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Toward evidence-based decision support systems to optimize pollination and yields in highbush blueberry

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Highbush blueberry (*Vaccinium* spp.) is a globally important fruit crop that depends on insect-mediated pollination to produce quality fruit and commercially viable yields. Pollination success in blueberry is complex and impacted by multiple interacting factors including flower density, bee diversity and abundance, and weather conditions. Other factors, including floral traits, bee traits, and economics also contribute to pollination success at the farm level but are less well understood. As blueberry production continues to expand globally, decision-aid technologies are needed to optimize and enhance the sustainability of pollination strategies. The objective of this review is to highlight our current knowledge about blueberry pollination, where current research efforts are focused, and where future research should be directed to successfully implement a comprehensive blueberry pollination decision-making framework for modern production systems. Important knowledge gaps remain, including how to integrate wild and managed pollinators to optimize pollination, and how to provide predictable and stable crop pollination across variable environmental conditions. In addition, continued advances in pesticide stewardship are required to optimize pollinator health and crop outcomes. Integration of on- and off-farm data, statistical models, and software tools could distill complex scientific information into decision-aid systems that support sustainable, evidence-based pollination decisions at the farm level. Utility of these tools will require multi-disciplinary research and strategic deployment through effective extension and information-sharing networks of growers, beekeepers, and extension/crop advisors.

KEYWORDS

Vaccinium, Integrated Crop Pollination, bees, sustainability, pollinator, crop yield, *Apis mellifera*, ecosystem service

Introduction

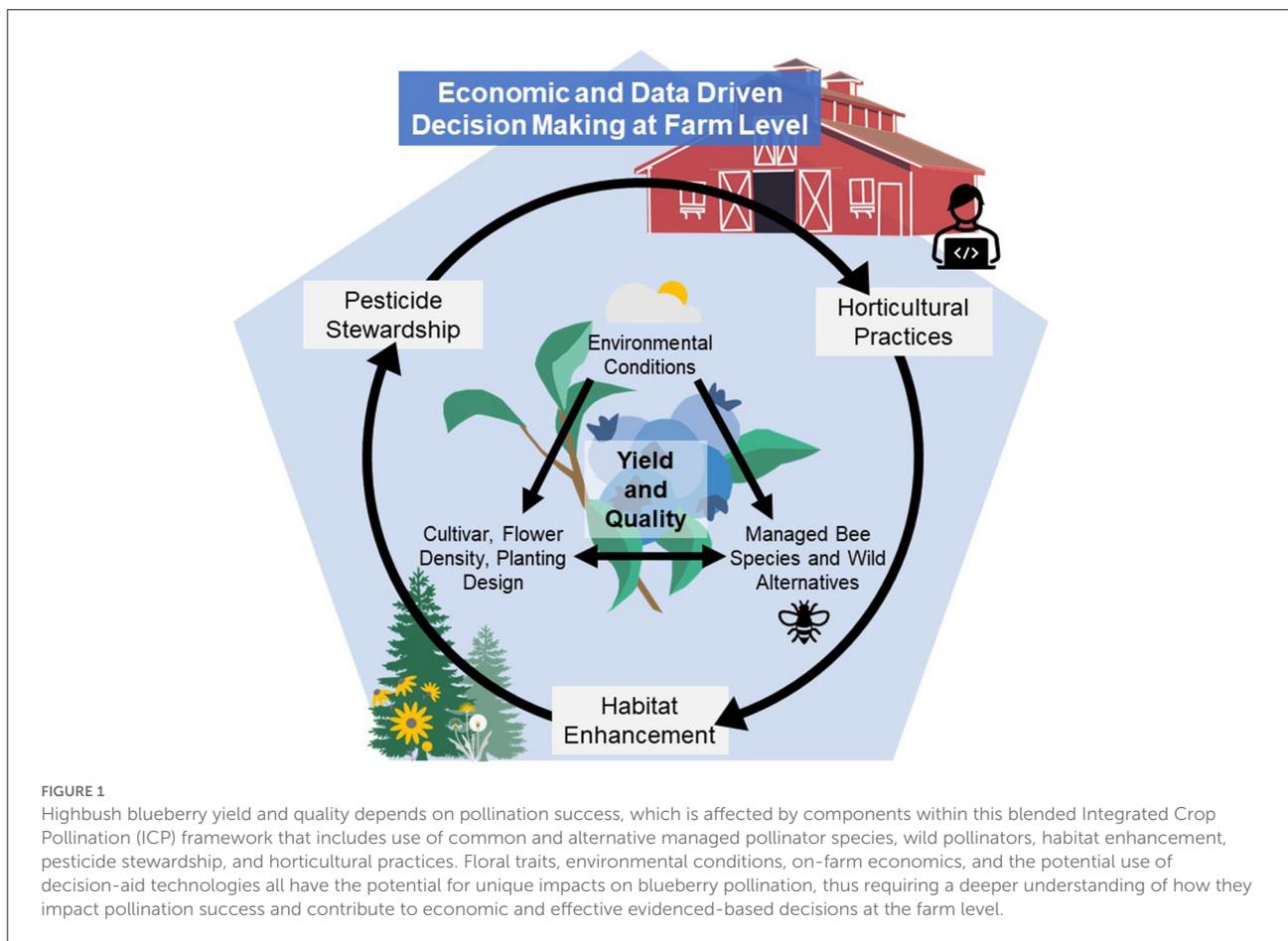
Highbush blueberry is a domesticated fruit crop from eastern North America that has gained cosmopolitan status in recent years due to its attractive fruit with human health benefits (Eck and Childers, 1966; Retamales and Hancock, 2018; Kalt et al., 2020). Global blueberry production has more than doubled since 2005 and expanded to all continents except Antarctica (Brazelton et al., 2021). Production systems of northern highbush blueberry (*Vaccinium corymbosum* L.) and southern highbush blueberry (complex hybrids of *V. corymbosum* and low-chill *Vaccinium* species) have rapidly modernized for efficient production with new cultivars and research-driven recommendations for irrigation, fertilization, harvesting, postharvest management, pruning and training, and pest and disease management. Parallel advances in pollination management, however, are lagging. There is a need for investment in research that can support evidence-based decision support systems to optimize sustainable pollination and ensure economical production of this globally important and expanding crop.

Insect-mediated pollination is needed to produce blueberries of marketable size for commercial production (MacKenzie, 1997; Retamales and Hancock, 2018; Martin et al., 2021). Blueberry fields frequently suffer from pollen limitation across different production regions, indicating optimal or maximum levels of insect-mediated pollination are not always achieved (Button and Elle, 2014; De Groot et al., 2015; Nicholson and Ricketts, 2019; Reilly et al., 2020). Wild pollinators alone are not sufficient in large and intensive crop systems where they are less abundant (Isaacs and Kirk, 2010), causing many growers to rely on renting managed western honey bee (*Apis mellifera* L.) and bumble bee (*Bombus* spp.) colonies for pollination services (Arrington and DeVetter, 2018a; Bobiwash et al., 2018; Cavigliasso et al., 2020; Mallinger et al., 2021). The number of honey bee colonies has globally increased over the last seven decades (Osterman et al., 2021a) and the supply of this pollinator to blueberry farms in North America has not experienced the decrease observed in other crops (Burgett et al., 2004, 2010; Aizen and Harder, 2009; Breeze et al., 2014). However, reliance only on honey bees may not be a viable long-term strategy for sustainable crop pollination in some regions given the increased expansion of pollinator-dependent crops relative to the supply of honey bees (Aizen and Harder, 2009; Breeze et al., 2014) and the potential for honey bee foraging to be inhibited by cool weather. Reported levels of honey bee colony mortality have been high in North American (Osterman et al., 2021a), and the health of both wild and managed bees is affected by individual or synergistic effects of poor nutrition, pesticide exposure, abiotic stressors, and pests and diseases that threaten the stability of pollination (Potts et al., 2010; Goulson et al., 2015), requiring a focus on overall pollinator health to ensure effective crop pollination.

Given these factors affecting honey bee and wild bee supply and health, blueberry pollination strategies should encompass the Integrated Crop Pollination (ICP) concept to move toward more resilient pollination systems and success for growers. Introduced by Isaacs et al. (2017), ICP is “the use of managed pollinator species in combination with farm management practices that support, augment, and protect pollinator populations to provide reliable and economical pollination of crops.” Implementation of ICP for blueberries will require understanding and addressing knowledge gaps within the fundamental components of ICP such as the use of common and alternative managed pollinator species, wild pollinators, habitat enhancement, pesticide stewardship, and horticultural practices. Only by understanding these components can advances be made in evidence-based decision support systems to optimize pollination and yield. The objective of this review is to highlight what is known about blueberry pollination within the context of ICP, where current efforts are focused, and where future research should be directed to support sustainable pollination strategies for profitable modern blueberry production systems (Figure 1). Floral traits of different cultivars, environmental factors that influence pollination, economics, and the use of decision-aid technologies will also be considered as components to blend within the ICP framework with the aim of better understanding and improving pollination for this globally expanding crop.

Pollination requirements

Highbush blueberry has the potential to set nearly 100% of its flowers into fruits when resources are not limiting (Ehlenfeldt, 2001; Kumarihami et al., 2021), but this may not be achieved if pollination is inadequate or disrupted. Cultivated highbush blueberries are highly dependent upon successful pollination, with individual flowers requiring deposition of about 30 to 100 pollen tetrads to maximize fruit set and fruit mass, and to minimize ripening time (Dogterom et al., 2000; Sun et al., 2021). While some parthenocarpy has been observed in some highbush blueberry genotypes, it yields generally small fruits and is insufficient at producing marketable yields for any cultivar (Harrison et al., 1993; MacKenzie, 1997; Kazokas, 2003; Ehlenfeldt and Vorsa, 2007; Ehlenfeldt, 2012). Insect pollinators are necessary due to low auto-fertility (*sensu* Rodger et al., 2021). Blueberry flowers excluded from insect pollinators have reduced fruit set, and any resulting berries are smaller than insect-pollinated flowers (Tuell and Isaacs, 2010a; Gibbs et al., 2016; Campbell et al., 2018). Low levels of auto-fertility in blueberry may be due to various aspects of floral development and morphology, including poricidal anthers that require sonication by insects to adequately release pollen (Cardinal et al., 2018; Cooley and Vallejo-Marín, 2021), and upside-down, urn-shaped flowers with a style sometimes shorter than the corolla that



limits pollen deposition on the stigma either by autonomous self-pollination or by wind pollination (Sampson et al., 2013).

Modern highbush blueberry cultivars have a relatively high degree of self-fertility, i.e., a high ability for flowers to set fruits when pollinated by self-pollen, including pollen derived from the same flower, from flowers of the same plant, or from plants of the same cultivar (Dogterom et al., 2000; Ehlenfeldt, 2001; Taber and Olmstead, 2016; Kendall et al., 2020). That is why many fields of northern highbush blueberry are established as single-cultivar blocks. Southern highbush blueberry, in contrast, is sometimes planted in mixed-cultivar configurations with overlapping bloom periods to promote cross-pollination (Mallinger and Phillips, 2022). Contrary to what many papers state due to a semantic confusion, the whole *Vaccinium* genus is self-compatible, meaning self-pollen can germinate in pollen tubes that can grow through the style and fertilize ovules to the same degree as cross-pollen (Garvey and Lyrene, 1987; Krebs and Hancock, 1988; Czesnik et al., 1989; Hokanson, 1995; Hokanson and Hancock, 2000; Schott, 2000; Brevis et al., 2006; Miller et al., 2011; Leposavić et al., 2021). But on the other hand, the *Vaccinium* genus is partially self-sterile (terminology proposed by Gibbs, 2014) as it is affected by

an early-acting inbreeding depression (EID) whereby embryos resulting from self-pollination may be partly aborted due to genetic load (Krebs and Hancock, 1990, 1991; Guillaume and Jacquemart, 1999; Rasp et al., 2004; Nuortila et al., 2006).

Consequently, as it is known from the early 20th century (Coville, 1921), many highbush blueberry genotypes show improved fertility with cross-pollination compared to self-pollination. For northern highbush, 70% of evaluated genotypes tested in the literature showed improved fruit set with hand cross-pollination, at least under certain conditions, and 86% showed improved fruit size (Supplementary Table 1). Likewise, southern highbush genotypes showed 63 and 65% improvement in fruit set and fruit size with hand cross-pollination, respectively. The magnitude of fertility gains may depend on the degree of inbreeding for a given genotype (Hellman and Moore, 1983; Krebs and Hancock, 1988, 1990) and on the pollen donor (White and Clark, 1939; Cremins, 1952; Gupton, 1984, 1997; Czesnik et al., 1989; Gupton and Spiers, 1994; Huang et al., 1997; Ehlenfeldt, 2003; Martin K. et al., 2019; Nagasaka et al., 2022). Cross-pollination can also result in a decrease of ripening time (Supplementary Table 1) and an increase of anthocyanin content (Doi et al., 2021). Insect pollinators vary

in their efficiency in cross pollination: high pollen loads on their bodies combined with foraging behavior across rows and cultivars can facilitate greater cross pollination by bumble bees (Miñarro and García, 2021), although in some cases honey bees have been observed to alternate between cultivars more than bumble bees (Estravis-Barcala et al., 2021b). Northern and southern highbush blueberry cultivars have similar levels of heterozygosity (Brevis et al., 2008) and are consequently similarly prone to EID. Domesticated blueberry cultivars have become increasingly inbred over time (Hancock and Siefker, 1982; Ehlenfeldt, 1994), which may increase their susceptibility to EID, indicating that the benefits of cross pollination will likely increase as new cultivars continue to be developed. Understanding the breeding history of modern cultivars and their levels of inbreeding will help to predict how well each cultivar will perform in single-cultivar plantings and which cultivars should be co-planted for effective cross-pollination.

Floral visitation

Floral visitation rates, driven by the diversity and abundance of the pollinator community and by the attractiveness of the crop flowers, are a major determinant of successful blueberry pollination. While considerable attention has been given to understanding the factors that influence pollinator abundance and diversity within blueberry fields (Isaacs and Kirk, 2010; Tuell and Isaacs, 2010a; Benjamin et al., 2014; Gibbs et al., 2016; Vieli et al., 2016; Graham et al., 2021a), neither diversity nor abundance of pollinators can positively influence pollination without successful recruitment (Gaines-Day and Gratton, 2016; Geslin et al., 2017a; Danka et al., 2019; Mallinger et al., 2021). Enhancing pollinator recruitment to crop flowers not only improves pollination but may also reduce the density of managed pollinators required, thereby reducing input costs.

Identifying and manipulating floral traits that maximize pollinator recruitment is key to optimizing pollination and tailoring pollination strategies to different blueberry cultivars. This is a promising avenue for crop breeding and is currently being explored in blueberry and other cropping systems (Ritzinger and Lyrene, 1999; Palmer et al., 2009; Bailes et al., 2015; Prasifka et al., 2018). Variation in floral rewards, including the quantity and quality of nectar and pollen, and in flower morphology and visual and olfactory cues can all influence pollinator attraction and subsequent pollination success (Prasifka et al., 2018; Cortés-Rivas et al., 2022 and references therein; Sampson et al., 2013; Vaudo et al., 2020). For example, honey bees showed greater visitation rates to blueberry flowers with wider floral tubes, specifically wider corolla opening diameters (Courcelles et al., 2013). Flower morphology can also interact with pollinator foraging behaviors: rates of nectar robbing or side working by carpenter bees (*Xylocopa* spp.) differed among blueberry cultivars and was

associated with differences in flower morphology (Sampson et al., 2004; Courcelles et al., 2013; Tucker et al., 2019). Bees are more likely to rob nectar from long and narrow blueberry flowers and more likely to make legitimate visits to shorter and wider blueberry flowers (Courcelles et al., 2013). In another example, individual flower size, corolla width, anther and pistil lengths, stigma-anther separation, and stigma protrusion across *Vaccinium* species was positively correlated with percent fruit set and/or berry weight following visits by the blueberry bee, *Osmia ribifloris* Cockerell (Sampson et al., 2013). Blueberry flowers can also differ in the degree to which petals are fused, but how these morphological traits affect pollinator recruitment is unknown (Arrington and DeVetter, 2018b).

Quantity and quality of blueberry rewards can also drive floral visitation rates. Honey bees primarily collect nectar from blueberry flowers and may respond to differences in nectar volume and sugar concentration found across cultivars (Jablonski et al., 1985; Bozek, 2021; Estravis-Barcala et al., 2021b). Bumble bees more frequently collect blueberry pollen than honey bees (Bobiwash et al., 2018; Miñarro and García, 2021) and may be affected by pollen traits including pollen chemistry, which has been found to differ across wild and cultivated blueberries and to affect bumble bee foraging preferences in other systems (Vaudo et al., 2016; Egan et al., 2018). For example, higher nectar volume increased honey and bumble bee visits to onion (*Allium cepa* L.) and zucchini (*Cucurbita pepo* L.) cultivars, while higher quantities of floral volatiles increased wild solitary bee visits to strawberry (*Fragaria x ananassa* Duch.) cultivars (Prasifka et al., 2018). Floral volatiles can indicate the age and pollination status of a flower, in turn signaling reward quantity and quality (Stout and Goulson, 2001). In blueberry, pollinators showed greater attraction to unvisited flowers that emitted greater amounts of floral volatiles (Rodríguez-Saona et al., 2011).

A promising new approach to enhance recruitment is feeding honey bee and bumble bee colonies with caffeine- or arginine-treated syrup flavored with crop flower scents just before bloom onset (Farina et al., 2020; Arnold et al., 2021; Estravis-Barcala et al., 2021a), training them to crop-specific rewards. Blueberry flower scents have been identified (Rodríguez-Saona et al., 2011; Forney et al., 2012; Huber, 2016) and could be used to aid bee recruitment. Brood, queen mandibular, and Nasonov pheromones are produced by honey bees for communication and manufactured versions of these pheromones are currently sold to growers to enhance honey bee recruitment (Free and Williams, 1970; Pankiw et al., 1994, 1998). Commercial bee attractants are also available on the market. The utility of these products when applied to blooming crops is questionable. Indeed, most studies have shown application of pheromones and attractants to be unreliable at increasing pollination and yield outcomes across various crops (Schultheis et al., 1994; Connell, 2000; Ellis and Delaplane, 2009; Williamson et al., 2018).

There are many opportunities to breed or manage the crop for more attractive flowers including accessible floral tubes to increase visitation rates and reduce nectar robbing, increased floral rewards (nectar and pollen) to enhance recruitment, and increased floral volatile emissions to signal attractive and rewarding flowers. These floral traits can be determined by genetic factors influenced by crop domestication (Egan et al., 2018) but recruitment can also be affected by environmental factors including temperature, water and nutrient availability, and interactions with herbivores and soil microorganisms (Lyrene, 1994; Cardel and Koptur, 2010; Halpern et al., 2010; Bruinsma et al., 2014; Brody et al., 2019; Rering et al., 2020). More studies are needed on the interaction of floral traits, rewards, and management to optimize floral visitation.

Horticultural factors

Horticultural factors such as field age, planting designs that include pollinizers, use of mulch, effective weed management, and conventional field management influence the probability of achieving higher yields (Retamales et al., 2015). Like most crops, soil conditions including plant nutrition and water availability directly affect blueberry productivity and need to be within an optimum range (Cameron et al., 1988; Bryla and Strik, 2015). Furthermore, soil conditions and pest and pathogen management may adjust allocation of resources to fruit and seed development independent of pollination so that pollination benefits may not be realized if soil conditions and pest and pathogen management are sub-optimal (Tamburini et al., 2019). Not only do these horticultural factors directly determine blueberry yield, but they also interact with pollination in complex ways that complicate our ability to quantify the benefits of insect-mediated pollination (Bos et al., 2007; Seppelt et al., 2011). For example, lack of pest control reduced yield of lowbush blueberry (*V. angustifolium* Ait.) independent of pollination and the highest yields were achieved when full, manual pollination was combined with the full input of recommended pesticides (Melathopoulos et al., 2014). Studies that attempt to disentangle the interaction between pollination and soil and pest and pathogen management in blueberry are lacking but needed given what has been shown in other cropping systems (Tamburini et al., 2019). Accounting for these other factors that contribute to yield will lend greater insight into the value of insect pollinators and build toward a more effective application of ICP.

Protected culture such as photo-selective nets and polytunnels can provide protection against environmental hazards such as hail, extremes in solar radiation, and vertebrate and arthropod pests (Wittwer and Castilla, 1995). Protected culture manipulates light quantity and quality, temperature, humidity, and airflow (Wittwer and Castilla, 1995; Shahak et al., 2008; Lobos et al., 2013) and can increase yields and advance

harvest timing compared to open-field production (Retamal-Salgado et al., 2015). However, these protective methods can negatively impact pollination and pollinator health (Kendall et al., 2021). Modifications in light intensity and wavelength can negatively impact the ability of some pollinating insects to forage and return to their nests given that they rely on polarized light from the sun for navigation (Evangelista et al., 2014). Hall et al. (2020) showed honey bee pollination deficits in the middle of 100-m long polytunnels can reduce blueberry fruit weight and yield compared to the edges. High temperatures in polytunnel middles can have lethal or sublethal effects on honey bees and greater humidity may have an additive effect by reducing honey bee capability to thermoregulate (Free and Spencer-Booth, 1962). Bumble bees, leafcutter bees (*Megachile* spp.), and mason bees (*Osmia* spp.) are reported to forage more efficiently in polytunnels compared to honey bees (Goodwin, 2012; as reviewed by Kendall et al., 2021). Because the use of protected culture has increased as the blueberry industry expands into new production regions and tries to capitalize on lucrative market windows, it is important to have a better understanding of how protected culture affects pollinators, so that these methods can be modified to optimize both crop protection and pollination.

Plant growth regulators are also sometimes used to overcome poor pollination. Gibberellic acid (GA₃) has received the most attention due to its role in increasing fruit set after a freeze event or physical injury (NeSmith et al., 1995). Controlled-environment studies have shown GA₃ increases fruit set in non-pollinated rabbiteye blueberry (*V. virgatum* Ait.) flowers with a trade off in delayed fruit development and weight (Williamson et al., 1996). In northern highbush blueberry, effects of GA₃ are subtle and inconsistent; its use may not always result in a yield response, and response to GA₃ depends on cultivar, application timing, pollination, and weather conditions (Hanson and Kelsey, 2019).

Managed honey bees

Honey bees have long been used for highbush blueberry pollination because their large population sizes and ease of transport facilitate the high densities needed to meet pollination requirements (Tuell and Isaacs, 2010a; Estravis-Barcala et al., 2021b; Mallinger et al., 2021). Stocking recommendations and practices are highly variable: earlier guides recommended stocking rates ranging from 1.2 to 25 honey bee colonies per hectare (Delaplane et al., 2000; Rucker et al., 2012), while current practices can range from 0 to 40 colonies per hectare (Gibbs et al., 2016; Mallinger et al., 2021). Colony stocking rate is poorly correlated with honey bee visitation and thus with blueberry yield, although honey bee visitation rates have been positively correlated with yield (Supplementary Table 2). Honey bees can become diluted in the landscape when there are natural habitats

or other blooming entomophilous crops, and they can also be attracted to some cultivars more than others, resulting in poor correlation between stocking rate and managed bee density in the field (Díaz et al., 2013; Gaines-Day and Gratton, 2016; Quinet et al., 2016; Estravis-Barcala et al., 2021b; Osterman et al., 2021b). Furthermore, there may be interactive effects between honey bees and wild bee densities that could affect pollination outcomes (Eaton and Nams, 2012).

Colony size and effective forager population can also vary considerably, ranging from 5,000 to 65,000 workers (Farrar, 1937; Schmickl and Crailsheim, 2007; Chabert et al., 2021). Larger honey bee colonies have higher foraging activity, increasing pollination within the same colony stocking rate (Geslin et al., 2017a; Cavigliasso et al., 2021). Farrar's (1937) study suggests that large colonies allocate an even higher proportion of their workers to the task of foraging, implying that large colonies would have a higher pollination performance than small colonies for the same number of workers provided in total. For some crops such as almond [*Prunus amygdalus* L., syn. *P. dulcis* (Mill.) DA Webb] or oilseed rape (*Brassica napus* L.) in hybrid seed production, growers request honey bee colonies with a minimum population size in their pollination contract, with increasing fees when colonies exceed the minimum request (Ovinge and Hoover, 2018; Goodrich, 2019; Goodrich and Goodhue, 2020). However, with the aim of promoting sustainable beekeeping for crop pollination, instead of absolutely meeting a standardized colony size that can be harmful for colonies (Durant, 2019), beekeepers could offset a low colony size by providing more colonies as long as the colonies are healthy with a laying queen alongside brood and enough empty combs (Sagili and Burgett, 2011). Combined, these functional differences based on colony size and forager population further complicate the utility of stocking density recommendations on a per colony basis. Assessing honey bee colony size can be done using the cluster size method (Nasr et al., 1990; Chabert et al., 2021) implemented with a beekeeper and/or an intermediary such as a bee broker (Goodrich, 2017), with thermographic imaging (Shaw et al., 2011; López-Fernández et al., 2018), or by assessing activity at hive entrances (Rodet and Henry, 2014; Ovinge and Hoover, 2018; Grant et al., 2021). When assessing honey bee colony sizes, it should be noted that the relationship between colony size and cluster size is exponential and not linear (Chabert et al., 2021).

In addition to colony stocking rates, Garibaldi et al. (2020) suggested identifying target pollinator densities to reach per flower in crops so that pollination is not limiting. These target densities can be assessed either empirically (Reilly et al., 2020; Chabert et al., 2022), or with a modular approach (Ne'eman et al., 2010; Garibaldi et al., 2020). With the modular approach, pistil receptivity lasts at least 4 days in highbush blueberry (Moore, 1964; Young and Sherman, 1978; Krebs and Hancock, 1990; Kirk and Isaacs, 2012), flowers require 5 to 15 bee visits to maximize fruit weight (Danka et al., 1993; Rogers et al., 2013;

Kendall et al., 2020), and honey bees visit about 5 blueberry flowers per minute (Shaw et al., 1939; Estravis-Barcala et al., 2021b; Sun et al., 2021). Based on the assumption of 6 hours of daily foraging activity, one blueberry field would require about 0.07 to 0.2 honey bees per 100 flowers (i.e., 0.2 to 0.6 honey bee visits per flower per hour). Empirically, Reilly et al. (2020) found that "Bluecrop" fields would require 16.7–26.3 bees per 100 m row to maximize fruit weight. Pollinator density estimates should always be associated with a flower count in pollination empirical studies (Chabert et al., 2022), highlighting the importance of developing simple and fast flower monitoring approaches with new methods such as image analysis with deep learning (Farjon et al., 2020; Hicks et al., 2021). Flower monitoring approaches could also be used by growers and crop advisors to assess pollination and inform pollination management.

Current recommendations indicate hive placement should begin when blueberry flowers are between 5 and 25% bloom (Howell et al., 1972) because honey bees may disperse onto alternative resources and forage less in the crop when placed before the onset of bloom (Jay, 1986). Some also advocate for the sequential introduction of colonies to crops resulting in higher bee densities in the crop and more bee movement between cultivars (Mayer, 1994; Shafir, 2011 and references therein). Sequential introduction or colony rotation could be applied in blueberry, especially in fields with mixed cultivars benefitting from cross-pollination, but it is unclear if any increase in pollination would offset the increased labor and transport costs. Many authors recommend placing colonies as close as possible to the crop and distributed as evenly as possible along the field to ensure effective and even pollination (Jay, 1986; Cunningham et al., 2016; Cavigliasso et al., 2021; Li et al., 2022), though these practices result in increased labor and transport costs for beekeepers and increased risk of pesticide drift. More investigations are required for creating recommendations on hive placement and density, so that target bee densities for maximum pollination and yields are achieved.

Alternative managed bees

Supplementing honey bees with other bee species can result in higher crop pollination (Rogers et al., 2013, 2014; Mallinger et al., 2021). Several researchers have investigated alternative managed pollinators for blueberry pollination (Table 1; Supplementary Table 3). Among the 16 species investigated other than the honey bee, 14 can be used in open field production, including 10 that are already commercially available, and four which have potential but require further investigation.

Bumble bees are the most widely used alternative managed pollinators of blueberry due to their ability to sonicate (King and Buchmann, 2003; Cardinal et al., 2018), frequency of collecting

TABLE 1 Alternative managed pollinator species other than the western honey bee (*Apis mellifera* L.) for highbush blueberry (*Vaccinium* spp.) pollination.

Part of the world	Species	Affinity for <i>Vaccinium</i> spp. pollen	Management status	Pollination performance compared to <i>A. mellifera</i>	Native range area
Northeast America	<i>Bombus impatiens</i>	Low to high	Currently managed	Improved	Northeastern America
	<i>Colletes validus</i>	High	Potentially manageable	Unknown	Northeastern America
	<i>Habropoda laboriosa</i>	High	Potentially manageable	Improved	Southeastern USA
	<i>Osmia lignaria lignaria</i>	Low to high	Currently managed	No improvement	Northeastern America
Northwest America	<i>Bombus huntii</i>	High	Currently managed	Unknown	Northwestern America, excluding extreme West
	<i>Bombus vosnesenskii</i>	Low	Currently managed	Unknown	Extreme West of North America
	<i>Osmia lignaria propinqua</i>	Low to high	Currently managed	No improvement	Northwestern America
	<i>Osmia ribifloris</i>	High	Potentially manageable	No improvement	Northwestern USA
South America	<i>Bombus pauloensis</i>	Unknown	Currently managed	Improved	South America
East Asia	<i>Apis cerana</i>	Unknown	Currently managed	Improved	East Asia
	<i>Anthophora villosula</i>	Unknown	Potentially manageable	Unknown	Eurasia
	<i>Megachile rotundata</i>	Low to high	Currently managed	Improved	Eurasia
	<i>Osmia cornifrons</i>	Low	Currently managed	Improved	East Asia
Europe	<i>Bombus terrestris</i>	Unknown	Currently managed	Improved	Europe
	<i>Anthophora villosula</i>	Unknown	Potentially manageable	Unknown	Eurasia
	<i>Megachile rotundata</i>	Low to high	Currently managed	Improved	Eurasia
Australia	<i>Tetragonula carbonaria</i>	Unknown	Currently managed	Unclear	Eastern Australia

See references listed in Supplementary Table 3.

blueberry pollen (Supplementary Table 3), ability to carry pollen on their bodies and deposit higher pollen loads on stigmas than honey bees (Dogterom, 1999; Rogers et al., 2013; Estravis-Barcala et al., 2021b; Sun et al., 2021), and ability to forage at lower air temperatures (Stubbs and Drummond, 2001; Tuell and Isaacs, 2010a). Usual stocking rates for bumble bee colonies range from 0.5 to 10 colonies per hectare (Tuell and Isaacs, 2010a; Estravis-Barcala et al., 2021b; Mallinger et al., 2021). While both bumble bees and the southeastern blueberry bee (*Habropoda laboriosa* Fabricius) can sonicate flowers (King and Buchmann, 2003; Cardinal et al., 2018), European leaf-cutting bees (*M. rotundata* Fabricius), orchard mason bees (*O. lignaria* Say), blueberry bees, and other bees are also able to collect pollen, deposit pollen on stigmas, and induce fertilization (Table 1; Supplementary Table 3). All the species also visit blueberry flowers for nectar (Stubbs et al., 1994; Dogterom, 1999; Javorek et al., 2002; Tuell and Isaacs, 2010a; Rogers et al., 2013; Estravis-Barcala et al., 2021b). Although nectar foragers are less efficient than pollen foragers for pollination (Javorek et al., 2002; Estravis-Barcala et al., 2021b), they can nevertheless carry pollen on their body (Dogterom and Winston, 1999; Hoffman et al., 2018; Estravis-Barcala et al., 2021b), contribute to blueberry pollination, and broaden the potential of alternative managed

species that can augment blueberry pollination. While the nest design for managed bumble bee colonies has been optimized for some species to make them commercially available, recent studies have also identified the preferred nesting material, nest hole diameter and attractant sprays to increase mason bee nesting success (Eraerts et al., 2022; Pinilla-Gallego et al., 2022). Further studies are required to optimize management and targeted application of solitary bees, especially ground nesting species (Cane, 1997; Mader et al., 2010; Leonard and Harmon-Threatt, 2019; Nelson et al., 2022), for blueberry pollination.

Precautions must be taken when considering honey bees and alternative managed bees outside of their native ranges, as they can become invasive and detrimental to native flora and/or entomofauna, or even for crop pollination (Goulson, 2003; Russo, 2016; Geslin et al., 2017b; Morales et al., 2017; Aizen et al., 2019, 2020; LeCroy et al., 2020; Russo et al., 2021). Managing bees within their native range can also be detrimental to wild entomofauna by competing for floral resources or nesting habitats, spreading pests and pathogens, eroding genetic diversity, and disrupting local adaptations by hybridization between native and commercial lines (Fürst et al., 2014; Lindström et al., 2016; Mallinger et al., 2017; Seabra et al., 2019; Bartomeus et al., 2020; Russo et al., 2021).

Wild pollinators and habitat enhancement

The contribution of wild bees and non-*Apis* insect pollinators depends on their pollination performance and abundance (Ne'eman et al., 2010). More specifically, this contribution can vary considerable from field to field, ranging from 12 to 82% (Isaacs and Kirk, 2010; see also Benjamin and Winfree, 2014; De Groot et al., 2015). A great diversity of wild bees has been found to visit blueberry flowers worldwide (De Groot et al., 2015; Martins et al., 2018; Graham et al., 2021a; Cortés-Rivas et al., 2022), and the pollination efficiency has been found to vary widely among bee species (Rogers et al., 2013, 2014; Sun et al., 2021; Cortés-Rivas et al., 2022) and blueberry cultivars (Cortés-Rivas et al., 2022). Differences in foraging behavior across pollinator taxa have been found in highbush blueberry cultivars as well (Courcelles et al., 2013; Estravis-Barcala et al., 2021b). Bumble bees and some solitary bees can sonicate and hence can release more pollen than honey bees and other insect pollinators who cannot sonicate (Buchmann, 1983; King and Buchmann, 2003; Cardinal et al., 2018; Cortés-Rivas et al., 2022). On the other hand, bumble bees and carpenter bees can sometimes steal nectar from blueberry flowers by using their mandibles to make a hole in the corolla and this foraging behavior reduces these species' pollination contribution (Sampson et al., 2004; Rogers et al., 2013), and can induce other bees to rob nectar (Dedej and Delaplane, 2004). Differences in pollination efficiency, foraging behavior, and abundance across different pollinator taxa can provide functional complementarity and stability for crop pollination when different taxa are present during the blueberry boom period (Blüthgen and Klein, 2011).

Although wild pollinators can contribute substantially to blueberry pollination, their abundance is often too low to fulfill commercial demands for pollination, especially in large fields (Isaacs and Kirk, 2010; Benjamin and Winfree, 2014; Gibbs et al., 2016). Variation in the abundance of wild bees visiting highbush blueberry flowers depends on many factors including production region (Gibbs et al., 2016), farm size (Isaacs and Kirk, 2010), farming practices (Nicholson et al., 2017; Mallinger et al., 2021), and the amount of semi-natural habitat (SNH) in the landscape around the farm (Gibbs et al., 2016; Nicholson et al., 2017). Increasing cover of intensive agriculture has a negative effect on wild bee visitation in blueberry fields (Benjamin et al., 2014; Nicholson et al., 2017), as agricultural intensification reduces species richness of pollinator assemblages and wild insect visitation (Klein et al., 2007; Garibaldi et al., 2011). In general, the amount of SNH enhances floral visitation by wild bees (Gibbs et al., 2016; Nicholson et al., 2017; Mallinger et al., 2021), but the landscape scale by which wild bees benefit from SNH depends on their body size. Smaller bees respond over shorter distances to local field conditions than those with larger body sizes that can utilize resources across the larger

landscape-scale (Benjamin et al., 2014). Conservation of SNH and implementing habitat enhancements near blueberry fields is therefore advised to provide nutritional and nesting resources for wild bees and boosting their local populations.

It has been recommended that agricultural landscapes should have at least 20% SNH to support agricultural productivity by improving pollination and other ecosystem services (e.g., as well as enhancing soil nutrition, pest control, and/or preventing floods and regulating climate; Garibaldi et al., 2021). Beyond conservation of SNH, pollinators and pollination also benefit from increasing landscape diversity (Martin E. A. et al., 2019), which has been found to support wild bee communities and their corresponding pollination services in blueberry. Reducing blueberry field size (Isaacs and Kirk, 2010), providing mass-flowering crops with complementary phenologies (Martins et al., 2018; Eeraerts, 2022), and reducing agricultural management intensity (e.g., organic management; Nicholson et al., 2017; Mallinger et al., 2021) are additional ways to promote landscape diversity and pollination by wild bees. Honey bee health will also benefit from the alternative forage provided by SNH and habitat enhancement efforts (Couvillon et al., 2014; Danner et al., 2017).

Creating SNH at larger scales may not be a plausible option for a single farmer given a lack of space as well as financial and logistical constraints (Osterman et al., 2021c). Decreasing agricultural intensity for pollination may also not be a realistic option for commercial blueberry growers. However, incorporation of small-scale habitat elements is one promising way to encourage wild bees. For example, hedgerows composed of linearly shaped plantings with flowering woody and herbaceous plants as well as flower strips of herbaceous plants placed at field margins do not take much land area and can be of high value to native pollinators, particularly if plant species are locally adapted (Garibaldi et al., 2014; Albrecht et al., 2020). The contribution of flower strips to blueberry pollination and yield has been investigated, with Blaauw and Isaacs (2014) concluding that these plantings can support higher crop yields 3 years after seeding, and are economical, even when considering the costs of establishment and maintenance. Careful selection of plant species is essential and should be done to support key pollinators of blueberry (Eeraerts et al., 2021; Windsor et al., 2021) while minimizing their potential to serve as alternative hosts to blueberry pests and diseases. An evaluation of hedgerows has not been carried out to date for blueberry systems and is challenging experimentally because it takes a considerable time for establishment and to observe the effects on pollinators and pollination (e.g., Morandin and Kremen, 2013). Nevertheless, the impacts of hedgerows and other perennial plantings on pollinators and pollination in blueberry should be studied as these elements can provide floral resources throughout the year (Timberlake et al., 2019), nesting habitat for wild bees (Eeraerts et al., 2021), and have great potential to enhance pollination

without requiring significant land area and changes to in-field production practices.

Wild bees, as well as alternative managed bees, are an important component of ICP and can complement honey bees as some of these non-*Apis* bees forage in suboptimal weather conditions, or early morning and late afternoon, when honey bees are less likely to forage (Tuell and Isaacs, 2010a; Rogers et al., 2013, 2014). Furthermore, wild bees may forage in different parts of the plant canopy and may also improve the foraging behavior and pollination efficiency of honey bees in some crop systems requiring cross-pollination (Tuell and Isaacs, 2009; Brittain et al., 2013; Eraerts et al., 2020). A mechanistic explanation regarding the positive interactive effect of non-*Apis* bees on honey bees is not entirely clear, but likely includes direct interactions between different kinds of bees during flower visitation (Greenleaf and Kremen, 2006; Carvalheiro et al., 2011) and indirect interactions between bees due to scent marks deposited on flowers after they have been visited (Stout and Goulson, 2001). This functional complementarity of foraging behavior contributes to the benefits of combining honey bees and non-*Apis* bees and their corresponding pollination contribution (Blüthgen and Klein, 2011). So far, these interactions between honey bees and non-*Apis* bees have not been investigated in blueberry but are expected to be similar.

Environmental factors

Temperature is a key driver of plant processes related to pollination such as bloom timing, bloom duration, pollen germination, pollen tube growth, ovule viability, flower longevity, and duration of flower receptivity. Studies investigating the effects of temperature on blueberry physiology are limited, especially as it relates to flower biology and reproduction, but are needed to inform adaptation strategies as the climate changes. Kirk and Isaacs (2012) compared blueberry bloom phenology in field-planted and greenhouse-potted bushes and found that flowering of potted bushes was delayed by ~100 growth degree days (GDD), which was likely attributed to potted bushes receiving a lower number of chilling hours than those assessed in the field. As climate change intensifies, the number of chilling hours experienced by blueberry plants will decrease in many key production regions and will likely impact bloom timing and characteristics. Variation in blueberry bloom timing may lead to complications with pollination such as phenological mismatch with the emergence of wild spring pollinators, and difficulties in predicting timing of honey bee hive placement.

Among the stages of plant reproductive development, sensitivity to heat extremes has been observed during pollen development, pollen germination, and pollen tube elongation for various crop plants (Mesihovic et al., 2016). However, pollen performance in blueberry is not well characterized

(Yang et al., 2019; Gan et al., 2020). Gan et al. (2020) explored pollen germination and pollen tube length for four commercially relevant northern highbush blueberry cultivars at 2, 7, 13, 18, and 24°C and found that germination generally increased from 2 to 24°C across all cultivars (besides “Liberty”, which peaked at 13 and 18°C). Pollen tube growth increased linearly across all cultivars from 2 to 24°C. Yang et al. (2019) assessed pollen germination and tube growth of “Gardenblue” rabbiteye blueberry in “Brightwell” pistils *in situ* and found that after 24 h over 90% of pollen on styles had germinated at 15, 20 and 25°C, while at 10, 30, and 35°C the percentage of the style with germinating pollen was 72, 63, and 57%, respectively. This study also reported that pollen failed to fully transverse the style at 35°C. Further limiting fertilization success, the same study reported that hot conditions at 30 and 35°C accelerated “Brightwell” ovule degradation after only 4 h and 74–100% after 120 h of exposure to these temperatures. Cooler temperatures (0 and 5°C) had less impact on “Brightwell” ovule degradation. Further investigations should explore thermotolerance capacities of blueberry pollen and ovaries for commercially important cultivars and develop an understanding of how environmental conditions can be incorporated into ICP programs for this crop.

Pesticide stewardship

During bloom, blueberry plants are susceptible to various fungal diseases such as mummy berry [*Monilinia vaccinii-corymbosi* (Reade) Honey], anthracnose (*Colletotrichum* spp.), and botrytis (*Botrytis cinerea* Pers.), and they can also become infected by viruses (Polashock et al., 2017). Blueberry fields may also need protection from insects including aphids that transmit viruses, fruitworm larvae that bore into developing berries, and various moth larvae that can defoliate bushes at this time of the season. Integrated pest management programs that incorporate monitoring, predictive models, resistant cultivars, and cultural controls have been developed to reduce the risk of economic injury from these pests (Rodriguez-Saona et al., 2019), but pesticide applications remain a common and frequent input in most blueberry production regions.

Bees can be exposed to pesticides via direct exposure during application, from landing on treated surfaces, through contaminated nectar and guttation fluid, and by residues collected in pollen and nectar. Pesticide residues are common in commercial honey bee colonies used for pollination (Mullin et al., 2010). In a recent study in Michigan blueberry farms, 22 pesticides were detected on average in pollen samples collected from bumble bee and honey bee colonies during bloom, even at sites that were not being sprayed (Graham et al., 2021b). As expected, the highest concentrations detected were pesticides applied during bloom, but the 80 identified active ingredients

also included various other pesticides likely collected from outside of blueberry farms. The chemical residues and their high concentrations highlight the need for development and adoption of practices that minimize the need for pesticide applications during crop flowering, combined with widespread awareness of exposure from neighboring lands.

Given their direct toxicity (Johnson et al., 2010) and potential to contribute to the stresses experienced by wild and managed bees (Goulson et al., 2015; Sánchez-Bayo et al., 2016), application of the most toxic insecticides is restricted during bloom. These limits, however, do not completely prevent risk of harm to bees and other pollinators. First, many wild pollinators have flight periods that extend before and after blueberry bloom, so they may not be protected by restrictions limited to bloom time. Label restrictions are also only for the few pesticides known to be acutely toxic, and not for the multiple other agrichemicals that can cause sublethal effects. Finally, pesticides applied elsewhere provide additional exposure routes for bees foraging outside the blueberry farms.

While it has been shown that wild bee communities in blueberry fields are less diverse in farms with higher pesticide toxicity (Tuell and Isaacs, 2010b), more research is needed to understand the effects of pesticide use on pollination outcomes. Many aspects of pesticide risk are profoundly understudied (Cullen et al., 2019), including combination exposures, synergistic effects (Siviter et al., 2021), effects of adjuvants and inactive ingredients (Straw et al., 2022; Wernecke et al., 2022), effects on developing bees (Claus et al., 2021), and effects on wild bees. Pollinator health risks from fungicides should be especially examined because exposure rates are so high (Graham et al., 2021b), and new research shows harm from fungicides to both bumble bees (for example Bernauer et al., 2015) and honey bees (Fisher et al., 2021). The Integrated Pest and Pollinator Management framework (Biddinger and Rajotte, 2015) can help balance the economic implications of spending money on pest control inputs vs. conserving wild pollinators and protecting honey bees. This approach can be tailored to blueberry settings using the regionally relevant community of insect and disease pests combined with the economics of pesticide and pollinator inputs (Egan et al., 2020).

Economic value of Integrated Crop Pollination

Successful application of integrated blueberry pollination strategies at the farm level will need to encompass economics to ensure farms remain profitable. The benefits of pollination in agricultural settings are typically measured in terms of crop yield and quality. For example, Rollin and Garibaldi (2019) conducted a meta-analysis of 22 studies, involving various crops grown in different countries, to examine the impact of honey bee densities on crop productivity variables such as fruit set,

seed set, fruit weight, and yield. They found that increased colony density and visitation rates augmented all productivity variables to a certain optimum, after which more honey bees do not increase pollination and yield any further. Several other studies documented positive linkages of pollination and crop productivity (see previous sections above). However, there are costs associated with implementing any pollination strategy and it is critical that benefits exceed costs to ensure a return on investment.

In the U.S., Hellerstein et al. (2017) conducted a national survey in 2015 and showed blueberry ranked third in terms of highest demand for honey bee pollination with rankings based on the total pollination fees paid for each crop determined by the total number of colonies used, price per colony, and total acreage pollinated. Only almond and apple (*Malus domestica* Borkh.) preceded blueberry, highlighting the significance of blueberry pollination. The *insect pollination economic value* (IPEV) of honey bee is known to be high (Morse and Calderone, 2000; Reilly et al., 2020; Jordan et al., 2021). Reilly et al. (2020) estimated the IPEV of seven crops [almond, apple, blueberry, pumpkin (*C. pepo* L.), sweet cherry (*Prunus avium* L.), tart cherry (*P. cerasus* L.), and watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai)] in major producing areas in the U.S. and placed it at ~\$6.4 billion by managed honey bees and \$1.5 billion by wild bees, with wild bees contributing \$50 million in blueberry. Jordan et al. (2021) considered all insect pollinators and estimated an average IPEV of \$34 billion for 75 crops across the U.S.

Insect pollination economic value estimates pertain to direct benefits of pollination services. However, there are limitations to the IPEV, such as the assumption of static pollination densities and constant dependency coefficients despite the crops being planted in different fields, production regions, and years (Melathopoulos et al., 2015). Also, there are indirect benefits to the environment (spillover pollination from surrounding landscapes), consumers (nutrition), and downstream industry sectors (e.g., livestock feed, food processing, consumer products) that must be considered to capture a full accounting of the economic benefits of crop pollination. Hence, values provided by the above studies can be considered conservative estimates but are useful to start framing the economic importance of pollinators. More holistic economic assessments that implement all components of ICP are also lacking. Consequently, comparing the costs of implementing an ICP framework to the contribution of improved pollination on the productivity of the cropping system are needed to determine its value for farmers.

Despite the economic value of wild bees in blueberry systems (Reilly et al., 2020), pollinator habitat establishment costs are perceived to be high and this in turn can be a barrier to implementing habitat elements that would benefit wild pollinators on farms (Garbach and Morgan, 2017). However, a multi-year study showed yield and profitability of blueberry fields adjacent to native wildflower plantings were greater than

fields without wildflowers and wildflower establishment costs could be recovered within 3–4 years (Blaauw and Isaacs, 2014). Landscape and management can influence the costs and benefits of maintaining or converting land into natural habitat that could benefit wild pollinators and their services (Magrath et al., 2019), underscoring the need for a robust understanding of these systems to develop accurate estimates for economic valuation. Of note is that blueberry is a perennial crop managed intensively for pest control. Pollinator habitat is typically located in non-arable land outside the crop fields. In some instances the extent of non-arable land can be considerable, but elsewhere, it may be limited. In these situations there may be direct and indirect opportunity costs that provide only small, private benefits to the grower making the investment (Lonsdorf et al., 2020). Few studies, in fact, have calculated the opportunity costs associated with converting land to other valuable uses. Some scenarios show the opportunity costs may outweigh the benefits accrued from additional wild pollination services (Magrath et al., 2019). More research should be dedicated to estimate opportunity costs against wild pollination benefits across different blueberry growing regions.

Decision aid systems

Effective implementation of improved blueberry pollination strategies that maximize profit may be aided by advances in and implementation of technologies like Big Data, Remote Sensing, Artificial Intelligence, and Cloud Computing which support “Agriculture 4.0.” This is poised to enable growers to be more efficient and economical in their production of quality crops while minimizing potential harms to agroecosystems through informed decisions when it comes to implementation of various agricultural practices. Decision aid or decision support systems (DAS or DSS, respectively) are tools that encompass quantitative models inside interactive software applications and can assist growers in making complex, evidence-based, and precise decisions (Jones et al., 1998). Effective utilization of DAS depends on upstream efforts to formulate models that provide predictions with sufficient accuracy and deliver resultant information in user-friendly platforms. The careful selection of model inputs, both decision variables and predictors, is an essential component of constructing a DAS that can effectively compare different courses of action. Model inputs may include historically collected data, routinely updated data streams, user input, and should be chosen to balance model accuracy with the cost efficiency and reliability of inputs (Zhai et al., 2020).

For optimization of pollination and yield in blueberry, a DAS should predict changes in crop pollination and yield components based on changes in managed and wild bee populations. In its simplest form, this model might be characterized by estimating the effect of pollinator density on pollinator visits, the effect of pollinator visits on fruit set, seed set, and berry size, and the impact of these three quantities

on yield. The impact of the number of honey bee hives on blueberry yield can depend on the densities of other bees in the surrounding area (Eaton and Nams, 2012). Thus, a DAS would likely benefit from including user inputs or data that characterizes wild pollinator populations in the surrounding area and components of ICP.

If a DAS is to be used to time the placement of honey bee colonies, it may be advantageous to model the timing of blueberry anthesis (Kirk and Isaacs, 2012). Phenology timing may be modeled based in part on temperature and heat accumulation to capture phenological effects on pollinator behavior as well as limit pollinator effects to the bloom window. Furthermore, as pollination is heavily weather dependent, the effect of meteorological variables on pollinator foraging activity and crop reproduction can be integrated too (Tuell and Isaacs, 2010a). Cultivar effects should also be accounted for given floral morphological traits and subsequent visitation rates by bees varies by cultivar (Courcelles et al., 2013).

The DAS approach has been developed in some cropping systems for pest management and irrigation to improve water use efficiency (Samietz et al., 2007; Jones et al., 2010; Bonfante et al., 2019). DAS is starting to be used to inform pollination-related decisions and could be a valuable tool for ICP. BEE-STEWARD is one research and decision-support software tool that can show how different environmental variables impact wild bumble bees in the landscape (Twiston-Davies et al., 2021). Climate-induced declines in fruit set in bog blueberry (*Vaccinium uliginosum* L.) has also been predicted to be mitigated with increases in honey bee and bumble bee densities using predictive modeling approaches based on the transfer learning concept to solve for data deficiency problems (Qu et al., 2021). More recently, an agent-based model was used in kiwi [*Actinidia chinensis* var. *deliciosa* (A. Chev)] to track and predict pollination outcomes in a dioecious crop under a range of management scenarios (Broussard et al., 2022). Similar approaches and platforms may be used to aid growers in making decisions integral to successful pollination. However, issues of interoperability, scalability, accessibility, and usability need to be addressed (Zhai et al., 2020). Other relevant challenges identified by Zhai et al. (2020) include adapting to uncertainty and dynamic factors to provide accurate decision support, incorporating knowledge from experts, enabling prediction and forecasts to enhance farm planning, and using historical information. Furthermore, release of DAS tools to growers needs to be synergized with extension education programs and training to ensure successful utilization.

Conclusion

Development of an integrated approach to sustainable blueberry pollination will require a thorough understanding of cultivar-specific pollination requirements within traditional and new production regions. Coordinated use of managed honey

bees, wild pollinators, and alternative managed bees where their use provides a return on investment will ensure resilience in blueberry pollination systems. However, this coordination should be integrated with an awareness of how horticultural factors, habitat enhancement, and pesticide stewardship also influence pollination and yield. At the same time, adoption of improved blueberry production systems will be most likely if their profitability can be documented, so there is a need to measure the costs of inputs and the value of returns to determine the economic viability of ICP approaches. Multidisciplinary research that includes the perspectives and experiences shared by growers, beekeepers, and extension/crop advisors will be needed to address knowledge gaps and translate information gained into practice at the farm level. Key gaps requiring research focus in honey bee dominated systems are the integration of wild and alternative managed pollinators to benefit from their pollination contribution, particularly when weather is suboptimal for honey bees. At the same time, honey bees are integral pollinators and research on efficacious honey bee deployment as a function of colony size, hive density, crop demand, and landscape structure are needed while encouraging pollinator recruitment and minimizing the potential negative effects on native insect populations. Research on habitat enhancement and landscape modification will also be needed to support all pollinators and attention should particularly be focused on how to realistically and economically achieve this at commercial scales. While pesticide stewardship is a relatively well-defined component of ICP, the role of horticultural practices remains ambiguous and will be an important area of future research. Many plant and soil factors seemingly independent of pollination may influence yield and crop quality outcomes in blueberry. Understanding and optimizing these factors within the ICP framework is expected to promote long-term crop yield and quality while enhancing growers' returns on their investments. With increasing availability of on- and off-farm data, statistical models, and software tools, there is also potential that the complexity of applying ICP on commercial blueberry farms could be simplified and made more accessible to growers and consultants. This could be accomplished through effective use of DAS that leverages existing and emerging information, adding new layers, and improved function as new research is completed. This must be blended with education and extension programs that encourage adoption, make adjustments when needed, and foster implementation to provide for more evidence-based blueberry pollination systems.

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Author contributions

LWD, RI, REM, SG, and AM procured funding. LWD, ME, and RI created the framework of the article. SC created tables (including [Supplementary Tables](#)) and KB created the figure and graphical abstract. All authors contributed to review of the literature, writing, critical review, and gave final approval for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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