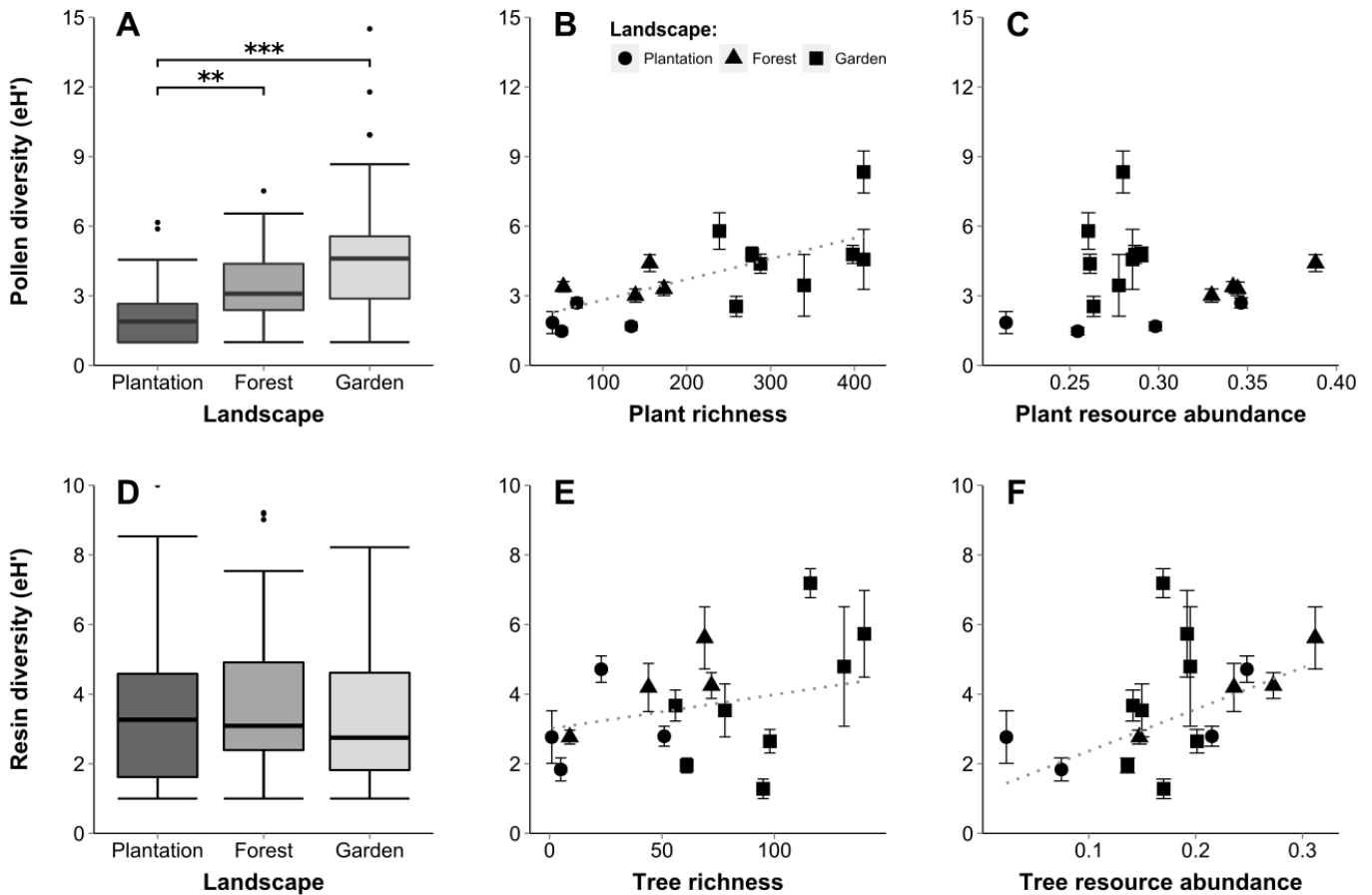
Figure IV.1. Diversity of pollen and resin types collected by bees in three different landscapes (**A**, **D**) and in relation to plant or tree species richness (**B**, **E**) or abundance (**C**, **F**). Bee hives were placed in plantations (dark grey bars/circle), forests (grey/triangle) and gardens (light grey/squares). Pollen and resin diversity are expressed as effective (i.e. the exponent of) Shannon diversity ($e^{H'}$). Asterisks indicate significant differences between landscapes (following Tukey's posthoc test: ** $P < 0.01$, *** $P < 0.001$; **A**). Boxplots display the median (thick bar), lower (0.25) and upper (0.75) quartile (grey box), minimum and maximum values (whiskers) and outliers of each dataset (i.e. dots). Means and standard errors of the effective Shannon diversity ($e^{H'}$) are presented (**B**, **C**, **E**, **F**) and dotted lines indicate significant correlations.

Resin diversity collected by bees was best explained by the interaction of tree richness, tree abundance and season (tree richness/abundance model, Table IV.2). It was similar across landscapes (Figure IV.1D), but significantly increased with tree richness in the surrounding habitat ($r = 0.16$, $P = 0.014$; Figure IV.1E) and even stronger with tree abundance ($r = 0.37$, $P < 0.001$; Figure IV.1F). Moreover, foraged resin diversity showed different seasonal trends for each landscape: while it tended to be highest in gardens and lowest in plantations in the cold season, this pattern was reversed in the dry

Table IV.2. Comparison of models including landscape (*Landscape model*) or plant/tree richness and plant/tree resource abundance (*Richness/abundance model*) as explanatory variables. Variance of fixed effects (marginal R^2: $_mR^2$) and variance of fixed and random effects (i.e. including effects of site; conditional R^2: $_cR^2$) of the most parsimonious models following AIC selection are given. Fixed effects tested in GLMMs: **Lds**: Landscapes; **Ssn**: Season; $_P$**Ric**: plant richness; $_T$**Ric**: tree richness; $_P$**Abd**: plant resource abundance; $_T$**Abd**: tree resource abundance. Asterisks (*****) indicate interaction between fixed effects, pluses (**+**) indicate no interaction and NULL indicates that the NULL-model (i.e. random site effects) explained the observed effects best.

Response variable	Landscape model	$_mR^2$	$_cR^2$	Richness/ abundance model	$_mR^2$	$_cR^2$
Pollen diversity	*Lds + Ssn*	0.40	0.50	$_P$*Ric* $_P$Abd + Ssn*	0.33	0.48
Resin diversity	*Lds * Ssn*	0.17	0.33	$_T$*Ric * $_T$Abd * Ssn*	0.29	0.33
Pollen nutritional quality (protein per foraging trip)	*Lds * Ssn*	0.27	0.43	$_P$*Ric* $_P$Abd * Ssn*	0.30	0.51
Nectar nutritional quality (sugar per foraging trip)	*Lds * Ssn*	0.09	0.17	$_P$*Ric* $_P$Abd * Ssn*	0.10	0.18
Resin antimicrobial activity	*NULL*	-	-	*NULL*	-	-

season.

Pollen evenness was best described with a model only including season, and was thus high in all landscapes (plantations: $J' = 0.79 \pm 0.16$; forests: $J' = 0.78 \pm 0.14$; gardens: $J' = 0.82 \pm 0.13$), but varied with season. Overall evenness was lowest in the dry season (dry season: $J' = 0.74 \pm 0.16$; wet season: $J' = 0.83 \pm 0.11$; cold season: $J' = 0.80 \pm 0.15$; GLMM: $\chi^2 = 13.84$, $df = 2$, $P < 0.001$). Pollen evenness increased with plant richness ($r = 0.15$, $P = 0.036$), but decreased with plant resource abundance ($r = -0.14$, $P = 0.047$).

Resin evenness was best explained by the NULL model (which only considers random site effects). Like pollen evenness, resin evenness was similarly high in all landscapes (plantations: $J' = 0.86 \pm 0.13$; forests: $J' = 0.85 \pm 0.12$; gardens: $J' = 0.86 \pm 0.11$), but did not change across seasons or with increasing tree richness or abundance.

4.4.3. *Resource functionality*

Protein content of pollen loads was best explained by the interaction of plant richness, plant resource abundance and season (plant richness/abundance model, Table IV.2).
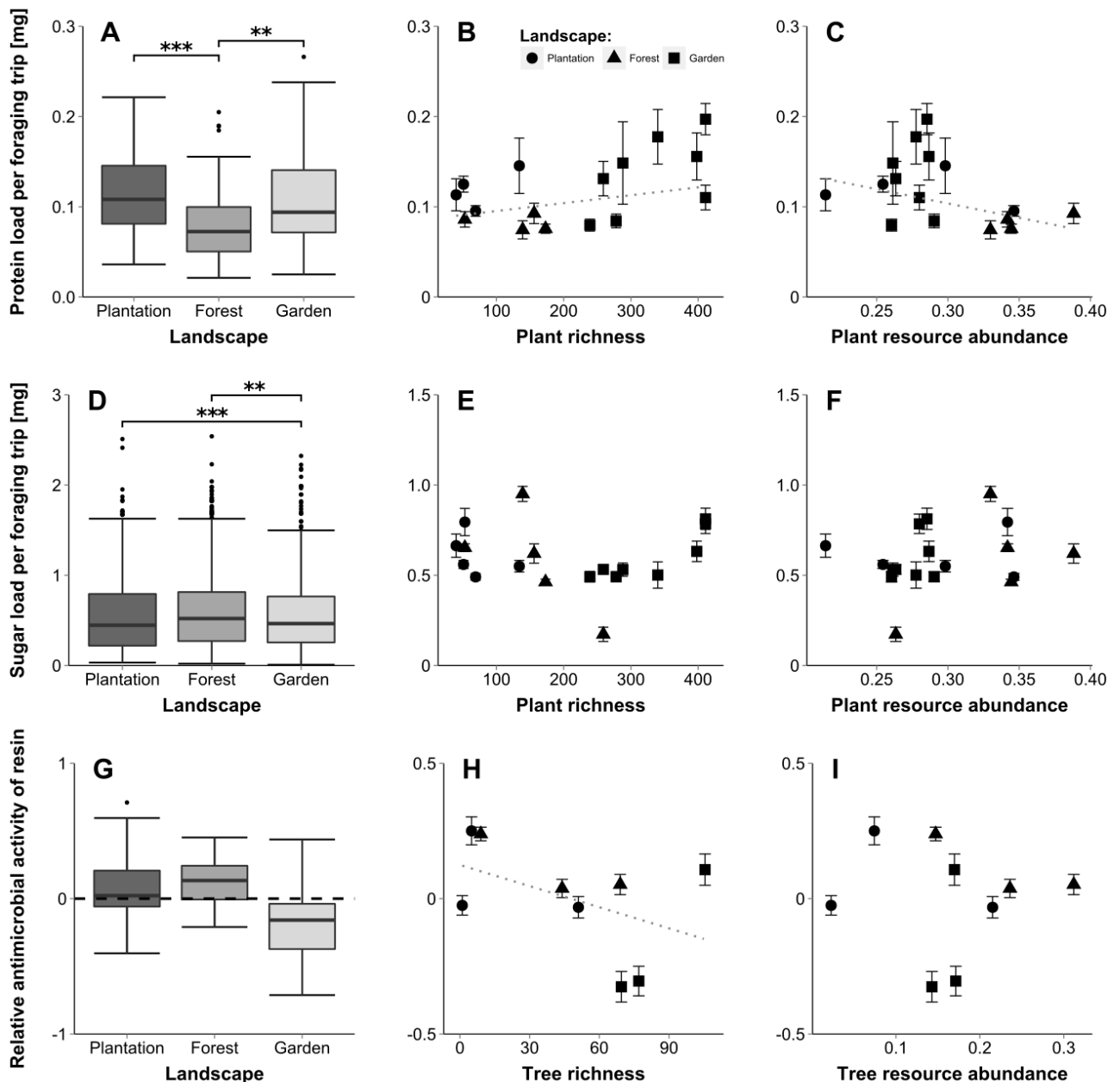
Figure IV.2. Functionality of resources collected by bees in three different landscapes (**A**, **D**) in relation to plant or tree species richness (**B**, **E**) or abundance (**C**, **F**). Pollen nutritional quality was measured as protein load per foraging trip (**A**-**C**), nectar nutritional quality as sucrose load per foraging trip (**D**-**F**) and resin functionality as relative antimicrobial activity of nest resin (**G**-**I**). Bee hives were placed in plantations (dark grey bars/circle), forests (grey/triangle) and gardens (light grey/squares). Pollen and resin diversity are expressed as effective (i.e. the exponent of) Shannon diversity ($e^{H'}$). Asterisks indicate significant differences between landscapes (following Tukey's posthoc test: ** $P < 0.01$, *** $P < 0.001$; **A**, **D**) and include (significant) opposing seasonal patterns between landscapes (**A**, **D**). Boxplots display the median (thick bar), lower (0.25) and upper (0.75) quartile (grey box), minimum and maximum values (whiskers) and outliers of each dataset (i.e. dots **A**, **D**, **G**). Means and standard errors of the effective Shannon diversity ($e^{H'}$) are presented (**B**, **C**, **E**, **F**, **H**, **I**) and dotted lines indicate significant correlations. The dashed horizontal line (**G**) indicates average antimicrobial activity of resin.

Protein content increased with surrounding plant richness ($r = 0.20$, $P = 0.004$, Figure IV.2B), but decreased with higher plant resource abundance ($r = -0.28$, $P < 0.001$, Figure IV.2C).However, protein loads per foraging trip showed no direct relationship with the diversity of pollen collected ($r = -0.05$, $P = 0.50$). Protein loads were overall significantly lower in forests compared to gardens and plantations (Figure IV.2A), but varied across seasons (i.e. protein content in forests tended to be low in the wet and dry season, but high in the cold season).

Likewise, protein loads of essential amino acids per pollen foraging trip were best described in the plant richness/abundance model and increased with surrounding plant richness ($r = 0.18$, $P = 0.007$), decreased with plant resource abundance ($r = -0.27$, $P < 0.001$) and were lowest in forests (plantations: 55.79 ± 22.84 µg; forests: 40.56 ± 20.24 µg; gardens: 55.83 ± 27.54 µg; GLMM: $\chi^2 = 38.08$, $df = 6$, $P < 0.001$).

Sucrose content of nectar per foraging trip was best explained by the interaction of plant richness, plant resource abundance and season (plant richness/abundance model). However, sucrose content was highly variable, and all composed models explained only little variance (Table IV.2). As sucrose intake patterns varied across seasons in different landscapes (i.e. effects of landscape interact with strong seasonal effects), model differences between landscapes (Figure IV.2D) mainly reflected different seasonal patterns. Sugar loads did not correlate with plant richness or plant resource abundance alone (plant richness: $r = 0.002$, $P = 0.92$; plant resource abundance: $r = 0.002$, $P = 0.92$; Figure IV.2E, F).

Relative antimicrobial activity of resin was best explained by the NULL model (which only considered random site effects). It was not correlated with foraged resin diversity ($r = -0.22$, $P = 0.56$) and even decreased with increasing tree richness ($r = -0.35$, $P < 0.001$; Figure IV.2H). Antimicrobial activity did also not significantly differ between landscapes when combining all microbes (Figure IV.2G). However, for *B. cereus* alone, mean growth inhibition was significantly higher in forests than in gardens (SM IV.5).

4.5. Discussion

Generalist consumers living in biodiverse ecosystems may benefit from the surrounding biodiversity through enhanced abundance and diversity of resources. We used a social bee species as model for a generalist herbivorous consumer (which entirely depends on plants for obtaining all resources required for nutrition and nesting)

to experimentally investigate how plant species richness and/or plant resource abundance associated with different landscapes/habitats influenced resource intake and corresponding resource functionality. We found that plant species richness and resource abundance better explained the bees' resource intake than landscape categories (except for pollen diversity). We should therefore be more cautious when solely taking into account the effect of different landscape or habitat categories on bee foraging behaviour and resource intake.

In agreement with our hypothesis, we found that the diversity of resources collected by bees continuously increased with increasing plant/tree species richness, suggesting that bees maximize resource diversity intake where possible. However, increased resource diversity did not result in increased resource functionality, as nutritional quality and antimicrobial activity were only slightly, if at all, affected by plant/tree species richness or resource abundance.

4.5.1. *Plant richness and resource abundance in landscapes*

Plant richness was closely linked to landscape and varied strongly with habitat type, thereby providing an adequate plant species richness gradient for assessing diversity effects. However, contrary to our expectations, our garden sites had an on average 2-3 times higher richness of plant species than natural forest or plantation sites, which has so far not been shown for a (sub)tropical region. Urban gardens typically comprise a diverse mix of native and exotic plants, which create a diverse and continuous supply of floral resources (Australia: Head et al. 2004; Europe: Loram et al. 2008). Generalist bee foragers are known to utilize both native and exotic flowering plants (Tepedino et al. 2008; Stout and Morales 2009; Williams et al. 2011; Threlfall et al. 2015) and in some cases even prefer horticultural plant hybrids over wild-types in gardens (Garbuzov and Ratnieks 2014), which renders urban areas with parks and gardens a very suitable foraging habitat for generalist bees. Our garden sites were further often close to patches of remnant vegetation, providing a mixture of habitats with a variety of native plants and trees. This combination of patches with diverse native and exotic plant species most likely explains why we found the greatest plant species richness and high resource abundance around urban sites in subtropical Australia.

Also in contrast to our expectations, plant richness around our forest sites varied between high richness to unexpectedly low richness. Low plant richness was found primarily in mature forested landscapes (heathland dominated by *Banksia* spp.), with dominant tree species well adapted to local climate and fire cycles (Bird et al. 2008). On

the other hand, forests with high plant richness were comprised of species-rich ecotones, like forest edges or transitions from rainforest to wet sclerophyll vegetation. Such moderately disturbed forests are known to have higher plant species richness and to support higher bee diversity than mature forests (Liow et al. 2001; Winfree et al. 2007).

As expected, we found plant richness to be lowest in macadamia plantations. However, some plantation sites had unexpectedly high plant diversity. Yet many of these plants were ground covering exotic weeds (51-65 %), which were persistently managed with mowing and herbicides and did not actually provide any floral resources for bees.

4.5.2. *Resource diversity and evenness*

As predicted, the diversity of pollen types collected by bees increased with increasing plant richness, but not plant abundance, and was thus highest in gardens, intermediate in forest and lowest in plantations. Average pollen diversity per hive at our forest sites was very similar to nest pollen diversity as reported for other bees in tropical forests (Ramirez Arriaga and Martinez Hernandez 1998; Vossler et al. 2010), yet pollen diversity collected in gardens exceeded the reported maximum diversity by 1.2 to 1.3 (plantations: $H' = 0.77 \pm 0.12$, forests: $H' = 1.04 \pm 0.24$ and gardens: $H' = 1.30 \pm 0.31$).

Generalist social bees, such as honeybees and stingless bees are known to forage pollen from a diverse spectrum of plant species (Ramirez Arriaga and Martinez Hernandez 1998; Odoux et al. 2012; Smith et al. 2012). Our study further showed that pollen diversity collected by *T. carbonaria* continuously increased with increasing plant species richness. Besides pollen, bees also maximized resin diversity intake in tree species rich environments, indicating that *T. carbonaria* generally follows a resource 'diversity maximization' strategy. A similar 'diversity maximization' strategy was found in saki monkeys (Palminteri et al. 2016), but has, to our knowledge, not been described in other animal species. However, many animal species, and in particular herbivores, are known to perform better on diets composed of diverse resources rather than only one resource type, as dietary mixing either improves nutritional balance or dilutes toxins (Glander 1982; Hägele and Rowell-Rahier 1999; Unsicker et al. 2008; Groendahl and Fink 2016; Palminteri et al. 2016).

As generalist (social) bees typically combine pollen from a variety of plant species at the colony level, pollen diversity likewise ensures composing a nutritionally balanced diet and the dilution of toxic plant compounds (Eckhardt et al. 2014; Irwin et al. 2014).

In fact, bees even incur greater foraging distances and higher energetic costs to maintain a polyfloral pollen diet (Williams and Tepedino 2003). Correspondingly, increasing resin diversity increases protection against multiple antagonists (Drescher et al. 2014). Thus maximizing resin diversity intake likely benefits stingless bees by increasing the functional diversity of the composed resin storage.

However, in contrast to pollen diversity, the diversity of resin types collected by our hives increased moderately with tree species richness and strongly with tree abundance. Unlike pollen, which is provided by many flowering plants, resin sources occur randomly, e.g. on wounded trees (Howard 1985; Roubik 1989; Langenheim 2003). Thus only a random subset of trees actually provides resin sources at any given time, which may in part explain the high variability observed between sites. However, increasing tree species richness likely directly increases the number of different potential resin sources. Further, tree abundance, as measured in our study, strongly corresponds to high numbers of common tree species, thus chances are higher that some trees of these species will secrete resin. Resin availability consequently increases with increasing numbers of tree species and common trees, which explains the observed positive correlation between resin diversity collected and tree species richness and abundance. The distribution of and pattern found for resin sources may be more comparable to non-plant resources, such as animal prey, whose encounter frequency and thus consumption rates also increase with overall abundance (likely driven by few specific prey species) and less (if at all) with species diversity (Hillebrand and Cardinale 2004).

While maximizing resource diversity may benefit bees (and other generalist consumers), it remains unclear how they regulate resource diversity intake. Individual consumers (which forage solitarily) can independently decide whether and when to switch sources in order to forage on diverse resources. In contrast, social (bee) foragers typically specialize on a single plant source for prolonged periods and up to their entire forager life-time (i.e. flower constancy: Grant 1950; Slaa et al. 2003). Moreover, both stingless bees and honeybees recruit foragers to rewarding food patches (von Frisch 1967; Nieh 2004), which typically favours abundant over high quality resources as colonies forage disproportionally on one to few specific abundant resources (Requier et al. 2015; Aleixo et al. 2017). However, many studies (including ours) investigating resource intake in generalist social bees found a relatively broad spectrum of resources collected in addition to the most abundant ones (Ramirez Arriaga and Martinez Hernandez 1998; Vossler et al. 2010; Requier et al. 2015; Kämper et al. 2016; Aleixo et al. 2017). Such disproportional foraging on few abundant and several less abundant

resources may be a consequence of increased overall foraging activity (or the proportion of a specific forager group, e.g. pollen foragers or scouts), which increases the chance that additional scouts or foragers discover and forage on new plant sources thereby increasing overall resource diversity intake. In fact, *T. carbonaria* responds to increased overall resource abundance in the habitat by increasing foraging activity (Kaluza et al. 2016), which supports the idea that 'diversity maximization' is regulated via increasing foraging activity at the colony level. Moreover, collected pollen diversity positively correlated with foraging activity, particularly in the plant species rich gardens (SM IV.6). Gardens offer a resource landscape with extremely high plant species richness but often comparatively small resource patches (i.e. more herbs, Appendix II: plant species list). Consequently, higher foraging activity likely results in passive resource maximization in diverse habitats, such as gardens, where any outgoing forager is likely to encounter a new patch or plant species. In contrast, higher foraging activity may not necessarily increase collected resource diversity in diverse habitats with larger resource patches (e.g. forests with mass-flowering trees), where most outgoing foragers are recruited to or encounter the same resource patch or plant species.

Evenness of foraged pollen and resin resources was high across habitats and seasons, indicating that bees always composed a diverse pollen diet or resin bouquet per day and did not show strong preferences for specific sources at particular days. Even in plantations during the short flowering periods of the dominant *Macadamia* trees, collected pollen diversity remained relatively stable (SM IV.4), suggesting that bees actively maximize daily resource diversity intake in habitats with low plant species richness, as a purely passive mechanism should have reduced pollen diversity due to the disproportional collection of abundant *Macadamia* pollen. This finding indicates that active or passive resource diversity maximization depends on habitat complexity and plant species richness or available resource diversity. However, future studies need to elucidate the precise mechanisms underlying resource diversity maximization, resource diversity and habitat complexity in *T. carbonaria* and other generalist consumers.

4.5.3. *Resource functionality*

Contrary to our predictions, neither resin antimicrobial activity nor pollen nutritional quality (i.e. the amount of protein collected per foraging trip) positively correlated with the diversity of collected resin or pollen types, respectively. Thus, increased diversity intake does not necessarily correlate with increased resource functionality, but rather results in average functionality for single quality measures. This finding is in

accordance with Alaux et al. (2010) and Di Pasquale et al. (2013) who showed that, while specific nutritional quality measures peak in single pollen types, pollen mixtures have average nutritional quality across nutrients.

In fact, in our study, pollen protein (and essential amino acid) content was better described by landscape than either plant species richness and/or abundance and was surprisingly low in forests and high in gardens and plantations. The low protein content found in pollen collected in forests cannot be attributed to quality limitations of pollen from plants of the indigenous Australian flora, as Rayner and Langridge (1985) found the protein content of honey bee collected pollen of Australian plants to often be even higher than in exotic plants. Instead, differences in protein loads may (at least partly) be explained by pollen load size, because pollen loads carried by single foragers in gardens had similar average protein concentrations (data not shown), but were larger compared to pollen loads in plantations. In plantations, pollen protein content showed high variability across seasons, but bees collected pollen with very high protein concentration during the macadamia flowering in the dry season, which resulted in overall highest protein content in plantations and indicates that macadamia pollen has comparatively high pollen protein content.

Similarly, resin from specific tree species can largely determine overall antimicrobial activity (Drescher et al. 2014), which may explain why resin antimicrobial activity did not correlate with resin diversity in our study. In fact, antimicrobial activity actually decreased with increasing plant richness (gardens), and variation in resin quality was best explained by site, indicating that it was mostly affected by the specific tree species composition at each site. Moreover, antimicrobial activity against *B. cereus* was highest in forests, further suggesting that antimicrobial properties were primarily driven by the presence of particular tree species, most likely typical and abundant forest trees (e.g. specific eucalypts). These findings suggest that few specific sources of high functional quality (e.g. a plant species with protein-rich pollen or highly antimicrobially active resin) may partly compensate low resource diversity, particularly when they are found in large quantities and occur at different times of the foraging season. As they are of high functionality (e.g. provide a protein-rich diet) they likely suffice to periodically cover a specific functional requirement.

In contrast to pollen and resin, nectar nutritional quality, i.e. sucrose intake per foraging trip, was high across landscapes, showing that resource availability and diversity did not determine nectar nutritional quality, but that bees had ample nectar foraging opportunities everywhere. *Tetragonula carbonaria* preferentially collects highly concentrated nectar ranging from 60-75 % sucrose content (Kaluza et al. 2016),

which was available from a number of plant species across landscapes. Many Australian plants are bird pollinated and produce an abundance of nectar (Ford et al. 1979) and thus offer plentiful carbohydrate resources, which in turn favour opportunistic social insects (Morton et al. 2011), as also shown here. Given the uniqueness of the Australian flora, results for interactions between plant diversity and nectar sugar content may be different at other continents.

Overall, our findings suggest that the diversity - resource functionality relationship depends more on plant (resource) community composition than plant species richness or diversity *per se*. However, studies investigating the relationship between resource diversity, composition and functionality are still extremely scarce, rendering broader inferences rather speculative. This relationship may however parallel the relationship between biodiversity and the functioning of specific ecosystem processes: specific ecosystem functions also appear to be determined by the identity and dominance of specific trait groups, and are thus influenced by community composition more strongly than by the number or abundance of species *per se* (Gagic et al. 2015).

Moreover, while we examined three functional variables in this study, we ignored other measures of resource functionality, e.g. overall nutritional composition (pollen and nectar), the presence of secondary compounds in floral resources or a repellence effect of resin against predators. Similar to the positive relationship between biodiversity and overall ecosystem functionality (Hooper et al. 2005; Tilman et al. 2014), the overall spectrum of functional resource effects most likely increases with increasing resource diversity, while specific resource functions may be fully provided by one or a few specific resources (Drescher et al. 2014). Bees and other consumers may consequently need to target a diverse and even resource intake to maintain a variety of functions associated with all resources. However, further comparative studies on resource intake in relation to biodiversity by different consumer species of ideally various trophic levels (i.e. other bee species and beyond) are needed in order to reveal whether the strategy of maximizing resource diversity is unique to Australian stingless bees or also applies to other generalist herbivores.

In this study, we were further able to separate the effects of plant species richness and plant resource abundance in landscapes on a single consumer, which has not been achieved before. Joined analyses of richness and abundance promise to be a sophisticated tool to identify driving factors in ecosystems, as demonstrated by Winfree et al. (2015) for bee species richness and abundance effects on ecosystem function. However, plant richness and resource abundance in our study were based on a rapid assessment approach, which limits more thorough conclusions. More detailed plant

data, e.g. on plant coverage (Hines and Hendrix 2005) or seasonal availability (Williams et al. 2012) would clearly improve deductions. A more comprehensive assessment of functions and resource effects would further be needed to entirely capture the quality and functionality of resources in relation to resource diversity.

4.5.4. *Conclusion*

Using bees as a model consumer, we found that this floral generalist attempts, where possible, to maximize the number of sources to collect from (resource 'diversity maximization' strategy). This resource use strategy has also been observed in primates (Palminteri et al. 2016) and agrees with the positive effects of resource mixing observed in herbivores (see above). It suggests that, at least for generalist consumers foraging on plants, resources need to fulfil a multitude of functions which may best be met by a multitude of resources (e.g. nutritional balance, toxin dilution), while specific functions (e.g. high pollen protein content, strong antimicrobial activity of resin) may be provided by one or a few resources. Depending on the surrounding plant (or prey) community, the functionality of resources may (e.g. pollen protein content, resin antimicrobial activity) or may not (e.g. nectar sugar content) be driven by the occurrence of specific plant sources. Single resources can thus cover specific functional needs even in impoverished landscapes (e.g. agricultural macadamia plantations). However, higher resource diversity safeguards a variety of functions by bolstering multiple aspects of resource functionality and providing insurance in spatiotemporally dynamic resource landscapes (Williams et al. 2012), which may ultimately determine a consumer's fitness and thus vulnerability.

While time and handling constraints may limit the number of different resources collected by solitary organisms or consumers of higher trophic levels (e.g. predators), resource diversity maximization may be facilitated by the social structure of insect colonies. Here, each forager can be highly specialized on and thus efficiently exploit one or a few resources, while the colony as a whole can increase overall resource diversity intake simply through increasing foraging activity. This unique way of partitioning resource collection renders social insects a very interesting study organism for further investigating the relationship between resource intake strategies and resource functionality in relation to available resource diversity.

4.6. Acknowledgements

4.7. References

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4.8. Supplementary material

SM IV.1. Calculation of plant resource abundance

To obtain a suitable measure for plant resource abundance (*A*) per study site, each plant species recorded during plant surveys was first categorized according to their abundance and life form/size (see main text). Plant categories were then replaced by values obtained through an optimization process. To assess plant resource abundance (*A*) for each site, values obtained through optimization were used to weigh relative frequencies of each category by including them in a factor matrix which was then multiplied with a frequency matrix.

Table IV.3. Factor matrix showing the optimized abundance estimates (*r*, *u*, *c*) and plant form estimates (*H*, *S*, *T*). The product of each combination is used as weighing factor for each category on respective study sites.

	Rare (*r*) = 0.5588	Uncommon (*u*) = 0.5594	Common (*c*) = 0.9017
Herb (*H*) = 0.3048	$rH = 0.14$	$uH = 0.14$	$cH = 0.24$
Shrub (*S*) = 0.4210	$rS = 0.20$	$uS = 0.20$	$cS = 0.34$
Tree (*T*) = 0.8405	$rT = 0.44$	$uT = 0.44$	$cT = 0.75$

The factor matrix (*fM*) is the product of values for rare (*r*), uncommon (*u*) and common (*c*) plants as well as for plants of different sizes, i.e. herb (*H*), shrub (*S*) and tree (*T;* Table 3). The plant species frequency matrix (*pM*) contains the number of plant species recorded for each category for a study site (*i*), each divided by the total number of all plant species (*ΣP*) recorded for the same site (Table IV.3).

The plant resource abundance (*A*) was then calculated by multiplying the factor matrix (Table 3) with the plant species frequency matrix (Table IV.4), resulting in a combined matrix for each study site (*i*). Resulting weighed values for all individual categories (e.g. rare herb on study site *i*) were summed up to obtain one plant resource abundance value for each study site, using the following equation:

$$A_i = \sum_i (fM \times pM_i)$$

Table IV.4. Frequency matrix to calculate the relative abundance (*r*) of all plants (*ΣP*) for each combination of plant abundance (*r*, *u*, *c*) and plant form (*H*, *S*, *T*) per study site (*i*).

	Rare (*r*)	Uncommon (*u*)	Common (*c*)
Herb (*H*)	$rHi/\sum Pi$	$uHi/\sum Pi$	$cHi/\sum Pi$
Shrub (*S*)	$rSi/\sum Pi$	$uSi/\sum Pi$	$cSi/\sum Pi$
Tree (*T*)	$rTi/\sum Pi$	$uTi/\sum Pi$	$cTi/\sum Pi$

SM IV.2. Palynological analysis of pollen by microscopy

Multiple studies of bee pollen foraging behaviour used palynological analyses to compare pollen types (Eltz et al. 2001; Vossler et al. 2010; Braga et al. 2012). This method is however problematic for our study region (Australia), because pollen cannot be as easily attributed to specific plant species as in temperate regions. There are at least 2800 native plant species in South East Queensland in addition to planted exotics from the tropics and subtropics from around the world. Pollen morphospecies can thus not easily be distinguished below family level in most cases, and a comprehensive pollen catalogue does not exist for this area. Moreover, the predominant plant family in forests, Myrtaceae, contains more than 5500 species. There are over 150 species of native Myrtaceae within our study area, which provide large quantities of pollen that is typically parasyncolpate and tricolpate and cannot be distinguished with light microscopy or scanning light microscopy (Thornhill et al. 2012). It is therefore not possible to palynologically match taxonomic groups of Myrtaceae (e.g. subfamily, tribes or genera) with distinct pollen morphological groups (Johnson and Briggs 1984). However these species often have different pollen colours which can be used to quickly categorize pollen types in the field (Leonhardt and Blüthgen 2012).

To evaluate whether both methods, i.e. identification by colour and pollen morphospecies, produce comparable results, we performed a palynological analysis of a subsample of corbicula pollen and compared diversity estimates obtained by morphospecies and pollen colour.

Methods

Corbicular pollen loads were collected from individual pollen foragers and each pollen load was deposited in a separate Eppendorf tube in the dry season in 2011. We identified pollen morphospecies of a total of 261 pollen loads collected from different study sites (147 per forests, 53 per plantations and 69 per gardens). The pollen colour of all samples was assessed, summing up to 19 different pollen colours and 63 pollen morphospecies.

Identification of pollen morphospecies

Permanent microscope slides were prepared to compare and, where possible, identify pollen morphospecies following a standard protocol of Beug (2004), including acetolysis and glycerine jelly mounting. Permanent pollen microscope slides were examined using a Leica DM 750 stereo microscope equipped with a Leica ICC 50 HD camera (Leica AG, Wetzlar, Germany) and compared with the software Leica Application Suite LAS EZ 2.0.0. First, we determined whether pollen samples were monofloral or polyfloral. Out of the 261 pollen loads, we identified 12 samples with polyfloral pollen, i.e. pollen collected from more than one plant species during a single foraging trip. Those polyfloral samples were excluded from further comparison of morphospecies types and pollen colours. The pollen morphospecies type in each sample was then characterized by shape (determined by equatorial and polar view), size, aperture and ornamentation of the pollen surface (Hesse et al. 2009) excluding pollen colour. Pollen morphospecies types with the same shape, aperture, surface ornamentation and similar size were considered identical across different pollen load samples / microscope slides.

Pollen morphospecies and color diversity

Numbers of pollen colours and pollen morphospecies were pooled across all hives per site for each observation day to obtain the maximum diversity of pollen types collected at the given site on the particular day. Diversity per site was calculated as the exponent of Shannon diversity ($e^{H'}$) for pollen colour and morphospecies and compared using linear regression.
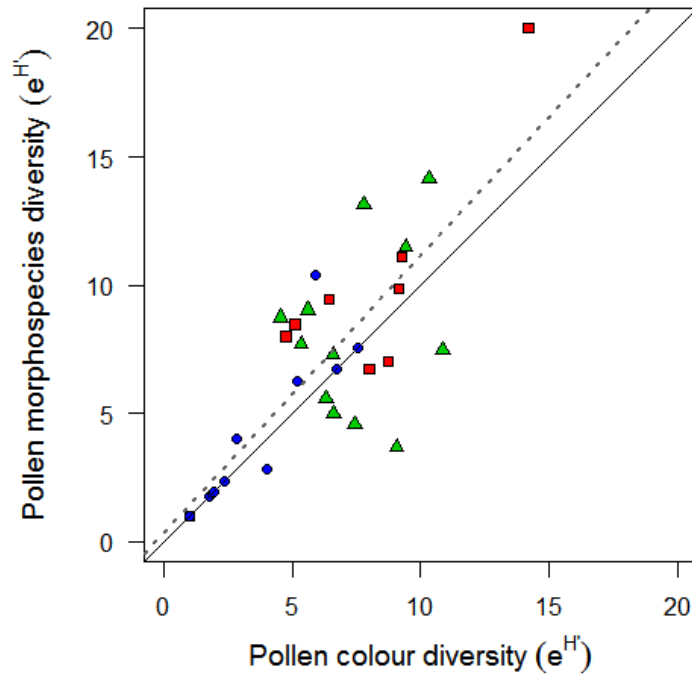
Figure IV.3 Comparison of pollen color and morphospecies diversity (exponent of Shannon diversity, $e^{H'}$) for corbicula pollen from plantations (blue circles), forests (green triangles) and gardens (red boxes), including the regression line (dotted).

Results and Discussion

Diversity of pollen morphospecies types was highly positively correlated with the diversity of pollen colours ($r = 0.81$, adjusted $R^2 = 0.65$, $P < 0.001$, Figure IV.3), rendering the two methods comparable. We found slightly higher pollen diversity for the palynological than colour assessment method. The highest variance between morphospecies and colour diversity was found for forests (Figure IV.3), which may be explained by the fact that Australian eucalypts mostly exhibit the same pollen characteristics and are often indistinguishable under the microscope. At study sites with many native Australian plants, pollen morphospecies may thus underestimate the plant species diversity foraged by bees, further rendering diversity assessment via pollen colour a valid method for rapid field assessment.

SM IV.3. Pollen DNA meta-barcoding

Pollen identification by DNA meta-barcoding has been shown to be more effective in identifying higher taxon richness than palynological methods without requiring expert knowledge (Keller et al. 2015). We therefore additionally validated our rapid colour assessment approach by analysing additional samples by DNA meta-barcoding and comparing colour and genetic diversity.

Methods

We collected 1330 corbicula pollen loads of returning foragers on 3 days for 8 study sites (521 loads in 3 gardens, 353 loads in 3 plantations and 456 loads in 2 forests) in the wet season in 2013. All forager loads of single garden sites and of paired forest and plantation sites were pooled across days, as paired forest and plantation sites had almost identical plant assemblages (according to our surveys), resulting in 8 samples for pollen meta-barcoding.

DNA from pollen grains was isolated as described by (Keller et al. 2015) using the Macherey-Nagel Food Kit (Düren, Germany) strictly according to the vendor's supplementary protocol for pollen preparation. Library preparation was performed according to the method described by (Sickel et al. 2015). As amplifying primers we used the well-established combination of plant barcoding primers ITS-S2F (White et al. 1990; Chen et al. 2010) with an Illumina specific scaffold design (Sickel et al. 2015). Each sample was assigned a different forward/reverse index combination for sample-specific labelling to multiplex samples on the same sequencing chip. For this study, we used 2 forward index sequences (SA507 – SB508) and 12 reverse indices (SA701 – SA712). These were processed together with 360 samples from other projects with other unique indices.

PCR was performed in three separate $10\,\mu L$ reactions in order to avoid PCR bias (Sickel et al. 2015). Each reaction contained $5\,\mu L$ 2x Phusion Master Mix (New England Biolabs, Ipswich, MA, USA), $0.33\,\mu M$ each of the forward and reverse primers, $3.34\,\mu L$ PCR grade water and $1\,\mu L$ DNA template. PCR conditions were as follows: initial denaturation at $95\,°C$ for 4 min, 37 cycles of denaturation at $95\,°C$ for 40 sec, annealing at $49\,°C$ for 40 sec and elongation at $72\,°C$ for 40 sec; followed by a final extension step at $72\,°C$ for 5 min. Triplicate reactions of each sample were combined after PCR and further processed as described in Sickel et al. (2015), including the required normalization, pooling and dilution steps. Quality of the library was controlled using a Bioanalyzer High Sensitivity DNA Chip (Agilent Technologies, Santa Clara, CA, USA) and quantified with the dsDNA High Sensitivity Assay (Life

Technologies GmbH, Darmstadt, Germany). 5 % Phix Control Kit v3 (Illumina Inc., San Diego, CA, USA) was added according to the Sample Preparation Guide (llumina Inc. 2013). Sequencing was performed on the Illumina MiSeq using 2x250 cycles v2 chemistry (Illumina Inc., San Diego, CA, USA).

Data was quality controlled, cleaned, taxonomically classified and prepared according to the scripts available at https://github.com/iimog/meta-barcoding-dual-indexing. Resulting files are directly importable into common statistical software, as e.g. R v.3.1.2 (R Development Core Team 2013) using the package phyloseq v.1.6.1 (McMurdie and Holmes 2013). To assess sufficiency of the sequencing depth, we created species accumulation curves for each sample using the vegan package v2.2-0 (Dixon 2003) in R v.3.1.2 (R Development Core Team 2013), excluding taxa accounting for less than 0.1 % of reads. Due to a more comprehensive taxon data base, identification efficiency is likely to be higher for exotic taxa than for Australian native plant species, though this does not affect the total number of identified taxa. The number of reads in each sample was used as abundance value for each taxon to calculate the exponent Shannon diversity per study site.

According to the colour categorization method, identical pollen colours are considered to be from the same source, but only when collected at the same site on the same day. Samples for DNA meta-barcoding however were pooled per site for all 3 observation days to minimize costs. We thus calculated the exponent Shannon diversity for single days for respective sites and took the mean of the 3 observation days, to compare the pollen colour diversity with the diversity measured by DNA meta-barcoding of respectively pooled samples.

Results and Discussion

Using DNA barcoding, we identified 294 plant taxa in 1330 single corbicula pollen loads, representing 31 colours. Thus, pollen colour diversity was generally lower than diversity estimated on molecular data except for one forest site ($r = 0.21$, $P = 0.60$, Figure IV.4). This demonstrates that pollen colour assessment generally underestimates the actual diversity of plants visited by bees for pollen foraging. In contrast, pollen colour assessment slightly overestimated evenness compared to molecular evenness ($r = 0.67$, $P = 0.06$, Figure IV.4). Pollen colour can thus be considered a conservative estimate of the bees' utilization of pollen diversity.
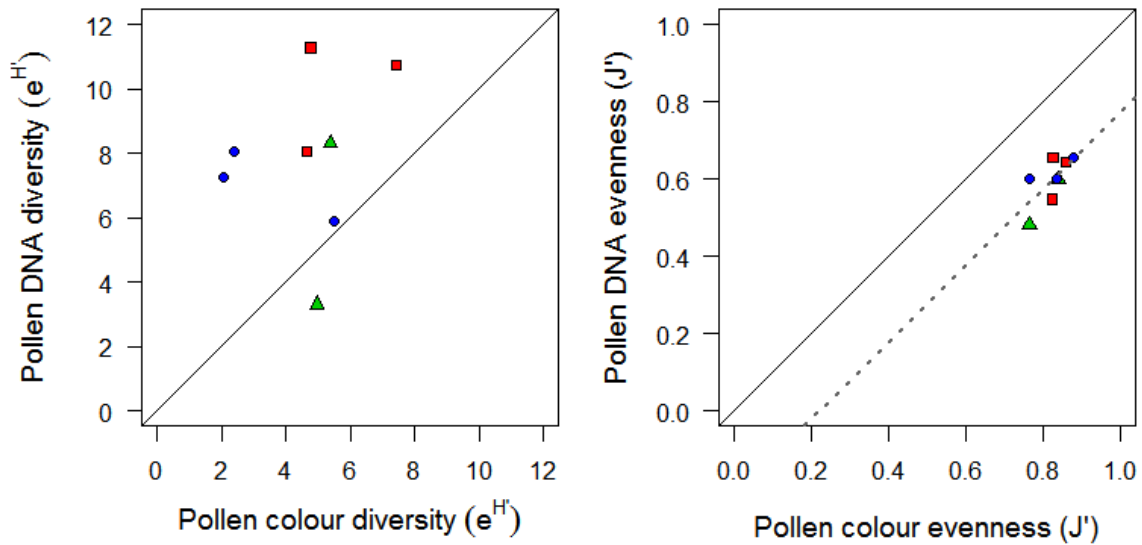
Figure IV.4. Comparison of pollen color and diversity estimated through meta-barcoding (exponent of Shannon diversity, $e^{H'}$) and evenness (Pielou's evenness, J') of corbicula pollen from plantations (blue circles), forests (green triangles) and gardens (red boxes), including the regression line (dotted).

SM IV.4. Variation in pollen diversity across seasons

Social bees are known to favour abundant resources, and colonies tend to forage disproportionally on few specific abundant resources when available (Requier et al. 2015; Aleixo et al. 2017). To investigate whether bees collect diverse resources across seasons and thus periods with mass-flowering resources (e.g. macadamia trees in plantations), bee resource intake was observed in different habitats (macadamia plantations, natural forests and urban gardens) across seasons.

Methods

Observations were conducted from September 2011 to September 2013, for three seasons per year, i.e. the dry season (September-December), wet season (January-April) and cold season (May-August). During observations, pollen loads of each pollen forager were removed from hind legs and pollen types were categorized by colour (see main text and other SM). The numbers of pollen categories were then pooled per site and day to assess pollen diversity. Diversity of pollen colours was then calculated as the exponent of Shannon diversity ($e^{H'}$) which is considered effective diversity and plotted against seasons for each habitat/landscape type.
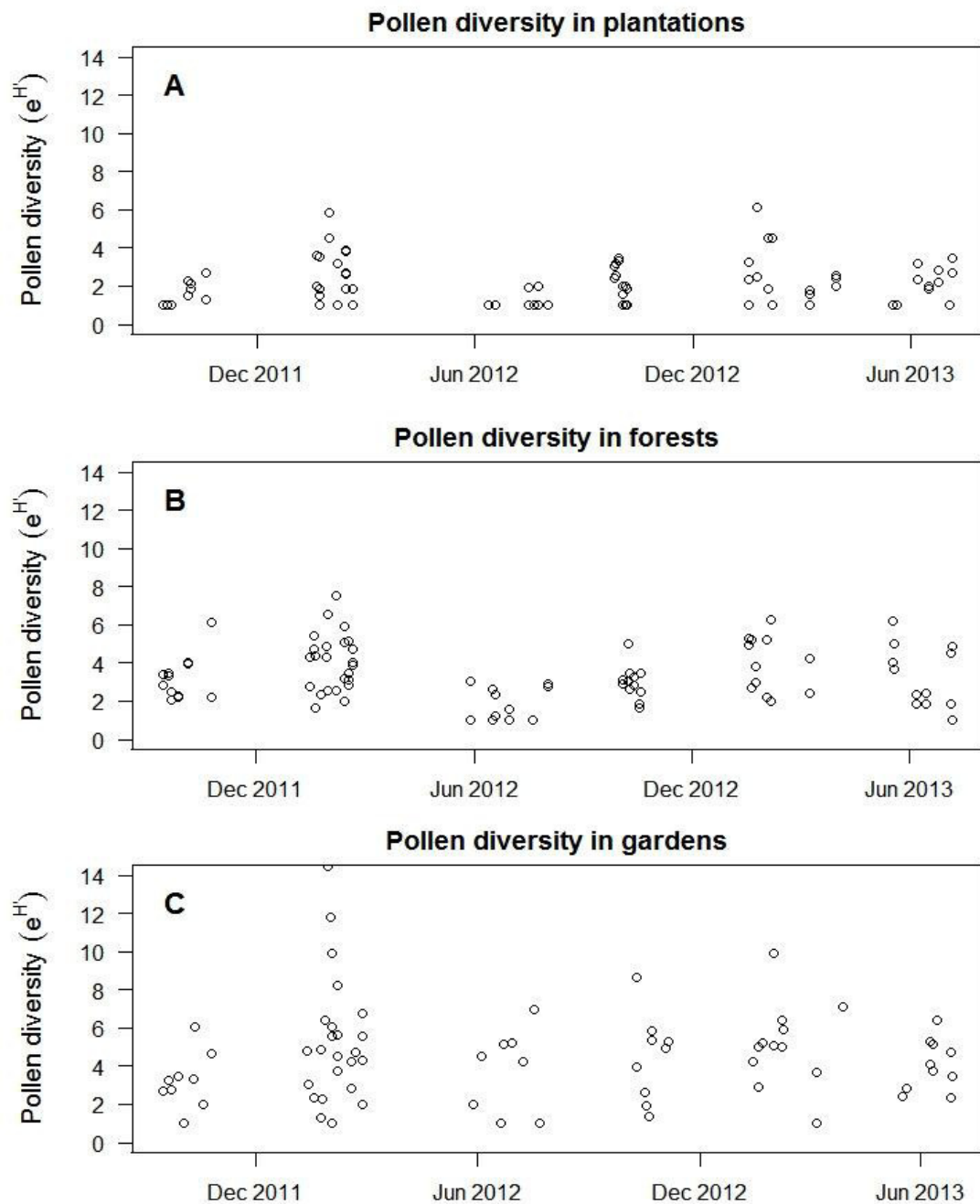
Figure IV.5. Diversity of pollen types (exponent of Shannon diversity, $e^{H'}$) collected by bees over time in three different landscapes, macadamia plantations (**A**), forests (**B**), and urban gardens (**C**). Note low seasonal variations in plantations.

Results and Discussion

In plantations, effective pollen diversity and variations in pollen diversity were similar in the cold and in the dry season (mean ± standard deviation: cold season: 1.61 ± 0.82; dry season: 1.73 ± 0.83; wet season: 2.38 ± 1.43; Figure IV.5). Pollen diversity was higher in forests and highest in gardens and peaked in the wet season in both habitats (forests: cold season: 2.55 ± 1.49; dry season: 3.10 ± 1.01; wet season: 4.03 ± 1.45; gardens: cold season: 3.93 ± 1.72; dry season: 3.85 ± 1.95; wet season: 5.23 ± 2.91; Figure IV.5).

Consequently, in our study, pollen diversity collected by bees in plantations remained relatively stable across seasons, suggesting that bees actively searched and foraged on other pollen sources in addition to the abundantly available macadamia pollen.

SM IV.5. Antimicrobial activity of resin against individual microbes

Antimicrobial effectivity of bee collected resin is considered among the most important functions of resin in bee nests (Simone-Finstrom and Spivak 2010), and was therefore used as a measure for resin quality in our study.

Methods

Resin samples were obtained and mixed from hive resin stores of all bee hives for each paired study site (3 per landscape type: plantation, forest and garden; see also main text). Microbial assays were repeated 5 times for each resin mix to determine the antimicrobial activity against three type-culture strains of microorganisms following Drescher et al. (2014): *Bacillus cereus* (ATCC 11788, Gram-positive bacterium), *Salmonella* Typhimurium (ATCC 13311, Gram-negative bacterium) and *Candida albicans* (laboratory strain of unicellular fungus).
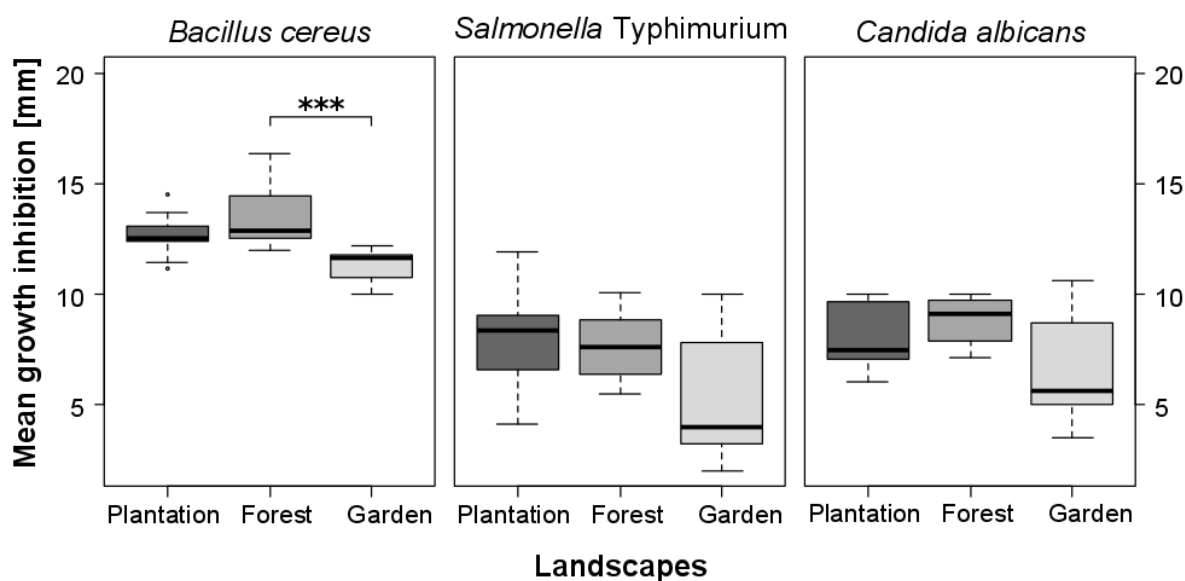
Figure IV.6. Mean growth inhibition of *Bacillus cereus*, *Candida albicans* and *Salmonella* Typhimurium by resin obtained from resin storages of bee hives placed in plantations (dark grey bars), forests (grey) and gardens (light grey). Significance levels (following Tukey-posthoc comparisons): *** $P < 0.001$.

Results and Discussion

Antimicrobial activity of resin (i.e. mean growth inhibition) against *B. cereus* was overall higher compared to other microorganisms and was significantly higher in forests compared to gardens (Figure IV.6). Microbial assays with *C. albicans* and *Salmonella* Typhimurium showed the same trend, with higher growth inhibition of forest resin compared to resin collected in gardens.

Bacillus cereus is known to be generally more susceptible, e.g. to antimicrobial agents in honey of *T. carbonaria,* than *C. albicans* or *Salmonella* Typhimurium (Boorn et al. 2010). However, while differences in antimicrobial activity were most pronounced for *B. cereus*, we did find similar trends across all tested microorganisms, suggesting that specific components with high antimicrobial properties against a variety of microorganisms were particularly available in forests, but lacking in gardens. The presence of those components may explain why antimicrobial activity did not correlate with tree species richness or collected resin diversity. It also suggests that high antimicrobial properties may be driven by the presence of particular tree species rather than overall tree diversity.
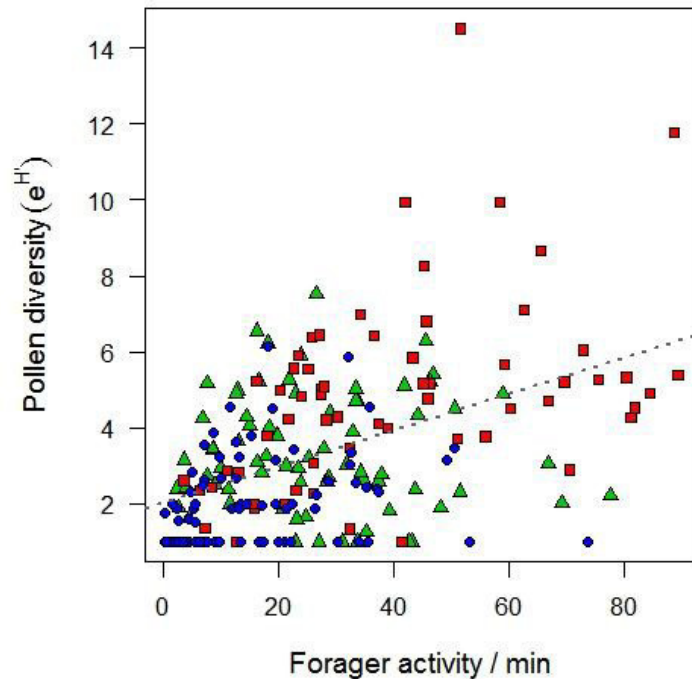
Figure IV.7. Relation of overall bee hive foraging activity and collected diversity (exponent of Shannon diversity, $e^{H'}$) of corbicula pollen in plantations (blue circles), forests (green triangles) and gardens (red boxes), including the regression line (dotted).

SM IV.6. Regulation of resource diversity maximization

Social bees recruit foragers to rewarding food patches (von Frisch 1967; Nieh 2004) and foraging activity positively correlates with overall resource abundance (Kaluza et al. 2016). In turn, higher foraging activity can increase the chance that additional scouts or foragers discover and forage on new plant sources. We thus explored the relationship of foraging activity and resource diversity intake.

Methods

For each hive foraging observation, the overall activity of each hive was recorded by counting the number of returning foragers for 3 minutes (see Kaluza et al. 2016). Twenty returning foragers were captured and pollen loads of pollen foragers removed from hind legs (see main text). Pollen types were categorized by colour and the numbers of pollen categories were pooled per site and day to assess pollen diversity. Diversity of pollen colours (calculated as the exponent of Shannon diversity $e^{H'}$) was then correlated with overall foraging activity using Pearson's correlation.

Results and Discussion

Pollen diversity increased with overall foraging activity of colonies (Pearson's correlation: $r = 0.46$, $P < 0.001$, Figure IV.7), but varied with habitat type: whereas diversity of pollen types increased with foraging activity in plantations and gardens, foraging activity did not correlate with pollen diversity in forests (plantations: $r = 0.25$, $P = 0.03$; gardens: $r = 0.48$, $P < 0.001$; forests: $r = -0.04$, $P = 0.71$). This finding suggests that the relationship between foraging activity and resource diversity depends on the surrounding environment and thus structure of foraging habitat (e.g. the size and distribution of resource patches).

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V. BIODIVERSITY DRIVES SOCIAL BEE FITNESS

5.1. Abstract

Widespread bee declines are likely driven by loss of plant biodiversity, as bee population dynamics directly depend on floral resource diversity and availability. While habitat biodiversity generally has a positive effect on bee fitness, no study has ever investigated how plant resource diversity and abundance as well as resulting changes of resource quantity and nutrient quality affect the fitness of the most important pollinators: the highly social bees.

In order to determine whether and how highly social bees depend on plant biodiversity, we monitored colony growth and fitness of a highly social bee species, *Tetragonula carbonaria* Smith, in relation to plant species richness and resource abundance as well as to patch sizes of various landscape types, ranging from natural habitats (forests) to anthropogenically altered habitats (agricultural plantations and suburban gardens). Colony reproduction and (colony and individual) fitness was further compared with the quantity and quality of food collected by colonies over two and a half years to elucidate the mechanisms underlying biodiversity effects on bee fitness.

Our extensive monitoring revealed that colony fitness (brood volume, hive-, queen- and worker reproduction) increased with increasing plant species richness and resource quantity (colony food stores), with highest plant species richness and consequently colony fitness in gardens. Interestingly, individual worker fitness was not affected by available resource diversity and abundance, showing that colonies do not increase the nutritional investment in single workers, but in overall worker population size. Moreover, resource nutrient quality and functionality also increased with plant species richness, but did not limit colony fitness.

Our study proves that high plant species richness provides continuous resource supply and thus promotes resource foraging and increases colony fitness. Biodiversity is therefore a key driver of (social) bee fitness by providing more foraging resources, even when only small, but florally diverse patches remain.

5.2. Introduction

The loss of pollinator diversity and abundance has raised global concern about the stability of pollination services for food production (Biesmeijer et al. 2006; Klein et al. 2007; Cameron et al. 2011; Goulson et al. 2015; Gill et al. 2016). Habitat loss and conversion (e.g. for agriculture) are key factors driving pollinator declines, as pollinators are affected by reductions in the diversity and abundance of flowering plants (Winfree et al. 2009; Potts et al. 2010; Winfree et al. 2011; González-Varo et al. 2013; Vanbergen and the Insect Pollinators Initiative 2013; Goulson et al. 2015). Bees are among the most important pollinators globally and depend entirely on floral resources for nutrition (Ollerton et al. 2011; Vaudo et al. 2015). Both the diversity and abundance of bee species tend to increase with plant diversity and are typically highest in natural and semi-natural habitats (referred to as natural habitat in the following; Winfree et al. 2009; Kennedy et al. 2013). In fact, bee diversity and abundance may be primarily driven by food (i.e. floral resource) availability and diversity (Hines and Hendrix 2005; Roulston and Goodell 2011; Winfree et al. 2011; Jha and Kremen 2013), because bees entirely depend on floral resources for food and nesting resources and thus their reproductive success. However, direct evidence for the importance of resource diversity and abundance for bee fitness is still scarce, and entirely lacking for highly social bee species, such as honeybees and stingless bees, which provide a significant proportion of overall pollination services (Goulson et al. 2015; Gill et al. 2016). In particular, no study has hitherto related bee fitness to plant resources available in the bees' habitats and to the quality and quantity of resources collected. In fact, all existing studies are limited to correlations between habitat characteristics and bee diversity and abundance, rendering it difficult to determine whether comparatively higher bee abundances (as observed in biodiverse habitats) actually reflect true population size or just forager concentration at rewarding resource patches (Crone and Williams 2016). This represents a major knowledge gap in understanding the impact of man-made habitat changes and biodiversity loss on bees.

Beside studies correlating landscape effects and bee occurrence, only a handful examined bee fitness in relation to (flowering) plant diversity (Goulson et al. 2002; Elliott 2009; Westphal et al. 2009; Williams et al. 2012; Renauld et al. 2016). Notably, they all found that habitat biodiversity had a positive effect on colony growth or offspring production. While all these studies were confined to species with seasonal life cycles, i.e. solitary bee species and (primitively eusocial) bumble bees, no study has as yet examined how floral resource diversity and abundance affect highly social bees with perennial life cycles. In such highly social bee colonies, resources determine the

survival and fitness of each colony member (individual fitness) as well as the colony as a whole (colony fitness; Brodschneider and Crailsheim 2010). Given the importance of highly social bees as pollinators and thus their contribution to global food security (Klein et al. 2007; Winfree 2010; Garibaldi et al. 2013; Vanbergen and the Insect Pollinators Initiative 2013), it is all the more surprising that we know very little about how resource diversity and abundance affect their fitness.

Moreover, many previous studies compared bee diversity or abundance between different landscapes (e.g. between disturbed and natural habitat) and emphasized the importance of larger areas of natural habitat for increased bee diversity and abundance (Söderström et al. 2001; Steffan-Dewenter 2003; Jauker et al. 2012; Rollin et al. 2013; Woodcock et al. 2013). However, these studies did not separate the underlying biodiversity effects. In fact, to date, no study has compared bee fitness between landscapes in relation to biodiversity and tested whether the frequently observed impact of landscape can be explained by underlying factors, such as available plant diversity and plant resource abundance or foraged resource quality and quantity.

Bees, particularly polylectic species, typically collect pollen and nectar from various plant species and store mixtures of these resources in the nest (Brodschneider and Crailsheim 2010; Leonhardt et al. 2014; Hülsmann et al. 2015). Nectar is converted into honey and represents the main source for sugars, while pollen provides proteins, lipids and all essential micro-nutrients (Roulston and Cane 2000a; Nicolson 2011). The nutritional composition of floral resources varies among and between plant species (Roulston and Cane 2000b; Weiner et al. 2010; Somme et al. 2015). The abundance of floral resources available in the environment consequently determines the quantity (i.e. the overall amount of resources collected) of food storage composed by bees, while the composition of resources determines the quality (i.e. the functional properties and nutritional composition) of the collected and stored food. Thus, generalist bees need to forage selectively to allocate resources of not only sufficient quantity, but also adequate nutritional quality (Vaudo et al. 2015).

Habitats with higher biodiversity and higher plant richness have a higher biomass productivity (Duffy et al. 2007; Grace et al. 2016) and plant species richness can thus directly enhance the quantity of resources (i.e. pollen and nectar) foraged in the surrounding landscape, which in turn increases overall resource intake (Kaluza et al. 2016a) as well as the diversity of resources collected (Kaluza et al. 2016b). However, whether plant species richness also positively affects colony fitness remains as yet unclear. Here, we present the first study that experimentally relates plant resource diversity and abundance to bee colony reproduction as well as to individual and colony

fitness. Because previous studies predominantly used specific landscape categories to predict bee species abundances and diversity, we further compare the predictive value of landscape types *vs.* measured plant species richness (i.e. resource diversity) and resource abundance to assess whether landscape categories adequately reflect biodiversity effects. We finally isolate the mechanisms by which resource diversity regulates bee (colony and individual) fitness by comparing the effect of resource quantity vs. quality in explaining fitness outcomes.

In order to address this question, we chose a generalist social bee species, the Australian stingless bee *Tetragonula carbonaria* Smith, as a model organism (Kaluza et al. 2016a). We placed bee colonies in different landscapes with varying plant species richness and thus resource diversity and abundance (Kaluza et al. 2016b), ranging from undisturbed natural habitats to anthropogenically altered habitats (agricultural plantations and suburban gardens). At our study sites, plant species richness was lowest in plantations and highest in gardens, and correlated with collected resource diversity (Kaluza et al. 2016b). We analysed colony reproduction and fitness in relation to surrounding plant species richness and resource abundance, as well as to resource quantity and quality over two and a half consecutive years. We hypothesise that increasing biodiversity (i.e. plant species richness) and corresponding increases in resource abundance strongly increase bee (colony and individual) fitness. We further predict that (colony and individual) fitness increase with both the quantity and the quality of resources (i.e. food stored in nests).

5.3. Methods

5.3.1. *Experimental setup*

The study was conducted from 2011 to 2014 in South East Queensland, Australia (24°38'-27°30' S, 152°6'-153°7' E). We placed bee hives along a gradient of varying plant resource diversity and abundance to quantify the influence of landscape-related plant species richness and resource abundance on bee and colony fitness. The gradient was established by selecting three landscape types characteristic for the region: (a) forests, ranging from costal forest to plant species rich rainforest ecotones, all of which represents the natural habitat of *T. carbonaria*, (b) macadamia plantations, i.e. intensively managed and low plant/resource diversity agricultural landscapes and (c) suburban gardens, comprising a highly diverse mix of native and exotic plant species

and abundant floral resources across the year (see Kaluza et al. 2016a for details).

Bee hives were placed at eight paired sites (replicates) per landscape type, with two bee hives per site at commencement in 2011. Due to early usurpation by another bee species in two hives, these hives have been excluded after the habituation phase resulting in 44 bee hives as the original setup. In plantations, bee hives were closed for 24 h when insecticides were applied on macadamia trees to prevent contamination.

Botanical surveys were conducted along four 500 m transects for each study site to assess plant species richness and to quantify plant resource abundance. Transects extend from the hives' location towards north, south, east and west. Plant form (categories: herb, shrub or tree) and abundance (rare, uncommon or common) of each plant species was recorded (see Kaluza et al. 2016b for details). The relative frequency for each combined category (plant form × abundance; e.g. rare herb) was calculated per site and multiplied with a weighing factor (obtained through model optimization for explaining variance in flight activity, see Kaluza et al. 2016b). The sum of all combined category values resulted in the plant resource abundance value calculated for each site.

We quantified the area of each landscape type (plantation, forest, garden) for each site within the bee's flight radius (assuming a 500 m flight radius around each bee hive, compare Smith et al. 2016) to compare landscape effects to effects of plant species richness and resource abundance. The area was quantified using aerial photos obtained by Google Earth and landscape patches were subsequently validated by ground surveys (Kaluza et al. 2016a).

5.3.2. *Hive reproduction*

Colonies of *T. carbonaria* were kept in wooden boxes (consisting of two boxes housing the brood and an additional box used as honey super) and artificially propagated to measure their reproductive output.

For most stingless bees, colony growth is limited by nesting space under natural conditions (Roubik 1989; Roubik 2006). We thus provided unlimited nesting space by performing hive splits (Heard 2016; hive: colony + wooden box) to separate resource effects from nesting space limitations. When a hive was split, brood and food storage were separated by a horizontal cut between the centre and bottom box and both hive parts were then equipped with new empty boxes (either one empty bottom box, or two: centre and super box; Figure V.1A insert). As a new queen is raised in the queen-less half of the hive (Heard 2016), a hive split effectively creates two daughter hives of the same lineage from one mother hive. Because of the slightly asymmetrical split, we kept

the daughter hive with brood and food storages (only) in the bottom box at the original location of the mother hive, to support hive recovery by returning foragers.

Hives were always propagated when they reached a total weight of 8.5 kg (weight empty box: 4.7 kg ± 0.6), equivalent to approximately 70 % nest space used and thus close to when the colony would initiate natural colony fission. The number of hives descending from one mother hive can thus be considered the reproductive output of the original mother hive.

5.3.3. *Fitness responses: a) Colony fitness*

Each bee hive was opened once per year in 2012 and 2013 to record fitness parameters and to obtain samples of pollen, honey and adult bees. At least one hive was opened at each paired site (1-4) in each season (wet, cold and dry; total of 35 in forests, 42 in gardens, 33 in plantations).

Nests of *T. carbonaria* consist of a circular brood in shape of an upright elongated sphere (ellipsoid) surrounded by honey and pollen storage pots (Figure V.1C). The brood itself varies in size depending on the colony, but is typically arranged in a spiral which perpetually grows upwards when new brood cells are build (Michener 1961; Brito et al. 2012). This advancing front of the brood continuously fills the empty space successively freed by hatching pupae on top. All open worker cells at the advancing front form one batch and are synchronously built and provisioned, with batch size directly corresponding to the number of workers produced per day (Yamane et al. 1995). Queens are continuously produced and queen pupae are easily identified by their larger size and location at the rim of the brood layers (Yamane et al. 1995).

The following parameters were recorded to assess colony fitness: (a) number of open worker cells, (b) number of queen pupae and (c) total brood volume. We were able to locate the advancing front in 56 % of cases when opening bee hives, which enabled standardized counts of (a) the number of open worker cells in the currently provisioned batch (worker reproduction) and (b) the number of queen pupae at the lowest brood layers with pupae above the advancing front (queen reproduction). For all opened hives, we measured the circumference of the largest brood layer at the cut face of the brood. Lastly, the width (w) and length (l) of the largest brood layer as well as the depth of the brood comb in the top (d_t) and bottom (d_b) box were quantified. Depth was measured by piercing the centre of both brood hemispheres with a long glass pipette. The total brood volume (V) was then calculated using the formula for an ellipsoid:

$$V = \frac{4}{3}\pi * \frac{w}{2} * \frac{l}{2} * \frac{(d_t + d_b)}{2}$$

5.3.4. *Fitness responses: b) Individual fitness*

We assessed the fitness of individual bees based on body size and body fat, which is known to correlate with the feeding status of insects (Roulston and Cane 2002; Quezada-Euan et al. 2011).

Bee body fat was measured using a protocol adapted from Cook et al. (2010). Before hives were opened to obtain samples (see above), we captured departing adult bees by placing a clean clear plastic bag over the entrance hole. Captured bees were killed by freezing and dried for 24 h at 50 °C to evaporate water and melt wax residuals. We then pooled 15 individuals per colony and weighed and extracted the bulk sample in chloroform for 24 h. Chloroform and dissolved lipids were removed and discarded. The procedure was repeated three times and remaining chloroform was evaporated in a heating cabinet for 48 h at 30 °C. The bulk sample was finally weighed again to determine weight loss (equivalent to the weight of lipids extracted from bees).

Bee body size was assessed in November 2012 for adult bees caught within a single season to ensure that differences in body size were related to site and not season. Ten bees per hive (for 13 hives at plantation, 15 at forest and 12 at garden sites) were dissected under a stereo microscope (Kyowa model SZM, Kyowa Optical Co. Ltd, Sagamihara, Japan) and individual body parts were mounted on clay. Head length and width, mesonotum length and width, upper and lower interocular distance as well as intertegular distance were measured (in mm) as biometric parameters (Cane 1987; Nagamitsu and Inoue 1998; Quezada-Euan et al. 2011). A principal component analysis (PCA) was performed on all biometric parameters and the first axis (explaining 61 % of the variance across samples) was determined as a single parameter describing body size.

5.3.5. *Food quantity and quality*

We quantified total food stored in hives and recorded quality measures to understand how colony and individual fitness was related to the amount and quality of resources collected by the workers per hive. The total quantity of food available within hives was estimated by weighing the whole hive, as overall colony weight is largely determined by food storage (about 80 % of total weight; Heard 2016). *Tetragonula carbonaria* stores honey and pollen in separate pots (Michener 1961), which allowed us to collect and mix honey and pollen samples from 1-10 pots of varying age per hive to reflect average food quality.

Honey samples were analysed for their sucrose and water content using hand-held

refractometers (sucrose: Eclipse Refractometer, Bellingham + Stanley Ltd., Lawrenceville, USA; water: HHR-2N Honey Refractometer, ATAGO Co. Ltd., Tokyo, Japan). Acidity of the honey was measured using standard pH-test strips.

Amino acid content in pollen samples was analysed by ion exchange chromatography (IEC: Biotronik, amino acid analyser LC 3000) as described in Kaluza et al. (2016b) and Leonhardt and Blüthgen (2012). The amino acid concentration (mg/g) was calculated using the molar mass of respective amino acids. Methionine, arginine, lysine, isoleucine, leucine, phenylalanine, histidine, valine and threonine were considered essential amino acids for bees. We additionally included proline in our analysis because of its importance for the flight muscle metabolism in adult bees (de Groot 1953; Micheu et al. 2000). A PCA was performed on all detected single amino acids and the first axis (explaining 80 % of the variance across samples) implemented in further statistical analysis (see SM V.1). We additionally used the sum of total protein (mg/g) and the sum of essential amino acids (mg/g) as response variables in the statistical analysis, as bees appear to be primarily affected by overall protein content rather than amino acid composition of pollen (reviewed by Ruedenauer et al. 2015).

We further performed a stoichiometric analysis on pollen following Minden and Kleyer (2014). All pollen material was milled at 300–400 revolutions ('pulverisette 7'; Fritsch, Idar-Oberstein, Germany) and dried at 70 °C for 4–5 h. In order to analyse carbon and nitrogen (C and N) 2–3 mg of material was placed in tin tubes (0.1 mg precision balance CP 225 D; Sartorius, Göttingen, Germany) and analysed using a CHNS Analyser Flash EA (Thermo Electron Corp., Waltham, MA, USA). All other elements (K, S, Mg, Ca, Na, P, Fe, B, Cu) were analysed using optical emission spectrometry with inductively coupled plasma (iCAP 6000, Thermo Scientific), for which 8-10 mg material was processed with nitric acid and hydrogen peroxide and subsequently measured following Murphy and Riley (1962). Micro-nutrients were also analysed as one combined factor, i.e. the first axis of a PCA (explaining 87 % of the variance across samples) comprising all elements except P, N and C, which were entered as separate factors in subsequent analyses (see SM V.1).

5.3.6. *Statistical analysis*

We composed a correlation matrix to identify correlations between all recorded variables, for explanatory variables (related to (a) biodiversity and (b) food resource quantity and quality) and response variables (related to (c) colony and (d) individual fitness; SM V.2). We performed separate models for plant species richness and

landscape areas to determine which variable provided more explanatory power in describing hive reproduction (SM V.3), because plant species richness was positively correlated with garden area, and negatively correlated with forest and plantation area (SM V.2). Plant species richness explained the observed variance best and was therefore tested in all subsequent analyses.

We used generalized linear mixed effect models (GLMM) to analyse the effect of fixed explanatory variables and random effects on colony fitness (i.e. hive reproduction, brood volume, queen reproduction, and worker reproduction) and individual fitness (i.e. worker body fat and worker body size). Because of co-variation between explanatory variables, we again performed separate analyses for biodiversity and resource related variables (SM V.2). In a first step, the effect of biodiversity-related explanatory variables (i.e. landscape types, plant species richness and resource abundance) on fitness response variables was tested (biodiversity models). In a second step, the effect of explanatory variables related to food resource quantity and quality (i.e. weight of pollen and honey storage, total protein in pollen and sucrose concentration in honey) was tested on the same fitness variables when recorded for the same day (i.e. brood volume, queen reproduction, worker reproduction and worker body fat).

We always started with the most complex model which included all explanatory variables and their interactions, followed by step-wise simplification of models by excluding interactions and variables. Model quality was evaluated using Akaike's Information Criterion (AIC), and the model with the lowest AIC value was considered the model with the highest explanatory value. Model selection was further confirmed by testing whether individual explanatory variables (remaining in the most parsimonious models) explained a significant proportion of the overall variance by comparing the model with a given explanatory variable to the same model without this variable (anova command in the lme4 package which compares two nested models using REML scores; library lme4: Bates et al. 2011). In order to compare effects of different explanatory variables on specific response variables, the explained variance (R^2) of the best model following AIC selection was calculated as described by Nakagawa and Schielzeth (2013), and compared between models (library MuMIn: Bartoń 2013).

Hive reproduction and queen reproduction were entered in GLMMs using a Poisson distribution. All other response variables (brood volume, worker reproduction, worker body fat and size) were analysed by GLMMs with Gaussian distribution. Variables were square root transformed where necessary (brood volume) to achieve normality. Hive was nested within site and entered as a random effect in all models (with the exception of hive reproduction: only site) to account for the nested study design. Variation

between years was considered by entering year as random factor in models for brood volume, worker reproduction and worker body fat. Differences between landscape types were assessed using Tukey's HSD post hoc test (package multcomp: Hothorn et al. 2008), and effects of plant richness were calculated using Spearman-rank correlation tests. All analyses were performed in R (R Development Core Team 2013).

Table V.1. Bee fitness response variables explained by biodiversity-related variables, i.e. plant species richness, resource abundance and landscape types (Biodiversity model), and resource quantity and quality variables (Resource model). Variance of fixed effects (marginal R^2: mR^2) and variance of fixed and random effects (i.e. including effects of site and year; conditional R^2: cR^2) of the most parsimonious models following AIC selection are given, as well as the AIC difference between the presented model and the NULL-model (Δ AIC). Fixed effects tested in GLMMs: ***pRi***: plant richness; ***Ls***: landscape types (plantation, forest, garden); ***W_{PH}***: weight pollen and honey stores. Asterisks indicate an interaction between fixed factors; ***NULL*** indicates that the NULL-model (i.e. random site and year effects) best explained the observed effects.

Response variable	Biodiversity model	Δ AIC	$_mR^2$	$_cR^2$	Resource model	Δ AIC	$_mR^2$	$_cR^2$
Hive reproduction	***pRi***	13.03	0.32	NA	NA			
Brood volume	***pRi***	18.88	0.28	0.60	***W_{PH}***	16.79	0.33	0.53
Queen reproduction	***pRi***	4.81	0.12	NA	***W_{PH}***	3.32	0.14	NA
Worker reproduction	***pRi * Ls***	9.46	0.39	0.39	***NULL***	-	-	-
Worker body fat	***NULL***	-	-	-	***NULL***	-	-	-
Worker body size	***NULL***	-	-	-	NA			

5.4. Results

5.4.1. *Colony fitness*

The original 46 mother hives as installed at sites in 2011 were propagated into a total of 93 bee hives by March 2014 (mean ± standard deviation; plantations: 3 ± 2 per site; forests: 3 ± 2; gardens: 6 ± 4; Figure V.1). Total hive reproduction was best explained by overall plant species richness in the surrounding landscape (biodiversity model, Table V.1; GLMM: $\chi^2 = 15.03$, $df = 1$; $P < 0.001$). The number of hives produced by a mother colony within 2 years significantly increased with increasing plant species richness (spearman correlation test: $r = 0.59$, $P < 0.001$), and was highest in gardens and lower in forests and plantations (Tukey test: plantations vs. forests: $P = 0.783$; forest vs. gardens: $P = 0.039$; plantations vs. gardens: $P = 0.007$).
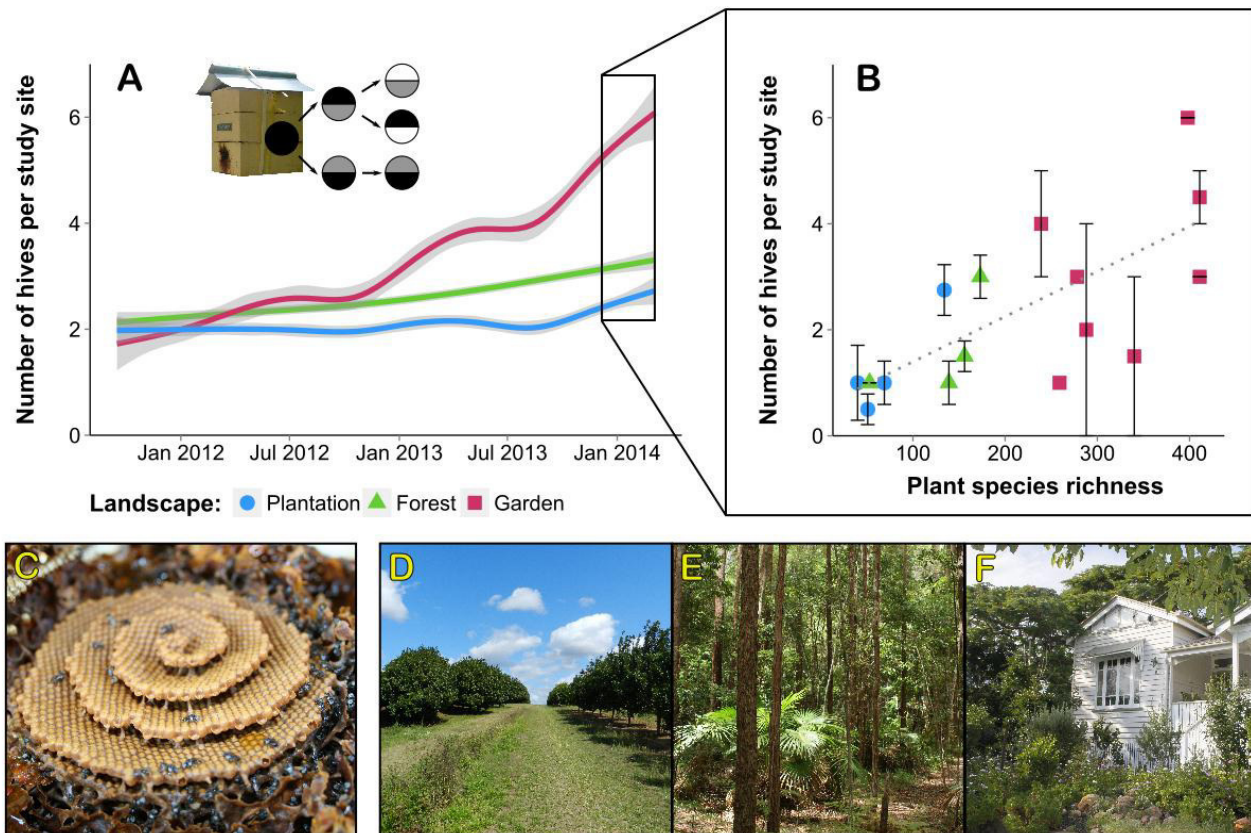
Figure V.1. Bee hive reproduction (number of hives per study site) over time (**A**) and in relation to plant species richness of study sites (**B**) in different landscapes: macadamia plantations (*blue circles*), natural forests (*green triangles*) and suburban gardens (*red squares*). Changes in average hive numbers per landscape type over two years are presented including standard errors (*grey margins*; **A**). Mean hive number of sites is presented with standard errors (**B**) and correlates with plant richness (*dotted line*). To separate resource effects from nest space limitations, hives were propagated by splitting the brood (*full circle*) and by then equipping each half with new boxes (step 1: *grey semi-circle*); splits were repeated when the brood was regrown (step 2, adding new boxes: *white semi-circle*) and the number of hives descending from the original colony thus represents the hive's reproduction (**A**, *insert*). Photos: advancing front of *T. carbonaria* brood (**C**), macadamia plantation (**D**), natural forest habitat (**E**) and suburban garden (**F**).

Both brood volume and queen reproduction (i.e. number of queen pupae) of bee hives were also best explained by plant species richness (Table V.1; brood volume: GLMM: $\chi^2 = 20.88$, $df = 1$; $P < 0.001$; queen reproduction: $\chi^2 = 6.82$, $df = 1$; $P = 0.009$) and likewise increased with plant species richness (brood volume: Figure V.2A, correlation test: $r = 0.54$, $P < 0.001$; queen reproduction: Figure V.2C, $r = 0.30$, $P = 0.002$). When testing for effects of resource quantity and quality, brood volume and

queen reproduction were best explained by and increased with food storage weight (resource model, Table V.1; brood volume: GLMM: $\chi^2 = 18.79$, $df = 1$, $P < 0.001$, Figure V.2B, correlation test: $r = 0.63$, $P < 0.001$; queen reproduction: $\chi^2 = 5.32$, $df = 1$, $P = 0.021$, Figure V.2D, $r = 0.49$, $P < 0.001$).

Worker reproduction (i.e. number of open worker cells per batch) was best explained by plant species richness interacting with landscape (Table V.1; landscape: GLMM: $\chi^2 = 9.64$, $df = 4$; $P = 0.047$; plant richness: GLMM: $\chi^2 = 13.61$, $df = 3$; $P = 0.003$; Figure V.2E). The number of worker cells increased with plant species richness in plantations (correlation test: $r = 0.68$, $P = 0.005$) and forests ($r = 0.51$, $P = 0.03$), but not in gardens ($r = 0.19$, $P = 0.379$). However, when testing for the effect of resource quantity and quality, the NULL-model (i.e. only random effects of sites and year) best explained observed variance (Table V.1).

5.4.2. *Individual fitness*

Fitness of individual workers, i.e. worker body fat and size, showed overall little variance across all observations and was best explained by random effects (i.e. NULL-models) in biodiversity models (Table V.1). Worker body fat was also best explained by the NULL-model when testing resource quantity and quality variables (data not available for body size).

5.5. Discussion

Multiple studies showed that natural habitat positively correlates with bee abundances (Ricketts et al. 2008; Winfree et al. 2009; Kennedy et al. 2013), but the mechanisms underlying this landscape effect have as yet not been experimentally investigated. Thus, our study is the first to demonstrate that bee fitness directly depends on plant biodiversity in a landscape, with higher plant species richness strongly increasing colony fitness through providing larger resource quantities. In fact, while the size of natural habitat was frequently discussed to explain bee population dynamics (Steffan-Dewenter 2003; Jauker et al. 2012; Rollin et al. 2013; Woodcock et al. 2013), we revealed overall plant species richness as significantly better predictor of fitness of a generalist bee species than the size of natural habitats (forests) or gardens. Moreover, we found even small patches of high plant species richness to provide sufficient resources and support bee colony fitness, as colonies were able to thrive in agricultural landscapes (plantations) if they had access to small patches of plant species rich habitats.
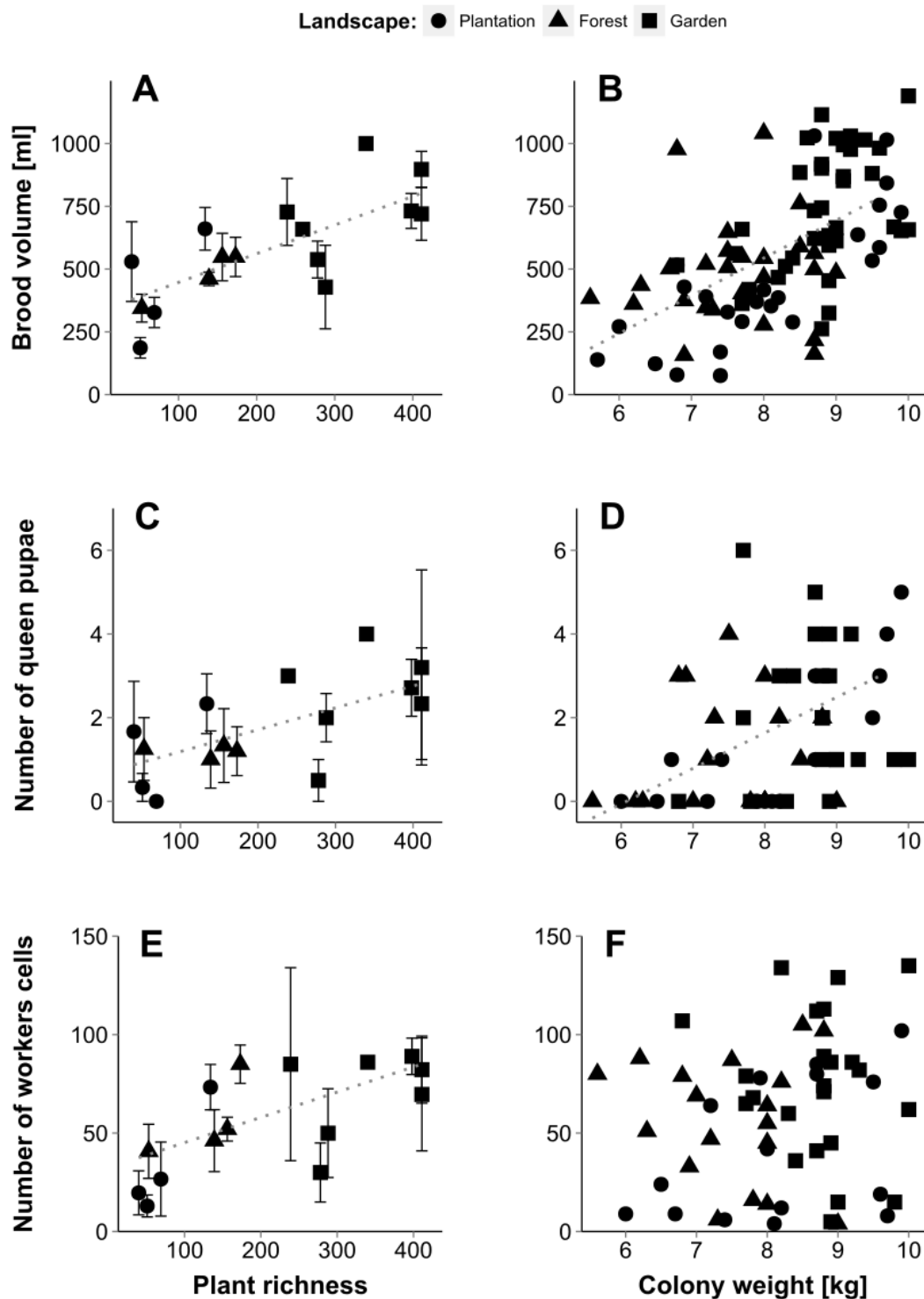
Figure V.2. Bee colony fitness parameters in relation to plant species richness (**A**, **C**, **E**) and total food quantity (**B**, **D**, **F**) in landscapes (plantation, forests and gardens). For plant species richness, means and standard errors are given per study site for all observations made during a two year period. Colony response variables were total brood volume, queen reproduction (number of queen pupae per hive observation) and worker reproduction (number of provisioned worker cells per hive observation). Dotted lines indicate significant correlations according to Spearman correlation tests.

V. Biodiversity drives social bee fitness

5.5.1. *Colony fitness*

Colony reproduction of *T. carbonaria* increased with plant species richness, and colony growth rates over time were almost exponential in landscapes with highest plant species richness (gardens). Likewise, brood volume increased with plant species richness, i.e. bee hives developed a larger forager population in landscapes with high plant species richness. Such a positive effect of plant species diversity on social bee colony growth (particularly in gardens) has also been shown for bumble bees in temperate climates (Goulson et al. 2002). Higher plant species richness, i.e. plant biodiversity, typically provides a broader spectrum of foraging resources, particularly in anthropogenically changed landscapes (e.g. gardens), because generalist bee foragers utilize resources from both native and exotic flowering plants (Tepedino et al. 2008; Stout and Morales 2009; Williams et al. 2011). High levels of plant diversity (as typically found in diverse environments) offer more foraging choices which are exploited by generalist bee species (Jha et al. 2013; Requier et al. 2015; Kaluza et al. 2016b). This allows bees to dilute toxic plant compounds or combine pollen from a variety of plants to maintain a nutritionally balanced diet (Williams and Tepedino 2003; Eckhardt et al. 2014; Irwin et al. 2014), which facilitates bee health (Alaux et al. 2010; Höcherl et al. 2012). Plant diversity may further indirectly benefit bees, because higher plant diversity positively correlates with a habitat's biomass and thus flower production (Duffy et al. 2007). Landscapes with higher plant diversity can also offer a wider range of flowering phenologies, thus providing a continuous floral resource supply across seasons which can bridge periods with otherwise low resource availability (Blüthgen and Klein 2011; Williams et al. 2012).

In contrast to plant species richness, resource abundance had a much weaker effect on bee fitness. Resource abundance in the surrounding landscape can directly limit foraging and reproduction of solitary and social bee species (Biesmeijer et al. 1999; Mattila and Otis 2006; Larsson and Franzén 2007; Westphal et al. 2009). However, note that the resource abundance measure used in our study estimates total resource abundance over the year and is independent of plant species richness. It strongly weighs abundant and large plant species over rare or herbaceous plants, thereby rating forests higher than gardens (Kaluza et al. 2016b). Thus, resource abundance can be high at sites with comparatively low plant species richness and high resource supply and bee colony resource intake may consequently be confined to specific time periods or seasons (e.g. macadamia flowering in the dry season; Kaluza et al. 2016a). The strong influence of plant species richness, but not resource abundance, as found in this study, consequently reveals that a continuous resource supply (as typically provided in biodiverse habitats)

is more important than overall food resource abundance.

In fact, Kaluza et al. (2016a) showed that *T. carbonaria* doubled its resource intake in highly diverse habitats (e.g. gardens) by increasing the hive's foraging activity compared to their natural environment (forests). This positive relationship between continuous resource supply and continuous resource intake in diverse landscapes most likely explains why brood volume was strongly determined by food quantity, which was also observed by Greco et al. (2011) for *T. carbonaria.* It shows that increased food storages allow colonies to rear and maintain a larger population, which in turn enhances foraging success (Figure V.3).

Moreover, like brood volume, queen reproduction also increased with plant species richness and the amount of food storage. Hitherto, most studies investigating colony fitness and associated queen reproduction focused on bumble bees (Goulson et al. 2002; Elliott 2009; Westphal et al. 2009; Williams et al. 2012), which show a specific seasonal life cycle. Bumble bees colonies grow by first producing cohorts of workers, until they switch to invest food storages into the production of males and queens towards the end of the flowering season (Crone and Williams 2016), which renders direct comparisons between bumble bees to other (tropical) social bees difficult. In contrast, most stingless bee colonies produce gynes (unmated queens) continuously throughout the year (Roubik 1989; van Veen and Sommeijer 2000; Sommeijer et al. 2003), and mechanisms which trigger or increase queen rearing in stingless bees are still largely unclear (Tarpy and Gilley 2004). Moo-Valle et al. (2001) showed that colonies which were artificially deprived of food reserves produced fewer queens, while increasing food reserves had no (positive) influence. Our study shows for the first time, that, under natural conditions, queen reproduction is indeed linked to food quantity in the nest, as suggested by Tarpy and Gilley (2004), indicating that stingless bee colonies significantly increase the number of the most costly and most important reproductives (likely in preparation of colony fission) in response to greater food storages in resource rich environments.

Interestingly, worker reproduction also increased with increasing plant species richness in plantations and forests, but did not increase further with higher plant species richness in gardens and was overall independent of resource quantity or quality. Worker reproduction is likely limited by batch size which may in turn be limited by brood architecture (i.e. form of the brood comb), as worker reproduction was positively correlated with brood circumference, but not with total brood volume. It thus seems likely that, when a given batch size is reached, *T. carbonaria* cannot further increase batch size in highly resource rich locations (e.g. gardens), but switches to provision
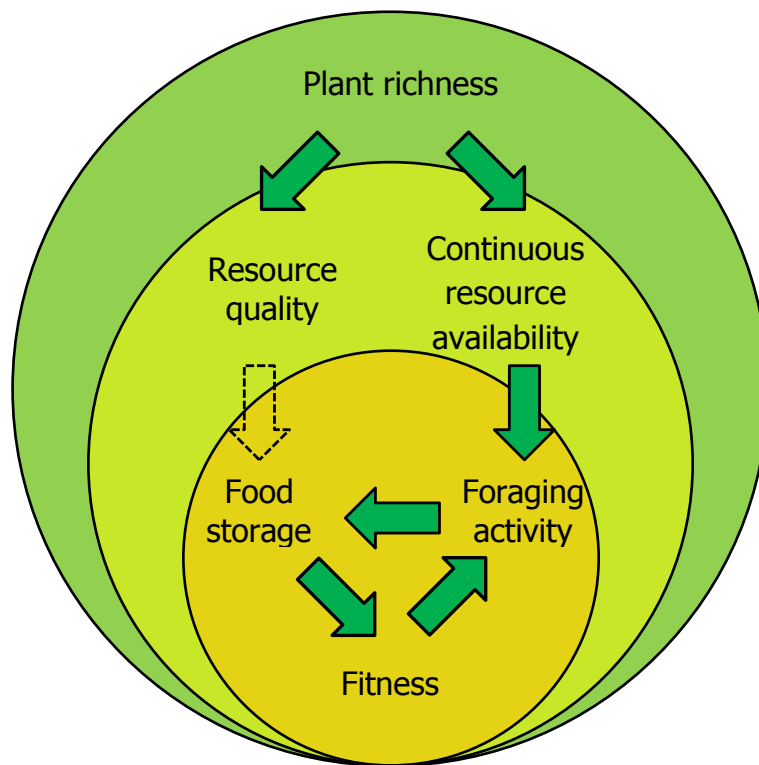
Figure V.3. Proposed mechanisms regulating social bee fitness. High plant species richness and thus continuous resource availability result in increased foraging activity and resource intake (e.g. in gardens: Kaluza et al. 2016a). Larger colony food storages benefit bee colony fitness (i.e. brood volume, queen- and worker reproduction) and in turn allow for larger colonies to increase their foraging activity. Resource quality increases with plant species richness, but does not limit bee fitness when nutrient limitation cannot be compensated by increased consumption.

more batches per day in order to increase the forager population.

Contrary to our predictions, resource quality did not significantly explain variations in colony fitness. Although we consider it likely that resource quality contributes to colony fitness and reproduction, our study shows that colony fitness is primarily driven by resource quantity, as was also found for bumble bee colony growth (Kämper et al. 2016). Limitations in resource quality may only become apparent when specific micro- or macro-nutrients are limited in such that they cannot be compensated by increased consumption (Simpson and Raubenheimer 2012). For example, we found phosphorus and other micro-nutrient minerals in pollen as well as sucrose in honey to increase with plant species richness, indicating a generally positive effect of biodiversity on the quality of allocated resources (Figure V.3), which may determine colony fitness when resource diversity is reduced, e.g. through increased brood worker mortality due to

nutritionally unbalanced cell provisions. Moreover, while we covered several quality measures for pollen and honey, we may have overlooked other important indicators of resource quality (e.g. antioxidants: Di Pasquale et al. 2013; sterols: Vanderplanck et al. 2014) or the effect of other non-food resources (e.g. resin: Drescher et al. 2014).

5.5.2. *Individual fitness*

Despite known positive effects of resource quantity and quality on worker body size, we found no effect of plant species richness and food storage on body size. Higher protein content and, to a lesser degree, increased pollen quantities (consumed by bee larvae) can increase offspring size in solitary bees and determine body weight and size in stingless bee workers (Roulston and Cane 2002; Quezada-Euan et al. 2011; Pech-May et al. 2012), which in turn increases the foraging range of workers (Araújo et al. 2004; Kuhn-Neto et al. 2009). Body fat can vary largely across workers, but was found to be inversely linked to worker size (mass) in bumble bees, where smaller bees possess proportionally more lipids (Couvillon et al. 2011). However in our study, body size was highly conserved across sites and thus landscapes with varying resource diversity. Likewise, worker body fat content was similar across sites over the entire year, and did not depend on resource quantity or quality.

Stingless bees, unlike honey bees or bumble bees, do not progressively feed brood, but mass provision cells and then seal them for the duration of the larval development (Michener 2007). Moreover, in honey bees, larval food is mainly of glandular origin, which may explain the relatively uniform size of adult honey bee workers compared to other bee taxa (Huang and Otis 1991; Roulston and Cane 2002). In contrast, stingless bees provision brood cells with honey and pollen directly, and food resources may thus influence worker size more strongly (Quezada-Euan et al. 2011). It is however unknown, whether stingless bees are able to assess the nutritional quality of larval food or target a fixed food volume per brood cell to determine the amount of food per cell necessary to rear a healthy bee. While we observed only minor variations in worker body fat and size with changing resource quantity and quality, overall colony brood volume increased with overall food storage levels. We therefore propose that *T. carbonaria,* and maybe other social bee species, do not adjust food quality or quantity per cell when facing resource limitations, but rather regulate the overall amount of brood produced.

5.5.3. *Conclusions*

This study is the first to experimentally demonstrate that social bee colony fitness is driven by biodiversity, i.e. plant species richness, in the surrounding habitat. Even small patches with high plant species richness (e.g. in gardens or plantations) provide a continuous supply in floral resources, to which bees respond with increasing resource intake and growing colony food storages, leading to increased queen-, worker- and ultimately hive reproduction. Though bee fitness was not limited by resource quality in this study, quality of food storage also increased with plant species richness. Fitness of individual workers was not affected by resource quality and quantity, and we propose that *T. carbonaria* (and potentially other social bees) do not alter the investment per brood cell, but rather regulate the overall amount of brood produced when food is limited. This highlights the importance of biodiversity as a key driver of (social) bee fitness through providing more and continuous foraging resources.

5.6.   Acknowledgments

5.7.   References

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5.8.   Supplementary material

SM V.1. Amino acids, macro- and micro-elements in nest pollen

Concentration of amino acids in nest pollen was determined as described in the main text. Methionine, arginine, lysine, isoleucine, leucine, phenylalanine, histidine, valine and threonine were considered essential amino acids for bees (Table V.2). We additionally included proline in our analysis because of its importance for the flight muscle metabolism in adult bees (de Groot 1953; Micheu et al. 2000). A principal component analysis (PCA) was performed on all detected single amino and the first axis (explaining 80 % of the variance across samples) implemented in further statistical analysis. We additionally used the sum of total protein (mg/g) as well as the sum of essential amino acids (mg/g) as response variable in the statistical analysis, as bees appear to be primarily affected by pollen overall protein content rather than amino acid composition (reviewed by Ruedenauer et al. 2015).

Stoichiometric analysis of elements were performed as described in the main text for nest pollen of each study site and boron, calcium, copper, iron, potassium, magnesium, manganese, sodium, sulphur and zinc were considered micro-nutrients (Table V.3). A principal component analysis was performed on all micro-elements, and the first axis of the PCA (explaining 87 % of the variance across samples) was used for further analyses. Phosphorus, nitrogen and carbon were entered as separate factors in subsequent analyses.

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Table V.2. Amino acids measured in nest pollen (mean ± sd [mg/g]) per study site (forests: F1a-F4b; gardens: G1a-G4b and plantations: P1a-P4b). Amino acids in bold and Proline are considered essential (summed up under total essential AAs).

Amino Acid	F1a	F1b	F2a	F2b	F3a	F3b	F4a	F4b
Asparagine acid	12.85 ± 3.56	11.97 ± 6.99	10.45 ± 2.28	10.19 ± 2.03	11.44 ± 2.66	11.25 ± 1.66	12.17 ± 1.78	12.52 ± 3.14
Hydroxyproline	1.09 ± 1.43	1.88 ± 0.77	0.43 ± 0.75	2.29 ± 2.65	0.77 ± 0.60	0.21 ± 0.42	0.58 ± 0.72	1.03 ± 0.86
Threonine	4.81 ± 1.87	4.16 ± 2.42	3.57 ± 0.37	3.86 ± 0.49	4.07 ± 1.08	4.23 ± 0.56	4.99 ± 0.83	5.36 ± 1.53
Serine	7.40 ± 2.12	6.25 ± 3.27	5.57 ± 0.85	6.22 ± 0.47	6.20 ± 1.42	5.87 ± 0.53	7.33 ± 0.90	7.43 ± 2.09
Glutamic acid	10.82 ± 3.24	9.54 ± 5.77	8.05 ± 1.69	8.37 ± 1.30	9.10 ± 3.04	8.04 ± 1.79	9.95 ± 2.32	10.16 ± 3.64
a-Aminoadipic acid	0	0	0	0	0	0	0.66 ± 0.85	0
Proline	16.01 ± 5.05	9.83 ± 4.62	14.17 ± 2.25	11.47 ± 3.71	10.85 ± 1.38	11.00 ± 3.13	15.24 ± 3.58	16.73 ± 6.05
Glycine	7.14 ± 1.71	5.49 ± 2.90	5.31 ± 0.59	5.29 ± 0.79	5.91 ± 1.31	5.61 ± 0.65	6.50 ± 0.92	6.64 ± 1.94
Alanine	7.98 ± 2.13	6.43 ± 3.30	5.93 ± 0.87	6.04 ± 0.68	6.83 ± 1.40	6.85 ± 0.81	7.28 ± 0.87	7.52 ± 1.90
Valine	3.44 ± 1.29	2.81 ± 1.64	2.47 ± 0.33	2.47 ± 0.31	2.72 ± 0.60	2.93 ± 0.36	3.11 ± 0.45	3.37 ± 0.79
Cysteine	0.45 ± 0.56	0.50 ± 0.57	0	0.10 ± 0.20	0.46 ± 0.31	0	0.46 ± 0.37	0.58 ± 0.14
Methionine	1.98 ± 0.73	1.80 ± 1.07	1.49 ± 0.12	1.3 ± 0.42	1.75 ± 0.52	1.74 ± 0.40	2.03 ± 0.32	2.15 ± 0.73
Isoleucine	2.61 ± 0.85	2.20 ± 1.13	2.04 ± 0.48	2.04 ± 0.39	1.96 ± 0.29	2.19 ± 0.20	2.46 ± 0.34	2.58 ± 0.63
Leucine	8.54 ± 2.37	7.14 ± 3.58	6.41 ± 1.29	6.69 ± 1.40	6.92 ± 0.84	7.06 ± 0.86	8.05 ± 1.27	8.20 ± 2.10
Tyrosine	2.78 ± 0.98	2.13 ± 1.45	1.73 ± 0.39	1.94 ± 0.40	2.22 ± 0.62	2.54 ± 0.38	2.56 ± 0.44	2.82 ± 0.70
beta-Alanine	0	0.19 ± 0.37	0	0	0.16 ± 0.33	0	0	0
Phenylalanine	4.42 ± 1.33	3.70 ± 2.05	3.43 ± 0.81	3.35 ± 0.69	3.55 ± 0.64	3.54 ± 0.52	4.16 ± 0.63	4.34 ± 1.26
Gamma amino butyric acid	0.92 ± 0.19	0.62 ± 0.18	0.72 ± 0.29	0.60 ± 0.20	0.74 ± 0.05	0.79 ± 0.31	0.80 ± 0.22	0.85 ± 0.22
Ornithine	0	0	0	0	0	0	0	0
Lysine	7.48 ± 1.96	7.08 ± 3.91	6.05 ± 2.21	6.79 ± 1.03	7.18 ± 1.23	7.01 ± 0.84	8.92 ± 1.43	8.17 ± 2.49
Histidine	3.02 ± 1.12	2.59 ± 1.35	1.99 ± 0.19	2.62 ± 0.59	2.24 ± 0.54	2.20 ± 0.17	2.59 ± 0.38	2.93 ± 0.81
Arginine	7.04 ± 2.90	5.43 ± 4.05	4.32 ± 1.21	3.91 ± 0.99	5.21 ± 1.50	5.29 ± 0.80	4.87 ± 0.69	5.50 ± 1.22
Total protein	110.77 ± 33.10	91.75 ± 49.29	84.15 ± 16.10	85.53 ± 11.36	90.28 ± 18.40	88.35 ± 11.45	104.71 ± 14.78	108.85 ± 30.14
Total essential AAs	59.35 ± 18.56	46.75 ± 25.27	45.95 ± 8.85	44.49 ± 8.33	46.44 ± 8.34	47.19 ± 6.40	56.42 ± 8.94	59.31 ± 17.17

Table V.2. continued.

Amino Acid	G1a	G1b	G2a	G2b	G3a	G3b	G4a	G4b
Asparagine acid	14.94 ± 6.77	14.35 ± 0.06	11.18 ± 1.9	12.83 ± 2.14	14.55 ± 4.04	15.92 ± 3.20	11.95 ± 3.48	11.25 ± 1.38
Hydroxyproline	0.54 ± 0.77	0.55 ± 0.62	0	0.54 ± 0.54	0.14 ± 0.32	0.52 ± 0.74	0.33 ± 0.45	0.31 ± 0.37
Threonine	6.17 ± 3.38	5.24 ± 0.58	3.93 ± 0.53	5.17 ± 1.07	5.10 ± 1.53	5.97 ± 1.21	4.94 ± 1.68	4.17 ± 0.70
Serine	8.32 ± 3.84	7.25 ± 0.74	5.92 ± 1.12	6.85 ± 1.03	7.21 ± 1.74	8.45 ± 1.48	6.67 ± 2.07	6.11 ± 0.81
Glutamic acid	11.84 ± 4.56	11.05 ± 0.55	9.37 ± 2.17	10.57 ± 1.69	11.61 ± 3.61	5.93 ± 6.44	9.98 ± 3.32	9.17 ± 1.61
a-Aminoadipic acid	0.15 ± 0.21	0	0	0	0	0	0	0
Proline	13.37 ± 7.50	13.37 ± 3.97	8.05 ± 1.76	10.40 ± 4.00	14.57 ± 4.33	14.87 ± 0.90	12.31 ± 1.88	0
Glycine	7.22 ± 2.45	6.40 ± 0.65	5.82 ± 1.17	6.22 ± 0.94	6.56 ± 1.46	7.42 ± 1.56	6.21 ± 1.79	5.81 ± 0.81
Alanine	9.04 ± 3.40	7.95 ± 0.90	7.11 ± 1.45	7.53 ± 1.09	8.09 ± 1.87	9.43 ± 1.91	7.39 ± 2.23	6.89 ± 0.98
Valine	4.29 ± 2.21	3.56 ± 0.33	2.85 ± 0.39	3.34 ± 0.63	3.49 ± 0.96	3.97 ± 0.73	3.33 ± 1.06	2.90 ± 0.53
Cysteine	0.79 ± 1.12	0.49 ± 0.07	0.22 ± 0.20	0.47 ± 0.46	0.43 ± 0.26	0.42 ± 0.60	0.21 ± 0.42	0.38 ± 0.34
Methionine	2.76 ± 1.51	2.26 ± 0.34	2.09 ± 0.60	2.01 ± 0.34	2.22 ± 0.62	2.59 ± 0.42	2.00 ± 0.62	1.93 ± 0.33
Isoleucine	3.65 ± 1.89	2.68 ± 0.37	2.24 ± 0.37	2.63 ± 0.36	2.76 ± 0.90	3.17 ± 0.48	2.66 ± 0.93	2.26 ± 0.38
Leucine	10.36 ± 3.83	8.47 ± 1.01	7.52 ± 1.45	8.36 ± 1.15	8.94 ± 2.69	9.65 ± 0.98	8.03 ± 2.48	7.37 ± 1.26
Tyrosine	3.71 ± 1.87	2.92 ± 0.36	2.27 ± 0.55	2.86 ± 0.65	2.95 ± 0.90	3.10 ± 0.21	2.83 ± 1.07	2.45 ± 0.49
beta-Alanine	0	0	0	0	0	0.37 ± 0.52	0	0
Phenylalanine	5.59 ± 2.08	4.51 ± 0.56	3.86 ± 0.84	4.42 ± 0.62	4.67 ± 1.48	5.13 ± 0.59	4.30 ± 1.47	3.75 ± 0.66
Gamma amino butyric acid	0.73 ± 0.41	0.99 ± 0.13	0.46 ± 0.02	0.58 ± 0.25	0.94 ± 0.31	1.04 ± 0.20	0.70 ± 0.15	0.79 ± 0.29
Ornithine	0	0	0	0	0	0	0	0
Lysine	9.95 ± 4.04	8.06 ± 1.30	7.33 ± 1.76	7.73 ± 1.55	9.03 ± 3.18	9.93 ± 1.68	7.50 ± 2.53	7.08 ± 1.05
Histidine	3.47 ± 1.99	2.75 ± 0.20	2.39 ± 0.47	2.70 ± 0.51	2.94 ± 0.57	3.59 ± 0.01	2.69 ± 0.86	2.65 ± 0.29
Arginine	7.86 ± 4.43	6.10 ± 0.48	5.45 ± 1.18	6.18 ± 1.14	6.28 ± 1.67	6.52 ± 1.02	5.48 ± 1.92	5.13 ± 0.94
Total protein	124.77 ± 58.26	108.96 ± 3.87	88.09 ± 15.05	101.38 ± 17.11	112.49 ± 31.36	117.97 ± 9.81	99.51 ± 29.43	92.64 ± 12.24
Total essential AAs	67.48 ± 32.86	57.01 ± 1.14	45.73 ± 7.10	52.93 ± 9.46	60.01 ± 17.70	65.38 ± 6.23	53.24 ± 15.13	49.49 ± 6.81

Table V.2. continued.

Amino Acid	P1a	P2a	P2b	P3a	P3b	P4a	P4b
Asparagine acid	13.42 ± 3.09	12.35 ± 1.05	12.00 ± 5.54	13.94 ± 3.51	12.83 ± 3.91	14.4 ± 4.93	11.32 ± 1.81
Hydroxyproline	0.71 ± 1.05	0.16 ± 0.27	0.24 ± 0.41	0.13 ± 0.29	0.16 ± 0.32	0.66 ± 0.98	1.14 ± 0.89
Threonine	5.06 ± 1.68	4.45 ± 0.74	4.66 ± 2.57	5.40 ± 1.26	4.97 ± 1.74	5.71 ± 2.33	4.35 ± 0.55
Serine	7.49 ± 1.83	7.03 ± 0.87	6.94 ± 3.40	8.10 ± 1.75	7.54 ± 2.37	8.52 ± 3.25	6.82 ± 1.04
Glutamic acid	12.78 ± 3.45	11.83 ± 2.21	12.08 ± 5.24	13.63 ± 3.19	12.74 ± 3.79	13.1 ± 6.31	9.98 ± 1.75
a-Aminoadipic acid	0	0	0	0	0	0.36 ± 0.44	0.88 ± 0.50
Proline	17.98 ± 4.49	19.67 ± 3.23	18.02 ± 12.71	18.71 ± 6.67	17.34 ± 6.17	17.54 ± 11.5	15.15 ± 3.27
Glycine	7.24 ± 1.38	6.87 ± 0.93	6.78 ± 3.25	7.92 ± 1.87	7.28 ± 2.26	7.75 ± 2.94	6.23 ± 0.86
Alanine	7.98 ± 1.47	7.40 ± 0.66	7.61 ± 2.67	8.66 ± 1.98	7.94 ± 2.47	8.53 ± 3.11	6.99 ± 1.17
Valine	3.54 ± 0.97	3.17 ± 0.33	3.17 ± 1.36	3.72 ± 0.84	3.47 ± 1.13	3.75 ± 1.40	2.94 ± 0.45
Cysteine	0.33 ± 0.39	0.21 ± 0.36	0.11 ± 0.18	0.40 ± 0.42	0.45 ± 0.34	0.48 ± 0.35	0.36 ± 0.25
Methionine	2.46 ± 0.64	2.35 ± 0.33	2.29 ± 1.38	2.84 ± 0.71	2.52 ± 0.94	2.79 ± 1.17	2.05 ± 0.32
Isoleucine	2.76 ± 0.65	2.48 ± 0.27	2.53 ± 1.21	2.84 ± 0.54	2.64 ± 0.95	3.00 ± 1.14	2.32 ± 0.49
Leucine	8.88 ± 1.90	8.17 ± 0.69	7.90 ± 3.76	9.40 ± 1.94	8.99 ± 3.19	9.12 ± 3.55	7.60 ± 1.64
Tyrosine	2.47 ± 0.70	2.23 ± 0.06	2.20 ± 1.18	2.79 ± 0.50	2.88 ± 1.04	2.91 ± 1.16	2.14 ± 0.37
beta-Alanine	0	0	0	0.26 ± 0.59	0	0	0
Phenylalanine	4.59 ± 1.02	4.37 ± 0.43	4.34 ± 2.25	5.02 ± 1.12	4.64 ± 1.65	4.93 ± 2.06	3.97 ± 0.83
Gamma amino butyric acid	0.73 ± 0.41	0.86 ± 0.34	0.95 ± 0.33	0.7 ± 0.46	0.73 ± 0.51	0.61 ± 0.27	0.89 ± 0.51
Ornithine	0	0	0	0	0.07 ± 0.14	0	0
Lysine	8.05 ± 1.02	7.48 ± 1.54	8.18 ± 4.24	9.29 ± 2.21	8.28 ± 2.82	10.19 ± 4.12	8.57 ± 1.86
Histidine	3.30 ± 0.48	2.82 ± 0.44	3.15 ± 1.30	3.52 ± 0.77	3.20 ± 1.15	3.54 ± 1.35	2.89 ± 0.63
Arginine	5.13 ± 1.19	4.81 ± 0.32	4.60 ± 2.60	6.6 ± 2.64	6.90 ± 3.93	6.52 ± 2.77	4.46 ± 0.93
Total protein	114.98 ± 23.79	108.7 ± 13.44	107.75 ± 53.89	123.88 ± 30.83	115.58 ± 38.37	124.41 ± 50.84	101.05 ± 17.13
Total essential AAs	61.76 ± 12.55	59.76 ± 7.77	58.84 ± 33.18	67.35 ± 17.11	62.96 ± 22.63	67.09 ± 29.99	54.31 ± 9.94

Table V.3. Stoichiometric analysis of elements in nest pollen (mean ± sd [mg/g]) per study site (forests: F1a-F4b; gardens: G1a-G4b and plantations: P1a-P4b). Macro-elements (bold) is the sum of Phosphorus, Nitrogen and Carbon, while micro-elements is the sum of all other elements.

Minerals	F1a	F1b	F2a	F2b	F3a	F3b	F4a	F4b
Boron	0.02 ± 0.02	0.03 ± 0.01	0.02	0.03 ± 0.02	0.02 ± 0.01	0.01	0.04 ± 0.01	0.01 ± 0.01
Calcium	1.40 ± 0.42	1.04 ± 0.38	1.30 ± 0.81	1.44 ± 0.30	2.46 ± 1.45	2.28 ± 0.28	1.63 ± 0.67	1.31 ± 0.48
Copper	0.02	0.01	0.01	0.01	0.02 ± 0.01	0.02 ± 0.01	0.01	0.01
Iron	0.06 ± 0.02	0.07 ± 0.02	0.04 ± 0.01	0.05 ± 0.02	0.06 ± 0.01	0.05 ± 0.01	0.04 ± 0.01	0.05 ± 0.01
Potassium	5.10 ± 0.75	4.61 ± 1.03	6.06 ± 1.04	5.53 ± 0.97	6.11 ± 0.84	6.41 ± 0.47	6.35 ± 0.67	6.53 ± 0.81
Magnesium	0.73 ± 0.12	0.70 ± 0.21	1.02 ± 0.18	0.78 ± 0.26	0.96 ± 0.08	1.02 ± 0.10	1.12 ± 0.22	1.07 ± 0.17
Manganese	0.03 ± 0.01	0.02	0.06	0.05 ± 0.01	0.12 ± 0.07	0.17 ± 0.11	0.05 ± 0.01	0.07 ± 0.03
Sodium	0.44 ± 0.10	0.51 ± 0.09	0.57 ± 0.09	0.48 ± 0.14	0.29 ± 0.13	0.26 ± 0.13	0.21 ± 0.10	0.21 ± 0.02
Sulphur	1.94 ± 0.39	1.57 ± 0.84	1.49 ± 0.21	1.57 ± 0.37	2.07 ± 0.30	2.00 ± 0.42	2.33 ± 0.51	1.95 ± 0.38
Zinc								
Phosphorus	3.64 ± 0.62	3.52 ± 1.82	4.14 ± 0.91	3.84 ± 0.74	4.89 ± 0.53	5.24 ± 0.15	5.00 ± 0.69	5.66 ± 2.17
Nitrogen	34.91 ± 5.69	33.17 ± 13.95	32.23 ± 0.70	27.06 ± 7.29	37.75 ± 8.65	38.63 ± 7.67	40.17 ± 6.27	34.72 ± 4.51
Carbon	465.16 ± 34.06	488.23 ± 17.91	481.23 ± 14.42	472.95 ± 112	473.64 ± 41.39	461.56 ± 39.27	524.60 ± 69.27	475.98 ± 39.87
Micro-elements	9.60 ± 1.25	8.35 ± 1.80	10.33 ± 1.18	9.76 ± 1.47	11.92 ± 2.26	11.89 ± 0.65	11.57 ± 0.73	10.97 ± 1.22
Macro-elements	503.71 ± 36.92	524.91 ± 4.56	517.60 ± 12.90	503.84 ± 118.72	516.27 ± 47.81	505.44 ± 46.85	569.77 ± 74.91	516.36 ± 44.65

Table V.3. continued.

Minerals	G1a	G1b	G2a	G2b	G3a	G3b	G4b	G4a
Boron	0.02 ± 0.01	0.02	0.01	0.02 ± 0.01	0.02	0.01	0.02	0.01
Calcium	2.26 ± 0.14	2.12 ± 0.30	2.23 ± 0.59	2.13 ± 0.76	2.33 ± 0.77	1.93 ± 0.17	2.28 ± 0.71	2.78 ± 1.32
Copper	0.01	0.01	0.01	0.01	0.02 ± 0.01	0.01	0.02	0.02 ± 0.01
Iron	0.08 ± 0.06	0.06 ± 0.01	0.05 ± 0.01	0.05 ± 0.01	0.05 ± 0.01	0.06	0.06 ± 0.02	0.05 ± 0.01
Potassium	6.14 ± 0.54	6.73 ± 0.96	6.31 ± 0.24	6.93 ± 0.60	7.50 ± 0.59	7.39 ± 0.98	7.24 ± 0.44	6.65 ± 0.25
Magnesium	1.44 ± 0.13	1.59 ± 0.35	1.38 ± 0.02	1.38 ± 0.30	1.41 ± 0.13	1.33 ± 0.10	1.50 ± 0.28	1.43 ± 0.09
Manganese	0.04	0.04 ± 0.01	0.04 ± 0.02	0.05 ± 0.02	0.03 ± 0.01	0.03	0.04 ± 0.01	0.05 ± 0.01
Sodium	0.58 ± 0.04	0.34 ± 0.12	0.40 ± 0.05	0.43 ± 0.16	0.22 ± 0.07	0.19 ± 0.01	0.32 ± 0.06	0.22 ± 0.06
Sulphur	2.30 ± 0.09	1.71 ± 0.48	1.71 ± 0.31	1.97 ± 0.30	1.90 ± 0.24	1.87 ± 0.12	2.11 ± 0.29	1.96 ± 0.41
Zinc	0.11 ± 0.14							
Phosphorus	5.49 ± 0.96	5.61 ± 1.23	5.51 ± 0.13	5.63 ± 0.96	5.51 ± 0.36	5.56 ± 0.14	5.64 ± 1.06	5.51 ± 0.25
Nitrogen	36.38 ± 3.78	35.13 ± 4.40	32.83 ± 1.83	33.69 ± 2.76	36.69 ± 1.50	40.19 ± 0.66	41.97 ± 21.24	33.72 ± 5.89
Carbon	486.45 ± 5.56	447.55 ± 40.66	500.87 ± 15.17	467.32 ± 23.93	485.53 ± 16.16	490.46 ± 1.54	480.38 ± 21.21	465.42 ± 50.19
Micro-elements	12.97 ± 0.80	12.43 ± 2.26	11.85 ± 0.42	12.67 ± 1.37	13.24 ± 1.52	12.56 ± 1.24	13.51 ± 0.99	13.01 ± 1.92
Macro-elements	528.33 ± 0.83	488.29 ± 46.23	539.21 ± 14.50	506.64 ± 26.84	527.72 ± 17.21	536.21 ± 1.02	527.99 ± 35.24	504.65 ± 56.07

Table V.3. continued.

Minerals	P1a	P2a	P2b	P3a	P3b	P4a	P4b
Boron	0.02 ± 0.01	0.01	0.03	0.01	0.01 ± 0.01	0.03 ± 0.02	0.03 ± 0.01
Calcium	1.55 ± 0.45	1.01 ± 0.61	1.56 ± 0.91	4.36 ± 8.06	5.56 ± 8.82	6.14 ± 9.37	0.99 ± 0.35
Copper	0.01			0.01	0.01 ± 0.01	0.01	
Iron	0.08 ± 0.03	0.07 ± 0.01	0.07 ± 0.01	0.08 ± 0.02	0.06 ± 0.01	0.07 ± 0.03	0.10 ± 0.07
Potassium	6.86 ± 1.22	7.30 ± 0.46	7.88 ± 0.07	7.02 ± 0.83	6.55 ± 0.83	6.51 ± 1.32	5.36 ± 0.95
Magnesium	1.12 ± 0.23	1.20 ± 0.15	1.75 ± 0.75	1.34 ± 0.25	1.19 ± 0.27	1.11 ± 0.15	0.99 ± 0.05
Manganese	0.03 ± 0.01	0.03	0.02 ± 0.01	0.04 ± 0.03	0.05 ± 0.04	0.02 ± 0.01	0.03 ± 0.03
Sodium	0.25 ± 0.04	0.22 ± 0.05	0.21 ± 0.10	0.41 ± 0.43	0.25 ± 0.10	0.39 ± 0.47	0.18 ± 0.05
Sulphur	1.94 ± 0.35	2.06 ± 0.07	1.84 ± 0.66	1.70 ± 1.49	2.00 ± 0.34	2.22 ± 0.23	2.17 ± 0.31
Zinc							
Phosphorus	4.92 ± 0.84	5.28 ± 0.31	5.85 ± 0.45	5.25 ± 0.51	4.80 ± 1.07	5.40 ± 0.94	4.47 ± 0.44
Nitrogen	32.87 ± 3.65	36.18 ± 2.32	30.03 ± 8.70	35.81 ± 3.26	35.02 ± 5.67	35.76 ± 3.42	35.87 ± 9.00
Carbon	478.39 ± 47.15	488.59 ± 3.16	473.34 ± 23.16	487.56 ± 16.39	481.31 ± 42.09	459.27 ± 55.20	497.5 ± 88.56
Micro-elements	11.57 ± 1.82	11.85 ± 0.67	13.24 ± 1.10	14.76 ± 6.27	15.56 ± 8.89	16.15 ± 10.41	9.60 ± 0.80
Macro-elements	516.18 ± 50.10	530.06 ± 4.27	509.22 ± 31.67	528.63 ± 18.90	521.14 ± 48.74	500.42 ± 57.14	537.84 ± 97.44

SM V.2. Correlation matrix

Spearman rank corellation matrix of explanatory variables related to biodiversity and food resource quantity and quality and of fitness response variables (Table V.4). Abbreviations as follows: pRi: plant species richness; pAb: plant resource abundance; G_A: garden area; F_A: forest area; P_A: plantation area; W_{PH}: weight pollen and honey stores (colony weight); Pr_P: total protein in pollen; eAA_P: essential amino acids in pollen; AA_P: all amino acids (first PCA axis); P_P: phosphorus in pollen; N_P: nitrogen in pollen; C_P: carbon in pollen; mn_P: micro nutrients in pollen (first PCA axis); S_H: sucrose concentration in honey; Wa_H: water concentration in honey; pH: pH of honey; V_B: brood volume in hives; C_B: brood circumference; Q_P: number of queen pupae; W_C: number of open worker cells; W_F: worker body fat.

Table V.4 a). Spearman corellations with biodiversity-related variables. Asterisks indicate significant correlations: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	pRi		pAb		G_A		F_A		P_A	
pAb	-0.11									
G_A	0.76	***	-0.29	**						
F_A	-0.38	***	0.88	***	-0.63	***				
P_A	-0.69	***	-0.13		-0.39	***	-0.06			
W_{PH}	0.50	***	-0.22	*	0.52	***	-0.35	***	-0.26	**
Pr_P	-0.09		-0.16		0.08		-0.19		0.27	**
eAA_P	-0.09		-0.18		0.06		-0.20		0.29	**
AA_P	-0.14		-0.17		0.02		-0.17		0.32	**
P_P	0.33	**	-0.33	**	0.44	***	-0.46	***	0.03	
N_P	0.12		0.10		0.11		0.01		0.02	
C_P	-0.02		0.06		-0.04		0.01		0.15	
mn_P	0.48	***	-0.17		0.47	***	-0.30	**	-0.32	**
S_H	0.21	*	-0.37	***	0.40	***	-0.46	***	-0.07	
Wa_H	-0.24	*	0.42	***	-0.36	***	0.47	***	0.13	
pH	0.02		-0.16		0.04		-0.06		-0.23	*
V_B	0.54	***	-0.21		0.44	***	-0.32	**	-0.30	**
C_B	0.48	***	-0.11		0.33	***	-0.20	*	-0.23	*
Q_P	0.30	**	-0.13		0.23	*	-0.15		-0.23	*
W_C	0.37	**	-0.09		0.19		-0.18		-0.08	
W_F	0.17		-0.07		0.01		-0.04		-0.16	

Table V.4 b). Spearman correlations with food resources quantity and quality variables (aberrations as above).

	W_{PH}		Pr_P		eAA_P		AA_P		P_P		N_P		C_P		mn_P		S_H		Wa_H		pH
Pr_P	0.07																				
eAA_P	0.06		0.98	***																	
AA_P	0.03		0.98	***	0.99	***															
P_P	0.20		0.40	***	0.37	***	0.35	***													
N_P	-0.02		0.52	***	0.52	***	0.50	***	0.45	***											
C_P	-0.07		0.17		0.22	*	0.20		0.04		0.53	***									
mn_P	0.29	**	-0.17		-0.19		-0.19		0.25	*	-0.06		-0.19								
S_H	0.28	**	-0.02		-0.01		-0.03		0.21	*	-0.16		-0.06		0.15						
Wa_H	-0.26	*	0.11		0.11		0.12		-0.21	*	0.20		0.14		-0.18		-0.95				
pH	0.06		-0.10		-0.13		-0.12		-0.01		-0.15		-0.16		-0.05		0.57	***	-0.61	***	
V_B	0.63	***	0.06		0.05		0.02		0.16		0.11		0.06		0.35	**	0.30	**	-0.28	*	0.02
C_B	0.56	***	0.07		0.06		0.04		0.15		0.13		0.11		0.15		0.29	**	-0.27	**	0.12
Q_P	0.49	***	-0.02		-0.03		-0.06		0.02		-0.03		0.18		0.10		0.18		-0.15		0.08
W_C	0.19		-0.07		-0.06		-0.06		0.11		0.09		0.10		0.19		0.06		-0.06		0.03
W_F	-0.15		0.16		0.21		0.19		0.00		0.32	**	0.40	***	-0.03		0.03		0.03		-0.11

Table V.4 c/d). Spearman correlations between fitness response variables (aberrations as above).

	V_B		C_B		Q_P		W_C
C_B	0.85	***					
Q_P	0.49	***	0.57	***			
W_C	0.17		0.40	**	0.32	**	
W_F	0.02		-0.02		-0.01		0.05

SM V.3. Selection of tested biodiversity variables

Several of the biodiversity-related explanatory variables were corellated (e.g. plant species richness with garden, forest and plantation area; SM V.2), but we aimed to select only independent explanatory variables for all subsequent analyses. For one response variable (hive reproduction), all (covarying) biodiversity-related explanatory variables were tested in separate models (Table V.5).

Plant species richness provided the highest explanatory power (over garden, forest and plantation area) and was thus subsequently used in all models for other response variables. Secondly, plant resource abundance was independent of plant species richness and consequently tested as independent explanatory variable in all following models. Landscape type was not correllated, as it was entered as categorial variable, and thus tested in all subsequent models.

Table V.5**.** Models testing the effect of single biodiversity-related explanatory variables on hive reproduction. Given are the AIC difference between the presented model and the NULL-model (**Δ AIC**), as well as the variance of the tested variable (marginal R^2: $_mR^2$).

Models	Δ AIC	$_mR^2$
Plant species richness model	13.03	0.32
Garden area model	5.28	0.24
Forest area model	-0.51	0.05
Plantation area model	1.11	0.10
Plant resource abundance model	-1.97	<0.01

VI.   SYNOPSIS

In the synopsis of this thesis I summarize the results of the presented studies and discuss broader implications of the findings. First, I will give an overview of the results of individual studies in relation to the proposed theoretical framework (Chapter I: Figure I.3). The thesis aimed to investigate how factors of landscape, foraging, resource quality/quantity and fitness influence each other, and I describe in the first section whether the observed links between these factors match the predictions of the theoretical framework (section 6.1).

Furthermore, I discuss implications of our research on social bee resource foraging and fitness in the two anthropogenically formed landscapes targeted in our study design: macadamia plantations and urban gardens. Section 6.2 focuses on the applied aspects of the presented research in agri- and meliponiculture, and highlights findings which can help improve the use of stingless bees for macadamia pollination. Next, I embed our research into the current knowledge of urban areas as bee habitat and identify knowledge gaps for future research (section 6.3).

Finally, I demonstrate and discuss the outstanding role of plant biodiversity on bee resource foraging and fitness and how this thesis advances our understanding of a key factor driving bee declines (section 6.4).

6.1. Summary of findings

SUMMARY OF FINDINGS IN RELATION
TO PREDICTIONS OF THE THEORETICAL FRAMEWORK

Across all presented studies, we step-wise investigated the relationships of plant biodiversity, foraging patterns, foraging/homing success, foraged resource quantity/quality and lastly individual/colony fitness of *Tetragonula carbonaria* as outlined in the presented theoretical framework (Chapter I: Figure I.3). First, we explored the relationship between resource availability, seasonality, foraging patterns and foraging success (Figure I.3A & B: right pathway; Chapter II). Additionally, we investigated whether landscape structure, habitat homogeneity or resource availability affects homing and thus foraging success (Figure I.3B; Chapter III). Next, we investigated how plant resource diversity influences diversity of foraged resources and whether it impacts on resource functionality and nutritional quality (Figure I.3A-C: left

pathway; Chapter IV). In a last step, we combined previous findings to explore how of plant biodiversity, resource quantity and quality impact on bee reproduction and individual or colony fitness (Figure I.3A-D; Chapter V).

In the first study, we investigated how forager numbers, foraging patterns and resource intake change between natural habitats (forests) and two landscapes modified by anthropogenic activities (plantations and gardens) and in response to landscape-scale seasonal availability of resources (Chapter II). We accounted for seasonal and weather influences (compare Figure I.3 A & B) and identified diverging seasonal foraging patterns between landscape types, but, beyond seasonal patterns, we found significant differences in the *total* resource intake over the whole year between landscapes.

Foraging activity as well as pollen and nectar forager numbers were found to be low in plantations, intermediate in forests and highest in suburban gardens. Likewise, sugar and pollen intake per minute was low in plantations, but contrary to our predictions, it was even higher in gardens than in forests. In contrast, resin intake was similar across landscapes, suggesting that bees maximize intake of food resources, but have a specific intake target for resin as nest material.

In summary, total resource availability and its seasonal changes in natural or altered landscapes can strongly impact on foraging patterns and thus resource intake of social bees, but bees respond differently to anthropogenic habitat alterations. Depending on the landscapes' resource availability, anthropogenic habitat can consequently either largely reduce foraging activity and success, as in agricultural monocultures, or increase resource intake well above rates found in natural habitats, as observed in suburban gardens.

The second study tested whether landscape structure (i.e. visual landmarks) and habitat homogeneity (homogenous or fragmented vegetation cover) can affect navigation and thus homing success in bees (Chapter III). Homing success and return speed was compared for both returning bees and nectar foragers between natural forests, with few landmarks but large proportions of vegetation cover, and anthropogenically modified landscapes (gardens and plantations), with many landmarks but fragmented vegetation cover.

Proportions of successfully returning nectar foragers and fastest return speed of both bees and foragers did however not differ between landscapes. In contrast, overall homing success (i.e. the proportion of bees returning within one hour) was highest in

both the visually/structurally most (forest) and least (garden) homogeneous landscape. These results indicate that landscape visual/structural alteration in disturbed landscapes may not provide more or less visual landmarks relevant to the bees' navigation than in undisturbed natural habitats. Instead, return speed may be primarily driven by resource availability in landscapes, which questions the importance of visual landmarks (i.e. elongated ground features) as suggested in previous studies.

The third study aims to improve our general understanding of whether and how biodiverse environments may benefit individual consumers by providing a higher diversity of resources to choose from (Chapter IV). We measured the diversity of bee collected resources of *T. carbonaria* (pollen and resin) in relation to plant species richness and plant resource abundance in different habitats (plantations, forests and gardens), observed whether bee consumers (actively or passively) maximize resource diversity intake and how collected resource diversity affects resource functionality and nutritional quality.

The diversity of foraged resources (pollen and resin) strongly increased with plant species richness and thus resource diversity as predicted by our theoretical framework (Figure I.3B), showing that bees maximize their resource diversity intake. Specifically in impoverished habitats (plantations), bees actively increased the diversity of foraged pollen resources (i.e. actively search for additional resources to maintain a diverse pollen diet), even when one resource was available in great abundance during macadamia flowering. Nevertheless, in habitats with highest plant species richness but comparatively small resource patches (gardens), foraged resource diversity continued to increase with highest foraging activity. Here, high resource diversity is available across seasons and higher foraging activity may thus result in passive resource maximization, where any outgoing forager is likely to encounter a new patch or plant species.

In contrast, resource nutritional quality (sucrose content of honey and total protein, amino acids or minerals in pollen) and functionality (antimicrobial activity of resin) did not increase with the diversity of collected resources as hypothesized (compare Figure I.3C). Instead, resource quality and functionality appeared to be primarily driven by the surrounding plant community composition and by the presence of specific plants/trees providing high quality pollen or resin. In generalist consumers, maximizing resource diversity intake may therefore primarily secure collection of sufficient amounts of resources across the entire foraging season, but it also increases chances that the allocated resources meet all functional needs.

In order to study plant resource effects on bee fitness, we monitored colony growth and fitness of *T. carbonaria* in relation to plant species richness, resource abundance and to patch sizes of various landscape types (plantations, forests and gardens; Chapter V). In a second step, we investigated the influence of quantity and quality of colony stored resources on bee fitness.

Our extensive monitoring revealed that colony reproduction and fitness (brood volume, hive-, queen- and worker reproduction) is primarily driven by plant species richness, with highest plant species richness resulting in highest fitness and reproduction in gardens. In contrast, resource abundance and landscape type played a minor role and thus even small patches with high plant species richness provided a sufficient and continuous supply in floral resources for bees to maintain high colony fitness. Furthermore, higher plant richness ensures continuous resource availability, to which bees respond with increasing resource intake and growing colony food storages, leading to increased colony reproduction and fitness as hypothesized (Figure I.3C/D).

However, while resource nutrient quality and functionality also increased with plant species richness, it did not limit colony fitness. Contrary to our hypothesis, individual worker fitness was not affected by available resource diversity and abundance, indicating that colonies do not increase the nutritional investment in single workers, but increase overall worker population size instead (compare Figure I.3).

Our study demonstrates that high plant species richness can provide continuous resource supply, promote resource foraging and increases colony fitness. Biodiversity is therefore a key driver of (social) bee fitness by providing more foraging resources, even when only small, but florally diverse patches remain.

6.2. Stingless bees in macadamia plantations

APPLIED ASPECTS OF THE RESEARCH:
STINGLESS BEE KEEPING FOR MACADAMIA POLLINATION

The stingless bee *Tetragonula carbonaria* is an effective pollinator of macadamia (*Macadamia integrifolia* Maiden and Betche × *M. tetraphylla* Johnson), an Australian indigenous rainforest tree, which is commercially grown for its edible nuts (Vithanage and Ironside 1986; Heard 1994; Heard and Exley 1994; Wallace et al. 1996). Stingless bee keeping in Australia, by bee enthusiasts as well as for crop pollination, has dramatically increased in recent years (Heard 2016). Macadamia pollination by *T. carbonaria* has thus not reached is full potential yet and a variety of findings in the

presented thesis can help developing a more efficient application of stingless bees in the macadamia industry.

This thesis investigated stingless bee fitness and reproduction in macadamia monocultures, thus looking at plantations from a bees' perspective. The presented findings can therefore help improve placement of stingless bee hives in plantations, protect the investment in hives and give recommendations for pollinator friendly layouts of (planned) macadamia plantations.

In general, bee hives in macadamia orchards showed a broad spectrum of fitness responses during our consecutive survey, from hive starvation to steady hive reproduction, even matching reproduction rates in natural forest habitats under best conditions (Chapter V). This highlights that bee hives are able to thrive in macadamia orchards when basic needs are met and that year-long placement of stingless bee hives in orchards is generally possible. Pollen and nectar resources are sufficiently available during macadamia flowering and nutritional quality of available pollen seems meet the bees' requirements (Chapter II & V). Analyses of protein content, amino acid composition and micro-nutrients provide indirect evidence that macadamia pollen may be of high nutritional value for bees (Chapter V). It is unclear, whether macadamia generally provides pollen of high nutritional quality or if high protein concentrations of bee-collected pollen are due to fertilizer usage in plantations, i.e. higher nitrogen deposition. Nitrogen deposition was found by Hoover et al. (2012) to affect plant traits and bee fitness, as nitrogen deposition changed nectar composition of pumpkin, which increased the nectar attractiveness for bee foragers, but reduced forager longevity. However, nutritional quality of macadamia pollen and nectar in comparison to other Australian plants, as well as the effect of nitrogen deposition on stingless bee foraging behaviour remain unknown and would require further research.

Our studies showed that, averaged over seasons, bee foraging activity, resource intake, foraged pollen diversity, bee fitness as well as hive reproduction in plantations stayed well below the controls in natural habitats (Chapter II, IV & V). The main reason for this was that foraging activity and resource intake dropped quickly and remained low outside macadamia flowering times (dry season; Chapter II). Bee hives in plantations consequently commanded smaller food storages which limited their fitness and reproduction (Chapter V). Resource availability across seasons is thus the critical limitation for bee keeping in macadamia plantations.

Fortunately, several positive findings from gardens are directly transferrable to

macadamia plantations. Plant species richness was a key driver in sustaining floral resource availability across seasons, and consequently allowed bees to maintain a larger forager population and collect greater food quantities (Chapter V). Thus, bee hives in plantations seem to need access to habitats with higher biodiversity within their 500m foraging range (compare to Smith et al. 2016), where plants with complementary flowering periods provide floral resources outside the dry season. In our study setup, these habitat patches were either remaining bush patches with mature eucalypts or gardens of neighbouring residents. In fact, over the range of our plantation study sites, we observed hives on one study site to persistently forage at one small, but very diverse garden in close proximity, which alone was sufficient to greatly boost hive reproduction at this site. Consequently, we found that plant richness, but not the size of forest or garden area determines hive reproduction (Chapter V). Thus even small patches of higher plant diversity should be able to sustain bee hives in macadamia plantations.

As a result of positive experience of stingless bee keeping in suburban gardens (Heard 2016), some macadamia growers started to remove stingless bee hives after the macadamia flowering into garden areas for recovery and rapid propagation. This thesis however supports that artificially enhancing plant diversity in remaining vegetation patches in and around the plantation could be sufficient to provide sufficient foraging opportunities throughout the year. Planting additional herbs with staggered flowering can thus be a cost efficient technique to attract wild pollinators and safeguard bees hives from food shortages (Nicholls and Altieri 2013; Williams et al. 2015).

The uniform layout of plantations was found to impair forager orientation and homing ability, as plantations lack visual landmarks and olfactory cues (e.g. different scents from various tree species) which are apparently necessary for foragers to quickly and successfully return to the hive. As a consequence, foragers returned later to the hive in macadamia plantations and resource intake was further reduced (Chapter III). Differences between macadamia trees are extremely small, as each tree row in macadamia orchards typically only contains macadamia plants that are genetic clones. Macadamia is predominantly insect pollinated but partially self-incompatible, and fruit set consequently increases through cross-pollination by insects between varieties, i.e. between tree lines (Trueman 2013). Bees (predominantly honey bees) are however known to mainly forage on and thus pollinate trees consecutively within one tree row in nut orchards, unless their foraging pattern is disrupted (Brittain et al. 2013). Thus breaking this foraging pattern to encourage bees to alternate between tree rows could potentially increase their pollination efficiency. Consequently, landmarks, gaps in tree

lines or small patches with other plant species (e.g. wind breaks or remnant vegetation) could increase the bees foraging speed and pollination efficiency.

6.3.   Urban habitat for bees

Suburban and urban garden sites in our studies had, to our surprise, highest plant species richness and average plant species richness in gardens was two and a half times higher than at forest sites, thus even exceeding plant richness of diverse natural forests featuring tall eucalypt sclerophyll with very diverse rainforest understory (Chapter II & IV). Bee hives in gardens had highest numbers of pollen and nectar foragers, highest foraging activity, highest sucrose and pollen intake rates and consequently largest reserves of stored food (Chapter II & V). Similar to hives in natural forests, bees collected great pollen diversity and returned quickly from foraging trips (Chapter III & IV). Nutritional quality of pollen (micro/macro elements, amino acids and total protein) and nectar/honey (sucrose), as well as resource functionality (antimicrobial activity of resin) was not limited in gardens (Chapter IV & V). As a consequence, colony fitness (queen reproduction, brood volume) of bee hives in gardens was generally high and reproduction followed an almost exponential growth, as it would typically be expected under ideal environmental conditions (Chapter V).

Only one previous study in a temperate climate revealed surprisingly high bee fitness in suburban gardens, where bumble bee colony growth was higher in gardens compared to improved farmland (Goulson et al. 2002). Goulson et al. (2002) however provided first evidence that improved plant resource availability and diversity in gardens may in fact support high bee abundances, as frequently observed in urban and suburban gardens in temperate zones (Eremeeva and Sushchev 2005; Hisamatsu and Yamane 2006; Fetridge et al. 2008; Matteson et al. 2008; Samnegård et al. 2011; Lowenstein et al. 2014; Baldock et al. 2015), though some studies noted exceptions (McKinney 2008; Bates et al. 2011). Higher bee abundances and visitation rates in urban habitats can lead to higher fruit and seed set in gardens and can thus directly affect human food production (Lowenstein et al. 2015; Theodorou et al. 2016). Surveys of bee abundances are however rare for subtropical urban environments (McIntyre and Hostetler 2001; Cane et al. 2006; Gotlieb et al. 2011; Wojcik and McBride 2012; Threlfall et al. 2015) and even fewer studied bees in tropical urban habitat (Zanette et al. 2005; Nemésio and Silveira 2007). Understanding the link of bee fitness, bee abundance and pollination service may however be specifically important in tropical environments, because dependency on bee pollinators increases towards the tropics (Winfree 2010; Ollerton et

al. 2011) and with generally higher biodiversity in tropical habitats, loss of natural habitat due to urbanization has even more devastating effects (Bradshaw et al. 2009; Seto et al. 2012). Ultimately, the global situation of bees in urban gardens remains unclear to date, but by providing the first bee fitness data for subtropical bees in urban habitat, this thesis contributes new insights and an incentive to find more generalized conclusions.

Furthermore, cities across the globe differ greatly in access to natural habitat, the availability of green space and total plant diversity. Even within cities, bee assemblages differ between neighbourhoods (Matteson et al. 2013; Lowenstein et al. 2014) or along urbanization gradients (McKinney 2008; Ahrné et al. 2009), and the value of urban bee habitat thus changes with socio-economic context or amount of sealed surfaces. Therefore, there is no unified definition of suburban or urban garden habitat. Consequently, studies can show seemingly conflicting evidence when using habitat categories, e.g. when comparing 'gardens' to 'rural habitats' (Bates et al. 2011; Baldock et al. 2015). It is therefore of great importance to identify the underlying key factors driving bee foraging and fitness in gardens, e.g. resource abundance and plant richness (Chapter IV & V).

It has been recently suggested to classify the current geological epoch as the 'Anthropocene', to acknowledge how human activities permanently reshaped the planet, as future geologists will find the dawn of the Anthropocene marked in ice and soil layers by ash, fertilizer, pesticides and plastic (Carey 2016). Human impacts are now at least as important as natural processes in ecosystems, adding new significant selection pressures on organisms, but also offering novel ecosystems for species to inhabit (Corlett 2015). The primary human habitats, cities, are predicted to expand massively in the next decades, with urban land cover increasing by 1.2 million km² until 2030, thus nearly tripling the global urban land area compared to 2000 (Seto et al. 2012). As a result, planning decisions for urban infrastructure made today will have vast impacts on how coming generations will live and if other species will be able to co-inhabit our urban environments. Urban planners are thus calling on ecologists to take a proactive role and help design better urban environments to achieve conservation goals (Chapin and Fernandez 2013; Felson et al. 2013). To understand whether and how species (e.g. bees) can actually adapt to urban habitat, comparative studies measuring fitness benefits of novel traits in urban environments will become increasingly relevant (Donihue and Lambert 2015).

Biodiversity trends in the Anthropocene depend on spatial scale, but while current knowledge is still patchy, it has been suggested that global plant diversity could actually increase due to hybridization of plants with introduced species (Thomas 2013; McGill et al. 2015). In urban habitats, plant richness was often found to increase with moderate urbanization due to high richness of introduced plants (McKinney 2008; Baldock et al. 2015), as garden owners often plant a diverse mix of native and exotic plants to feature flowers in multiple seasons (Head et al. 2004; Loram et al. 2008; Shwartz et al. 2014). While this is often done purely for aesthetical reasons, high plant richness and season-long flowering also provides a continuous supply of floral resources for many pollinators and can thus support larger bee populations (Antonini and Martins 2003; Hülsmann et al. 2015).

Our studies revealed that increased resource foraging and fitness of bees in urban gardens is directly driven by plant species richness (Chapter II-V). We thus found that bees can clearly benefit from increasing plant richness and utilize native and exotic plants alike. Our findings are however likely limited to generalist social bees, as some bee species may depend on (specific) native plants more strongly and will consequently be absent in urban habitats (Pardee and Philpott 2014; Harrison and Winfree 2015). Our results highlight that, while overall plant diversity is of critical importance for generalist social bees, plant richness can be natural or artificial and can be provided by native as well as exotic plants and by maintaining plant diversity in cities we may be able to create a nurturing environment for humans as well as other species. Social bees show a great potential to thrive in urban habitats, yet whether they can actually adapt to man-made habitats beyond mere co-existence remains to be investigated.

6.4. Effects of plant biodiversity on social bees

While it has been long observed that biodiverse natural and semi-natural habitats support highest bee species richness and abundance (Winfree et al. 2009; Kennedy et al. 2013), the mechanisms, *how* biodiversity may benefit bee species, remained unknown. Conversely, studies occasionally found surprisingly high bee abundance and diversity in disturbed or otherwise anthropogenically formed habitat, such as gardens (Winfree et al. 2007; Fetridge et al. 2008; Gotlieb et al. 2011; Hinners et al. 2012), but plant biodiversity as underlying concept driving bee fitness and consequently bee populations has not yet been systematically investigated.

We predicted two main conceptual paths of how higher biodiversity may affect bee

foraging and ultimately bee fitness (Chapter I: Figure I.3A & B): (a) via higher plant species richness and thus greater resource diversity and (b) via continuous plant resource availability across seasons. First, we found that bees can greatly utilize high resource diversity in diverse habitats and even maximize the diversity of collected plant resources (Chapter IV). Second, we found that bees are able to maintain high or highest foraging activity and thus resource intake across all seasons in landscapes with highest plant biodiversity (i.e. gardens in our study; Chapter II).

Of the predicted second tier effects of biodiversity, namely on resource quality and quantity (Figure I.3C), we found clear evidence that foraged resource quantity (overall food stores in the nest) is highest in the habitats with highest plant richness (Chapter V). In contrast, quality of resources collected by foragers and in nest storage pots were typically independent of overall plant species richness (amount of pollen protein, amino acids, sugar concentration of nectar or honey, antimicrobial activity of resin), but some measurements of resource quality were found to increase with plant richness (phosphorus and other micro nutrients in pollen, Chapter V). Instead, the presence of specific plant species providing high quality resources (e.g. protein-rich macadamia pollen) or resource compounds (as contained in resins of some eucalypt trees) seem to be more relevant to maintain resource quality and functionality (Chapter IV). Single resources can thus even be found in high quality in impoverished landscapes (e.g. macadamia plantations). However, as nutritional bottlenecks or dependencies on particular plant species (or specific plant resources) are often unknown for bee species, higher plant biodiversity can clearly safeguard for resource quality limitations as well.

Overall, bee hive reproduction benefits from greater plant species richness, as high plant species richness supports a continuous resource supply and, in total, greater colony food storages (Figure I.3D). Both the overall colony population (brood volume) and the number of reproductive animals (queens) increase with plant richness and resource quantity (i.e. colony food stores, Chapter V). In contrast, fitness of individual workers was not linked to plant biodiversity, i.e. plant species richness. While fitness of individuals can be impaired by reduced resource quantity or quality (Quezada-Euan et al. 2011; Pech-May et al. 2012), the colonies in our study seem to primarily reduce the total number of workers produced when facing resource scarcities, instead of producing workers with lower fitness (Chapter V).

Theoretical predictions and integrative models highlight that habitats with higher biodiversity and higher plant richness have a higher biomass productivity (Duffy et al. 2007; Grace et al. 2016) and thus produce a greater total abundance of plant resources to be exploited by consumers. In our studies, we quantified the total plant resource

abundance available per plot per year. Our measurement of plant resource abundance strongly weighs common species over rare ones and flowering trees over herbs, thereby rating forests higher than gardens. However, we found total plant resource abundance (summed up over the whole year) to be weaker predictor of bee foraging and fitness than plant species richness *per se*. While both plant richness and overall plant resource abundance affected the diversity of foraged resources, only plant richness directly affected bee fitness (Chapter IV & V).

Higher plant biodiversity in landscapes can also offer a wider range of flowering phenologies (i.e. flowers might be available in different months), and phenological complementarity is predicted to provide more continuous resource availability across seasons (Blüthgen and Klein 2011). In fact, continuously high floral resource availability in landscapes was shown to improve bee fitness and increase overall diversity and abundance of bee species (Hines and Hendrix 2005; Williams et al. 2012). These findings are in accordance with our studies, as we observed continuously high foraging rates (and consequently larger food stores) in habitats with highest plant species richness (i.e. gardens; Chapter II). By investigating total plant resource abundance and plant richness effects separately, our results further support that (at least generalist social) bee species foraging and fitness seem to be more directly limited by continuous resource availability, which we attribute to lower plant species richness (Chapter V). Thus food resources do not only need to be available in sufficient abundance, they need to be dependably available over long periods for bee colonies to successively build up the colony population, including foragers and reproductives. This limitation gains even more importance when the total foraging and reproduction period is shorter, e.g. in temperate zones (Williams et al. 2012; Requier et al. 2015). While social bee colonies can respond to a temporal overabundance of food resources by increasing foraging activity (Chapter II), a colony needs to have a large enough population to recruit for foraging. A small bee colony may benefit only little from pulsed mass flowering, as they first need to invest the freshly foraged resources into new worker reproduction. New workers of these colonies may thus hatch too late to utilize abundant, but short-lived resources, resulting in comparatively lower food intake for weak colonies (e.g. in plantations, Chapter II & V). In contrast, colonies maintaining greater food stores and a larger worker population may be quicker to respond and with greater reward to pulsed floral resources, but face higher costs to maintain the larger population. These costs can however be met when food resources are continuously available and colonies command larger food reserves (e.g. in gardens, Chapter II & V). Forests had on average a higher number of flowering trees and thus greater plant

resource abundance than gardens, yet gardens provided higher plant richness and thus a continuous resource availability, allowing colonies to maintain larger food storages in nests and consequently promoted higher fitness and colony reproduction (Chapter IV & V). Social bee fitness thus thrives in biodiverse habitats, as they provide continuous resource availability which in turn helps maintain greater colony resource reserves. Our studies therefore illustrate the mechanisms, how plant biodiversity can affect social bee fitness. While we identified multiple complex interactions between the studied factors, the study system seems to be less complex than anticipated, as important fitness factors were strongly driven by plant species richness (Figure V.3). Consequently, this thesis highlights the outstanding role of plant biodiversity on bee resource foraging and fitness.

Studying bee fitness in response to resource availability and diversity in landscapes greatly improves our understanding of the relationship between plant biodiversity and bee populations (Crone and Williams 2016), as it helps separating true bee population size effects from short term behavioural responses to resource abundance (Chapter I). National scale assessments showed that bee abundance is typically limited by plant abundance and thus plant resources (Biesmeijer et al. 2006; Baude et al. 2016), but existing large scale studies are limited to temperate climate zones. Generalist social bees are of even greater importance in (sub-) tropical climate zones, as they often dominate tropical bee communities (Klein et al. 2007; Winfree 2010). As bee population trends in subtropical and tropical systems however remain critically understudied (Goulson et al. 2015), this thesis adds an important perspective, underlining that findings investigating the plant resource - bee abundance relationship may be in fact universal across climate zones. Moreover, while some studies previously showed the positive influence of plant species richness on bee abundance (Antonini and Martins 2003; Hülsmann et al. 2015), our work provides a mechanistic framework (at least for generalist social bees) and identifies how biodiversity can drive bee abundance.

Expanded to a general scope, plant biodiversity, regardless whether it is provided by native or exotic plants, seems to be of critical importance to protect food security for bees and to ensure not only short term survival, but indeed reproduction of bees. Habitats with greater biodiversity can thus support greater bee abundances, safeguard bee population survival and increase the resilience of the whole system. Human food production widely benefits from wild bees for their free pollination services, and human food security is consequently affected by biodiversity as well. It thus remains imperative to maintain or create biodiverse landscapes to create refuges for both humans and wild bees.

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Results of generalized linear mixed effect models (exported from R Statistics). Models show the effects of landscape and season on various foraging parameters in the stingless bee *Tetragonula carbonaria*.

Activity

```
> summary(model_activity)
Linear mixed model fit by REML
Formula: activity_l_sqrt ~ landscape + (1 | site/as.factor(activity_data$hive))
   Data: activity_data
  AIC  BIC logLik deviance REMLdev
 1459 1482 -723.3     1449    1447
Random effects:
 Groups                                Name        Variance Std.Dev.
 as.factor(activity_data$hive):site (Intercept) 0.0000   0.0000
 site                                 (Intercept) 1.1192   1.0579
 Residual                                         2.8604   1.6913
Number of obs: 366, groups: as.factor(activity_data$hive):site, 48; site, 12

Fixed effects:
            Estimate Std. Error t value
(Intercept)   3.2605     0.5635   5.787
landscape_F   1.5693     0.7950   1.974
landscape_G   2.5217     0.7992   3.155

Correlation of Fixed Effects:
            (Intr) lands_F
landscape_F -0.709
landscape_G -0.705  0.500
```

Pollen foragers / min

```
> summary(model_forager)
Generalized linear mixed model fit by the Laplace approximation
Formula: For_a ~ landscape * season_total + (1 | site/as.factor(activity_data$hive))
   Data: activity_data
  AIC  BIC logLik deviance
 2549 2591  -1263     2527
Random effects:
 Groups                            Name        Variance Std.Dev.
 as.factor(activity_data$hive):site (Intercept) 0.66363  0.81464
 site                              (Intercept) 0.22739  0.47685
Number of obs: 366, groups: as.factor(activity_data$hive):site, 48; site, 12

Fixed effects:
                          Estimate Std. Error z value Pr(>|z|)
(Intercept)                 0.6396     0.3599   1.777  0.07554 .
landscape_F                 0.3462     0.4932   0.702  0.48274
landscape_G                 2.1401     0.4837   4.424 9.67e-06 ***
season_wet                 -1.1453     0.1473  -7.777 7.43e-15 ***
season_cold                 0.3146     0.1166   2.697  0.00699 **
landscape_F:season_wet      1.0787     0.1948   5.537 3.08e-08 ***
landscape_G:season_wet      0.4705     0.1722   2.732  0.00630 **
landscape_F:season_cold     0.2694     0.1735   1.553  0.12042
landscape_G:season_cold    -1.0811     0.1502  -7.197 6.15e-13 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr) lands_F lands_G seas_wet seas_col lands_F:seas_wet lands_G:seas_wet lands_F:seas_col
landscape_F     -0.730
landscape_G     -0.744  0.543
season_wet      -0.194  0.141   0.144
season_cold     -0.195  0.143   0.145   0.500
lands_F:seas_wet  0.146 -0.246 -0.109 -0.756   -0.378
lands_G:seas_wet  0.165 -0.121 -0.200 -0.855   -0.427   0.646
lands_F:seas_col  0.131 -0.224 -0.098 -0.336   -0.672   0.575            0.287
lands_G:seas_col  0.152 -0.111 -0.185 -0.388   -0.776   0.293            0.530            0.522
```

Nectar foragers / min

```
> summary(model_forager)
Generalized linear mixed model fit by the Laplace approximation
Formula: For_a ~ landscape * season_total + (1 | site/as.factor(activity_data$hive))
   Data: activity_data
  AIC  BIC logLik deviance
 2963 3006  -1470     2941
Random effects:
 Groups                             Name        Variance Std.Dev.
 as.factor(activity_data$hive):site (Intercept) 0.14985  0.38711
 site                               (Intercept) 0.11623  0.34092
Number of obs: 366, groups: as.factor(activity_data$hive):site, 48; site, 12

Fixed effects:
                       Estimate Std. Error z value Pr(>|z|)
(Intercept)              1.1531     0.2248   5.129 2.92e-07 ***
landscape_F              0.7314     0.3086   2.370 0.017786 *
landscape_G              1.9093     0.3075   6.209 5.33e-10 ***
season_wet               0.3460     0.1014   3.411 0.000646 ***
season_cold              0.5323     0.1078   4.939 7.86e-07 ***
landscape_F:season_wet   0.2335     0.1306   1.788 0.073742 .
landscape_G:season_wet  -0.7672     0.1302  -5.893 3.79e-09 ***
landscape_F:season_cold -0.1799     0.1401  -1.284 0.199054
landscape_G:season_cold -1.3774     0.1431  -9.624  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
             (Intr) lands_F lands_G seas_wet seas_col lands_F:seas_wet lands_G:seas_wet lands_F:seas_col
landscape_F   -0.729
landscape_G   -0.731  0.533
season_wet    -0.353  0.257   0.258
season_cold   -0.308  0.224   0.225  0.693
lands_F:seas_wet  0.274 -0.349 -0.200 -0.777   -0.538
lands_G:seas_wet  0.275 -0.200 -0.339 -0.779   -0.540   0.605
lands_F:seas_col  0.237 -0.297 -0.173 -0.533   -0.769   0.707           0.415
lands_G:seas_col  0.232 -0.169 -0.277 -0.522   -0.753   0.405           0.651           0.579
```

Resin foragers / min

```
> summary(model_forager)
Generalized linear mixed model fit by the Laplace approximation
Formula: For_a ~ landscape * season_total + (1 | site/as.factor(activity_data$hive))
   Data: activity_data
   AIC  BIC logLik deviance
 970.6 1014 -474.3    948.6
Random effects:
 Groups                               Name        Variance Std.Dev.
 as.factor(activity_data$hive):site (Intercept) 0.21301  0.46153
 site                               (Intercept) 0.33580  0.57948
Number of obs: 366, groups: as.factor(activity_data$hive):site, 48; site, 12

Fixed effects:
                          Estimate Std. Error z value Pr(>|z|)
(Intercept)                 0.6522     0.3524   1.850   0.0642 .
landscape_F                -0.1723     0.4988  -0.346   0.7297
landscape_G                -0.8150     0.5292  -1.540   0.1235
season_wet                 -0.7831     0.1420  -5.516 3.47e-08 ***
season_cold                -0.9863     0.1750  -5.637 1.73e-08 ***
landscape_F:season_wet      1.2056     0.2206   5.466 4.61e-08 ***
landscape_G:season_wet      2.0332     0.2792   7.282 3.30e-13 ***
landscape_F:season_cold     1.3649     0.2509   5.441 5.30e-08 ***
landscape_G:season_cold     2.0386     0.3026   6.737 1.61e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr) lands_F lands_G seas_wet seas_col lands_F:seas_wet lands_G:seas_wet lands_F:seas_col
landscape_F   -0.707
landscape_G   -0.666  0.471
season_wet    -0.227  0.161  0.151
season_cold   -0.147  0.104  0.098  0.380
lands_F:seas_wet 0.146 -0.330 -0.097 -0.644  -0.245
lands_G:seas_wet 0.116 -0.082 -0.447 -0.508  -0.193  0.327
lands_F:seas_col 0.103 -0.246 -0.068 -0.265  -0.697  0.562            0.135
lands_G:seas_col 0.085 -0.060 -0.386 -0.220  -0.578  0.142            0.733            0.403
```

Unsuccessful foragers / min

```
> summary(model_forager)
Generalized linear mixed model fit by the Laplace approximation
Formula: For_a ~ landscape * season_total + (1 | site/as.factor(activity_data$hive))
   Data: activity_data
  AIC  BIC logLik deviance
 1534 1577 -755.9     1512
Random effects:
 Groups                                Name        Variance Std.Dev.
 as.factor(activity_data$hive):site (Intercept) 0.068885 0.26246
 site                                 (Intercept) 0.369838 0.60814
Number of obs: 366, groups: as.factor(activity_data$hive):site, 48; site, 12

Fixed effects:
                          Estimate Std. Error z value Pr(>|z|)
(Intercept)                1.66014    0.32767   5.066 4.05e-07 ***
landscape_F               -0.34368    0.46428  -0.740    0.459
landscape_G               -0.23717    0.46760  -0.507    0.612
season_wet                -0.54834    0.08451  -6.488 8.69e-11 ***
season_cold               -0.47989    0.09365  -5.125 2.98e-07 ***
landscape_F:season_wet     0.72380    0.13459   5.378 7.53e-08 ***
landscape_G:season_wet     0.99684    0.14853   6.712 1.93e-11 ***
landscape_F:season_cold    1.07364    0.14077   7.627 2.41e-14 ***
landscape_G:season_cold    1.49531    0.15131   9.883  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
                (Intr) lands_F lands_G seas_wet seas_col lands_F:seas_wet lands_G:seas_wet lands_F:seas_col
landscape_F     -0.706
landscape_G     -0.701  0.495
season_wet      -0.164  0.116   0.115
season_cold     -0.119  0.084   0.083  0.478
lands_F:seas_wet 0.103 -0.222  -0.072 -0.628   -0.300
lands_G:seas_wet 0.093 -0.066  -0.256 -0.569   -0.272   0.357
lands_F:seas_col 0.079 -0.175  -0.055 -0.318   -0.665   0.609            0.181
lands_G:seas_col 0.073 -0.052  -0.218 -0.296   -0.619   0.186            0.688            0.412
```

Proportion of pollen foragers

```
> summary(model_prop)
Generalized linear mixed model fit by the Laplace approximation
Formula: prop ~ landscape * season_total + (1 | site/as.factor(proportion$hive))
   Data: proportion
  AIC  BIC logLik deviance
 1696 1740 -836.8     1674
Random effects:
 Groups                            Name        Variance Std.Dev.
 as.factor(proportion$hive):site (Intercept) 0.481790 0.69411
 site                             (Intercept) 0.093858 0.30636
Number of obs: 414, groups: as.factor(proportion$hive):site, 49; site, 12

Fixed effects:
                          Estimate Std. Error z value Pr(>|z|)
(Intercept)               -1.40694    0.26392  -5.331 9.77e-08 ***
landscape_F               -0.03722    0.36537  -0.102 0.918862
landscape_G                0.32456    0.37454   0.867 0.386179
season_wet                -1.06527    0.12499  -8.523  < 2e-16 ***
season_cold               -0.19096    0.12293  -1.553 0.120329
landscape_F:season_wet     0.75939    0.17611   4.312 1.62e-05 ***
landscape_G:season_wet     0.93296    0.19393   4.811 1.50e-06 ***
landscape_F:season_cold    0.59049    0.17869   3.305 0.000951 ***
landscape_G:season_cold   -0.02848    0.19942  -0.143 0.886436
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr) lands_F lands_G seas_wet seas_col lands_F:seas_wet lands_G:seas_wet lands_F:seas_col
landscape_F   -0.722
landscape_G   -0.705  0.509
season_wet    -0.228  0.165   0.161
season_cold   -0.182  0.132   0.128   0.393
lands_F:seas_wet 0.162 -0.287 -0.114 -0.710   -0.279
lands_G:seas_wet 0.147 -0.106 -0.341 -0.645   -0.253   0.457
lands_F:seas_col 0.125 -0.204 -0.088 -0.271   -0.688   0.429            0.174
lands_G:seas_col 0.112 -0.081 -0.274 -0.242   -0.616   0.172            0.527            0.424
```

Proportion of nectar foragers

```
> summary(model_prop)
Generalized linear mixed model fit by the Laplace approximation
Formula: prop ~ landscape * season_total + (1 | site/as.factor(proportion$hive))
   Data: proportion
  AIC  BIC logLik deviance
 1768 1812 -872.9     1746
Random effects:
 Groups                            Name         Variance Std.Dev.
 as.factor(proportion$hive):site (Intercept) 0.154868 0.39353
 site                            (Intercept) 0.060565 0.24610
Number of obs: 414, groups: as.factor(proportion$hive):site, 49; site, 12

Fixed effects:
                         Estimate Std. Error z value Pr(>|z|)
(Intercept)             -1.18047    0.18419  -6.409 1.47e-10 ***
landscape_F              0.52127    0.25790   2.021  0.04326 *
landscape_G              1.36665    0.26666   5.125 2.97e-07 ***
season_wet               0.82250    0.09733   8.450  < 2e-16 ***
season_cold              0.35407    0.11360   3.117  0.00183 **
landscape_F:season_wet  -0.32605    0.14019  -2.326  0.02003 *
landscape_G:season_wet  -1.36592    0.15745  -8.675  < 2e-16 ***
landscape_F:season_cold -0.50418    0.16141  -3.124  0.00179 **
landscape_G:season_cold -1.57039    0.18151  -8.652  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
                (Intr) lands_F lands_G seas_wet seas_col lands_F:seas_wet lands_G:seas_wet lands_F:seas_col
landscape_F     -0.714
landscape_G     -0.691  0.493
season_wet      -0.367  0.262   0.253
season_cold     -0.277  0.198   0.192  0.532
lands_F:seas_wet 0.255 -0.395  -0.176 -0.694   -0.369
lands_G:seas_wet 0.227 -0.162  -0.440 -0.618   -0.329    0.429
lands_F:seas_col 0.195 -0.277  -0.135 -0.375   -0.704    0.521            0.232
lands_G:seas_col 0.174 -0.124  -0.323 -0.333   -0.626    0.231            0.536            0.440
```

Proportion of resin foragers

```
> summary(model_prop)
Generalized linear mixed model fit by the Laplace approximation
Formula: prop ~ landscape * season_total + (1 | site/as.factor(proportion$hive))
   Data: proportion
  AIC  BIC logLik deviance
 1046 1090 -511.9     1024
Random effects:
 Groups                            Name         Variance Std.Dev.
 as.factor(proportion$hive):site (Intercept) 0.19004  0.43594
 site                             (Intercept) 0.15235  0.39032
Number of obs: 414, groups: as.factor(proportion$hive):site, 49; site, 12

Fixed effects:
                           Estimate Std. Error z value Pr(>|z|)
(Intercept)                 -1.7761     0.2537  -7.001 2.55e-12 ***
landscape_F                 -0.3064     0.3639  -0.842   0.3999
landscape_G                 -1.6359     0.4131  -3.960 7.48e-05 ***
season_wet                  -0.0735     0.1282  -0.573   0.5665
season_cold                 -0.7177     0.1747  -4.108 3.99e-05 ***
landscape_F:season_wet       0.2777     0.1984   1.400   0.1615
landscape_G:season_wet       1.2815     0.2730   4.694 2.68e-06 ***
landscape_F:season_cold      0.6398     0.2453   2.608   0.0091 **
landscape_G:season_cold      1.6301     0.3081   5.291 1.22e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
                (Intr) lands_F lands_G seas_wet seas_col lands_F:seas_wet lands_G:seas_wet lands_F:seas_col
landscape_F     -0.697
landscape_G     -0.614  0.428
season_wet      -0.323  0.225  0.198
season_cold     -0.200  0.139  0.123  0.406
lands_F:seas_wet 0.209 -0.389 -0.128 -0.646    -0.262
lands_G:seas_wet 0.152 -0.106 -0.550 -0.470    -0.191   0.304
lands_F:seas_col 0.142 -0.245 -0.087 -0.289    -0.712   0.464           0.136
lands_G:seas_col 0.113 -0.079 -0.446 -0.230    -0.567   0.149           0.670            0.404
```

Proportion of unsuccessful foragers

```
> summary(model_prop)
Generalized linear mixed model fit by the Laplace approximation
Formula: prop ~ landscape * season_total + (1 | site/as.factor(proportion$hive))
   Data: proportion
  AIC  BIC logLik deviance
 1315 1359 -646.3     1293
Random effects:
 Groups                             Name         Variance Std.Dev.
 as.factor(proportion$hive):site (Intercept) 0.073002 0.27019
 site                               (Intercept) 0.039313 0.19828
Number of obs: 414, groups: as.factor(proportion$hive):site, 49; site, 12

Fixed effects:
                         Estimate Std. Error z value Pr(>|z|)
(Intercept)             -0.52873    0.14537  -3.637 0.000276 ***
landscape_F             -0.29187    0.21154  -1.380 0.167664
landscape_G             -0.90446    0.22397  -4.038 5.38e-05 ***
season_wet              -0.10878    0.09066  -1.200 0.230218
season_cold              0.12967    0.10310   1.258 0.208488
landscape_F:season_wet  -0.42379    0.14324  -2.959 0.003091 **
landscape_G:season_wet   0.26478    0.16016   1.653 0.098291 .
landscape_F:season_cold -0.26426    0.15700  -1.683 0.092344 .
landscape_G:season_cold  0.87028    0.16969   5.129 2.92e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr) lands_F lands_G seas_wet seas_col lands_F:seas_wet lands_G:seas_wet lands_F:seas_col
landscape_F   -0.687
landscape_G   -0.649  0.446
season_wet    -0.391  0.268   0.254
season_cold   -0.296  0.203   0.192   0.483
lands_F:seas_wet 0.247 -0.453 -0.160 -0.633  -0.306
lands_G:seas_wet 0.221 -0.152 -0.515 -0.566  -0.273  0.358
lands_F:seas_col 0.194 -0.316 -0.126 -0.317  -0.657  0.477            0.180
lands_G:seas_col 0.180 -0.124 -0.412 -0.293  -0.608  0.186            0.564            0.399
```

Pollen load size

```
> summary (model_loads)
Linear mixed model fit by REML
Formula: loads ~ season_total + (1 | site/as.factor(loads_data$hive))
   Data: loads_data
   AIC   BIC logLik deviance REMLdev
 349.2 371.6 -168.6    325.8    337.2
Random effects:
 Groups                           Name         Variance  Std.Dev.
 as.factor(loads_data$hive):site (Intercept) 0.0042788 0.065413
 site                             (Intercept) 0.0350893 0.187321
 Residual                                     0.1564168 0.395496
Number of obs: 307, groups: as.factor(loads_data$hive):site, 51; site, 12

Fixed effects:
               Estimate Std. Error t value
(Intercept)     1.13301    0.08045  14.083
season_wet      0.19143    0.06342   3.018
season_cold    -0.19940    0.07067  -2.821

Correlation of Fixed Effects:
           (Intr) seas_wet
season_wet  -0.638
season_cold -0.495  0.628
```

Pollen intake (mg / min)

```
> summary(model_pollen)
Generalized linear mixed model fit by the Laplace approximation
Formula: pollen ~ landscape + season_total + (1 | site/as.factor(pollen_total_data$hive))
   Data: pollen_total_data
  AIC  BIC logLik deviance
 1364 1391 -674.8     1350
Random effects:
 Groups                                  Name        Variance Std.Dev.
 as.factor(pollen_total_data$hive):site (Intercept) 0.163616 0.40449
 site                                    (Intercept) 0.034804 0.18656
Number of obs: 366, groups: as.factor(pollen_total_data$hive):site, 48; site, 12

Fixed effects:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)      1.34266    0.16133   8.322  < 2e-16 ***
landscape_F      0.45453    0.21187   2.145 0.031925 *
landscape_G      0.78638    0.21104   3.726 0.000194 ***
season_wet      -0.14157    0.06161  -2.298 0.021568 *
season_cold     -0.21523    0.06791  -3.169 0.001528 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) lands_F lands_G seas_wet
landscape_F -0.695
landscape_G -0.696  0.539
season_wet  -0.268 -0.032 -0.037
season_cold -0.220 -0.010 -0.028  0.623
```

Nectar concentration

```
> summary(model_concentration)
Linear mixed model fit by REML
Formula: concentration ~ landscape * season_total + (1 | site/as.factor(conc_data$hive))
   Data: conc_data
   AIC    BIC logLik deviance REMLdev
 22336 22406 -11156    22339   22312
Random effects:
 Groups                         Name        Variance Std.Dev.
 as.factor(conc_data$hive):site (Intercept) 12.204   3.4934
 site                           (Intercept) 30.185   5.4941
 Residual                                   263.589  16.2354
Number of obs: 2647, groups: as.factor(conc_data$hive):site, 53; site, 12

Fixed effects:
                        Estimate Std. Error t value
(Intercept)               68.916      3.043  22.651
landscape_F               -0.503      3.885  -0.130
landscape_G               -7.592      4.305  -1.763
season_wet               -10.944      1.580  -6.926
season_cold               -6.189      1.828  -3.385
landscape_F:season_wet    -7.336      2.227  -3.294
landscape_G:season_wet     1.981      2.449   0.809
landscape_F:season_cold   -5.224      2.557  -2.043
landscape_G:season_cold   -1.843      2.752  -0.670

Correlation of Fixed Effects:
              (Intr) lands_F lands_G seas_wet seas_col lands_F:seas_wet lands_G:seas_wet lands_F:seas_col
landscape_F   -0.676
landscape_G   -0.691  0.529
season_wet    -0.442  0.357   0.314
season_cold   -0.346  0.272   0.245   0.673
lands_F:seas_wet 0.305 -0.494 -0.211 -0.710   -0.478
lands_G:seas_wet 0.281 -0.245 -0.450 -0.646   -0.434  0.457
lands_F:seas_col 0.250 -0.381 -0.177 -0.481   -0.715  0.661            0.311
lands_G:seas_col 0.229 -0.184 -0.337 -0.447   -0.664  0.317            0.599            0.475
```

Sugar intake (mg / min)

```
> summary(model_sugar)
Generalized linear mixed model fit by the Laplace approximation
Formula: sugar ~ landscape * season_total + (1 | site/as.factor(sugar_data$hive))
   Data: sugar_data
     AIC     BIC  logLik deviance
 1899619 1899662 -949799  1899597
Random effects:
 Groups                           Name        Variance Std.Dev.
 as.factor(sugar_data$hive):site (Intercept) 0.274801 0.52421
 site                            (Intercept) 0.062475 0.24995
Number of obs: 366, groups: as.factor(sugar_data$hive):site, 48; site, 12

Fixed effects:
                          Estimate Std. Error z value Pr(>|z|)
(Intercept)               6.892722   0.189490   36.38  < 2e-16 ***
landscape_F               0.981429   0.260355    3.77 0.000164 ***
landscape_G               2.688392   0.260819   10.31  < 2e-16 ***
season_wet                1.025930   0.005464  187.75  < 2e-16 ***
season_cold               0.997624   0.005853  170.44  < 2e-16 ***
landscape_F:season_wet    0.146078   0.006782   21.54  < 2e-16 ***
landscape_G:season_wet   -1.635497   0.006530 -250.46  < 2e-16 ***
landscape_F:season_cold  -0.828214   0.007529 -110.00  < 2e-16 ***
landscape_G:season_cold  -2.318527   0.007370 -314.60  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr) lands_F lands_G seas_wet seas_col lands_F:seas_wet lands_G:seas_wet lands_F:seas_col
landscape_F   -0.728
landscape_G   -0.727  0.529
season_wet    -0.025  0.018   0.018
season_cold   -0.023  0.016   0.016   0.786
lands_F:seas_wet  0.020 -0.023 -0.015 -0.806   -0.634
lands_G:seas_wet  0.021 -0.015 -0.021 -0.837   -0.658    0.674
lands_F:seas_col  0.018 -0.020 -0.013 -0.611   -0.777    0.768            0.512
lands_G:seas_col  0.018 -0.013 -0.018 -0.625   -0.794    0.503            0.703            0.617
```

7.2.   Appendix II: plant species list

List of recorded plant species. Given are plant species, the plant form (i.e. size and thus number of flowers per plant; $_p$F, **H**: herb; **S**: shrub; **T**: tree) and its status ($_p$S, **N**: native, **E**: exotic)in the study region. Study sites are coded as follows: **F1**-**F4** (**a/b**) are paired forest study sites, **G1a**-**G4b** single garden sites and **P1**-**P4** (**a/b**) paired plantation sites. Letters indicate abundance of the plant species per respective study site: **r**: rare (1-5 individuals) per plant species, **u**: uncommon (6-16 individuals) and **c**: common (>16 individuals), pages 207-242.

	Family	Genus	Species	$_p$F	$_p$S	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
1	Acanthaceae	*Barleria*	*obtusa*	S	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
2	Acanthaceae	*Barleria*	*repens*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
3	Acanthaceae	*Brunoniella*	*australis*	H	N	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4	Acanthaceae	*Dyschoriste*	*depressa*	H	E	.	.	.	.	.	.	.	.	.	.	c	.	.	.	.	.
5	Acanthaceae	*Graptophyllum*	*ilicifolium*	S	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
6	Acanthaceae	*Graptophyllum*	*reticulatum*	S	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
7	Acanthaceae	*Hypoestes*	*aristata*	H	E	.	.	.	.	.	.	.	.	.	.	r	u	.	.	.	.
8	Acanthaceae	*Hypoestes*	*phyllostachya*	H	E	.	.	.	.	u	.	.	.	.	.	c	c	.	.	.	.
9	Acanthaceae	*Justicia*	*betonica*	H	E	.	.	.	.	.	.	r	.	.	.	c	.	.	.	.	.
10	Acanthaceae	*Justicia*	*brandegeeana*	H	E	.	.	.	.	.	.	.	.	u	.	.	r	.	.	.	.
11	Acanthaceae	*Odontonema*	*tubaeforme*	S	E	.	.	.	.	.	.	.	.	r	r	c	.	.	.	.	.
12	Acanthaceae	*Pseuderanthemum*	*variabile*	H	N	.	r	r	c	.	.	.	.	.	.	.	.	u	.	.	.
13	Acanthaceae	*Rostellularia*	*obtusa*	H	N	.	.	.	.	.	.	.	.	.	.	.	.	u	.	.	.
14	Acanthaceae	*Ruellia*	*tweediana*	H	E	.	.	.	.	.	.	r	.	c	u	.	c	.	.	.	.
15	Acanthaceae	*Thunbergia*	*alata*	H	E	.	.	.	u	.	.	.	.	.	.	r	.	.	.	.	.
16	Acanthaceae	*Thunbergia*	*grandiflora*	H	E	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
17	Acanthaceae	*Thunbergia*	*laurifolia*	H	E	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
18	Adoxaceae	*Sambucus*	*nigra*	S	E	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
19	Adoxaceae	*Sambucus*	*sp.*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
20	Adoxaceae	*Viburnum*	*odoratissimum*	S	E	.	.	.	.	.	.	r	r	.	r	.	r	.	.	.	.

	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
21	Adoxaceae	*Viburnum*	*tinus*	S	E	.	.	.	.	.	.	.	.	r	.	u	u	.	.	.	.
22	Agavaceae	*Agave*	*angustifolia*	H	E	.	.	.	.	.	.	u	.	r	.	.	.	.	.	.	.
23	Agavaceae	*Agave*	*attenuata*	H	E	.	.	.	.	c	u	.	c	u	c	r	u	.	.	.	.
24	Agavaceae	*Agave*	*sisalana*	S	E	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.
25	Agavaceae	*Agave*	*sp.*	H	E	.	.	.	.	r	.	u	.	.	.	u	.	.	.	.	.
26	Agavaceae	*Agave*	*sp. 2*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
27	Agavaceae	*Agave*	*sp. 3*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
28	Agavaceae	*Yucca*	*gigantea*	S	E	.	.	.	.	c	u	.	c	r	u	u	u	.	.	.	.
29	Aizoaceae	*Carpobrotus*	*sp.*	H	N	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.
30	Aizoaceae	*Sesuvium*	*portulacastrum*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
31	Aizoaceae	*Tetragonia*	*tetragonioides*	H	N	.	.	.	.	c	.	.	.	.	.	r	.	.	.	.	.
32	Alliaceae	*Nothoscordum*	*borbonicum*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.
33	Alliaceae	*Tulbaghia*	*violacea*	H	E	.	.	.	.	.	.	.	.	.	.	u	c	r	.	.	.
34	Alstroemeriaceae	*Alstroemeria*	*pulchella*	H	E	.	.	.	.	.	.	r	.	.	.	r	.	.	.	.	.
35	Altingiaceae	*Liquidambar*	*styraciflua*	T	E	.	.	.	.	r	r	.	.	.	.	r	.	.	.	.	.
36	Amaranthaceae	*Alternanthera*	*dentata*	H	E	.	.	.	.	c	.	r	r	u	c	.	r	.	.	.	.
37	Amaranthaceae	*Alternanthera*	*denticulata*	H	N	.	.	.	.	r	u	.	.	.	.	.	.	c	c	c	c
38	Amaranthaceae	*Alternanthera*	*nana*	H	N	.	.	.	.	.	.	.	.	.	c	.	.	.	r	.	.
39	Amaranthaceae	*Alternanthera*	*pungens*	H	E	.	.	.	.	.	.	.	.	r	.	.	u	.	.	r	.
40	Amaranthaceae	*Amaranthus*	*hypochondriacus*	H	E	.	.	.	.	.	.	.	.	.	r	u	.	.	.	.	.
41	Amaranthaceae	*Amaranthus*	*viridis*	H	E	.	.	.	.	c	c	u	u	c	c	c	c	c	c	c	u
42	Amaranthaceae	*Beta*	*vulgaris*	H	E	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
43	Amaranthaceae	*Celosia*	*cristata*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
44	Amaranthaceae	*Gomphrena*	*celosioides*	H	E	.	.	.	c	c	c	.	u	u	c	.	c	c	c	c	.
45	Amaryllidaceae	*Agapanthus*	*africanus*	H	E	.	.	.	.	.	.	u	c	.	c	c	.	.	.	.	.
46	Amaryllidaceae	*Agapanthus*	*praecox*	H	E	.	.	.	.	u	.	.	c	.	.	c	c	.	.	r	.
47	Amaryllidaceae	*Allium*	*cepa*	H	E	.	.	.	.	.	.	r	.	r	u	.	.	.	.	r	.
48	Amaryllidaceae	*Allium*	*sativum*	H	E	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
49	Amaryllidaceae	*Allium*	*schoenoprasum*	H	E	.	.	.	.	.	.	.	r	u	.	u	r	.	.	.	.
50	Amaryllidaceae	*Allium*	*sp.*	H	E	.	.	.	.	.	.	u	.	.	.	.	.	r	.	.	.
51	Amaryllidaceae	*Allium*	*tuberosum*	H	E	.	.	.	.	c	.	r	r	r	r	.	.	.	.	.	.
52	Amaryllidaceae	*Clivia*	*miniata*	H	E	.	.	.	.	.	.	r	.	r	r	r	r	r	r	.	.

	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
53	Amaryllidaceae	*Crinum*	*pedunculatum*	H	N	.	u	r	.	.	r	r	.	.	r	.	r	.	.	.	.
54	Amaryllidaceae	*Hippeastrum*	*reginae*	H	E	.	.	.	.	c	.	.	r	.	.	u	.	.	.	.	.
55	Amaryllidaceae	*Hippeastrum*	*sp.*	H	E	.	.	.	.	.	u	u	.	.	.	.	r	.	.	r	.
56	Amaryllidaceae	*Hymenocallis*	*× festalis*	H	E	.	.	.	.	.	.	c	.	c	c	.	r	.	.	.	.
57	Amaryllidaceae	*Hymenocallis*	*littoralis*	H	E	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.
58	Amaryllidaceae	*Proiphys*	*cunninghamii*	H	N	.	.	.	.	.	.	.	.	r	r	r	r	.	.	.	.
59	Amaryllidaceae	*Scadoxus*	*multiflorus*	H	E	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
60	Amaryllidaceae	*Zephyranthes*	*candida*	H	E	.	.	.	.	.	.	.	r	c	u	c	c	.	.	.	.
61	Amaryllidaceae	*Zephyranthes*	*rosea*	H	E	.	.	.	.	r	.	.	.	u	.	u	.	.	.	.	.
62	Anacardiaceae	*Euroschinus*	*falcata*	T	N	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
63	Anacardiaceae	*Mangifera*	*indica*	T	E	.	.	.	u	r	c	u	r	u	u	c	r	.	.	.	.
64	Anacardiaceae	*Pistacia*	*sp.*	T	E	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
65	Anacardiaceae	*Pleiogynium*	*timorense*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
66	Anacardiaceae	*Rhodosphaera*	*rhodanthema*	T	N	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.
67	Anacardiaceae	*Schinus*	*terebinthifolius*	T	E	.	.	.	.	.	r	c	c	r	u	u	r	.	.	r	.
68	Angiopteridaceae	*Angiopteris*	*evecta*	S	N	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
69	Annonaceae	*Annona*	*squamosa*	T	E	.	.	.	.	.	r	.	.	.	.	r	.	.	.	.	.
70	Annonaceae	*Melodorum*	*leichhardtii*	H	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
71	Annonaceae	*Polyalthia*	*nitidissima*	T	N	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
72	Apiaceae	*Apium*	*graveolens*	H	E	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
73	Apiaceae	*Cyclospermum*	*leptophyllum*	H	E	.	.	.	.	c	u	.	c	r	.	c	c	c	c	c	.
74	Apiaceae	*Eryngium*	*foetidum*	H	E	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
75	Apiaceae	*Hydrocotyle*	*acutiloba*	H	N	.	.	.	.	.	c	.	.	.	r	.	r	.	.	c	.
76	Apiaceae	*Petroselinum*	*crispum*	H	E	.	.	.	.	r	r	r	.	c	.	u	r	.	.	.	.
77	Apiaceae	*Platysace*	*linearifolia*	S	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
78	Apocynaceae	*Adenium*	*obesum*	S	E	.	.	.	.	.	r	.	.	u	c	r	.	.	.	.	.
79	Apocynaceae	*Adenium*	*sp.*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
80	Apocynaceae	*Allamanda*	*cathartica*	H	E	.	.	.	.	c	u	r	u	u	u	.	r	.	.	.	.
81	Apocynaceae	*Alstonia*	*constricta*	T	N	.	c	.	.	.	r	.	.	.	.	.	.	.	.	.	.
82	Apocynaceae	*Alyxia*	*magnifolia*	S	N	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
83	Apocynaceae	*Alyxia*	*ruscifolia*	S	N	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
84	Apocynaceae	*Araujia*	*sericifera*	H	E	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.

7.2. Appendix II: plant species list

	Family	Genus	Species	$_PF$	$_PS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
85	Apocynaceae	*Asclepias*	*curassavica*	S	E	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.
86	Apocynaceae	*Carissa*	*macrocarpa*	S	E	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.
87	Apocynaceae	*Carissa*	*ovata*	S	N	.	u	r	.	.	.	.	.	.	.	.	.	.	.	.	.
88	Apocynaceae	*Cascabela*	*thevetia*	S	E	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.
89	Apocynaceae	*Catharanthus*	*roseus*	H	E	.	.	.	.	.	c	c	.	c	c	u	c	.	.	.	.
90	Apocynaceae	*Chonemorpha*	*fragrans*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
91	Apocynaceae	*Gomphocarpus*	*physocarpus*	S	E	.	u	.	.	.	.	.	.	.	.	r	.	.	.	.	.
92	Apocynaceae	*Hoya*	*australis*	H	N	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.
93	Apocynaceae	*Mandevilla*	*sanderi*	H	E	.	.	.	.	.	c	r	.	.	c	.	r	.	.	.	.
94	Apocynaceae	*Mandevilla*	*sp.*	S	E	.	.	.	.	c	.	.	c	c	.	.	.	.	.	.	.
95	Apocynaceae	*Marsdenia*	*sp.*	H	-	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
96	Apocynaceae	*Nerium*	*oleander*	S	E	.	.	.	.	r	r	c	r	r	u	r	.	.	.	r	.
97	Apocynaceae	*Pachypodium*	*lamerei*	S	E	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
98	Apocynaceae	*Parsonsia*	*sp.*	H	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
99	Apocynaceae	*Parsonsia*	*straminea*	H	N	.	r	.	r	.	.	.	.	.	r	.	.	.	.	r	u
100	Apocynaceae	*Plumeria*	*obtusifolia*	S	E	.	.	.	.	.	r	u	c	.	r	.	.	.	.	.	.
101	Apocynaceae	*Plumeria*	*rubra*	T	E	.	.	.	.	c	c	c	c	c	c	c	c	.	.	.	.
102	Apocynaceae	*Secamone*	*elliptica*	H	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
103	Apocynaceae	*Tabernaemontana*	*divaricata*	S	E	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.
104	Apocynaceae	*Tabernaemontana*	*pandacaqui*	S	N	.	r	u	.	.	.	.	.	.	.	.	.	.	.	.	.
105	Apocynaceae	*Thevetia*	*peruviana*	S	E	.	.	.	.	.	.	u	.	.	.	.	.	.	.	.	.
106	Apocynaceae	*Trachelospermum*	*jasminoides*	S	E	.	.	.	.	u	r	r	c	c	c	c	u	.	.	.	.
107	Apocynaceae	*Vinca*	*sp.*	S	E	.	.	.	.	c	.	.	c	.	.	.	.	.	.	.	.
108	Araceae	*Alocasia*	*× amazonica*	H	N	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
109	Araceae	*Alocasia*	*brisbanensis*	H	N	.	.	.	.	.	.	.	.	.	.	r	.	r	.	r	.
110	Araceae	*Alocasia*	*sp.*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
111	Araceae	*Anthurium*	*sp.*	H	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
112	Araceae	*Colocasia*	*esculenta*	H	E	.	.	.	.	.	u	.	.	.	.	.	c	.	.	.	.
113	Araceae	*Dieffenbachia*	*seguine*	H	E	.	.	.	.	r	.	r	.	r	.	r	.	.	.	.	.
114	Araceae	*Epipremnum*	*aureum*	H	E	.	.	.	.	r	.	r	.	r	r	c	r	.	.	.	.
115	Araceae	*Epipremnum*	*pinnatum*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
116	Araceae	*Gymnostachys*	*anceps*	H	N	.	.	c	c	.	.	.	.	.	.	.	.	.	.	.	.

#	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
117	Araceae	*Monstera*	*deliciosa*	S	E	.	.	.	r	r	r	r	r	u	r	u	r	.	.	r	.
118	Araceae	*Philodendron*	*bipinnatifidum*	S	E	.	.	.	.	c	r	r	.	r	u	r	r	.	.	.	.
119	Araceae	*Philodendron*	*erubescens*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
120	Araceae	*Philodendron*	*scandens*	H	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
121	Araceae	*Philodendron*	*sp.*	S	E	.	.	.	.	.	.	r	.	.	.	.	.	.	.	r	.
122	Araceae	*Philodendron*	*xanadu*	S	E	.	.	.	.	u	.	c	c	c	c	u	u	.	.	.	.
123	Araceae	*Pothos*	*longipes*	H	N	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
124	Araceae	*Spathiphyllum*	*sp.*	H	E	.	.	.	.	.	.	u	u	r	.	.	r	.	.	.	.
125	Araceae	*Syngonium*	*podophyllum*	H	E	.	.	.	.	c	u	u	u	c	c	c	c	.	.	c	.
126	Araliaceae	*Astrotricha*	*latifolia*	S	N	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.
127	Araliaceae	*Astrotricha*	*sp.*	S	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
128	Araliaceae	*Hedera*	*helix*	H	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
129	Araliaceae	*Polyscias*	*balfouriana*	S	E	.	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.
130	Araliaceae	*Polyscias*	*elegans*	T	N	.	c	c	c	.	.	.	.	.	.	r	.	.	.	.	.
131	Araliaceae	*Schefflera*	*actinophylla*	T	E	.	.	r	u	u	u	c	r	c	c	u	u	.	.	r	.
132	Araliaceae	*Schefflera*	*arboricola*	S	E	.	.	.	.	u	u	r	r	u	c	r	r	.	.	.	.
133	Araucariaceae	*Agathis*	*robusta*	T	N	.	.	.	.	.	.	r	.	r	.	u	c	.	.	.	.
134	Araucariaceae	*Araucaria*	*bidwillii*	T	N	.	.	.	.	.	.	.	.	.	.	r	u	.	.	.	.
135	Araucariaceae	*Araucaria*	*cunninghamii*	T	N	.	r	u	.	r	r	.	.	r	r	u	u	.	c	.	.
136	Araucariaceae	*Araucaria*	*heterophylla*	T	E	.	.	.	.	r	.	.	.	r	r	r	.	.	.	.	.
137	Arecaceae	*Archontophoenix*	*alexandrae*	T	N	.	.	.	.	c	c	c	c	c	c	c	c	.	.	r	r
138	Arecaceae	*Archontophoenix*	*cunninghamiana*	T	N	.	.	c	c	.	.	.	.	.	.	r	.	.	.	.	.
139	Arecaceae	*Calamus*	*muelleri*	H	N	.	.	c	r	.	.	.	.	.	.	.	.	.	.	.	.
140	Arecaceae	*Caryota*	*mitis*	T	E	.	.	.	.	.	.	u	.	.	r	.	.	.	.	.	.
141	Arecaceae	*Caryota*	*sp.*	T	E	.	.	.	.	r	.	.	r	.	.	.	.	.	.	.	.
142	Arecaceae	*Chamaedorea*	*cataractarum*	S	E	.	.	.	.	u	r	.	u	.	r	r	.	.	.	.	.
143	Arecaceae	*Chamaedorea*	*elegans*	S	E	.	.	.	.	u	u	c	r	u	u	r	.	.	.	.	.
144	Arecaceae	*Cocos*	*nucifera*	T	E	.	.	.	.	r	c	r	.	.	r	.	.	.	.	.	.
145	Arecaceae	*Dypsis*	*decaryi*	T	E	.	.	.	.	u	u	.	r	r	.	r	.	.	.	.	.
146	Arecaceae	*Dypsis*	*leptocheilos*	T	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
147	Arecaceae	*Dypsis*	*lutescens*	S	E	.	.	.	.	c	c	c	c	c	c	c	u	.	.	r	.
148	Arecaceae	*Howea*	*forsteriana*	T	N	.	.	.	.	.	.	.	.	r	r	r	.	r	.	.	.

	Family	Genus	Species	$_P$F	$_P$S	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
149	Arecaceae	*Livistona*	*australis*	T	N	.	.	c	c	.	.	.	c	.	.	.	.	.	.	.	.
150	Arecaceae	*Livistona*	*decora*	T	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
151	Arecaceae	*Livistona*	*lanuginosa*	T	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
152	Arecaceae	*Livistona*	*sp.*	T	N	.	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.
153	Arecaceae	*Phoenix*	*canariensis*	T	E	.	.	.	.	r	r	r	u	r	.	.	.	.	.	.	.
154	Arecaceae	*Phoenix*	*dactylifera*	T	E	.	.	.	.	r	.	.	u	.	.	r	.	.	.	.	.
155	Arecaceae	*Phoenix*	*roebelenii*	S	E	.	.	.	.	.	.	.	r	.	r	u	r	.	.	.	.
156	Arecaceae	*Ravenea*	*rivularis*	S	E	.	.	.	.	u	u	.	c	.	.	.	.	.	.	.	.
157	Arecaceae	*Rhapis*	*excelsa*	S	E	.	.	.	.	r	.	u	u	u	u	.	u	.	.	.	.
158	Arecaceae	*Roystonea*	*regia*	T	E	.	.	.	.	r	u	u	r	r	.	.	.	.	.	.	.
159	Arecaceae	*Syagrus*	*romanzoffiana*	T	E	.	.	.	.	c	.	c	c	c	c	c	c	.	.	.	.
160	Arecaceae	*Trachycarpus*	*fortunei*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
161	Arecaceae	*Washingtonia*	*robusta*	T	E	.	.	.	.	u	r	.	r	.	.	.	.	.	.	.	.
162	Arecaceae	*Wodyetia*	*bifurcata*	T	N	.	.	.	.	u	.	r	u	.	u	r	.	.	.	.	.
163	Aristolochiaceae	*Aristolochia*	*elegans*	H	E	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
164	Aristolochiaceae	*Pararistolochia*	*praevenosa*	H	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
165	Asclepiadaceae	*Stephanotis*	*floribunda*	H	E	.	.	.	.	.	.	.	.	r	.	.	r	.	.	.	.
166	Asparagaceae	*Asparagus*	*aethiopicus*	H	E	.	.	.	.	r	c	u	r	c	u	u	u	.	.	u	.
167	Asparagaceae	*Asparagus*	*africanus*	H	E	.	.	.	.	.	r	.	.	.	c	c	r	.	.	.	.
168	Asparagaceae	*Asparagus*	*densiflorus*	H	E	.	.	.	.	.	r	.	.	u	.	r	.	.	.	.	.
169	Asparagaceae	*Asparagus*	*officinalis*	H	E	.	.	.	.	u	.	r	.	.	.	.	r	.	.	.	.
170	Asparagaceae	*Asparagus*	*plumosus*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
171	Asparagaceae	*Asparagus*	*retrofractus*	S	E	.	.	.	.	.	.	.	.	c	.	r	.	.	.	.	.
172	Asparagaceae	*Asparagus*	*virgatus*	S	E	.	.	.	.	.	c	.	u	.	u	c	c	.	.	.	.
173	Asparagaceae	*Aspidistra*	*elatior*	H	E	.	.	.	.	.	.	.	.	r	u	c	c	.	.	.	.
174	Asparagaceae	*Beaucarnea*	*recurvata*	S	E	.	.	.	.	c	r	u	u	r	u	u	r	.	.	.	.
175	Asparagaceae	*Chlorophytum*	*comosum*	H	E	.	.	.	.	u	r	u	.	r	.	r	.	.	.	.	.
176	Asparagaceae	*Chlorophytum*	*laxum*	H	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
177	Asparagaceae	*Laxmannia*	*compacta*	H	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
178	Asparagaceae	*Liriope*	*muscari*	H	E	.	.	.	.	c	c	c	u	c	.	c	c	.	.	.	.
179	Asparagaceae	*Lomandra*	*banksii*	H	N	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
180	Asparagaceae	*Lomandra*	*filiformis*	H	-	.	.	.	.	.	.	.	.	.	.	.	.	u	.	.	.

	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
181	Asparagaceae	*Lomandra*	*glauca*	H	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
182	Asparagaceae	*Lomandra*	*hystrix*	H	N	.	c	c	.	.	.	.	.	c	.	.	c	.	.	.	.
183	Asparagaceae	*Lomandra*	*laxa*	H	N	r	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.
184	Asparagaceae	*Lomandra*	*longifolia*	H	N	.	c	c	c	r	.	c	c	.	c	c	c	.	.	.	.
185	Asparagaceae	*Lomandra*	*multiflora*	H	N	.	u	.	c	.	.	.	.	.	.	.	.	.	.	.	.
186	Asparagaceae	*Ophiopogon*	*japonicus*	H	E	.	.	.	.	c	u	r	c	c	c	c	c	.	.	.	.
187	Asparagaceae	*Polygonatum*	*odoratum*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
188	Asteraceae	*Ageratina*	*riparia*	H	E	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.
189	Asteraceae	*Ageratum*	*houstonianum*	H	E	.	c	.	c	.	c	u	.	c	r	c	c	c	c	c	c
190	Asteraceae	*Ambrosia*	*artemisiifolia*	H	E	.	.	.	.	.	.	.	.	u	u	.	.	.	.	.	.
191	Asteraceae	*Argyranthemum*	*frutescens*	H	E	.	.	.	.	.	.	.	.	r	r	.	r	.	.	.	.
192	Asteraceae	*Artemisia*	*absinthium*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
193	Asteraceae	*Artemisia*	*ludoviciana*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
194	Asteraceae	*Aster*	*sp.*	H	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
195	Asteraceae	*Aster*	*subulatus*	H	E	.	.	.	.	r	u	.	r	.	.	.	r	u	c	r	.
196	Asteraceae	*Baccharis*	*halimifolia*	S	E	.	.	.	.	.	.	r	.	.	.	r	.	.	.	.	r
197	Asteraceae	*Bidens*	*bipinnata*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
198	Asteraceae	*Bidens*	*pilosa*	H	E	.	c	.	c	.	c	c	u	c	c	c	c	c	c	c	c
199	Asteraceae	*Centaurea*	*sp.*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
200	Asteraceae	*Centipeda*	*minima*	H	N	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
201	Asteraceae	*Centratherum*	*punctatum*	H	E	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
202	Asteraceae	*Chrysanthemum*	*× morifolium*	H	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
203	Asteraceae	*Chrysanthemum*	*pacificum*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
204	Asteraceae	*Chrysanthemum*	*paludosum*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
205	Asteraceae	*Chrysanthemum*	*sp.*	H	E	.	.	.	.	.	r	u	.	.	.	.	.	.	.	.	.
206	Asteraceae	*Chrysocephalum*	*apiculatum*	H	N	.	c	.	.	.	.	.	.	.	.	c	.	.	.	.	.
207	Asteraceae	*Cirsium*	*vulgare*	H	E	.	.	.	.	.	.	.	.	.	.	u	.	.	r	u	.
208	Asteraceae	*Conyza*	*bonariensis*	H	E	.	c	.	c	.	.	.	.	.	c	c	c	c	.	.	.
209	Asteraceae	*Conyza*	*sp.*	H	E	.	.	.	.	c	c	c	c	c	.	.	.	.	c	c	.
210	Asteraceae	*Coreopsis*	*lanceolata*	H	E	.	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.
211	Asteraceae	*Cosmos*	*sp.*	H	E	.	.	.	.	.	.	.	.	r	u	r	.	.	.	.	.
212	Asteraceae	*Crassocephalum*	*crepidioides*	H	E	.	c	.	c	.	.	r	.	.	.	u	u	u	.	.	c

	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
213	Asteraceae	*Cyanthillium*	*cinereum*	S	N	.	c	c	c	.	.	.	.	.	.	.	.	r	.	r	.
214	Asteraceae	*Dahlia*	*sp.*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
215	Asteraceae	*Eclipta*	*prostrata*	H	N	.	r	.	.	u	.	.	.	.	.	.	.	.	r	.	.
216	Asteraceae	*Emilia*	*sonchifolia*	H	E	.	c	.	c	c	.	c	c	c	.	u	c	c	c	.	c
217	Asteraceae	*Epaltes*	*australis*	H	N	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
218	Asteraceae	*Erigeron*	*glaucus*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
219	Asteraceae	*Erigeron*	*karvinskianus*	H	E	.	.	.	.	.	.	.	.	u	r	r	r	.	.	.	.
220	Asteraceae	*Euchiton*	*involucratus*	H	N	.	.	.	.	.	.	.	.	.	.	.	.	c	u	c	.
221	Asteraceae	*Euryops*	*chrysanthemoides*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
222	Asteraceae	*Galinsoga*	*parviflora*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	c	.	c	c
223	Asteraceae	*Gamochaeta*	*coarctata*	H	E	.	.	.	.	.	.	.	.	r	c	.	c	u	.	.	.
224	Asteraceae	*Gazania*	*rigens*	H	E	.	.	.	.	.	.	.	c	.	u	.	.	c	.	.	.
225	Asteraceae	*Gazania*	*sp.*	H	E	.	.	.	.	c	c	.	c	.	r	.	u	.	.	.	.
226	Asteraceae	*Gerbera*	*sp.*	H	E	.	.	.	.	u	u	.	r	u	u	.	.	.	.	.	.
227	Asteraceae	*Glossocardia*	*bidens*	H	N	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
228	Asteraceae	*Helianthus*	*annuus*	H	E	.	.	.	.	r	.	r	.	.	r	.	r	.	.	.	.
229	Asteraceae	*Helichrysum*	*italicum*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
230	Asteraceae	*Hypochaeris*	*alba*	H	E	.	.	.	.	c	c	.	.	c	.	.	.	c	c	c	.
231	Asteraceae	*Hypochaeris*	*albiflora*	H	E	.	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.
232	Asteraceae	*Hypochaeris*	*glabra*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	c	.	.	c
233	Asteraceae	*Hypochaeris*	*microcephala*	H	E	.	.	.	c	.	.	u	.	.	.	.	.	.	.	.	.
234	Asteraceae	*Hypochaeris*	*radicata*	H	E	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.	c
235	Asteraceae	*Jacobaea*	*maritima*	H	E	.	.	.	.	.	.	.	.	r	r	.	u	.	.	.	.
236	Asteraceae	*Lactuca*	*sativa*	H	E	.	.	.	.	.	.	u	.	.	.	c	c	r	.	.	.
237	Asteraceae	*Lactuca*	*serriola*	H	E	.	.	.	.	.	.	.	.	.	.	c	.	r	.	.	.
238	Asteraceae	*Leucanthemum*	*× superbum*	H	E	.	.	.	.	.	.	r	.	.	.	u	r	.	.	.	.
239	Asteraceae	*Montanoa*	*hibiscifolia*	S	E	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
240	Asteraceae	*Osteospermum*	*fruticosum*	H	E	.	.	.	.	.	.	r	r	r	r	r	.	r	.	r	.
241	Asteraceae	*Ozothamnus*	*diosmifolius*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.	.
242	Asteraceae	*Picris*	*angustifolia*	H	N	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
243	Asteraceae	*Praxelis*	*clematidea*	H	E	u	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
244	Asteraceae	*Pterocaulon*	*redolens*	H	N	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.

	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
245	Asteraceae	*Sigesbeckia*	*orientalis*	H	-	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
246	Asteraceae	*Soliva*	*anthemifolia*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	c	.
247	Asteraceae	*Sonchus*	*oleraceus*	H	E	.	.	.	.	c	.	.	u	c	c	u	u	c	r	c	c
248	Asteraceae	*Sphagneticola*	*trilobata*	H	E	.	.	.	.	c	c	c	.	c	c	u	c	.	.	.	.
249	Asteraceae	*Synedrella*	*nodiflora*	H	E	.	.	.	.	.	c	.	u	c	c	c	.	.	c	.	.
250	Asteraceae	*Tagetes*	*patula*	H	E	.	.	.	.	u	c	.	r	c	c	r	.	.	.	.	.
251	Asteraceae	*Taraxacum*	*officinale*	H	E	.	.	.	.	.	c	c	.	r	r	c	u	.	.	c	.
252	Asteraceae	*Tithonia*	*diversifolia*	S	E	.	.	.	.	.	.	.	.	.	.	c	c	.	.	.	.
253	Asteraceae	*Tridax*	*procumbens*	H	E	.	.	.	.	c	c	.	c	c	c	c	u	.	.	.	.
254	Asteraceae	*Xanthium*	*occidentale*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
255	Asteraceae	*Xanthium*	*spinosum*	H	E	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
256	Asteraceae	*Xerochrysum*	*bracteatum*	H	N	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
257	Asteraceae	*Zinnia*	*peruviana*	H	E	.	.	.	.	.	.	.	.	r	r	u	.	.	.	.	.
258	Atherospermataceae	*Daphnandra*	*apatela*	T	N	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
259	Avicenniaceae	*Avicennia*	*marina*	T	N	.	.	.	.	.	.	.	.	.	c	u	c	.	.	.	.
260	Balsaminaceae	*Impatiens*	*hawkeri*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
261	Balsaminaceae	*Impatiens*	*sodenii*	H	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
262	Balsaminaceae	*Impatiens*	*sp.*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
263	Balsaminaceae	*Impatiens*	*walleriana*	H	E	.	.	.	.	u	u	r	.	r	.	.	.	.	.	.	.
264	Basellaceae	*Anredera*	*cordifolia*	H	E	.	.	.	.	.	.	.	.	r	r	c	c	.	.	.	.
265	Basellaceae	*Basella*	*alba*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
266	Begoniaceae	*Begonia*	*sp.*	S	E	.	.	.	.	.	c	r	r	r	r	r	r	.	.	.	.
267	Berberidaceae	*Nandina*	*domestica*	S	E	.	.	.	.	c	r	u	u	c	c	r	r	.	.	.	.
268	Betulaceae	*Betula*	*nigra*	T	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
269	Bignoniaceae	*Campsis*	*radicans*	H	E	.	.	.	.	.	.	.	.	r	.	.	r	.	.	.	.
270	Bignoniaceae	*Dolichandra*	*unguis-cati*	H	E	.	.	.	.	.	.	.	.	.	u	c	c	.	.	.	.
271	Bignoniaceae	*Jacaranda*	*mimosifolia*	T	E	.	.	.	.	.	r	u	r	c	c	c	c	.	.	.	.
272	Bignoniaceae	*Pandorea*	*jasminoides*	H	N	.	.	.	.	r	.	u	r	r	r	r	u	.	.	.	.
273	Bignoniaceae	*Pandorea*	*pandorana*	H	N	.	u	c	r	.	.	.	.	.	r	r	r	.	.	.	.
274	Bignoniaceae	*Podranea*	*ricasoliana*	H	E	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.
275	Bignoniaceae	*Pyrostegia*	*venusta*	H	E	.	.	.	.	r	r	r	.	.	r	r	r	.	.	.	.
276	Bignoniaceae	*Radermachera*	*sinica*	T	E	.	.	.	.	r	r	r	r	r	.	.	r	.	.	.	.

#	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
277	Bignoniaceae	*Radermachera*	*sp.*	S	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
278	Bignoniaceae	*Saritaea*	*magnifica*	H	E	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.
279	Bignoniaceae	*Spathodea*	*campanulata*	T	E	.	.	.	r	.	r	u	.	u	r	r	r	.	.	.	.
280	Bignoniaceae	*Tabebuia*	*aurea*	T	E	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.
281	Bignoniaceae	*Tabebuia*	*rosea*	T	E	.	.	.	.	.	.	r	.	u	u	.	.	.	.	.	.
282	Bignoniaceae	*Tabebuia*	*sp.*	T	E	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
283	Bignoniaceae	*Tecoma*	*stans*	T	E	.	.	.	.	r	u	r	.	r	r	r	r	.	.	.	.
284	Bignoniaceae	*Tecomanthe*	*hillii*	H	N	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.	.
285	Bignoniaceae	*Tecomaria*	*capensis*	S	E	.	.	.	.	.	.	r	.	.	.	u	.	.	.	.	.
286	Boraginaceae	*Ehretia*	*acuminata*	T	N	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.
287	Boraginaceae	*Heliotropium*	*amplexicaule*	H	E	.	r	.	.	c	r	.	.	u	r	r	r	.	u	.	.
288	Brassicaceae	*Brassica*	*rapa*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
289	Brassicaceae	*Capsella*	*bursa-pastoris*	H	E	.	.	.	.	c	c	.	.	.	.	c	c	c	c	c	u
290	Brassicaceae	*Cardamine*	*flexuosa*	H	E	.	.	.	.	.	.	.	.	c	.	.	.	.	.	.	c
291	Brassicaceae	*Cardamine*	*hirsuta*	H	E	.	.	.	.	.	r	.	.	.	.	.	.	r	c	c	.
292	Brassicaceae	*Eruca*	*sativa*	H	E	.	.	.	.	u	u	r	u	.	.	r	.	.	.	.	.
293	Brassicaceae	*Lepidium*	*sp.*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
294	Brassicaceae	*Lobularia*	*maritima*	H	E	.	.	.	.	r	r	.	r	r	u	r	.	.	.	.	.
295	Brassicaceae	*Raphanus*	*raphanistrum*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	u
296	Brassicaceae	*Raphanus*	*sativus*	H	E	.	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.
297	Bromeliaceae	*Ananas*	*comosus*	H	E	.	.	.	.	.	u	r	u	r	r	.	r	.	.	.	.
298	Bromeliaceae	*Billbergia*	*sp.*	H	E	.	.	.	.	c	u	c	c	c	u	c	c	.	.	.	.
299	Bromeliaceae	*Tillandsia*	*usneoides*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
300	Buxaceae	*Buxus*	*sempervirens*	S	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
301	Buxaceae	*Buxus*	*sp.*	S	-	.	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.
302	Cactaceae	*Echinopsis*	*sp.*	H	E	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.
303	Cactaceae	*Echinopsis*	*sp. 2*	H	E	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
304	Cactaceae	*Hylocereus*	*undatus*	H	E	.	.	.	.	.	.	r	.	r	r	.	.	.	.	.	.
305	Cactaceae	*Opuntia*	*sp.*	S	E	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
306	Cactaceae	*Opuntia*	*tomentosa*	S	E	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.
307	Cactaceae	*Schlumbergera*	*sp.*	H	E	.	.	.	.	.	.	r	.	r	r	.	.	.	.	.	.
308	Cactaceae	*Selenicereus*	*grandiflorus*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.

#	Family	Genus	Species	$_p$F	$_p$S	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
309	Caesalpiniaceae	*Barklya*	*syringifolia*	T	N	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
310	Caesalpiniaceae	*Bauhinia*	*× blakeana*	T	E	.	.	.	.	.	.	.	.	c	r	u	r	.	.	r	.
311	Caesalpiniaceae	*Bauhinia*	*galpinii*	S	E	.	.	.	.	.	r	.	r	r	.	r	r	.	.	r	.
312	Caesalpiniaceae	*Cassia*	*fistula*	T	E	.	.	.	.	.	r	r	r	.	r	r	.	.	.	.	.
313	Caesalpiniaceae	*Cassia*	*javanica*	T	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
314	Caesalpiniaceae	*Peltophorum*	*pterocarpum*	T	E	.	.	.	.	.	.	.	.	r	.	.	r	.	.	.	.
315	Caesalpiniaceae	*Schotia*	*brachypetala*	T	E	.	.	.	.	.	r	.	.	r	r	r	r	.	.	.	.
316	Campanulaceae	*Lobelia*	*erinus*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
317	Campanulaceae	*Lobelia*	*membranacea*	H	N	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	u
318	Campanulaceae	*Lobelia*	*purpurascens*	H	N	.	.	c	c	.	.	c	c	.	.	.	.	.	.	u	.
319	Campanulaceae	*Wahlenbergia*	*communis*	H	N	.	.	.	.	.	c	.	.	r	.	.	.	c	c	u	.
320	Campanulaceae	*Wahlenbergia*	*sp.*	H	N	.	c	.	r	.	.	.	.	.	.	c	.	.	.	.	r
321	Cannabaceae	*Aphananthe*	*philippinensis*	T	N	.	c	r	.	.	.	.	.	.	.	.	.	.	.	.	.
322	Cannaceae	*Canna*	*indica*	S	E	.	.	.	.	.	.	.	.	c	u	.	c	.	.	.	.
323	Cannaceae	*Canna*	*sp.*	H	E	.	.	.	.	.	c	u	r	.	.	u	.	.	.	r	.
324	Capparaceae	*Capparis*	*arborea*	S	N	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
325	Capparaceae	*Capparis*	*sarmentosa*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
326	Caprifoliaceae	*Abelia*	*× grandiflora*	S	E	.	.	.	.	.	.	r	.	r	r	r	u	.	.	.	.
327	Caprifoliaceae	*Lonicera*	*japonica*	H	E	.	.	.	.	.	r	r	.	c	r	.	.	.	.	.	.
328	Caprifoliaceae	*Lonicera*	*sp.*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
329	Cardiopteridaceae	*Citronella*	*moorei*	T	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
330	Caricaceae	*Carica*	*papaya*	T	E	.	.	.	.	.	u	u	r	u	u	u	u	.	.	.	.
331	Caryophyllaceae	*Dianthus*	*sp.*	H	E	.	.	.	.	c	.	.	.	c	u	.	.	.	.	.	.
332	Caryophyllaceae	*Drymaria*	*cordata*	H	E	.	.	.	c	.	.	c	r	r	.	r	c	r	.	c	c
333	Caryophyllaceae	*Stellaria*	*media*	H	E	.	.	.	.	.	r	.	.	u	.	.	.	.	.	c	c
334	Casuarinaceae	*Allocasuarina*	*littoralis*	T	N	c	c	.	c	.	.	.	.	r	.	.	.	.	.	.	c
335	Casuarinaceae	*Allocasuarina*	*torulosa*	T	N	.	.	c	.	.	.	.	.	.	.	r	.	.	.	r	.
336	Casuarinaceae	*Casuarina*	*cunninghamiana*	T	N	.	.	.	.	.	.	.	.	.	.	.	.	.	c	u	.
337	Casuarinaceae	*Casuarina*	*equisetifolia*	T	N	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
338	Casuarinaceae	*Casuarina*	*glauca*	T	N	.	.	.	.	.	.	.	.	u	c	r	.	.	.	.	.
339	Chenopodiaceae	*Atriplex*	*sp.*	H	N	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.
340	Clusiaceae	*Hypericum*	*calycinum*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.

#	Family	Genus	Species	$_p$F	$_p$S	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
341	Colchicaceae	*Gloriosa*	*superba*	H	E	.	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.
342	Combretaceae	*Quisqualis*	*indica*	H	E	.	.	.	.	.	.	.	.	c	r	r	r	.	.	.	.
343	Commelinaceae	*Callisia*	*fragrans*	H	E	.	.	.	.	.	c	.	c	c	c	c	c	.	.	.	.
344	Commelinaceae	*Callisia*	*repens*	H	E	.	.	.	.	.	c	r	r	c	c	c	.	.	.	.	.
345	Commelinaceae	*Commelina*	*diffusa*	H	N	.	c	.	.	.	.	c	.	c	c	r	c	.	.	.	.
346	Commelinaceae	*Commelina*	*lanceolata*	H	N	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
347	Commelinaceae	*Commelina*	*sp.*	H	E	.	.	.	.	.	.	.	.	c	.	.	.	.	.	.	.
348	Commelinaceae	*Dichorisandra*	*thyrsiflora*	S	E	.	.	.	.	.	.	.	.	r	r	c	.	.	.	.	.
349	Commelinaceae	*Murdannia*	*graminea*	H	N	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
350	Commelinaceae	*Pollia*	*crispata*	H	N	.	.	.	.	.	.	.	.	.	.	.	c	.	.	.	.
351	Commelinaceae	*Tradescantia*	*fluminensis*	H	E	.	.	.	.	.	.	.	.	.	.	u	c	.	.	.	.
352	Commelinaceae	*Tradescantia*	*pallida*	H	E	.	.	.	.	.	.	.	.	u	u	.	.	.	.	.	.
353	Commelinaceae	*Tradescantia*	*spathacea*	H	E	.	.	.	.	c	c	c	u	c	c	u	u	.	.	.	.
354	Commelinaceae	*Tradescantia*	*zebrina*	H	E	.	.	.	.	.	.	r	.	.	.	c	.	.	.	.	.
355	Convolvulaceae	*Convolvulus*	*erubescens*	H	N	.	.	.	.	c	c	.	.	.	.	.	.	c	c	r	.
356	Convolvulaceae	*Cuscuta*	*australis*	H	N	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
357	Convolvulaceae	*Dichondra*	*repens*	H	N	.	r	.	u	c	.	c	.	c	.	.	c	.	.	u	.
358	Convolvulaceae	*Evolvulus*	*alsinoides*	H	N	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
359	Convolvulaceae	*Evolvulus*	*nuttallianus*	H	E	.	.	.	.	.	r	.	.	r	.	r	.	.	.	.	.
360	Convolvulaceae	*Evolvulus*	*pilosus*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
361	Convolvulaceae	*Ipomoea*	*batatas*	H	E	.	.	.	.	.	u	.	.	c	r	r	.	.	.	r	.
362	Convolvulaceae	*Ipomoea*	*cairica*	H	E	.	.	.	.	.	c	r	.	r	u	u	r	.	.	.	.
363	Convolvulaceae	*Ipomoea*	*horsfalliae*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
364	Convolvulaceae	*Ipomoea*	*indica*	H	E	.	.	.	.	.	.	.	.	.	.	c	c	.	.	.	.
365	Convolvulaceae	*Ipomoea*	*quamoclit*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
366	Convolvulaceae	*Polymeria*	*calycina*	H	N	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
367	Costaceae	*Costus*	*comosus*	H	E	.	.	.	.	.	r	.	.	r	.	.	u	.	.	.	.
368	Crassulaceae	*Bryophyllum*	*delagoense*	H	E	.	.	.	.	.	.	.	.	r	r	c	c	.	.	.	.
369	Crassulaceae	*Bryophyllum*	*pinnatum*	H	E	.	.	.	.	.	r	.	.	r	.	u	.	.	.	.	.
370	Crassulaceae	*Kalanchoe*	*blossfeldiana*	H	E	.	.	.	.	.	r	.	.	.	.	u	.	.	.	.	.
371	Crassulaceae	*Kalanchoe*	*fedtschenkoi*	H	E	.	.	.	.	u	u	r	r	.	.	u	.	.	.	.	.
372	Crassulaceae	*Kalanchoe*	*thyrsiflora*	H	E	.	.	.	.	r	u	.	u	r	r	r	.	.	.	.	.

#	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
373	Cucurbitaceae	*Cucumis*	*sativus*	H	E	.	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.
374	Cucurbitaceae	*Cucurbita*	*moschata*	H	E	.	.	.	.	.	.	r	.	u	r	u	r	.	.	.	.
375	Cucurbitaceae	*Momordica*	*charantia*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
376	Cunoniaceae	*Ceratopetalum*	*gummiferum*	T	N	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
377	Cunoniaceae	*Davidsonia*	*pruriens*	T	N	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.
378	Cunoniaceae	*Schizomeria*	*ovata*	S	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	.
379	Cuppressaceae	*Taxodium*	*distichum*	T	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
380	Cupressaceae	*Callitris*	*columellaris*	T	N	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.
381	Cupressaceae	*Callitris*	*sp.*	T	N	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.
382	Cupressaceae	*Cupressus*	*× leylandii*	T	E	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
383	Cupressaceae	*Cupressus*	*sempervirens*	T	E	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.	.
384	Cupressaceae	*Cupressus*	*sp.*	T	E	.	.	.	.	r	r	.	r	.	r	r	.	.	.	.	.
385	Cupressaceae	*Juniperus*	*conferta*	S	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
386	Cupressaceae	*Juniperus*	*horizontalis*	S	E	.	.	.	.	r	.	.	.	r	.	.	.	.	.	.	.
387	Cupressaceae	*Platycladus*	*orientalis*	T	E	.	.	.	.	.	.	r	r	r	.	.	.	.	.	.	.
388	Dilleniaceae	*Hibbertia*	*aspera*	S	N	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.
389	Dilleniaceae	*Hibbertia*	*scandens*	H	N	.	.	r	u	.	.	r	.	r	.	.	.	.	.	.	.
390	Dilleniaceae	*Hibbertia*	*sp.*	S	N	.	.	r	.	.	.	.	.	.	r	.	.	.	.	.	.
391	Dilleniaceae	*Hibbertia*	*stricta*	S	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
392	Dioscoreaceae	*Dioscorea*	*transversa*	H	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	.
393	Dracaenaceae	*Dracaena*	*fragrans*	S	E	.	.	.	.	r	r	.	r	u	u	u	u	.	.	.	.
394	Dracaenaceae	*Dracaena*	*marginata*	S	E	.	.	.	.	.	.	u	.	.	.	u	r	.	.	.	.
395	Dracaenaceae	*Dracaena*	*reflexa*	S	E	.	.	.	.	c	c	r	c	c	c	r	.	.	.	.	.
396	Dracaenaceae	*Sansevieria*	*trifasciata*	H	E	.	.	.	.	r	r	c	r	c	u	c	u	.	.	.	.
397	Droseraceae	*Drosera*	*burmannii*	H	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
398	Droseraceae	*Drosera*	*peltata*	H	N	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
399	Droseraceae	*Drosera*	*sp.*	H	N	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
400	Ebenaceae	*Diospyros*	*fasciculosa*	T	N	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
401	Ebenaceae	*Diospyros*	*pentamera*	T	N	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.
402	Ebenaceae	*Diospyros*	*virginiana*	T	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
403	Elaeocarpaceae	*Elaeocarpus*	*eumundi*	T	N	.	.	.	u	.	.	.	.	r	r	r	.	.	.	.	.
404	Elaeocarpaceae	*Elaeocarpus*	*grandis*	T	N	.	.	u	r	.	.	.	.	u	r	r	u	.	.	.	.

7.2. Appendix II: plant species list

	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
405	Elaeocarpaceae	*Elaeocarpus*	*obovatus*	T	N	.	.	r	.	.	.	r	.	.	.	.	r	.	.	.	.
406	Elaeocarpaceae	*Elaeocarpus*	*reticulatus*	T	N	.	.	c	c	.	.	r	.	r	r	r	r	.	.	.	c
407	Elaeocarpaceae	*Elaeocarpus*	*sp.*	T	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
408	Elaeocarpaceae	*Sloanea*	*australis*	T	N	.	.	u	u	.	.	.	.	.	.	.	.	.	.	.	.
409	Ericaceae	*Acrotriche*	*aggregata*	S	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	.
410	Ericaceae	*Leucopogon*	*leptospermoides*	S	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
411	Ericaceae	*Rhododendron*	*indicum*	S	E	.	.	.	.	.	r	.	c	r	.	.	.	.	.	.	.
412	Ericaceae	*Rhododendron*	*sp.*	S	E	.	.	.	.	.	.	u	.	r	u	.	r	.	.	.	.
413	Ericaceae	*Trochocarpa*	*laurina*	T	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	.
414	Ericaceae	*Vaccinium*	*sp.*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
415	Euphorbiaceae	*Acalypha*	*australis*	H	E	.	.	.	.	.	r	.	c	.	.	.	.	.	.	.	.
416	Euphorbiaceae	*Acalypha*	*capillipes*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
417	Euphorbiaceae	*Acalypha*	*hispaniolae*	H	E	.	.	.	.	.	r	.	.	.	c	.	.	.	.	.	.
418	Euphorbiaceae	*Acalypha*	*sp.*	S	E	.	.	.	.	u	.	.	.	.	.	u	.	.	.	.	.
419	Euphorbiaceae	*Acalypha*	*wilkesiana*	S	E	.	.	.	.	u	u	u	r	u	r	.	u	.	.	.	.
420	Euphorbiaceae	*Aleurites*	*moluccanus*	T	N	.	.	.	.	.	.	r	.	.	.	r	r	.	.	.	.
421	Euphorbiaceae	*Codiaeum*	*variegatum*	S	E	.	.	.	.	r	r	c	c	c	u	r	c	.	.	r	.
422	Euphorbiaceae	*Croton*	*sp.*	S	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
423	Euphorbiaceae	*Euphorbia*	*cotinifolia*	S	E	.	.	.	.	.	.	u	.	.	r	.	.	.	.	.	.
424	Euphorbiaceae	*Euphorbia*	*cyathophora*	H	E	.	.	.	.	u	c	.	.	.	.	c	.	.	.	.	.
425	Euphorbiaceae	*Euphorbia*	*grantii*	S	E	.	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.
426	Euphorbiaceae	*Euphorbia*	*hirta*	H	E	.	.	.	.	.	c	.	.	.	.	.	.	.	c	.	u	.
427	Euphorbiaceae	*Euphorbia*	*leucocephala*	S	E	.	.	.	.	r	r	c	u	r	.	r	r	.	.	.	.
428	Euphorbiaceae	*Euphorbia*	*milii*	H	E	.	.	.	.	.	.	u	.	.	.	.	r	.	.	.	.
429	Euphorbiaceae	*Euphorbia*	*peplus*	H	E	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
430	Euphorbiaceae	*Euphorbia*	*prostrata*	H	E	.	.	.	.	c	r	.	c	c	.	.	.	.	c	c	.
431	Euphorbiaceae	*Euphorbia*	*pulcherrima*	S	E	.	.	.	.	.	.	r	r	u	r	r	.	.	.	.	.
432	Euphorbiaceae	*Euphorbia*	*sp.*	S	-	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
433	Euphorbiaceae	*Euphorbia*	*tithymaloides*	S	E	.	.	.	.	r	r	r	.	r	.	r	.	.	.	.	.
434	Euphorbiaceae	*Excoecaria*	*agallocha*	T	N	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
435	Euphorbiaceae	*Homalanthus*	*populifolius*	T	N	.	.	.	.	.	.	r	.	.	.	r	.	.	.	.	r
436	Euphorbiaceae	*Macaranga*	*tanarius*	T	N	.	.	.	u	r	u	r	.	u	.	u	u	.	.	.	.

#	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
437	Euphorbiaceae	*Mallotus*	*claoxyloides*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
438	Euphorbiaceae	*Mallotus*	*discolor*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
439	Euphorbiaceae	*Mallotus*	*philippensis*	T	N	.	r	.	u	.	.	.	.	r	.	u	r	.	.	.	.
440	Euphorbiaceae	*Manihot*	*esculenta*	S	E	.	.	.	.	.	c	.	.	.	u	.	.	.	.	.	.
441	Euphorbiaceae	*Petalostigma*	*pubescens*	S	N	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
442	Euphorbiaceae	*Ricinocarpos*	*pinifolius*	S	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
443	Euphorbiaceae	*Ricinus*	*communis*	S	E	.	.	.	.	.	c	.	.	r	.	.	.	.	.	.	.
444	Eupomatiaceae	*Eupomatia*	*bennettii*	S	N	.	.	r	r	.	.	.	.	.	.	r	.	.	.	.	.
445	Eupomatiaceae	*Eupomatia*	*laurina*	S	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	.
446	Fabaceae	*Abrus*	*precatorius*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
447	Fabaceae	*Acacia*	*amblygona*	S	-	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
448	Fabaceae	*Acacia*	*attenuata*	S	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
449	Fabaceae	*Acacia*	*concurrens*	T	N	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
450	Fabaceae	*Acacia*	*disparrima*	T	N	c	c	r	c	.	.	r	.	r	.	u	c	.	.	r	c
451	Fabaceae	*Acacia*	*fimbriata*	T	N	.	.	.	.	.	.	.	.	r	r	u	r	.	.	.	.
452	Fabaceae	*Acacia*	*flavescens*	S	N	c	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
453	Fabaceae	*Acacia*	*juncifolia*	S	N	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
454	Fabaceae	*Acacia*	*leiocalyx*	T	N	.	c	.	.	.	.	r	.	.	.	.	.	.	.	c	.
455	Fabaceae	*Acacia*	*leptocarpa*	T	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
456	Fabaceae	*Acacia*	*longissima*	T	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
457	Fabaceae	*Acacia*	*maidenii*	T	N	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.
458	Fabaceae	*Acacia*	*melanoxylon*	T	N	.	.	r	u	.	.	r	r	.	.	r	.	.	.	.	u
459	Fabaceae	*Acacia*	*oshanesii*	T	N	.	.	c	c	.	.	.	.	.	.	.	.	.	.	.	.
460	Fabaceae	*Acacia*	*podalyriifolia*	T	N	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
461	Fabaceae	*Acacia*	*suaveolens*	S	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
462	Fabaceae	*Acacia*	*ulicifolia*	S	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
463	Fabaceae	*Albizia*	*lebbeck*	T	N	.	.	.	.	.	r	.	.	.	.	r	.	.	.	.	.
464	Fabaceae	*Aotus*	*lanigera*	S	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
465	Fabaceae	*Archidendron*	*sp.*	T	N	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.
466	Fabaceae	*Austrosteenisia*	*blackii*	H	-	.	u	.	r	.	.	.	.	.	.	.	.	.	.	.	.
467	Fabaceae	*Caesalpinia*	*ferrea*	T	E	.	.	.	.	r	r	r	.	u	c	r	c	.	.	r	.
468	Fabaceae	Caesalpinia	pulcherrima	S	E	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.

	Family	Genus	Species	$_p$F	$_p$S	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
469	Fabaceae	*Caesalpinia*	*scortechinii*	H	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
470	Fabaceae	*Callerya*	*megasperma*	H	N	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.
471	Fabaceae	*Calliandra*	*haematocephala*	S	E	.	.	.	.	r	u	r	.	c	c	r	.	.	.	.	.
472	Fabaceae	*Calliandra*	*surinamensis*	S	E	.	.	.	.	r	.	.	.	r	r	r	r	.	.	.	.
473	Fabaceae	*Canavalia*	*rosea*	H	N	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.
474	Fabaceae	*Castanospermum*	*australe*	T	N	.	.	.	.	.	r	r	r	r	.	r	u	.	.	r	.
475	Fabaceae	*Chamaecrista*	*rotundifolia*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
476	Fabaceae	*Chamaecrista*	*sp.*	H	E	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
477	Fabaceae	*Cochliasanthus*	*caracalla*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
478	Fabaceae	*Colvillea*	*racemosa*	T	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
479	Fabaceae	*Crotalaria*	*mitchellii*	H	N	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
480	Fabaceae	*Crotalaria*	*sp.*	H	E	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.	c
481	Fabaceae	*Cullen*	*tenax*	H	N	.	.	.	.	.	.	.	.	c	.	.	.	.	.	.	.
482	Fabaceae	*Delonix*	*regia*	T	E	.	.	.	.	u	r	u	r	c	u	u	c	.	.	.	.
483	Fabaceae	*Desmodium*	*rhytidophyllum*	H	N	.	.	.	u	.	.	.	.	.	.	.	.	.	r	.	.
484	Fabaceae	*Desmodium*	*sp.*	H	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	u
485	Fabaceae	*Desmodium*	*uncinatum*	H	E	.	.	.	c	.	.	u	r	.	r	u	c	.	.	.	c
486	Fabaceae	*Desmodium*	*varians*	H	N	.	.	.	.	.	.	.	.	u	.	.	.	.	.	.	.
487	Fabaceae	*Dillwynia*	*floribunda*	S	N	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
488	Fabaceae	*Erythrina*	*crista-galli*	T	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
489	Fabaceae	*Glycine*	*clandestina*	H	N	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
490	Fabaceae	*Glycine*	*cyrtoloba*	H	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	c	.
491	Fabaceae	*Glycine*	*sp.*	H	N	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.
492	Fabaceae	*Glycine*	*tabacina*	H	N	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
493	Fabaceae	*Gompholobium*	*pinnatum*	H	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
494	Fabaceae	*Hardenbergia*	*violacea*	H	N	.	.	.	c	.	.	.	.	r	r	.	r	.	.	.	.
495	Fabaceae	*Hovea*	*acutifolia*	S	N	.	.	c	c	.	.	.	.	r	.	.	.	.	.	.	.
496	Fabaceae	*Indigofera*	*linnaei*	H	E	.	.	.	.	.	.	.	.	c	c	.	.	.	.	.	.
497	Fabaceae	*Indigofera*	*sp.*	H	E	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
498	Fabaceae	*Indigofera*	*spicata*	H	E	.	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.
499	Fabaceae	*Inga*	*edulis*	T	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
500	Fabaceae	*Jacksonia*	*scoparia*	S	N	.	c	.	u	.	r	.	.	.	.	.	.	.	.	.	.

	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
501	Fabaceae	*Leucaena*	*leucocephala*	T	E	.	.	.	r	.	u	r	.	c	c	c	c	.	.	.	.
502	Fabaceae	*Macroptilium*	*atropurpureum*	H	E	.	r	.	c	c	u	c	c	c	c	.	c	r	c	r	c
503	Fabaceae	*Macroptilium*	*lathyroides*	H	E	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.
504	Fabaceae	*Millettia*	*pinnata*	T	N	.	.	.	.	r	.	.	.	r	.	.	r	.	.	.	.
505	Fabaceae	*Mimosa*	*pudica*	H	E	.	.	.	.	.	u	.	.	.	.	.	.	.	.	u	.
506	Fabaceae	*Mirbelia*	*rubiifolia*	H	-	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
507	Fabaceae	*NA*	*unknown sp. 17*	H	N	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.
508	Fabaceae	*Neptunia*	*gracilis*	H	N	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.
509	Fabaceae	*Phaseolus*	*vulgaris*	H	E	.	.	.	.	.	.	.	.	r	.	r	.	r	.	.	.
510	Fabaceae	*Phyllota*	*phylicoides*	S	-	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
511	Fabaceae	*Platylobium*	*formosum*	S	N	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
512	Fabaceae	*Pultenaea*	*euchila*	S	-	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.
513	Fabaceae	*Pultenaea*	*myrtoides*	S	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
514	Fabaceae	*Pultenaea*	*villosa*	S	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	c
515	Fabaceae	*Rhynchosia*	*minima*	H	N	.	.	.	.	.	c	.	c	.	.	.	.	.	c	.	.
516	Fabaceae	*Schizolobium*	*parahyba*	T	E	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
517	Fabaceae	*Senna*	*pendula*	S	E	.	.	.	r	.	.	c	.	u	r	r	r	.	.	.	u
518	Fabaceae	*Senna*	*septemtrionalis*	S	E	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
519	Fabaceae	*Senna*	*sp.*	S	E	.	r	.	.	.	.	.	.	.	.	.	r	.	.	.	.
520	Fabaceae	*Sesbania*	*punicea*	S	E	.	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.
521	Fabaceae	*Sesbania*	*sp.*	S	E	.	.	.	.	.	u	.	.	.	.	.	.	.	.	.	.
522	Fabaceae	*Stylosanthes*	*sp.*	H	E	.	.	.	.	r	c	.	.	.	.	.	.	.	r	.	.
523	Fabaceae	*Tamarindus*	*indica*	T	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
524	Fabaceae	*Tephrosia*	*sp.*	H	E	.	c	.	.	c	.	.	.	.	.	.	.	.	.	u	.
525	Fabaceae	*Tephrosia*	*sp. 2*	H	E	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
526	Fabaceae	*Tipuana*	*tipu*	T	E	.	.	.	.	.	r	.	.	.	r	u	c	.	.	.	.
527	Fabaceae	*Trifolium*	*repens*	H	E	.	.	.	c	.	.	.	.	.	r	.	.	c	.	.	c
528	Fabaceae	*Vigna*	*speciosa*	H	E	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
529	Fabaceae	*Vigna*	*unguiculata*	H	E	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
530	Fabaceae	*Wisteria*	*sinensis*	H	E	.	.	.	.	.	r	.	.	.	.	r	u	r	.	.	.
531	Flagellariaceae	*Flagellaria*	*indica*	H	N	.	.	c	u	.	.	.	.	.	.	.	.	r	.	.	.
532	Geraniaceae	*Geranium*	*solanderi*	H	N	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.

	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
533	Geraniaceae	*Pelargonium*	*hortorum*	H	E	.	.	.	.	u	r	u	r	c	.	c	r	.	.	.	.
534	Geraniaceae	*Pelargonium*	*peltatum*	H	E	.	.	.	.	.	.	.	.	.	r	u	.	.	.	.	.
535	Geraniaceae	*Pelargonium*	*sp.*	H	E	.	.	.	.	.	r	r	.	r	r	.	.	.	.	.	.
536	Gesneriaceae	*Columnea*	*× banksii*	H	E	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
537	Gesneriaceae	*Streptocarpus*	*caulescens*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
538	Goodeniaceae	*Goodenia*	*glabra*	H	N	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
539	Goodeniaceae	*Goodenia*	*rotundifolia*	H	N	.	u	c	u	.	.	.	.	.	.	.	.	.	.	.	.
540	Goodeniaceae	*Scaevola*	*sp.*	H	N	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.
541	Goodeniaceae	*Velleia*	*spathulata*	H	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
542	Haemodoraceae	*Anigozanthos*	*sp.*	H	N	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.
543	Haloragaceae	*Gonocarpus*	*micranthus*	H	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
544	Haloragaceae	*Gonocarpus*	*tetragynus*	H	N	u	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
545	Haloragaceae	*Haloragis*	*heterophylla*	S	-	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
546	Hamamelidaceae	*Loropetalum*	*chinense*	S	E	.	.	.	.	r	.	.	.	r	.	.	.	.	.	r	.
547	Heliconiaceae	*Heliconia*	*pendula*	S	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
548	Heliconiaceae	*Heliconia*	*psittacorum*	S	E	.	.	.	.	.	.	r	.	.	r	c	c	.	.	.	.
549	Heliconiaceae	*Heliconia*	*sp.*	S	E	.	.	.	.	r	.	.	c	r	.	.	.	.	.	r	.
550	Hemerocallidaceae	*Dianella*	*brevipedunculata*	H	N	.	u	.	.	r	r	r	.	u	r	.	r	.	.	.	.
551	Hemerocallidaceae	*Dianella*	*caerulea*	H	N	.	c	u	.	.	.	r	.	.	.	u	.	.	.	.	u
552	Hemerocallidaceae	*Dianella*	*longifolia*	H	N	.	c	.	.	.	.	.	.	r	.	r	.	.	.	.	.
553	Hemerocallidaceae	*Dianella*	*revoluta*	H	N	.	.	c	r	.	.	.	.	.	.	r	.	.	.	.	.
554	Hemerocallidaceae	*Dianella*	*sp.*	H	N	.	.	.	.	u	c	.	.	.	.	.	.	.	.	.	.
555	Hemerocallidaceae	*Dianella*	*tasmanica*	H	N	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
556	Hemerocallidaceae	*Geitonoplesium*	*cymosum*	H	N	.	u	c	u	.	.	.	.	r	r	r	.	.	.	.	.
557	Hydrangeaceae	*Hydrangea*	*macrophylla*	S	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
558	Hypoxidaceae	*Hypoxis*	*pratensis*	H	-	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
559	Hypoxidaceae	*Molineria*	*capitulata*	H	N	.	.	.	.	.	.	.	.	.	.	c	.	.	.	.	.
560	Iridaceae	*Dietes*	*bicolor*	H	E	.	.	.	.	u	u	c	u	c	u	u	c	.	.	.	.
561	Iridaceae	*Dietes*	*grandiflora*	H	E	.	.	.	.	c	.	.	r	c	.	c	c	.	.	.	.
562	Iridaceae	*Freesia*	*laxa*	H	E	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
563	Iridaceae	*Gladiolus*	*communis*	H	E	.	.	.	.	.	.	r	.	u	r	r	u	.	.	.	.
564	Iridaceae	*Iris*	*germanica*	H	E	.	.	.	.	.	.	.	.	.	.	r	u	.	.	.	.

	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
565	Iridaceae	*Neomarica*	*northiana*	H	E	.	.	.	.	.	.	.	.	.	.	c	.	.	.	.	.
566	Iridaceae	*Patersonia*	*sericea*	H	-	c	u	.	r	.	.	.	.	.	.	.	.	.	.	.	.
567	Juglandaceae	*Carya*	*illinoinensis*	T	E	.	.	.	.	.	.	r	.	r	.	r	r	.	.	.	.
568	Lamiaceae	*Clerodendrum*	*floribundum*	T	N	.	c	u	c	.	.	.	.	.	.	.	.	.	.	.	.
569	Lamiaceae	*Clerodendrum*	*splendens*	H	E	.	.	.	.	.	r	.	u	u	c	r	r	.	.	.	.
570	Lamiaceae	*Lavandula*	*dentata*	H	E	.	.	.	.	c	.	.	.	r	c	u	.	.	.	.	.
571	Lamiaceae	*Lavandula*	*stoechas*	H	E	.	.	.	.	.	.	.	r	.	.	u	.	.	.	.	.
572	Lamiaceae	*Melissa*	*officinalis*	H	E	.	.	.	.	.	.	r	.	r	r	.	.	.	.	.	.
573	Lamiaceae	*Mentha*	*× piperita*	H	E	.	.	.	.	.	.	r	.	.	u	r	r	.	.	.	.
574	Lamiaceae	*Mentha*	*piperita*	H	E	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
575	Lamiaceae	*Mentha*	*spicata*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
576	Lamiaceae	*NA*	*unknown sp. 02*	H	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
577	Lamiaceae	*Ocimum*	*basilicum*	H	E	.	.	.	.	.	u	u	u	c	c	c	u	.	.	.	.
578	Lamiaceae	*Origanum*	*vulgare*	H	E	.	.	.	.	r	.	.	.	r	c	r	u	.	.	.	.
579	Lamiaceae	*Orthosiphon*	*aristatus*	S	N	.	.	.	.	.	.	.	.	.	r	.	u	.	.	.	.
580	Lamiaceae	*Plectranthus*	*amboinicus*	H	E	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
581	Lamiaceae	*Plectranthus*	*graveolens*	H	N	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
582	Lamiaceae	*Plectranthus*	*scutellarioides*	H	E	.	.	.	.	.	.	.	.	u	.	r	.	.	.	.	.
583	Lamiaceae	*Plectranthus*	*sp.*	H	-	.	.	.	.	r	r	.	.	.	.	r	.	.	.	.	.
584	Lamiaceae	*Plectranthus*	*verticillatus*	H	E	.	.	.	.	.	.	r	r	r	u	u	u	.	.	.	.
585	Lamiaceae	*Rosmarinus*	*officinalis*	H	E	.	.	.	.	u	r	r	r	c	c	u	u	.	.	.	.
586	Lamiaceae	*Salvia*	*elegans*	S	E	.	.	.	.	.	.	.	r	.	.	r	.	.	.	.	.
587	Lamiaceae	*Salvia*	*guaranitica*	H	E	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
588	Lamiaceae	*Salvia*	*leucantha*	S	E	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
589	Lamiaceae	*Salvia*	*officinalis*	H	E	.	.	.	.	r	.	.	.	r	.	r	r	.	.	.	.
590	Lamiaceae	*Salvia*	*sp.*	H	E	.	.	.	.	r	.	.	.	r	r	r	.	.	.	.	.
591	Lamiaceae	*Salvia*	*splendens*	H	E	.	.	.	.	u	.	.	.	c	u	.	.	.	.	.	.
592	Lamiaceae	*Stachys*	*arvensis*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
593	Lamiaceae	*Tetradenia*	*riparia*	S	E	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
594	Lamiaceae	*Thymus*	*vulgaris*	H	E	.	.	.	.	.	.	.	.	u	c	r	c	.	.	.	.
595	Lamiaceae	*Vitex*	*sp.*	T	-	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
596	Lamiaceae	*Westringia*	*fruticosa*	S	N	.	.	.	.	u	.	r	.	c	u	.	.	.	.	.	.

	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
597	Lauraceae	*Cassytha*	*glabella*	H	-	.	c	.	c	.	.	.	.	.	.	.	.	.	.	.	.
598	Lauraceae	*Cinnamomum*	*camphora*	T	E	.	.	c	r	.	r	r	.	.	r	u	r	.	.	r	r
599	Lauraceae	*Cryptocarya*	*glaucescens*	T	N	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
600	Lauraceae	*Cryptocarya*	*laevigata*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
601	Lauraceae	*Cryptocarya*	*macdonaldii*	T	N	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.
602	Lauraceae	*Cryptocarya*	*microneura*	T	N	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.
603	Lauraceae	*Cryptocarya*	*obovata*	T	N	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
604	Lauraceae	*Cryptocarya*	*triplinervis*	T	N	.	c	.	.	.	.	.	.	.	.	.	.	.	.	r	.
605	Lauraceae	*Endiandra*	*discolor*	T	-	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
606	Lauraceae	*Endiandra*	*muelleri*	T	-	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
607	Lauraceae	*Endiandra*	*pubens*	T	N	.	.	r	u	.	.	.	.	.	.	.	.	.	.	.	.
608	Lauraceae	*Endiandra*	*sieberi*	T	N	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
609	Lauraceae	*Laurus*	*nobilis*	S	E	.	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.
610	Lauraceae	*Neolitsea*	*dealbata*	T	N	.	.	u	c	.	.	.	.	.	.	r	.	.	.	.	.
611	Lauraceae	*Persea*	*americana*	T	E	.	.	.	.	.	.	.	.	r	r	r	r	.	.	.	.
612	Laxmanniaceae	*Cordyline*	*petiolaris*	S	N	.	.	r	.	.	.	.	.	.	c	.	u	.	.	.	.
613	Laxmanniaceae	*Cordyline*	*rubra*	S	N	.	.	c	u	.	.	c	.	.	r	.	r	.	.	.	.
614	Laxmanniaceae	*Cordyline*	*sp.*	S	-	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
615	Laxmanniaceae	*Cordyline*	*stricta*	S	N	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
616	Laxmanniaceae	*Cordyline*	*terminalis*	S	E	.	.	.	.	u	r	.	u	u	r	.	r	.	.	.	.
617	Lecythidaceae	*Planchonia*	*careya*	T	N	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
618	Leguminosae	*Phanera*	*purpurea*	T	E	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
619	Lentibulariaceae	*Utricularia*	*caerulea*	H	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
620	Linderniaceae	*Lindernia*	*crustacea*	H	-	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
621	Linderniaceae	*Torenia*	*fournieri*	H	E	.	.	.	.	.	.	.	.	.	u	r	.	.	.	.	.
622	Loganiaceae	*Mitrasacme*	*sp.*	H	-	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
623	Loranthaceae	*NA*	*unknown sp. 01*	H	N	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
624	Luzuriagaceae	*Drymophila*	*moorei*	H	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
625	Lythraceae	*Cuphea*	*carthagenensis*	H	E	.	.	.	.	c	c	.	.	.	.	c	.	c	c	u	.
626	Lythraceae	*Cuphea*	*hyssopifolia*	H	E	.	.	.	.	.	.	.	.	r	c	u	.	u	.	.	.
627	Lythraceae	*Lagerstroemia*	*sp.*	T	E	.	.	.	.	r	u	u	u	u	c	u	r	.	.	.	.
628	Lythraceae	*Lagerstroemia*	*speciosa*	T	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.

	Family	Genus	Species	ₚF	ₚS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
629	Lythraceae	*Lythrum*	*salicaria*	H	-	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
630	Lythraceae	*NA*	*unknown sp. 16*	H	-	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.
631	Lythraceae	*Punica*	*malus*	T	E	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
632	Magnoliaceae	*Magnolia*	*figo*	S	E	.	.	.	.	r	r	.	r	c	u	r	.	.	.	r	.
633	Magnoliaceae	*Magnolia*	*grandiflora*	T	E	.	.	.	.	.	.	r	r	c	u	u	.	.	.	.	.
634	Magnoliaceae	*Magnolia*	*sp.*	T	E	.	.	.	.	.	.	r	.	.	r	r	.	.	.	.	.
635	Malpighiaceae	*Galphimia*	*gracilis*	S	E	.	.	.	.	.	.	.	.	r	.	u	r	.	.	.	.
636	Malvaceae	*Abutilon*	*× hybridum*	S	E	.	.	.	.	.	.	.	.	r	r	c	u	.	.	.	.
637	Malvaceae	*Abutilon*	*oxycarpum*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
638	Malvaceae	*Abutilon*	*pictum*	S	E	.	.	.	.	r	.	.	r	.	.	.	.	.	.	.	.
639	Malvaceae	*Brachychiton*	*acerifolius*	T	N	.	.	.	.	r	.	.	r	u	c	u	r	.	.	.	.
640	Malvaceae	*Brachychiton*	*bidwillii*	S	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
641	Malvaceae	*Brachychiton*	*discolor*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
642	Malvaceae	*Brachychiton*	*populneus*	T	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
643	Malvaceae	*Brachychiton*	*rupestris*	T	N	.	.	.	.	r	r	.	.	.	.	r	r	.	.	.	.
644	Malvaceae	*Brachychiton*	*sp.*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
645	Malvaceae	*Commersonia*	*bartramia*	T	N	.	u	u	r	.	.	.	.	.	.	r	.	.	.	.	.
646	Malvaceae	*Commersonia*	*fraseri*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
647	Malvaceae	*Commersonia*	*salviifolia*	S	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
648	Malvaceae	*Hibiscus*	*heterophyllus*	S	N	.	.	c	u	.	.	.	.	.	.	r	.	.	.	.	.
649	Malvaceae	*Hibiscus*	*mutabilis*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
650	Malvaceae	*Hibiscus*	*rosa-sinensis*	S	E	.	.	.	.	c	c	c	c	c	u	c	c	.	.	r	.
651	Malvaceae	*Hibiscus*	*sabdariffa*	S	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
652	Malvaceae	*Hibiscus*	*splendens*	S	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
653	Malvaceae	*Hibiscus*	*sturtii*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
654	Malvaceae	*Hibiscus*	*tiliaceus*	T	N	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.
655	Malvaceae	*Lagunaria*	*patersonia*	T	N	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.
656	Malvaceae	*Malva*	*parviflora*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	u
657	Malvaceae	*Malvastrum*	*americanum*	H	E	.	.	.	.	c	c	.	.	c	c	c	c	c	.	c	.
658	Malvaceae	*Modiola*	*caroliniana*	H	E	.	.	.	.	.	.	r	.	.	.	.	.	u	.	.	c
659	Malvaceae	*Sida*	*cordifolia*	H	E	.	u	.	.	.	.	.	.	.	.	.	.	r	.	c	.
660	Malvaceae	*Sida*	*rhombifolia*	H	E	.	.	.	.	c	u	c	.	c	u	c	c	r	c	u	c

	Family	Genus	Species	$_p$F	$_p$S	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
661	Malvaceae	*Sterculia*	*quadrifida*	T	N	.	u	.	c	r	.	.	.	r	.	r	r	.	.	.	.
662	Malvaceae	*Urena*	*lobata*	H	E	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
663	Marantaceae	*Calathea*	*sp.*	H	E	.	.	.	.	r	u	.	.	.	.	.	.	.	.	.	.
664	Melastomataceae	*Melastoma*	*affine*	S	-	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
665	Melastomataceae	*Melastoma*	*malabathricum*	S	-	.	.	.	r	.	.	.	.	.	.	.	.	r	.	.	u
666	Melastomataceae	*Tibouchina*	*granulosa*	S	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
667	Melastomataceae	*Tibouchina*	*lepidota*	S	E	.	.	.	.	.	.	u	r	.	r	.	r	.	.	.	.
668	Melastomataceae	*Tibouchina*	*sp.*	S	E	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.
669	Meliaceae	*Aglaia*	*brownii*	S	N	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.
670	Meliaceae	*Azadirachta*	*indica*	T	E	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.
671	Meliaceae	*Melia*	*azedarach*	T	N	.	u	.	u	.	u	r	.	u	.	r	r	.	.	.	.
672	Meliaceae	*Synoum*	*glandulosum*	T	N	.	.	c	c	.	.	.	.	.	.	.	.	.	.	.	.
673	Meliaceae	*Toona*	*ciliata*	T	N	.	.	.	r	.	.	.	.	.	.	r	r	.	.	r	.
674	Meliaceae	*Turraea*	*pubescens*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
675	Menispermaceae	*Echinostephia*	*aculeata*	H	-	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
676	Menispermaceae	*Pleogyne*	*australis*	H	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	.
677	Menispermaceae	*Stephania*	*japonica*	H	N	.	.	c	c	.	.	.	.	r	.	.	.	.	.	c	.
678	Monimiaceae	*Wilkiea*	*macrophylla*	S	N	.	.	u	u	.	.	.	.	.	.	.	.	.	.	.	.
679	Moraceae	*Artocarpus*	*altilis*	T	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
680	Moraceae	*Ficus*	*benjamina*	T	E	.	.	.	.	u	r	u	.	c	u	.	c	.	.	r	.
681	Moraceae	*Ficus*	*binnendijkii*	T	E	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
682	Moraceae	*Ficus*	*carica*	T	E	.	.	.	.	.	.	.	.	u	r	u	.	.	.	.	.
683	Moraceae	*Ficus*	*coronata*	T	N	.	.	c	u	.	.	.	.	r	.	r	u	.	.	.	.
684	Moraceae	*Ficus*	*elastica*	T	E	.	.	.	.	.	.	r	.	r	.	r	.	.	.	.	.
685	Moraceae	*Ficus*	*fraseri*	T	N	.	u	.	r	.	.	.	.	.	.	r	.	.	.	.	.
686	Moraceae	*Ficus*	*macrophylla*	T	N	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.
687	Moraceae	*Ficus*	*microcarpa*	T	N	.	.	.	r	.	r	.	.	.	.	r	r	.	.	.	.
688	Moraceae	*Ficus*	*obliqua*	T	N	.	r	.	.	.	.	.	r	.	r	r	u	.	.	r	.
689	Moraceae	*Ficus*	*pumila*	H	E	.	.	.	.	.	.	.	.	r	r	u	.	.	.	.	.
690	Moraceae	*Ficus*	*virens*	T	N	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
691	Moraceae	*Morus*	*nigra*	T	E	.	.	.	.	.	r	.	.	r	.	u	u	.	.	.	.
692	Moraceae	*Trophis*	*scandens*	H	N	.	c	c	c	.	.	.	.	.	.	r	.	.	.	.	.

	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
693	Musaceae	*Musa*	*acuminata*	S	E	.	.	.	.	r	r	r	r	u	u	c	r	.	.	.	.
694	Myrsinaceae	*Aegiceras*	*corniculatum*	T	N	.	.	.	.	.	.	.	.	.	c	u	r	.	.	.	.
695	Myrsinaceae	*Ardisia*	*crenata*	S	E	.	.	.	r	.	.	.	r	u	.	.	.	.	.	r	.
696	Myrsinaceae	*Ardisia*	*elliptica*	S	-	.	.	.	.	.	.	.	u	.	.	.	.	.	.	.	.
697	Myrsinaceae	*Lysimachia*	*arvensis*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
698	Myrsinaceae	*Myrsine*	*variabilis*	T	N	.	c	c	u	.	.	.	.	.	.	r	.	.	.	.	.
699	Myrtaceae	*Acca*	*sellowiana*	T	E	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.
700	Myrtaceae	*Acmena*	*hemilampra*	T	N	.	.	.	.	.	.	r	.	u	.	r	.	.	.	.	.
701	Myrtaceae	*Acmena*	*ingens*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
702	Myrtaceae	*Angophora*	*leiocarpa*	T	N	u	u	.	.	.	.	.	.	.	.	.	.	.	.	r	.
703	Myrtaceae	*Asteromyrtus*	*symphyocarpa*	S	N	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
704	Myrtaceae	*Austromyrtus*	*dulcis*	H	N	.	.	.	.	.	.	r	.	.	.	u	.	.	.	.	.
705	Myrtaceae	*Austromyrtus*	*glabra*	H	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
706	Myrtaceae	*Backhousia*	*citriodora*	T	N	.	.	.	.	.	.	.	.	u	.	r	r	.	.	r	.
707	Myrtaceae	*Backhousia*	*myrtifolia*	T	N	.	.	c	u	.	.	.	.	r	.	.	.	.	.	.	.
708	Myrtaceae	*Baeckea*	*frutescens*	S	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
709	Myrtaceae	*Chamelaucium*	*uncinatum*	S	N	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
710	Myrtaceae	*Corymbia*	*citriodora*	T	N	.	.	.	.	.	.	r	r	.	r	r	c	.	.	.	.
711	Myrtaceae	*Corymbia*	*ficifolia*	T	N	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
712	Myrtaceae	*Corymbia*	*gummifera*	T	N	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.
713	Myrtaceae	*Corymbia*	*intermedia*	T	N	c	c	c	c	.	r	.	.	.	.	c	c	.	.	c	c
714	Myrtaceae	*Corymbia*	*ptychocarpa*	T	N	.	.	.	.	r	.	r	.	r	u	r	r	.	.	r	.
715	Myrtaceae	*Corymbia*	*tessellaris*	T	N	.	c	.	.	.	.	r	c	.	.	u	.	.	.	.	.
716	Myrtaceae	*Corymbia*	*torelliana*	T	N	.	.	.	.	.	r	r	.	r	r	r	r	.	.	r	.
717	Myrtaceae	*Corymbia*	*trachyphloia*	T	N	.	.	u	r	.	.	.	.	.	.	.	.	.	.	.	c
718	Myrtaceae	*Decaspermum*	*sp.*	S	N	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
719	Myrtaceae	*Eucalyptus*	*acmenoides*	T	N	.	c	.	r	.	.	.	.	.	.	u	u	.	.	.	.
720	Myrtaceae	*Eucalyptus*	*cloeziana*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
721	Myrtaceae	*Eucalyptus*	*crebra*	T	N	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
722	Myrtaceae	*Eucalyptus*	*curtisii*	T	N	.	.	.	.	.	.	.	.	.	r	r	r	.	r	.	.
723	Myrtaceae	*Eucalyptus*	*exserta*	T	N	.	u	.	.	.	.	.	.	.	.	.	.	.	.	r	.
724	Myrtaceae	*Eucalyptus*	*grandis*	T	N	.	.	c	u	.	.	r	.	r	r	r	.	.	.	.	.

	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
725	Myrtaceae	*Eucalyptus*	*latisinensis*	T	N	c	c	.	.	.	.	.	.	.	.	.	.	.	.	.	u
726	Myrtaceae	*Eucalyptus*	*microcorys*	T	N	.	.	c	c	.	.	r	.	.	r	.	u	.	.	.	r
727	Myrtaceae	*Eucalyptus*	*moluccana*	T	N	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
728	Myrtaceae	*Eucalyptus*	*pilularis*	T	N	.	.	c	c	.	.	.	.	.	.	.	.	.	.	.	c
729	Myrtaceae	*Eucalyptus*	*portuensis*	T	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	u	.
730	Myrtaceae	*Eucalyptus*	*propinqua*	T	N	.	.	c	.	.	.	.	.	.	.	u	c	.	.	.	.
731	Myrtaceae	*Eucalyptus*	*racemosa*	T	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	c
732	Myrtaceae	*Eucalyptus*	*resinifera*	T	N	.	.	c	c	.	.	r	.	.	.	.	.	.	.	.	.
733	Myrtaceae	*Eucalyptus*	*robusta*	T	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	c
734	Myrtaceae	*Eucalyptus*	*siderophloia*	T	N	.	.	c	.	.	.	.	.	.	r	u	u	.	.	.	.
735	Myrtaceae	*Eucalyptus*	*tereticornis*	T	N	.	c	c	.	r	.	r	.	r	.	u	c	.	.	u	u
736	Myrtaceae	*Eugenia*	*reinwardtiana*	S	N	.	.	.	.	r	.	r	.	.	.	r	r	.	.	.	.
737	Myrtaceae	*Eugenia*	*uniflora*	S	E	.	u	.	.	r	r	u	r	u	u	r	r	.	.	r	.
738	Myrtaceae	*Gossia*	*inophloia*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
739	Myrtaceae	*Leptospermum*	*luehmannii*	T	N	.	.	.	.	.	r	.	.	.	r	r	.	.	.	.	.
740	Myrtaceae	*Leptospermum*	*petersonii*	T	N	.	.	.	.	.	r	.	r	.	r	r	r	.	.	.	.
741	Myrtaceae	*Leptospermum*	*scoparium*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
742	Myrtaceae	*Leptospermum*	*sp.*	S	N	c	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
743	Myrtaceae	*Leptospermum*	*trinervium*	S	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
744	Myrtaceae	*Lophostemon*	*confertus*	T	N	.	c	c	c	.	r	.	.	.	r	c	c	.	.	.	.
745	Myrtaceae	*Lophostemon*	*grandiflorus*	T	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	c	.
746	Myrtaceae	*Lophostemon*	*suaveolens*	T	E	.	c	.	.	.	u	r	.	.	.	.	.	.	.	c	u
747	Myrtaceae	*Melaleuca*	*armillaris*	T	N	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
748	Myrtaceae	*Melaleuca*	*bracteata*	T	N	.	.	.	.	u	u	r	r	c	u	u	u	.	.	r	.
749	Myrtaceae	*Melaleuca*	*citrina*	T	N	.	.	.	.	.	.	u	.	.	.	.	.	.	.	.	.
750	Myrtaceae	*Melaleuca*	*fluviatilis*	T	N	.	.	.	.	.	r	.	r	.	r	.	.	.	.	.	.
751	Myrtaceae	*Melaleuca*	*leucadendra*	T	N	.	.	.	.	r	r	.	u	r	u	.	r	.	.	r	.
752	Myrtaceae	*Melaleuca*	*linarifolia*	T	N	.	.	.	.	.	.	u	u	.	.	u	r	.	.	.	.
753	Myrtaceae	*Melaleuca*	*nodosa*	T	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
754	Myrtaceae	*Melaleuca*	*quinquenervia*	T	N	.	.	.	.	.	.	c	c	.	r	.	r	.	.	u	c
755	Myrtaceae	*Melaleuca*	*saligna*	T	N	.	.	u	.	r	.	r	.	r	u	r	r	.	.	.	.
756	Myrtaceae	*Melaleuca*	*sp.*	T	N	.	.	.	.	r	.	.	.	r	.	.	.	.	.	r	.

7.2. Appendix II: plant species list

	Family	Genus	Species	$_p$F	$_p$S	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
757	Myrtaceae	*Melaleuca*	*sp. 2*	S	N	.	.	.	.	.	.	u	.	r	r	.	.	.	.	.	.
758	Myrtaceae	*Melaleuca*	*sp. 3*	T	N	.	.	.	.	r	.	.	.	r	.	.	.	.	.	.	.
759	Myrtaceae	*Melaleuca*	*styphelioides*	T	N	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
760	Myrtaceae	*Melaleuca*	*thymifolia*	S	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
761	Myrtaceae	*Melaleuca*	*trichostachya*	T	N	.	.	r	.	u	.	.	r	u	r	.	.	.	.	.	.
762	Myrtaceae	*Melaleuca*	*viminalis*	T	N	.	.	.	.	c	u	c	c	c	c	u	u	.	.	r	.
763	Myrtaceae	*Melaleuca*	*viridiflora*	T	N	c	c	.	.	u	.	.	.	.	.	.	.	.	.	r	.
764	Myrtaceae	*Metrosideros*	*collina*	S	E	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.
765	Myrtaceae	*Metrosideros*	*excelsa*	S	E	.	.	.	.	r	.	u	r	.	u	.	r	.	.	.	.
766	Myrtaceae	*Metrosideros*	*sp.*	S	E	.	.	.	.	.	.	r	u	.	r	.	.	.	.	.	.
767	Myrtaceae	*NA*	*unknown sp. 18*	T	N	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
768	Myrtaceae	*Ochrosperma*	*lineare*	S	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
769	Myrtaceae	*Pilidiostigma*	*rhytispermum*	S	N	.	.	c	c	.	.	.	.	.	.	.	.	.	.	.	.
770	Myrtaceae	*Plinia*	*cauliflora*	S	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
771	Myrtaceae	*Psidium*	*cattleianum*	T	E	.	.	.	.	.	r	.	r	.	.	r	.	.	.	.	.
772	Myrtaceae	*Psidium*	*guajava*	T	E	.	.	.	u	.	r	.	.	r	.	r	r	.	.	.	.
773	Myrtaceae	*Rhodamnia*	*rubescens*	T	N	.	.	u	u	.	.	.	.	.	.	.	.	.	.	.	.
774	Myrtaceae	*Rhodamnia*	*sp.*	T	N	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
775	Myrtaceae	*Sannantha*	*similis*	S	N	.	.	.	.	.	.	r	.	r	.	r	.	.	.	.	.
776	Myrtaceae	*Sannantha*	*sp.*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
777	Myrtaceae	*Sannantha*	*virgata*	S	E	.	.	u	.	r	r	.	.	.	.	.	.	.	.	u	.
778	Myrtaceae	*Syncarpia*	*glomulifera*	T	N	.	.	c	c	.	.	.	.	.	.	.	.	.	.	.	c
779	Myrtaceae	*Syzygium*	*× wilsonii*	T	N	.	.	r	.	r	r	c	.	c	u	.	c	.	.	.	.
780	Myrtaceae	*Syzygium*	*australe*	T	N	.	r	r	.	c	u	.	.	c	c	.	.	.	.	.	.
781	Myrtaceae	*Syzygium*	*crebrinerve*	T	-	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.
782	Myrtaceae	*Syzygium*	*francisii*	T	N	.	.	.	.	.	.	u	.	r	r	.	r	.	.	.	.
783	Myrtaceae	*Syzygium*	*jambos*	T	N	.	.	.	.	.	r	r	.	r	.	.	r	.	.	.	.
784	Myrtaceae	*Syzygium*	*luehmannii*	T	N	.	.	r	.	u	u	c	r	c	c	c	c	.	u	.	.
785	Myrtaceae	*Syzygium*	*mooreii*	T	N	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
786	Myrtaceae	*Syzygium*	*oleosum*	T	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
787	Myrtaceae	*Syzygium*	*paniculatum*	T	N	.	.	.	.	c	c	c	.	c	c	c	c	.	.	.	.
788	Myrtaceae	*Syzygium*	*smithii*	T	N	.	.	c	c	.	r	.	c	c	.	.	r	.	u	r	.

	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
789	Myrtaceae	*Syzygium*	*sp.*	T	N	.	.	.	.	.	.	r	.	r	.	r	.	.	.	.	.
790	Myrtaceae	*Syzygium*	*wilsonii*	S	N	.	.	.	.	.	r	r	u	.	r	r	r	.	.	.	.
791	Myrtaceae	*Tristaniopsis*	*laurina*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
792	Myrtaceae	*Waterhousea*	*floribunda*	T	N	.	.	c	.	.	.	u	.	u	c	u	r	.	.	.	.
793	Myrtaceae	*Xanthostemon*	*chrysanthus*	T	N	.	.	.	.	c	u	r	u	c	c	.	u	.	.	.	.
794	NA	*NA*	*unknown sp. 03*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
795	NA	*NA*	*unknown sp. 04*	H	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	u	.
796	NA	*NA*	*unknown sp. 05*	S	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
797	NA	*NA*	*unknown sp. 06*	S	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
798	NA	*NA*	*unknown sp. 07*	S	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
799	NA	*NA*	*unknown sp. 08*	H	-	.	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.
800	NA	*NA*	*unknown sp. 09*	S	-	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
801	NA	*NA*	*unknown sp. 10*	S	-	.	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.
802	NA	*NA*	*unknown sp. 11*	H	-	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
803	NA	*NA*	*unknown sp. 12*	H	-	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
804	NA	*NA*	*unknown sp. 13*	S	-	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
805	NA	*NA*	*unknown sp. 14*	H	-	.	.	.	.	.	.	.	.	.	.	.	.	c	.	.	.
806	NA	*NA*	*unknown sp. 15*	H	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
807	Nephrolepidaceae	*Nephrolepis*	*cordifolia*	H	N	.	.	.	.	u	c	c	u	c	c	c	c	.	.	c	.
808	Nephrolepidaceae	*Nephrolepis*	*sp.*	H	E	.	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.
809	Nyctaginaceae	*Boerhavia*	*sp.*	H	E	.	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.
810	Nyctaginaceae	*Bougainvillea*	*sp.*	H	E	.	.	.	.	c	u	u	r	u	u	c	c	.	.	.	.
811	Nyctaginaceae	*Mirabilis*	*jalapa*	H	E	.	.	.	.	.	.	.	.	c	.	r	.	.	.	.	.
812	Nymphaeaceae	*Nymphaea*	*caerulea*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
813	Ochnaceae	*Ochna*	*serrulata*	S	E	.	.	c	u	.	u	u	.	u	c	c	c	.	.	.	.
814	Oleaceae	*Chionanthus*	*ramiflorus*	T	-	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.
815	Oleaceae	*Jasminum*	*laurifolium*	S	E	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.
816	Oleaceae	*Jasminum*	*nudiflorum*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
817	Oleaceae	*Jasminum*	*officinale*	H	E	.	.	.	.	.	.	r	.	u	.	r	.	.	.	.	.
818	Oleaceae	*Jasminum*	*polyanthum*	H	E	.	.	.	.	.	.	.	.	r	.	r	u	r	.	.	.
819	Oleaceae	*Jasminum*	*sambac*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
820	Oleaceae	*Jasminum*	*simplicifolium*	H	-	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.

#	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
821	Oleaceae	*Ligustrum*	*sinense*	S	E	.	.	.	.	.	.	.	.	r	u	.	.	.	.	.	.
822	Oleaceae	*Notelaea*	*longifolia*	T	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	.
823	Oleaceae	*Notelaea*	*microcarpa*	T	N	.	c	.	.	.	.	.	.	.	.	r	.	.	.	.	.
824	Oleaceae	*Olea*	*europaea*	T	E	.	.	.	.	r	r	.	.	c	r	r	.	.	.	.	.
825	Onagraceae	*Gaura*	*lindheimeri*	H	E	.	.	.	.	.	.	.	u	.	.	.	.	.	.	.	.
826	Onagraceae	*Ludwigia*	*octovalvis*	H	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	c
827	Onagraceae	*Ludwigia*	*peploides*	H	E	.	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.
828	Onagraceae	*Ludwigia*	*sp.*	H	-	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.
829	Onagraceae	*Oenothera*	*lindheimeri*	H	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
830	Onagraceae	*Oenothera*	*sp.*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	.	c	r	.
831	Orchidaceae	*Cymbidium*	*madidum*	H	N	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
832	Orchidaceae	*Cymbidium*	*sp.*	H	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
833	Orchidaceae	*Dendrobium*	*bigibbum*	H	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
834	Orchidaceae	*Dendrobium*	*sp.*	H	E	.	.	r	.	r	r	.	r	r	.	r	.	.	.	.	.
835	Orchidaceae	*Dendrobium*	*speciosum*	H	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
836	Orchidaceae	*Dipodium*	*variegatum*	H	N	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
837	Orchidaceae	*Epidendrum*	*radicans*	H	E	.	.	.	.	r	u	u	u	.	r	c	r	.	.	.	.
838	Orchidaceae	*Geodorum*	*densiflorum*	H	N	.	u	r	.	.	.	.	.	.	.	.	.	.	.	.	.
839	Orchidaceae	*Oncidium*	*altissimum*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
840	Orchidaceae	*Oncidium*	*varicosum*	H	E	.	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.
841	Orchidaceae	*Phaius*	*australis*	H	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
842	Orchidaceae	*Pterostylis*	*sp.*	H	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
843	Orchidaceae	*Vanda*	*sp.*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	r	.	.	.
844	Oxalidaceae	*Averrhoa*	*carambola*	T	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
845	Oxalidaceae	*Oxalis*	*corniculata*	H	E	.	.	c	u	c	c	c	.	r	c	c	c	c	c	c	.
846	Oxalidaceae	*Oxalis*	*corymbosa*	H	E	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.	u
847	Oxalidaceae	*Oxalis*	*debilis*	H	E	.	.	.	.	.	.	u	.	r	.	u	c	.	.	.	.
848	Oxalidaceae	*Oxalis*	*sp.*	H	-	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
849	Pandanaceae	*Freycinetia*	*scandens*	T	N	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
850	Pandanaceae	*Pandanus*	*tectorius*	T	N	.	.	r	.	u	.	r	c	r	.	r	.	.	.	r	.
851	Passifloraceae	*Passiflora*	*edulis*	H	E	.	.	.	r	r	r	r	u	u	u	u	r	.	.	.	.
852	Passifloraceae	*Passiflora*	*foetida*	S	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.

	Family	Genus	Species	$_p$F	$_p$S	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
853	Passifloraceae	*Passiflora*	*suberosa*	H	E	.	c	c	c	c	u	r	u	r	.	u	r	.	.	.	.
854	Passifloraceae	*Passiflora*	*subpeltata*	H	E	.	.	.	u	.	.	.	.	.	.	.	u	.	.	.	u
855	Petiveriaceae	*Rivina*	*humilis*	H	E	.	.	.	.	.	u	.	.	c	r	c	u	.	.	.	.
856	Philydraceae	*Philydrum*	*lanuginosum*	H	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	u
857	Phyllanthaceae	*Breynia*	*disticha*	S	E	.	.	.	.	.	r	r	.	r	.	.	.	.	.	.	.
858	Phyllanthaceae	*Breynia*	*oblongifolia*	S	N	.	c	r	c	.	.	.	r	.	.	u	r	.	.	c	.
859	Phyllanthaceae	*Bridelia*	*exaltata*	T	N	.	u	.	.	.	.	.	.	.	.	r	.	.	.	.	.
860	Phyllanthaceae	*Bridelia*	*sp.*	T	N	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
861	Phyllanthaceae	*Eustrephus*	*latifolius*	H	N	.	c	c	c	.	.	.	.	.	.	.	.	.	.	c	.
862	Phyllanthaceae	*Glochidion*	*ferdinandi*	T	N	.	c	c	c	.	.	u	c	.	.	c	r	.	.	.	.
863	Phyllanthaceae	*Glochidion*	*sumatranum*	T	N	.	.	c	c	.	.	.	.	.	.	.	.	.	.	u	c
864	Phyllanthaceae	*Phyllanthus*	*myrtifolius*	S	E	.	.	.	.	.	.	r	.	.	r	.	.	.	.	r	.
865	Phyllanthaceae	*Phyllanthus*	*sp.*	H	E	.	u	.	c	.	.	.	.	.	.	.	.	.	.	.	.
866	Phyllanthaceae	*Phyllanthus*	*tenellus*	H	E	.	.	.	.	.	u	c	.	c	c	c	c	r	.	.	.
867	Phyllanthaceae	*Phyllanthus*	*virgatus*	H	N	.	.	.	.	c	u	.	c	c	.	.	.	c	c	c	.
868	Pinaceae	*Pinus*	*sp.*	T	E	.	.	r	r	.	.	r	.	.	.	r	.	.	.	.	c
869	Piperaceae	*Peperomia*	*sp.*	H	E	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.
870	Piperaceae	*Piper*	*hederaceum*	H	N	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.
871	Pittosporaceae	*Auranticarpa*	*rhombifolia*	T	N	.	.	.	.	.	r	r	.	.	.	r	.	.	.	.	.
872	Pittosporaceae	*Billardiera*	*scandens*	H	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	.
873	Pittosporaceae	*Bursaria*	*spinosa*	S	N	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
874	Pittosporaceae	*Hymenosporum*	*flavum*	T	N	.	.	.	.	.	.	r	r	r	.	u	u	.	.	r	.
875	Pittosporaceae	*Pittosporum*	*multiflorum*	S	-	.	.	.	u	.	.	.	.	.	.	.	u	.	.	.	.
876	Pittosporaceae	*Pittosporum*	*revolutum*	S	N	.	r	c	r	.	.	.	.	.	.	r	.	.	.	.	.
877	Pittosporaceae	*Pittosporum*	*tobira*	S	E	.	.	.	.	r	.	.	r	.	.	.	.	.	.	.	.
878	Pittosporaceae	*Pittosporum*	*undulatum*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
879	Plantaginaceae	*Angelonia*	*angustifolia*	H	E	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
880	Plantaginaceae	*Bacopa*	*monnieri*	H	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
881	Plantaginaceae	*Penstemon*	*sp.*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
882	Plantaginaceae	*Plantago*	*lanceolata*	H	E	.	.	.	.	.	.	.	.	.	c	c	c	.	.	.	.
883	Plantaginaceae	*Plantago*	*sp.*	H	E	.	.	.	.	.	.	.	.	.	c	.	.	.	.	.	.
884	Plantaginaceae	*Scoparia*	*dulcis*	H	E	.	u	.	c	.	.	.	.	.	.	.	.	.	.	.	.

	Family	Genus	Species	$_p$F	$_p$S	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
885	Plumbaginaceae	*Limonium*	*sp.*	H	E	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.	.
886	Plumbaginaceae	*Plumbago*	*auriculata*	S	E	.	.	.	.	.	r	r	.	c	c	c	.	.	.	.	.
887	Plumbaginaceae	*Plumbago*	*zeylanica*	H	N	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.
888	Podocarpaceae	*Podocarpus*	*elatus*	T	N	.	.	.	.	r	.	r	.	.	.	r	u	.	.	.	.
889	Polygonaceae	*Antigonon*	*leptopus*	H	E	.	.	.	.	.	.	.	.	r	r	.	r	.	.	.	.
890	Polygonaceae	*Homalocladium*	*platycladum*	S	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
891	Polygonaceae	*Persicaria*	*attenuata*	H	N	.	.	.	.	u	c	.	.	.	.	.	.	.	c	.	c
892	Polygonaceae	*Persicaria*	*maculosa*	H	E	.	.	.	.	.	c	.	.	.	.	.	.	.	c	.	.
893	Polygonaceae	*Persicaria*	*sp.*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	u
894	Polygonaceae	*Persicaria*	*strigosa*	H	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	u
895	Polygonaceae	*Rumex*	*sp.*	H	E	.	.	.	.	u	c	u	.	c	u	.	c	.	.	.	c
896	Portulacaceae	*Crassula*	*ovata*	S	E	.	.	.	.	r	u	u	r	c	c	.	r	.	.	.	.
897	Portulacaceae	*Portulaca*	*oleracea*	H	E	.	.	.	.	c	c	c	u	c	c	u	u	c	c	.	.
898	Portulacaceae	*Portulaca*	*pilosa*	H	E	.	.	.	.	c	c	.	.	r	.	.	c	r	c	c	u
899	Portulacaceae	*Portulacaria*	*afra*	S	E	.	.	.	.	u	u	.	r	r	.	r	r	.	.	.	.
900	Primulaceae	*Embelia*	*australiana*	H	N	.	u	r	.	.	.	.	.	.	.	.	.	.	.	.	.
901	Primulaceae	*Samolus*	*repens*	H	-	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
902	Proteaceae	*Banksia*	*aemula*	S	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
903	Proteaceae	*Banksia*	*ericifolia*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
904	Proteaceae	*Banksia*	*integrifolia*	T	N	.	.	.	r	.	.	r	r	r	.	r	r	.	.	.	.
905	Proteaceae	*Banksia*	*oblongifolia*	S	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
906	Proteaceae	*Banksia*	*robur*	S	N	c	.	.	.	.	.	r	r	r	.	.	r	.	.	.	c
907	Proteaceae	*Banksia*	*spinulosa*	S	N	.	.	.	r	.	.	r	.	r	.	r	.	.	.	.	.
908	Proteaceae	*Buckinghamia*	*celsissima*	T	N	.	.	.	.	r	r	r	u	c	u	r	u	.	.	r	.
909	Proteaceae	*Conospermum*	*taxifolium*	S	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
910	Proteaceae	*Grevillea*	*× bipinnatifida*	S	N	.	.	.	.	u	.	r	r	r	.	r	.	.	.	.	.
911	Proteaceae	*Grevillea*	*× hodgei*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
912	Proteaceae	*Grevillea*	*× humilis*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
913	Proteaceae	*Grevillea*	*× pteridifolia*	T	N	.	.	.	.	r	r	r	.	r	u	r	.	.	.	.	.
914	Proteaceae	*Grevillea*	*× whiteana*	T	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
915	Proteaceae	*Grevillea*	*baileyana*	T	N	.	.	.	.	.	.	r	.	r	r	r	.	.	.	r	.
916	Proteaceae	*Grevillea*	*banksii*	S	N	.	u	.	.	r	.	.	.	r	r	.	r	.	.	.	.

	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
917	Proteaceae	*Grevillea*	*flexuosa*	S	N	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
918	Proteaceae	*Grevillea*	*formosa*	S	N	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
919	Proteaceae	*Grevillea*	*robusta*	T	N	.	.	.	.	.	u	.	.	u	u	u	u	.	.	.	.
920	Proteaceae	*Grevillea*	*sp.*	S	N	.	.	.	.	.	r	.	.	r	r	.	r	.	.	.	.
921	Proteaceae	*Grevillea*	*sp. 2*	S	N	.	.	.	.	.	.	.	.	.	u	.	r	.	.	.	.
922	Proteaceae	*Grevillea*	*sp. 3*	T	N	.	.	.	.	u	.	r	r	.	.	.	.	.	.	.	.
923	Proteaceae	*Grevillea*	*venusta*	S	N	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
924	Proteaceae	*Hakea*	*actites*	S	-	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
925	Proteaceae	*Hakea*	*florulenta*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
926	Proteaceae	*Helicia*	*glabriflora*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
927	Proteaceae	*Leucadendron*	*galpinii*	S	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
928	Proteaceae	*Leucadendron*	*laureolum*	S	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
929	Proteaceae	*Leucadendron*	*stelligerum*	S	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
930	Proteaceae	*Lomatia*	*silaifolia*	S	-	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.
931	Proteaceae	*Lomatia*	*sp.*	S	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
932	Proteaceae	*Macadamia*	*integrifolia*	T	N	.	.	.	c	.	r	u	r	u	c	u	u	c	c	c	c
933	Proteaceae	*Persoonia*	*cornifolia*	T	-	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	r
934	Proteaceae	*Persoonia*	*iogyna*	T	-	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
935	Proteaceae	*Persoonia*	*virgata*	S	N	c	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.
936	Proteaceae	*Protea*	*sp.*	S	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
937	Proteaceae	*Serruria*	*× florida*	S	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
938	Proteaceae	*Stenocarpus*	*sinuatus*	T	N	.	.	r	.	r	.	r	.	r	r	r	r	.	.	.	.
939	Proteaceae	*Xylomelum*	*benthamii*	T	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
940	Putranjivaceae	*Drypetes*	*deplanchei*	T	N	.	c	.	.	.	.	.	.	.	.	.	.	r	.	.	.
941	Ranunculaceae	*Aquilegia*	*vulgaris*	H	E	.	.	.	.	r	.	.	.	.	r	.	.	.	.	.	.
942	Ranunculaceae	*Clematis*	*aristata*	H	N	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
943	Ranunculaceae	*Delphinium*	*sp.*	H	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
944	Rhamnaceae	*Alphitonia*	*excelsa*	T	N	.	c	c	c	.	r	r	.	.	.	u	u	.	.	r	u
945	Rhamnaceae	Alphitonia	petriei	T	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
946	Rhamnaceae	*Emmenosperma*	alphitonioides	T	N	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.
947	Ripogonaceae	*Ripogonum*	*album*	H	-	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
948	Ripogonaceae	*Ripogonum*	*elseyanum*	H	N	.	.	c	r	.	.	.	.	.	.	.	.	.	.	.	.

	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
949	Rosaceae	*Cotoneaster*	*coriaceus*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
950	Rosaceae	*Eriobotrya*	*japonica*	T	E	.	.	.	.	.	.	.	.	r	r	c	u	.	.	.	.
951	Rosaceae	*Fragaria*	*× ananassa*	H	E	.	.	.	.	r	.	r	c	.	.	r	.	.	.	r	.
952	Rosaceae	*Prunus*	*persica*	T	E	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.	.
953	Rosaceae	*Rhaphiolepis*	*indica*	S	E	.	.	.	.	r	u	c	r	u	u	r	u	.	.	.	.
954	Rosaceae	*Rosa*	*banksiae*	H	E	.	.	.	.	.	r	r	r	.	r	.	.	.	.	.	.
955	Rosaceae	*Rosa*	*sp.*	S	E	.	.	.	.	c	u	u	r	u	u	c	u	.	.	.	.
956	Rosaceae	*Rubus*	*moluccanus*	S	N	.	.	c	c	.	.	.	.	.	.	r	.	.	.	r	.
957	Rosaceae	*Rubus*	*rosifolius*	S	N	.	.	.	.	.	.	.	.	.	.	r	u	.	.	.	.
958	Rosaceae	*Rubus*	*sp.*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
959	Rosaceae	*Spiraea*	*cantoniensis*	S	E	.	.	.	.	.	.	r	.	.	r	r	.	.	.	.	.
960	Rousseaceae	*Abrophyllum*	*ornans*	T	N	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.
961	Rubiaceae	*Atractocarpus*	*fitzalanii*	T	N	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
962	Rubiaceae	*Coffea*	*arabica*	S	E	.	.	.	.	.	.	r	.	r	r	u	.	.	.	.	.
963	Rubiaceae	*Cyclophyllum*	*coprosmoides*	T	N	.	c	c	r	.	.	.	.	.	.	r	.	.	.	.	.
964	Rubiaceae	*Gardenia*	*jasminoides*	S	E	.	.	.	.	r	r	c	c	c	c	u	.	.	.	.	.
965	Rubiaceae	*Ixora*	*coccinea*	S	E	.	.	.	.	u	c	c	r	u	.	r	r	.	.	.	.
966	Rubiaceae	*Ixora*	*sp.*	S	E	.	.	.	.	r	u	.	.	.	.	.	.	.	.	.	.
967	Rubiaceae	*Morinda*	*jasminoides*	H	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	.
968	Rubiaceae	*Nauclea*	*orientalis*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
969	Rubiaceae	*Oldenlandia*	*galioides*	H	-	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
970	Rubiaceae	*Oldenlandia*	*mitrasacmoides*	H	-	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
971	Rubiaceae	*Pavetta*	*australiensis*	S	N	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
972	Rubiaceae	*Pavetta*	*capensis*	S	E	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.
973	Rubiaceae	*Pentas*	*lanceolata*	S	E	.	.	.	.	u	u	.	r	c	.	.	.	.	.	.	.
974	Rubiaceae	*Psychotria*	*daphnoides*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
975	Rubiaceae	*Psychotria*	*loniceroides*	S	N	.	.	u	u	.	.	.	.	.	.	r	.	.	.	.	.
976	Rubiaceae	*Psydrax*	*lamprophylla*	T	-	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
977	Rubiaceae	*Richardia*	*brasiliensis*	H	E	.	c	.	.	.	.	.	.	.	u	.	.	.	.	.	.
978	Rubiaceae	*Rogiera*	*amoena*	S	E	.	.	.	.	.	.	r	r	.	r	r	r	r	.	.	.
979	Rubiaceae	*Serissa*	*japonica*	S	E	.	.	.	.	r	r	.	.	.	.	.	r	.	.	.	.
980	Rubiaceae	*Spermacoce*	*multicaulis*	H	N	.	c	.	.	.	c	.	.	.	.	.	.	.	.	r	.

#	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
981	Rubiaceae	*Spermacoce*	*sp.*	S	-	.	.	.	.	.	.	.	.	.	.	.	.	.	c	.	.
982	Rutaceae	*Acronychia*	*laevis*	T	N	.	c	r	.	.	.	.	.	.	.	.	.	.	.	.	.
983	Rutaceae	*Acronychia*	*oblongifolia*	T	N	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
984	Rutaceae	*Casimiroa*	*edulis*	T	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
985	Rutaceae	*Citrus*	*× latifolia*	S	E	.	.	.	.	r	.	r	r	u	r	.	r	.	.	.	.
986	Rutaceae	*Citrus*	*× limon*	S	E	.	.	.	r	r	u	r	u	u	.	u	r	.	.	.	.
987	Rutaceae	*Citrus*	*× sinensis*	T	E	.	.	.	.	.	.	.	.	r	r	.	r	.	.	.	.
988	Rutaceae	*Citrus*	*australis*	S	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
989	Rutaceae	*Citrus*	*hystrix*	S	E	.	.	.	.	.	.	.	.	r	r	r	r	r	.	r	.
990	Rutaceae	*Citrus*	*japonica*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
991	Rutaceae	*Citrus*	*paradisi*	T	E	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.
992	Rutaceae	*Citrus*	*reticulata*	T	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
993	Rutaceae	*Citrus*	*sp.*	T	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
994	Rutaceae	*Flindersia*	*australis*	T	N	.	.	.	r	.	r	.	.	r	.	r	r	.	.	.	.
995	Rutaceae	*Flindersia*	*bennettiana*	T	N	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.
996	Rutaceae	*Flindersia*	*brayleyana*	T	N	.	.	.	r	.	.	r	.	.	.	r	.	.	.	r	.
997	Rutaceae	*Flindersia*	*schottiana*	T	N	.	r	r	u	.	.	.	.	r	.	r	r	.	.	.	.
998	Rutaceae	*Flindersia*	*xanthoxyla*	T	N	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
999	Rutaceae	*Melicope*	*elleryana*	T	N	.	.	.	r	.	.	.	.	r	r	u	r	r	.	r	.
1000	Rutaceae	*Melicope*	*rubra*	S	N	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
1001	Rutaceae	*Microcitrus*	*sp.*	S	N	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
1002	Rutaceae	*Murraya*	*koenigii*	H	E	.	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.
1003	Rutaceae	*Murraya*	*paniculata*	S	N	.	.	.	.	c	c	c	c	c	c	c	.	.	.	u	.
1004	Rutaceae	*Phebalium*	*sp.*	H	N	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
1005	Rutaceae	*Zieria*	*laxiflora*	S	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1006	Rutaceae	*Zieria*	*minutiflora*	S	N	.	.	u	c	.	.	.	.	.	.	.	.	.	.	.	.
1007	Rutaceae	*Zieria*	*smithii*	S	N	.	.	r	c	.	.	.	.	.	.	.	.	.	.	.	.
1008	Salicaceae	*Scolopia*	*braunii*	T	-	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.
1009	Sapindaceae	*Acer*	*palmatum*	T	E	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
1010	Sapindaceae	*Alectryon*	*connatus*	T	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
1011	Sapindaceae	*Alectryon*	*coriaceus*	T	N	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
1012	Sapindaceae	*Alectryon*	*tomentosus*	T	N	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.

	Family	Genus	Species	pF	pS	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
1013	Sapindaceae	*Cardiospermum*	*grandiflorum*	H	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
1014	Sapindaceae	*Cedrela*	*sp.*	T	E	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
1015	Sapindaceae	*Cupaniopsis*	*anacardioides*	T	N	.	u	.	.	c	u	r	r	c	u	u	r	.	.	.	.
1016	Sapindaceae	*Cupaniopsis*	*parvifolia*	T	N	.	u	.	.	.	.	.	.	.	.	.	r	.	.	.	.
1017	Sapindaceae	*Dimocarpus*	*longan*	T	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
1018	Sapindaceae	*Diploglottis*	*australis*	T	N	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
1019	Sapindaceae	*Dodonaea*	*triquetra*	S	N	.	.	c	c	.	.	.	.	.	.	.	.	.	.	.	.
1020	Sapindaceae	*Elattostachys*	*nervosa*	T	N	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
1021	Sapindaceae	*Guioa*	*acutifolia*	T	-	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
1022	Sapindaceae	*Guioa*	*semiglauca*	T	N	.	.	.	c	.	.	.	.	.	.	.	r	.	.	.	.
1023	Sapindaceae	*Harpullia*	*pendula*	T	N	.	.	.	.	r	r	r	.	u	c	u	c	.	.	r	.
1024	Sapindaceae	*Jagera*	*pseudorhus*	T	N	.	u	u	u	.	.	.	.	r	.	u	r	.	.	r	.
1025	Sapindaceae	*Koelreuteria*	*elegans*	T	E	.	.	.	.	.	r	.	.	.	r	r	r	.	.	r	.
1026	Sapindaceae	*Koelreuteria*	*paniculata*	T	-	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
1027	Sapindaceae	*Litchi*	*chinensis*	T	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
1028	Sapindaceae	*Mischarytera*	*lautereriana*	T	N	.	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.
1029	Sapindaceae	*Sarcopteryx*	*stipata*	T	N	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.
1030	Sapotaceae	*Chrysophyllum*	*cainito*	T	E	.	.	.	.	.	.	.	.	r	.	.	r	.	.	.	.
1031	Scrophulariaceae	*Buddleja*	*davidii*	S	E	.	.	.	.	.	r	.	c	r	r	.	.	.	.	.	.
1032	Scrophulariaceae	*Eremophila*	*debilis*	H	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
1033	Scrophulariaceae	*Eremophila*	*sp.*	S	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
1034	Scrophulariaceae	*Myoporum*	*montanum*	S	N	.	.	.	.	c	.	.	.	.	.	.	.	.	.	.	.
1035	Scrophulariaceae	*Myoporum*	*sp.*	S	N	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.
1036	Scrophulariaceae	*Russelia*	*equisetiformis*	S	E	.	.	.	.	r	u	.	r	u	r	r	.	.	.	.	.
1037	Simaroubaceae	*Ailanthus*	*triphysa*	T	N	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
1038	Smilacaceae	*Smilax*	*australis*	H	N	.	.	c	c	.	.	.	.	.	.	r	r	.	.	.	.
1039	Smilacaceae	*Smilax*	*glyciphylla*	H	N	.	.	c	u	.	.	.	.	.	.	.	.	.	.	.	.
1040	Solanaceae	*Brugmansia*	*× candida*	S	E	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
1041	Solanaceae	*Brugmansia*	*sp.*	S	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
1042	Solanaceae	*Brunfelsia*	*bonodora*	S	E	.	.	.	.	u	.	u	.	c	c	u	u	.	.	.	.
1043	Solanaceae	*Brunfelsia*	*pauciflora*	S	E	.	.	.	.	.	u	.	r	.	.	.	.	.	.	.	.
1044	Solanaceae	*Capsicum*	*baccatum*	H	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.

	Family	Genus	Species	$_PF$	$_PS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
1045	Solanaceae	*Capsicum*	*frutescens*	H	E	.	.	.	.	u	u	u	.	u	u	c	r	.	.	.	.
1046	Solanaceae	*Capsicum*	*sp.*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
1047	Solanaceae	*Cestrum*	*parqui*	S	E	.	.	.	.	r	.	r	.	c	u	c	u	.	.	.	.
1048	Solanaceae	*Datura*	*stramonium*	S	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
1049	Solanaceae	*Lycianthes*	*rantonnetii*	H	-	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
1050	Solanaceae	*Lycopersicon*	*esculentum*	H	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	u
1051	Solanaceae	*Petunia*	*× hybridum*	H	E	.	.	.	.	c	c	r	r	r	r	c	.	.	.	r	.
1052	Solanaceae	*Physalis*	*minima*	S	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	u
1053	Solanaceae	*Physalis*	*peruviana*	H	E	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.
1054	Solanaceae	*Solanum*	*betaceum*	T	E	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.
1055	Solanaceae	*Solanum*	*capsicoides*	H	E	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
1056	Solanaceae	*Solanum*	*chrysotrichum*	S	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	u
1057	Solanaceae	*Solanum*	*densevestitum*	S	-	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1058	Solanaceae	*Solanum*	*lycopersicum*	H	E	.	.	.	.	.	.	.	.	r	u	u	c	u	.	.	.
1059	Solanaceae	*Solanum*	*mauritianum*	S	E	.	.	.	u	.	.	r	.	r	.	.	u	.	.	.	c
1060	Solanaceae	*Solanum*	*melongena*	H	E	.	.	.	.	.	.	.	.	c	.	.	.	.	.	.	.
1061	Solanaceae	*Solanum*	*nigrum*	H	E	.	c	.	u	c	u	r	.	c	u	c	c	c	c	c	c
1062	Solanaceae	*Solanum*	*seaforthianum*	H	E	.	u	.	u	.	.	r	.	.	.	.	.	.	.	r	.
1063	Solanaceae	*Solanum*	*stelligerum*	S	-	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1064	Solanaceae	*Solanum*	*torvum*	S	E	.	r	.	.	.	.	.	.	r	.	.	r	r	u	r	.
1065	Solanaceae	*Solanum*	*tuberosum*	H	E	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.
1066	Solanaceae	*Solanum*	*viridifolium*	S	N	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.	.
1067	Sparrmanniaceae	*Corchorus*	*cunninghamii*	H	N	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
1068	Sterculiaceae	*Argyrodendron*	*actinophyllum*	T	N	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
1069	Strelitziaceae	*Ravenala*	*madagascariensis*	T	E	.	.	.	.	u	.	u	r	.	r	r	.	.	.	.	.
1070	Strelitziaceae	*Strelitzia*	*nicolai*	S	E	.	.	.	.	.	.	.	.	.	.	u	.	r	.	.	.
1071	Strelitziaceae	*Strelitzia*	*reginae*	S	E	.	.	.	.	u	u	r	c	c	u	c	u	.	.	r	.
1072	Surianaceae	*Guilfoylia*	*monostylis*	S	N	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
1073	Tamaricaceae	*Tamarix*	*aphylla*	T	E	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
1074	Theaceae	*Camellia*	*japonica*	S	E	.	.	.	.	.	.	.	.	r	r	r	.	r	.	.	.
1075	Theaceae	*Camellia*	*sasanqua*	S	E	.	.	.	.	r	.	r	u	r	r	r	u	.	.	.	.
1076	Thymelaeaceae	*Phaleria*	*clerodendron*	T	N	.	.	.	.	r	.	r	.	r	r	r	.	.	.	.	.

	Family	Genus	Species	$_pF$	$_pS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
1077	Thymelaeaceae	*Phaleria*	*sp.*	S	N	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
1078	Thymelaeaceae	*Pimelea*	*latifolia*	S	-	.	.	.	u	.	.	.	.	.	.	.	.	.	.	.	.
1079	Thymelaeaceae	*Pimelea*	*linifolia*	H	N	.	.	c	.	.	.	.	.	.	.	.	r	.	.	.	.
1080	Thymelaeaceae	*Wikstroemia*	*indica*	S	N	.	.	r	u	.	.	.	.	.	.	.	.	.	.	.	.
1081	Tropaeolaceae	*Tropaeolum*	*majus*	H	E	.	.	.	.	r	u	.	.	c	r	u	r	.	.	.	.
1082	Typhaceae	*Typha*	*orientalis*	S	N	.	.	.	.	.	.	.	.	.	.	.	c	.	.	.	c
1083	Ulmaceae	*Celtis*	*sinensis*	T	E	.	.	.	.	.	.	.	.	c	c	c	c	.	.	.	.
1084	Ulmaceae	*Trema*	*tomentosa*	S	N	.	u	.	r	.	.	.	.	.	.	r	u	.	.	.	.
1085	Urticaceae	*Pilea*	*microphylla*	H	E	.	.	.	.	.	.	u	c	r	.	.	u	.	.	.	.
1086	Urticaceae	*Pipturus*	*argenteus*	S	N	.	.	.	.	.	.	.	.	r	.	r	r	.	.	.	.
1087	Verbenaceae	Citharexylum	spinosum	T	E	.	.	.	.	.	r	.	r	r	r	r	.	.	.	r	.
1088	Verbenaceae	*Duranta*	*erecta*	S	E	.	.	.	.	c	c	c	u	c	c	u	u	.	.	.	.
1089	Verbenaceae	*Lantana*	*× montevidensis*	S	E	.	.	.	.	.	r	.	.	u	.	.	.	.	.	.	.
1090	Verbenaceae	*Lantana*	*camara*	S	E	.	c	c	c	.	r	.	.	r	.	u	.	.	.	.	c
1091	Verbenaceae	*Lantana*	*montevidensis*	S	E	.	.	.	.	.	.	r	.	r	r	u	r	.	.	.	.
1092	Verbenaceae	*Lippia*	*nodiflora*	H	E	.	.	.	.	.	r	.	.	r	.	.	.	.	.	.	.
1093	Verbenaceae	*Petrea*	*volubilis*	H	E	.	.	.	.	.	r	.	.	.	.	r	r	.	.	.	.
1094	Verbenaceae	*Verbena*	*bonariensis*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
1095	Verbenaceae	*Verbena*	*litoralis*	H	E	.	.	.	.	r	.	.	.	u	.	r	.	.	c	.	.
1096	Verbenaceae	*Verbena*	*rigida*	H	E	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
1097	Verbenaceae	*Verbena*	*sp.*	S	E	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
1098	Veronicacea	*Antirrhinum*	*majus*	H	E	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.
1099	Violaceae	*Hybanthus*	*stellarioides*	H	N	.	r	u	.	.	.	.	.	.	.	.	.	.	.	.	.
1100	Violaceae	*Viola*	*hederacea*	H	N	.	.	.	r	c	.	.	.	.	r	u	r	.	.	.	.
1101	Vitaceae	*Cayratia*	*clematidea*	H	N	.	.	.	.	.	.	.	.	r	.	r	r	.	.	.	.
1102	Vitaceae	*Cissus*	*antarctica*	H	N	.	.	c	u	.	.	.	.	.	.	r	r	.	.	.	.
1103	Vitaceae	*Cissus*	*hypoglauca*	H	N	.	.	c	c	.	.	.	.	.	.	.	.	.	.	.	.
1104	Vitaceae	*Cissus*	*rhombifolia*	H	E	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.
1105	Vitaceae	*Clematicissus*	*opaca*	H	N	.	c	c	.	.	.	.	.	.	.	.	.	.	.	.	.
1106	Vitaceae	*Tetrastigma*	*nitens*	H	N	.	.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
1107	Vitaceae	*Vitis*	*vinifera*	H	E	.	.	.	.	r	.	.	.	r	r	r	r	.	.	.	.
1108	Xanthorrhoeaceae	*Aloe*	*arborescens*	S	E	.	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.

	Family	Genus	Species	$_PF$	$_PS$	F1 ab	F2 ab	F3 ab	F4 ab	G1 a	G1 b	G2 a	G2 b	G3 a	G3 b	G4 a	G4 b	P1 ab	P2 ab	P3 ab	P4 ab
1109	Xanthorrhoeaceae	*Aloe*	*vera*	H	E	.	.	.	.	u	u	r	.	r	r	u	.	.	.	.	.
1110	Xanthorrhoeaceae	*Hemerocallis*	*lilioasphodelus*	H	E	.	.	.	.	.	.	.	.	.	.	u	.	.	.	.	.
1111	Xanthorrhoeaceae	*Hemerocallis*	*sp.*	H	E	.	.	.	.	.	c	.	.	.	.	c	r	.	.	.	.
1112	Xanthorrhoeaceae	*Phormium*	*sp.*	H	E	.	.	.	.	r	.	.	r	.	.	.	.	.	.	.	.
1113	Xanthorrhoeaceae	*Xanthorrhoea*	*fulva*	H	N	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1114	Xanthorrhoeaceae	*Xanthorrhoea*	*johnsonii*	S	N	.	c	c	.	r	.	r	.	.	.	r	.	.	.	r	.
1115	Xanthorrhoeaceae	*Xanthorrhoea*	*latifolia*	H	N	c	u	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1116	Xanthorrhoeaceae	*Xanthorrhoea*	*macronema*	H	N	.	.	u	u	.	.	.	.	.	.	.	.	.	.	.	c
1117	Xanthorrhoeaceae	*Xanthorrhoea*	*sp.*	S	N	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
1118	Xyridaceae	*Xyris*	*operculata*	H	-	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1119	Zamiaceae	*Cycas*	*revoluta*	S	E	.	.	.	.	u	r	c	c	u	u	r	r	.	.	.	.
1120	Zamiaceae	*Lepidozamia*	*peroffskyana*	S	N	.	.	.	.	.	.	.	.	r	r	.	r	.	.	.	.
1121	Zamiaceae	*Macrozamia*	*lucida*	S	N	.	.	c	.	.	.	.	.	.	.	r	.	.	.	.	.
1122	Zamiaceae	*Zamia*	*furfuracea*	H	E	.	.	.	.	r	r	.	.	r	r	.	.	.	.	.	.
1123	Zingiberaceae	*Alpinia*	*caerulea*	S	N	.	.	r	u	.	.	u	.	r	r	r	c	.	.	.	.
1124	Zingiberaceae	*Alpinia*	*zerumbet*	S	E	.	.	.	.	.	u	.	.	r	c	r	c	.	.	r	.
1125	Zingiberaceae	*Curcuma*	*longa*	H	E	.	.	.	.	.	r	.	r	r	.	.	.	.	.	.	.
1126	Zingiberaceae	*Hedychium*	*coronarium*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
1127	Zingiberaceae	*Zingiber*	*officinale*	H	E	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	.
1128	Zingiberaceae	*Zingiber*	*sp.*	H	E	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.

VIII. ACKNOWLEDGEMENTS

Acknowledgements

DECLARATION

Declaration according to § 9 section 2 e)-f) and section 3 of the Doctoral Regulations of 2011 of the Faculty of Sustainability, Leuphana University Lüneburg

I hereby declare that I have not taken or registered to take another examination to receive a doctoral degree.

I hereby declare that the dissertation, in its present or any other version, has not yet been submitted to any other university for review.

I hereby certify that the submitted dissertation entitled 'Impacts of landscape resource diversity and availability on bee foraging and fitness' has been written by me without using any unauthorized aids. I did not use any aids and writings other than those indicated. All passages taken from other writings either verbatim or in substance have been marked by me accordingly.

Erklärungen gem. § 9 Abs. 2 e)-f) und Versicherung gem. § 9 Abs. 3 der Promotionsordnung 2011 der Fakultät Nachaltigkeit der Leuphana Universität Lüneburg

Hiermit erkläre ich, dass ich mich bisher keiner anderen Doktorprüfung unterzogen oder zu einer solchen Prüfung angemeldet habe.

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Ich versichere, dass ich die eingereichte Dissertation „Impacts of landscape resource diversity and availability on bee foraging and fitness" selbständig und ohne unerlaubte Hilfsmittel verfasst habe. Anderer als der von mir angegebenen Hilfsmittel und Schriften habe ich mich nicht bedient. Alle wörtlich oder sinngemäß anderen Schriften entnommene Stellen habe ich kenntlich gemacht.

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