



Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Review

The effect of protective covers on pollinator health and pollination service delivery



Liam K. Kendall^{a,b,1}, Lisa J. Evans^{c,*,1}, Megan Gee^d, Tobias J. Smith^{a,e}, Vesna Gagic^a, Juan D. Lobaton^a, Mark A. Hall^f, Jeremy Jones^a, Lindsay Kirkland^a, Manu E. Saunders^a, Carolyn Sonter^a, Brian T. Cutting^c, Sophie Parks^g, Katja Hogendoorn^h, Cameron Spurrⁱ, Alistair Gracie^j, Melinda Simpson^k, Romina Rader^a

^a School of Environmental and Rural Sciences, University of New England, Armidale, NSW 2351, Australia

^b CSIRO Agriculture, GPO Box 2583, Brisbane, QLD 4001, Australia

^c Plant & Food Research Australia, c/o Queensland University of Technology, Brisbane, QLD 4000, Australia

^d The New Zealand Institute for Plant & Food Research, Christchurch 8140, New Zealand

^e School of Biological Sciences, University of Queensland, St Lucia, QLD 4072, Australia

^f Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW 2753, Australia

^g NSW Department of Primary Industries, Central Coast Primary Industries Centre, Ourimbah Campus, NSW 2258, Australia

^h The University of Adelaide, School of Agriculture, Food and Wine, Adelaide, SA 5005, Australia

ⁱ Seed Purity, Margate, TAS 7054, Australia

^j Tasmanian Institute of Agriculture, University of Tasmania, Sandy Bay, TAS 7005, Australia

^k NSW Department of Primary Industries, Wollongbar Agricultural Institute, Wollongbar, NSW 2477, Australia

ARTICLE INFO

Keywords:

Covered cropping
Ecosystem services
Bee orientation
Pollinator management
Pollinator fitness
Protected agriculture
Stocking rate

ABSTRACT

Protective covers (i.e., glasshouses, netting enclosures, and polytunnels) are increasingly used in crop production to enhance crop quality, yield, and production efficiency. However, many protected crops require insect pollinators to achieve optimal pollination and there is no consensus about how best to manage pollinators and crop pollination in these environments. We conducted a systematic literature review to synthesise knowledge about the effect of protective covers on pollinator health and pollination services and identified 290 relevant studies. Bees were the dominant taxon used in protected systems (90%), represented by eusocial bees (e.g., bumble bees (*Bombus* spp.), honey bees (*Apis* spp.), stingless bees (Apidae: Meliponini) and solitary bees (e.g., *Amegilla* spp., *Megachile* spp., and *Osmia* spp.). Flies represented 9% of taxa and included Calliphoridae, Muscidae, and Syrphidae. The remaining 1% of taxa was represented by Lepidoptera and Coleoptera. Of the studies that assessed pollination services, 96% indicate that pollinators were active on the crop and/or their visits resulted in improved fruit production compared with flowers not visited by insects (i.e., insect visits prevented, or flowers were self- or mechanically pollinated). Only 20% of studies evaluated pollinator health. Some taxa, such as mason or leafcutter bees, and bumble bees can function well in covered environments, but the effect of covers on pollinator health was negative in over 50% of the studies in which health was assessed. Negative effects included decreased reproduction, adult mortality, reduced forager activity, and increased disease prevalence. These effects may have occurred as a result of changes in temperature/humidity, light quality/quantity, pesticide exposure, and/or reduced access to food resources. Strategies reported to successfully enhance pollinator health and efficiency in covered systems include: careful selection of bee hive location to reduce heat stress and improve dispersal through the crop; increased floral diversity; deploying appropriate numbers of pollinators; and manipulation of flower physiology to increase attractiveness to pollinating insects. To improve and safeguard crop yields in pollinator dependent protected cropping systems, practitioners need to ensure that delivery of crop pollination services is compatible with suitable conditions for pollinator health.

* Corresponding author.

E-mail address: lisa.evans@plantandfood.co.nz (L.J. Evans).

¹ LK Kendall and LJ Evans contributed equally to this work as first authors.

<https://doi.org/10.1016/j.agee.2021.107556>

Received 19 August 2020; Received in revised form 23 June 2021; Accepted 24 June 2021

Available online 21 July 2021

0167-8809/© 2021 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Many agricultural crops traditionally grown in open fields are now being produced in covered environments (e.g., glasshouses, hail netting, and polytunnels; Fig. 1; Baudoin et al., 2017; Castilla, 2002; Cook and Calvin, 2005; Nordey et al., 2017; Reddy, 2016), as these systems can help growers to overcome the challenges associated with extreme weather, pests, pathogens, and contamination by foreign pollen (Amarante et al., 2011; Lloyd et al., 2005; Morison et al., 2000). By modifying the growing environment, covered systems can also enhance crop production by providing warmer conditions for precocious bud initiation (Renquist, 2005; Retamal-Salgado et al., 2015), and increasing fruit quality, yield (Mditshwa et al., 2019; Parks et al., 2019), and efficiency of water and fertilizer use through the capture and reuse of leachates (Grewal et al., 2011; van Kooten et al., 2006). Yet, despite the numerous benefits of protected cropping, covers can be detrimental to some aspects of production, including pollination.

Many covered crops benefit from the movement of viable and compatible pollen (Baudoin et al., 2013, 2017). However, the physical barrier presented by glass, plastic, or small-aperture mesh can restrict wind and pollinator movement, and there has been concern about pollinator performance in these environments since covers were first deployed at scale (Jensen and Malter, 1995). The environmental conditions created under covers can be unfavourable to flying insects and can detrimentally affect pollinator behaviour, activity levels, and survival (e.g., Birmingham and Winston, 2004; da Silva et al., 2017; Evans et al., 2019; Pinzauti, 1994). As a result, inappropriately managed covered crops can result in lower pollination rates and reduced yields (Dag, 2008).

Currently, there is a lack of consensus on how best to manage pollination in these modified environments. It is generally accepted that some managed pollinators are better suited than others to conditions under covers. For example, bumble bees are used widely for pollination of glasshouse grown tomatoes (Velthuis and Van Doorn, 2006). However, changes within and surrounding the production environment can affect the activity levels and flower-visiting behaviour of many insect pollinators (Bates et al., 2011; Kremen et al., 2002; Saturni et al., 2016;

Stavert et al., 2018). Ultimately, these behavioural changes are likely to have consequences (+ or -) for pollination and pollinator management. Development of system-specific approaches for managing pollinators in covered systems has the potential to improve and safeguard yields through increased pollination efficiency and sustainable use of pollinators.

Here, we undertake a systematic review of published empirical literature to synthesise what is known about the effect of protective covers on pollinator health and pollination services. We also synthesise findings relating to the effectiveness of the approaches taken to mitigate poor pollinator health and/or pollination service and the constraints within which pollination management occurs. Finally, we identify knowledge gaps and provide recommendations for improved pollinator health and pollination under protective covers.

2. Materials and methods

We conducted a systematic search using Scopus, Centre for Agriculture and Bioscience (CAB), and ProQuest databases, to identify peer-reviewed journal articles and technical publications related to pollination management in protected cropping environments. We restricted our search to studies that considered plants and insect pollinators confined together within a covered cropping system. We did not include studies that focused solely on plant pollination in the absence of insects. Searches were current as of February 2020. Our search terms (provided in Supplementary Materials) returned a total of 2097 papers. We removed duplicate records as well as papers that could not be accessed or interpreted. We further narrowed our results to include only empirical studies; review papers were scanned for relevant information but were not included directly in our results.

A total of 290 relevant studies progressed to data extraction. Each of the relevant papers was searched for data related to the following 8 factors: (1) cover type, (2) research focus, (3) type of assessment, (4) focal pollinator species, (5) crop species, (6) experimental design, (7) impacts of covers, and (8) mitigation of negative impacts.

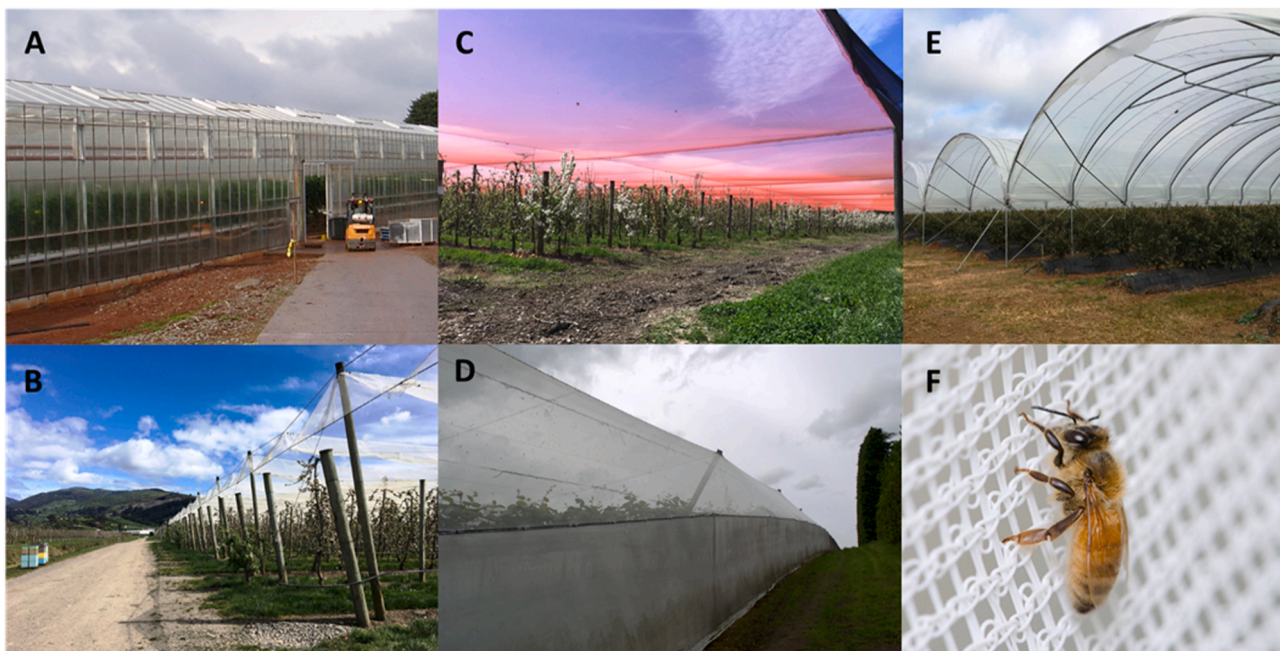


Fig. 1. Different types of covers and covered systems used to protect commercial crops: (a) tomatoes in a climate-controlled glasshouse; (b) apples under white and (c) coloured hail netting; (d) kiwifruit fully enclosed with hail netting and wind cloth; (e) blueberries in polytunnels; (f) a honey bee on high-thread-density wind cloth on the side of a netted enclosure.

- (1) Cover types included: glasshouses (synonymous with greenhouse), polytunnels (or hoop houses), and netting (hail or bird netting). Some studies were conducted in experimental enclosures, some covering only a small number of plants. For the purpose of this review, we categorised experimental enclosures according to construction material, as either plastic enclosures (including vinyl houses) or screen cages (including insect proof mesh and shade cloth). These were analysed along with experiments conducted in full-scale production environments.
- (2) Topics of research focus included: pollination service, pollinator health, or 'other' pollinator behaviour unrelated to foraging/pollination (e.g., virus transmission), and effects of transgenic plants on pollinators.
- (3) We noted how these studies assessed their research focus (type of assessment). Pollination success was either directly assessed as yield quantity and/or quality or inferred from pollinator foraging activity or pollen deposition rates, and pollinator health was assessed by comparisons of colony strength, population/colony activity, population/colony survival, or genetic effects.
- (4) Focal pollinator species were recorded and then categorised under: bees, flies and other insects. This included commercially managed species, propagated/domesticated species, and pollinators introduced from the wild.
- (5) The identity and number of vegetable, fruit, and other commodity crops that were used in trials under covers were recorded.
- (6) Experimental design was recorded in terms of the number of studies comparing covered vs uncovered treatments, insect visited vs non-insect visited treatments, or insect 'A' vs insect 'B' treatments.
- (7) We recorded when factors that may affect pollinators under covers were taken into consideration. These factors included: temperature/humidity, light, orientation ability, pollinator resources, and pesticide application (Dag, 2008).
- (8) We noted if methods to mitigate adverse effects of covers were deployed and/or directly tested, for example: introducing floral diversity, artificial feeding of pollinators, strategic placement of pollinator units (e.g., hives), and accurate stocking rates.

To synthesise the outcomes of the reviewed studies, a vote counting approach was employed to independently evaluate pollination services, pollinator health, and mitigation methods across relevant papers. We compared the number of positive studies (studies showing benefit) with the number of neutral studies (studies showing no change) and negative

studies (studies showing harm).

3. Results and discussion

3.1. Overview of candidate papers

Our systematic review returned 290 relevant research studies (reference list provided in [Supplementary Material](#)), where plants and pollinators were under a cover. Interest in the subject area has grown over recent years, with the number of relevant research studies increasing three-fold in the previous two decades, including studies in at least 40 countries (Fig. 2A). Early research predominantly focused on *Apis* spp., but in the past 25 years there has been increasing interest in *Bombus* spp., as well as other species of bees and flies. The last 10 years has seen an increase in the number of studies on stingless bees (Fig. 2B). Of these studies, 43% were conducted in glasshouses, 16% in poly-tunnels and 13% under netting. Other studies were conducted in experimental enclosures, including screen cages (22%) and plastic enclosures (6%; Fig. 3A).

Studies have assessed commercially managed species, propagated/domesticated species, and pollinators introduced from the wild. An indication of the current scalability of a range of different species is provided in Table 1. Bees were the dominant taxon (90%, Fig. 3B) and were represented by eusocial bumble bees (*Bombus* spp.), honey bees (*Apis* spp.) and stingless bees (Apidae: Meliponini); semi-social species (e.g., *Xylocopa* spp. that exhibit communal nesting and some shared care of offspring); and solitary bees (e.g., *Amegilla* spp., *Megachile* spp. and *Osmia* spp.). Flies represented 9% of taxa and included Calliphoridae, Muscidae, and Syrphidae. Lepidoptera and Coleoptera represented the remaining 1% of taxa (0.7% and 0.3% respectively).

Forty-five vegetable, fruit, and other commodity crops were used in trials under covers (Fig. 3C). The most-represented crops were tomato (*Solanum lycopersicum*), strawberry (*Fragaria* spp.), capsicum (*Capsicum* spp.), melon (Cucurbitaceae sp.) and cucumber (*Cucumis sativus*). This reflects the historical and continuing trend towards covered production of these crops in many important growing regions (Popsimonova et al., 2019). The significance of covered production is also reflected in the development of parthenocarpic/seedless varieties (e.g., seedless cucumber), due to their lower requirements for pollination services in glasshouses (and growing consumer demand for these products) (Badgery-Parker and James, 2010), as well as increasing interest in non-biological pollination (e.g., Potts et al., 2018; Yang and Miyako, 2020).

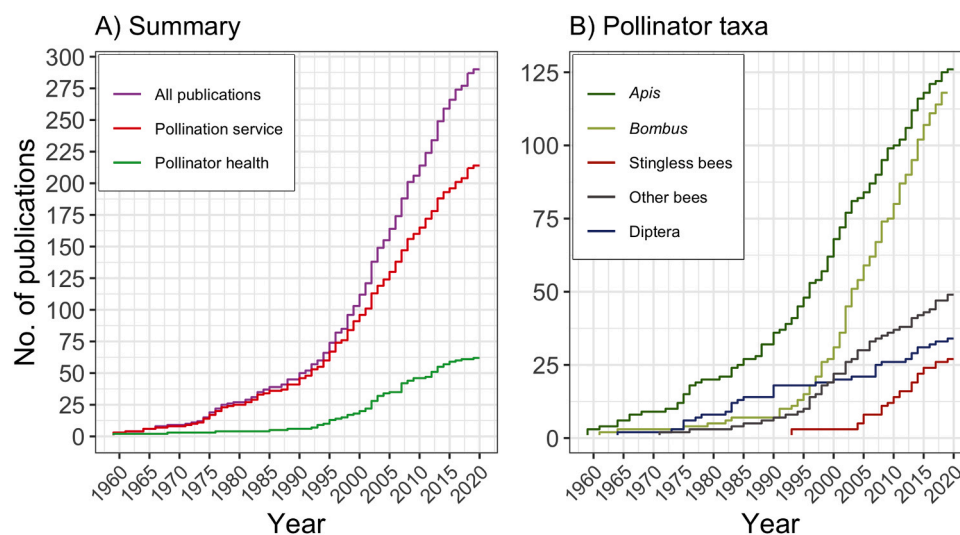


Fig. 2. Cumulative number of relevant publications per year with main topics related to (A) pollination services and pollinator health and (B) pollinator taxa in covered cropping.

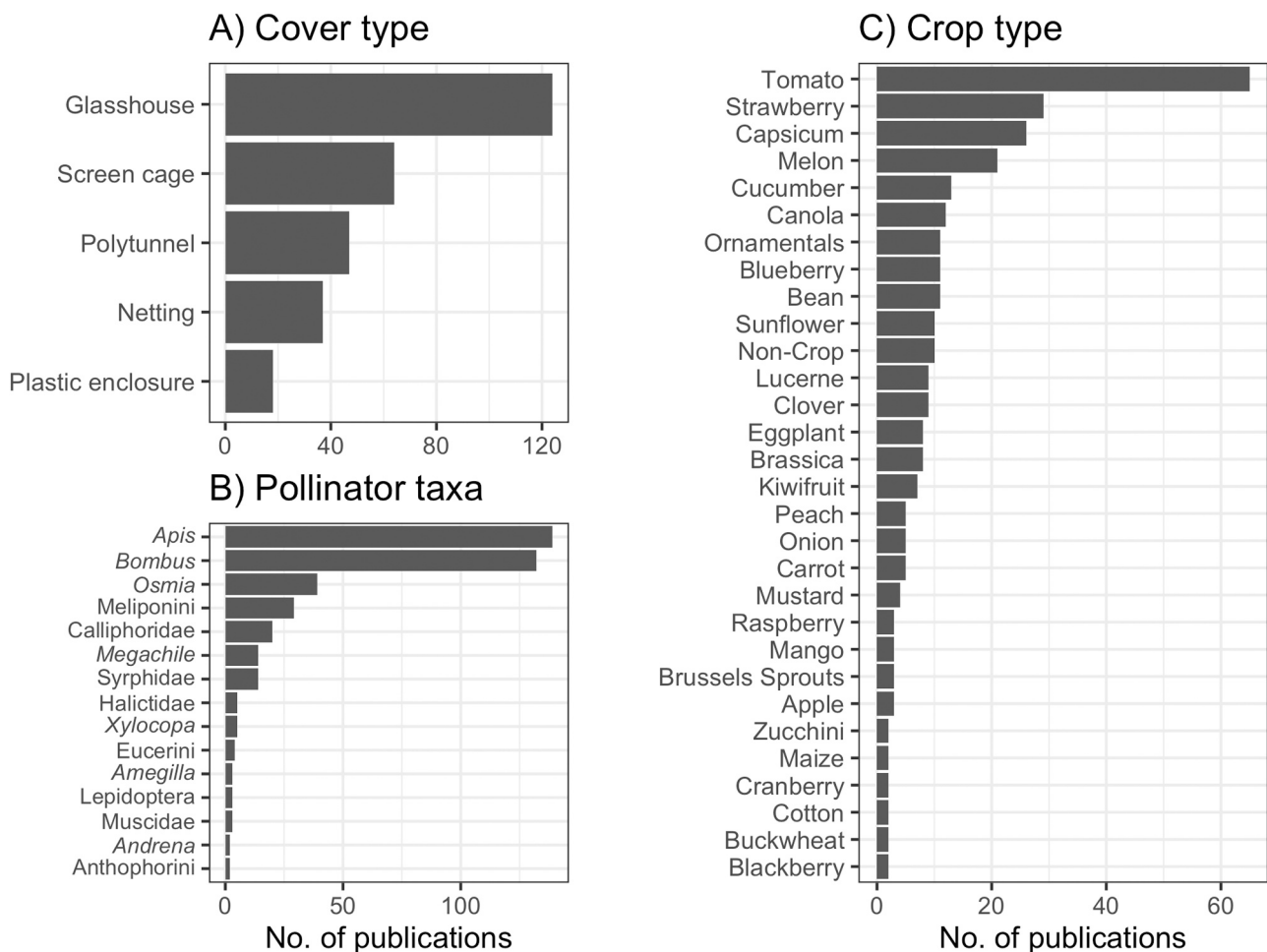


Fig. 3. (A) Frequency distribution of cover types, (B) pollinator taxa, and (C) crop types. Only pollinator taxa and crop species present in more than one study are shown. All taxa and crop species are provided in [Table S1](#).

3.2. Pollination service

All relevant publications were classified according to their focus; pollination service, pollinator health, or other (if neither pollination service nor pollinator health were assessed). Twenty-four studies assessed both pollination service and pollinator health and were thus added to both categories, generating a total of 314 records. Sixty-eight percent of studies ($n = 213$) focused on pollination ([Fig. 4](#)). Most often studies were conducted as comparisons of pollinator species effectiveness or tested the effectiveness of a particular insect pollinating a crop. Pollination success was measured directly as yield quantity and/or quality (55% of studies), inferred from pollinator foraging activity (10% of studies), or approximated through other metrics including comparisons of pollen transfer efficiency and/or seed production per flower visit (3% of studies). Most (205) studies reported improved pollination success using insects in covered systems; their data indicated that tested taxa visited the target crop flowers or improved fruit/seed set, compared with a control treatment. Only 21% of studies included direct comparison of insect visits and pollination success between covered environments and open (control) environments. More often, comparisons were drawn between insect visited flowers and unvisited flowers (i.e., insect visits were prevented, or flowers were self- or mechanically pollinated) and any mentioned effects of covers on pollination were inferred from expected insect activity patterns in covered vs open environments.

Thirty-three studies compared the effectiveness of different pollinator species under protected cropping, relative to conditions without

pollinators. Studies comparing pollination effectiveness within genera, such as within different *Bombus* spp., *Apis* spp., or among members of the same tribe (e.g., stingless bee species), found their performance as pollinators to be similar ([Chang et al., 2001](#); [dos Santos et al., 2008](#); [Greco et al., 2011a](#); [Strange, 2015](#)). Comparisons of pollinator effectiveness among genera identified differences in the performance of pollinator taxa, but these differences were crop specific. For example, bumble bees and buzz-pollinating stingless bees (*Melipona quadrifasciata*) were similarly effective pollinators of glasshouse tomatoes ([Hikawa and Miyana, 2009](#); [Silva-Neto et al., 2019](#)) and were both more effective than honey bees, in terms of yield, fruit quantity, and fruit weight ([Banda and Paxton, 1991](#); [dos Santos et al., 2009](#)). Pollination of parthenocarpic glasshouse cucumber by stingless bees resulted in greater fruit set and greater fruit weight than pollination by honey bees or with bees excluded ([Nicodemo et al., 2013](#)). However, bumble bees and honey bees were equally effective pollinators of strawberries in terms of fruit weight and yield ([Paydas et al., 1998](#); but see: [Zaitoun et al., 2006](#)) and honey bees and *Osmia cornuta* were similarly effective pollinators of blackberry (*Rubus fruticosus*), in terms of drupelet number and berry weight ([Pinzauti et al., 1997](#)). [Goubara and Takasaki \(2003\)](#) evaluated the flight activity and floral visitation patterns of 17 solitary bee species and a hover fly (*Eristalis tenax*) to lettuce flowers in open fields, glasshouses, and cages. Of the evaluated taxa, 10 bee species were found to actively forage on lettuce flowers and *Lasioglossum villosulum trichopse*, *Andrena knuthi*, and *O. cornifrons* were the most common flower visitors. Comparisons among Diptera showed that *Calliphora vicina* was superior to *Musca domestica* for pollination and seed

Table 1

The outcome (negative/neutral/positive) of studies that measured pollinator health, i.e., colony growth or activity at the front of the hive. Where multiple species were compared in a single study these have been recorded separately. An indication of the current scalability of each different species is provided.

		Population survival or growth			Activity at nest			Current scalability			
		Negative	Neutral	Positive	Negative	Neutral	Positive	From wild	Propagated /domesticated	Limited commercial production	Widespread commercial production
	Pollinator species	Declined or didn't reach potential	Sustained (w/ intervention)	Sustained (w/o intervention)	Increased	Reduced	Sustained (w/ intervention)	Sustained			
Bumble bees	<i>Bombus impatiens</i>	3				1		5			x
	<i>Bombus terrestris</i>		1					1			xG
	<i>Bombus occidentalis</i>	3*									x [†]
Honey bees	<i>Apis mellifera</i>	8*		1 ^o		1		1			xG
Mason bees	<i>Osmia cornuta</i>	2			1						x
	<i>Osmia cornifrons</i>				2					x	
	<i>Osmia pumila</i>			1				x			
	<i>Osmia sanrafaelae</i>				1				x		
	<i>Osmia californica</i>		1						x		
Leafcutter bees	<i>Megachile rotundata</i>				1						xG
	<i>Megachile concinna</i>				1				x		
	<i>Megachile pacifica</i>				1				x		
Stingless bees	<i>Tetragonula carbonaria</i>				1						x
	<i>Austroplebeia australis</i>				1					x	
	<i>Tetragonisca angustula</i>			1							x
	<i>Nannotrigona testaceicornis</i>			1						x	
	<i>Tetragonula minangkabau</i>			1					x		
	<i>Nannotrigona perilampoides</i>	1					2			x	
	<i>Melipona quadrifasciata</i>	2 ^o								x	
	<i>Melipona subnitida</i>	2								x	
	<i>Scaptotrigona</i> sp.		1						x	x	
Squash bees	<i>Eucera pruinosa</i>	1							x		
Sweat bees	<i>Lasioglossum apristum</i>		1							x	
Hover flies	<i>Episyrphus balteatus</i>	2	3		1						x
	<i>Eupeodes corollae</i>		1								x
	<i>Sphaerophoria rueppellii</i>		1								x
Blow flies	<i>Calliphora albifrontalis</i>	1								x	

*Colonies assessed in glasshouses over summer stayed stable but those assessed in winter declined in adult bees (Whittington and Winston, 2003). * Brood increased in weaker colonies but declined in larger colonies (Pinzauti, 1994). ^oColonies used were smaller than standard sized colonies (Keasar et al., 2007). ^o 16% of colonies experienced severe declines in strength, the remaining colonies grew in strength (Del Sarto et al., 2005).

[†]Historically only, commercial and wild populations of *B. occidentalis* populations have been decimated by disease (Thorp et al., 2003; Rao et al., 2011). 'G' denotes a global distribution.

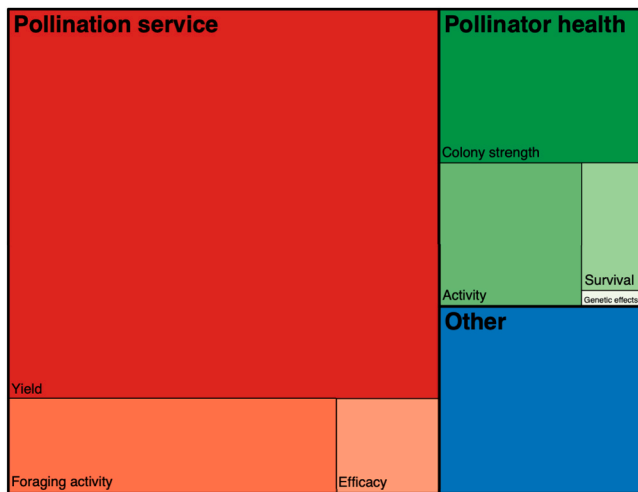


Fig. 4. Tree map showing the proportion of reviewed publications to assess 'pollination service' (orange squares), 'pollinator health' (green squares), and 'other' topics (blue square), and the indicators used. Examples of 'other' topics include virus transmission, pollinator behaviour unrelated to foraging/pollination, and effects of transgenic plants on pollinators.

production of caged leek (Clement et al., 2007).

A number of studies compared the effectiveness of bee pollination in comparison with hand-held vibrating pollination wands, for crops such as tomato e.g., *Bombus* spp. (Banda and Paxton, 1991; Houbaert and Jacobs, 1992; Martín-Closas et al., 2007), *Xylocopa* spp. (controls plants were shaken by hand, Hogendoorn et al., 2000), *Melipona quadrifasciata* (Del Sarto et al., 2005) and *Amegilla chlorocyanea* (Hogendoorn et al., 2006). Most commonly, bees were found to improve fruit set and fruit quality more so than pollination wands (Hogendoorn et al., 2006; Houbaert and Jacobs, 1992; Martín-Closas et al., 2007).

3.3. Pollinator Health

Only 20% of studies ($n = 62$) investigated pollinator health within covered environments (Fig. 4). After excluding the 14 pesticide exposure studies (where the covered environment was not of particular interest), 29% of studies ($n = 14/48$) reported that pollinator populations/colonies grew under covers and 17% ($n = 8/48$ studies) reported that populations/colonies sustained their numbers. Growing or stable populations were observed for several species of bumble bees, mason bees, leafcutter bees, stingless bees, and hover flies (Table 1). However, in 54% of studies ($n = 26/48$), the covers had a negative effect, contributing to a decline in pollinator numbers (Table 1). *Apis mellifera* was the most commonly studied taxon ($n = 11$ studies) and population decline and/or reduced colony activity was reported in 81% of studies. However, negative effects have been observed across many other pollinator taxa, including in 50% of studies assessing *Bombus* sp., which are commonly used for pollination in commercial glasshouses.

Negative effects included reduced reproduction (*Apis mellifera*: Lepore and Pinzauti, 1994; *Melipona subnitida*: Bomfim et al., 2014; *Nannotrigona perilampoides*: Cauich et al., 2004; *Melipona subnitida*: Bomfim et al., 2014; da Silva et al., 2017), a loss of adults (*A. mellifera*: Evans et al., 2019; *Bombus* spp: Birmingham and Winston, 2004; *Calliphora albifrontalis*: Cook et al., 2020), decreased forager activity measured at colony entrances (*A. mellifera*: Evans et al., 2019; Lepore and Pinzauti, 1994; Morison et al., 2000; Pinzauti, 1994; Meliponini: Bomfim et al., 2014), and increased disease prevalence (*A. mellifera*: Morimoto et al., 2011; Pinzauti, 1994).

3.4. Factors affecting pollinators under covers and mitigation of negative effects of covers

We identified studies that investigated or incorporated factors that may affect pollinators under covers, and studies that investigated methods of mitigating adverse effects of covers on pollinators. Forty percent of studies ($n = 116/290$) measured or accounted for one or more factors that have previously been identified as contributing to adverse effects on pollinator health (see: Dag, 2008). These factors included: temperature/humidity, light penetration (UV light and light intensity), pollinator orientation (flight behaviour and direction, homing ability), pollinator resources (hive nectar and/or pollen reserves and nutrient deficiency of the crop), and chemical exposure (pesticides). A smaller number of studies (14%, $n = 39/290$) explored techniques for mitigating negative effects of the aforementioned factors (Fig. 5).

3.4.1. Temperature and humidity

In the absence of effective climate control, protective covers restrict the air flow and alter air temperature and relative humidity surrounding the crop (reviewed in: Mditshwa et al., 2019). Completely enclosed environments can experience higher or lower temperatures and higher relative humidity (e.g., netting can increase humidity by 3.2 – 12.9%: Mditshwa et al., 2019; Parks et al., 2019). We found that patterns in temperature and humidity in covered systems have been investigated in conjunction with pollinator activity, pollinator survival, or pollination in 42 studies. Similar to open production environments, some pollinators perform better than others in the climate created by covers (e.g., Greco et al., 2011a; Pineda and Marcos-García, 2008c). However, the conditions under covers, and therefore the suitability of different pollinators, can be largely dependent on the local climatic conditions. A pollinator-crop pairing that works well in one region or in a particular covered environment may be less effective elsewhere. For example, several tropical stingless bee species perform well under protective covers (Bartelli and Nogueira-Ferreira, 2014; dos Santos et al., 2009; Greco et al., 2011a; Nicodemo et al., 2013). However, consistently high ambient temperatures (>39 °C) in glasshouses in north-eastern Brazil reduced foraging activity and induced declines in colony strength of the native stingless bee *Melipona subnitida*, as nest temperatures frequently exceeded their critical maximum (da Silva et al., 2017).

Environmental conditions can also vary spatially within covered systems and may impact pollinator activity (Hall et al., 2020; Stewart et al., 2010). In ~100 m long polytunnels in NSW Australia, average temperatures increased with increasing distance from the ends of the tunnel, and the higher temperatures in the centre of the tunnels were correlated with reduction in visits to flowers by pollinators, and decreased fruit set and fruit quality (Hall et al., 2020). Alternatively, such effects may be due to a pollinator's reluctance to venture very far into covered rows and/or blocks (Middleton and McWaters, 2000), or result from relatively small foraging ranges of some species of pollinators; in this case *Tetragonula carbonaria* was studied, which has been demonstrated to travel < 100 m from a colony in cultivated macadamia (Evans et al., 2021). In covered systems, the concurrent use of multiple pollinator taxa which differ in their temperature/humidity thresholds for foraging (described below) and foraging range, may improve pollination outcomes.

Covered crop growers may have the option of selecting the most suitable pollinator species for their locality and covered system, based on the optimum foraging temperatures of the species. Generally, flies and bumble bees occur in higher numbers and/or are more active feeders in cooler conditions when compared with honey bees. For example, *Calliphora vicina* forages most actively at < 20 °C (Howlett, 2012), *Eristalis tenax* between $\geq 5 - < 30$ °C (Jarlan et al., 1997; Howlett and Gee, 2019), and *B. terrestris* has a minimum foraging temperature of 3 °C (Stelzer et al., 2010) and exhibits optimal activity between 19.6 and 24 °C in glasshouses (Roman and Szczesna, 2008). Other species of blowflies (*C. vomitoria*, *Lucilia caesar* and *L. sericata*) will forage between

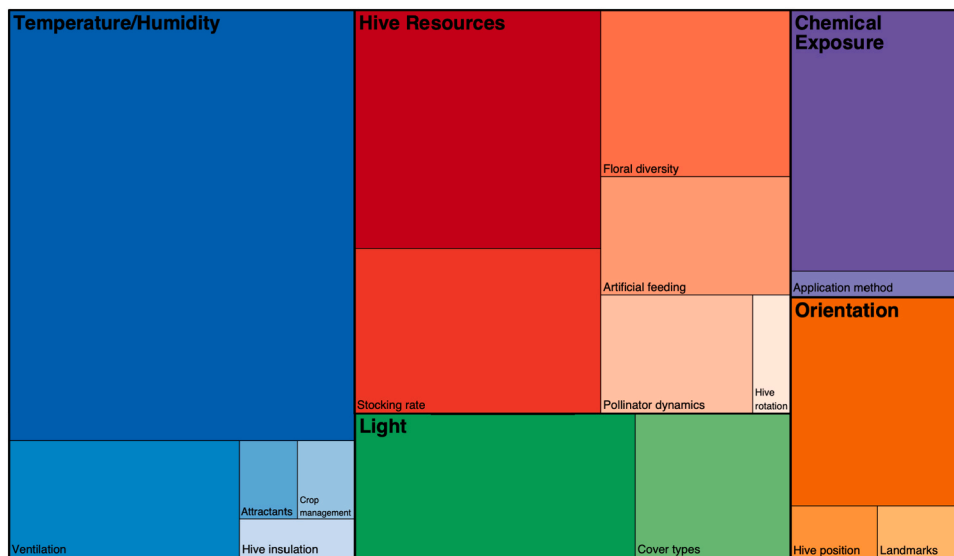


Fig. 5. Tree map showing the proportion of publications considering factors associated with crop covers that can negatively affect pollination service and/or pollinator health, and the proportion of publications investigating corresponding methods of mitigation. Squares with bold text indicate the number of papers that considered these effects. Other squares indicate the number of papers that also considered mitigation approaches associated with: 'temperature/humidity' (blue squares), 'light penetration' (green squares), 'hive resources' (red squares), 'chemical exposure' (purple squares), and 'orientation' ability (orange squares). Further details on the mitigation approaches trialled and the outcomes (+ or -) are provided in Table 3.

14 and 28 °C (maximum range assessed) but spend less time on each flower between 26 and 28 °C (Currah and Ockendon, 1984). These pollinators may be useful for covered crops flowering in early spring, in cooler climates, or under cover types that reduce ambient air temperatures. Other pollinator species exhibit increased foraging activity above 20 °C. The minimum temperature threshold for flight in honey bees is predicted to be between 12 and 13 °C, but maximum activity occurs between 26.5 and 27 °C (Danka et al., 2006). For stingless bees, optimal foraging temperatures can range from 14° to 35°C (Hilário et al., 2000; Cauich et al., 2004). For example: between 20 and 35 °C in *Nannotrigona perilampoides* (Cauich et al., 2004), 27–28 °C in *Austroplebeia australis* (Greco et al., 2011a) and 29 – 31 °C in *Tetragonula carbonaria* (Greco et al., 2011a). Relative humidity can also affect foraging activity in stingless bees, and optimal relative humidity for foraging varies across species. The optimal temperature range and relative humidity for 22 Brazilian stingless bee species are summarised by Hilário et al. (2000). Many of these species may be well-suited for covered crops in warmer climates or in covered environments with limited climate control.

Growers can modify their covered system to better suit either a target pollinator or a broader diversity of pollinators. Four studies tested this approach, by comparing pollinator activity on flowers and pollination when modifying the covered system to improve ventilation. Modifications included installing screen vents in glasshouses, opening sides of glasshouses, and opening the ends of tunnels. Several studies showed increased pollinator activity on the crop when ventilation was introduced (e.g., *Apis mellifera*: Dag and Eisikowitch, 1999; hover flies: Pineda and Marcos-García, 2008a; Pineda and Marcos-García, 2008c). In addition to lowering air temperatures, opening up the enclosures made the crop accessible to wild pollinators from outside, which could also help to explain the increase in activity on flowers (Dag and Eisikowitch, 1999). However, opening enclosures should be done with caution, due to the risk of pest incursion, and escape of commercially managed pollinators which can pose risks to wild populations of pollinators occupying the surrounding environment (Mallinger et al., 2017; Bartomeus et al., 2020). Furthermore, for seed production, the exclusion of pollen incursion from external sources is necessary to prevent outcrossing and maintain varietal purity (George, 2009). Alternatively, rather than modifying the enclosure, pollinators can be manipulated directly to increase their efficacy in these environments. For example, bee colonies can be placed throughout covered systems to encourage an even spread of pollinators/pollination (Middleton and McWaters, 2000). Commercially produced 'Pollination Stations' (structures for protecting bumble bee colonies from extreme heat) can help to maintain lower

average colony temperatures and reduce temperature fluctuations. These stations can improve colony reproduction and forager activity compared with control colonies (Martínez et al., 2014). Similarly, insulative foam or hive designs with insulative properties are often used to protect honey bee and stingless bee hives from extreme temperatures, including in protected cropping environments.

In addition to directly influencing foraging activity and pollinator survival, both temperature and humidity affect the production of pollen and nectar by crop flowers (Dag, 2008), and as a consequence can alter the foraging behaviour of pollinators (Corbet, 1990; Free, 1993). High temperatures and relative humidity can lower the sugar concentration of nectar, making the flower less attractive to pollinators (Corbet, 1990; Dag, 2008; Free, 1993), though it may be possible to mitigate effects of nectar-sugar concentration with other management practices. A single study from our review looked at a method of modifying flowers to increase their attractiveness to bees in a covered system. Dag and Eisikowitch (2000) successfully used carbon dioxide to enhance the sugar content of nectar, which resulted in increased flower visitation by honey bees. In another study, a temporary increase in foraging activity was achieved by exposing *B. terrestris* hives to a foraging recruitment pheromone in a glasshouse setting (Molet et al., 2009), however the efficacy of this pheromone and other volatile attractants to enhance flower visitation has not been trialled in covered systems.

3.4.2. Light

Protective covers are designed to modify the quantity and/or quality of sunlight reaching plants, in order to enhance their growth. Different growing conditions necessitate varying degrees of light transmission, for example, plastic nets that selectively reduce solar radiation have been developed for arid and tropical locations. The desired light transmission can be achieved by modifying the weave density and/or the colour of the plastic (Middleton and McWaters 1996, Stamps, 2009; Maraveas, 2020).

Pollinator performance was assessed in relation to the quantity (intensity) of light or UV transmittance under covers in 14 of the reviewed studies. The reported effects of light intensity on pollinator activity varied across studies. For example, foraging activity of *Nannotrigona perilampoides* was positively correlated with light intensity in one study on greenhouse tomato (Palma et al., 2008b) but not another (Cauich et al., 2004). *B. impatiens* foraging activity was positively correlated with light intensity in habanero pepper crops (Palma et al., 2008a) but not tomato (Palma et al., 2008b; Roman and Szczesna, 2008). However, where assessed, low UV transmittance consistently interfered with bee activity and orientation (described in detail in Section 3.4.3).

Whilst a wide variety of polyethylene and netting covers are available for growers to use, only five studies have compared pollinator performance under different cover types. Two studies showed differences in bee behaviour with the type of polyethylene cover. *B. impatiens* were more active on the crop and adults were less likely to fail to return to hives in commercial glasshouses constructed from materials that transmit an extended range of UV light (Magnani et al., 2007; Morandin et al., 2001a). However, in a follow-up study, Morandin et al. (2002) recorded no difference in *B. impatiens* activity levels across four experimental enclosures constructed from different polyethylene covers, although these authors acknowledge that their custom-built glasshouses may have been too small for accurate observation of foraging behaviour. Vaissiere et al. (2000) compared *A. mellifera* hive health in apple orchards under two different types of hail netting covers (clear and black thread) and in uncovered orchards. These authors found hive strength declined significantly under both types of netting, with colonies losing between 3000 and 7000 bees per season, whilst colonies in uncovered orchards increased in strength.

Prior to installing protective covers, growers should seek guidance from manufacturers regarding their product's light transmission and its compatibility with pollinators. Manufacturers quantify light transition using a shading factor (SF %), which describes the amount of light loss - a relative proportion of absorbed and reflected radiation, in either the visible range of solar radiation (380–760 nm) or photosynthetically active radiation PAR range (400–700 nm) (Kittas et al., 2014). Separate shading factors for direct versus diffuse radiation may also be available (Kotilainen et al., 2018). Larger bodied pollinator species (e.g. *Bombus* spp.) are possibly better suited for use under covers with uniformly high shading factors, because the visual capabilities of insects can increase with body size (Spaethe, 2003; Taylor et al., 2019). For example, individual bumble bees with larger body size have better object resolution than smaller conspecifics (Spaethe, 2003), and can fly under lower light intensities (Kapustjanskij et al., 2007). Operating under low light is certainly possible for bees and other insects with nocturnal or crepuscular lifestyles (e.g., *Megalopta genalis*, *Apis dorsata*, *Trigonisca pipioli* and *Lepidoptera* spp.), as these species have eyes that are adapted to such conditions (Dorey et al., 2020; Tichit, 2021).

Spectral wavebands and their proportions (transmitted light quality/colour) also differ between cover types, but inconsistencies in the way these values are reported has made it difficult to generate comparisons among products (Kotilainen et al., 2018). Insect pollinators use colour to evaluate ambient light for navigation and/or in object recognition (van der Kooi et al., 2021). The spectral wave bands of greatest importance are likely to be those to which their eyes are most receptive, including: UV ~ 350 nm, green ~530 nm, and blue ~ 440 nm (Briscoe and Chittka, 2001; for taxon-specific receptivity see: van der Kooi et al., 2021).

3.4.3. Pollinator orientation

Covers are likely to reduce or alter the visual cues that bees use to navigate when foraging. Such cues include the position of the sun and polarised UV light (used by honey bees and bumble bees: Collett et al., 2013; Frisch, 1967; Meyer-Rochow, 1981) and landmarks on the horizon (Fry and Wehner, 2002; Plowright et al., 1995). Blacquière et al. (2006) showed that bumble bees and honey bees fail to return to their hives under polycarbonate covers, which do not transmit any UV light.

An additional challenge that pollinators may face in covered systems is uneven dispersion of light. Social bees are positively phototactic when returning to their nest (Menzel and Greggers, 1985) and bright areas such as corners and ventilation systems may function as "light traps" that attract bees (Pinzauti, 1994). In particular, losses of bumble bees through ventilation systems have been found to be greater under covers that transmit less UV light, as the high contrast between the light transmitted through the covering and light entering the ventilation systems can increase the attractiveness of the ventilation systems (Morandin et al., 2002). These factors may result in bees being lost from

hives and/or not visiting the crop.

Loss of adult bees from honey bee colonies can occur over the duration of their deployment under covers, but the largest losses have been observed soon after hives were introduced into covered systems (Evans et al., 2019). Remaining honey bee foragers either learnt to orient (Dyer and Chittka, 2004), or were perhaps replaced by new recruits that adapt better to foraging under covers (Bartelli et al., 2014; Cauch et al., 2004). For these reasons, bee colonies are sometimes introduced earlier than required for pollination, to allow time for bees to acclimatise or become conditioned (e.g., Higo et al., 2004; Morandin et al., 2001a). Alternatively, experienced foragers can be removed prior to deploying colonies in the covered environment to avoid losses (Bartelli and Nogueira-Ferreira, 2014; Cauch et al., 2004), although this is only of benefit if the colonies are managed and other colonies (e.g., at an apiary site) are able to accept the removed workers.

Ten studies specifically investigated how pollinator orientation and/or forager distribution was affected within covered systems (e.g., Bartelli et al., 2014; Birmingham and Winston, 2004; Free and Racey, 1966). Two of these studies also investigated management practices to improve the orientation and distribution of honey bees or bumble bees. Hive placement was found to be important for optimising honey bee activity across polytunnel-grown melon flowers (Dag and Eisikowitch, 1995). Hives located at the northern end of tunnels (upwind) were more active on the crop compared with hives located at the southern end of the tunnel, perhaps because these colonies were exposed to the southern air flow from the glasshouse, which increased their foraging inside. The increase in honey bee activity was correlated with improved fruit set (Dag and Eisikowitch, 1995). A second study investigated the use of visual landmarks to improve the ability of bumble bees to return to their hives and prevent colony losses (Birmingham and Winston, 2004). *B. occidentalis* and *B. impatiens* colonies were provided unique pattern cues at the hive entrances and landmarks hung in the general vicinity of the hives. The landmarks did not prevent drifting of bees between colonies or bee losses, but they were correlated with shorter foraging trips, potentially increasing foraging efficiency and/or colony performance.

3.4.4. Pollinator resources

Crop covers that fully enclose the crop inherently restrict pollinator access to alternative food sources. This can be beneficial for pollination because it prevents pollinators from leaving the crop to forage on competing floral resources in the wider landscape (Palmer-Jones and Forster, 1972). However, it can be challenging to determine whether enough resources exist within the covered system to sustain pollinator populations. If resources are insufficient in quantity, pollinator numbers will rapidly decline (Cook et al., 2020). Brood production requires a sufficient supply of water, carbohydrates (nectar), and a diversity of protein and micronutrients from pollen (Alaux et al., 2010; Di Pasquale et al., 2013; Foley et al., 2012; Hendriksma and Shafir, 2016). As such, prolonged restriction to a mono-floral environment can prevent sustained colony development in eusocial bees due to lack of nutritional value of the crop (Free, 1993).

Twenty-five studies from our review provided pollinators with food supplements, such as honey, sucrose solution or manufactured pollen substitutes either in hives (Bartelli and Nogueira-Ferreira, 2014; Bezabih and Gebretsadiikan, 2014; Cauch et al., 2004; Evans et al., 2019) or in the surrounding environment (Bell et al., 2006; Orbán et al., 2012); potted flowering plants (Hogendoorn et al., 2000; Keasar et al., 2007); and water sources (Cauch et al., 2004; Cook et al., 2020). However, only four studies directly assessed the benefits of providing food supplements, and eight studies assessed the benefits of increasing floral diversity in covered systems. When assessed, providing supplementary resources did not consistently improve pollinator performance. There was no increase in *B. occidentalis* brood production or colony longevity when colonies were fed pollen supplements containing a diversity of pollen types (Whittington and Winston, 2003). Providing water had no effect on survival of the fly *Calliphora albifrontalis* in covered blueberry

(Cook et al., 2020). However, honey bees fed supplementary pollen were more active on melons (Iselin et al., 1974). These results may indicate that these particular resources were already sufficient in two of the tested systems, but the benefits of artificially feeding are likely to be variable for insect taxon, crop, and covered system. Supplementary feeding of sucrose has successfully been used in glasshouses to increase the proportion of pollen foragers relative to nectar foragers in honey bee colonies (Free and Racey, 1966), a useful management strategy for crops where pollen foragers are more effective pollinators than nectar foragers (Free and Spencer-Booth, 1961; Goodwin and Houten, 1991). Sucrose feeding is also standard practice for crops that do not produce nectar, such as kiwifruit and tomato (Goodwin and Houten, 1991; Velthuis and Van Doorn, 2006).

Increased access to floral diversity, through the inter-planting of crops, inclusion of additional floral resources, or by allowing pollinators to forage outside the covered system (e.g., deployment of honey bee hives with double entrances) typically yielded positive results. Floral diversity has been related to decreased brood parasitism (*Osmia pumila*: Goodell, 2003), increased brood production (*A. mellifera*: Sabara and Winston, 2003), increased population size (Syrphidae: Pineda and Marcos-García, 2008b; van Rijn et al., 2013; but see Pineda and Marcos-García, 2008a), and increased activity on crops (*A. mellifera*: Vaisiere and Froissart, 1996). In addition to supporting pollinator health and activity, secondary plantings under covers can enhance biological control of crop pests (Parolin et al., 2012) and reduce reliance on pesticides (discussed in Section 3.4.5). The provision of nest-building resources for eusocial species (e.g., resins) may improve defences against pathogens and infections of brood and food storage (Michener and Michener, 1974; Roubik, 1989), as well as pollinator performance, although this has not been investigated in protected cropping environments.

Appropriate stocking rates for managed pollinators can help facilitate improved pollinator performance in covered systems. Too few (or ineffective) pollinators can lead to reduced crop yield, yet too many pollinators may damage flowers and reduce yields (Morandin et al., 2001b; Sáez et al., 2014) and/or reduce pollinator population longevity due to limited resources (Cook et al., 2020). Fully enclosed systems exclude wild pollinators, so only managed pollinators are available to pollinate the crop. For this reason, optimal stocking rates in covered systems may be quite different from those developed for open production systems. So far, recommended stocking guides have been devised for a small number of pollinator-crop pairings (Table 2). To improve the management of pollination in protected crops, guidelines for optimal stocking rates need to be developed for the majority of pollinator-crop pairings.

A small number of studies have considered the dynamics of individual pollinators or colonies and modified 'standard' practices to improve pollinator performance. For example, smaller dispensable honey bee hives or microcolonies have been used successfully to pollinate melons grown in polytunnels (Keasar et al., 2007). This particular study was undertaken to increase the cost effectiveness of using honey bees in enclosures; the loss of small hives is better than the loss of standard pollination units. However, smaller honey bee colonies within

netting enclosures have also fared better than larger colonies; the former increasing in adult bee numbers and brood size whilst the latter declined (Free, 1993; Pinzauti, 1994). The reason for this is not yet well understood, but the initial difficulties for colonies negotiating a covered environment may disrupt brood production, because brood size establishment corresponds with the amount of food resources entering the colony (Pinzauti, 1994). Switching honey bee colonies halfway through bloom has been trialled as a way of maintaining the interest among foragers for the target crop (Palmer-Jones and Forster, 1972), but this could also prevent colony decline, by reducing the duration of residence under cover.

3.4.5. Chemical exposure

Whilst covers can help growers prevent contamination from pathogens and colonisation by insects, the controlled climatic conditions, high density of plants, and lack of natural enemies can exacerbate certain pest and disease problems (Gullino et al., 2020). Thus, pesticide application is a necessary management practice for most crops grown in protected environments. The detrimental impacts of pesticide exposure to pollinator health and pollination service provision are fairly well-documented (e.g., Desneux et al., 2007; Stanley et al., 2015; van der Sluijs et al., 2013), however, the ways in which pesticide-pollinator interactions differ in protected environments are not well understood.

In some covered environments, pesticide exposure risk may be heightened because pollinators do not have access to alternative forage, it follows that insects would instead be forced to forage on treated crop flowers, increasing pesticide exposure. The persistence of pesticides on crops can also be increased by covers; the usual modes of degradation of pesticides include hydrolysis (rainfall), photodegradation (UV light) and volatilisation (Cessna et al., 2005), all of which are typically lessened in protected environments. The persistence of residues for several pesticides was increased on raspberry crops (foliage and berries) grown under high tunnels, compared with open fields, and was even greater for covers with reduced UV transmission (Leach et al., 2017). Similar patterns have been found in leafy greens and berries (Allen et al., 2015). Prolonged residual action of pesticides in protected environments may lead to enhanced pest suppression (and therefore fewer pesticide applications) but could also lead to increased exposure risk to pollinators after each application - residues from acaricides used to control spider mite have been identified as posing unacceptable risk to honey bees in covered strawberries (Wang et al., 2018). Some pesticides can bioaccumulate in plant tissues, and the extended growing period in glasshouses may increase this effect (Arias et al., 2021) with potential to affect pollinators, especially if the compounds are present in flowers.

Only one study in our review directly evaluated pesticide effects on pollinator health and pollination service under covers. Alarcón et al. (2005) evaluated the effect on bumble bee health and pollination service of different application methods for the systemic insecticide thiamethoxam. Pollination levels were higher when the pesticide was applied through drip irrigation as opposed to foliar sprays, but there was no significant difference detected in the survival of bumble bee workers. Though there are few empirical studies directly assessing pollinator exposure to pesticides in protected cropping environments, there is

Table 2

Recommended pollinator stocking rates currently available for covered crops.

Crop species	Pollinator	Stocking rate	Reference
Strawberries	<i>Apis mellifera</i>	10,000–15,000 bees/1000 m of tunnel or glasshouse	Lieten (1993)
Strawberries	<i>Bombus</i> sp.	60–100 bees/700–1000 m of tunnel or glasshouse	Lieten (1993)
Green kiwifruit	<i>B. terrestris</i>	660 foraging bees/ha	Pomeroy and Fisher (2002)
Gold kiwifruit	<i>B. terrestris</i>	914 foraging bees/ha	Cutting et al. (2018)
Tomato	<i>B. impatiens</i>	2000 foraging bees ha/day	Morandin et al. (2001a)
Tomato	<i>Amegilla chlorocyanea</i>	282 nesting female bees/ha	Hogendoorn et al. (2007)
'Braeburn' apples	<i>Osmia cornuta</i>	1 female and 1 male/ tree	Ladurner et al. (2004)
Hybrid red rape	<i>Osmia cornuta</i>	1 female and 3 males/ plant	Ladurner et al. (2002)
Capsicum	<i>Tetragonula carbonaria</i>	One colony/1900 plants	Greco et al. (2011b)

Table 3
Mitigation approaches trialled and their outcomes (-/+/=).

Factors associated with crop covers	Mitigation method	Taxa assessed	Implementation	Outcome (-/+/=)	Publications	
Temperature / humidity	Ventilation	<i>Episyrrhus balteatus</i>	Side walls open vs closed, assessed residence time	+	Pineda and Marcos-García (2008a)	
		<i>Eupeodes corolla</i>	Side walls open vs closed, assessed abundance	+	Pineda and Marcos-García (2008c)	
Hive resources	Ventilation	<i>Episyrrhus balteatus</i>				
		<i>Sphaerophoria rueppellii</i>				
		<i>Apis mellifera</i>	Tunnels open at end	+	Dag and Eisikowitch (1999)	
		<i>Apis mellifera</i>	Screen vent	=	Sabara et al. (2003)	
		<i>Apis mellifera</i>	Screen vent	=	Sabara and Winston (2003)	
		<i>Apis mellifera</i>	Different types of ventilation	=	Celli and Giordani 1981	
		Attractants	<i>Bombus terrestris</i>	Recruitment pheromone	+	Molet (2009)
			<i>Apis mellifera</i>	CO ² treatment to increase nectar	+	Dag and Eisikowitch (2000)
		Crop management	<i>Bombus terrestris</i>	Hive shelter	+	Martínez et al. (2014)
		Floral diversity	<i>Osmia pumila</i>	Floral richness	+	Goodell (2003)
	<i>Episyrrhus balteatus</i>		Floral richness	+	van Rijn et al. (2013)	
	<i>Episyrrhus balteatus</i>		Flowers with more accessible nectar + pollen	+	van Rijn and Wäckers (2013)	
	<i>Episyrrhus balteatus</i>		Floral diversity	=	Pineda and Marcos-García (2008b)	
	<i>Eupeodes corolla</i>		Co-flowering plants	+	Pineda and Marcos-García (2008c)	
	<i>Episyrrhus balteatus Sphaerophoria rueppellii</i>					
	<i>Apis mellifera</i>		Allowed outside access	+	Vaissiere and Froissart (1996)	
	<i>Apis mellifera</i>		Allowed outside access	+	Sabara and Winston (2003)	
	Stocking rate		<i>Bombus terrestris</i>	Stocking rate for green kiwifruit	+	Pomeroy and Fisher (2002)
			<i>Bombus impatiens</i>	Stocking rate for tomatoes	+	Morandin et al. (2001b)
		<i>Amegilla chlorocyanea</i>	Stocking rate for tomatoes	+	Hogendoorn, Coventry, Keller (2007)	
<i>Bombus terrestris</i>		Stocking rate for tomato seed	+	Pinchinat, Bilinski, Ruskowski (1979)		
<i>Bombus hypnorum</i>						
<i>Bombus agrorum</i>						
<i>Osmia lignaria</i>		Stocking rate for hybrid rap	+	Ladurner, Santi, Maccagnani Maini (2002)		
<i>Apis mellifera</i>						
<i>Apis mellifera</i>		Number of bees for strawberries	+	Lieten (1993)		
<i>Bombus sp.</i>						
Artificial feeding	<i>Tetragonula carbonaria</i>	Stocking rate for capsicums	+	Greco et al. (2011b)		
	<i>Bombus terrestris</i>	Stocking rate for gold kiwifruit	+	Cutting et al. (2018)		
	<i>Apis mellifera</i>	Density of bees and blueberries	+	Dedej and Delaplane (2003)		
	<i>Bombus occidentalis</i>	Supplementary pollen	=	Whittington and Winston (2003)		
	<i>Calliphora albifrontalis</i>	Water provision	=	Cook et al. (2020)		
	<i>Apis mellifera</i>	Supplementary pollen	+	Iselin et al. (1974)		
	<i>Apis mellifera</i>	Sucrose feeding to increase pollen collection	+	Free and Racey (1966)		
	<i>Bombus impatiens</i>	Feeder location	+	Orbán, Plowright, Plowright (2012)		
	Pollinator dynamics	<i>Apis mellifera</i>	Small colonies	+	Keasar et al. (2007), Pinzauti (1994)	
		<i>Episyrrhus balteatus</i>	Younger adults	+	Pineda and Marcos-García (2008a)	
<i>Apis mellifera</i>		Amount of brood	=	Sabara et al. (2003)		
Hive rotation	<i>Apis mellifera</i>	Amount of brood	=	Sabara and Winston (2003)		
	<i>Apis mellifera</i>	Hive rotation	-(pollination)	Palmer-Jones and Forster (1972)		
Light	Cover type	<i>Bombus impatiens</i>	Assessed activity and loss	+	Morandin et al. (2001a)	
		<i>Bombus impatiens</i>	Assessed activity level and photo-response	=	Morandin et al. (2002)	
		<i>Bombus terrestris</i>	Assessed activity	+	Magnani et al. (2007)	
		<i>Apis mellifera</i>	Assessed colony strength	-	Vaissiere et al. (2000)	
Orientation	Hive position	<i>Apis mellifera</i>	North vs South placement	+	Dag and Eisikowitch (1995)	
	Landmarks	<i>Bombus occidentalis</i>	Assessed return to colonies	=	Birmingham and Winston (2004)	
Chemical exposure	Application method	<i>Bombus impatiens</i>				
		<i>Bombus terrestris</i>	Drip application	=(bees) +(pollination)	Alarcón et al. (2005)	

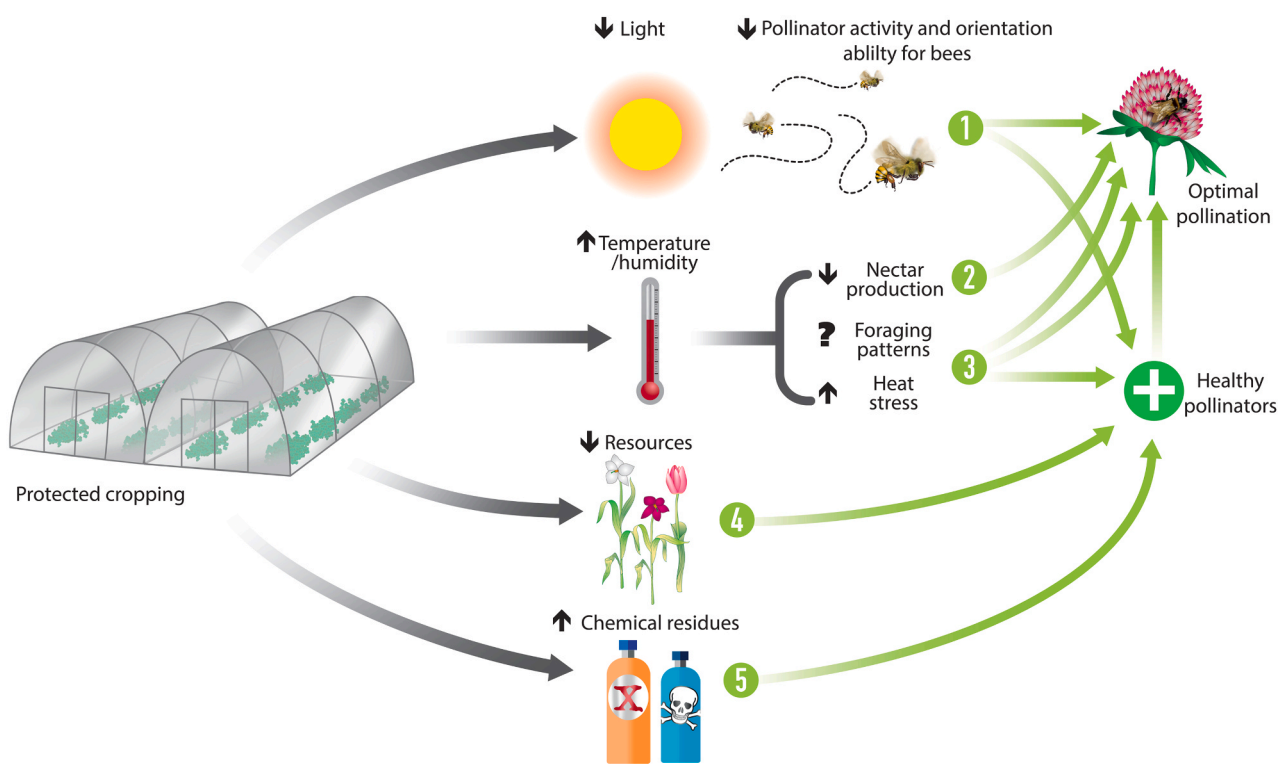
growing recognition among researchers, extension agents, and growers that these issues need to be considered. Best management guidelines have been developed to include practices that minimise pesticide risks, including activities promoting improved hygiene to reduce outbreaks, pest and disease monitoring instead of calendar sprays, the use of natural enemies (Badgery-Parker, 2015) and banker plants (Payton Miller and Rebek, 2018) for sustained, non-chemical control of pest populations. Adopting new best practice can have multiple benefits; the greenhouse tomato industry has been able to successfully deploy bumble bees for pollination while substantially reducing pesticide use (Velthuis and van Doorn, 2006).

4. Knowledge gaps

Significant knowledge gaps need to be overcome to ensure the continued development and adoption of best practice for effective and sustainable pollination in protected cropping environments. Of the studies that provided details of pollination services under protected covers (n = 213), 96% confirmed that introduced insects provided a pollination service. However, only 21% of these studies compared this pollination service provision between covered and uncovered (control)

environments. Hence, while information is available about pollinator performance under covers relative to other pollinators, mechanical pollination, or self-pollination, much less is known about how pollinator performance changes between environments. Pollinators are generally expected to perform better outside, relative to covered systems, therefore direct experimental comparisons of pollinator foraging behaviour and pollination success across these environments will help elucidate if, or under what conditions, different pollinator species under-perform (i.e. uncovered environments provide a 'standard practice' comparison).

Despite the economic importance of maintaining healthy pollinator populations, only 20% of studies investigated the effect of crop covers on the health of pollinators. If the health of pollinator populations declines during the flowering period (as observed in 54% of studies where pollinator health was assessed) pollination services may be suboptimal. Moreover, replacing pollinators can be expensive for growers (Bir-ningham and Winston, 2004), and the decline of perennial bee colonies (e.g., honey and stingless bees) can lead to increased hive rental prices and tight restrictions on hive use in covered crops (Evans et al., 2019). Further research is needed to both identify the optimal foraging and breeding conditions (e.g., temperature, humidity, and light intensity) for a wide range of pollinator taxa and to better understand how different



Potential intervention points to improve pollinator health and pollination	
<p>1 - Consider cover type, some materials better than others</p> <ul style="list-style-type: none"> - Consider hive placement - Select appropriate pollinator(s) 	<p>4 - Provide outside access</p> <ul style="list-style-type: none"> - Supplementary feeding - Use companion planting - Use appropriate stocking rates of managed pollinators - Rotate managed pollinators - Consider hive setup
<p>2 - Use practices to regulate or increase plant nectar production</p>	<p>5 - Consider method of application</p> <ul style="list-style-type: none"> - Use biocontrol of pests and diseases
<p>3 - Use temperature regulation systems or include ventilation</p> <ul style="list-style-type: none"> - Use insulation with hives - Select appropriate pollinator(s) 	

Fig. 6. Possible effects for pollinators and/or pollination that can occur in covered cropping systems and potential intervention points for mitigating these effects (numbers 1–5).

covered systems impact the health of pollinator populations. These results will enable us to identify the most effective taxa for different covered systems and for growers it will allow risk spreading through diversification of pollination services.

To date, only a small number of studies ($n = 39$) have explored techniques for improving pollinator performance under covers. Whilst some successful mitigation approaches have been identified (see Table 3), many options for intervention remain underexplored. For example, management practices such as the inclusion of additional floral resources in production systems (e.g., banker plants) and safer types and methods of pesticide application, have received some attention in uncovered production systems, however, much less is known about their applicability for pollinators in growing systems under cover. Further, the approach used may vary depending on the type of covered system as these can be fully closed with introduced pollinators, or semi-closed with introduced and/or wild pollinators given access to both the internal and external environment.

Finally, the global increase in protected cropping (and other controlled environment agriculture) will likely necessitate the commercial production of a greater variety of pollinator taxa. The logistics and economic costs versus the benefits of employing pollinators other than honey bees and bumble bees, as well as the necessary mitigation practices, have rarely been considered in production environments of scale, but are likely to be of importance to growers.

4.1. Strategies to mitigate poor pollinator health and pollination

Covers can modify the conditions experienced by pollinators within crops, sometimes with negative consequences. However, some successful mitigation approaches have been developed (possible negative consequences and mitigation approaches are summarised in Fig. 6). High temperatures and altered light can reduce foraging activity or interfere with navigation. Increasing ventilation in glasshouses and tunnels, achieved by opening sides or ends, can reduce temperatures and lead to increases in pollinator foraging activity. Selection of crop covers that better optimise light conditions for pollinators may also be beneficial.

Covers can also limit pollinator access to the biological resources they require and consequently diminish pollinator health. Increasing and diversifying biological resources for pollinators through food supplements, outside access, or banker plants has potential as a strategy to improve pollinator performance. Moreover, there is evidence that other management practices for pollinators, including introducing smaller colonies, consideration of colony position within the crop, and age of adults released (for *Episyrphus balteatus*) can be useful for improving pollinator performance.

In practice, the above measures should be incorporated as part of an integrated crop management strategy that considers both crop production and the requirements of insect pollinators. These measures could improve pollinator health and pollination services whilst also promoting a more biodiverse growing system with reduced reliance on chemical-based pesticides.

Author contributions

Liam K. Kendall, Lisa J. Evans, Romina Rader and Tobias J. Smith conceived review. Liam K. Kendall, Lisa J. Evans, Romina Rader, Megan Gee, Tobias J. Smith, Vesna Gagic, Juan D. Lobaton, Mark Hall, Jeremy Jones, Lindsay Kirkland, Manu E. Saunders, Carolyn Sonter developed search terms and conducted the review of articles. Brian T. Cutting, Sophie Parks, Katja Hogendoorn, Cameron Spurr, Alistair Gracie, Melinda Simpson provided expert opinion and edits. Liam K. Kendall and Lisa J. Evans summarised the data and jointly wrote the manuscript and all authors contributed to or approved the final version.

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.

Acknowledgements

We thank Bruce White for useful discussions in the early stages of this review, Melissa Broussard and our anonymous reviewers for their helpful feedback, and Tony Corbett of PFR for preparation of the summary graphic. This project was delivered by Hort Innovation, from the Australian Government Department of Agriculture, Water and the Environment as part of its Rural R&D for Profit programme and Plant and Food Research, NSW Department of Primary Industries, University of New England, University of Adelaide, University of Tasmania and Seed Purity Pty Ltd: Novel technologies and practices for the optimisation of pollination within protected cropping environments, contract no. CON-001793. Liam K. Kendall and Romina Rader were also funded by the Ian Potter Foundation (Australia) and Liam K. Kendall by a Commonwealth Scientific and Industrial Research Organisation (CSIRO) PhD top-up scholarship. Lisa J. Evans was also supported by Zespri Group Limited and the New Zealand Ministry for Primary Industries Sustainable Farming Fund (SFF): optimising pollination of Gold3 kiwifruit under hail netting, contract no. 404958.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2021.107556](https://doi.org/10.1016/j.agee.2021.107556).

References

- Alarcón, A.L., Cánovas, M., Senn, R., Correia, R., 2005. The safety of thiamethoxam to pollinating bumble bees (*Bombus terrestris* L.) when applied to tomato plants through drip irrigation. *Commun. Agric. Appl. Biol. Sci.* 70, 569–579.
- Alaux, C., Ducloz, F., Crauser, D., Conte, Y.L., 2010. Diet effects on honeybee immunocompetence. *Biol. Lett.* 6, 562–565.
- Arias, L.A., Garzón, A., Ayarza, A., Aux, S., Bojacá, C.R., 2021. Environmental fate of pesticides in open field and greenhouse tomato production regions from Colombia. *Environ. Adv.* 3, 100031.
- Allen, G., Halsall, C.J., Ukpebor, J., Paul, N.D., Ridall, G., Wargent, J.J., 2015. Increased occurrence of pesticide residues on crops grown in protected environments compared to crops grown in open field conditions. *Chemosphere* 119, 1428–1435.
- Amarante, C.V.T., Steffens, C.A., Argenta, L.C., 2011. Yield and fruit quality of 'Gala' and 'Fuji' apple trees protected by white anti-hail net. *Sci. Hortic.* 129, 79–85.
- Badgery-Parker, J., 2015. Keep it CLEAN: Reducing Costs and Losses in the Management of Pests and Diseases in the Greenhouse. NSW Agriculture.
- Badgery-Parker, J., James, L., 2010. Commercial Greenhouse Cucumber Production. Industry & Investment NSW.
- Banda, H.J., Paxton, R.J., 1991. Pollination of Greenhouse Tomatoes by Bees. *International Society for Horticultural Science (ISHS)*, Leuven, Belgium, pp. 194–198.
- Bartelli, B.F., Nogueira-Ferreira, F.H., 2014. Pollination services provided by *Melipona quadrifasciata* Lepeletier (Hymenoptera: Meliponini) in greenhouses with *Solanum lycopersicum* L. (Solanaceae). *Sociobiology* 61, 510–516.
- Bartelli, B.F., Santos, Resende, Nogueira-Ferreira, F.H., A.O., 2014. Maintenance of colonies and foraging behaviour of *Melipona quadrifasciata* (Hymenoptera, Meliponina) in a greenhouse of *Lycopersicon esculentum* (Solanaceae). *Sociobiology* 61, 60–67.
- Bartomeus, I., Molina, F.P., Hidalgo-Galiana, A., Ortego, J., 2020. Safeguarding the genetic integrity of native pollinators requires stronger regulations on commercial lines. *Ecol. Solut. Evid.* 1, e12012.
- Bates, A.J., Sadler, J.P., Fairbrass, A.J., Falk, S.J., Hale, J.D., Matthews, T.J., 2011. Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *PLoS One* 6, 23459.
- Baudoin, W., Nono-Womdim, R., Lutaladio, N., Hodder, A., Castilla, N., Leonardi, C., De Pascale, S., Qaryouti, M. and Duffy, R., 2013. Good agricultural practices for greenhouse vegetable crops: principles for mediterranean climate areas. *FAO Plant Production and Protection Paper No. 217*.
- Baudoin, W., Nersisyan, A., Shamilov, A., Hodder, A., Gutierrez, D., De Pascale, S., Nicola, S., Gruda, N., Urban, L., Tany, J., 2017. Good Agricultural Practices for greenhouse vegetable production in the South East European countries. *FAO Plant Production and Protection Paper No. 230*.

- Bell, M.C., Spooner-hart, R.N., Haigh, A.M., 2006. Pollination of greenhouse tomatoes by the Australian bluebanded Bee *Amegilla (Zonamegilla) holmesi* (Hymenoptera: Apidae). *J. Econ. Entomol.* 99, 437–442.
- Bezabih, G., Gebretsadikan, K., 2014. Managed honeybees (*Apis mellifera* L.) increase onion (*Allium cepa*) seed yield and quality. *Livestock Research for Rural Development* 26, 1.
- Birmingham, A.L., Winston, M.L., 2004. Orientation and drifting behaviour of bumblebees (Hymenoptera: Apidae) in commercial tomato greenhouses. *Can. J. Zool.* 82, 52–59.
- Blacqui re, T., van der Aa-Furn e, J., Cornelissen, B., Donders, J., 2006. Behaviour of honey bees and bumble bees beneath three different greenhouse claddings. In: *Proc. Neth. Entomol. Soc. meeting* 17, 93–102.
- Bomfim, I.G.A., De, M., Bezerra, A.D., Nunes, A.C., De Arago, F.A.S., Freitas, B.M., 2014. Adaptive and foraging behavior of two stingless bee species (Apidae: Meliponini) in greenhouse mini watermelon pollination. *Sociobiology* 61, 502–509.
- Briscoe, A.D., Chittka, L., 2001. The evolution of color vision in insects. *Annu. Rev. Entomol.* 46, 471–510.
- Castilla, N., 2002. Current situation and future prospects of protected crops in the Mediterranean region. *Acta Hortic.* 582, 135–147.
- Cauich, O., Javier, J.G., Quezada-eu n, N., Macias-macias, J.O., Reyes-oregel, V., Medina-peralta, S., Parra-tabla, V., 2004. Behavior and pollination efficiency of *Nannotrigona perilampoides* (Hymenoptera: Meliponini) on greenhouse tomatoes (*Lycopersicon esculentum*) in subtropical M xico. *J. Econ. Entomol.* 97, 475–481.
- , 2004CELLI, G; GIORDANI, G (1981) Importanza economica e biologica dell'ape (*Apis mellifera* L.) per la fruttificazione del melone (*Cucumis melo* L.) in coltura protetta. *Bollettino dell' Instituto di Entomologia della Universita di Bologna* 36: 91–114.
- Cessna, A.J., Wolf, T.M., Stephenson, G.R., Brown, R.B., 2005. Pesticide movement to field margins: routes, impacts and mitigation. *Field weed, boundary habitats: implications for weed. Insect Dis. Manage* 1, 69–112.
- Chang, Y., Lee, M., Mah, Y., 2001. Pollination on strawberry in the vinyl house by *Apis mellifera* L. and *A. cerana* Fab. *Acta Hortic.* 561, 257–262.
- Clement, S.L., Hellier, B.C., Elbersen, L.R., Staska, R.T., Evans, M.A., 2007. Flies (Diptera: Muscidae: Calliphoridae) are efficient pollinators of *Allium ampeloprasum* L. (Alliaceae) in field cages. *J. Econ. Entomol.* 100, 131–135.
- Collett, M., Chittka, L., Collett, Thomas, S., 2013. Spatial memory in insect navigation. *Curr. Biol.* 23, 789–800.
- Cook, D.F., Deyl, R.A., Mickan, B.S., Howse, E.T., 2020. Yield of southern highbush blueberry (*Vaccinium corymbosum*) using the fly Calliphora albifrontalis (Diptera: Calliphoridae) as a pollinator. *Austral Entomol.* 59, 345–352.
- Cook, R., Calvin, L., 2005. Greenhouse Tomatoes Change the Dynamics of the North American Fresh Tomato Industry Economic Research Report Number 2. Economic Research Service, United States Department of Agriculture.
- Corbet, S.A., 1990. Pollination and the weather. *Isr. J. Bot.* 39, 13–30.
- Currah, L., Ockendon, D.J., 1984. Pollination activity by blowflies and honeybees on onions in breeders' cages. *Ann. Appl. Biol.* 105, 167–176.
- Cutting, B.T., Evans, L.J., Paugam, L.I., McBrydie, H.M., Jesson, L.K., Pomeroy, N., Janke, M., Jacob, M., Pattemore, D.E., 2018. Managed bumble bees are viable as pollinators in netted kiwifruit orchards. *N. Z. Plant Prot.* 71, 214–220.
- da Silva, M.A., Ferreira, N.D.S., Teixeira-Souza, V.H.D.S., Maia-Silva, C., de Oliveira, F.D. A., Hrcir, M., 2017. On the thermal limits for the use of stingless bees as pollinators in commercial greenhouses. *J. Apic. Res.* 56, 81–90.
- Dag, A., 2008. Bee pollination of crop plants under environmental conditions unique to enclosures. *J. Apic. Res.* 47, 162–165.
- Dag, A., Eiskowitch, D., 1995. The influence of hive location on honeybee foraging activity and fruit set in melons grown in plastic greenhouses. *Apidologie* 26, 511–519.
- Dag, A., Eiskowitch, D., 1999. Ventilation of greenhouses increases honey bee foraging activity on melon, *Cucumis melo*. *J. Apic. Res.* 38, 169–175.
- Dag, A., Eiskowitch, D., 2000. The effect of carbon dioxide enrichment on nectar production in melons under greenhouse conditions. *J. Apic. Res.* 39, 88–89.
- Danka, R.G., Sylvester, H.A., Boykin, D., 2006. Environmental influences on flight activity of USDA–ARS Russian and Italian stocks of honey bees (Hymenoptera: Apidae) during almond pollination. *J. Econ. Entomol.* 99, 1565–1570.
- Dedej, S., Delaplane, K.S., 2003. Honey bee (Hymenoptera: Apidae) pollination of rabbiteye blueberry *Vaccinium ashei* var. 'Climax' is pollinator density-dependent. *J. Econ. Entomol.* 96 (4), 1215–1220. Aug 1.
- Del Sarto, M.C.L., Peruquetti, R.C., Campos, L.A.O., 2005. Evaluation of the Neotropical stingless bee *Melipona quadrifasciata* (Hymenoptera: Apidae) as pollinator of greenhouse tomatoes. *J. Econ. Entomol.* 98, 260–266.
- Desneux, N., Decourtye, A., Delpuech, J.-M., 2007. The sublethal effects of pesticides on beneficial arthropods. *Annu. Rev. Entomol.* 52, 81–106.
- Di Pasquale, G., Salignon, M., Le Conte, Y., Belzuces, L.P., Decourtye, A., Kretschmar, A., Suchail, S., Brunet, J.L., Alaux, C., 2013. Influence of pollen nutrition on honey bee health: Do pollen quality and diversity matter? *PLoS One* 8, 72016.
- Dorey, J.B., Fagan-Jeffries, E.P., Stevens, M.I., Schwarz, M.P., 2020. Morphometric comparisons and novel observations of diurnal and low-light-foraging bees. *JHR* 79, 117–144.
- dos Santos, S.A., Roselino, A.C., Hrcir, M., Bego, L.R., 2009. Pollination of tomatoes by the stingless bee *Melipona quadrifasciata* and the honey bee *Apis mellifera* (Hymenoptera, Apidae). *Genet. Mol. Res.* 8, 751–757.
- dos Santos, S.A.B., Roselino, A.C., Bego, L.R., 2008. Pollination of cucumber, *Cucumis sativus* L. (Cucurbitales: Cucurbitaceae), by the stingless bees *Scaptotrigona* aff. *deplis* Moure and *Nannotrigona testaceicornis* Lepelletier (Hymenoptera: Meliponini) in greenhouses. *Neotrop. Entomol.* 37, 506–512.
- Dyer, A.G., Chittka, L., 2004. Bumblebee search time without ultraviolet light. *J. Exp. Biol.* 207, 1683–1688.
- Evans, L.J., Cutting, B.T., Jochym, M., Janke, M.A., Felman, C., Cross, S., Jacob, M., Goodwin, M., 2019. Netted crop covers reduce honeybee foraging activity and colony strength in a mass flowering crop. *Ecol. Evol.* 9, 5708–5719.
- Evans, L.J., Jesson, L., Read, S.F.J., Jochym, M., Cutting, B.T., Gayrard, T., Jammes, M.A. S., Roumier, R., Howlett, B.G., 2021. Key factors influencing forager distribution across macadamia orchards differ among species of managed bees. *Basic. Appl. Ecol.* 53, 74–85.
- Foley, K., Fazio, G., Jensen, A.B., Hughes, W.O.H., 2012. Nutritional limitation and resistance to opportunistic *Aspergillus* parasites in honey bee larvae. *J. Invertebr. Pathol.* 111, 68–73.
- Free, J.B., 1993. *Insect Pollination of Crops*. Academic Press.
- Free, J.B., Racey, P.A., 1966. The pollination of *Freesia refracta* in glasshouses. *J. Apic. Res.* 5, 177–182.
- Free, J.B., Spencer-Booth, Y., 1961. The effect of feeding sugar syrup to honey-bee colonies. *J. Agric. Sci.* 57, 147–151.
- Frisch, K., 1967. *The Dance Language and Orientation of Bees*. Oxford University Press, London.
- Fry, S.N., Wehner, R., 2002. Honey bees store landmarks in an egocentric frame of reference. *J. Comp. Physiol. A.* 187, 1009–1016.
- Goodell, K., 2003. Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. *Oecologia* 134, 518–527.
- Goodwin, R.M., Houten, A.T., 1991. Feeding sugar syrup to honey bee (*Apis mellifera*) colonies to increase kiwifruit (*Actinidia deliciosa*) pollen collection: effects of frequency, quantity and time of day. *J. Apic. Res.* 30, 41–49.
- Goubara, M., Takasaki, T., 2003. Flower visitors of lettuce under field and enclosure conditions. *Appl. Entomol. Zool.* 38, 571–581.
- Gullino, M.L., Albajes, R., Nicot, P.C. (Eds.), 2020. *Integrated Pest and Disease Management in Greenhouse Crops*. Springer, Switzerland.
- Greco, M.K., Spooner-Hart, R.N., Beattie, G.A.C., Barchia, I., Holford, P., 2011a. Australian stingless bees improve greenhouse *Capsicum* production. *J. Apic. Res.* 50, 102–115.
- Greco, M.K., Spooner-Hart, R.N., Beattie, G.A.C., Barchia, I., Holford, P., 2011b. Stocking rates of *Trigona carbonaria* for the pollination of greenhouse capsicums. *J. Apic. Res.* 50, 299–305.
- George, R., 2009. *Vegetable Seed Production*, 3rd edition.. CABI, Wallingford.
- Grewal, H.S., Maheshwari, B., Parks, S.E., 2011. Water and nutrient use efficiency of a low-cost hydroponic greenhouse for a cucumber crop: an Australian case study. *Agric. Water Manag.* 98, 841–846.
- Hall, M.A., Jones, J., Rocchetti, M., Wright, D., Rader, R., 2020. Bee visitation and fruit quality in berries under protected cropping vary along the length of polytunnels. *J. Econ. Entomol.* 113, 1337–1346.
- Hendriksma, H., Shafir, S., 2016. Honey bee foragers balance colony nutritional deficiencies. *Behav. Ecol. Sociobiol.* 70, 509–517.
- Higo, H.A., Rice, N.D., Winston, M.L., B., L., 2004. Honey bee (Hymenoptera: Apidae) distribution and potential for supplementary pollination in commercial tomato greenhouses during winter. *J. Econ. Entomol.* 97, 163–170.
- Hikawa, M., Miyanaaga, R., 2009. Effects of pollination by *Melipona quadrifasciata* (Hymenoptera: Apidae) on tomatoes in protected culture. *Appl. Entomol. Zool.* 44, 301–307.
- Hil rio, S.D., Imperatriz-Fonseca, V.L., Kleinert, A., 2000. Flight activity and colony strength in the stingless bee *Melipona bicolor bicolor* (Apidae, Meliponinae). *Rev. Bras. De Biol.* 60, 299–306.
- Hogendoorn, K., Coventry, S., Keller, M.A., 2007. Foraging behaviour of a blue banded bee, *Amegilla chlorocyanea* in greenhouses: Implications for use as tomato pollinators. *Apidologie* 38, 86–92.
- Hogendoorn, K., Gross, C.L., Sedgley, M., Keller, M.A., 2006. Increased tomato yield through pollination by native Australian *Amegilla chlorocyanea* (Hymenoptera: Anthophoridae). *J. Econ. Entomol.* 99, 828–833.
- Hogendoorn, K., Steen, Z., Schwarz, M.P., 2000. Native Australian carpenter bees as a potential alternative to introducing bumble bees for tomato pollination in greenhouses. *J. Apic. Res.* 39, 67–74.
- Houbaert, D., Jacobs, F.J., 1992. Accelerated fruit setting of tomatoes by insect pollination. In: *Bees for pollination. Proc. EC Workshop*, 207–218.
- Howlett, B.G., 2012. Hybrid carrot seed crop pollination by the fly *Calliphora vicina* (Diptera: Calliphoridae). *J. Appl. Entomol.* 136, 421–430.
- Howlett, B.G., Gee, M., 2019. The potential management of the drone fly (*Eristalis tenax*) as a crop pollinator in New Zealand. *N. Z. Plant. Prot.* 72, 221–230.
- Iselin, W.A., Jensen, M.H., Spangler, H.G., 1974. The pollination of melons in air inflated greenhouses by honey bees. *Environ. Entomol.* 3, 664–666.
- Jarlan, A., De Oliveira, D., Gingras, J., 1997. Pollination by *Eristalis tenax* (Diptera: Syrphidae) and seed set of greenhouse sweet pepper. *J. Econ. Entomol.* 90, 1646–1649.
- Jensen, M.H., Malter, A.J., 1995. *Protected Agriculture: A Global Review*. World Bank Publications, Washington DC.
- Kapustjanskij, A., Streinzer, M., Paulus, H.F., Spaeth, J., 2007. Bigger is better: Implications of body size for flight ability under different light conditions and the evolution of alloethism in bumblebees. *Funct. Ecol.* 21, 1130–1136.
- Keasar, T., Shihadeh, S., Shmida, A., Majali, N., Weil, D., Reuven, N., 2007. An evaluation of mini-nucleus honey bee hives for the pollination of honeydew melons in enclosures. *J. Apic. Res.* 46, 264–268.
- Kitta, E., Baillie, A.D., Katsoulas, N., Rigakis, N., Gonz lez-Real, M.M., 2014. Effects of cover optical properties on greenhouse radiative environment and sweet pepper productivity. *Biosyst. Eng.* 122, 115–126.

- Kotilainen, T., Robson, T.M., Hernández, R., 2018. Light quality characterization under climate screens and shade nets for controlled-environment agriculture. *PLoS One* 13, 0199628.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *PNAS* 99, 16812–16816.
- Ladurner, E., Recla, L., Wolf, M., Zelger, R., Burgio, G., 2004. *Osmia cornuta* (Hymenoptera Megachilidae) densities required for apple pollination: A cage study. *J. Apic. Res.* 43, 118–122.
- Ladurner, E., Santi, F., Maccagnani, B., Maini, S., 2002. Pollination of caged hybrid red rape with *Osmia cornuta* and *Apis mellifera* (Hymenoptera Megachilidae and Apidae). *B. Insect* 55, 9–11.
- Leach, H., Wise, J.C., Isaacs, R., 2017. Reduced ultraviolet light transmission increases insecticide longevity in protected culture raspberry production. *Chemosphere* 189, 454–465.
- Lepore, A., Pinzauti, M., 1994. The behaviour of *Apis mellifera* L. and *Osmia cornuta* Latreille in apricot pollination in confined environments Atti XVII Congresso Nazionale Italiano di Entomologia, Udine, Italy, 13–18 Giugno 1994., 851–854.
- Lieten, F., 1993. Fruit misshaping of strawberries: over-visiting. *Fruiteelt* 6, 27–29.
- Lloyd, A., Hamacek, E., George, A., Nissen, R., Waite, G., 2005. Evaluation of exclusion netting for insect pest control and fruit quality enhancement in tree crops. *Acta Hort.* 694, 253–258.
- Magnani, G., Filippi, F., Pinzauti, M., Bonora, M., Calderisi, M., 2007. Activity of bumblebees: (*Bombus terrestris* L.) on tomato grown under differently stabilized covering films. *Colt. Prote* 36, 73–83.
- Mallinger, R.E., Gaines-Day, H.R., Gratton, C., 2017. Do managed bees have negative effects on wild bees?: a systematic review of the literature. *PLoS One* 12, 0189268.
- Maraveas, C., 2020. The sustainability of plastic nets in agriculture. *Sustainability* 12, 3625.
- Martin-Closas, L., Puigdomènech, P., Pelacho, A.M., 2007. Pollination techniques for the improvement of greenhouse tomato production in two crop cycles. *Acta Hort.* 761, 327–332.
- Martínez, F.D., García, F.J.S., Hernández, M.S., Ferre, F.C., 2014. Evaluation of a novel bumble bee pollination station under summer greenhouse conditions. *J. Apic. Res.* 53, 408–412.
- Mditshwa, A., Magwaza, L.S., Tesfay, S.Z., 2019. Shade netting on subtropical fruit: effect on environmental conditions, tree physiology and fruit quality. *Sci. Hortic.* 256, 108556.
- Menzel, R., Greggers, U., 1985. Natural phototaxis and its relationship to color-vision in honeybees. *J. Comp. Physiol. A* 157, 311–321.
- Meyer-Rochow, V.B., 1981. Electrophysiology and histology of the eye of the bumblebee *Bombus hortorum* (L.) (Hymenoptera: Apidae). *J. R. Soc. N. Z.* 11 (2), 123–153.
- Michener, C.D., Michener, C.D., 1974. The Social Behavior of the Bees: A Comparative Study. Harvard University Press.
- Middleton, S., McWaters, A., 1996. Hail Netting to Increase Apple Orchard Productivity. Horticultural Research and Development Corporation NSW, Australia.
- Middleton, S., McWaters, A., 2000. Bee Pollination Under Netting. Pome fruit Australia, pp. 16–24.
- Molet, M., Chittka, L., Raine, N.E., 2009. Potential application of the bumblebee foraging recruitment pheromone for commercial greenhouse pollination. *Apidologie* 40, 608–616.
- Morandin, L.A., Laverty, T.M., Gegear, R.J., Kevan, P.G., 2002. Effect of greenhouse polyethylene covering on activity level and photo-response of bumble bees. *Can. Entomol.* 134, 539–549.
- Morandin, L.A., Laverty, T.M., Kevan, P.G., 2001a. Bumble bee (Hymenoptera: Apidae) activity and pollination levels in commercial tomato greenhouses. *J. Econ. Entomol.* 94, 462–467.
- Morandin, L.A., Laverty, T.M., Kevan, P.G., 2001b. Effect of bumble bee (Hymenoptera: Apidae) pollination intensity on the quality of greenhouse tomatoes. *J. Econ. Entomol.* 94, 172–179.
- Morimoto, T., Kojima, Y., Toki, T., Komeda, Y., Yoshiyama, M., Kimura, K., Nirasawa, K., Kadowaki, T., 2011. The habitat disruption induces immune-suppression and oxidative stress in honey bees. *Ecol. Evol.* 1, 201–217.
- Morison, N., Vaissière, B., Martin, F., Pécaut, P., Cambon, G., 2000. Pollination of globe artichoke (*Cynara scolymus* L.) by honey bees (*Apis mellifera* L.) to produce hybrid seed under enclosure. *Apidologie* 31, 115–128.
- Nicodemo, D., Malheiros, E.B., Jong, D.D., Couto, R.H.N., 2013. Enhanced production of parthenocarpic cucumbers pollinated with stingless bees and Africanized honey bees in greenhouses. *Semin.: Ciências Agrar.* 34, 3625.
- Nordey, T., Basset-Mens, C., De Bon, H., Martin, T., Déletré, E., Simon, S., Parrot, L., Despretz, H., Huat, J., Biard, Y., Dubois, T., 2017. Protected cultivation of vegetable crops in sub-Saharan Africa: limits and prospects for smallholders. A review. *Agron. Sustain Dev.* 37, 1–20.
- Orbán, L.L., Plowright, C.M.S., Plowright, R.C., 2012. The effect of feeder location on pollen collection by bumble bees in a tomato greenhouse in Ontario, Canada. *J. Econ. Entomol.* 105, 34–39.
- Palma, G., Quezada-Euán, J.J., Meléndez-Ramírez, V., Irigoyen, J., Valdovinos-Núñez, G. R., Rejón, M., 2008a. Comparative efficiency of *Nannotrigona perillampoides*, *Bombus impatiens* (Hymenoptera: Apoidea), and mechanical vibration on fruit production of enclosed habanero pepper. *J. Econ. Entomol.* 101, 132–138.
- Palma, G., Quezada-Euán, J.J.G., Reyes-Oregel, V., Meléndez, V., Moo-Valle, H., 2008b. Production of greenhouse tomatoes (*Lycopersicon esculentum*) using *Nannotrigona perillampoides*, *Bombus impatiens* and mechanical vibration (Hym.: Apoidea). *J. Appl. Entomol.* 132, 79–85.
- Palmer-Jones, T., Forster, I.W., 1972. Measures to increase the pollination of lucerne (*Medicago sativa* Linn.). *N. Z. J. Agric. Res.* 15, 186–193.
- Parolin, P., Bresch, C., Desneux, N., Brun, R., Bout, A., Boll, R., Poncet, C., 2012. Secondary plants used in biological control: a review. *Int. J. Pest Manage.* 58, 91–100.
- Parks, S., Spohr, L., Olesen, T., Jarvis, J., 2019. The effect of environmental control and plant density on cucumber crop performance in Australian conditions. *Fruits* 74, 66–72.
- Paydas, S., Eti, S., Kaftanoglu, O., Yasa, E., Derin, K., 1998. Effects of pollination of strawberries grown in plastic greenhouses by honeybees and bumblebees on the yield and quality of the fruits. *Acta Hort.* 513, 443–452.
- Payton Miller, T.L., Rebeck, E.J., 2018. Banker plants for aphid biological control in greenhouses. *J. Integr. Pest Man* 9, 9.
- Pinchinat, B., Bilinski, M., Ruszkowski, A., 1979. Possibilities of applying bumble bees as pollinator vectors in tomato F1 hybrid seed production. *Proc. Fourth. Int. Symp. on Pollinat.* 1978., Maryland, 73–90.
- Pineda, A., Marcos-García, M.Á., 2008a. Evaluation of several strategies to increase the residence time of *Episyrphus balteatus* (Diptera:Syrphidae) releases in sweet pepper greenhouses. *Ann. Appl. Biol.* 152, 271–276.
- Pineda, A., Marcos-García, M.Á., 2008b. Use of selected flowering plants in greenhouses to enhance aphidophagous hoverfly populations (Diptera:Syrphidae). *Ann. Soc. Entomol. Fr.* 44, 487–492.
- Pineda, A., Marcos-García, M.Á., 2008c. Seasonal abundance of aphidophagous hoverflies (Diptera: Syrphidae) and their population levels in and outside Mediterranean sweet pepper greenhouses. *Ann. Entomol. Soc. Am.* 101, 384–391.
- Pinzauti, M., 1994. Pollinator behaviour and activity in colonies of *Apis mellifera* in confined environments. *Ethol. Ecol. Evol.* 6, 101–106.
- Pinzauti, M., Lazzarini, D., Felicioli, A., 1997. Preliminary investigation of *Osmia cornuta* Latr. (Hymenoptera, Megachilidae) as a potential pollinator for blackberry (*Rubus fruticosus* L.) under confined environment. *Acta Hort.* 437, 329–334.
- Plowright, C.M.S., O'Connell, C.E., Roberts, L.J., Reid, S.L., 1995. The use of proximal and distal cues in nest entrance recognition by bumble bees. *J. Apic. Res.* 34, 57–64.
- Pomeroy, N., Fisher, R.M., 2002. Pollination of kiwifruit (*Actinidia deliciosa*) by bumble bees (*Bombus terrestris*): Effects of bee density and patterns of flower visitation. *N. Z. Entomol.* 25, 41–49.
- Popsimonova, G., Benko, B., Karic, L., Gruda, N., 2019. 8989849. FAO Good agricultural practices for greenhouse vegetable production in the South East European countries.
- Potts, S.G., Neumann, P., Vaissière, B., Vereecken, N.J., 2018. Robotic bees for crop pollination: Why drones cannot replace biodiversity. *Sci. Total Environ.* 642, 665–667.
- Rao, S., Stephen, W.P., Kimoto, C., DeBano, S.J., 2011. The status of the 'red-listed' *Bombus occidentalis* (Hymenoptera: Apiformes) in northeastern Oregon. *Northwest Sci.* 85 (1), 64–67.
- Reddy, P.P., 2016. Sustainable Crop Protection under Protected Cultivation. Springer, Singapore.
- Renquist, S., 2005. An evaluation of blueberry cultivars grown in plastic tunnels in Douglas County, Oregon. *Int. J. Fruit. Sci.* 5, 31–38.
- Retamal-Salgado, J., Bastías, R.M., Wilckens, R., Paulino, L., 2015. Influence of microclimatic conditions under high tunnels on the physiological and productive responses in blueberry O'Neal. *Chilean. J. Agric. Res.* 75, 291–297.
- Roman, A., Szczesna, N., 2008. Assessment of the flying activity of the buff-tailed bumblebee (*Bombus terrestris* L.) on greenhouse-grown tomatoes. *J. Apic. Sci.* 52, 93–101.
- Roubik, D., 1989. Ecology and Natural History of Tropical Bees. Cambridge University Press, New York.
- Sabara, H.A., Winston, M.L., 2003. Managing honey bees (Hymenoptera:Apidae) for greenhouse tomato pollination. *J. Econ. Entomol.* 96, 547–554.
- Sáez, A., Morales, C.L., Ramos, L.Y., Aizen, M.A., 2014. Extremely frequent bee visits increase pollen deposition but reduce drupelet set in raspberry. *J. Appl. Ecol.* 51, 1603–1612.
- Saturni, F.T., Jaffé, R., Metzger, J.P., 2016. Landscape structure influences bee community and coffee pollination at different spatial scales. *Agric. Ecosyst. Environ.* 235, 1–12.
- Silva-Neto, C.D.M.E., Ribeiro, A.C.C., Gomes, F.L., Melo, A.P.C.D., Oliveira, G.M.D., Faquinello, P., Franceschinelli, E.V., Nascimento, A.D.R., 2019. The stingless bee mandacaia (*Melipona quadrifasciata* Lepelletier) increases the quality of greenhouse tomatoes. *J. Apic. Res.* 58, 9–15.
- Spaethe, J., 2003. Interindividual variation of eye optics and single object resolution in bumblebees. *J. Exp. Biol.* 206, 3447–3453.
- Stamps, R.H., 2009. Use of colored shade netting in horticulture. *HortScience* 44, 239–241.
- Stanley, D.A., Garratt, M.P.D., Wickens, J.B., Wickens, V.J., Potts, S.G., Raine, N.E., 2015. Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature* 528, 548–550.
- Stavert, J.R., Pattemore, D.E., Bartomeus, I., Gaskett, A.C., Beggs, J.R., 2018. Exotic flies maintain pollination services as native pollinators decline with agricultural expansion. *J. Appl. Ecol.* 55, 1737–1746.
- Stelzer, R.J., Chittka, L., Carlton, M., Ings, T.C., 2010. Winter active bumblebees (*Bombus terrestris*) achieve high foraging rates in urban Britain. *PLoS One* 5 (3), 9559.
- Stewart, X.C., Rojas, E.S., Gleason, M.L., 2010. Influence of row covers on muskmelon pollination in the absence of bacterial wilt. *Phytopathology* 100, 3340.
- Strange, J.P., 2015. *Bombus huntii*, *Bombus impatiens*, and *Bombus vosnesenskii* (Hymenoptera: Apidae) pollinate greenhouse-grown tomatoes in western North America. *J. Econ. Entomol.* 108, 873–879.
- Taylor, G.J., Tichit, P., Schmidt, M.D., Bodey, A.J., Rau, C., Baird, E., 2019. Bumblebee visual alloverly results in locally improved resolution and globally improved sensitivity. *Elife* 8, e40613.

- Tichit, P., 2021. The Visual Ecology of Bees - Tales of Diverse Eyes and Behaviours. Lund University, Lund (Phd thesis).
- Thorp, R.W., Strickler, K., Cane, J.H., 2003. Bumble bees (Hymenoptera: Apidae): commercial use and environmental concerns. For nonnative crops, whence pollinators of the future 21–40.
- Vaissiere, B.E., Froissart, R., 1996. Pollination of cantaloupes under spunbonded row cover by honey bees (Hymenoptera: Apidae) in West Africa. *J. Econ. Entomol.* 89, 1213–1222.
- Vaissiere, B.E., Morison, N., Crete, X., Ferre, G., Matti, M., Vilain, J., 2000. Incidence des filets paragrele sur les abeilles et la pollinisation des pommiers (Effects of nets against hail on honeybees and the pollination of apple trees). *Arboric. Fruit.* 544, 19–25.
- van der Kooi, C.J., Stavenga, D.G., Arikawa, K., Belušić, G., Kelber, A., 2021. Evolution of insect color vision: From spectral sensitivity to visual ecology. *Annu. Rev. Entomol.* 66, 435–461.
- van der Sluijs, J.P., Simon-Delso, N., Goulson, D., Maxim, L., Bonmatin, J.M., Belzunces, L.P., 2013. Neonicotinoids, bee disorders and the sustainability of pollinator services. *Curr. Opin. Environ. Sustain* 5, 293–305.
- van Kooten, O., Heuvelink, E., Stanghellini, C., 2006. New developments in greenhouse technology can mitigate the water shortage problem of the 21st century. *Acta Hortic.* 767, 45–52.
- van Rijn, P.C.J., Kooijman, J., Wäckers, F.L., 2013. The contribution of floral resources and honeydew to the performance of predatory hoverflies (Diptera: Syrphidae). *Biol. Control.* 67, 32–38.
- Velthuis, H.H., Van Doorn, A., 2006. A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. *Apidologie* 37, 421–451.
- Wang, Z., Cang, T., Wu, S., Wang, X., Qi, P., Wang, X., Zhao, X., 2018. Screening for suitable chemical acaricides against two-spotted spider mites, *Tetranychus urticae*, on greenhouse strawberries in China. *Ecotoxicol. Environ. Saf.* 163, 63–68.
- Whittington, R., Winston, M.L., 2003. Are bumble bee colonies in tomato greenhouses obtaining adequate nutrition? *Can. Entomol.* 135, 883–892.
- Yang, X., Miyako, E., 2020. Soap bubble pollination. *iScience* 23, 101188.
- Zaitoun, S.T., Al-Ghzawi, A.A.-M., Shannag, H.K., Al-Tawaha, A.R.M., 2006. Comparative study on the pollination of strawberry by bumble bees and honeybees under plastic house conditions in Jordan valley. *J. Food Agric. Environ.* 4, 237–240.