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Research Article

Honey bees as potential vectors of the invasive rust pathogen *Austropuccinia psidii*: nutritional mutualism and implications for pathogen spread

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Abstract

Myrtle rust fungus, *Austropuccinia psidii* (Basidiomycota, Pucciniales), infects more than 500 species in the Myrtaceae family and is a significant threat to keystone plant taxa, particularly in Australia. Urediniospores are primarily dispersed by wind, but there are several reports of animal-mediated dispersal events. Recent observations of *Apis mellifera* (Western honey bees) collecting urediniospores of *A. psidii* raise the possibility of a novel mutualistic interaction between these two alien species. Here, we test two key conditions required for such a mutualism: (1) that spores remain viable after entering hives and (2) that they provide nutritional benefit to the pollinator. We show that *A. psidii* spores remain viable for at least nine days within honey bee colonies and match or exceed the nutritional quality of known high-protein pollens. Trials using artificial rearing of bee larvae further demonstrate that *A. psidii* spores support normal development and survival in honey bee brood. These findings suggest that spore foraging may not be an aberration, but a viable foraging strategy for honey bees. Our results support the hypothesis of a mutualism and dispersal of these plant pathogens, whereby nutritional benefits to *A. mellifera* facilitate the long-distance dispersal and epidemiology of *A. psidii*. This has implications for models of pathogen spread, especially in regions where managed hives are regularly transported over long distances in agricultural pollination services landscapes. Recognising pollinators as potential vectors of invasive plant pathogens is essential for developing more effective biosecurity and conservation strategies.

Key words: *Apis mellifera*, biosecurity, honey bee nutrition, mutualism, myrtle rust, pollination, urediniospores, vector-mediated spread

Introduction

The invasive rust fungus *Austropuccinia psidii* (Basidiomycota, Pucciniales), the causative agent of myrtle rust, is a significant threat to biodiversity across the Southern Hemisphere. Originating in Central and South America, *A. psidii* has spread rapidly in recent decades, detected in Australia in 2010, South Africa in 2013 and New Zealand in 2017 (Carnegie et al. 2010; Roux et al. 2013; Carnegie et al. 2016; Carnegie and Pegg 2018). The pathogen infects more than 500 species in the Myrtaceae family, which is an ecologically and culturally significant family for many countries, notably in Australia, where 17% of endemic vegetation is at risk from the pathogen (Makinson et al. 2020). In some cases, infection has resulted in localised dieback, reproductive failure and population collapse, prompting national biosecurity interventions and conservation concern (Pegg et al. 2018; Fensham and Radford-Smith 2021).

Fungi typically generate small reproductive propagules (spores) for dispersal primarily by wind or water (Nagarajan and Singh 1990; Shaw 1999). *Austropuccinia psidii* produces vast quantities of small, lightweight urediniospores that can be transported by wind over long distances and are adapted for aerial transport across heterogeneous landscapes. However, urediniospores are known to be produced in the floral tissues of infected plants, with *A. psidii* reported to infect floral tissues in multiple host species (Langrell et al. 2008). Recent field observations include observations which suggest that *Apis mellifera* [Western honey bees (Hymenoptera, Apidae)] foragers may actively collect *A. psidii* urediniospores from infected host plants, storing them in their pollen baskets and returning them to the hive in a manner that is visually and behaviourally indistinguishable from pollen foraging (Pattemore et al. 2018; Schmid et al. 2021; Fig. 1). This raises the possibility that *A. psidii* may benefit from animal-mediated dispersal.

In gymnosperms, animal-mediated pollination is thought to have evolved from small, abundant pollen grains dispersed by wind that were utilised by the emerging insect taxa and developed into specialised and mutualistic plant–pollinator interactions (Labandeira 1998; Bronstein et al. 2006; Cardinal and Danforth 2013). The radiation of angiosperms and their pollinators, together with the evolution of specialised floral traits, exemplifies the mutualistic advantages of this relationship: enhanced pollen dispersal specificity and plant reproductive efficiency, while providing pollinators with vital nutrients such as crude protein, essential amino acids (EAAs), lipids, vitamins and minerals (De Groot 1953; Kay and Sargent 2009; Vaudo et al. 2015).

The concept that fungi might form mutualistic or semi-mutualistic relationships with animal vectors is not unprecedented, but remains poorly understood. Fungi also generate small reproductive propagules — spores — for dispersal by wind or water (Nagarajan and Singh 1990; Shaw 1999). Confirmed examples of utilisation by animals are comparatively rare. Nonetheless, recent studies have begun to document insects, particularly bees, deliberately collecting fungal spores or mycelium, including

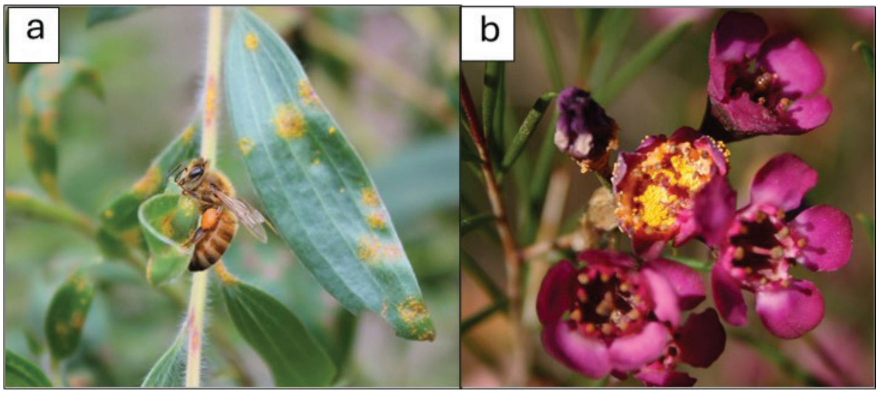

Figure 1. Foraging of urediniospores by bees on plants infected with myrtle rust. **a.** Honey bee forager collecting *Austropuccinia psidii* urediniospores from leaves of broadleaf paperbark [*Melaleuca quinquenervia* (Myrtales, Myrtaceae)], Bungawalbin, New South Wales, Australia; **b.** *A. psidii* urediniospores in the opening of a Geraldton wax [*Chamelaucium uncinatum* (Myrtales, Myrtaceae)] flower bud in Brisbane, Queensland, Australia. Photographs by Geoff Pegg.

from plant pathogens in the genera *Botrytis*, *Cladosporium* and *Colletotrichum* (Pattemore et al. 2018; Parish et al. 2020). Honey bees have been reported collecting urediniospores of *Melampsora larici-populina* (Basidiomycota, Pucciniales) (Shaw 1999). Furthermore, some fungi are now known to produce pseudoflowers — morphological mimics of true flowers, presumably to attract insect visitors and facilitate reproductive processes (Laraba et al. 2020). These findings suggest that animal-mediated dispersal of fungi may be more common and ecologically relevant than previously recognised.

Critically, *A. psidii* urediniospores share several characteristics with typical pollen grains — they are bright yellow, morphologically similar in size and shape and present in dense quantities on infected plant surfaces. These visual and physical traits likely resemble foraging cues that honey bees use when evaluating potential protein sources. If the urediniospores confer nutritional benefits, their collection may represent deliberate foraging behaviour rather than a foraging error.

Within the context of biological incursions, "invasional mutualisms" occur when introduced species facilitate each other's success, often exacerbating the speed and scale of invasion and cascading ecological impacts (Simberloff and Von Holle 1999; Ricciardi 2007; Traveset and Richardson 2014). The interactions between *A. psidii* and *A. mellifera* potentially fit this mutualism framework. While the rust gains a new mode of urediniospores dispersal, the bee may obtain an alternative source of protein, especially under conditions of floral resource scarcity induced by infection of the plant.

Such a relationship would challenge two central assumptions in both pollination ecology and plant pathology: first, that pollen is the sole natural source of protein in the honey bee diet; and second, that rust fungi rely solely on abiotic dispersal. Recent research has begun to challenge this paradigm. In a laboratory study, adult worker bees fed diets containing fungal spores showed increased longevity compared to those fed pollen-only diets (Parish et al. 2020). However, larval bees have higher nutritional needs than adults and dietary deficiencies at this stage can result in reduced body size and impaired immune function, with long-term effects on colony vitality (Crailsheim 1990; Allsopp et al. 2003).

The protein content of pollen varies widely amongst plant species — from 2% to over 60% dry mass — and a threshold of at least 20% protein is required to maintain colony health (Roulston et al. 2000; Somerville and Nicol 2006; Wright et al. 2018). Moreover, a full complement of 10 EAAs must be present above minimum concentrations to support brood development. Whether fungal spores and especially those from invasive pathogens like *A. psidii*, can support larval development remains a critical, unexplored question.

To demonstrate a novel, context-dependent mutualism, three conditions must be satisfied: (1) viable *A. psidii* urediniospores must be collected and transported by bees; (2) the urediniospores must confer nutritional benefits to the bees; and (3) bees must subsequently deposit viable urediniospores on susceptible host tissues, resulting in new infections.

In this study, we address the first two conditions of this hypothesis. We investigate whether *A. psidii* urediniospores collected by *A. mellifera* remain viable in hive environments over multiple days. We also assess the nutritional composition of the spores (specifically: total protein and EAA content) and conduct artificial larval feeding experiments to test their effects on honey bee development. By doing so, we evaluate the plausibility of a mutualistic relationship between an invasive rust pathogen and a globally managed pollinator and explore the ecological and biosecurity implications of pollinator-mediated fungal dispersal.

Materials and methods

(a) Collection of *A. psidii* urediniospores by honey bees (*A. mellifera* sp.)

Three honey bee colonies were placed at three sites with active outbreaks of myrtle rust in Queensland, Australia, in December 2017. A further six colonies were placed at four sites (three sites with one hive each and one site with three subsites each with one hive) in Brisbane in January 2018. Two weeks after placement, pollen-foraging bees returning to the hives were sampled individually or in groups of five, although groups of 25 were collected from colonies at two of the sites in Queensland in 2017. Pollen cell contents were sampled individually from four cells inside the honey bee hive at one site in 2017 and from five cells each out five of the six hives in 2018 (Pattemore et al. 2018).

Samples were collected in sterile plastic 1 ml Eppendorf or 50 ml Falcon tubes, frozen at -20 °C and urediniospores extracted from samples by washing on the same day. Bees were washed individually or in batches of five or 25 (dictated by the pooling of bees at the time of sample collection) to remove spores by agitation for 20 min in 0.05% Tween®80. The bees were removed from the wash, which was then centrifuged, the supernatant removed and the pellet dried. The pellet was frozen in liquid nitrogen and ground with a micropestle, re-suspended in extraction buffer (0.5% SDS, 50 mM Tris, 25 mM EDTA and 1 μg/ml RNase, pH 8) and incubated at 50 °C for 30 min. Protein contaminants were removed by precipitation with potassium acetate and DNA was precipitated with isopropanol, washed twice with 70% ethanol, dried and re-suspended in 200 μl of TE buffer and stored at -20 °C.

The method of Baskarathevan et al. (2016) was adapted to detect *A. psidii* urediniospores via qPCR. For confirmation of spore presence via PCR, 3 μl of extract was used in a reaction which included PpsiITS1F/R primers and PpsiITS1P Taqman probe, SensiFAST Probe (no Rox) reaction buffer and water. Samples were amplified in a RotorGene 6000 Real Time Thermocycler (72-well carousel; Generi Biotech) using a two-step PCR profile: one initial cycle at 95 °C for 5 min followed by 40 cycles at 95 °C for 15 s and 60 °C for 45 s. Fluorescence was detected using the Green channel and Auto-Gain optimisation was used before the first acquisition. Urediniospore counts were quantified by conducting a serial dilution of urediniospores from a stock solution of ~ 440,000 spores/ml to construct a standard curve, which was then applied to the average threshold cycles of three replicates of each sample in order to calculate a corresponding calculated concentration (spore count).

(b) Viability of *A. psidii* urediniospores in the honey bee hive

Six honey bee colonies were placed in known areas of myrtle rust outbreaks for two weeks in January 2018 before being moved into containment cages in Brisbane, Australia, for a further two weeks to prevent fresh *A. psidii* spores entering the hive (Pattemore et al. 2018; see Suppl. material 1). *A. psidii* urediniospores collected from *Syzygium jambos* were placed in 5-ml micro Eppendorf tubes with a paper plug to prevent bees from foraging on the spores ("Day Zero samples or "D0"). Up to 100 bees were collected from inside each hive into 50-ml falcon tubes containing *A. psidii* urediniospores, chilled briefly on ice and then tipped gently to coat with dry myrtle rust spores. Coated bees were then placed in batches of five bees in plastic queen bee cages with a sugar cube and then five cages were placed back into each source colony into the brood nest along with five tubes of urediniospores (D0). Bees remained alive in the cages, were free to groom and consume the spores and were able to be fed by uncaged nest mates.

Urediniospores in tubes were collected on D0 (day zero control), 1, 4, 7 and 9. Spores were washed from the tubes with 0.05% Tween 80, placed directly on to water agar, covered in paraffin wax and incubated in the dark for 24–48 h at 22 °C. One cage of bees from each hive was sampled on each of D0, 1, 4, 7 and 9. Sampled bees were washed, as described above, to remove spores in 0.05% Tween 80. Washed spores were placed directly on to water agar, covered in paraffin wax and incubated in the dark for 24–48 h at 22 °C. After incubation for 24 to 48 hours, germinated and un-germinated spores in each of 'three fields of view' on each plate were counted using an inverted microscope (Pattemore et al. 2018).

Statistical analysis

Urediniospores viability was analysed with generalised mixed-effects model with a binomial error family and logit link function. The full model included a fixed effect term for the number of days since recovery of the spores and random effects terms for honey bee colony and experimental batch. Statistical evidence in support of the fixed term was determined with a likelihood ratio test against the null model, using the evidence scale as described in Muff et al. (2021). These analyses and subsequent mixed modelling analyses were carried out in R (version 4.0.0) (R Core Team 2014) using the *lme4* package (version 1.1-23) (Bates et al. 2015).

(c) Nutritional composition of *A. psidii* spores

The nutritional value and composition of *A. psidii* urediniospores to honey bees was compared with *Melampsora* sp. urediniospores (hybridised in New Zealand between *Melampsora medusae* and *Melampsora larici-populina*, causing poplar rust) and pollen from staminate kiwifruit flowers [*Actinidia chinensis* (Actinidiaceae, Ericales)] and the flowers of willow trees [*Salix* spp. (Salicaceae, Malpighiales)], all of which are present in early- to mid-spring in New Zealand.

Pollen and rust urediniospores collection

In 2019, pollen-producing willow catkins were broken from ten trees and 1.5 kg of whole male kiwifruit flowers were removed from vines in the Waikato Region of New Zealand and placed into paper bags. For willow pollen, the paper bags were directly transported to the laboratory at ambient temperature, then placed in an incubator to dry at ~ 25 °C for 48 h. The kiwifruit flowers first required to be processed through a flower mill to separate the anthers before they could be placed in an incubator to dry at ~ 25 °C for 48 h. Once dried, pollen was separated from the catkins and anthers using a pollen cyclone vacuum (cyclone extractor pump connected to a portable 12V car battery) and refined by sifting through a fine sieve (BD Biosciences cell strainer 100 μm) to remove any plant material. Dried, refined pollen was stored in a glass vial at -20 °C until use in chemical analysis or artificial rearing trials (no samples were stored > 3 months before use).

Urediniospores: In 2019, urediniospores of two species of rust (*A. psidii* and *Melampsora* sp.) were collected from their respective host plants, grown in bio-containment greenhouses at Plant & Food Research in Hamilton, New Zealand. A surface vacuum pump (Burkard Manufacturing Co. Cyclone surface sampler) was used to separate the spores from infected leaves and shoots. Collected spores were placed into 1.5–2 ml Eppendorf tubes and then stored at -20 °C until used in chemical analysis or *in vitro* rearing trials (no samples were stored for > 3 months before use).

Protein analyses

Total crude nitrogen was measured by the Waikato Stable Isotope Unit (University of Waikato). Approximately 10 mg subset sample from each test diet was suspended in ethanol for transport and then dried using a nitrogen stream before analysis (Azilawati et al. 2014). The crude nitrogen abundance was determined using a fully automated Europa Scientific 20/20 isotope ratio mass spectrometer (IRMS) with a measurement precision of ± 0.1% (Ramirez-Matiz 2020). The protein content was estimated by multiplying the crude nitrogen value by 6.25 (Roulston et al. 2000; Szczêsna 2006; Azilawati et al. 2014; Pamminger et al. 2019).

Amino acid analyses

The amino acid content, including the ten EAAs for honey bee nutrition (arginine, histidine, iso-leucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine), of the pollen and urediniospores (n = 1 per diet source) were analysed by the Nutrition Laboratory at Massey University following AOAC (Association of Official Agricultural Chemists International) 994.12 standard methods. Again, these subsamples were taken from the same batches used in the larval feeding trials, suspended in ethanol for transport and dried using a nitrogen stream before analysis (Brodschneider and Crailsheim 2010; Azilawati et al. 2014). We compared the levels of each EAAs found to assess the overall quality of each amino acid source (Brodschneider and Crailsheim 2010).

(d) Nutritional value of *A. psidii* urediniospores to honey bees

Artificial rearing of honey bee larvae on urediniospores and pollen diets

Larval honey bees were artificially reared on four diet treatments, each of which contained the standard diet incorporated with one of the four treatments (pollen or urediniospores) or the standard artificial diet (mixture of Royal jelly, D-Glucose, D-Fructose, Bacto yeast extract and water) (Schmehl et al. 2016). Four brood source honey bee colonies were selected, based on in-hive brood survival rates above > 80% survival of larvae from 1-day-old to capping (Mortensen et al. 2019). Rearing of honey bee larvae was performed as described in Crailsheim et al. (2015) and Schmehl et al. (2016). Two plates (48 individuals per plate) were grafted per colony and diet treatments were evenly distributed between source colonies by each row (8 individuals) on each plate receiving one treatment (16 individuals per source colony per diet treatment, 64 individuals per diet treatment overall).

Pollen or urediniospores treatments were added to the larval diets on the last two days of feeding (D4 and D5) to reflect how larvae are fed pollen in the hive and to ensure any larval mortality that occurred was due to the diet treatment, rather than grafting error (US EPA 2015; OECD 2016). On D4, 0.68 mg of either urediniospores or pollen was added per 40 µl of diet C. On D5, 1.36 mg of rust spores or pollen was added per 50 µl of diet C (Schmehl et al. 2016). Survival and developmental stage were recorded daily. At adult emergence, fresh and dry weights were measured for each bee (Human et al. 2013), excluding one plate of 48 individuals that quickly moved between wells when the lid of the plate was lifted post adult emergence. The bees were dried following standard protocols (Human et al. 2013), with bees being dried in open Eppendorf tubes in an incubator, set at 60 °C until the dry weight showed constant weight in successive measures, typically 7 days. Survival rate, developmental time and fresh and dry weights were compared between individuals reared on the standard artificial diet to individuals reared on diets containing pollen or urediniospores.

Statistical analyses

We used linear mixed-effects models for the analysis of the time to pupation, time to emergence, fresh weight and dry weight of adult honey bees and generalised mixed-effects model with a binomial error family and logit link function for the survival rate of honey bee larvae (Bates et al. 2015). The full models included a fixed effect term for the treatment (diet type) and a random effect term for the rearing plate nested within the colony. Statistical evidence of pairwise differences between the diets was determined using estimated marginal means, with Tukey p-value adjustment for multiple comparisons (R-package *emmeans*; version 1.5.3.) (Lenth 2024).

We used generalised linear models with a binomial error distribution and logit link function to assess the relationship between diet composition (EAAs and protein) and larval survival across treatments. The EAA values or protein content for the standard artificial diet were not measured directly. For the EAA comparison, we instead assigned from the baseline EAA requirements for honey bee health reported by De Groot (1953). Each EAA was first tested individually in separate binomial GLMs to identify potential associations with survival rates. For EAAs showing significant or marginal effects, treatment-level differences and treatment × EAA interactions were examined where appropriate. The relationship between protein content and survival was evaluated for pollen and rust diets using an additional binomial GLM.

All raw larval-rearing data, qPCR Ct values are archived on Figshare (DOI 10.6084/m9.figshare.16569369).

Results

(a) Collection rates of *A. psidii*

With the initial trial in Brisbane, in December 2017, honey bee colonies were placed into known outbreaks sites of myrtle rust (Fig. 2a). *A. psidii* spores were detected in 45% of pollen cells from the hives and on 48% of returning foragers bodies (Fig. 2b). However, the estimated urediniospore counts per sample were low, typically fewer than 10 spores per slide.

(b) Viability of *A. psidii* spores in honey bee hives

All tube samples and 50% of caged bee samples, at day 9 had *A. psidii* urediniospores. The germination rates had an average of 16% and 12.1% for urediniospores extracted from bees and plastic discs, respectively, compared with the starting mean germination rates of 22% and 32%, respectively (Fig. 2b). There was strong evidence that the percentage of urediniospores on plastic discs that germinated declined by 10.1% per day, while there was no clear trend of a decline in viability on bees (Fig. 2b).

(c) Protein and EAA's of urediniospores spores

Urediniospores of both rust species had lower protein content than pollen of the host plant. Kiwifruit pollen had the highest percentage of protein (43.13%), followed by willow pollen (31.88%), *A. psidii* urediniospores (22.5%) and finally *Melampsora* sp. urediniospores (16.25%). All pollen and urediniospore samples contained the ten EAAs in amounts above the minimum thresholds required for full protein absorption by honey bees (De Groot 1953; Somerville and Nicol 2006) (Fig. 3d).

(d) Honey bee larvae survival, development and weight on rust and pollen diets

Larval pupation time was not significantly affected by diet treatment (LRT: $p = 0.083$, $\chi^2 = 8.253$, 4 df) and all larvae pupated at the mean age of 14 days after oviposition (Fig. 3a). The type of diet significantly affected the day of adult emergence (LRT: $p < 0.001$, $\chi^2 = 30.94$, 4 df), with bees emerging as adults fastest in the kiwifruit pollen treatment (average 20.370 ± 0.072 days), which was significantly earlier than those on the poplar rust (20.789 ± 0.067 days) and standard treatment (20.843 ± 0.059 days) diets. Willow pollen treatment (20.547 ± 0.069 days) and *A. psidii* treatment (20.708 ± 0.066 days) were intermediate and did not differ significantly from either the earliest or latest emerging groups. Poplar rust and the standard control treatment did not differ significantly from each other and both exhibited the highest number of days to emerge (Fig. 3a).

Bees raised on different treatments affected fresh weight (LRT: $p = 0.027$, $\chi^2 = 10.94$, 4 df), with bees reared on a diet containing *Melampsora* sp. urediniospores being significantly lower in weight than bees reared on either the standard diet or the kiwifruit pollen treatment. Bees reared on *A. psidii* spores had lower fresh

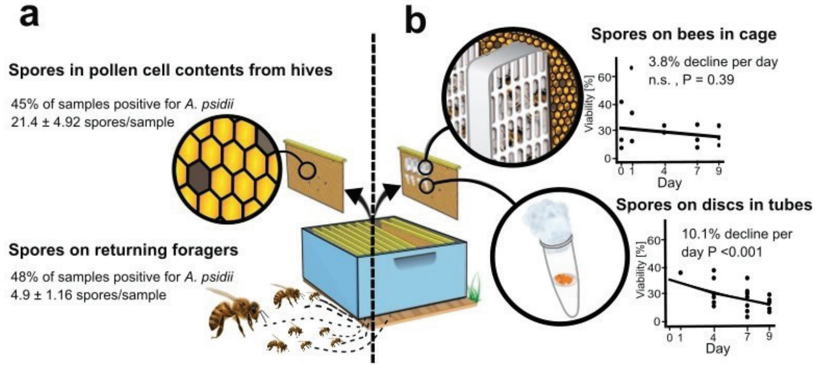

Figure 2. Presence and survival of *Austropuccinia psidii* urediniospores ("spores") in western honey bees (*Apis mellifera*) colonies in Queensland, Australia. **a.** Percentage of samples of pollen cell contents (n = 29 samples from 6 hives; Suppl. material 1) and returning foragers (n = 67 samples from 9 hives; Suppl. material 1) collected from hives two weeks after being placed at sites with known *A. psidii* outbreaks that were positive for *A. psidii* and the mean ± SE of site means of number of spores calculated per sample; **b.** Decline in *A. psidii* urediniospores viability over nine days of spores recovered from bees dosed with urediniospores and placed in cages within the hive and from urediniospores placed on plastic discs and contained in Eppendorf™ tubes closed with cotton wool and placed in hives. Decline in viability was modelled using a binomial generalised mixed-effects model.

weight than those reared on the artificial diet, but not compared to those reared on either pollen treatment (Fig. 3b). There was no significant difference between diet treatments and the dry weight of bees (LRT: $p > 0.05$, $\chi^2 = 3.758$, 4 df: Fig. 3b).

Bee survival differed significantly amongst diet treatments (GLM, LRT: $\chi^2 = 15.38$, df = 4, $p = 0.0040$; Fig. 3c). Mean (± SE) survival probabilities were highest for the kiwifruit pollen diet (88.5 ± 4.4%), followed by willow pollen (86.9 ± 4.3%), the standard artificial diet (83.6 ± 4.7%), *A. psidii* diet (78.7 ± 5.2%) and lowest for *Melampsora* sp. diets (62.3 ± 6.2%). Post-hoc Tukey comparisons indicated that survival on the *Melampsora* sp. diet (only treatment to fail minimum *in vitro* survival threshold > 70% (Human et al. 2013) was significantly lower than on the kiwifruit pollen diet ($z = 3.021$, $p = 0.0213$) and willow pollen diet ($z = -3.004$, $p = 0.0224$). No other pairwise differences were statistically significant (all $p > 0.07$).

Total EAA concentration was not significantly associated with larval survival (GLM, LRT: $\chi^2 = 1.63$, *df* = 1, $p = 0.202$). However, when EAAs were examined individually, threonine concentration showed a significant negative association with survival (GLM, slope = –0.417, $p = 0.013$), with weaker trends for leucine ($p = 0.053$) and isoleucine ($p = 0.064$). Protein content had a positive correlation with survival (LRT: $p < 0.001$, $\chi^2 = 14.15$, 1 df), with survival increasing 60–80% as protein content tripled.

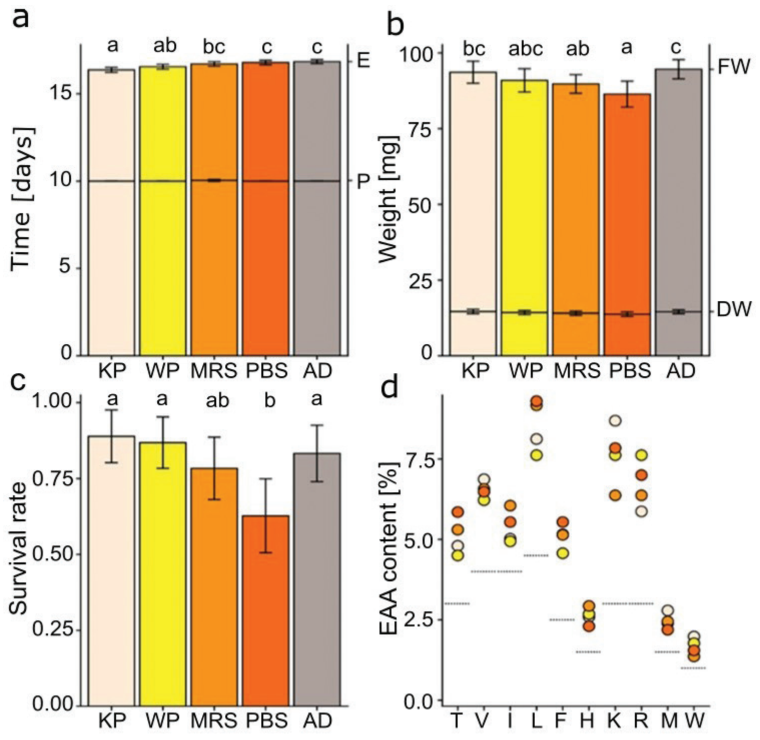

Figure 3. Nutritional value of *Austropuccinia psidii* urediniospores. **a.** Mean age in days from oviposition at pupation (P) and emergence (E) in larvae fed diets of kiwifruit (*Actinidia chinensis*) pollen (KP), willow (*Salix* spp.) pollen (WP), myrtle rust (*Austropuccinia psidii*) urediniospores (MRS), poplar rust (*Melampsora* sp.) urediniospores (PRS) and an artificial diet (AD). There were no significant differences in mean time to pupation, but there were significant differences in mean time to emergence; **b.** Mean dry weight (DW) and fresh weight (FW) of emerged bees. There were no significant differences in DW of emerged bees, but there were significant differences in fresh weight on different diets; **c.** Mean larval survival rate; **d.** Content of 10 essential amino acids (EAA) in KP, WP, MRS, PRS and AD; horizontal dashed lines indicate EAA absorption threshold. EAA abbreviations: T = threonine; V = valine; I = isoleucine; L = leucine; F = phenylalanine; H = histidine; K = lysine; R = arginine; M = methionine; W = tryptophan. Error bars in panels a, b and c indicate 95% confidence intervals around the means. Treatments with at least one lowercase letter in common indicate no significant difference between means based on a linear mixed-effects model (**a, b**) or a binomial generalised linear mixed-effects model (**c**).

Discussion

This study challenges two common assumptions in plant pathology and pollinator ecology: first, that rust fungi rely solely on the wind for dispersal of urediniospores and second, that pollen is the only natural protein source available to honey bees.

We found that *A. psidii* urediniospores are transported into and stored in pollen in hives by foraging honey bees and may remain viable for at least nine days. Urediniospores were detectable both on returning foragers and within pollen storage cells, even though it seems that, in our trials, there was no significant foraging event on the *A. psidii* spores where many workers are recruited to forage on the same source. These viable spores persisted despite grooming behaviour and colony exposure. This suggests that even limited or incidental collection can result in the introduction of viable inoculum into the hive environment and that bees actively transport viable urediniospores.

By demonstrating that *A. psidii* spores remain viable after hive entry and support larval development in *A. mellifera*, we provide evidence of a potentially mutualistic interaction between two invasive species. Such interactions exemplify "invasional mutualism", in which alien species facilitate one another's establishment and spread (Simberloff and Von Holle 1999; Traveset and Richardson 2014), with important consequences for biological invasion dynamics and management.

While *A. psidii* is primarily a wind-dispersed pathogen (Nagarajan and Singh 1990; Shaw 1999), our results confirm that insect-vectored dispersal is biologically plausible and may be under-recognised in current epidemiological models. Notably, the nine-day persistence of viable spores is congruent with the typical time of transport of commercial hives between sites (3–7 days), suggesting that long-distance transport of infectious spores via managed hives cannot be discounted. This represents a potentially critical, human-assisted vector pathway that has not been incorporated into existing biosecurity frameworks for myrtle rust.

Indicative nutritional analyses of the diet treatments showed that *A. psidii* urediniospores meet or exceed the crude protein and essential amino acid (EAA) thresholds required for honey bee development (De Groot 1953; Roulston et al. 2000). Chemical analyses of subset samples from each diet source were conducted using the same source used to rear larvae, providing a representative indication of the nutritional profiles experienced during the feeding trials. *A. psidii* spores contained protein levels and all ten EAAs comparable to those of willow pollen, a known high-quality dietary resource for *A. mellifera*. Furthermore, larvae reared on diets containing *A. psidii* spores developed at rates and achieved weights similar to those fed willow and kiwifruit pollen. Together, these findings suggest that differences in the balance of specific amino acids — rather than total EAA abundance may underlie observed variation in larval survival amongst diet treatments.

Qualitatively, the total EAA concentration was not strongly related to survival, suggesting that overall EAA abundance alone does not explain variation amongst treatments. Instead, survival was more closely linked to the relative balance of specific amino acids, with threonine showing the clearest negative association and leucine and isoleucine also displaying weaker trends. Such imbalances have been shown in other studies to disrupt protein synthesis and limit the growth of bees, even when total amino acid availability meets baseline requirements (De Groot 1953; Brodschneider and Crailsheim 2010; DeGrandi-Hoffman et al. 2013).

Crude protein content, however, was a strong positive predictor of survival across treatments, with higher-protein diets supporting substantially greater brood survival. This aligns with previous findings that pollen sources, rich in protein, promote larval survival and adult bee health (Crailsheim 1990; Allsopp et al. 2003; Camilli et al. 2021). In contrast, larvae fed diets containing *Melampsora* sp. urediniospores had reduced survival and lower fresh body weight, likely due to sub-threshold protein content or undetected toxicological interactions. Together, these results highlight and demonstrate that, while *A. psidii* urediniospores can serve as a high-quality protein and amino acid source for honey bee larvae, not all fungal spores are equal in their nutritional value to bees.

Notably, the performance of larvae on *A. psidii* urediniospores suggests that the decision by bees to collect these spores is not maladaptive. In resource-scarce environments — such as those caused by drought, habitat loss or plant pathogen-induced floral decline — these spores could provide a valuable alternative protein source. Foraging plasticity in *A. mellifera* may, thus, enable bees to derive benefit from a novel and potentially widespread nutritional source during an outbreak of myrtle rust.

Although fungal spores might provide an additional protein source for hives in the short term, they are not likely to be a long-term substitute for floral resources. Indeed, continuous interactions between *A. psidii* and bees could ultimately lead to reduced floral resources already pressured by anthropogenic stressors and biodiversity loss. Myrtle rust disproportionately impacts Myrtaceae species that are rich sources of pollen and nectar for a wide range of pollinators, including *Melaleuca*, *Backhousia* and *Rhodomyrtus* (Pegg et al. 2017; Williams 2018; Fensham and Radford-Smith 2021). As these floral resources decline, both specialist and generalist pollinators face increasing foraging stress, particularly in fragmented or urban landscapes that are already experiencing reduced floral diversity (Xiao et al. 2016).

Under such conditions, bees may increasingly turn to alternative protein sources, such as fungal urediniospores. This behavioural shift could enhance the pathogen's spread, thereby further reducing floral resources and reinforcing the cycle, a positive ecological feedback loop that compounds the impacts of invasion. Over time, this dynamic may destabilise plant–pollinator networks and forest regeneration, particularly in regions with high Myrtaceae endemism.

While generalist foragers like *A. mellifera* may buffer their colony health by switching to spores or non-Myrtaceae pollen sources, the long-term ecological cost could be substantial, especially for specialist pollinators that lack such flexibility. These dynamics warrant close attention in conservation planning, particularly for ecosystems already under stress from climate change and land-use conversion.

These findings extend a growing body of work implicating pollinators, including *A. mellifera*, in the spread of plant pathogens, such as *Erwinia amylovora* (Enterobacterales, Erwiniaceae) (Thomson et al. 1992; Mukhtar et al. 2024), *Pseudomonas syringae* pv. *actinidiae* (Pseudomonadales, Pseudomonadaceae) (Pattemore et al. 2014) and fungal pathogen *Uromyces Pisi* (Pucciniales, Pucciniaceae) (Pfunder and Roy 2000). Despite mounting evidence of vector-mediated pathogen dispersal by honey bees, current national and regional biosecurity strategies do not yet include the potential of apiculture in the spread of plant pathogens. Neither the Australian Myrtle Rust Action Plan (Makinson et al. 2020) nor the New Zealand surveillance plan (Ministry of Primary Industries 2019) includes beekeeping and commercial pollination services in its list of assessed dispersal pathways or regulatory targets. Integrating pollinator movement into myrtle rust management plans could help limit the geographic expansion of *A. psidii* and protect biodiversity in areas vulnerable to rust outbreaks.

Conclusion and future directions

Our study provides empirical support for two of the three conditions necessary for a functional mutualism between *A. psidii* and *A. mellifera*: (1) that spores remain viable after bee-mediated transport and (2) that bees derive a nutritional benefit from collecting and consuming them. The third condition (successful infection of a new host following pollinator-mediated dispersal) remains unconfirmed, but is biologically plausible, especially given observations and reports of *A. psidii* infecting floral tissues in multiple host species (Langrell et al. 2008).

We propose that honey bees be explicitly considered in both epidemiological models of *A. psidii* spread and the formulation of management and containment strategies. As both the host range and distribution of *A. psidii* continue to expand, recognising non-traditional vectors, such as pollinators, is essential for slowing its spread and reducing its ecological impact.

Further work should experimentally test the final condition for mutualism (host infection via bee-vectored spores) and quantify the relative contribution of insect-mediated versus windborne dispersal across different landscapes and seasons. Such data are vital for forecasting future spread, prioritising vulnerable habitats and designing effective, evidence-based interventions.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

D.P. and G.P. conceived of the Australian field trials and D.P., G.P., C.H., M.Ba. and M.Bu. designed and conducted the Australian trials. D.P., A.M., J.B. and S.S.C. conceived and designed the nutritional trials; S.S.C. and A.M. conducted the nutritional trials. All authors contributed

to writing the manuscript. M.J. and S.S.C. conducted the statistical analyses. D.P. secured the funding for both trials.

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Data availability

All datasets generated and/or analysed during the current study are openly available in the Figshare repository under the following DOIs:

- Spore viability in tubes: https://doi.org/10.6084/m9.figshare.30625499.v1
- Spore viability in washes: https://doi.org/10.6084/m9.figshare.30625520.v1
- Amino acid content: https://doi.org/10.6084/m9.figshare.30621362.v1
- Larval survival and mortality: https://doi.org/10.6084/m9.figshare.30625529.v1
- Larval age at emergence: https://doi.org/10.6084/m9.figshare.30621230.v1
- Larval age at pupation: https://doi.org/10.6084/m9.figshare.30621293.v1
- Dry weight of emerged bees: https://doi.org/10.6084/m9.figshare.30621308.v1
- Fresh weight of emerged bees: https://doi.org/10.6084/m9.figshare.30625484.v1

Supplementary Information is available for this paper. Correspondence and requests for materials should be addressed to Sacchi Shin-Clayton at hshi980@auckland.ac.nz.

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Supplementary material 1

Pollen Cell Samples

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Data type: pdf

Explanation note: Number of samples of pollen cell contents and returning foragers from honey bee (Apis mellifera) hives in Queensland, Australia in Summer 2017–18.

Link: https://doi.org/10.3897/neobiota.106.169027.suppl1