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The impact of mass-flowering crops on bee pathogen dynamics

Tina Tuerlings [1], Louella Buydens [1], Guy Smagghe, Niels Piot *

Laboratory of Agrozoology, Department of Plants and Crops, Faculty of Bioscience Engineering, Coupure links 653, Ghent University, Ghent, Belgium

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ABSTRACT

Nearly two fifths of the Earth's land area is currently used for agriculture, substantially impacting the environment and ecosystems. Besides the direct impact through land use change, intensive agriculture can also have an indirect impact, for example by changing wildlife epidemiology. We review here the potential effects of mass-flowering crops (MFCs), which are rapidly expanding in global cropping area, on the epidemiology of known pathogens in bee pollinators. We bring together the fifty MFCs with largest global area harvested and give an overview of their pollination dependency as well as their impact on bee pollinators. When in bloom these crops provide an abundance of flowers, which can provide nutrition for bees and increase bee reproduction. After their short bloom peak, however, the fields turn into green deserts. These big changes in floral availability strongly affect the plant-pollinator network, which in turn affects the pathogen transmission network, mediated by shared flowers. We address this dual role of flowers provided by MFCs, serving as nutritional resources as well as pathogen transmission spots, and bring together the current knowledge to assess how MFCs could affect pathogen prevalence in bee pollinator communities.

1. Introduction

The current epoch, the Anthropocene, is characterized by the unprecedented and often irreversible impact of humans on the planet (Lewis and Maslin, 2015). Landscape alterations for agriculture, currently occupying nearly two-fifths of the earth's land surface (Food and Agriculture Organization of the United Nations (2021)), substantially impact the environment and ecosystems (e.g. Tscharntke et al., 2005). A significant portion of the global cropping area is designated to the cultivation of agricultural crops that provide abundant floral resources during a short, synchronized bloom period of a few weeks, also referred to as mass-flowering crops (MFCs) (Fig. 1 and Table 1).

Up to 90% of flowering plants depend on pollination for successful reproduction, hence most of the MFCs do as well (Ollerton et al., 2011). However, intensively managed MFC monocultures can have a negative impact on the pollinator community (Eeraerts et al., 2017, 2021). Agricultural intensification is seen as one of the main drivers of bee decline (Goulson et al., 2015). As these intensifications are frequently accompanied with the destruction of semi-natural habitat and increased use of fertilizer and pesticides, they often reduce both richness and abundance of non-crop floral resources (Rajaniemi, 2002; Tscharntke et al., 2005; Eeraerts et al., 2017; Proesmans et al., 2019; Raven and Wagner, 2021). However, bee pollinator decline is a multifactorial problem where several main drivers such as pathogens and agricultural intensification can interact, aggravating their negative effect on bees (Goulson et al., 2015), for instance by the synergistic effects of pesticide exposure and pathogen infection (Vidau et al., 2011; Grassl et al., 2018; Harwood and Dolezal, 2020).

Bees, both wild and managed species, are host to an abundance of different pathogens ranging from eukaryotic pathogens to viruses (see e.g. Ravoet et al., 2014; Yañez et al., 2020), mostly with an oral-fecal transmission route (Durrer and Schmid-Hempel, 1994; Graystock et al., 2015; Burnham et al., 2021). Pathogens are naturally present in a dynamic host-pathogen equilibrium (Henson et al., 2009; Rabajante et al., 2015). However, disturbing this equilibrium may result in increasing negative effects exerted by pathogens on their hosts, ultimately resulting in an important role of pathogens as drivers of bee decline (Meeus et al., 2018).

MFCs as a part of intensive agriculture may disturb the host-pathogen dynamics by changing the amount and composition of available natural and agricultural floral resources. These floral resources have a dual role for the presence and impact of pathogens on bees. On the one hand, floral resources provide a spot for pathogen infection, as floral resources are shared by different bees enabling inter- and intra-

* Corresponding author.
E-mail address: niels.piot@ugent.be (N. Piot).
[1] these authors contributed equally.

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species transmission (Durrer and Schmid-Hempel, 1994; Graystock et al., 2015; Figueroa et al., 2019). On the other hand, they provide nutrition needed for the bees' survival, reproduction and host defense mechanisms against pathogen infections.

This dual role is rarely recognized in studies addressing pathogen prevalence in bees. In the past few years, a handful of studies addressed the plant-pollinator network as a means to explain pathogen prevalence (e.g. Figueroa et al., 2020; Graystock et al., 2020; Piot et al., 2020), where shared flowers are a potential hub for pathogen transmission. Other studies, mostly under controlled conditions, looked at the role of nutrition on the impact of pathogens on their host. With this review, we aim to bring together these two aspects and address the potential effects of intensive MFCs on the presence and impact of pathogens in bee pollinators (Fig. 2). In a first part, we discuss how MFCs may impact pathogen transmission, mediated by the floral network, while a second part is focusing on the role of MFCs as a source of nutrition and its consequences for the host defense mechanisms.

2. The effect of MFCs on pathogen transmission via flowers

Most of the pathogens found in bees have an oral-fecal transmission route (Singh et al., 2010; Tian et al., 2018; Figueroa et al., 2019; Yañez et al., 2020), where infective particles are shed via the feces and picked up by a naive host, who can subsequently become infected. As many pollinators are somehow connected with one another through shared floral resources, inter- and intra-species transmission may occur via flowers. Here, infected hosts can leave behind infective particles on a flower during visitation, either through defecation or external vectoring (where the particles adhere to the outside of the bee) (Figueroa et al., 2019; Piot et al., 2020). These infective particles can be taken up by the next visitor of the flower and induce an infection. This route of transmission where shared flowers act as transmission hubs has been shown for multiple pathogens, both single-cell pathogens as well as viruses (Durrer and Schmid-Hempel, 1994; Graystock et al., 2015; Burnham et al., 2021).

Plant-pollinator networks give an informative (graphical) representation of the interactions between pollinators, the flowers they visit and the interaction-specific visitation frequencies for a certain period and location (Bascompte et al., 2003; Memmott et al., 2004). Given the flower-mediated nature of transmission for multiple bee pathogens, plant-pollinator networks can shape the route of pathogen transmission in pollinator communities (Proesmans et al., 2021). Plant-pollinator network analyses showed that generalist bees can connect different bee species through their broad diet, which gives them a pivotal role in the transmission of pathogens (Figueroa et al., 2020; Piot et al., 2020). Networks with a higher connectance (i.e. the proportion of realized links between the present plant and bee species) can display lower probabilities of disease transmission (Figueroa et al., 2020). In these high connectance networks, an infected bee would visit more plant species and disseminate infection across more flower species (instead of a similar number of flowers from a single plant species), which in turn would lower the likelihood of a susceptible bee encountering a contaminated flower (Benadi and Pauw, 2018; Figueroa et al., 2020). Additionally, bee densities and bee species traits, such as specialism, body size and foraging range, can also shape pathogen prevalence (Cohen et al., 2021), possibly by influencing inter- or intra-species encounters on the same flower, resulting in altered chances of pathogen transmission.

The impact of MFCs on floral resources is twofold. When in bloom, they significantly increase the amount of available floral resources at a location [e.g. oilseed rape (*Brassica napus*) fields in bloom provide ca. 600 flowers per m^2 (estimated from Pertl et al., 2002 and Kuai et al., 2015)]. After blooming, they transform into a green desert with very few floral rewards. This sharp change in the number of available floral resources may have an effect on the bee pollinator density on these flowers. Consequently, one might hypothesize that this transition significantly alters the present plant-pollinator network and hence pathogen transmission dynamics (Fig. 2 upper part). However, contrasting findings have been reported on the effect of MFCs on bee densities, with studies reporting an increase in bee densities (host concentration), while others show a decrease (host dilution).

2.1. Host density

2.1.1. Host concentration

During bloom, MFCs can attract wild pollinators (Table 1) and increase bee densities in these fields and adjacent habitats (Westphal et al., 2003; Holzschuh et al., 2013). For example, crops like sunflower, oilseed rape and field bean are highly attractive to honey bees, bumble bees and solitary bees (Table 1). In landscapes comprised of MFCs with successive blooming periods, bee densities can increase in the MFC flowering later in the season, as has been observed for bumble bees in sunflower fields when relatively high covers of oilseed rape were blooming first (Riedinger et al., 2014). Next to sequential flowering of MFCs within the same year, successive blooming of MFCs between years may also display a positive effect on bee densities due to higher reproduction (Kallioniemi et al., 2017). Higher bee densities may consequently increase pathogen transmission and prevalence (Fig. 2 upper right). Cohen et al. (2021)

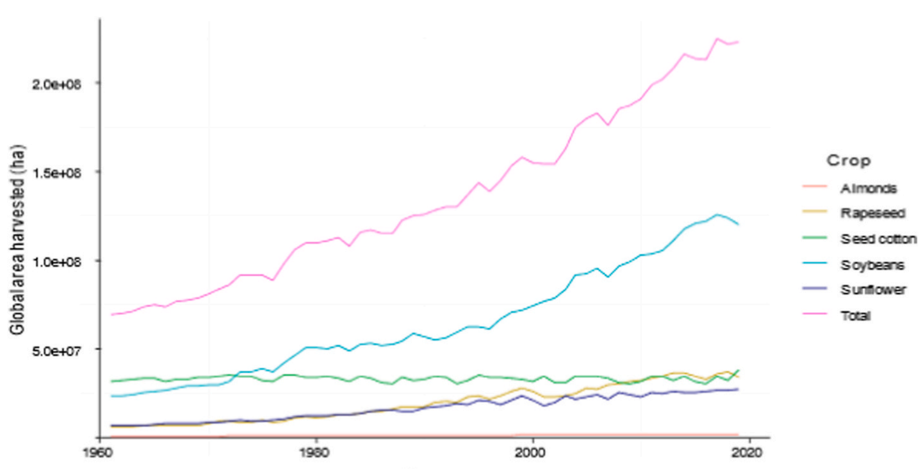

Fig. 1. Chronological trend (1961–2019) of the global land area (ha) used for crops; red: almonds; ochre: rapeseed; green: seed cotton; light blue: soybeans; dark blue: sunflower; purple: the sum of 5 MFCs with biggest global land area used in 2019 (see Table 1); data from the Food and Agriculture Organization of the United Nations (2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
List of fifty mass-flowering crops (MFCs), based on data of the Food and Agriculture Organization of the United Nations, 2021. We selected the MFCs with the largest global area harvested and which met the following criteria: i) flowering peak lasts for maximum 2 months (except for sunflowers), ii) flowers are attractive to bees, and iii) sexual reproduction. MFCs are sorted in decreasing global total area harvested.

Type of (main) plant product	Mass-flowering crop	*Plant species name*	Total area harvested (ha) [17]	Field size (ha) with largest production [154]	Animal pollination, impact on fruit/seed set	Pollinator community [6,8,16]	Blooming period (season)	Blooming time	Attractiveness of flower to bees [8]			
									Nectar to honey bees	Pollen to honey bees	Bumble bees	Solitary bees
Legume	Soybean	*Glycine max, G. soja*	120 501 628	500–1000	increase [6], yield increase associated with an increase of seed number [16]	honey bees (*Apis mellifera*), bumble bees, solitary bees (*Megachile rotundata*)	early summer [25]	50–60 days [25]	+	+	+	+
Fiber	Seed cotton	*Gossypium hirsutum, G. barbadense, G. arboreum, G. herbaceum*	38 640 608	2–5	increase [6], increased fiber and seed production, increased yield quantity and quality [16]	honey bees (*Apis* spp.), bumble bees, solitary bees (*Halictus* spp., *Anthophora* spp., *Xylocopa* spp., *Megachile* spp., *Nomia* spp., *Ptilothrix* spp.), wasps	summer [26]	4–6 weeks [27]	+	–	+	+
Oil	Oilseed rape, canola	*Brassica napus*	34 030 921	100–200	increase [6], increased fruit set, yield, and the number of seeds per pod [16] bee density.	honey bees (*A. mellifera*), bumble bees, solitary bees (*Andrena* spp., *Osmia cornifrons, Osmia lignaria lignari, Osmia rufa, Halictus* spp., *Megachile* spp.), hoverflies; *Episyrphus balteatus, Eristalis tenax*,	winter type: late spring [28]	3–4 weeks [29]	++	++	+	++
Fruit	Almond	*Amygdalus communis*	33066183	100–200	increased nut set and nut yield [129]	honey bees (*A. mellifera*), bumble bees, solitary bees (*Osmia cornuta*), flies	early spring [30]	2–3 weeks [30]	+	++	+	+
Oil, seed	Sunflowers	*Helianthus annuus*	27368766[a]	100–200	increase [6], increased yield, significant role of honey bees [16]	honey bees (*Apis cerana, A. mellifera*), bumble bees, solitary bees (*Halictus* spp., *Dieunomia* spp., *Megachile* spp., *Melissodes* spp., *Svastra* spp., *Xylocopa* spp.), stingless bees (*Trigona iridipennis*)	late summer [31]	8–12 weeks [31]	++	++	++	++
Legume	Cow peas	*Vigna unguiculata*	14447336	1–2	increase [6]	ants, honey bees and bumble bees	autumn [32]	1 day [32]	+	–	+	+
Seed	Sesame seed	*Sesamum indicum*	12821752	2–5	Increased seed yield [132]	honey bees (*A. cerana, A. mellifera*), solitary bees, wasps, flies	mid- to late summer [131]	30–50 days [130]	++	+	N/AV	+
Latex	Rubber	*Hevea brasiliensis*	12339058	<1	150% seed yield increase [14]	stingless bees, small carpenter bees, sweat bees, hoverflies [118]	early spring [34]	a few weeks to months [35]	N/AV	N/AV	N/AV	N/AV
Seed	Cocoa	*Theobroma cacao*	12234311[b]	2–5	increased fruit set [134]	cecidomyiid midges, ceratopogonid midges, stingless bees, sweat bees [133]	late summer to autumn [36]	a week, a few times a year [153]	N/AV	N/AV	N/AV	N/AV
Fruit	Coconut	*Cocos nucifera*	11807156	<1	increase [6]	honey bees, stingless bees	monthly [37]	two weeks [37]	+	+	+	+
Seed	Coffee	*Coffea arabica, C. canephora, C. liberica*	11120498	1–2	increase [6], *C. arabica*: Increased fruit set, *C. canephora*: increased fruit production [16]	honey bees (*Apis dorsata, A. mellifera*), stingless bees (*Trigona [Lepidotrigona] terminata*), solitary bees (*Creightonella frontalis, Xylocopa* spp., *Zonohirsuta dejeanii*)	spring [38]	weeks to months, depending on rain [38]	–	+	N/AV	+

(*continued on next page*)

Table 1 (*continued*)

Type of (main) plant product	Mass-flowering crop	*Plant species name*	Total area harvested (ha) [17]	Field size (ha) with largest production [154]	Animal pollination, impact on fruit/ seed set	Pollinator community [6,8,16]	Blooming period (season)	Blooming time	Attractiveness of flower to bees [8]			
									Nectar to honey bees	Pollen to honey bees	Bumble bees	Solitary bees
Legume	Peas	*Pisum sativum*	9948508[c]	500–1000	higher yield [23]	bumble bees, solitary bees (*Eucera dalmatica, Xylocopa* spp.)	Late spring and summer [39]	2–3 weeks [40]	+	+	+	+
Nut and fruit	Cashew	*Anacardium occidentale*	7585083[d]	2–5	up to 200% yield increase [135]	honey bees (*A. dorsata*, *A. mellifera*), stingless bees, bumble bees, solitary bees (*Centris tarsata*), butterflies, flies, hummingbirds	Late spring, early summer [41,42]	2–3 months [41,42]	+	+	N/AV	N/AV
Legume	Pigeon peas	*Cajanus cajan*	5616153	2–5	seed number and weight increase [136,137]	honey bees (*Apis florea, A. dorsata*), solitary bees (*Megachile* spp., *Xylocopa* spp., *Chalicodoma* spp.)	late spring, early summer [128]	up to a month [128]	+	+	+	+
Fruit	Mango, Guava, Guayaba	*Mangifera indica, Psidium guajava*	5588716[e]	5–10	increase [6]	mango: honey bees, stingless bees (*Trigona*), flies, ants, wasps - guava: honey bees (*A. mellifera*), stingless bees (*Trigona cupira*), bumble bees (*Bombus mexicanus*), solitary bees (*Lasioglossum* spp.)	Mango: winter and early spring [45] Guava: Two to three flowering periods: Early spring late spring, and autumn [43]	mango: 25–30 days flower initiation to full bloom [45] - guava: 4 weeks [44]	N/AV	N/AV	N/AV	N/AV
Fruit	Tomato	*Lycopersicon esculentum*	5030545	2–5	increase [6]	honey bees (*A. mellifera*), stingless bees (*Melipona quadrifasciata, Nannotrigona perliampoides*), bumble bees (*Bombus hypnorum, B. thoracobombus, B. pascuorum, B. sonorus, B. terrestris, B. vosnesenskii*), solitary bees (*Amegilla chlorocyanea, A. zonamegilla), A. holmesi, Xylocopa*)	summer [46]	3 weeks [47]	–	–	+	+
Legume	Lentils	*Lens culinaris*	4800017	<1	no signs of increase, low amount of cross pollination [138]	Honey bees, bumble bees, hover flies [139], *Megachile*	summer [152]	a month [19,48]	+	+	–	+
Fruit	Apple	*Malus domestica*	4717384	10–20	increase [6]	honey bees (*A. cerana*, A. mellifera), bumble bees, solitary bees (*Andrena, Anthophora, O. cornifrons, O. lignaria propinqua, O. rufa, Anthidium, Halictus, Habropoda*), hover flies (*Eristalis cerealis, E. tenax*)	late spring [49]	3–10 days [49]	+	++	+	++
Fruit	Orange	*C. sinensis, C. aurantium*	4060129	2–5	little [6]	honey bees (*A. cerana, A. mellifera),* bumble bees, solitary bees (*Andrena, Xylocopa*)	spring [120]	Up to a month [120]	++	++	+	+
Leaves	Tobacco	*Nicotiana tabacum*	3619118	10–20	N/AV	honey bees [155], hummingbirds	summer to autumn [121]	weeks to months [121]	–	+	+	+

(*continued on next page*)

Table 1 (*continued*)

Type of (main) plant product	Mass-flowering crop	*Plant species name*	Total area harvested (ha) [17]	Field size (ha) with largest production [154]	Animal pollination, impact on fruit/ seed set	Pollinator community [6,8,16]	Blooming period (season)	Blooming time	Attractiveness of flower to bees [8]			
									Nectar to honey bees	Pollen to honey bees	Bumble bees	Solitary bees
Fruit	Watermelon	*Citrullus lanatus*	3084217	10–20	increase [6]	honey bees (*A. cerana*), bumble bees (*Bombus californicus, B. impatiens, B. vosnesenskii*), solitary bees (*Halictus tripartitus, Peponapis pruinosa, Agapostemon, Floridegus, Halictus, Hoplitus, Melissodes*)	late spring - early summer [50]	1 day [50]	+	+	+	+
Fruit	Tangerines, mandarins, clementines, satsumas	*Citrus tangerina, Citrus reticulata*	2756887	5–10	variable effects of added bee pollination [140]	*Andrena* spp., *Xylocopa* spp.	early spring [51,53,55], clementines: spring [54]	citrus trees: several weeks [52]	++	++	+	+
Seed	Okra, gumbo	*Abelmoschus esculentus*	2729811	100–200	increase [6]	honey bees (*A. cerana*), solitary bees (*Halictus* spp.)	summer [56]	1 day [57]	+	+	+	+
Fruit	Plum, greengage, mirabelle, sloe	*Prunus mume, P. domestica, P. spinosa*	2727745[f]	10–20	increase [6]	honey bees (*A. mellifera*), bumble bees, solitary bees (*Osmia lignaria propinqua, Anthophora* spp.), flies	Japanese plum, sloe early spring [58] [61], European plum (greengage): mid-spring [59], mirabelle plum: spring [60]	Japanese plum: 1 month [58]	+	+	+	+
Legume	Field bean (broad bean)	*Vicia faba*	2577201[g]	<1	increase [6]	honey bees (*A. mellifera*), bumble bees (*Bombus lapidarius, B. pascuorum, B. hortorum*), solitary bees (*Anthophora plumipes, Eucera* spp., *Megachile rotundata, Xylocopa* spp.)	spring - early summer [62]	two weeks [63]	++	++	++	+
Fruit	Cucumber, Gherkin	*Cucumis sativus*	2231402	>1000	increase [6], 10% increase in production, larger, heavier, and longer cucumbers [16]	honey bees (*A. mellifera*), bumble bees (*Bombus impatiens*), solitary bees (*Melissodes* spp., *Andrena* spp.)	late spring - summer [64]	2–3 weeks [65]	+	+	+	+
Spice (leaves, seeds, fruit)	Anise, Badian, Fennel, Coriander	*Pimpinella anisum, Illicium verum, Foeniculum vulgare, Coriandrum sativum*	2080000	2–5	Anise: Increasing seed yield, Coriander - higher seed set and yield [16]	Coriander: honey bees (*A. cerana, A. dorsata, A. florea, A. mellifera*), stingless bees, solitary bees Fennel: honey bees (*A. florea, A. mellifera*)	anise: early - midsummer [66], badian: early spring [68], fennel: summer [70], coriander: spring [71]	anise: 20–25 days [67], badian: several months [69], fennel: months [70], coriander: up to one month [72]	+	+	+	+
Fruit	Chile pepper, Red pepper, Bell pepper, Green pepper, Allspice, Pimento	*Capsicum annuum, C. fructescens, Pimenta dioica (syn. P. officinalis, P. dioica)*	1990926[h]	2–5	increase [6], Capsicum annuum: Increased fruit weight, width, volume and quality, increased	honey bees, stingless bees (*Melipona favosa, M. subnitida*), bumble bees (*B. impatiens, B. terrestris*), solitary bees (*O. cornifrons, Megachile rotundata*), hover flies (*Eristalis tenax*), for Pimento: honey bees,	*Capsicum annuum*: early summer [73], *Capsicum fructescens*: late summer [74], *Pimento dioica*: summer [75]	1 day [76]	–	+	++	+

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International Journal for Parasitology: Parasites and Wildlife 18 (2022) 135–147

Table 1 (*continued*)

Type of (main) plant product	Mass-flowering crop	*Plant species name*	Total area harvested (ha) [17]	Field size (ha) with largest production [154]	Animal pollination, impact on fruit/ seed set	Pollinator community [6,8,16]	Blooming period (season)	Blooming time	Attractiveness of flower to bees [8]			
									Nectar to honey bees	Pollen to honey bees	Bumble bees	Solitary bees
					seed weight and quality [16]	*Halictus* spp., *Exomalopsis* spp., *Ceratina* spp.						
Fruit	Eggplant (Aubergine)	*Solanum melongena*	1847787	<1	increase [6]	honey bees (*Apis mellifera*), bumble bees, solitary bees, stingless bees	summer [77]	up to a month [77]	–	–	++	+
Grain	Buckwheat	*Fagopyrum esculentum*	1673478	10–20	up to 50 times increase [141]	honey bees	late summer, early autumn [78]	up to 10 weeks [78]	++	+	+	+
Fruit	Pumpkin, Squash, Gourd, Marrow, Zucchini	*Cucurbita maxima, C. mixta, C. moschata, C. pepo*	1539023	1–2	essential [6]	honey bees (*A. cerana*, *A. mellifera*), stingless bees (*Scaptotrigona depilis*), solitary bees (*Pithitis smaragdula Peponapis limitaris, P. pruinosa, Xenoglossa* spp., *Ceratina* spp., *Agapostemon* spp., *Melissodes* spp., *Peponapis* spp.)	early summer [122]	up to a week [123]	+	+	++	+
Fruit	Peach, Nectarine	*Prunus persica, Persiva laevis*	1527052	1000–10000	increase [6]	honey bees (*A. mellifera*), bumble bees, solitary bees (*O. cornifrons, O. lignaria propinqua*), flies	spring [79]	a few weeks [80]	+	+	+	+
Fruit	Pear	*Pyrus communis*	1379387	10–20	increase [6], increased fruit size [16]	honey bees (*A. mellifera*), bumble bees, solitary bees (*Osmia* spp., *Andrena* spp.), flies (*Eristalis* spp.)	late winter - early spring [81]	2 weeks [82]	+	+	+	+
Fruit	Lemon, Lime	*Citrus limon, C. aurantifolia, C. limetta*	1226617	2–5	increase [6]	honey bees (*A. cerana*, *A. mellifera*), bumble bees	most common in early spring [124]	a few weeks [124]	++	++	N/AV	+
Fruit	Cantaloupe and other melons	*Cucumis melo*	1039691	10–20	increase [6]	honey bees (*A. mellifera*), bumble bees, solitary bees (*Ceratina* spp., *Peponapis* spp., *Melissodes* spp., *Agapostemon* spp.)	summer [125]	a few weeks, one day per flower [125]	+	+	+	+
Fruit	Persimmons	*Diospyros kaki*	992425	10–20	increase [142]	honey bees (*A. cerana*, *A. mellifera*), bumble bees, solitary bees	late spring [151]	a few weeks [151]	+	+	+	+
Legume	Lupin	*Lupinus* sp.	887111	20–50	increased crop yield [143]	honey bees, bumble bees (*Bombus terrestris, B. pascuorum, B. lapidarius*), solitary bees (*Megachile ericetorum, Andrena wilkella*) [143]	late spring - early summer [86]	2 months [87]	–	+	++	+
Seed	Mustard	*Brassica alba, B. hirta, Sinapis alba, B. nigra, S. nigra*	850079[i]	<1	increased fruit set and seed yield [156]	honey bees (*A. mellifera*), solitary bees (*O. cornifrons, O. lignaria lignaria*)	mid-spring [88]	7–15 days [89]	++	++	+	+
Fruit	Avocado	*Persea americana*	726660	1000–10000	increased production and weight of fruit [16]	honey bees, stingless bees, solitary bees	spring [93]	2 months [93]	+	+	N/AV	+
Oil, seed	Safflower	*Carthamus tinctorius*	652780	2–5	increased yield [144]	honey bees (*A. cerana, A. mellifera*), solitary bees	early summer [126	2–3 weeks [126]	+	+	N/AV	+
Nut	Chestnut	*Castanea sativa*	595703	200–500		honey bees, solitary bees	early summer [95]	a few week [95]	++	++	+	+

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Table 1 (*continued*)

Type of (main) plant product	Mass-flowering crop	*Plant species name*	Total area harvested (ha) [17]	Field size (ha) with largest production [154]	Animal pollination, impact on fruit/ seed set	Pollinator community [6,8,16]	Blooming period (season)	Blooming time	Attractiveness of flower to bees [8]			
									Nectar to honey bees	Pollen to honey bees	Bumble bees	Solitary bees
					higher quality nuts and higher yield [145]							
Fruit	Apricot	*Prunus ermeniaca*	561750	10–20	higher fruit yield, higher size and quality of fruit [146]	honey bees (*A. mellifera*), bumble bees, solitary bees (*O. cornifrons, O. lignaria propinqua*), flies	early spring [96]	a few weeks [96]	++	++	++	+
Spice	Cardamom	*Elettaria cardamomum*	450728[j]	1–2	higher yield [147]	honey bees (*A. cerana, A. dorsata, A. florea*), solitary bees	mid-spring to mid-summer [97]	a few months [97]	N/AV	N/AV	N/AV	N/AV
Fruit	Sweet cherry	*Prunus avium*	443771	2–5	increase yield and fruit set [148]	honey bees (*A. mellifera*), bumble bees, solitary bees (*Osmia lignaria*), flies	spring [98]	7–24 days [98]	+	++	+	++
Fruit	Strawberry	*Fragaria* ssp.	396401	10–20	bigger fruit, higher fruit yield [149]	honey bees (*A. mellifera*), stingless bees (*Trigona angusula, T. tetragonula, T. minangkabau, Nannotrigona testaceicornis*), bumble bees, solitary bees (*O. cornuta, Andrena, Halictus*), hover flies	*Fragaria ananassa*: late spring [99]	a few weeks [99]	+	+	+	+
Fruit	Grapefruit	*Citrus maxima; C. grandis; C. paradisi*	346191	>1000	increase [6]	honey bees (*A. cerana, A. mellifera*), bumble bees	spring [127]	a few weeks [52]	++	++	+	N/AV
Fruit	Kiwifruit	*Actinidia deliciosa, A. chinensis*	268788	2–5	increased fruit set and yield, higher fruit breadth, longer fruits, heavier fruits [16], variable, 40% increase [10]	honey bees (*A. mellifera*), bumble bees (*B. terrestris, Bombus haemorrhoidalis*), solitary bees, *Eristalis tenax*,	*Actinidia deliciosa*: summer [101] *Actinidia chinensis:* late spring [102]	a few weeks [101 102]	+	+	+	+
Spice (leaves)	Yerba mate	*Ilex paraguariensis*	264699	2–5	insects fundamental [12]	N/AV	late autumn - early winter [103]	weeks to months [103]	N/AV	N/AV	N/AV	N/AV
Fruit	Sour cherry	*Prunus cerasus*	224237	1–2	increased yield [150]	honey bees (*A. mellifera*), bumble bees, solitary bees, flies	early spring [104]	6 days [105]	N/AV	N/AV	N/AV	N/AV
Fruit	Raspberry, Blackberry, Cloudberry, Northern Dewberry, Southern Dewberry	*Rubus idaeus, R. fruticosus, R. chamaemorus, R. flagellaris, R. trivalis*	127578[k]	5–10	more and better fruit [13]	honey bees (*A. mellifera*), bumble bees, solitary bees (*Osmia aglaia, O. cornuta, Andrena* spp., *Coletes* spp., *Halictus* spp.), hover flies (*Eristalis* spp.)	*Rubus idaeus, Rubus flagellaris, Rubus trivalis*: late spring - early summer [109,111,112], *Rubus fruticosus*: spring [110]	a few weeks [110]	+	+	++	+, ++ for blackberry

Type of plant product: product used from the crops; Mass-flowering crop: common name of the MFC; Plant species name: scientific name(s) of the MFC; Total area harvested (ha):the total global area harvested (ha); Average field size: average field size used for the MFC based on Ricciardi et al. (2018) (see supplementary file for details); Animal pollination impact on fruit/seed set: the impact of animal pollination on fruit or seed set; Pollinator community: bee pollinator community that visits the MFC based on references mentioned in the header, unless stated differently in the specific cell; Blooming period: season of bloom; Blooming time: average time of bloom; Attractiveness to bees: for honey bees both attractiveness of the pollen and nectar are given, for bumble bees and solitary bees no distinction was made and we reported flower attractiveness due to lack of data to separate pollen and nectar for these species. Letters in column of area harvested refer to commodity description of reference, which differs from the description of mass-flowering crops (a: Sunflower seed; b: Cocoa, beans; c: Peas, dry and green; d: Cashew nuts, with shell and cashew apple; e: Mangoes, mangosteens, guavas; f: Plums and sloes; g: Broad beans, horse beans, dry; h: Chilies and peppers, dry + green; i: Mustard seeds; j: Nutmeg, mace and cardamoms; k: Raspberry). N/AV: data is unavailable. Attractiveness taken from USDA (2007), "-" = not attractive, "+" = attractive under certain conditions, and "++" = high attractiveness in all cases (used references indicated by number between brackets, see supplementary information for full reference list of the table).

observed a higher wild bee density in MFCs, which was associated with an increase in pathogen prevalence.

An additional factor which may lead to host concentration is the deployment of honey bee hives, which are transported between locations. These hives (often multiple) are regularly placed near or in MFC fields just before bloom and often remain there a while after bloom to ensure crop pollination. This results in a surge of the amount of honey bee hosts present at that location (Eeraerts et al., 2017) [average size of a managed European honey bee hive ~20 000 bees/colony during late spring-summer (Ippolito et al., 2021), of which around 4.1% on average are foragers (Danka et al., 1986)]. Furthermore, honey bees are host to a variety of pathogens (Ellis and Munn, 2005). Infective hives could act as a source of pathogens, which they may spread to wild pollinators via shared flowers (pathogen spillover) (McMahon et al., 2015; González-Varo and Vilà, 2017; Dalmon et al., 2021; Nanetti et al., 2021). This likely increases pathogen prevalence in the pollinator community (Fig. 2 upper right). Pathogen-free managed colonies could also increase local pathogen prevalence through spillback mechanisms, where managed bees get infected with pathogens acquired from the environment and subsequently reinfect other wild bees (Kelly et al., 2009; Graystock et al., 2016; Pereira et al., 2021).

2.1.2. Host dilution

Piot et al. (2021) showed that pathogen transmission was diluted during the peak bloom of mass-flowering fruit trees and suggested that a reduced host density is one of the potential underlying causes (Fig. 2 upper left). Holzschuh et al. (2016) found that increasing the cover of mass-flowering crops that are attractive to bees can lead to a dilution of honey bee, bumble bee and solitary bee populations in these fields, despite attracting them from the surrounding landscape. A similar result was reported by Shaw et al. (2020) and Eeraerts et al. (2017) who showed that an increasing cover of MFCs negatively affected bee abundance and richness in the MFCs. However, Eeraerts et al. (2017) only detected this dilution for non-*Apis* bee pollinators. For managed honey bees they found an increasing abundance with increasing MFC cover, which they attribute to the placement of honey bee hives for pollination purposes (Eeraerts et al., 2017). Wild pollinators may have been unable to increase their population size in proportion to the increase in MFC cover (Holzschuh et al., 2016). This was empirically confirmed for bumble bees by Proesmans et al. (2019) who showed that their reproduction rates decreased with increasing cover of mass-flowering orchards.

2.2. Other factors

When assessing the effect of MFCs on pathogen prevalence, several factors are at play next to host densities, such as field size (Holzschuh et al., 2016), flower abundance (Graystock et al., 2020) and floral characteristics (Adler et al., 2018). For example, one might expect that encounters, or the likelihood of defecating on the flower, could be more likely to happen on sunflowers (MFC studied by Cohen et al., 2021), compared to the blossoms of apple or sweet cherry (MFCs studied by Piot et al., 2021). Next to differences in size and morphology, the average time spent on the flowering unit also differs, e.g. ~116 s and ~11 s on a sunflower head and a single cherry flower by honey bees, respectively (Nderitu et al., 2008; Eeraerts et al., 2020).

Furthermore, the broader landscape needs to be accounted for as well, since semi-natural elements surrounding MFC fields may also impact bee populations and pathogen dynamics. Cohen et al. (2021) found that pathogen prevalence was diluted instead of amplified for MFC sites that were accompanied by a high non-crop floral abundance. After mass-flowering, the bees that foraged on the MFCs now need to forage on the plants in the surrounding landscape (González-Varo et al., 2017; Heller et al., 2019). When the floral abundance is lower here (Mallinger et al., 2019), this may lead to higher floral visitation frequencies and bee densities on these flowers (González-Varo et al., 2017; Benadi et al., 2018). This can in turn lead to an increase in pathogen transmission and prevalence (Fig. 2 upper part) in the area surrounding MFCs after bloom (Piot et al., 2021).

3. The effect of MFCs on floral nutrition

3.1. MFCs and the nutritional landscape

In addition to their role in pathogen transmission, flowers also provide the essential nutritional resources for bees to survive and reproduce. A bee's diet is dependent on the floral preferences of the bees, but is also greatly influenced by the availability and quality of floral resources (Parreño et al., 2021). Bees need both energetic 'fuel' as well as essential components for physiological development. The former is provided by nectar, the latter by pollen (Nicolson, 2011). Pollen is the main source of essential elements, such as proteins, amino acids and vitamins, and can have different nutritional values depending on the plant source (Di Pasquale et al., 2013). Many essential and non-essential amino acids are present in varying amounts in pollen and can each have a different role in bee health. Pollen can affect metabolism, immunity, detoxification against pesticides, and tolerance to pathogens (Alaux et al., 2010; Di Pasquale et al., 2013; Roger et al., 2017; Barascou et al., 2021). The quality of a pollen diet is determined by both the diversity and the nutritional content of pollen. It is important to note that nutritional requirements differ between bee species. The definition of quality is therefore different depending on bee species (Parreño et al., 2021; Barraud et al., 2022). For example, low amino acid and sterol content has been shown to negatively impact the development of bumble bees and mason bees, while honey bees were not impacted by these low contents (Barraud et al., 2022). Bumble bees re-assess pollen quality continuously to improve the colony health, as poor pollen diets decreased larval and pupal masses and increased larval ejection in bumble bees (Ruedenauer et al., 2016; Roger et al., 2017). In general, it has been shown that a quality diet, with abundant and diverse food, can significantly increase a bee's health and fitness (de Groot, 1952; Pernal and Currie, 2000; Pirk et al., 2010; Parreño et al., 2021).

Despite the quantity of flowers offered by MFCs, they do not always provide a sufficient quality (Schmidt et al., 1995). Some MFC pollen contain little sterol or have low protein levels [e.g. sunflower pollen (Nicolson and Human, 2013), which is a typical mass-flowering monoculture] and this can deteriorate colony development of bumble bees (Moerman et al., 2017; McAulay and Forrest, 2019).

Legume (Fabaceae) pollen, which includes many MFCs (see Table 1), is protein-rich (Hanley et al., 2008). Yet, high protein content is not always beneficial for pollinators, as it was recently shown that pollen with a high protein content had a negative impact on honey bee survival (Barraud et al., 2022). MFCs can have high nectar concentrations and are often more attractive (see Table 1) than existent flowers in field margins (Esquivel et al., 2021), but they can become a sugar trap when pollen quality is inadequate, undermining the pollinators' health. For example sunflower, which is rich in hexose, is highly attractive to bees (see Table 1) (Neff and Simpson, 1990), but does not provide a quality diet for them (Nicolson et al., 2013; Giacomini et al., 2021). The differences in the nutritional composition of MFCs and the differences in nutritional requirements of bee species emphasize the importance of a sufficient amount of alternative floral resources. This to overcome nutritional stress, caused by MFCs with poor quality bee nutrition or the lack of resources after their short blooming period (see Table 1). For example, McAulay et al. (2019) showed that a mixed pollen diet can overcome the effect of the low nutritive quality of sunflower pollen in bumble bee development (McAulay et al., 2019). It could therefore be hypothesized that next to altering the plant-pollinator transmission network, the implementation of MFCs can also significantly alter the nutritional landscape (Fig. 2 bottom part). This in turn could impact the defense mechanisms of bees against pathogens.

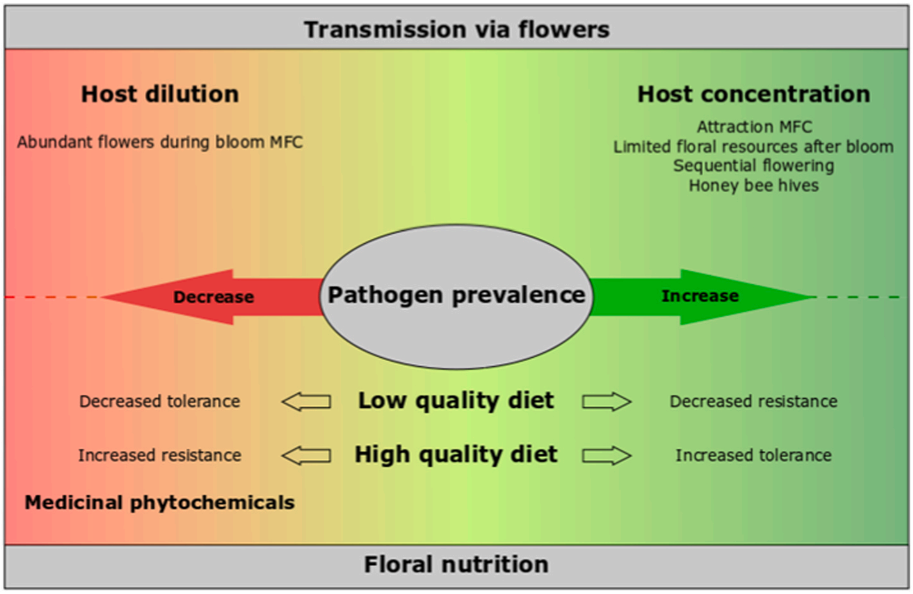

Fig. 2. *Graphical representation of the potential effects of MFCs on bee pathogen prevalence. Floral resources act both as an encounter spot between species, allowing inter- and intra-species transmission* ***(upper part of the figure)*** (Durrer and Schmid-Hempel, 1994; Graystock et al., 2015; Adler et al., 2018; Piot et al., 2020)*, as well as nutritional sources, impacting host defense mechanisms* ***(bottom part of the figure)*** (Alaux et al., 2010; Roger et al., 2017)*. When in bloom, MFCs produce an abundance of flowers that might attract pollinators (Host concentration), which could increase their densities and pathogen transmission potential (green arrow)* (Cohen et al., 2021)*. When MFCs are present for several consecutive years or different MFCs in the same region have sequential blooming periods, this can result in higher bee densities over time* (Riedinger et al., 2014; Kallioniemi et al., 2017)*. During bloom, the large abundance of flowers may also act as a dilutor where pollinators are less likely to visit the same flower (Host dilution). This reduces the likelihood of pathogen transmission and consequently pathogen prevalence (red arrow)* (Piot et al., 2021)*. However, after the bloom of the MFC, all present pollinators are forced to forage on the remaining non-crop floral resources, which are often not abundant. This increases the use of shared flowers (Host concentration) and the subsequent potential for pathogen transmission and pathogen prevalence (green arrow). The quantity of available non-crop flowers may therefore have an important impact on the effect of MFCs on pathogen prevalence* (Cohen et al., 2021; Piot et al., 2021)*. The use of honey bees to ensure pollination of MFCs often results in the placement of multiple hives in or near a MFC field. This significantly increases the number of pollinators present in that region and may result in an increased transmission potential (Host concentration). MFCs can also alter the nutritional landscape (bottom part of the figure), which can affect the bees' nutritional status and their defense mechanisms used to combat pathogen infections. Depending on which defense mechanism is affected, a different outcome of pathogen prevalence is expected. If the MFC has a low nutritional quality and little to no alternative floral resources are present, host defenses may be weakened. A weakened host resistance likely results in an increase in pathogen prevalence (green arrow), while a weakened host tolerance likely has the opposite outcome (red arrow). If the MFC provides an adequate quality of nutrition, their abundance will provide a good nutritional landscape for pollinators, strengthening their defense mechanisms. This can result in either an increase (if pathogen tolerance is increased) or a decrease (if pathogen resistance is increased) in pathogen prevalence. Some MFCs can provide antipathogenic secondary metabolites* (Fatrcová-Šramková et al., 2016) *which may reduce pathogen prevalence (red arrow).* . (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2. MFCs may alter the host defense mechanisms

Hosts have two main defense mechanisms, i.e. pathogen resistance and pathogen tolerance. Whereas the former is the ability to avoid and/or reduce a pathogen infection, the latter can be defined as the ability of a host to limit the negative impact of pathogen infection, without limiting pathogen reproduction within the host (Kutzer and Armitage, 2016). Bees with a sub-optimal diet may have a decreased pathogen resistance against infection for a certain pathogen. This can be the result of a compromised constitutive immunity, which was shown for bumble bees, where a poor quality diet reduced immune gene expression (Brunner et al., 2014). Similarly, unrestricted access to high quality diet increased the constitutive immunity in bumble bees (Roger et al., 2017). In honey bees, polyfloral diets increased the glucose oxidase activity, which plays a role in social immunity by producing an antiseptic compound (Alaux et al., 2010). Amino acids are likely the limiting factor here, since essential amino acids are needed in a certain amount and proportion for general bee health (Alaux et al., 2010; Barraud et al., 2022). Arginine is an essential amino acid and a precursor of nitric oxide, which is thought to be a key effector molecule against diseases in invertebrates (Negri et al., 2017). Arginine is present in pollen of MFCs like squash, sunflower and rape, where it is documented to be below minimum requirements for honey bee health (Taha et al., 2019). Micronutrients are also suggested to play a key role. For example, Dolezal et al. (2019) found that honey bees that were fed with high quality pollen had a lower mortality upon infection with Israeli acute paralysis virus (IAPV) and had a higher calcium and iron content compared to those fed on lower quality pollen or no pollen (Dolezal et al., 2019). Although they did not find a direct relation, micronutrients such as iron have been shown to play a role in *N. ceranae* infections (Rodríguez-García et al., 2021) and insect pathogen interactions in general (Hrdina and Iatsenko, 2022). The precise role of micronutrients in host pathogen interactions still remains understudied, yet their role in a healthy bee diet and bee immune response warrants further research (Hrdina et al., 2022). Increased pollen diet quality has also been shown to reduce pathogen induced mortality in honey bees for *Nosema ceranae* (Di Pasquale et al., 2013) and *Aspergillus fumigatus* (Foley et al., 2012). However, the observed effects are not always clear. Figueroa et al. (2021) found no interaction effect of *C. bombi* infection and pollen starvation on the survival of two solitary bees (*Osmia lignaria* and *Megachile rotundata*) (Figueroa et al., 2021). Both quantity and quality of pollen as well as nectar have a potential impact on pathogen burden in bees. High sugar concentrations increased survival after infection of bumble bees with *Crithidia bombi* (Sadd, 2011). Starvation stress, on the other hand, increased the *C. bombi* as well as Slow bee paralysis virus (SBPV) induced mortality in bumble bees (Brown et al., 2000; Manley et al., 2017).

Although these studies provide valuable information on the impact of pathogens on their host under nutritional stress, the impact of nutrition on within-host dynamics is also important, as it provides information on the replication of the pathogen and spread via the feces, which impacts the overall pathogen prevalence in the bee community. Sadd (2011) showed that the amounts of infective *C. bombi* cells shed in the feces as well as infection intensities in the gut were lower when bumble bees were fed low concentrations of sugar water (Sadd, 2011). The same effect was seen with *C. bombi* in another bumble bee species, where lack of pollen and low sugar concentration reduced *C. bombi* counts in the gut (Conroy et al., 2016). In honey bees, an increased virus titer was observed when they were supplemented with pollen (DeGrandi-Hoffman et al., 2010).

Depending on which of the two defense mechanisms is affected (pathogen tolerance and/or pathogen resistance), a different outcome is expected (Fig. 2 bottom part). A good quality diet can enhance pathogen resistance (Huang, 2012) and can in this way reduce the pathogens' spreading (Fig. 2 bottom left). Furthermore, a good quality diet could increase pathogen tolerance in bees (Dolezal et al., 2019), but this mechanism has a different outcome. As pathogen tolerance does not limit pathogen reproduction, the increase of pathogen loads in the host with no fitness cost for the host will likely result in increased pathogen transmission to the environment via the feces (Otterstatter and Thomson, 2006) (Fig. 2 bottom right). Pollen from MFCs can be highly nutritious, such as pollen from rapeseed or legumes (Hanley et al., 2008; Huang, 2012). During the peak bloom of MFCs, the increased abundance and nutritious pollen of floral resources can both lower pathogen prevalence by reducing its reproduction in the host (resistance), yet it may also result in an increased pathogen prevalence by allowing the pathogen to reproduce without or with less fitness costs to the host (tolerance) (Fig. 2 bottom part). When the floral resources of MFCs are of insufficient quality, the process would be opposite and the outcome equally unknown.

Current knowledge on the precise defense mechanisms affected by nutrition in different bee species is still mostly lacking, especially in field studies. A recent study, however, showed that pathogen loads [i.e. Black queen cell virus (BQCV), Deformed wing virus (DWV) and *Nosema bombi*] in *Bombus impatiens* were associated with lower quality landscapes, yet in their study McNeil et al. (2020) also found a link with honey bee hive density. These results highlight the difficulty of elucidating the precise underlying mechanism of pathogen prevalence in field studies, as multiple uncontrollable factors may be at play as well. Although we strongly encourage further research on this topic both in lab and field studies, we believe current evidence already strongly suggests that MFCs may alter the nutritional landscape. This can in turn affect the bees' defense mechanisms and subsequent pathogen prevalence in that region. This is particularly true for wild bees, as honey bees are mostly well monitored by the beekeeper and often supplemented with additional food when needed (Mortensen et al., 2019), while wild bees do not have this safety net.

3.3. Secondary metabolites of MFCs

Besides pollen content and nectar amounts, a third nutritional factor can affect pathogen dynamics. Secondary metabolites are chemical compounds produced by plants and often play a role in the interaction with the environment. These phytochemicals such as alkaloids are used as a defense tactic against herbivores (Adler, 2000). While some secondary metabolites can be toxic to bees in high concentrations (Baracchi et al., 2015; Stevenson et al., 2017), several studies have highlighted the medicinal effect of these compounds for bees when taken in small amounts through nectar and pollen. Both viral as well as single cellular pathogens appear to be affected by several phytochemicals (Aurori et al., 2016; Palmer-Young et al., 2017). These compounds also occur in many MFCs [see e.g. Palmer-Young et al. (2019)]. One well-studied case is sunflower, of which the pollen decreased *C. bombi* infection in bumble bees and sunflower honey decreased *N. ceranae* infection in honey bees (Gherman et al., 2014; Giacomini et al., 2018; LoCascio et al., 2019). Although several compounds of sunflower pollen have been tested individually, such as the major secondary metabolite of the sunflower pollen, triscoumaroyl spermidine and several fatty acids, the precise underlying mechanisms of the medicinal effect have not yet been elucidated (Adler et al., 2020).

4. Conclusion

Within this review we tried to bring together current knowledge on bee epidemiology and the potential impact of MFCs. Currently, only two studies directly address the role of MFCs on pathogen prevalence in bees. Although both studies focused on different MFCs and differ in their experimental design [i.e. Piot et al. (2021) looked at the pathogen prevalence in the collected pollen during and after bloom of sweet cherry and apple orchards, while Cohen et al. (2021) investigated pathogen prevalence in wild bees in sunflower fields and non-crop flowering fields], they both reported an effect on pollinator epidemiology and addressed the need for sufficient non-crop flowering habitat to support a healthy pollinator community. As the total land use of MFCs continues to increase (Fig. 1), strongly altering the (nutritional) landscape and plant-pollinator transmission networks, we encourage further research on the impact of MFCs on bee epidemiology. Although studies, incorporating the plant-pollinator network as a tool to explain the observed pathogen prevalence, are increasing over the last few years, studies with regard to the effect of nutrition on the host defense mechanisms are still scarce. Assessing the impact of nutrition in the field is very difficult. Furthermore, comparisons between studies are often hard due to the different methodologies used to assess the quality of the nectar and pollen content, which in turn results in divergent data. Moreover, the nutritional quality of flowers can be affected by multiple factors, such as soil type, climate and used cultivar (see e.g. Alqudah et al., 2011; Nickless et al., 2017; Fairhurst et al., 2021). Nonetheless, a solid framework on the impact of nutrition on host-pathogen interactions in bees under controlled conditions is also still largely missing, and this should provide the solid basis for field studies. During the past decade, multiple studies have investigated the impact of different pathogens on bee species, providing the foundation for triple interaction studies, where the impact of nutrition on the host-pathogen interaction is incorporated. We strongly encourage further research in this field as this will increase our knowledge on underlying mechanisms in pathogen dynamics in wild bees. From what is currently known, we can already acknowledge the irrefutable role of good landscape management, where sufficient (semi-)natural habitat is retained. This is important to provide alternative flowers to overcome both the low(er) nutritional quality of some MFCs, preventing nutritional stress, which can impact pathogen prevalence, as well as to reduce the concentration effect of bees on flowers after the bloom of the MFC and reduce pathogen transmission.

Conflicts of interest

Declarations of interest: none.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijppaw.2022.05.001.

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