Pollination of the wet forest herb *Pollia crispata* (Commelinaceae)

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Abstract: The flower structure of *Pollia crispata* (R.Br.) Benth. allows access by a taxonomically diverse assemblage of pollinating insects. Patterns of flower anthesis, and removal of pollen, suggest adaptation to diurnal flower visitors. Flowers are pollinated by insects, but *Pollia crispata* can produce viable seeds independent of insect pollination, and plants can reproduce and spread vegetatively subsequent to founding events. The composition of the pollinator fauna is dominated by syrphid flies, halictid bees and the apid bee *Trigona carbonaria*, but most insect visitors observed have broader recorded flower host ranges. In general, the insects recorded from *Pollia crispata* flowers are restricted to the understorey and ground strata of regional subtropical rainforests.

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Introduction

In Australia, herbs in the genus *Pollia* (family Commelinaceae) comprise two endemic species, *Pollia crispata* (R.Br.) Benth. and *Pollia macrophylla* (R.Br.) Benth. (Harden 1993). *Pollia crispata* occurs in New South Wales and Queensland, *Pollia macrophylla* is restricted to Queensland (Hnatiuk 1990).

Pollia crispata (Figures 1, 2) is found along creeklines in montane and subcoastal rainforest and wet sclerophyll forest, and can form dense spreading mats on sunlit creek margins, drainage lines and associated slopes where soil moisture levels are high. These habitats are vulnerable to invasion by exotic weeds, such as the related South American weed Tradescantia fluminensis. Like most flowering plants of the subtropical rainforest understorey in Australia, no information is available on flower visitors, or reproductive ecology of Pollia crispata. Despite the species frequently occurring in dense populations very few, if any, visitors to flowers are normally observed by casual observation. The principal aim of this study was to identify flower visitors and potential pollinators.

Methods

The study was largely confined to a single patch of *Pollia crispata* plants growing along a shallow drainage line in regenerating mixed wet sclerophyll forest and subtropical rainforest at Lorien Wildlife Refuge (31°45′00′′S, 152°32′30″E, approximately 100 m a.s.l.), north of Taree on the New South Wales north coast. This patch constituted the largest known population at the location. The two intergrading forest communities had been logged, or structurally damaged as a result of logging, in the late 1970s.

Observations of plants and flower visitors were undertaken (collectively over 34 days) during 1996, and from 1998 until January 2003. These extended from mid November until late



Fig. 2. *Pollia crispata* clump in wet sclerophyll forest, Lorien Wildlife Refuge



Fig. 1. Pollia crispata flowers

February (the general period of flowering), and comprised 1–3 hours each day of observation. The timing of individual daily observations commenced as early as 0830 hours and as late as 1940 hours (dusk). Throughout each day flowers received intermittent and dappled sunlight and were frequently fully shaded. Most insects visited between early daylight and midday (>0800–1200 hours), and observations in 1999–2003 were generally restricted to this period. Daily weather conditions were usually hot, to very hot and humid. The 2001–2002 season of observation coincided with pronounced drought conditions, and drought conditions preceded the 2002–2003 season of flowering.

In addition to the Lorien site, flowering plants were briefly observed in montane warm temperate rainforest at Coombadjha Creek (approximately 1000 m a.s.l.), Washpool National Park northwest of Grafton, in 1997, and in subtropical rainforest at Gumbaynggir Nature Reserve (previously League Scrub Flora Reserve) (> 900 m a.s.l.) near Bowraville in 1998 and 2001.

Flower structure and pollen were examined using a light microscope. To determine if *Pollia crispata* is dependent on pollinators for pollen transfer, a total of thirty-two unopen flowers, distributed between three plants, were covered with fine nylon bags to exclude pollinators. The flowers were enclosed on the 27 December 1998, and the bags later removed on 8 March 1999, by which time flowering of the population had ceased.

The behaviour of all insects on flowers was observed. Voucher specimens of all insect species visiting flowers were collected, using a small hand-held net, for identification and examination of pollen loads (Table 1). Pollen from individual insects was compared with voucher pollen collected from *Pollia crispata*. Voucher insect specimens are deposited in the Australian Museum (Sydney), Museum Victoria (Melbourne) and the Lorien Wildlife Refuge field research collection. Undescribed halictid bees, collected during the study, have been deposited in Museum Victoria. Australian plant names follow Harden (1990–93).

Results

Pollia crispata is a perennial, annually flowering herb and individual plants grow vegetatively from adventitious stem roots. In 1996 the *Pollia crispata* clump at Lorien Wildlife Refuge covered an area approximately 3×5 m and available flowers comprised more than 100 inflorescences. By November 2000 the population had expanded vegetatively to an area approximately > 10 m $\times 5$ m. However, plants (in dense shade) close to regenerating wet sclerophyll forest and rainforest had died back, or 'opened-up' (i.e. foliage no longer formed a closed mat), exposing bare ground. These heavily shaded plants were much lower than those growing in sunlit conditions (average < 0.33 m, as opposed to > 0.75 m in height). By late 2001 some grass, ferns and additional herb

species (e.g. *Lobelia*, *Pratia*) had begun to colonise open ground space previously covered by the dense *Pollia* mat, and by January 2003 ferns had largely replaced the original *Pollia* population and *Pollia* had colonised adjacent open areas.

The flowers of *Pollia crispata* are actinomorphic, bisexual, approximately 8–9 mm wide, in terminal inflorescences; petals 3 coloured white, sepals 3 coloured greenish-white; gynoecium superior, style long and narrow; stamens 3; with 2–3 long staminodes or non-functional stamens. Flowers do not appear to produce nectar and there are no obvious nectar guides (and nectar guides and patterns were not apparent under ultra violet light). Flowers open sequentially each morning and appear slightly protogynous. The perianth is open and shallow and does not restrict access. However, each petal can act as a landing platform, if orientated downwards, in which case the lower petal is 'pseudolobellate'. Pollen is bright yellow, dry and easily displaced from anthers; pollen exine pattern is reticulate. The bright-coloured pollen appears to convey the main visual recruitment signal.

Bagged flowers set seed but actual numbers were not counted as the presentation of the hard nut-like seeds made it difficult to assign them to individual flowers. Twenty seeds collected from bagged flowers were sown in pots; 5 seeds germinated and grew to mature plants, and these had flowered by January 2003. The formation of viable seeds indicates that *Pollia crispata* is not dependent upon insect pollinators for fertilisation to occur.

By mid-January 2002 local drought conditions at the Lorien site were severe, and although plants possessed numerous flower buds none were open. Flower buds were progressively aborted such that none were available later in the flowering season to flower-visiting insects.

Insects were not observed to visit flowers during the night or during rain. All flower visitors were able to contact the stigma and stamens and are considered potential pollinators.

Pollen from daily-opening flowers had normally been removed by insects by 1300 hours. In general, abundance of insects decreased when flowers were in full sun and insects were absent in late afternoon and at dusk. The majority of insect species observed visited shaded flowers, and flowers in dappled sunlight, even when flowers were hidden by low overhanging ferns. Many species were not observed visiting flowers in full sunlight. Exceptions were several species of Syrphini (Diptera: Syrphidae) (Melangyna damastor [Walker], Syrphini species 1, 2, Betasyrphus sp.) which preferred sunlit flowers. The syrphid Episyrphus sp. was common most seasons but generally restricted its visits to shaded and dapple-lit flowers. Most halictid bees were very timid and easily disturbed. On one occasion (13 December 2001) the large trap-lining anthophorine bee Amegilla bombiformis (Smith) approached flowers at the Lorien site but did not land.

Table 1. Biotic pollen vectors, showing number of individuals, dates observed and main sites of pollen lodgement, visiting *Pollia crispata* flowers, Lorien Wildlife Refuge

Dates observed = dates when taxa were observed on flowers; no. individuals = number of specimens examined for pollen; n/a = no apparent pollen; 'home' pollen = approximate percentage of *Pollia* pollen on number of individuals examined for pollen; number of additional foreign pollen species in brackets; letters assigned to undescribed *Lasioglossum* spp. are K. Walker interim identification codes.

Taxa No. individuals % home pollen Dates observed Main sites of pollen lodgement

DIPTERA

Bombyliidae

Geron nigrocciput Evenhuis 2 n/a 27.12.98, 30.11.01, 4.12.01, 18.12.01, 9.1.03

Syrphidae: Syrphini

Betasyrphus sp.

16.12.99, 3.2.00

face, pro-, meso- and hind femora, ventrites generally, lateral margins of basal metasomal segments, but particularly sternopleura and mesopleura

Episyrphus sp./spp. 5 >99-100 15.11.96,17.11.96, 26.12.98, 28.12.98, 31.12.98, 31.199, 11.12.99, 19.1.00, 3.2.00, 4.2.00, 25.2.00, 30.11.01, 8.1.03 ventral areas, thorax, fore, mid and hind legs, inner ocular margins (comb-like long setae on mid femora)

Melanogyna damastor (Walker) 1 100 15.11.96, 29.11.96, 26.12.98, 24.11.99, 9.12.99, 5.12.0, 13.12.01 thorax and forelegs generally

Syrphini sp. 1 2 100 26.12.98, 29.12.98, 31.12.98, 11.12.99, 19.1.00, 30.11.01 scattered grains on whole body surface and face, but particularly ventrites, sternopleural and pteropleural regions

Syrphini sp. 2 1 100 31.12.99

scattered occasional grains on hind femora, anepisternites, sternopleural and pteropleural regions

Syrphini sp. 3 1 ~50 (2) 30.11.01 notopleuron, isolated grains on body generally

HYMENOPTERA

Apidae

Amegilla ?pulchra (Smith) 1 >50 26.12.98, 18.12.00, 4.12.01 hind tibiae and femora

Apis mellifera Linnaeus 4 100 4.2.00, 23.11.00, 3.12.00, 18.12.00, 23.12.00, 30.11.01, 4.12.01, 13.12.01, 18.12.01, 16.1.03 corbiculae — hind leg, scattered grains elsewhere

Exoneura sp. 0 8.1.03

Trigona carbonaria Smith 2 100 15.11.96, 2.12.96, 3.12.96, 27.12.98, 23.11.00, 3.12.00, 18.12.00,

15.11.96, 2.12.96, 3.12.96, 27.12.98, 23.11.00, 3.12.00, 18.12.00 23.12.00, 30.11.01, 4.12.01, 13.12.01,18.12.01, 8.1.03, 9.1.03, 16.1.03

corbiculae - hind leg, scattered grains elsewhere

Colletidae-Hylaeinae

Amphylaeus nubilosellus (Cockerell) 1 100
9.12.99
scattered few grains on body and wings generally

Hemirhiza melliceps Cockerell 3 100
29.12.98, 3.1.99, 11.12.99
few (or no) grains scattered on body surface generally, or few grains restricted to meso— or metasoma

Halictidae

Lasioglossum (Austrevylaeus) 1 100 sp. nov. 'J' 4.1.99, 9.12.99, 3.2.00

ventral surface and legs generally, particularly hind femora and basal ventrites, propodeum and mesasomal metapleuron

Lasioglossum (Austrevylaeus) 6 100 sp. nov. 'L'

2.12.96, 3.12.96, 27.12.98, 29.12.98, 31.12.98, 3.1.99, 13.12.99, 19.12.99, 19.1.00, 4.12.01, 8.1.03

hind femora, tibiae and tarsomeres, ventral scopae of metasoma, lateral basal margin of mesosoma

Lasioglossum (Austrevylaeus) 2 ~60–100 (2) sp. nov. 'Y'

9.12.99, 3.2.00

ventral surface and legs generally, particularly hind femora and ventrites 1-3

Lasioglossum (Callalictus) 1 100 tooloomense (Cockerell)

9.12.99

ventral surface and hind legs generally, especially hind femora

Lasioglossum (Chilalictus) 1 <50 (2, ?3) convexum (Cockerell)

5.12.01, 8.1.03

base of propodeum, metapleura, base of metasoma and mid legs, but particularly hind legs

Lasioglossum (Chilalictus) 5 <40–100 (2, ?3) polygoni (Cockerell) 29.12.98, 9.12.99, 16.12.99, 3.2.00, 18.12.00, 8.1.03

ventral surface generally, but particularly propodeum, hind legs and ventrites $1\!-\!2$

Lasioglossum (Parasphecodes) 4 >99–100 (1, ?2) atronitens (Cockerell)

29.12.98, 31.12.98, 30.11.01, 4.12.01, 16.1.03

hind femora, tibiae and tarsomeres, ventral surface of metasoma, base of propodeum, scattered grains on body surface generally

Lasioglossum (Parasphecodes)

leichardti (Cockerell) 2 >99->90 (2) 3.2.00, 30.11.01, 5.12.01, 8.1.03

base of propodeum, ventral surface generally, but particularly hind legs and basal half of metasoma

Lasioglossum (Parasphecodes) 5 >95–100 (2) musicum (Cockerell)

26.12.98, 29.12.98, 3.1.99, 19.12.99, 18.12.00, 23.12.00, 30.11.01, 5.12.01

petiole, propodeum and mesosomal metapleura, basal segment of metasoma, ventral surface generally, hind trochanter, femora, tibiae and tarsomeres

Lasioglossum sp. 1 100 3.1.99

hind tibiae and tarsomeres, ventral scopae of metasoma

Nomia aurantifer Cockerell 1 100 19.12.99, 18.12.00, 13.12.01, 8.1.03

scattered grains over whole body, but especially ventral surface generally, apex of metasoma, hind tibiae and hind femora

Formicidae

Myrmecia nigrocincta Smith 0 30.11.01, 4.12.01, 9.1.03

Myrmecia ?tarsata Smith 0 23.11.00, 3.12.00, 30.11.01, 4.12.01, 9.1.03

REPTILIA

Scincidae

Saproscincus ?galli Wells 0 and Wellington 3.1.99 There was annual and daily variation in the number of insect taxa visiting flowers (see Table 1). No insects were recorded on some days. Greater numbers of taxa were observed visiting flowers at the Lorien site during the summer of 1998– 1999 and 2000–2001, although approximately equal time was spent each year (until January 2002) observing flowers (Table 1). Only four taxa were observed in 1996 and this relatively low diversity may be related to the smaller patch size of the *Pollia* population at that time, because numbers of available flowers/inflorescences can influence visitation. In most years Episyrphus sp. and Lasioglossum sp. nov. 'L' were the most commonly observed flower visitors. For example, Lasioglossum sp. nov. 'L' comprised 48 % and Episyrphus sp. comprised 32 % of visits to Pollia crispata flowers during 1 hour of morning observations (on the 3 January 1999) out of twenty-five visits by 6 insect taxa. However, both species were rarely seen in 2001–2002.

No insects were observed visiting flowers at Washpool National Park during brief daytime inspections. Three species of syrphid fly (*Melangyna damastor*, *Syrphini* sp. 2, *Betasyrphus* sp.), and the bees *Trigona carbonaria* Smith and *Lasioglossum musicum* (Cockerell) were observed on *Pollia crispata* flowers at Gumbaynggir Nature Reserve. These species were also recorded from Lorien Wildlife Refuge. At Lorien Wildlife Refuge, in 1998–1999, visits by *Trigona carbonaria* occurred when most of the *Pollia crispata* population was in flower but *Trigona* was not observed when flower numbers diminished later in the flowering season.

Pollen loads are in part related to the amount of time spent foraging, but except for the bombyliid fly Geron nigrocciput Evenhuis all bees and flies examined carried Pollia crispata pollen (Table 1). The 2 hylaeine bees (Amphylaeus nubilosellus [Cockerell], Hemirhiza melliceps Cockerell), however, only carried occasional scattered pollen grains. The syrphids appear to be pollen feeders, and except for the longtongued bee Amegilla ?pulchra (Smith) and Geron nigrocciput, other visitors were relatively short-tongued insects whose visits to *Pollia* flowers are unimpeded owing to the shallow open structure of the perianth. Amegilla ?pulchra foraged rapidly, was easily disturbed, and moved quickly between individual flower clusters. The introduced honey bee Apis mellifera Linnaeus was observed visiting Pollia crispata flowers only in the 2000–2001 and 2001–2002 seasons. In an attempt to remove pollen Apis occasionally agitated flowers by shaking, but did not 'buzz' flowers. On the 4 December 2001 a single Lasioglossum musicum attempted briefly to 'buzz' flowers. Beetles, which regionally are a common element of entomophilous subtropical rainforest trees (Williams 1995), were not observed on Pollia flowers.

Of particular interest were observations on the 3 January 1999 of a small skink, *Saproscincus ?galli* Wells and Wellington. The skink climbed with agility over and between *Pollia* plants using its tail to grasp stems, and on one occasion leaping > 25 cm from leaf to branch. The skink frequently contacted flowers but no attempt was made to isolate pollen from its body.

Three new Lasioglossum bee species, in the subgenus Austrevylaeus, were collected during this study. One of these, Lasioglossum sp. nov. 'L', is a distinctive black species with golden yellow setae on the thorax. However, to date only females have been collected and males remain unknown at the site. During observations Lasioglossum sp. nov. 'L' restricted its foraging to Pollia crispata and did not visit adjoining co-flowering Lobelia sp. (Campanulaceae). Pollen loads on the 6 individuals examined consisted of 'home' pollen only. This species preferred very shaded flowers but otherwise exhibited no obvious foraging pattern. Generally no more than 4 Lasioglossum sp. nov. 'L' bees were observed at any one time at the Pollia clump. Individuals would spend up to approximately three minutes collecting pollen from individual flowers and used fore and mid-legs to pack pollen into hind-leg scopae and setae on the abdominal ventrites.

Discussion

World wide the Commelinaceae comprise 42 genera and approximately 620 species, mainly distributed in the Tropics (Harden 1993). With the exception of brief observations on *Commelina cyanea* (Williams 1993) flower visitors and pollinators of the Australian Commelinaceae flora are unrecorded.

The daily patterns of flower opening and removal of pollen by insects indicates adaptation to diurnal visitors by Pollia crispata. Although flowers are allophilic, offering unrestricted access to a taxonomically broad range of invertebrate flower visitors, the pollinator fauna of *Pollia crispata* is apparently dominated by syrphid flies, halictid bees, and Trigona carbonaria. However, Kato (2000) has recorded small Lasioglossum bees, and the beetle genera Protaetia (Scarabaeidae) and Chlorophorus (Cerambycidae), visiting white-flowered, actinomorphic, Pollia japonica in the Ryukyu Archipelago, Japan. Halictid and syrphid-dominated plantpollinator relationships are also recorded for Australian ground orchids in the genus Thelymitra, and the ground stratum more generally (Dafni & Calder 1987). Trigona carbonaria is recorded from numerous flowering subtropical rainforest plants in the study region and elsewhere (Williams 1995, Williams & Adam 1997, G. Williams unpubl. data).

The related herb *Commelina cyanea* is also visited and pollinated by bees and syrphid flies. Williams (1993) records native halictid, colletid and trap-lining anthophorine bees (e.g. *Amegilla ?pulchra, Nomia aurantifer* [Cockerell]), and the syrphid fly *Syritta* sp. as pollinators. Contrary to the actinomorphic open and white flowers of *Pollia crispata*, flowers of *Commelina cyanea* are bright blue and slightly zygomorphic suggesting that flower shape and colour may be poor indicators of pollinator taxa. This is supported by the observations of Kato and Miura (1996) who recorded syrphid flies as the pollinators of blue-flowered, actinomorphic, *Commelina communis* and pink-flowered, zygomorphic, *Murdannia keisak* (Commelinaceae) in a Japanese lowland marsh community. Hingston and McQuillan (2000), investigating plant-flower visitor associations in a range of

Tasmanian vegetation formations, found that flower pollination syndromes may be unreliable predictors of pollinators. Rather, occupation of a particular vegetation stratum may be a better predictor of pollinator association in wet forest types.

A number of the flower visitors recorded during this study have broader wet forest host plant associations in the Taree region. At Lorien Wildlife Refuge Episyrphus sp., was occasionally observed on adjacent Aneilema acuminatum (Commelinaceae) herbs (this is an endemic genus restricted to the Northern Territory, Queensland and New South Wales [Harden 1993]) (G. Williams unpubl. data). Syrphini sp. 1 was observed on male flowers of Clematis glycinoides (Ranunculaceae). In addition to Commelina cyanea, Nomia aurantifer is recorded from the flowers of the small mangrove tree Aegiceras corniculatum (Myrsinaceae) and the mass-flowering canopy vine Austrosteenisia blackii (Fabaceae) (Williams 1993). Lasioglossum musicum occasionally visited Rubus rosifolius (Rosaceae) shrubs on rainforest margins, Lasioglossum atronitens (Cockerell) was also collected from Dianella caerulea (Liliaceae) and the scrambling vine Hibbertia scandens (Dilleniaceae), and Lasioglossum tooloomense (Cockerell) was also a rare visitor to Dianella caerulea (G. Williams unpubl. data). Lasioglossum polygoni (Cockerell) is recorded from the shrub Senna acclinis (Caesalpinioideae) (Williams 1998) and the subcanopy tree Diospyros australis (Ebenaceae) (Williams & Adam 1997). Amphylaeus nubilosellus and Hemirhiza melliceps have been regionally recorded from a number of rainforest canopy and understorey trees and shrubs (Williams 1998, Williams & Adam 1997). At Gumbaynggir Nature Reserve Lasioglossum musicum was also collected buzz-pollinating adjacent flowering Senna × floribunda (Caesalpinioideae), a native of Mexico, that now occurs throughout coastal New South Wales. Melanogyna damastor is encountered in sunlight wet forest margins on the New South Wales north coast on numerous low-flowering plants (G. Williams unpubl. data). The native bees Amegilla ?pulchra, Amphylaeus nubilosellus, Hemirhiza melliceps, Lasioglossum atronitens, Lasioglossum convexum (Cockerell), Lasioglossum leichardti (Cockerell), Lasioglossum musicum, Lasioglossum polygoni and Trigona carbonaria, however, have ecological and floral host ranges not limited to wet forest types (Cardale 1993, Walker 1995).

With the exception of *Amphylaeus nubilosellus*, the insects visiting *Pollia crispata* flowers appear to be restricted to understorey strata (including open forest floor areas) in the study region. Many taxa visiting *Pollia crispata* could best be described as cryptic visitors as these preferred shaded or dapple-lit flowers and individual foraging events were commonly inconspicuous. Williams and Adam (1997) indicated that *Hemirhiza melliceps* foraged preferentially at shaded flowers of the rainforest understorey and observations during this study confirm this. Notable exceptions, during the study, to apparent cryptic foraging behaviour were a number of *Syrphini* and *Amegilla ?pulchra*.

Pollination of *Pollia crispata* (and potentially that of the additional Commelinaceae mentioned here, Commelina cyanea and Aneilema acuminatum) differs from the entomophilous pollination strategy of mass-flowering subtropical rainforest canopy trees. In the latter, pollination is primarily achieved by a diverse assemblage of ecologically generalist Diptera, Coleoptera and Hymenoptera (Williams 1995, Williams & Adam 2001), within which Syrphidae (and especially *Syrphini*) and native Apoidea are only a small or inconsequential proportion (Williams 1995, Williams & Adam 1997). The pollinator relationships found in *Pollia crispata* are more typical of those documented in the rainforest understorey, where plant-pollinator mutualisms are generally more specialised and pollinator assemblages on individual plants are less diverse (e.g. Hamilton 1897, Williams & Adam 1994, 1999, Williams et al. 2001), and groups such as bees are more prominent (e.g. Gross 1993, Williams 1998). Rainforest understorey communities, however, are vulnerable to piecemeal clearing for recreational facilities, paths and roads, and to blanket invasion by exotic weeds such as Tradescantia fluminensis and Asparagaceae (Williams & Adam 1999, Williams & Gerrand 1998).

However, *Pollia crispata* is not totally dependent on pollinators. Individual plants are able to self-pollinate, and founding populations can expand by root growth from stolons; as was the case in the principal study population at Lorien Wildlife Refuge. Restrictions to colonisation appear to be absence of moist areas and dense shading.

Two of the seasonally most abundant pollinators observed during this study, *Episyrphus* sp. and *Lasioglossum* sp. nov. 'L', have restricted ecological ranges and were not collected by Williams (1995) during the extensive sampling of massflowering rainforest canopy trees in the region. *Lasioglossum* sp. nov. 'L' is presently known only from Lorien Wildlife Refuge and is currently known only from *Pollia crispata*. These apparently restricted vertical ranges and plant associations, within wet forest strata, suggest that the loss of relatively common or localised native understorey plants, and clearing of the entire understorey stratum, may have important impacts on pollinator faunas, with individual species being susceptible to local extinction.

Volant insects can exhibit limited ability to enter, and cross, cleared landscape matrices (see Campbell & Brown 1994). Consequently, pollinators with restricted host associations may be unable to recolonise isolated vegetation remnants even if suitable host plants are reintroduced. Loss of pollinators, and subsequent breakdown in plant-pollinator relationships may have important flow-on impacts on the maintenance of floristic and overall biological diversity in reserves.

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