

Standard yet unusual mechanisms of long-distance dispersal: seed dispersal of *Corymbia torelliana* by bees

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ABSTRACT

Mellitochory, seed dispersal by bees, has been implicated in long-distance dispersal of the tropical rain forest tree, *Corymbia torelliana* (Myrtaceae). We examined natural and introduced populations of *C. torelliana* for 4 years to determine the species of bees that disperse seeds, and the extent and distance of seed dispersal. The mechanism of seed dispersal by bees was also investigated, including fruit traits that promote dispersal, foraging behaviour of bees at fruits, and the fate of seeds. The fruit structure of *C. torelliana*, with seed presented in a resin reward, is a unique trait that promotes seed dispersal by bees and often results in long-distance dispersal. We discovered that a guild of four species of stingless bees, *Trigona carbonaria*, *T. clypearis*, *T. sapiens*, and *T. hockingsi*, dispersed seeds of *C. torelliana* in its natural range. More than half of the nests found within 250 m of fruiting trees had evidence of seed transport. Seeds were transported minimum distances of 20–220 m by bees. Approximately 88% of seeds were dispersed by gravity but almost all fruits retained one or two seeds embedded in resin for bee dispersal. Bee foraging for resin peaked immediately after fruit opening and corresponded to a peak of seed dispersal at the hive. There were strong correlations between numbers of seeds brought in and taken out of each hive by bees ($r = 0.753–0.992$, $P < 0.05$), and germination rates were $95 \pm 5\%$. These results showed that bee-transported seeds were effectively dispersed outside of the hive soon after release from fruits. Seed dispersal by bees is a non-standard dispersal mechanism for *C. torelliana*, as most seeds are dispersed by gravity before bees can enter fruits. However, many *C. torelliana* seeds are dispersed by bees, since seeds are retained in almost all fruits, and all of these are dispersed by bees.

Keywords

Corymbia, *Eucalyptus*, long-distance dispersal, resin, stingless bees, *Trigona*.

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INTRODUCTION

Long-distance seed dispersal is currently of intense interest, as rare long-distance dispersal events have a disproportionate influence on plant population dynamics (Cain *et al.*, 2000; Higgins *et al.*, 2003; Nathan, 2005, 2006). Rare long-distance dispersal events have also been shown to play a crucial role in plant invasion dynamics, vegetation response to climate change, and biodiversity conservation (Richardson *et al.*, 2000; Soons & Ozinga, 2005; Trakhtenbrot *et al.*, 2005). Long-distance dispersal can result from exceptional behaviour of the standard dispersal agent, for example, wind-dispersed seeds travelling long distances in thermal updrafts, or by non-standard agents such as unusual dispersal syndromes not commonly reported in the literature (Higgins *et al.*, 2003; Nathan, 2006). Non-standard animal agents such as emus and white-tailed deer disperse

seeds long distances, thus impacting on plant migration, plant invasion, gene flow, and metapopulation dynamics (Myers *et al.*, 2004; Calviño-Cancela *et al.*, 2006). In general, however, mechanisms of long-distance dispersal are poorly characterized in the literature, and there is a lack of fundamental knowledge of traits that promote long-distance dispersal (Higgins *et al.*, 2003; Nathan, 2006).

Mellitochory, seed dispersal by bees, is an unusual seed-dispersal syndrome reported for three unrelated tropical rain forest species: a eucalypt, *Corymbia torelliana* (Wallace & Trueman, 1995); a tree legume, *Zygia racemosa* (Bacelar-Lima *et al.*, 2006); and an epiphyte, *Coussapoa asperifolia* ssp. *magnifolia* (Garcia *et al.*, 1992). Bees forage for resin at or inside fruits, transport seeds to their nest, and then discard seeds at the nest (Wallace & Trueman, 1995; Bacelar-Lima *et al.*, 2006). In *C. torelliana*, seeds are known to be dispersed long distances by bees (Wallace &

Trueman, 1995; Cain *et al.*, 2000). Little is known about the traits of *C. torelliana* that promote foraging by bees, and the consequences for seed dispersal, including long-distance dispersal.

Seed dispersal by animals is considered to be a diffuse mutualism, since seed dispersal rarely involves a tightly coevolved relationship between only two partners (Stanton, 2003). Instead, plants are usually coevolved with multispecies guilds of dispersers, and associations between partners are loose and general (Howe & Smallwood, 1982; Stanton, 2003; Bollen *et al.*, 2004). In *Z. racemosa* and *C. asperifolia*, several species of meliponine bees are implicated in seed dispersal (Garcia *et al.*, 1992; Bacelar-Lima *et al.*, 2006). In *C. torelliana*, seeds are only known to be dispersed by one species of stingless bee, *Trigona carbonaria*, outside the tree's natural range (Wallace & Trueman, 1995). In Australia, there are approximately 12 species of stingless bees in two genera, *Trigona* and *Austroplebeia* (Cardale, 1993; Dollin *et al.*, 1997; Franck *et al.*, 2004). At least four species of *Trigona* occur in the natural range of *C. torelliana* (Dollin *et al.*, 1997), but it is not known whether these species disperse seeds.

The aim of this study was to investigate seed dispersal by stingless bees in the natural range of *C. torelliana*. In addition, we examined the mechanism of seed dispersal by bees, including fruit traits of *C. torelliana* that promote dispersal by bees, foraging behaviour of bees at fruits, and the fate of seeds. We specifically addressed the following questions: (1) How widespread is bee dispersal and what species of bees disperse seeds of *C. torelliana* in the natural range? (2) How do fruits present and release resin and seed? (3) How and when do bees forage for resin and transport seeds? (4) What is the fate of seeds?

METHODS

Study species

The study was conducted over four fruiting seasons (2001–05) of *C. torelliana* in both its natural range in the wet tropics of northern Queensland, Australia, and in subtropical southern Queensland where the species has been introduced. In its natural range, the species occurs in tropical rain forest and rain forest margins and grows to 30 m tall (Hill & Johnson, 1995).

Seed dispersal in the natural range of *C. torelliana*

Populations of *C. torelliana* were studied over 4 years in the natural range between Shipton's Flat, near Cooktown (15°48'30" S, 145°13'55" E), and Kirrima State Forest, near Ingham (18°09'45" S, 145°41'55" E) (Fig. 1). We surveyed fruiting *C. torelliana* trees in natural populations at seven sites for the presence of resin-foraging bees using Zeiss 8 × 30 binoculars. Planted trees at three sites in the natural range were also examined, and bees were collected for identification. Between one and five trees with fresh mature fruits were observed for 5-min periods between 08:00 h and 18:00 h during sunny weather conducive to bee activity.

We also surveyed the sites for nests of stingless bees. Where nests were found, the bee species were identified where possible,

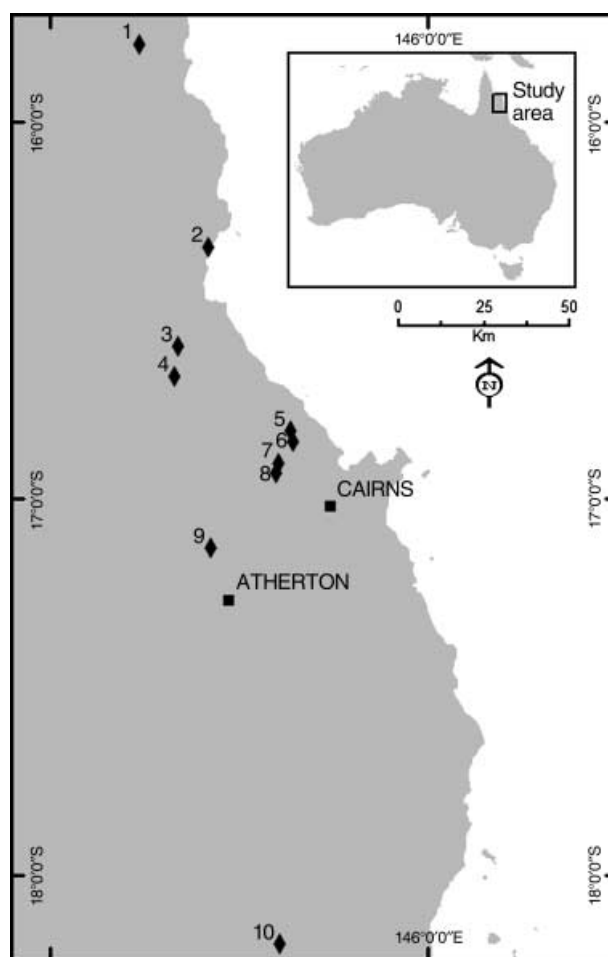


Figure 1 Map of study region showing site locations in the natural range of *Corymbia torelliana*.

and distance to nearest fruiting *C. torelliana* was recorded. In the *T. carbonaria* group, identification is based on the internal nest structure, but examination inside nests was not always possible. We examined nests for evidence of seed transport; for example, seeds adhering on the nest surface, seeds, or seedlings under the nest, bees carrying seeds into or out of the nest and, where possible, seeds inside the nest.

Mechanisms of bee dispersal

Study site

Experimental studies of fruit development, seed release, and foraging behaviour were conducted at Gympie, Australia (25°59' S, 154°45' E), on 12 planted trees of *C. torelliana* where fruits were readily accessible. Eleven of the trees had flowered heavily in October 2001 and had many maturing fruits. Four *T. carbonaria* hives propagated in wooden boxes after the method of Heard (1988) were transported to the study site in November 2001. Hives were 60–120 m away from the nearest fruiting *C. torelliana*. We observed fruit development, resin-foraging

behaviour, and seed transport at weekly intervals for 10 weeks between December 2001 and February 2002.

Fruit development and seed release

Six trees of *C. torelliana* were randomly selected and, from each, three large fruit clusters were haphazardly chosen for observation. All clusters had more than 150 fruits and were within 3 m of the ground. We examined the changes in fruit morphology on 10 fruits from each of the three fruit clusters each week ($n = 180$ per week). Colour and stage of valve opening were recorded for each fruit, and fruit were longitudinally sectioned to determine whether resin and seeds were present.

We also examined the proportion of seeds retained in the fruit for seed dispersal by bees. Three fruit clusters per tree were selected haphazardly on four trees. On each cluster, we enclosed five fruits per bunch in paper bags ($n = 60$). Fruits were allowed to dehisce naturally, and were then removed from the tree after 4 weeks and the number of seeds in the bag counted. The dehisced fruits were longitudinally sectioned and we recorded where resin was placed and the number and location of retained seeds.

Resin foraging and fate of seeds

Studies on resin foraging by *T. carbonaria* and seed transport were conducted at the same weekly intervals. Six trees of *C. torelliana* were randomly selected and from each a large fruit cluster was haphazardly chosen for observation. All clusters had more than 150 fruits and were within 3 m of the ground. Fruits were observed with Zeiss 8 × 30 binoculars where necessary. Each week, we observed each fruit cluster for 10 min every 2 h between 08:00 h and 18:00 h to assess the number of bees foraging for resin, number of bees with resin, and number of bees carrying seeds.

At the *T. carbonaria* hives, we recorded the number of bees entering with seeds, and the number of bees leaving the hive with seeds in two consecutive 5-min intervals by watching the hive entrance. Observations were repeated on all hives every 2 h between 08:00 h and 18:00 h once each week throughout the study ($n = 20$). Correlations between numbers of seeds transported into and out of hives were calculated on totals for each day for each hive using Pearson's correlation coefficients ($n = 10$).

Seeds were collected from the hive entrance and from underneath each of the four hives to establish viability of seed dispersed by *T. carbonaria*. Where possible, seeds were divided into subsamples of 10 and germinated by incubating on damp filter paper, under constant light, at 25 °C for 20 days (Boland *et al.*, 1980; Wallace & Trueman, 1995).

RESULTS

Seed dispersal in the natural range of *C. torelliana*

Foraging by stingless bees for resin was observed in all *C. torelliana* fruiting populations, both natural and planted, in all years of the study (Table 1). Bees foraging for resin on amenity plantings of *C. torelliana* were identified as *T. carbonaria* group or *T. sapiens*.

In total, 50 stingless bee nests were located in the natural range of *C. torelliana*. More than half of the 19 nests found within 250 m of fruiting *C. torelliana* had evidence of seed transport (Table 2). Four species of stingless bees, *Trigona carbonaria*, *T. clypearis*, *T. sapiens*, and *T. hockingsi*, were confirmed as seed transporters at three sites, in both disturbed and undisturbed habitats (Tables 2 and 3). Seed transport was observed directly at six nests of at least two species, and seeds were also found inside nests, on nest entrances, and underneath other nests (Table 3).

Table 1 Habitat type, number of observation days, years, and sites where stingless bees were observed foraging on fruits of *Corymbia torelliana* in the species' natural range. Sites are shown in Fig. 1.

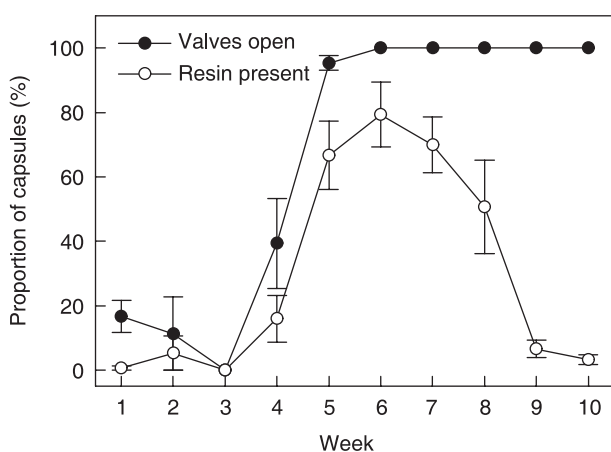
Habitat	No. of observation days	Years	Sites
Undisturbed rain forest margins	4	2002, 2003, 2004	1, 6, 8
Disturbed rain forest margins	6	2002, 2004	3, 5, 7
Rain forest	1	2003	10
Amenity plantings	12	2002, 2003, 2004, 2005	2, 4, 9

Table 2 Nests of stingless bees examined for evidence of seed transport of *Corymbia torelliana* in its natural range. Table shows species (or *Trigona carbonaria* group, where internal nest structure could not be examined to distinguish between *T. carbonaria* and *T. hockingsi*), total number of nests of each species examined, number of each species' nests within 250 m of fruiting *C. torelliana*, and number of these nests with evidence of seed transport.

Species	Total nests found	Nests within 250 m of <i>C. torelliana</i>	Nests with seed transport
<i>Trigona sapiens</i>	11	6	4
<i>Trigona hockingsi</i>	2	2	1
<i>Trigona clypearis</i>	12	5	2
<i>Trigona carbonaria</i>	3	3	2
<i>Trigona carbonaria</i> group	10	2	2
<i>Trigona</i> sp.	11	0	0
<i>Austroplebeia</i> sp.	1	1	0
Total	50	19	11

Table 3 Nests of *Trigona* spp. with evidence of seed transport in the natural range of *Corymbia torelliana*. Table shows: species of bee (or group, where internal nest structure could not be examined), map reference, distance to nearest fruiting *C. torelliana*, location of seed at the nest, and habitat type.

Species	Map ref.	Distance (m)	Location of seeds	Habitat
<i>T. carbonaria</i>	1	50	Inside nest; on nest surface	Undisturbed
	1	50	Inside nest; on nest surface	Undisturbed
<i>T. hockingsi</i>	5	20	Transport in/out of nest; on, under and inside nest; seedling establishment (39 seedlings within 2-m radius of nest)	Moderately disturbed
<i>T. carbonaria</i> group	5	20	On and under nest; seedling establishment (1 seedling within 2-m radius of nest)	Disturbed
	1	50	Transport into nest; on nest entrance	Undisturbed
<i>T. clypearis</i>	2	220	On nest entrance	Disturbed
	2	210	On nest entrance	Disturbed
<i>T. sapiens</i>	5	50	Transport in/out of nest	Disturbed
	5	100	Transport in/out of nest, seedling establishment (60 seedlings within 2-m radius of nest)	Disturbed
	5	100	Transport in/out of nest	Disturbed
	5	50	Transport into nest	Disturbed

**Figure 2** The timing of valve opening and availability of resin in *Corymbia torelliana* fruits. Means and standard errors are presented. Observations were conducted weekly, with week 1 commencing 19 December 2001.

Bees dispersed many seeds over minimum distances of 20–220 m, and established seedlings were found under three nests of least two species (Table 3). Where seedling establishment was found, seedlings were clumped within 2 m of the nest entrance.

Mechanisms of bee dispersal

Fruit development and seed release

Fruits were green until mid-December (week 2), and between weeks 3–5 most fruits turned brown, fruit valves began to open, and seeds were released (Fig. 2). *C. torelliana* produced 15.6 ± 1.8 seeds per fruit, and most (88.4%) of these were released immediately when valves opened and were then dispersed by gravity. However, seeds were retained in

$85.6 \pm 6.1\%$ of fruits, with an average of 2.1 ± 0.3 seeds remaining per fruit. When valves opened, resin was secreted from behind the valves, forming sticky droplets at the margins. All seeds remaining in the fruit were embedded in these resin droplets. Resin was not available to foraging bees until valves opened and most seeds were released, forming a hollow fruit structure into which bees could enter. The resin available in fruits diminished towards the end of the observation period (Fig. 2). No seeds were found in fruits when the resin was depleted.

Resin foraging by *T. carbonaria* and fate of seeds

The peak of foraging by *T. carbonaria* occurred between weeks 3–5 during initial valve opening and seed release (Fig. 3). After valve opening, bees foraged in all remaining weeks of the study but, as the resin resources depleted, bees did not obtain resin (Figs 2 & 3a,b). Seed transport peaked immediately after valve opening, when around 25% of foragers transported seeds (Figs 2 & 3c). Bees foraged for resin by flying in diminishing circles around fruit clusters, and landing on the surface of a fruit. Bees then entered the fruit head-first, collecting resin in their mandibles (Fig. 4a). While inside the fruit, bees turned their body around 180° and collected more resin from other valves. Bees usually left the fruit head-first, sometimes carrying a seed (Fig. 4b,c).

Returning foragers carried seeds into the nest in resin attached to their corbiculae at all hives. Usually one or two *C. torelliana* seeds were attached to resin in the corbiculae of the bees, but one individual was observed entering the hive with four seeds. Hive-cleaning bees were observed carrying seeds away from the hive in their mandibles and forelegs. Seeds were mostly discarded within a few metres of the entrance, and discarded seeds were sometimes encased in a garbage pellet consisting of bee faeces. Both inward and outward transport of seed at hives peaked in the fourth week of observations, coinciding with the period of rapid

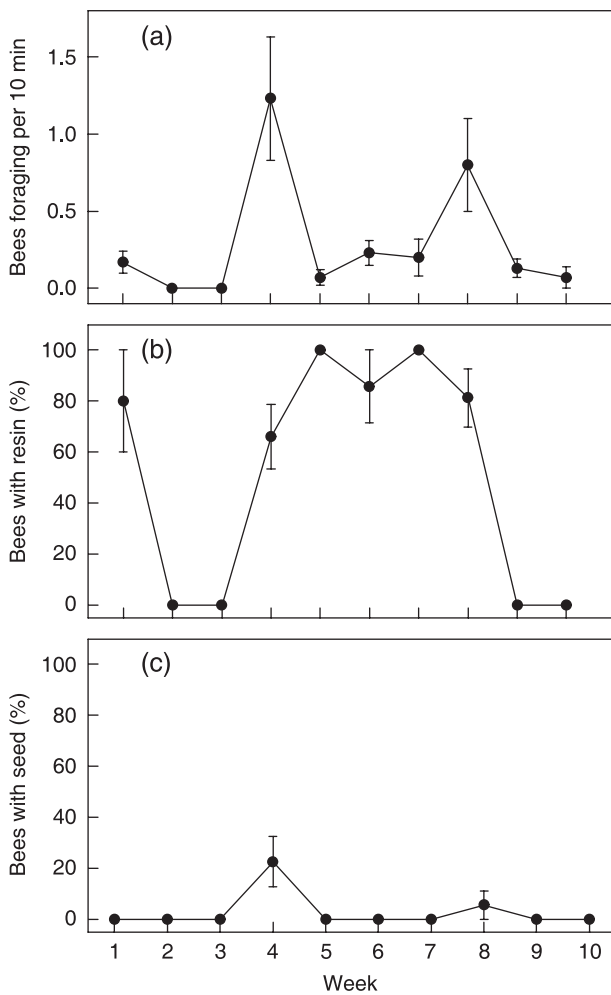


Figure 3 (a) Number of *Trigona carbonaria* foraging at *Corymbia torelliana* fruit clusters. (b) Percentage of foraging *T. carbonaria* that obtained resin at fruit clusters. (c) Percentage of foraging bees carrying seeds at the fruit. Means and standard errors per 10-min observation are presented. Means are calculated from all fruit clusters over all times of the day ($n = 30$). Observations were conducted weekly, with week 1 commencing 19 December 2001.

valve opening and greatest foraging at the fruits (Figs 2, 3 & 5). The peak of seed transport out of the hive corresponded closely with seed transport into the hive (Fig. 5). Seed transport out of each hive was highly correlated with seed transport into the hive (hive 1, $r = 0.753$, $P < 0.05$, and hives 2, 3, and 4, $r = 0.821$, 0.992 , 0.943 , respectively, $P < 0.01$). Germination rates of bee-dispersed seeds were very high, with $95 \pm 5\%$ for seeds from under the hive, and $92 \pm 2\%$ for seeds taken from resin around the hive entrance.

DISCUSSION

Morphological dispersal syndromes, such as the classic, well-documented dispersal syndromes (van der Pijl, 1982), are considered to be the 'standard' means of dispersal for plant species, and if other agents are involved they are considered as

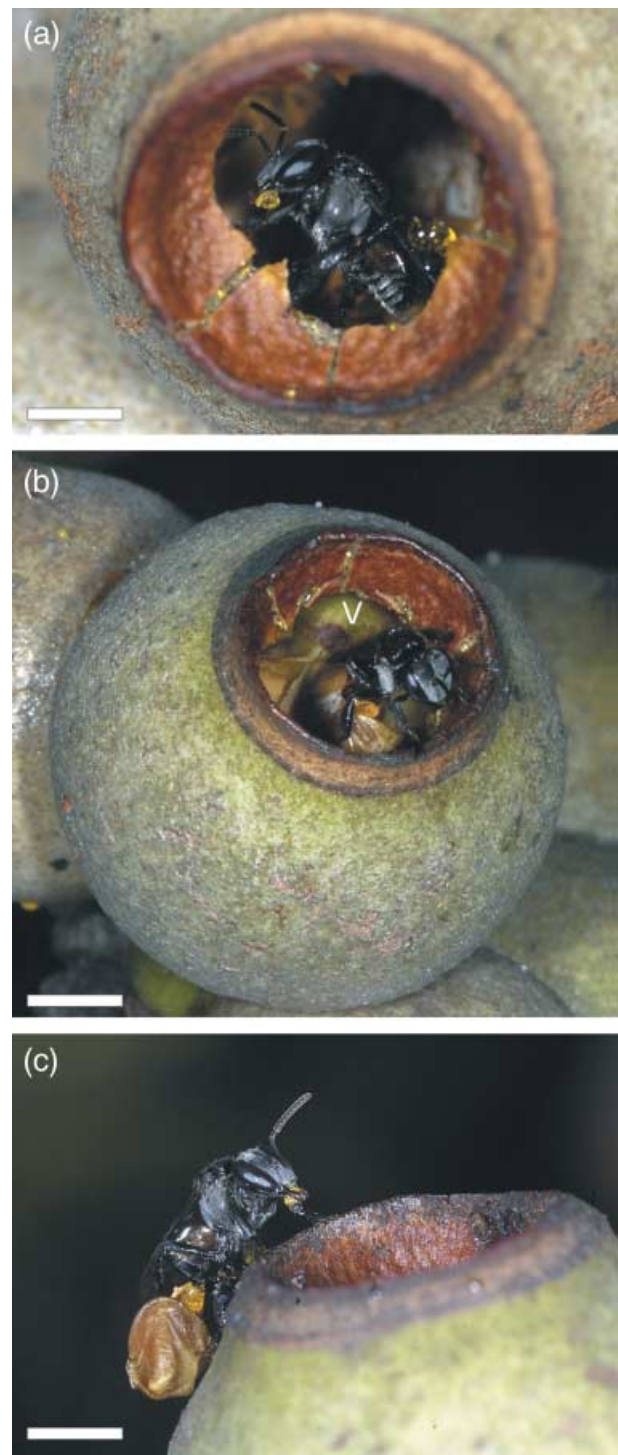


Figure 4 (a) *Trigona carbonaria* foraging for resin inside fruit of *Corymbia torelliana*. Note resin in mandibles and corbiculae. Scale bar = 1.6 mm. (b) *T. carbonaria* emerging from fruit with resin and seed attached, 'v' indicates retracted valve. Scale bar = 2.5 mm. (c) *T. carbonaria* at fruit entrance carrying resin and seed of *C. torelliana*. Scale bar = 1.5 mm. Photographs courtesy of Robert B. Luttrell.

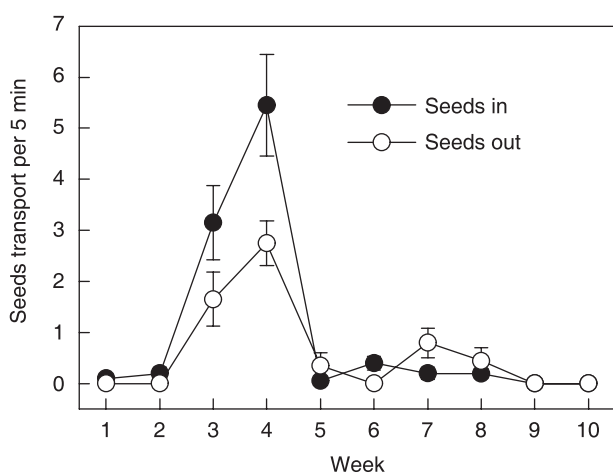


Figure 5 Number of bees entering and leaving hives of *Trigona carbonaria* with seeds for each 5-min observation period. Observations were carried out on four propagated hives. Means and standard errors are presented. Observations were conducted weekly, with week 1 commencing 19 December 2001.

'non-standard' (Higgins *et al.*, 2003). The morphological dispersal syndrome concept emphasizes processes that move a majority of seeds rather than the rarer processes that move a small proportion of seeds (Higgins *et al.*, 2003). Here, we describe a plant with unusual morphological adaptations that benefit only a small proportion of its seeds. Our results showed that *C. torelliana* has a 'bet-hedging' strategy of seed dispersal, with gravity dispersal of 88% of seeds, coupled with bee dispersal for 12% of seeds. Thus, *C. torelliana* has two standard mechanisms of seed dispersal, as it has morphological adaptations to both gravity dispersal and bee dispersal. However, dispersal by bees is rare compared with gravity dispersal.

C. torelliana had unique fruit adaptations to promote bee dispersal. When fruits dehisced, fruit valves collapsed and withdrew into the fruit, allowing seeds to be released and dispersed by gravity (Boland, 1976; Carr & Carr, 1987). This resulted in a hollow fruit that allowed foragers of *Trigona* to enter to collect resin (Wallace & Trueman, 1995). We found resin droplets at the margins of the valves in all fruits and, in 86% of fruits, one or more seeds remained embedded in resin droplets. Furthermore, bees transported seeds soon after fruits commenced valve opening. Seed turnover in the hives was rapid, with strong correlations between seeds entering and leaving the hives, and seeds dispersed outside of the hives were capable of germination. This suggests that many seeds reached their final dispersal location, often at long distances from the parent tree, soon after fruit opening. The valves and resin droplets of *C. torelliana* fruits are a seed-presentation mechanism that attracts stingless bees and enables rapid seed dispersal.

Resin veins in the wood tissue of eucalypts (*Corymbia*, *Eucalyptus*, and *Angophora*), commonly referred to as kino veins, are formed in response to injury and help to prevent pathogen invasion (Tippett, 1986). To our knowledge, the mechanism of resin production in the fruits is unique to *C. torelliana*.

However, the species is known to form hybrids with its closest relatives, the spotted gum group (*C. maculata*, *C. henryi*, and *C. citriodora*) and other more distant relatives such as *C. tessellaris* (Hill & Johnson, 1995; Lee, 2007). Hybrids form naturally in the wild where the species overlap, near amenity plantings where *C. torelliana* has been introduced, and are also produced by artificial crossing in eucalypt breeding programs (Hill & Johnson, 1995; Potts & Dungey, 2004; Lee, 2007; Trueman & Richardson, 2007). Fruit- and seed-dispersal characteristics of these hybrids have not yet been investigated.

Long-distance dispersal is now recognized as critically important for plant population dynamics and plant communities (Cain *et al.*, 2000; Higgins *et al.*, 2003; Nathan, 2005; Soons & Ozinga, 2005; Trakhtenbrot *et al.*, 2005; Nathan, 2006). Dispersal of *C. torelliana* seeds by bees is the longest known distance for any insect-mediated seed dispersal. Ants are the most common insect dispersers, but ant dispersal is usually restricted to a short range from the parent. Mean dispersal distances for ants are less than 1 m (Gomez & Espadaler, 1998) with the longest recorded dispersal distance being 180 m (Whitney, 2002). In contrast, final dispersal locations were 60–120 m from the nearest parent trees in our study site in the subtropics and sometimes > 200 m from the nearest parent tree in wild populations in the tropics. Actual dispersal distances are likely to be much further, as the distance to the nearest parent tree has been shown to underestimate true dispersal distance (Mack, 1995; Nathan & Muller-Landau, 2000). Molecular data have shown that seed is being transported from trees much further than the nearest tree, where the nearest tree is 100 m from the nest (Stokoe, unpublished data). There are also anecdotal reports of bees carrying *C. torelliana* seeds over 1 km (L. Bird, R. Luttrell, pers. comm.).

Dispersal over such long distances has important consequences for the population dynamics of *C. torelliana*, both in its natural range and in areas where it has been introduced. Eucalypt seeds dispersed by gravity rarely travel more than 50 m, and eucalypt seeds of similar size to *C. torelliana* only travel around 20 m when dispersed by gravity and wind (Cremer, 1977). Models of seed dispersal show that even a small proportion of seeds (0.1%) moving long distances can lead to an order of magnitude increase in predicted spread rate (Higgins & Richardson, 1999). Long-distance dispersal may already have important consequences for the population dynamics of *C. torelliana* outside its natural range. For example, *C. torelliana* is rapidly colonizing natural forest and is now considered an invasive species in areas where it has been introduced and co-occurs with *T. carbonaria* (Wallace & Trueman, 1995). Seed-dispersal mutualisms are known to be crucial in assisting plant invasions but usually generalist vertebrate dispersers are implicated in widespread invasions due to their long-distance dispersal (Richardson *et al.*, 2000).

Stingless bees foraged for resin in fruits throughout the natural range of *C. torelliana* in all habitat types, and in both natural populations and amenity plantings. Four species of bee, *Trigona carbonaria*, *T. clypearis*, *T. sapiens*, and *T. hockingsi*, were confirmed as seed transporters in the natural range. Therefore, mellitochory, like other seed-dispersal syndromes (Howe &

Smallwood, 1982; Stanton, 2003) is a diffuse mutualism involving guilds of stingless bee species. An unidentified species of *Austroplebeia* occurred at one of the sites and bees of this genus are also known to collect plant resin (Michener, 1961; Cardale, 1993).

Providing resin to attract bees requires an energetic investment by *C. torelliana*. If only a small proportion of seeds can be dispersed by bees, then what is the trade-off to the species to offset the energetic costs? Possible benefits of seed dispersal are (1) escape from density-dependent mortality near the parent, (2) colonization of rare or unpredictable sites, and (3) directed dispersal to more favourable microhabitats (Howe & Smallwood, 1982). We observed a clumped distribution of *C. torelliana* dispersed by bees, resulting in a high density of *C. torelliana* seedlings near the nest. Hence, these seeds dispersed by bees are not likely to escape from density-dependent mortality.

The colonization hypothesis provides one explanation for the evolution of bee-mediated dispersal in *C. torelliana*. Bee-mediated dispersal and, in particular, long-distance dispersal is likely to transport seeds to rare sites not available to gravity-dispersed seeds, including sites at higher elevation. While only a small proportion of seeds is available for bee transport, each mature *C. torelliana* tree produces many thousands of fruits (Lee, unpublished data). With one or two seeds remaining in each of 86% of the fruits, each individual has thousands of opportunities for colonization of rare sites via bee dispersal.

Directed dispersal is another possible explanation for adaptations of *C. torelliana* to seed dispersal by bees. Directed dispersal to more nutrient-rich sites near ant nests is proposed as a selective advantage for many ant-dispersed species. In these species, the directed-dispersal hypothesis is supported in about half of the studies where it was tested, with consistent evidence for both tropical forest species and trees (Giladi, 2006). Similarly, stingless bees potentially alter soil nutrients by disposing of garbage pellets near their nests (Roubik, 1989), and we observed that some discarded seeds were encased in bee faeces. However, we propose that the most likely benefit of seed dispersal by bees is directed dispersal to a higher light environment. Light levels are limiting to seedling establishment in rain forests of the wet tropics, and small-seeded plants are especially sensitive to low light levels (Osunkoya *et al.*, 1994). Stingless bees generally colonize hollows in dead trees and fallen logs (Michener, 1961; Dollin *et al.*, 1997), and *T. carbonaria* only flies from the nest when solar radiation is above 15 Wm⁻² (Heard & Hendrikz, 1993). Therefore, mellitochory is likely to disperse seeds to canopy gaps, rain forest margins, and disturbed areas, areas with a higher light environment that provide ideal conditions for seedling establishment.

ACKNOWLEDGEMENTS

We thank P. Collier, S. Khan, R. Stokoe, and S. Trueman for field assistance, R. Jenkins for help with mapping, and S. Trueman for helpful comments on the manuscript. This work was funded in part by an Australian Research Council Linkage Grant to HW and DL. All experiments comply with the current laws of Australia.

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