Initial floral visitor identity and foraging time strongly influence blueberry reproductive success

Liam K. Kendall[a,b,]*, Jamie R. Stavert[b,c], Vesna Gagic[d], Mark Hall[e], Romina Rader[b]

[a]*Centre for Environmental and Climate Science, Lund University, Sölvegatan 37, Lund S-223 62, Sweden*
[b]*School of Environmental and Rural Sciences, University of New England, Armidale, NSW 2351, Australia*
[c]*Department of Conservation, Te Papa Atawhai, Auckland, New Zealand*
[d]*CSIRO Agriculture, GPO Box 2583, Brisbane, QLD 4001, Australia*
[e]*Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith NSW 2751, Australia*

Abstract

Priority effects occur when the order of species arrival affects subsequent ecological processes. The order that pollinator species visit flowers may affect pollination through a priority effect, whereby the first visitor reduces or modifies the contribution of subsequent visits. We observed floral visitation to blueberry flowers from honeybees, stingless bees or a mixture of both species and investigated how (i) initial visits differed in duration to later visits; and (ii) how visit sequences from different pollinator taxa influenced fruit weight. Stingless bees visited blueberry flowers for significantly longer than honeybees and maintained their floral visit duration, irrespective of the number of preceding visits. In contrast, honeybee visit duration declined significantly with an increasing number of preceding visits. Fruit weight was positively associated with longer floral visit duration by honeybees but not from stingless bee or mixed species visitation. Fruit from mixed species visits were heavier overall than single species visits, because of a strong priority effect. An initial visit by a stingless bee fully pollinated the flower, limiting the pollination contribution of future visitors. However, after an initial honeybee visit, flowers were not fully pollinated and additional visitation had an additive effect upon fruit weight. Blueberries from flowers visited first by stingless bees were 60% heavier than those visited first by honeybees when total floral visitation was short (∼1 min). However, when total visitation time was long (∼ 8 min), blueberry fruit were 24% heavier when initial visits were from honeybees. Our findings highlight that the initial floral visit can have a disproportionate effect on pollination outcomes. Considering priority effects alongside traditional measures of pollinator effectiveness will provide a greater mechanistic understanding of how pollinator communities influence plant reproductive success.

Introduction

The order of species arrival to ecological communities can strongly influence subsequent ecological processes such as

*Corresponding author at: Centre for Environmental and Climate Science, Lund University, Sölvegatan 37, Skåne, S-223 62 Lund, Sweden.
E-mail address: liam.k.kendall@gmail.com (L.K. Kendall).

species' establishment and population growth or reproduction ("priority effects", reviewed in Fukami, 2015). Priority effects can occur through niche pre-emption, whereby early-arriving species exploit and/or monopolise resources, limiting the survival of later-arriving competitively similar species (Hernandez & Chalcraft, 2012). Alternatively, priority effects can arise when early arriving species modify niche conditions, which then inhibit or facilitate the establishment of later arriving species (D'Antonio & Vitousek, 1992; Odion et al., 2010). Priority effects can also affect ecosystem functions such as pollination. For example, colonisation of flowers by nectar-inhabiting bacteria, as opposed to yeasts, can reduce nectar pH and sugar concentration, resulting in decreased nectar consumption and pollination success of honeybees and hummingbirds (Good et al., 2014; Vannette et al., 2013). However, little is known about the role priority effects play in mediating pollination success, such as through the order in which different pollinator species visit individual flowers.

Most flowering plants benefit from animal-mediated pollination to some degree (Ollerton et al., 2011) and successful plant reproduction can be directly influenced by interactions amongst pollinator species and differences in efficiency and foraging behaviour (Brittain et al., 2013; Carvalheiro et al., 2011; Chagnon et al., 1989). Indirect interactions amongst pollinator species on the same flowers may manifest as pollinator-specific priority effects when the initial floral visitor pre-empts (prevents) or modifies (changes) floral niche conditions for future visitors, leading to changes in pollination success. For example, pre-emptive effects can occur if the initial visitor deposits or depletes the greatest amount of pollen. For example, in *Pedicularis chamissonis* (Orobanchaceae), pollen deposited by bumblebees during initial visits, accounted for over 50% of the total pollen deposited (Kawai & Kudo, 2008). Further blueberry fruit set was 40 − 60% higher in flowers visited once compared to unvisited flowers, but this only increased a further 10 − 27% after five visits (Kendall et al., 2020). Pre-emptive effects can negatively impact pollination success if the first floral visitor is an ineffective but adequate pollinator, resulting in suboptimal fertilisation of ovules, which then limits the ability of a more effective pollinator to improve fertilisation in a following visit (MacInnis & Forrest, 2019). Variation in floral resource availability may cause both pre-emptive and niche modification priority effects. For example, pollen and nectar removal (and thus availability) by floral visitors typically declines after the initial visit (Harder, 1990; Thomson, 1986; Young & Stanton, 1990) and per visit pollen deposition rates, as well as flower handling time are both negatively linked to nectar availability (Hodges & Wolf, 1981; Thomson, 1986). Accordingly, pollinator-specific priority effects may result from the initial floral visitor disproportionately influencing pollination outcomes, yet this remains untested.

Here, we investigate how priority effects can influence pollination success through (i) variations in the order of species visits to flowers and (ii) visit duration. We use a pollinator-dependant blueberry cultivar (*Vaccinium corymbosum*) as our model plant species. To test if priority effects influence pollination success, we compared fruit weight resulting from single and mixed species visitation sequences (1 − 15 visits) from the two known dominant and effective pollinators in this system (Kendall et al., 2020); the honeybee, *Apis mellifera*, and a stingless bee, *Tetragonula carbonaria*.

Specifically, we address the following research questions:

1 How does floral visit duration vary amongst the two dominant pollinator species in response to the number of preceding floral visits?
2 How do mixed floral visits from honeybees and stingless bees affect fruit weight compared to visitation by either species alone?
3 How does species identity and foraging time of the first floral visitor (i.e., pollinator priority effects) affect fruit weight?

Materials and methods

Study system

This study was conducted on a large-scale berry farm located on the North Coast of New South Wales, Australia (29.990232°S, 153.143171°E). We undertook our study in monocultural stands of southern highbush blueberry (*V. corymbosum* interspecific hybrid, cultivar Snowchaser (Patented US20080196128)) This cultivar is self-compatible but dependant on pollination by managed and wild bees (Kendall et al., 2020). Most farms stock honeybee (*A. mellifera*) colonies for pollination services at a rate of 5 - 7 hives per hectare. A native stingless bee, *T. carbonaria*, is naturally common in this region and nests in native vegetation within and around farms. Other native bees, such as *Xylocopa* spp. and *Exoneura* spp. are also present but are rarely observed visiting blueberry flowers and are presumed to not contribute considerably to blueberry pollination in this region (Kendall et al., 2020).

Commercial blueberry cultivars benefit considerably from insect pollination to obtain improved fruit quality and yield e.g., earlier harvest, improved fruit set and larger fruit (Benjamin & Winfree, 2014; Cane, 2005; Nicholson & Ricketts, 2019). Fruit weight is positively related to both the number of pollen grains deposited on the stigma and seed set (Dogterom 2000). Blueberry flowers are urceolate (urn-shaped), and in open flowers, the anthers remain enclosed within the corolla and a single stigma protrudes at or slightly above the corolla aperture. Blueberry stigmas remain receptive for three − five days (Brevis et al., 2006).

Measuring floral visitation and pollinator effectiveness

We conducted pollinator effectiveness experiments across two flowering seasons (May) in three blocks in 2017 and

these were repeated in one block in 2018. We observed 829 individual pollinator visits to blueberry flowers ($n = 214$ floral visitation sequences) and the fruit weight resulting from 610 pollinator visits ($n = 124$ floral visitation sequences). To have full control over the visits of individual flowers, we placed organza bags (mesh size < 0.1 mm) over developing shoots and tagged developing flowers before anthesis. We un-bagged flowers upon anthesis and observed visits on flowers from the two dominant pollinator species (honeybees and stingless bees) (See Appendix A: Table 1 for details of replication and distribution of treatment flowers between plants, cropping blocks and flowering seasons). For each pollinator visit, we recorded species identity and visit duration in seconds. We observed multiple flowers within the inflorescences concurrently, until one flower reached a maximum number of visits (i.e., 10 or 15 visits) or for as long as weather conditions were favourable and insect activity remained high. Each treatment flower was only observed on a single day. This resulted in a dataset with visit foraging times within floral visitation sequences from honeybees (range: $1 − 7$ visits per flower), stingless bees (range: $1 − 5$ visits per flower) or a mixture of honeybee and stingless bee visits (range: $2 − 15$ visits per flower) (See Appendix A: Table 2 for description of replication). We then re-bagged all flowers for the duration of flowering (2−5 days), to prevent further visitation from pollinators. Overall probability of fruit set across experimental flowers was high (75%, 161 of 214) and we were able to collect 124 fruit (77%). The remaining fruit (37) were lost prior to collection due to damage or commercial collection. We picked the fruit upon ripening and measured fruit weight (grams) on the same day using an analytical balance.

Data analysis

Visit duration in response to previous visitation

To test if floral visit duration differed between pollinating taxa and in response to the number of preceding visits to flowers, we specified a generalized linear mixed-effects model (GLMM). We modelled individual visit duration (seconds) as a function of pollinating taxon (honeybees or stingless bees) in interaction with the visit number in the sequence and in addition to whether the floral visitation sequence was single species (i.e., honeybees or stingless bees) or both species (categorical: two levels). We log-transformed visit number prior to analysis as it improved the model fit. We fitted this model with a *truncated negative binomial* distribution (with a linear parametrisation) and allowed the dispersion parameter to vary between pollinator species as stingless bee visit durations were significantly more dispersed than honeybees. We fitted this model with one nested random effect: *'flower ID'* nested within *'plant',* nested within *'cropping block'*, nested within *'year'* due to the dependence between visits to the same flower and

inflorescences of the same plant, and because visitation data were collected from three cropping blocks and across two years.

Species composition effects on fruit weight

To test how floral visitation from either bee species or a species mixture affected fruit weight, we undertook two analyses. First, we specified an LMM that modelled blueberry fruit weight as a function of pollinator taxa (honeybees, stingless bees, or a mixture of both). This model contained a nested random effect of *'plant',* nested in *'cropping block',* nested in *'year'*. Secondly, we modelled individual fruit weight as a function of the total visit duration (seconds) by each bee species or a mixture of both species. We fitted the honeybee and stingless bee models with a random effect of *'plant'* nested in *'cropping block'* and the mixed species model with a random effect of *'plant'*. Differences in random effect structures are a result of honeybee and stingless bee visitation sequences being measured only in 2017, across three (honeybee) or two (stingless bee) blocks. Although we recorded in mixed species visits in both years, year was not included in that model as it had extremely low variance, which resulted in model non-convergence.

Priority effects

To identify if priority effects influenced blueberry fruit weight, we subsetted each dataset to only include blueberries produced because of mixed pollinator visits (visits from both honeybees and stingless bees). To test if the initial visit had a disproportionate effect upon pollination success, relative to any subsequent floral visitation to the same flower, we categorised each fruit as being produced from a flower initially visited by either a honeybee or a stingless bee. With these data, we specified two LMMs to estimate fruit weight: 1) as a function of the initial floral visitor (honeybee or stingless bee) in interaction with the total remaining floral visit duration (i.e., total floral visit duration minus the first visit), and 2) as a function of the initial floral visit duration in interaction with total remaining floral visit duration. Initial floral visit duration and total floral visit duration were scaled and centred prior to analyses to reduce multicollinearity amongst predictor variables (Zuur et al., 2009). We fitted these models with a random effect of *'plant'* as all data were collected in a single cropping block. We did not include an additional random effect of year as it had extremely low variance, and resulted in non-convergence.

We assessed the importance of each 'priority effect' model by comparing it to a null model containing only total visit duration (i.e., fruit weight $\sim$ total visit duration) using the small sample-size corrected Akaike-Information Criterion (AIC_C) (Akaike, 1974; Hurvich & Tsai, 1993) and a likelihood-ratio test. Models were fitted with Maximum-Likelihood to enable comparison of fixed effects with a

likelihood-ratio test (Luke, 2017; Pinheiro & Bates, 2000). To report the final model estimates, these were then refit using Restricted Maximum-Likelihood (Luke, 2017).

Relationship between the number of visits and total visit duration

We assessed the correlation between total number of visits and total visit duration using Spearman rank correlation tests independently for honeybee visits, stingless bee visits and mixed species visits. These were highly correlated in all three groups (honeybees: $\rho = 0.64$, $P < 0.001$; stingless bee: $\rho = 0.59$, $P < 0.001$; mixed species: $\rho = 0.44$, $P < 0.002$). Therefore, we repeated all analyses of species composition effects and priority effects models, with identical model formulations as described above, except with the total number of visits (or the total number of visits after the initial visit) as the primary predictor variable (See Appendix A: Section 2 for these results).

All analyses were conducted in *R* v3.6.1 (R Core Team, 2021). We specified all models using the *glmmTMB* package v.0.2.3 (Brooks et al., 2017). All presented models passed tests of model residuals for uniformity and over- and under-dispersion from the *DHARMa* package v.0.2.2 (Hartig, 2019). We assessed the VIF amongst predictive variables in each model using the *performance* package v.0.4.0 (Lüdecke et al., 2021). Across all models, we found low collinearity amongst predictors (VIF < 3). We calculated post-hoc marginal mean differences between pollinator taxa and slope contrasts using the *emmeans* package v1.3.5 (Lenth, 2019). Summary tables of all model parameters are provided within Appendix A.

Results

In total, we recorded 829 individual pollinator visits to blueberry flowers ($n = 214$ floral visitation sequences) and the fruit weight resulting from 610 pollinator visits ($n = 124$ floral visitation sequences).

How does floral visit duration vary among pollinator taxa in response to the number of preceding visits?

We found that stingless bees visited blueberry flowers for significantly longer than honeybees ($z = 6.46$, $P = <0.001$) (Fig. 1). Visit duration by honeybees declined significantly with an increasing number of previous visits ($z = -3.22$, $P = 0.001$). In contrast, stingless bees maintained their floral visit duration, irrespective of the number of preceding visits (interaction term: $z = 2.2$, $P = 0.02$). In mixed species floral visitation sequences, floral visits by either bee species were significantly longer in duration ($z = 3.16$, $P = 0.002$).

How do multiple floral visits from honeybees and stingless bees combined affect fruit weight when compared to visitation by either individual species?

We found that fruit weight from flowers visited by both species (i.e., mixed visits) were heavier than those visited by honeybees ($z = 3.75$, $P = <0.001$) or stingless bees ($z = 2.09$, $P = 0.04$) alone (Fig. 2A). We found no difference in fruit weight resulting from flowers visited by either honeybees or stingless bees. Fruit weight was positively related to total visit duration by honeybees ($z = 6.44$, $P = < 0.001$), but not stingless bees ($z = 1.4$, $P = 0.16$) or when both species visited the same flowers ($z = 1.58$, $P = 0.12$) (Fig. 2B).

Does the identity and visit foraging time of the first floral visit (i.e., pollinator priority effects) in a floral visitation sequence affect fruit weight outcomes?

We found evidence of a strong priority effect due to the duration (seconds) and species identity of the initial visit (Fig. 3A and Fig. 3B, respectively). Models containing either initial visit duration or initial species identity had lower AIC values than a null model which contained only total visit duration (initial visit duration model: $\Delta AIC = 5.02$, χ^2: 9.02, $P = 0.01$; initial visitor species: $\Delta AIC = 4.45$, $\chi^2 = 8.45$, $P = 0.02$). The initial visit duration model did not outperform the initial visitor identity model (ΔAIC: 0.57).

Fruit weight increased linearly with total visit duration when initial visits were short in duration as the interaction between initial visit and total visit duration was significantly negative. Further, total visit duration in interaction with initial visitor identity had a strong effect on blueberry fruit weight. Fruit produced from flowers that received their first visit from a stingless bee were heavier than those initially visited by a honeybee. However, as total visit duration increased, fruit weight from flowers initially visited by a honeybee increased ($\beta = 0.17 \pm 0.06$, z: 2.788, $P = 0.005$), There was no relationship between increased total visit duration and fruit weight for flowers initially visited by a stingless bee ($\beta = -0.11 \pm 0.09$, t-ratio: -1.28, $P = 0.21$). For example, fruit from flowers initially visited by stingless bees were 60% heavier than those first visited by honeybees where flowers were visited for ~1 min. In contrast, when flowers were visited for ~ 8 min, fruit from flowers initially visited by honeybees were only 24% heavier in fruit weight compared to those first visited by stingless bees.

Discussion

In this study, we demonstrated that when two bee species (honeybees and stingless bees) visit the same flowers, a pollinator-specific priority effect occurs due to the identity and
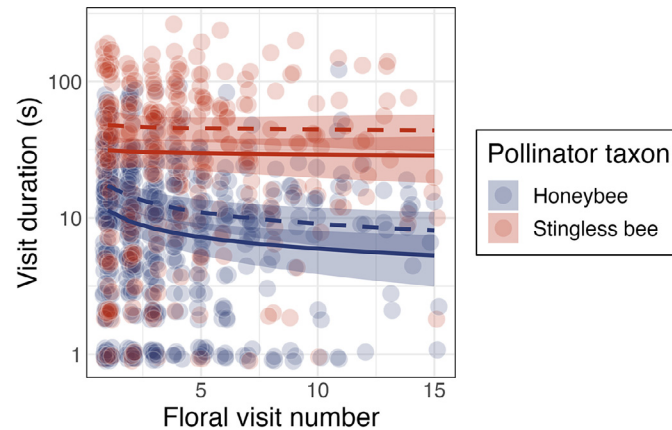
Fig. 1. Floral visit duration from honeybees and stingless bees in relation to the number of preceding visits to blueberry flowers. Lines indicate model-estimated lines of best fit for single species visitation sequences (solid lines) and mixed species visitation sequences (dashed lines). Shaded ribbons are the model-estimated 95% confidence intervals. Circles are the actual data. Y-axis is presented on the log-10 scale to improve visualisation.
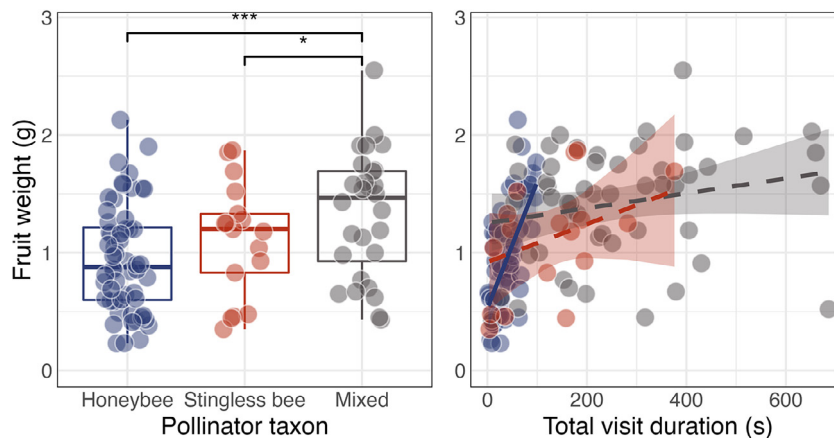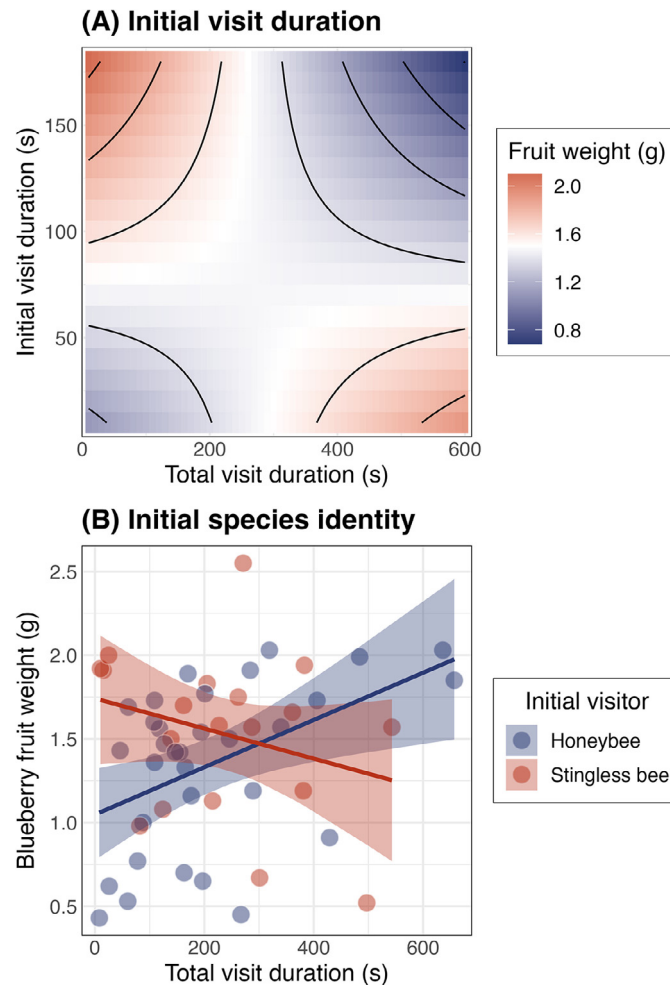

Fig. 2. Blueberry fruit weight from flowers visited by honeybees, stingless bees or a mixture of honeybees and stingless bees (left) and relationship between fruit weight and total visit duration (seconds) (right). On the left plot, lines and asterisks indicate significant differences in fruit weight resulting from mixed species visits and single species visits. On the right plot, lines indicate model-estimated lines of best fit. Shaded ribbons are the model-estimated 95% confidence intervals. The solid line indicates a significant slope between fruit weight and total visit duration (honeybees). Dashed lines indicate a non-significant slope (stingless bees or mixed species visits). Circles are the actual data. * $P = 0.04$, *** $P = <0.001$.

visit duration of the initial visitor. An initial visit by a stingless bee fully pollinated the flower, limiting the pollination contribution of future visitors. However, after an initial honeybee visit, flowers were not fully pollinated and additional visitation then had an additive effect upon fruit weight. We found similar trends in floral visit sequences consisting of either species alone. These findings indicate that priority effects can arise from the order that species visit flowers which, in turn, can strongly affect plant reproductive success and crop pollination service delivery.

The identity of the first floral visitor strongly drove the priority effects that we observed. We found that initial floral visits from stingless bees were significantly longer than those from honeybees and when stingless bees were the initial visitor, resulting fruits were heavier. Stingless bees and honeybees exhibited marked differences in their foraging behaviour on blueberry flowers. Stingless bees are small enough to forage inside blueberry flowers, directly contacting the anthers and the stigma (LK Kendall, personal observation), whereas honeybees can only insert their proboscis or forelegs into the flower (Cane & Payne, 1993; Courcelles et al., 2013). Further, whereas honeybees predominantly collect nectar from blueberry flowers (Miñarro & Garcia, 2021), stingless bee foragers collect both pollen and nectar (LK Kendall, unpublished data). This distinct foraging behaviour of stingless bees, combined with high resource availability present at the initial visit (Harder, 1990; Kawai & Kudo, 2008), may increase geitonogamous (self-pollination via a vector) pollen deposition and pollen receipt, which is associated with fruit weight increases in this blueberry cultivar (Kendall et al., 2020), and limit the contribution of any further pollen deposited by future visitors.

(A) Initial visit duration

(B) Initial species identity

Fig. 3. Priority effects in blueberry fruit weight from mixed visit sequences (≥ 2 visits). (A) initial visit duration model: The response surface demonstrates the interactive effect of initial visit duration and total visit duration. It shows that heavier fruit are obtained from either, (i) long initial visits, when the total visit duration is short or, (ii) long total visit duration, when the initial visit is short. Conversely, lighter fruit are obtained when either, (i) initial visit and total visit duration are both short, or (ii) initial visit and total visit duration are both long. (B) initial species identity model. Solid lines indicate model-estimated lines of best fit. Shaded ribbons are the model-estimated 95% confidence intervals. Circles are the actual data. In both plots, total visit duration is the entire duration of floral visitation, after the initial visit.

The lack of relationship between fruit weight and visit duration after an initial stingless bee visit, as well as in stingless bee only visitation sequences, is suggestive of a strong pre-emptive priority effect for pollination success as subsequent visitation had no effect on fruit weight (MacInnis & Forrest, 2019; Parker et al., 2016). In contrast, when honeybees are the initial visitor or the only visitor in a visitation sequence, the effect of additional visits is additive; the cumulative effect of longer total visitation sequences, including those involving both bee species, is heavier fruit. Honeybees are, in general, less effective pollinators than wild bee species (Page et al., 2021). As such, an initial visit by a honeybee does not have the same limiting effect as a stingless bee, and the effect of subsequent floral visitation is likely more reflective of patterns in decreasing floral resource availability.

We found that priority effects were not only a result of the initial visitors' identity but also influenced by the length of time different species spent on a flower relative to the number of preceding visits. Honeybee floral visit duration decreased logarithmically in visitation sequences. Reduced floral handling time can be result of decreased floral resource availability and/or reduced floral scent emissions (Rodriguez-Saona et al., 2011; Thomson, 1986; Young & Stanton, 1990). Further, honeybees (Giurfa, 1993), and stingless bee species (e.g., *Trigona* spp., Boogert et al., 2006; Goulson et al., 2001) mark flowers with scents that allow conspecific foragers to discriminate between rewarding (e.g., nutrient-rich unvisited flowers) and unrewarding (e.g., previously visited nutrient poor flowers) (Goulson, 2009; Stout & Goulson, 2001). Collectively, reduced resource availability and floral odours, combined with the presence of scent marks, may modify floral niche conditions negatively for later conspecific visitors, making flowers less attractive and reducing floral visitation.

We found that the duration of stingless bee visits to blueberry flowers was the same irrespective of the number of preceding visits. Smaller-bodied bees (e.g., stingless bees) have lower metabolic rates and resource requirements than larger bees and can therefore forage more effectively on low-reward or resource-depleted flowers (Corbet et al., 1995; Goulson et al., 2001). Accordingly, the lack of relationship between stingless bee visit duration and the number of preceding visits may be a result of stingless bees collecting less resources per visit, so that floral resources deplete slower in response to further visits. Further, differences in resource depletion rate between honeybees and stingless bees may also explain why in mixed species visits, both bee species visited flowers for significantly longer periods of time.

As in many ecological research studies, experimental and analytical methods employed during the study can impact the interpretation of results. In this study, total floral visit duration and the number of visits were highly correlated, and we found that trends in fruit weight were near-identical between model specifications using either total visit duration or number of visits (See Appendix A: Section 2). However, our analyses showed that for honeybees, total visit duration better predicted fruit weight increases than the total number of visits. Thus, total visit duration better accounted for behavioural changes in honeybees (i.e., declining visit duration with increasing number of preceding visits) in floral visit sequences. Accordingly, total floral visit duration may be a more useful predictor of pollination outcomes, such as fruit weight, than the total number of visits.

It remains unclear how generalisable our results are to other blueberry types, and other plant species, due to differences in floral traits, pollination syndromes, and pollinator communities. We used a self-compatible blueberry cultivar in this study. However, some blueberry types are self-incompatible (i.e., rabbiteye, *V. virgatum,* Sampson & Cane, 2000) and require cross-pollination for improved reproduction. Second, blueberries have poricidal anthers, which are well-adapted to buzz-pollination (Buchmann, 1983). Neither pollinator species in our study buzz-pollinates, yet stingless bees may be able to overcome this by releasing pollen mechanically by directly foraging inside the corolla. It would therefore be interesting to assess priority effects in blueberry between buzz-pollinating and non-buzz-pollinating species. Nonetheless, the diversity in form and function of plants and their pollinators will present substantial challenges in assessing priority effects in the pollination of other plant species.

Our results may have implications for biodiversity ∼ ecosystem functioning relationships. Previous work has demonstrated that stingless bees and honeybees are similarly effective pollinators of blueberry, on a per visit basis, in terms of fruit set (Kendall et al., 2020). Yet, our results demonstrate that plant reproductive outcomes are shaped by patterns in floral visitation throughout a flower's blooming period. Interactions between pollinator species can have synergistic effects upon pollination (Brittain et al., 2013; Chagnon et al., 1989; Eeraerts et al., 2020). Our results add additional insight into interactive effects, by demonstrating that they can result in more than one mechanism that improves pollination success, which may then increase ecosystem service resilience. Further, our results demonstrate that native stingless bees could be prioritised for blueberry crop-pollination services. Growers may be able to achieve increased yields, alongside greater conservation outcomes, by focussing their efforts on sustaining native populations of stingless bees, without large densities of stocked honeybees that may negatively impact native bee communities (Wojcik et al., 2018).

In conclusion, our study is one of the first to demonstrate the presence of priority effects in pollination systems. We have shown that priority effects can occur through the initial floral visit having a disproportionately strong effect on plant reproductive outcomes. This has important implications for pollination ecology research, as it contributes further mechanistic understanding of the complexity of plant ∼ pollinator interactions, thus helping to overcome shortcomings of experimental pollination methods, such as discrepancies between pollen deposition and receipt (cf Stavert et al., 2020.). Investigation of priority effects in other plant species and in more diverse pollinator communities is now required to better understand the interaction between plant species, pollinator communities, and the mechanisms by which priority effects influence plant reproductive success.

Data availability

All data and accompanying R code are available on GitHub (https://github.com/liamkendall/berrymixer).

Appendix A. Supplementary data Supplementary data associated with this article can be found, in the online version, at 10.1016/j.baae.2022.02.009.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Liam K. Kendall: Conceptualization, Visualization, Data curation, Formal analysis, Writing − original draft, Writing − review & editing. **Jamie R. Stavert:** Formal analysis, Writing − original draft, Writing − review & editing. **Vesna Gagic:** Formal analysis, Writing − original draft, Writing − review & editing. **Romina Rader:** Conceptualization, Visualization, Writing − original draft, Writing − review & editing.

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Supplementary materials

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