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Review

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

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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.

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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.

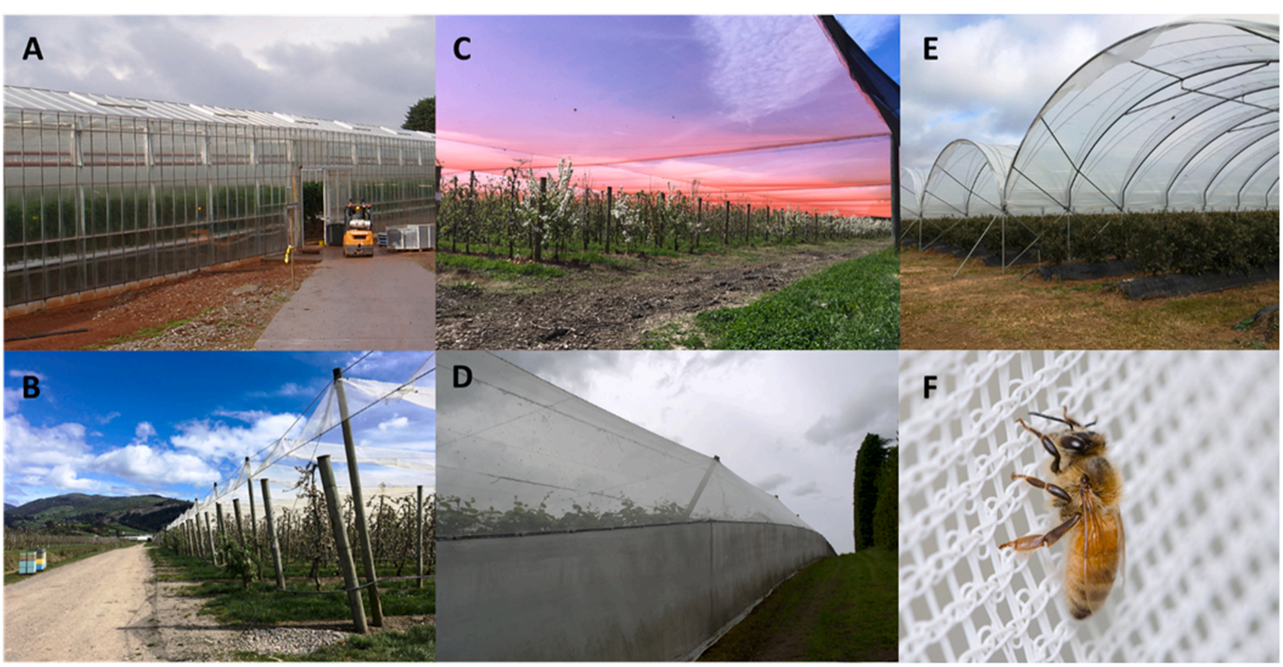

Fig. 1. Different types of covers and covered systems used to protect commercial crops: (a) tomatoes in a climate-controlled glasshouse; (b) apples under white and (c) coloured hail netting; (d) kiwifruit fully enclosed with hail netting and wind cloth; (e) blueberries in polytunnels; (f) a honey bee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

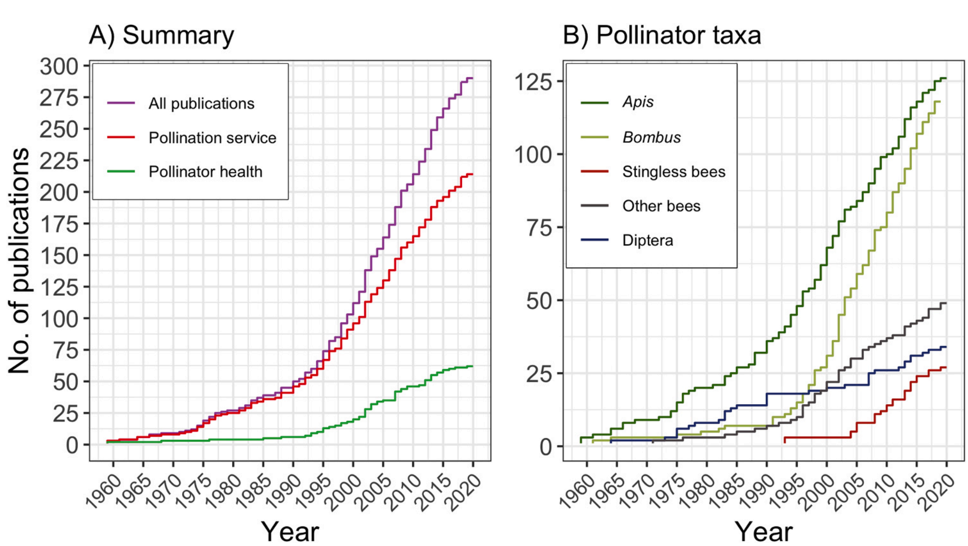

Fig. 2. Cumulative number of relevant publications per year with main topics related to (A) pollination services and pollinator health and (B) pollinator taxa in covered cropping.

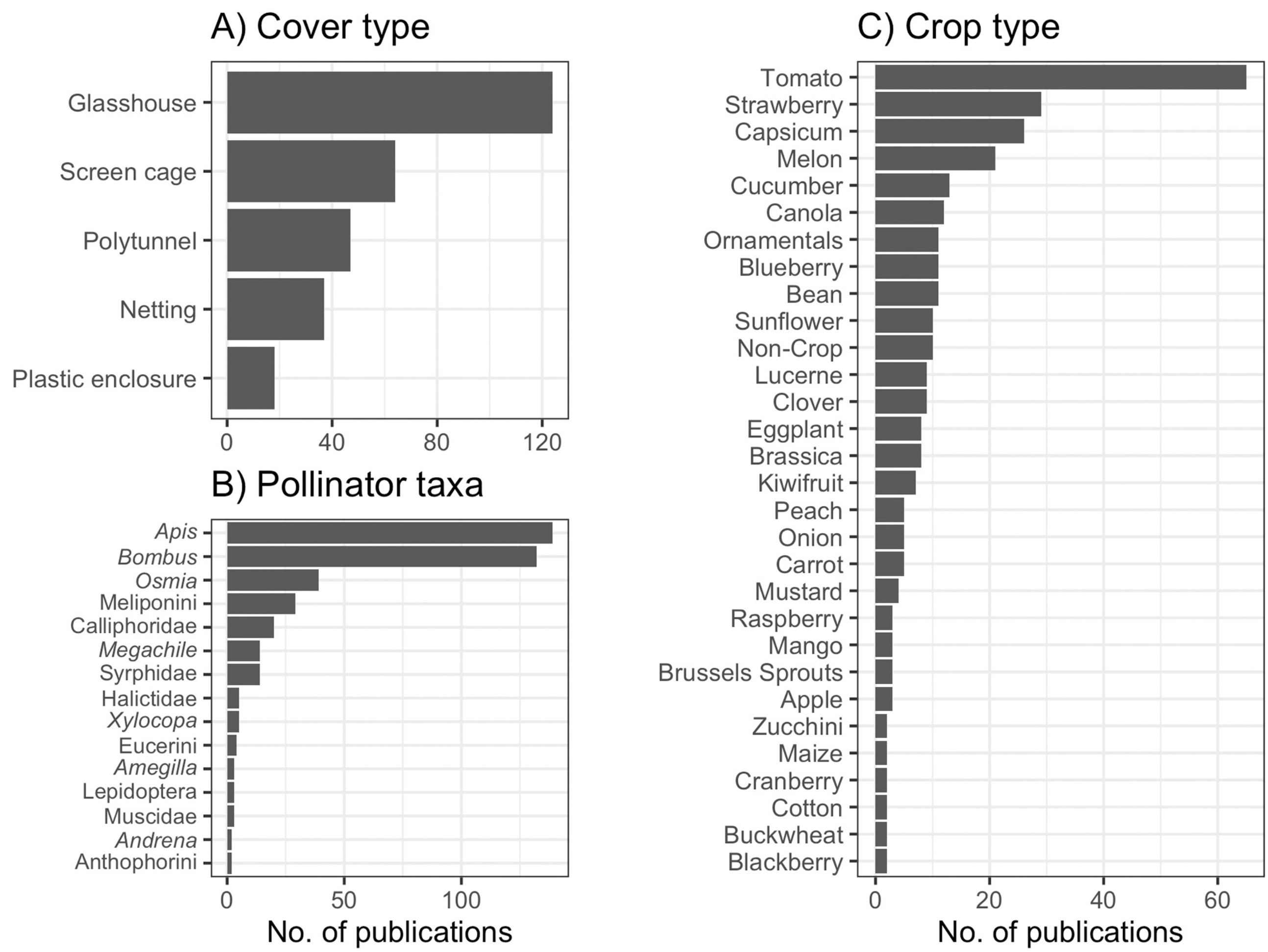

Fig. 3. (A) Frequency distribution of cover types, (B) pollinator taxa, and (C) crop types. Only pollinator taxa and crop species present in more than one study are shown. All taxa and crop species are provided in Table S1.

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 Miyanaga, 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	*Bombus impatiens*	3				1		5				x
	Bombus terrestris		1					1				xG
	Bombus occidentalis	3*										x[†]
Honey bees	*Apis mellifera*	8⁎		1[φ]		1		1				xG
Mason bees	*Osmia cornuta*	2			1							x
	Osmia cornifrons				2						x	
	Osmia pumila			1					x			
	Osmia sanrafaelae				1					x		
	Osmia californica		1							x		
Leafcutter bees	*Megachile rotundata*				1							xG
	Megachile concinna				1					x		
	Megachile pacifica				1				x			
Stingless bees	*Tetragonula carbonaria*				1							x
	Austroplebeia australis				1						x	
	Tetragonisca angustula			1								x
	Nannotrigona testaceicornis			1							x	
	Tetragonula minangkabau			1						x		
	Nannotrigona perilampoides	1					2				x	
	Melipona quadrifasciata	2[υ]									x	
	Melipona subnitida	2									x	
	Scaptotrigona sp.		1						x	x	x	
Squash bees	*Eucera pruinosa*	1							x			
Sweat bees	*Lasioglossum apristum*		1							x		
Hover flies	*Episyrphus balteatus*	2	3		1							x
	Eupeodes corollae		1									x
	Sphaerophoria rueppellii		1									x
Blow flies	*Calliphora albifrontalis*	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). [φ]Colonies used were smaller than standard sized colonies (Keasar et al., 2007). [υ] 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.

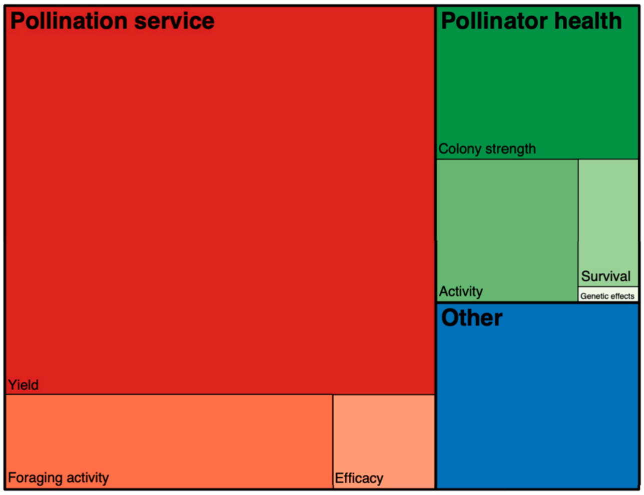

Fig. 4. Tree map showing the proportion of reviewed publications to assess 'pollination service' (orange squares), 'pollinator health' (green squares), and 'other' topics (blue square), and the indicators used. Examples of 'other' topics include virus transmission, pollinator behaviour unrelated to foraging/pollination, 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 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:* Bomfin 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 ≥ 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 glasseshouses (Roman and Szczesna, 2008). Other species of blowflies (*C. vomitoria, Lucilia caesar and L. sericata*) will forage between

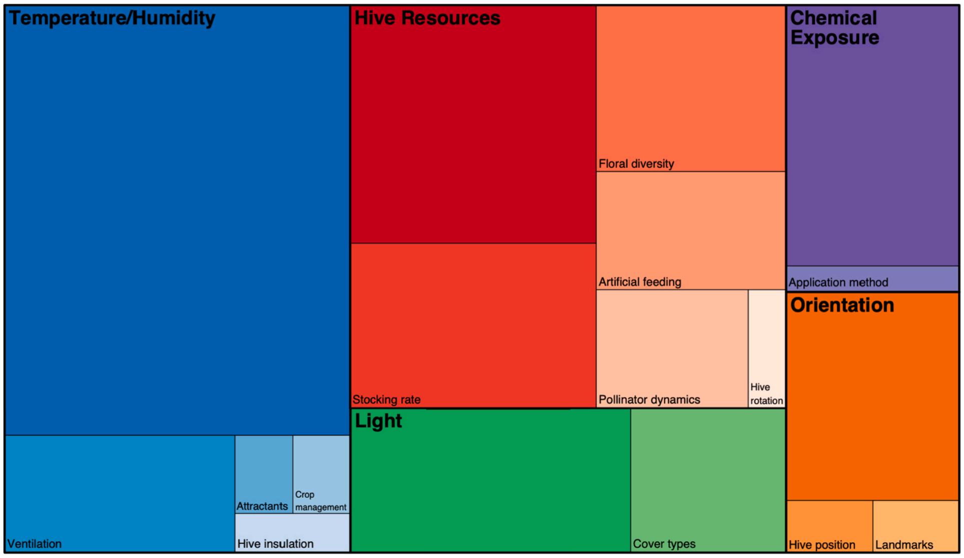

Fig. 5. Tree map showing the proportion of publications considering *factors associated with crop covers* that can negatively affect pollination service and/or pollinator health, and the proportion of publications investigating corresponding *methods of mitigation*. Squares with bold text indicate the 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; Cauich 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; Cauich 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 Gebretsadikan, 2014; Cauich 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 (Cauich 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*: Vaissiere 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	Socking rate	Reference
Strawberries	*Apis mellifera*	10,000–15,000 bees/1000 m of tunnel or glasshouse	Lieten (1993)
Strawberries	*Bombus* sp.	60–100 bees/700–1000 m of tunnel or glasshouse	Lieten (1993)
Green kiwifruit	*B. terrestris*	660 foraging bees/ha	Pomeroy and Fisher (2002)
Gold kiwifruit	*B. terrestris*	914 foraging bees/ha	Cutting et al. (2018)
Tomato	*B. impatiens*	2000 foraging bees ha/day	Morandin et al. (2001a)
Tomato	*Amegilla chlorocyanea*	282 nesting female bees/ha	Hogendoorn et al. (2007)
'Braeburn' apples	*Osmia cornuta*	1 female and 1 male/ tree	Ladurner et al. (2004)
Hybrid red rape	*Osmia cornuta*	1 female and 3 males/ plant	Ladurner et al. (2002)
Capsicum	*Tetragonula carbonaria*	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	*Episyrphus balteatus*	Side walls open vs closed, assessed residence time	+	Pineda and Marcos-García (2008a)
		Eupeodes corolla	Side walls open vs closed, assessed abundance	+	Pineda and Marcos-García (2008c)
		Episyrphus balteatus			
		Sphaerophoria rueppellii			
		Apis mellifera	Tunnels open at end	+	Dag and Eisikowitch (1999)
		Apis mellifera	Screen vent	=	Sabara et al. (2003)
		Apis mellifera	Screen vent	=	Sabara and Winston (2003)
		Apis mellifera	Different types of ventilation	=	Celli and Giordani 1981
	Attractants	*Bombus terrestris*	Recruitment pheromone	+	Molet (2009)
	Crop management	*Apis mellifera*	CO^2 treatment to increase nectar	+	Dag and Eisikowitch (2000)
	Hive insolation	*Bombus terrestris*	Hive shelter	+	Martínez et al. (2014)
Hive resources	Floral diversity	*Osmia pumila*	Floral richness	+	Goodell (2003)
		Episyrphus balteatus	Floral richness	+	van Rijn et al. (2013)
		Episyrphus balteatus	Flowers with more accessible nectar + pollen	+	van Rijn and Wäckers (2013)
		Episyrphus balteatus	Floral diversity	=	Pineda and Marcos-García (2008b)
		Eupeodes corolla	Co-flowering plants	+	Pineda and Marcos-García (2008c)
		Episyrphus balteatus Sphaerophoria rueppellii			
		Apis mellifera	Allowed outside access	+	Vaissiere and Froissart (1996)
		Apis mellifera	Allowed outside access	+	Sabara and Winston (2003)
	Stocking rate	*Bombus terrestris*	Stocking rate for green kiwifruit	+	Pomeroy and Fisher (2002)
		Bombus impatiens	Stocking rate for tomatoes	+	Morandin et al. (2001b)
		Amegilla chlorocyanea	Stocking rate for tomatoes	+	Hogendoorn, Coventry, Keller (2007)
		Bombus terrestris	Stocking rate for tomato seed	+	Pinchinat, Bilinski, Ruszkowski (1979)
		Bombus hypnorum			
		Bombus agrorum			
		Osmia lignaria	Stocking rate for hybrid rap	+	Ladurner, Santi, Maccagnani Maini (2002)
		Apis mellifera			
		Apis mellifera	Number of bees for strawberries	+	Lieten (1993)
		Bombus sp.			
		Tetragonula carbonaria	Stocking rate for capsicums	+	Greco et al. (2011b)
		Bombus terrestris	Stocking rate for gold kiwifruit	+	Cutting et al. (2018)
		Apis mellifera	Density of bees and blueberries	+	Dedej and Delaplane (2003)
	Artificial feeding	*Bombus occidentalis*	Supplementary pollen	=	Whittington and Winston (2003)
		Calliphora albifrontalis	Water provision	=	Cook et al. (2020)
		Apis mellifera	Supplementary pollen	+	Iselin et al. (1974)
		Apis mellifera	Sucrose feeding to increase pollen collection	+	Free and Racey (1966)
		Bombus impatiens	Feeder location	+	Orbán, Plowright, Plowright (2012)
	Pollinator dynamics	*Apis mellifera*	Small colonies	+	Keasar et al. (2007),Pinzauti (1994)
		Episyrphus balteatus	Younger adults	+	Pineda and Marcos-García (2008a)
		Apis mellifera	Amount of brood	=	Sabara et al. (2003)
		Apis mellifera	Amount of brood	=	Sabara and Winston (2003)
	Hive rotation	*Apis mellifera*	Hive rotation	-(pollination)	Palmer-Jones and Forster (1972)
Light	Cover type	*Bombus impatiens*	Assessed activity and loss	+	Morandin et al. (2001a)
		Bombus impatiens	Assessed activity level and photo-response	=	Morandin et al. (2002)
		Bombus terrestris	Assessed activity	+	Magnani et al. (2007)
		Apis mellifera	Assessed colony strength	–	Vaissiere et al. (2000)
Orientation	Hive position	*Apis mellifera*	North vs South placement	+	Dag and Eisikowitch (1995)
	Landmarks	*Bombus occidentalis*	Assessed return to colonies	=	Birmingham and Winston (2004)
		Bombus impatiens			
Chemical exposure	Application method	*Bombus terrestris*	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 (Birmingham 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

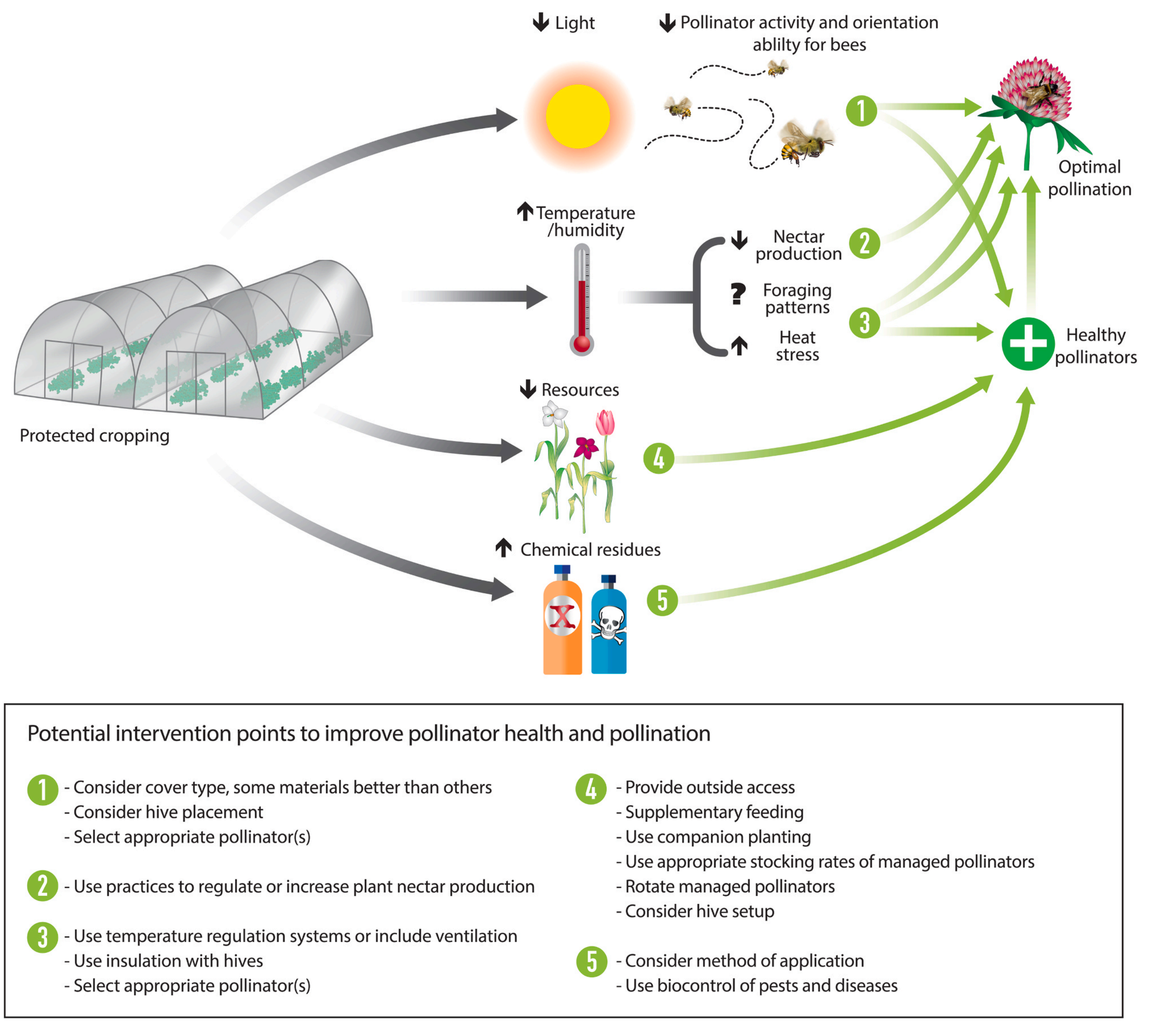

Fig. 6. Possible effects for pollinators and/or pollination that can occur in covered cropping systems and potential intervention points for mitigating these effects (numbers 1–5).

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

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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.

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