

IS EARLY SEASON POLLINATION TO LOWBUSH BLUEBERRY AN
ECOSYSTEM SERVICE OR DISSERVICE?

by

Laurel Schut

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ABSTRACT

Insect-mediated pollination is frequently identified as an important ecosystem service to agricultural production. In contrast, ecosystem disservices are rarely considered. Using selective exclusion of early season (wild) versus late season (wild and managed) pollinators, this study explores the potential for early season pollination disservice on commercial lowbush blueberry production (*Vaccinium angustifolium*). Contrary to the hypothesis of disservice, the results indicate that early season pollinators are important to production; pre-harvest berry drop, shatter, and sugar content were consistent across pollination treatments, even though early season pollinated plots exhibited heavier berries. Ancillary results found that (1) early flowering clones were more productive than late flowering clones, and (2) that shatter was extremely high, outweighing ripe yield. Though a disservice was not identified, it is hoped that this thesis prompts other industries to critically evaluate the alignment (or misalignment) of pollination and harvest that may inadvertently lead to disservice and decreased yields.

LIST OF ABBREVIATIONS USED

Bx	Brix
EC	Early Clone
EPO	Early Pollination Only
g	Grams
kg	Kilograms
LC	Late Clone
LPO	Late Pollination Only
MEA	Millennium Ecosystem Assessment
SCOPE	Scientific Committee on Problems of the Environment
WHO	World Health Organization

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I came to this graduate research as an International Development Studies (IDS) scholar. During my undergraduate degree, I became particularly interested in understanding the linkages of global food systems to food security. This led me to my honours undergraduate research on fisheries transitions and the challenges of sustainable certification processes for small-scale producers in Vietnam. While this previous work on sustainable fisheries may not seem related to the graduate research presented herein, the common thread is a critical engagement with the issue of *food availability*, one of the three key pillars towards ensuring food security (the other two being *food access* and *food use*) (WHO, 2006).

My interest in pollination specifically began during an international exchange to the University of Sydney, Australia. While abroad, I attended a panel discussion entitled “*Food Security Needs Bee Security*” as part of the 2011 Sydney Food Festival. The panel presented a seemingly simplified underpinning of a complex set of problems (food security) to one problem (bee security), which left me simultaneously fascinated, alarmed, and keen to learn more. Five years later, this graduate research has afforded me the opportunity to expand my knowledge and interest of food systems, critically engage with an amazingly complex topic (plant-pollinator interactions), and develop new skills to complement my social science background.

More broadly, pollination and its connection to ongoing food security concerns has recently attracted considerable attention. Its rise in the public spotlight links inextricably links food security to pollinator health (Allen-Wardell et al. 1998; Kevan et al. 2001; Kevan & Phillips, 2001; Potts et al. 2010; Kevan & Menzel, 2012; Bailes et al. 2015). In addition to peer-reviewed literature, popular media outlets such as TIME Magazine, BBC, The New York Times, and National Geographic have all ran stories in the last three years alone on how pollinators provide an irreplaceable yet threatened ecosystem service that must be valued and protected. But the complexity of these problems needs to be grounded in very specific phenomena.

In this thesis, I use lowbush blueberry in Atlantic Canada as a study system to examine how early season versus late season pollination in a managed agro-ecosystem influences yield, and more specifically, test whether early season pollination (that which occurs before the introduction of managed pollinators) may instead function as an ecosystem *disservice* that decreases crop productivity in this particular context. Though lowbush blueberry is not a ‘staple food’ and thus not critical towards maintaining food security, this crop serves as an excellent study system because it is highly managed, requires biotic pollination, and has a relatively long bloom period. As such, in comparison to other commercial crops with shorter bloom periods, lowbush blueberry’s relatively long bloom allows for more nuanced testing of how early versus late season pollination influences yield. To the best of my knowledge, this is the first study that examines how pollination timing (early versus late season) influences final yield outcomes in a heterogeneously blooming commercial fruit crop. As a result, I hope that this thesis research serves as an exemplar for other managed crops that require biotic pollination,

and prompts other industries to critically evaluate the alignment (or misalignment) of pollination and harvest that may inadvertently lead to disservice and decreased yields.

1.1 Food security via Managed Agro-Ecosystems

While the noun is singular, food security is not a single problem. Current debates on food security show a wide array of perspectives on the issue. For example, some argue that current levels of food production will not meet the needs of a growing global population (Ehrlich, Ehrlich, & Daily, 1993; Tilman et al. 2011), while others argue that it is instead more of an issue of adequate food distribution (Godfray et al. 2010). Some push for a strengthening of global trade (Gillson & Fouad, 2015), while others believe that global trade makes countries more vulnerable to food price shocks and other food security challenges (Suweis et al. 2015). Still others argue that national food security programs are imperative (Toledo & Barbara, 2006). And there are a range of opinions on whether globalization will worsen or solve the persistence of food insecurity and poverty in rural communities (Wade, 2004; Hill & Rapp, 2009). These are just a few examples – there are many more points of concern, each with their own handful of diverse perspectives.

Food security has been defined as existing “when all people at all times have access to sufficient, safe, nutritious food to maintain a healthy and active life” (World Health Organization, 2006, p. 1). As outlined by the World Health Organization (WHO, 2006), it can then be broken down further into three main pillars: food *availability* (sufficient quantities of food available on a consistent basis), food *access* (having sufficient resources to obtain appropriate foods for a nutritious diet), and food *use*

(appropriate use based on knowledge of basic nutrition and care, as well as adequate water and sanitation).

Continued agricultural production is therefore a critical component to ensuring continued food availability, the first pillar of food security. Indeed, aggregate world food production has grown by 145% since the 1960s (FAO, 2009). This increase in production, commonly referred to as the ‘Green Revolution’, was the result of several important shifts in production, including the development of new high-yielding crop varieties, the expansion of irrigation infrastructure, and the application of new fertilizers and pesticides (Evenson & Gollin, 2003; FAO, 2015). Although certainly true for agricultural production in general (however basic), modern commercial agriculture has become an especially managed system, or agro-ecosystem, that is operated with specific intentions of desired results (Swinton, 2008, p. 28). Such managed agro-ecosystems are characterized by a continuous feedback loop in which human behaviour influences ecosystem function, ecosystem function impacts ecosystem services, and ecosystem services then effect human behaviour (Daily, 1997; Antle & Capalbo, 2002; Swinton, 2008; Fig 1).

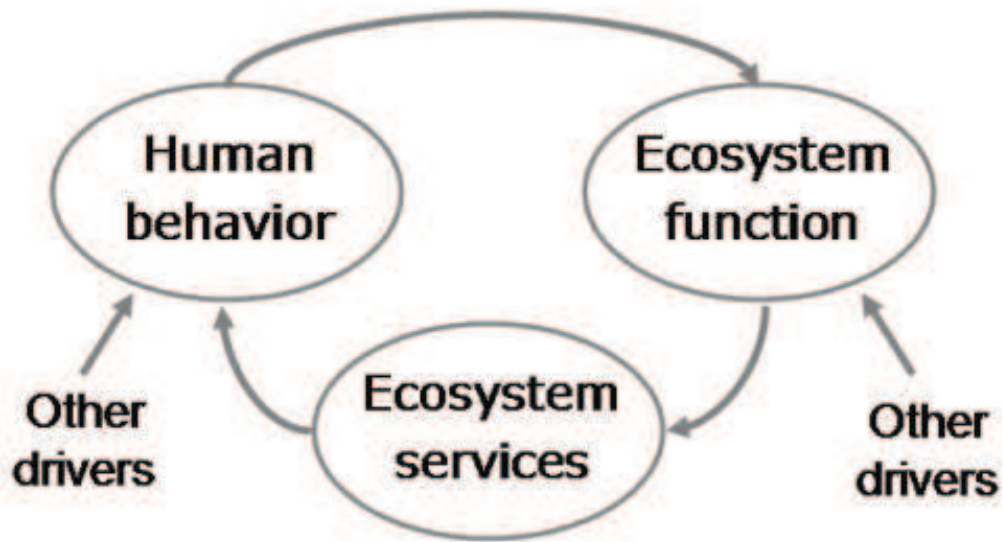


Figure 1. Relationship between human behaviour, ecosystem function, and ecosystem services. Adapted from Daily (1997) by Swinton (2008).

In other words, human can intentionally or unintentionally affect processes in natural systems (Antle & Capalbo, 2002, p. 7). As Swinton (2008, p. 28) describes,

What ecologists call “human disturbance” agriculturalists call “management.” But farmers who manage those ecosystems influence flows of many ecosystem services, whether they think about it or not.

But what are the potential consequences of shifting food production to intentionally *managed* systems, when not all aspects of production are, nor can be, actively regulated or controlled? Pollination is an excellent example of this challenge.

Plants achieve pollination through a range of abiotic and biotic mechanisms. Abiotic mechanisms include wind pollination (anemophily) and water pollination (hydrophily). Biotic pollination is very important for the reproduction of wild angiosperms and many crops (Klein et al. 2007). Pollinators as biotic agents, or vectors, move pollen from the male anthers of a flower to the female stigma of a flower, therein facilitating the act of plant fertilization (syngamy) (Mauseth, 2008). Pollinators are therefore widely recognized as an important input to agricultural production (Klein et al. 2007; Winfree et al. 2011; Lautenbach et al. 2012), especially in light of the Green Revolution's intensification of production (Aizen et al. 2008). Recently, there has been a disproportionate increase in the land cultivated for pollinator-dependent crops, and global demand for these crops has increased (Aizen et al. 2008). To accommodate demand, many managed agro-ecosystems manipulate and manage specific pollinator species, most commonly honeybees (*Apis mellifera*), which are either maintained by farmers themselves or rented and transported as a piece of the managed agro-ecosystem model of current agricultural production (James & Pitts-Singer, 2008; vanEngelsdorp & Meixner, 2010). However, thousands of wild (unmanaged) pollinator species exist (Michener, 2000). Of these, bees are the most common, but others include certain species of: ants, butterflies, wasps, flies, birds, bats, rodents, monkeys, lizards, and snakes (Cruden & Hermann-Parker, 1979; Herre, 1989; Gautier-Hion & Maisels, 1994; Oleson & Valido, 2003; Fleming, Geiselman, & Kress, 2009; Oilerton, Winfree, & Tarrant, 2011; Rader et al. 2015). In many settings, wild pollinators may be native species but can also include a suite of non-native, naturalized species (Crane, 1982; Goulson, 2010). Importantly, these wild species provide their pollination services to the process of human agricultural production free of charge. Understanding how these unmanaged wild pollinator species

contribute in highly managed agro-ecosystems is an important part of understanding the consequences of our deliberate management strategies.

1.2 The Rise and Popularization of Ecosystem Services

Since the 1990s, ecosystem services have become an increasingly popular way to conceptualize the numerous direct and indirect benefits of ecosystems on human wellbeing (Costanza et al. 1997; Daily, 1997; Millennium Ecosystem Assessment, 2005). The first chapter in Daily's 1997 publication of *Nature's Services: Societal Dependence On Natural Ecosystems*, a cornerstone publication of the ecosystem service literature, defined ecosystem services as "the conditions and processes through which natural ecosystems, and the processes that make them up, sustain and fulfill human life" (p. 3). Shortly thereafter, the Millennium Ecosystem Assessment (MEA) described ecosystem services as "the benefits people obtain from ecosystems" (MEA, 2005, p. V). The MEA categorized ecosystem services into four classifications: provisioning services (such as water), regulating services (such as flood control), cultural services, and supporting services (such as nutrient cycling) (MEA, 2005, p. V).

Although idea of ecosystem services has gained substantial momentum from the 1990s onward, the concept is not new. Even at the time of its rise in popularity, academics recognized the ongoing history of ecosystem services. In the second chapter of Daily's 1997 publication, Mooney & Ehrlich (1997) note that "the notion that natural ecosystems help to support society probably traces back to the time when our ancestors were first able to have notions" (p. 11). They argue that its origins can be more formally traced back to 1864, with George Perkins Marsh's publication of *Man and Nature*, and is

again revisited by Leopold (1949), Carson (1962), the *Study of Critical Environmental Problems* (1970), and SCOPE (Scientific Committee on Problems of the Environment) (1991), among others.

Ecosystem services can also be interpreted from various vantage points. Many scholars frame ecosystem services as beneficial ecosystem functions with an objective to increase public attention to biodiversity conservation strategies (Chan et al. 2006; Armsworth et al. 2007; Turner et al. 2007). Others focus more attention on methods that estimate ecosystem service monetary value (Costanza et al. 1997; Heal, 2000; Fisher & Turner, 2008; de Groot et al. 2012), arguing that they should be incorporated into “the total economic value of the planet” due to their direct and/or indirect contributions to human welfare (Costanza et al. 1997, p. 253). The MEA argued strongly that ecosystem services be implemented into policy measures, and ecosystem services have since appeared in economic decision-making, including Markets for Ecosystem Services and Payments for Ecosystem Services schemes (Engel et al. 2008; Gómez-Baggethun et al. 2010).

1.3 Pollination as an Ecosystem Service

Plants vary in their dependence on biotic pollinators. Some, such as lowbush blueberry, cucumber, pumpkin, and mango (among others), rely on pollinators for virtually 100% of their pollination and subsequent fruit production and are described as *pollinator dependent* species. To a lesser extent, pollinators also benefit *pollinator-mediated* plant species, which are self-fertile but receive some benefit (ranging from minimal to substantial) from animal pollination, either by increasing quantity and/or

quality of fruit production (Richards, 2001; Winfree, 2008; Aizen et al. 2009). Pollinator-mediated crops include oil-seed rape, sunflowers, cotton, pepper, and tomatoes, among others (Richards, 2001). Furthermore, although most monoecious (separate male and female flowers on the same individual) species are self-fertile and wind-pollinated, productivity of some monoecious plants is enhanced by insect visitation (i.e. coconut) (Richards, 2001).

As a provisioning ecosystem service, Klein et al. (2007) found that 20% of current agricultural production in terms of volume comes from crops whose production is enhanced to some degree with pollination, 15% from crops that increase seed production with animal pollination (the distinction between pollinator-mediated and pollinator dependent was not given), but that the large majority (60%) of current agricultural production is from pollinator independent crops, such as cassava, corn, rice, potato, wheat, and yam (with 5% left unevaluated). Using Klein et al.'s estimates of the proportion of crop production dependent on animal pollinators, Eilers et al. (2011) found that the large majority of calories (78.83%) in the human diet from agricultural crops are derived from pollinator *independent* crop production, with 18.59% from pollinator mediated crops, and only 2.58% from crops that are pollinator dependent. This illustrates humanity's overwhelming reliance on pollination independent crops, which coincides with the doubling of production of staple crops in the past 50 years as a result of new crop strains, agrochemicals, irrigation, and new agricultural techniques (Shetty, 2011). What is remarkable is that despite the relatively minimal contribution to overall global production in terms of volume, the trend in popular media and culture has been to prioritize bees as a requirement for ongoing food security and an important, and overwhelmingly positive, ecosystem service.

However, it should be noted that certainty in dependency studies is difficult to achieve. Melathopoulos et al. (2015) examined the studies upon which Klein et al. (2007) based their analyses and found that for many crops, estimates of dependency were based upon singular studies, often with only one cultivar represented per crop, on one field, and/or in one country. These estimates of dependence therefore present a static assessment of pollinator influence, and are poorly equipped to consider how consumer choices, farming patterns, and agricultural technology would respond to changes in pollination services (Melathopoulos et al. 2014a).

Yet despite this uncertainty, pollination continues to be highlighted as a monotonically positive ecosystem service in scholarly discourse and as a trending issue in mainstream media. Rarely are the possible negative consequences of such ‘services’ on human wellbeing ever considered, especially in the managed agro-ecosystem context. But as Swinton (2008) states, “farmers who manage those ecosystems influence flows of many ecosystem services, whether they think about it or not” (p. 28). Agricultural management decisions do not exist in a void. For every action, there is a reaction – and they may not always produce positive consequences.

1.4 Ecosystem Disservices

Similar to ecosystem services, the idea that non-human life and ecosystem processes can *harm* us is conceptually as old as human society. Shortly after ecosystem services’ rise to popularity in the literature, other scholars began to examine the ecosystem service framework from a more critical lens, specifically the overwhelming and problematic tendency to consider only the positive values of ecosystems (Zhang et al.

2007; Dunn, 2010). Assuming that ecosystems provide only positive externalities is to ignore half of the picture – to choose to see only the good and not the bad (Dunn, 2010). According to these critiques, ecosystem service scholarship needs to expand its scope and acknowledge that nature also provides us with many *disservices* that can inhibit human development and economic growth by reducing productivity and/or increasing production costs (Zhang et al. 2007). Others argued that in addition to economic costs, ecosystem disservices can be even more detrimental to humans – pathogen prevalence is a salient example that nature can “often harm and kill us” (Dunn, 2010, p. 555).

While the concept of ecosystem disservices presents the opposite side of the coin to ecosystem services, understanding what exactly is being referred to is important. Thus, while ecosystem *services* point to the *positive* effects that ecosystems provide human well-being, ecosystem *disservices* refer to the *negative* effects that ecosystems have *on humans*. As a result, most disservice literature to date has focused on human-dominated ecosystem types, such as agricultural landscapes and urban environments (Döhren & Haase, 2015).

Ecosystem services that are typically described in modern agro-ecosystems include pollination, regulation of soil and water quality, support for biodiversity, and cultural services (Power, 2010; Swinton et al. 2007), but this is challenging given the nature of the setting. For example, if producers are actively inputting managed, rented pollinators into their landscapes, should they still be viewed as an positive *ecosystem* service to production, even though they not a product or function of the surrounding ecosystem? Similarly, should cattle be viewed as ecosystem services for their nutrient production and grazing, or as economic investments that already have associated costs?

Ecosystem disservices to agro-ecosystems, on the other hand, can also take many forms, and usually inhibit economic growth to agriculture by reducing productivity and/or increasing production costs (Zhang et al. 2007). These can include pest damage, competition for water from other ecosystems, and competition for pollination (Zhang et al. 2007), but also sedimentation of waterways and increases to greenhouse gas emissions (Power, 2010). From this literature, I identify dichotomous pairings of services and disservices in managed agro-ecosystems: regulation of water quality but also nutrient runoff and sedimentation of waterways; support for biodiversity but also habitat loss and poisoning of non-target species; pollination but also competition for pollination, and so on. What appears to be occurring, at least in the case of some phenomena, is a *sliding scale of service to disservice*. As Zhang et al. (2007) observe,

The flows of these services and disservices directly depend on how agricultural ecosystems are managed and upon the diversity, composition, and functioning of remaining natural ecosystems in the landscape (p. 253).

Yet the notion that pollination could be an ecosystem disservice to agricultural production is far less represented. The work by Zhang et al. (2007) identifies competition for pollination as a possible disservice, in that nearby flowering non-crop plants may detract from overall crop pollination, and other authors have identified possible competition *between* pollinators, with varying results (Bushmann, 1996; Steffan-Dewenter & Tschardtke, 2000). More recently, Klein et al. (2015) found that excess pollination can reduce fruit quality and the production of leaves for photosynthesis in fruit tree performance. Klein et al. (2015) provide a highly relevant example of how common practices in industrial agricultural production can actually give rise to these disservices in the first place. Perhaps the most well established example of pollination disservice, although frequently not identified as such, is the excess pollination that occurs in apple,

pear, etc., that results in fruitlet thinning. These insect-pollinated crop species commonly set more fruit than optimal from an economic production perspective (Bos et al., 2007a; Bos et al., 2007b). When this occurs, growers may mechanically or chemically thin flowers and/or fruitlets in order to alter resource allocation and increase fruit size, value, and quality at harvest (Free, 1993; Jackson, 1989).

1.5 Lowbush Blueberry (*Vaccinium angustifolium*)

The field research for this thesis was conducted on lowbush blueberry (*Vaccinium angustifolium*), a perennial, native deciduous shrub that grows in treeless barrens, fields, and burned over areas across northeastern North America. Importantly, lowbush blueberry was chosen as the study system for this thesis research because it is a pollinator dependent crop, as the diversity of self-sterile genotypes (often referred to as ‘clones’) require pollinators to cross-pollinate (Bell et al. 2009). Lowbush blueberry flowers have poricidal anthers, which require pollen to be shaken out through small holes. The pollen grains are relatively large and heavy, and thus the clones are effectively unable to rely on wind-pollination (Jesson et al. 2014). Bees are assumed to be the primary pollinators for the crop (Javorek et al. 2002; Cutler et al. 2015), but nocturnal pollination by other insects may also contribute significantly to fruit set (Cutler et al. 2012; Manning & Cutler, 2013).

Furthermore, although commercially managed, lowbush blueberry is an inherently ‘wild’ species. Commercial fields are not sown; instead, forest land is cleared and levelled to facilitate the natural propagation of individual clones, most already present in the pre-existing forested areas, via rhizome growth. Clones vary widely within fields with regards to many biological traits, including age, height, colour and hue, phenology, and

yield (Bell et al. 2009). After a relatively long propagation period that can range from 2-10 years, management strategies focus on optimizing growth, including fertilization, irrigation, and prevention of harvest losses from diseases, weeds, and insect pests (Drummond, 2000; Yarborough, 2012). Due to this unique growth and field development, a particularly unique management strategy on lowbush blueberry is bi-annual mechanical mowing and/or burning aimed to promote plant growth, encourage more synchronistic blooms, and increase fruit yield. Fields are therefore managed and harvested on two-year cycles and alternate between vegetative and fruiting (yield) years (DeGomez, 1988). Once established and given favourable environmental conditions, blueberry clones can have life spans that exceed over 200 years (Eaton and Hall, 1961; Vander Kloet, 1988; Drummond et al. 2008). At the end of the fruiting season, commercial fields are harvested all at once using specialized machines (McIsaac, 1997).

Despite its identification as a 'wild' crop, commercial lowbush blueberry production in Atlantic Canada is also heavily managed, including insect, weed, vertebrate pest, and disease management interventions (Agriculture & Agri-Food Canada, 2012; Yarborough, 2012; Delbridge & Rogers, 2013). Most producers also actively manage for adequate pollination services. Typically, pollination and fruit set extends from late May to mid June in the south of its geographic range, and from mid to late June in the north of its geographic range (Bell & Burchill, 1955). Although wild pollinators are present within the landscape throughout the duration of bloom, many growers also provide additional pollination supplied by commercial pollination service providers during 'peak bloom' (Javorek et al. 2002; Cutler et al. 2015). Ground-nesting pollinators may nest within fields as the soil is not disturbed by cultivation (MacKenzie et al. 2004; Bushmann & Drummond, 2015). Similarly, as all fields are converted directly from forest, edges are

often wild or largely undisturbed habitat (Drummond, 2003). However, there can be as much as a two-week delay from when clones begin blooming to when managed pollinators are moved into fields.

1.6 Hypothesis and Study Predictions

I posit that commercial lowbush blueberry crop production may experience significant losses from early season pollination that occurs before the introduction of managed pollinators, which would be measurable as premature berry development, ripening, and pre-harvest berry drop. Furthermore, early pollinated flowers may inhibit the development of fruit set later in the season, as is the case in both strawberry (Gardner et al. 1952) and almond production (Ortega et al. 2004). If this occurs, early season pollination to this crop could constitute an ecosystem disservice that detracts from final yield by reducing the amount of harvested berries, or by reducing berry sweetness should the production of many early-season berries reduce plant resources available to late-season berries.

I tested this hypothesis of ecosystem disservice by selectively excluding early (wild) pollinators and late (wild and managed) pollinators from both early and late blooming clones, and then measured the effects on total and ripe yield at harvest, berry drop both mid-season and during the harvest process, fruit sweetness, and fruit size. Should the hypothesis of disservice be true, I predicted plots exposed to early season pollination to exhibit:

1. Lower total yield and ripe yield levels at harvest,

2. Higher levels of mid-season berry drop and shatter at harvest due to early ripening and fruit drop,
3. Increased berry sweetness at harvest as a result of the relatively longer ripening time, and,
4. Smaller berry size at harvest as a consequence of larger berries being dropped before final yield.

1.7 Organization of Thesis

Two chapters form the remainder of this thesis. Chapter 2 was written as a stand-alone article that will be submitted to an academic journal with myself as lead author and Dr. Peter Tyedmers, Dr. Chris Cutler, and Dr. Andony Melathopoulos included as co-authors. In Chapter 2, methods and results are presented on early versus late season pollination impacts to lowbush blueberry production, along with a discussion on overall impacts to production and how these results relate to the broader discourse on ecosystem services versus disservices, pollinator influence, and food production. Chapter 3 concludes the thesis with discussions on wild versus managed pollinators, implications for lowbush blueberry producers, research limitations and future research opportunities, and a final word on ecosystem services versus disservices.

2.1 Abstract

Insect-mediated pollination is frequently identified as an important ecosystem service to agricultural production. In contrast, ecosystem *disservices* are often not considered in current estimates of service provisioning. This study explores pollinator service versus disservice in fruit production, using lowbush blueberry as a study system. This crop is highly managed, requires insect pollination, and has a long bloom period; when combined, these characteristics may cause a portion of early season pollination to result in premature ripening and pre-harvest loss. To test this, I exposed early and late flowering clones to early (wild) pollination only or late (wild and managed) pollination only, and found that early pollination only plots (1) produced over 70% of the total production produced by late pollination only plots, (2) retained their berries just as well as late pollination only plots, and (3) did not exhibit relatively higher levels of shatter at harvest, despite producing heavier berries. Furthermore, sugar content was unaffected by treatment. These results suggest that early pollination to lowbush blueberry does not present an ecosystem disservice.

2.2 Introduction

Since the 1990s, the idea of ecosystem services has become an increasingly popular way to conceptualize the numerous direct and indirect benefits of ecosystems on human wellbeing (Costanza et al. 1997; Daily, 1997; MEA, 2005). In contrast, ecosystem

disservices are often not acknowledged or considered in the current estimates of service provisioning. Yet the existence of beneficial services to humanity necessitates the recognition that nature also provides disservices that can reduce the productivity of various human systems, increase production costs, and/or pose direct threats to human health (Dunn, 2010; Lyytimaki et al. 2008; Zhang et al. 2007).

Insect-mediated pollination is frequently identified as a regulating ecosystem service (Costanza et al. 1997; Schulp et al. 2013; Winfree et al. 2011), whose role in the production of many agricultural crops is well studied (Klein et al. 2007; Lautenbach et al. 2012) and broadly recognized in popular culture (Walsh, 2013). In certain instances, however, pollination, or a portion of pollination, can be an ecosystem disservice. For example, many insect pollinated crop species set more fruit than optimal from a profitability perspective (Bos et al. 2007a; Bos et al. 2007b). When this occurs, growers may mechanically or chemically thin flowers and/or fruitlets in order to alter resource allocation and increase fruit size, value, and quality at harvest (Free, 1993; Jackson, 1989). Similarly, Klein et al. (2015) found that excess pollination in almond can reduce fruit quality and leaf production, compromising the photosynthetic capacity of trees, while Klatt et al. (2014) found that pollen limitation in commercially important strawberry varieties results in lower amounts of deformed fruit. These crop-specific yield responses to pollination intensity are clear examples of how pollination as an ecosystem service can transform into a disservice that detracts from overall production (Zhang et al. 2007). Yet pollination continues to be commonly viewed as a monotonically positive service, despite recent evidence that what actually happens as a result of management strategies may be a disservice to final production.

Commercial lowbush blueberry (syn. “wild blueberry”, *Vaccinium angustifolium* Aiton) production is an excellent system to explore pollinator service and disservice. Self-sterile blueberry plants (‘clones’) are pollinator-dependent, and benefit from the presence of wild pollinators (Javorek et al. 2002; Fulton, 2013). The bloom period of lowbush blueberry lasts approximately four weeks, exceeding that of many pollinator dependent crops like apple (Whiting et al. 2015) or almond (Ortega, 2004), but being comparable to other crops like canola (oilseed rape) (McGregor, 1981). Bloom is also quite heterogeneous due to considerable clonal diversity within fields, with early and late blooming clones, and a sequential succession of floral bloom and senescence (Bell et al. 2009; VanderKloet, 1988). Furthermore, although wild pollinators are present throughout the bloom, most growers augment the natural pollinator force with managed honeybees (*Apis mellifera* L.) or bumble bees (*Bombus impatiens* Cresson) at approximately 25% bloom, such that the crop experiences an intense pulse of pollination (Drummond, 2002; Eaton et al. 2004). In contrast to the prolonged period over which fruit are potentially set, lowbush blueberries in commercial production are harvested from each field during a single mechanized harvest event. I therefore posit that commercial lowbush blueberry crop production may experience significant losses from early season pollination that occurs before the introduction of managed pollinators, which may result in premature berry development, ripening, and pre-harvest berry drop. If this occurs, early season pollination to this crop could constitute an ecosystem disservice that detracts from final yield by reducing the amount of harvested berries, or by reducing berry sweetness should the production of many early-season berries reduce plant resources available to late-season berries. Similar examples of this intra-plant competition for resource allocation can be seen in strawberry (Gardner et al. 1952), almonds (Ortega et al. 2004), and

cranberries (Birrenkott & Stang, 1990; Brown & McNeil, 2006). In such cases, as might be the case with lowbush blueberry, developing fruit compete for finite plant resources, such as photosynthates (Gifford and Evans, 1981; Stephenson, 1981). Such intra-plant resource competition may lead early set fruit to produce an inhibitory substance that causes late set flowers and fruit to abort (Van Steveninck, 1959).

I tested this hypothesis by selectively excluding early (wild) pollinators and late (wild and managed) pollinators from both early and late blooming clones, and then measured the effects on total and ripe yield at harvest, berry drop both mid-season and during the harvest process, fruit sweetness, and fruit size. Should the hypothesis of disservice be true, I predicted plots exposed to early season pollination to exhibit: (1) lower total yield and ripe yield levels at harvest as a result of (2) higher levels of mid-season berry drop and shatter at harvest due to early ripening and fruit drop; (3) increased berry sweetness at harvest as a result of the relatively longer ripening time; and (4) smaller berry size at harvest as a consequence of larger berries being dropped before final yield.

2.3 Materials and Methods

2.3.1 Pollination Exclusion

The experiment was conducted from 12 May to 14 August, 2014 on ten (10) well-established commercial blueberry fields located in the eastern part of the province of

Prince Edward Island, Canada (Fig 2). Fields averaged 11.5 ha (max=27.0 ha, min=5.4 ha), and all were owned and/or managed by a single company and therefore subjected to consistent management practices. Managed pollinator stocking densities averaged 8 honeybee colonies per ha as well as 4 bumblebee colonies per ha. In order to minimize soil and climate variability and their potential influences on the study results, the 10 agricultural fields were all intentionally located on similar agricultural landscapes located within an 80 km radius.



Figure 2. Locations of the 10 lowbush blueberry experimental fields in the eastern part of the province of Prince Edward Island (PEI), Canada.

In each field, a 100 m transect was established 25 m from and parallel to the northern field edge. A total of twelve experimental plots measuring 1 m² each were established along and within 6 m of each transect. The experimental plots were located on clones of a consistent size class (total area of 1-2m²) with comparable stem densities. Criterion used to establish the twelve experimental plots was the relative timing of clonal

bloom within each plot, such that six early blooming clones (EC) and six late blooming clones (LC) were selected in each field. Overall flower density and relative flowering phenology of the experimental plots was estimated at the onset of bloom by counting the number of stems in five randomly selected 10 x 10 cm subplots within each 1 m² plot, along with the total number of open flowers present in the subplots.

After six EC and six LC plots were established in each field, plots were randomly assigned to one of two treatments: exposure to early pollination only (EPO) or late pollination only (LPO). This resulted in three replicates of each of the following treatments based on the bloom timing and insect pollinator access: early blooming clone, early pollination only (EC-EPO); early blooming clone, late pollination only (EC-LPO); late blooming clone, early pollination only (LC-EPO); and late blooming clone, late pollination only (LC-LPO). In addition to experimental plots, five control plots were established at approximately 0, 25, 50, 75, and 100 m along the transect. These control plots experienced no pollinator exclusion treatment, nor any specific clonal designation based on timing of bloom, and were open to pollinators throughout the entire bloom period. That is, control plots mimicked normal pollination of clones in commercial fields. Experimental clones had similar stem densities with no bare patches. Pollination treatments were established by placing pollinator exclusion tents (Type 2 mesh, Vilutis and Co, Inc., Frankfort, Illinois) over clones at the appropriate time. Exclusion tents were supported by four PVC pipes (1 m long, 2.5 cm diameter) placed vertically into the ground at the corners of the plot. Excess tent material was gathered at the ground and securely pinned to limit insect access (Fig 3). LPO plots were set before bloom began (~ <1% bloom for early and late clones) and remained covered until 3-9 June, just before the introduction of managed bumble bees and honeybees into fields. Tents were then

removed from LPO plots and re-installed on EPO plots. Tents remained over EPO plots until the end of bloom (31 June). Throughout the experiment exclusion tents were monitored to ensure bees and other potential pollinators were excluded. Electronic temperature monitors (Onset Corporation HOBO data loggers) were used inside and outside two randomly selected plots to ensure that the exclusion tents did not adversely affect plot air temperature.



Figure

3.

Pollination exclusion tent design in Mount Vernon, Prince Edward Island.

2.3.2 Flower and Fruit Development

Twenty-five (25) stem clippings were collected at evenly spaced intervals along the 100 m transect at: (1) the onset of bloom (early June), (2) peak bloom (mid June), (3) initial fruit set (late June - early July; two weeks after bloom), and (4) final fruit set (early to mid August). The number of flowers and fruit per stem were counted and recorded. Additionally, I randomly selected and tagged three 'typical' stems in each plot at the beginning of the field experiment and on seven dates from the beginning of June until the day of harvest in mid August counted closed flowers, open flowers, diseased flowers, dropped flowers, green berries, pink berries, and ripe berries. On the day of harvest, berries on these stems were collected, weighed, and frozen.

2.3.3 Berry Drop

Three perforated catchments measuring approximately 28 cm x 7 cm were installed in each plot. These catchments were made of clear plastic embroidery mesh with 2 mm holes, fastened into half-cylinder shapes using three electrical ties, and then secured into the ground with two agricultural staples (Fig 4). Beginning mid-July until harvest, I recorded the number of dropped flowers, green berries, pink berries, and ripe berries in each catchment on a weekly basis, removing all fallen flowers and berries after counting. After harvest, I estimated berry drop per 1 m² by summing the data for the three catchments and then multiplying the combined catchment area (approximately 0.05 m²) by 20.

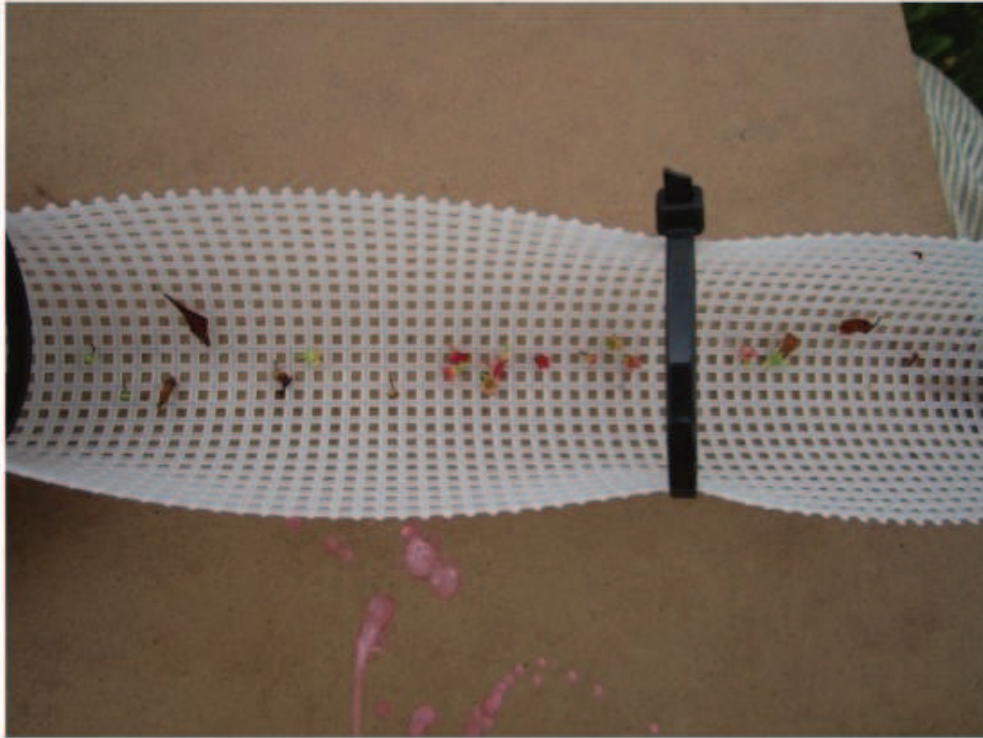


Figure 4. Perforated plastic mesh berry catchment. Three catchments were installed in each experimental and control plot.

2.3.4 Fruit Yield, Ripeness, and Sugar Content

From 11-14 August, I harvested all experimental and control plots using lowbush blueberry hand-rakes. The timing of plot harvest was aligned with commercial harvest in order to represent typical blueberry harvest. Total yield (kg) of all ripe and unripe berries was measured for each plot. Sub-samples of berries (~375 mL) were also collected from each plot and returned to the laboratory to calculate the mass and percentage of ripe vs. green berries per plot. Sub-samples were frozen and subsequently measured for sugar content. This consisted of crushing 20 berries in a mechanical press and separating seeds and pulp from juice with a paper filter. Twenty berries gave ~0.75 mL pure juice from which sugar concentrations were measured using a Euromex digital hand refractometer

(Euromex Microscopes Holland), with an accuracy of 0.1° Bx across a range of 0 to 35° Bx.

Unlike other fruit crops that can be picked individually by hand, the small size of lowbush blueberries requires hand or mechanical raking, a process that results in some lost berries. The number of ripe berries that fell to the ground during harvesting (“shatter”) was recorded for each plot using three 10 x 10 cm subplots. Estimates of total shatter per 1 m² were calculated after harvest by summing the total number of dropped berries from three subplots, generating a mass value using the plot-level data for mean mass per ripe berry, and then multiplying this value by 3.33 to arrive at a rough estimate of shatter per 1 m².

2.3.5 Data Analyses

Analyses were conducted on the data pooled per field. I first confirmed whether the bloom phenology of early, late, and control clones was significantly different using a one-way analysis of variance (ANOVA), and then separated the means using Tukey’s Honest Significant Difference (HSD) test (Gotelli & Ellison, 2013).

For each of the six dependent parameters (total yield, ripe yield, pre-harvest drop, shatter, sweetness, and berry size), I began with a one-way ANOVA model to test for significant differences among the four manipulated treatment plots (EC-EPO; EC-LPO; LC-EPO; LC-LPO) and the control plots (open pollination with randomly selected clones). Total yield data were log-transformed and ripe yield data were square root transformed to normalize error variance before analysis (Gotelli & Ellison, 2013). Where these models detected significant treatment effects, means were separated using Tukey’s

HSD. I then explored the interaction effect of pollinator exclusion and clone phenology by running fixed effects two-way ANOVA with interaction models on warranted parameters (Gotelli & Ellison, 2013). These two-way ANOVA models were only run for parameters that showed a significant treatment effect according to the one-way ANOVA models. All one-way and two-way ANOVA models met the statistical assumptions of independence, normality, and homogeneity of variances (Logan, 2010). All analyses were conducted in the R statistical environment (R Development Core Team, 2013).

2.4 Results

2.4.1 Early and Late Clones

Flowering phenology at peak bloom differed among the three clone treatment groups ($F = 6.844$, $df = 2, 24$, $P = 0.004$) such that early clones had just over 20% more open flowers than late clones, but neither early clones nor late clone plots were significantly different from the field average (Fig 5).

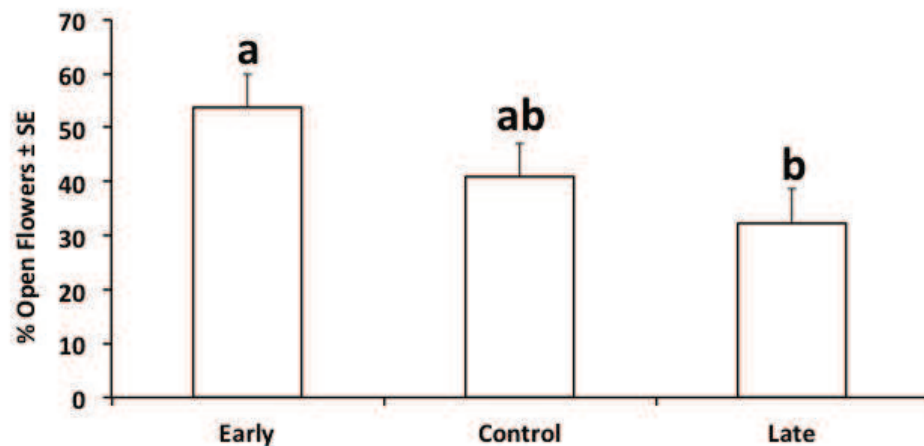


Figure 5. Percentage of open flowers for early clones, late clones, and controls across 10 lowbush blueberry fields in Prince Edward Island, 8 - 9 June 2014. Bar with different letters above them are significantly different, Tukey HSD ($P < 0.05$).

2.4.2 Fruit Quantity

I found significant differences amongst the treatment and control plots for both total yield ($F = 13.12$, $df = 4, 44$, $P = <0.001$) and ripe yield ($F = 8.06$, $df = 4, 44$, $P = <0.001$). As expected, EPO plots produced less overall than LPO plots, the latter of which had similar total yield to (in LC) or much higher yields (in EC) when compared to the controls (Fig 6A). However, there was no benefit to early pollination restriction on ripe yield, as all treatments had consistent levels with the exception of LC-EPO plots that were largely closed to pollinators during their bloom (Fig 6B). Importantly, the timing of pollination did not result in disproportionately more fruit yield whether the clones were late or early blooming. Looking at clone phenology more closely, total yield was 1.9 times greater and ripe yield was 2.3 times greater from plots established on early blooming clones as compared to plots on late blooming clones (Fig 7). Finally, in contrast to my prediction, I found no significant interaction between pollinator exclusion and clone phenology on these endpoints (Table 1).

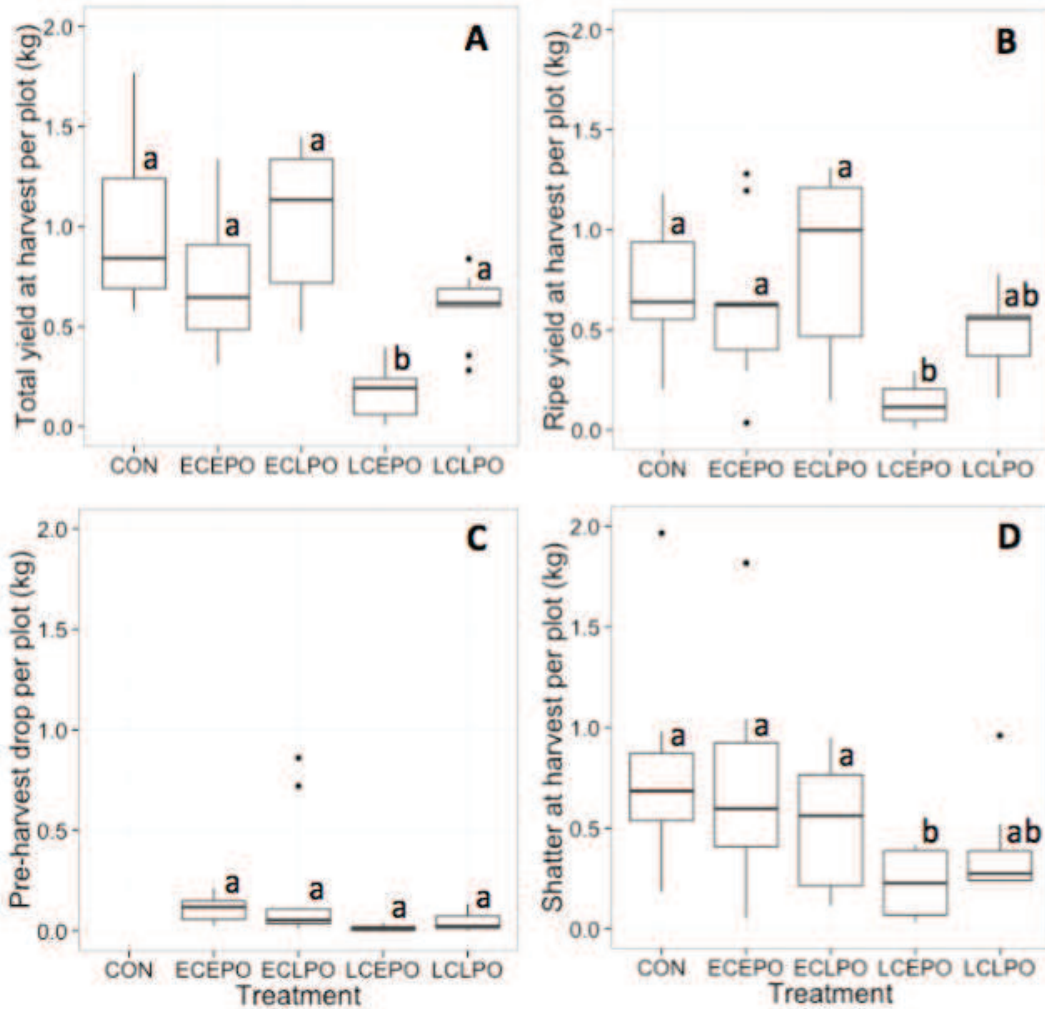


Figure 6. Total berry production (kg) per m² for each pollination treatment and clone phenology combination on lowbush blueberry: (A) total fruit yield (ripe and unripe) (kg) at harvest; (B) ripe fruit yield (kg) at harvest; (C) pre-harvest berry drop (kg); and (D) ripe shattered berries per plot (kg) at harvest ($n = 4$ plots per treatment group per field, 5 plots per control group per field). Tukey HSD post-hoc test results are depicted as smaller case letters. No data were available for pre-harvest berry drop on control plots. CON = control; EC = early clone; LC = late clone; EPO = early pollination only; LPO = late pollination only.

Table 1. Results of two-way ANOVA models analyzing the effects of clonal flowering time (clone) and pollination treatment (early pollination only or late pollination only) on lowbush blueberry total yield (kg), ripe yield (kg), pre-harvest ripe drop (kg), shatter at harvest (kg), sugar concentration (Bx), and ripe berry size at harvest (g).

Factors, by variables	Df	<i>F</i>	<i>P</i>
Total yield (kg)			
Clone	1	38.19	<0.001
Pollination	1	22.89	<0.001
Clone × Pollination	1	2.21	0.146
Error	36		
Ripe yield (kg)			
Clone	1	20.05	<0.001
Pollination	1	13.67	<0.001
Clone × Pollination	1	2.35	0.134
Error	36		
Pre-harvest ripe drop (kg)			
Clone	1	6.25	0.017
Pollination	1	1.31	0.260
Clone × Pollination	1	0.29	0.595
Error	36		
Shatter at harvest (kg)			
Clone	1	10.14	0.004
Pollination	1	0.22	0.639
Clone × Pollination	1	3.55	0.070
Error	28		
Sugar concentration (Bx)			
Clone	1	1.73	0.197
Pollination	1	0.19	0.664
Clone × Pollination	1	0.10	0.749
Error	36		
Ripe berry size (g)			
Clone	1	0.02	0.894
Pollination	1	6.92	0.012
Clone × Pollination	1	0.04	0.843
Error	36		

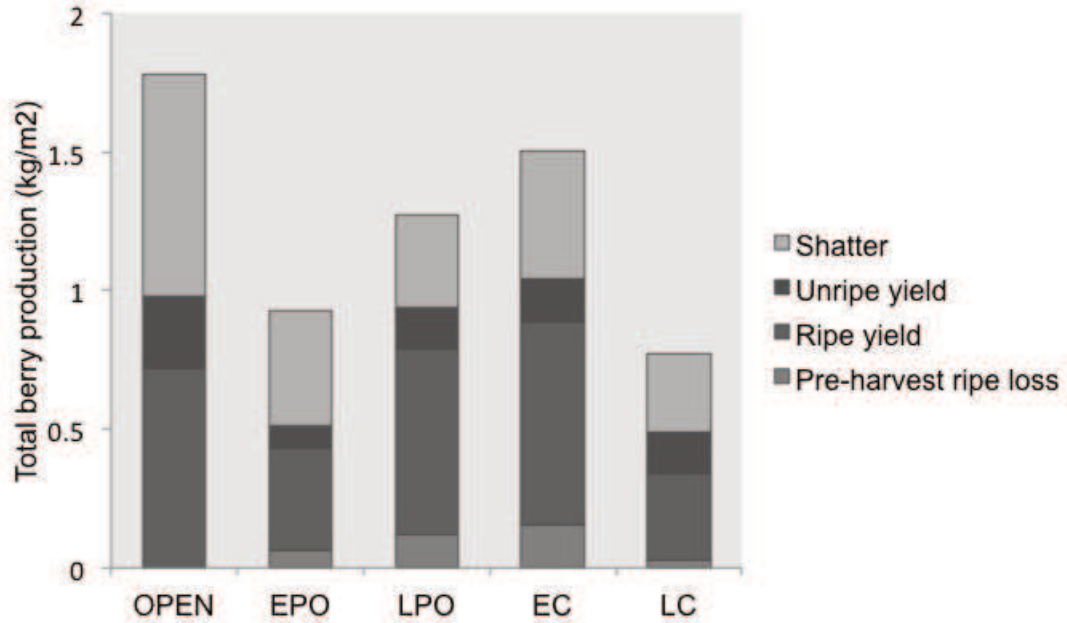


Figure 7. Mean overall berry production for pollination timing and clone phenology including pre-harvest ripe loss, ripe yield, unripe yield, and shatter at harvest. Pre-harvest berry loss was not measured for the control plots. OPEN = control; EC = early clone; LC = late clone; EPO = early pollination only; LPO = late pollination only.

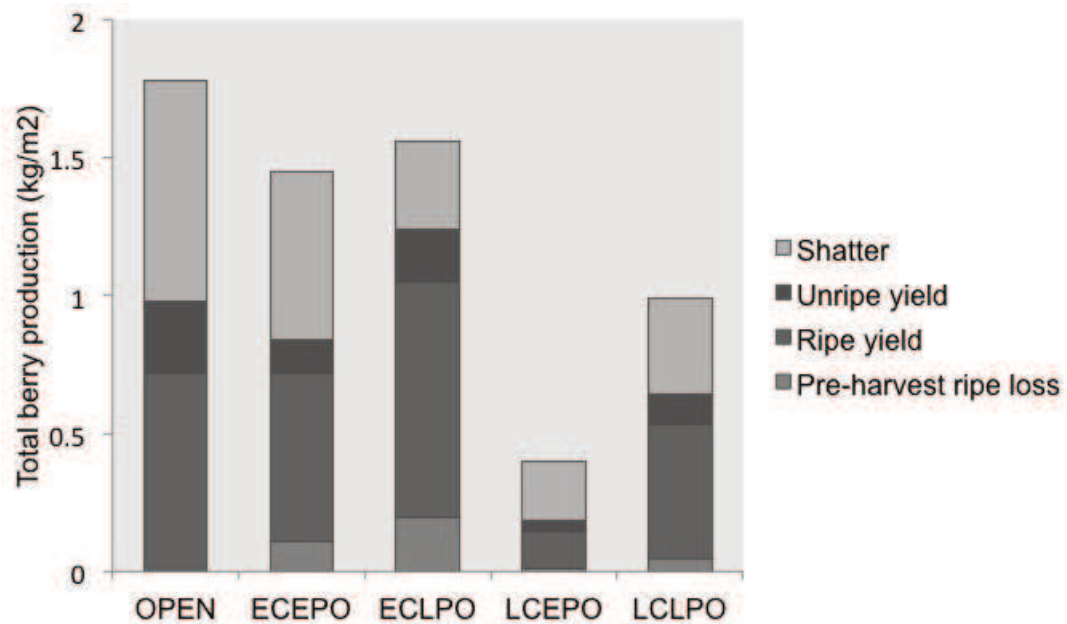


Figure 8. Mean overall berry production for each pollination treatment and clone phenology combination, including pre-harvest ripe loss, ripe yield, unripe yield, and shatter at harvest. Pre-harvest berry loss was not measured for the control plots. OPEN = control; EC = early clone; LC = late clone; EPO = early pollination only; LPO = late pollination only.

2.4.3 Pre-harvest Berry Drop

Contrary to my prediction that abundant early pollination would lead to increased levels of pre-harvest berry drop, I found no significant differences in pre-harvest berry drop among pollination treatments ($F = 2.615$, $df = 3,36$, $P = 0.066$) (Fig 6C). Overall, the measured amount of pre-harvest berry drop relative to total berry production was small across all treatments (Fig 7, Fig 8). Furthermore, there was no interaction of clonal diversity and pollination treatment on pre-harvest berry drop, meaning timing of pollination did not result in disproportionately more pre-harvest loss whether the clones were early or late blooming (Table 1).

2.4.4 Shatter at Harvest

There was a significant treatment effect on shatter at harvest ($F = 2.882$, $df = 4,35$, $P = 0.037$). However, contrary to my prediction that shatter would be highest for plots exposed to abundant early pollination, pollination treatment was not a significant factor. The rate of shatter at harvest was consistent across all experimental treatments, with the exception of LC-EPO plots that produced very few berries overall (Fig 6D). There was no interaction of clone phenology and pollination treatment on shatter at harvest (Table 1). Overall, shatter at harvest was much higher than anticipated, and in some cases actually exceeded the ripe yield that was collected for consumption (0.8 kg/m^2 versus 0.72 kg/m^2 in control plots, respectively) (Fig 7, Fig 8).

2.4.5 Berry Quality

Contrary to my prediction that sugar content would be higher in berries with the longest ripening time, I found no significant difference in sugar concentration amongst the treatment and control plots ($F = 0.581$, $df = 4, 45$, $P = 0.678$). Mean sugar concentration for the four treatments and control groups are as follows: EC-EPO=15.5° Bx±0.39; LC-EPO=14.4° Bx±0.79; EC-LPO=15° Bx±0.54; LC-LPO=14.3° Bx±0.74; control=14.9° Bx±0.41. There was also no significant interaction of clone and pollination treatment on berry quality (Table 1).

2.4.6 Berry Weight

Pollination treatment had a significant effect on berry size ($F = 6.92$, $df = 4, 45$, $P = 0.012$). In contrast to my prediction that late pollination plots would produce heavier berries, I found that plots exposed to early pollination produced ripe berries that were 0.05 g heavier than those exposed to late pollination only (Table 1) (0.43 g/berry and 0.38 g/berry, respectively). Interestingly, berries in the control plots were the smallest at harvest, weighing an average of 0.36 g/berry. There was no interaction of pollination timing and clone phenology on berry weight (Table 1).

2.5 Discussion

Pollination is largely viewed as a positive ecosystem service (Costanza et al. 1997; Klein et al. 2007; Winfree et al. 2011; Lautenbach et al. 2012; Schulp et al. 2013), although instances of disservice have started to emerge as a result of agricultural management practices (Bos et al. 2007a; Bos et al. 2007b; Klein et al. 2015). Yet despite the combination of a wide pollination window and considerable early pollination prior to the introduction of managed pollinators, and despite the industry practice of conducting a singular, mechanized harvest, the results of this study show that early season pollination to lowbush blueberry does not present an ecosystem disservice (although it should be noted that a disservice effect in a perennial like lowbush blueberry may appear in conditions where clones experience more stress).

As predicted, I found clear pollination treatment effects for both total yield and ripe yield showing significant increases to yield for LPO. However, though *total* berry harvest in LPO plots was greater or similar to control plots (depending on the relative timing of clone flowering), when saleable *ripe* berries are considered, the benefits of excluding all early season pollination input was small and only occurred in clones that flowered early. Furthermore, and in contrast to my predictions, plots exposed to EPO retained their berries throughout the season just as well as LPO plots and did not exhibit relatively higher levels of shatter at harvest, despite having significantly heavier individual berries. This restriction of pollination and fruit set aligns well with other fruit crops where fruit thinning is common practice (Free, 1993; Jackson, 1989), and suggests that lowbush blueberry production also benefits from a lessening of the demands on plants' resources with regards to increasing fruit size at harvest. Finally, while I anticipated berry sugar content to be highest in berries with the longest ripening time, I

found sugar content at harvest to be unaffected by pollination treatment, suggesting that early pollination to lowbush blueberry does not affect berry quality, as measured by sweetness.

One of several surprising results of this study was that although EPO plots produced comparatively less overall, they still produced over 70% of the total production (pre-harvest drop, ripe yield, unripe yield, and shatter combined) per m² than was produced by LPO plots. In other words, plots exposed to late-season, wild and managed pollinators combined produced only 30% more total production than plots exposed to early-season, solely wild pollination.

Therefore, instead of presenting an ecosystem disservice, it appears that early-pollination to lowbush blueberry is instead very helpful to ensuring high levels of yield. For example, I found that EC set more fruit than LC, suggesting that early (wild) pollinators may be more important to lowbush blueberry production than many growers currently believe (Hanes et al. 2013). It is also striking that EC-EPO plots set the same yield as EC-LPO plots; that is, early flowering clones that were excluded from managed pollinators *set the same yield* as early flowering clones that were exposed to managed pollinators. This raises an interesting question on how much pollination is in fact coming from LPO (i.e. additional managed bee inputs) in the first place. Although lowbush blueberry producers invest heavily in managed pollinators, and there is evidence that additions of managed pollinators can boost blueberry fruit set and yield (Aras et al 1996; Stubbs and Drummond 2001), my findings and those of others indicate use of managed bees does not always benefit blueberry production. For example, a recent study by Jesson et al. (2014) found that lowbush blueberry fields *without* managed pollinators were as likely to have high levels of fruit production as fields *with* managed pollinators. Other

recent studies on lowbush blueberry have found that managed honeybees have no effect on yield when wild bee populations are high, and in fact compete for pollination with wild species and ultimately decrease wild species floral visitation rates (Hicks, 2011; Eaton & Nams, 2012; Mallinger & Gratton, 2015). In valuing managed pollination benefit, Winfree et al. (2011) argued that additional increments of honeybee pollination need to be valued *after* wild bee increments have been added. Using this approach to pricing the contributions of managed and wild bees, the yield determined for the LPO treatment in this study and attributed to managed pollinators is therefore even less important from a production standpoint than the results of this study suggest at the surface.

The importance of wild pollinator services to yield in pollinator-dependent crops is not limited to lowbush blueberry. Within the last decade, many other studies have confirmed that wild insects provide better quality pollination and enhance crop productivity even amongst crop species that are relatively novel in their ranges and with which they have not co-evolved (Greenleaf & Kremen, 2006; Winfree et al. 2007; Hoehn et al. 2008; Carvalheiro et al. 2011; Garibaldi et al. 2013). Garibaldi et al. (2013) found wild bees to enhance fruit set of crops regardless of honeybee abundance, and that managed honeybee pollinators should not be viewed as a substitute for wild pollinators.

My work found that clone phenology (early versus late blooming) significantly affected total yield, ripe yield, berry drop, and shatter, and that early flowering clones were comparatively more productive than late flowering clones. Additionally, clonal phenology did not significantly interact with pollination timing. This raises an interesting question on why early flowering clones are so much more productive than late flowering

clones. Future research is therefore needed to determine if early clone productivity is a result of environmental factors (i.e. more water early in the season) or genetic factors.

To the best of my knowledge, this is the first study examining the effect of the timing of pollination on yield in a heterogeneously blooming crop. Although early and late clones were different from one another, neither were significantly different from the field on average and as such, their identification and inclusion in the study design was necessary to understanding and representing the unique, heterogeneous phenology of this system. Producers may therefore consider limiting establishment of late flowering clones to enhance bloom and harvest synchronization. However, with the potential of long winters and late-spring frosts, the presence of late flowering clones may provide insurance to final production. More research on active clonal management is needed.

Surprisingly, the process responsible for the largest loss of yield was the harvest event itself. From data collected on control plots, I found the average rate of shatter at harvest to be *more* than the ripe yield actually harvested for consumption. This was also the case for EPO plots, but for LPO plots shatter was markedly reduced to just under 50% of the ripe yield actually harvested for consumption – a rate of loss that in most industries would still be considered extremely high. It is important to note here that I collected the harvest data using careful hand-raking, and therefore suspect that the rate of shatter in this study might be an underestimate of current harvest practices, as previous studies have estimated mechanical harvesting to be between only 60-76% as effective as manual harvesting (Hall, Craig & Lawrence, 1983; Marra et al. 1989).

I know of no other commercial fruit industry that leaves more than half of its potential yield and revenue available at the time of harvest to degrade in the fields. In other crops, such as grape production, shatter levels can reach 20% of total production,

especially as fruit increase in maturity (Crisosto, 2015). Given the scale of this loss, it is surprising that I could find no extant literature on loss via shatter in lowbush blueberry production. As such, suggestions for future research include collecting more robust and direct data to monitor shatter: (i) at various points in the harvest period, (ii) with various methods of harvesting, (iii) under various chemical and organic treatments, and (iv) under various temperatures and weather patterns. This could lead to strategies to substantially increase marketable yield with little additional expenditure.

Finally, this study adds to the awareness of ecosystem disservices to ecosystem services science. Returning to the potential nature of pollination as an ecosystem service or disservice depending on prevailing conditions, it appears clear that as current commercial agricultural practice typically creates intensively managed ecosystems, producers are therefore highly influential in managing – and altering – the flows of these concrete services and disservices based on management choices. Yet to date, the active management choice by most producers is to manage pollination inputs in a manner that universally augments what is otherwise available on the assumption that if some is good, more must always be better (Benjamin & Winfree, 2014). Although not the case for lowbush blueberry, there are other pollination-dependent systems in which managed pollinator resources, beyond a certain point, undermine production (McClure & Cline, 2014; Klein et al. 2015). What must therefore be stressed is that pollination is neither inherently a service or disservice until appropriated for human food production.

The ecosystem service framework has become an increasingly popular way for a wide range of groups, including academics, environmental organizations, national governments, and international organizations, to conceptualize the benefits of nature (MEA, 2005; Ruhl & Salzman, 2007; Maes et al. 2012; Schulp et al. 2013). Pollinators have been particularly highlighted as an exceptionally valuable ecosystem service, perhaps due to their recent media visibility and the seemingly simplistic relationship between pollination and human welfare; this is especially true with regards to literature on pollinator importance for agricultural production and maintaining ongoing food security (Klein et al. 2007; Aizen et al. 2008; Winfree, 2008; Eilers et al. 2011; Garibaldi et al. 2011; Garibaldi et al. 2013). Given the broad identification and usage of pollination as an ecosystem service, it is important to understand how both ecosystem services *and* *disservices* unfold in managed agro-ecosystems.

In this thesis (Chapter 2), I assessed the impacts of early season (wild) pollination versus late season (wild and managed) pollination on lowbush blueberry production in Atlantic Canada in order to understand how pollination timing might influence yield. In particular, this thesis explored ecosystem services versus disservices in a managed agro-ecosystem of a ‘wild’ crop species. I hypothesized that in this context, early season pollination could constitute an ecosystem disservice that detracts from final yield by reducing the amount of harvested berries and/or by reducing berry sweetness should the production of many early-season berries reduce plant resources available to late-season berries. Field research consisted of an extensive pollinator exclusion experiment, followed by four months of consistent crop monitoring, including early season and late

season pollinator exclusion to early and late flowering lowbush blueberry clones, followed by the collection of various at-harvest and post-harvest metrics.

Results of my analyses show that early pollination does not present an ecosystem disservice to lowbush blueberry yield or berry sweetness. Instead, I found that although *total* berry harvest in late pollination only plots was greater or similar to control plots (depending on the relative timing of clone flowering), when saleable *ripe* berries are considered, the benefits of excluding all early season pollination input was small and only occurred in clones that flowered early. What's more, I found that early pollination only plots produced over 70% of the total production per m² than was produced by late pollination only plots. In other words, plots exposed to late-season, wild *and* managed pollinators combined produced only 30% more total production than plots exposed to early-season, solely wild pollination. Importantly, I also found that plots exposed to early pollination only retained their berries throughout the season just as well as late pollination only plots, and did not exhibit relatively higher levels of shatter at harvest, despite producing significantly heavier individual berries. Finally, I found sugar content at harvest to be unaffected by pollination treatment or clonal phenology.

3.1 Wild Versus Managed Bees

Though not the explicit objective of this thesis, the results of my research highlight the relative importance of wild pollinators to lowbush blueberry production. For example, I found that EC-EPO plots set the same yield as EC-LPO plots; that is, early flowering clones that were excluded from managed pollinators *set the same yield* as early flowering clones that were exposed to managed pollinators. This ultimately raises an

interesting question on how much pollination is in fact coming from late pollination only plots (i.e. additional managed bee inputs) in the first place. In valuing the managed pollination benefit in this context, Winfree et al. (2011) argue that additional increments of honeybee pollination need to be valued *after* wild bee increments have been added. Using this approach to understanding the contributions of managed and wild bees, the yield determined for the late pollination only treatment in this study and attributed to managed pollinators is therefore even less important from a production standpoint than the results of this study suggest at the surface.

The appreciation and even pricing of benefits of managed honeybee contributions as secondary to wild bee contributions is important (Winfree et al. 2011), and is substantiated within the growing body of literature on pollinator effectiveness, both in lowbush blueberry and in agricultural production more broadly. Although lowbush blueberry producers invest heavily in managed pollinators, and there is evidence that additions of managed pollinators can boost blueberry fruit set and yield (Aras et al 1996; Stubbs and Drummond 2001), my findings and those of others indicate use of managed bees does not always benefit blueberry production. A recent study conducted in Atlantic Canada's lowbush blueberry industry found that fields *without* managed pollinators were as likely to have high levels of fruit production as fields *with* managed pollinators (Jesson et al. 2014). Similarly, others have found that managed honeybees have no effect on lowbush blueberry yield when wild bee populations are high, and in fact compete for pollination with wild species and ultimately decrease wild species floral visitation rates (Eaton & Nams, 2012; Hicks, 2011; Mallinger & Gratton, 2015).

Yet the continued usage of managed pollinators in this industry speaks to a concern of pollen limitation (not enough pollen transfer, with lower yield as a result), yet

augmentation of pollinator communities in general does not necessarily produce the desired outcome of increased yield (Fulton et al. 2015; Melathopoulos, 2015). In a recent study on mitigating the effects of pollen limitation via managed pollinator increases, Fulton et al. (2015) found no significant increase to lowbush blueberry reproduction with pollinator augmentation. Similarly, Melathopoulos (2014b; 2015) found little evidence to support the claim that lowbush blueberry yield is determined by pollinator abundance. Instead of adding more managed pollinators such as honeybees, bumble bees, and/or leaf cutter bees, the authors argue that management practices such as increasing outcross pollen receipt and bolstering plant resources would have a greater return on investment. It is therefore not just the *quantity* of pollinators available, but the *quality* of pollination that is being performed (Hoehn et al. 2008; Garibaldi et al. 2013).

This qualitative difference between wild versus managed bees can be attributed, at least in part, to their respective abilities to carry and effectively transfer pollen per floral visitation. These pollen carrying loads are highly variable among pollinator species in lowbush blueberry, ranging from a few hundred to more than 110,000 pollen grains per individual pollinator (Moisan-Desseres et al. 2014). Wild pollinator species *Bombus* spp. and *Andrena* spp. are particularly effective at carrying high pollen loads in this crop (Javorek et al. 2002; Moisan-Deserres et al. 2014; Melathopoulos, 2015). As compared to managed pollinators, these wild pollinators carry more weight – literally and figuratively. For example, as Javorek et al. (2002) found that “*A. mellifera* would have to visit a flower four times to deposit the same amount of pollen as single visits by *Bombus* spp. queens or *Andrena* spp.” (p. 345).

The importance of wild pollinator services to yield in pollinator-dependent crops is not limited to lowbush blueberry. Within the last decade, many other studies comparing

wild versus managed pollinators have confirmed that wild insects provide better quality pollination and enhance crop productivity even amongst crop species that are relatively novel in their ranges and with which they have not co-evolved (Greenleaf & Kremen, 2006; Winfree et al. 2007; Hoehn et al. 2008; Carvalheiro et al. 2011; Garibaldi et al. 2013). In one particularly large meta-study produced by Garibaldi et al. (2013), wild bees were found to enhance fruit set of crops regardless of honeybee abundance. Though wild bees have been shown to provide importance insurance against ongoing honeybee losses (Winfree et al. 2007), managed honeybee pollinators should not be viewed as a substitute for wild pollinators (Garibaldi et al. 2013). Wild pollinators are therefore a valuable input to many agricultural crop species, including lowbush blueberry, and their importance to continued production should not be overlooked.

3.2 Practical Implications for Producers

While the symbiotic relationship between the lowbush blueberry plant and its pollinators is becoming more clear (Stubbs & Drummond, 2001; Javorek et al. 2002; Cutler et al. 2012; Drummond, 2012; Cutler et al. 2015), there has been comparatively little qualitative research on growers' perceptions of the influence of wild versus managed pollinators. A recent study by Hanes et al. (2013) found that lowbush blueberry growers in Maine, USA felt considerable uncertainty concerning wild pollinators' contribution to yield, as well as how to accurately monitor their population sizes. The study concluded that while most growers agreed that wild pollinators are important, they were still only viewed as supplementary to honeybee usage and a way to provide insurance in cases such as poor weather, when the pollinating effectiveness of the honeybee is reduced. These

results are echoed in Nova Scotia and other parts of Atlantic Canada, where the demand for honeybees is increasing: 5,000-6,000 colonies have been shipped into Nova Scotia from central Canada in the last two years to augment the ~20,000 colonies already in the province in order to service crops such as lowbush blueberry (Melathopoulos, 2016).

In this thesis research, I found that early flowering clones set more fruit than late flowering clones, suggesting that early (wild) pollinators may be more important to lowbush blueberry production than many growers currently believe (Hanes et al. 2013). Furthermore, the uncertainty regarding wild pollinators in Hanes et al.'s study stands in contrast with recent literature on the value of wild pollinators to lowbush blueberry production (Javorek et al. 2002; Hicks, 2011; Eaton & Nams, 2012; Jesson et al. 2014; Moisan-Deserres et al. 2014; Cutler et al. 2015; Fulton et al. 2015; Mallinger & Gratton, 2015; Melathopoulos, 2015) as well as other many other agricultural production systems (Greenleaf & Kremen, 2006; Winfree et al. 2007; Hoehn et al. 2008; Carvalheiro et al. 2011; Garibaldi et al. 2013). This incongruence is especially concerning for several reasons. Firstly, from an economic perspective, I posit that managed pollinator costs in this particular industry perhaps may not be worth the return on yield. As such, there is still a greater need for sharper analyses on the marginal return of investment of honeybee inputs in this industry, particularly at the individual field level as the size and health wild pollinator populations may vary depending on location; performing such analysis will be a crucial step towards maximizing possible yield and minimizing potential costs. Secondly, biodiversity conservation efforts may be limited if growers remain uncertain as how to identify and monitor wild populations and their respective habitats. Making recent information available to growers will help to remove uncertainties regarding the

contribution of wild pollinators; these could include workshops on wild bee identification and population monitoring, and educational newsletters.

3.3 Research Challenges

Conducting research in a non-controlled environment presents many variables and unexpected difficulties. The first major challenge encountered in this project was how to accurately monitor berry development and loss throughout the season on a per stem basis. Tracking the same stems throughout the season would have been novel and instrumental in illustrating when berries were aborted from the clones, and also give the ratios of how many set berries made it to harvest for both pollination treatments as well as for the open pollinated control plots. The initial plan for this monitoring was to fashion plastic mesh cones around a set number of individual stems in each experimental plot to be used to monitor flower and fruit fates, so that when berries dropped they would collect at the bottom of the cone for analysis. In practice, however, this design was neither effective at collecting the berries, nor practical in terms of the time required for installation on each stem. Given this unexpected hurdle, the design was shifted to a plastic mesh half-cylinder catchment installed on the ground. The major limitation to this design was that I was no longer able to monitor the fate of berries per stem, as the catchments collected dropped berries from all surrounding stems. Furthermore, catchment data on the control plots was lost in the translation of data from paper to electronic format, highlighting the value of setting out a specific method of data management at the beginning of the project.

Although this method of data collection had significant limitations, it nevertheless still proved useful at providing a glimpse at the rate of berry drop occurring throughout

the season. Future studies should consider revising this design, or the idea of a per stem cone design, in order to improve the accuracy of the data collected. This information would be extremely valuable in furthering our understanding of lowbush blueberry phenology and seasonal yield development.

The second major challenge to this thesis research was identified in hindsight. In order to account for the variance in bloom time between clones, the design of this study included open control plots and the selection of an equal number of both early flowering and late flowering clones to compose the experimental plots subjected to the pollination treatments. In retrospect, however, the selection of only early flowering and late flowering clones may have been problematic: focusing exclusively on the notably early and late clones, without assessing what the ‘typical’ clone flowering time was in each of the ten fields, could have potentially skewed the data towards the clonal outliers that were perhaps not representative of the field on the whole. To ensure that the data was indeed representative of the fields, I therefore had to perform additional and unanticipated post-hoc analyses for each field using bloom estimates from each plot versus transect clipping data and then run a one-way ANOVA with Tukey’s Honest Significant Difference to determine if the bloom timing was significantly different. The results of these analyses showed that the clonal variation did represent the fields on average, and therefore did not affect the validity of the study. However, had the results been different, this would have been a major issue with regards to the design of the study. Future studies on lowbush blueberry should therefore consider clonal variation, but should also include randomly selected clones to better represent the ‘typical’ clone in each field that is used.

3.4 Research Opportunities

Some of the unanticipated results of this thesis research may prove to be an important bridge in identifying future research opportunities. Firstly, I found that the largest cause of yield loss in my study occurred as a result of the harvest event itself. The average rate of shatter at harvest ranged from 45% to over 100% relative to the ripe yield actually harvested for consumption, depending on pollination treatment, with open pollinated plots experiencing the most shatter at harvest. Even at the lowest estimate, this is a rate of loss that in many other agricultural systems would be considered extremely high. For example, a shatter rate of 20% in grape production is considered very high (Crisosto, 2015), which increases substantially with delayed harvest (Christensen et al. 1995). Furthermore, the actual rate of shatter for lowbush blueberry fields in commercial production is likely to be much higher than I found when hand-raking plots; this is because mechanical harvesting now dominates commercial production and previous studies have estimated mechanical harvesting in lowbush blueberry fields to be between only 60-76% as effective as manual harvesting (Hall, Craig & Lawrence, 1983, Marra et al. 1989). Positively, Farooque et al. (2014) found that un-harvested berries remaining on lowbush blueberry clones and losses through mechanical harvesting are significantly lower than ground shatter, yet these losses still contribute to an already substantial extent of lost income.

I know of no other commercial fruit industry that leaves more than half of its potential yield and revenue available at the time of harvest to degrade in the fields. Given the scale of this loss, it is surprising that I could find no extant, specific literature on loss via ground shatter in lowbush blueberry production. As such, future research is needed to collect more robust and direct data to monitor shatter: (i) at various points in the harvest

period (i.e. an earlier harvest versus a later harvest), (iii) with various methods of harvesting, (iii) under various chemical and organic treatments, and (iv) under various temperatures and weather conditions patterns. Such research could lead to strategies to substantially increase marketable yield with little additional production expenditure.

The second area of opportunity relates to the productivity of early clones as compared to late clones. Contrary to my hypothesis that early flowering clones would have fewer berries at harvest due to early ripening and wastage, the results of this study indicate that early flowering clones produced *more* yield at harvest than late flowering clones. In fact, I found clone phenology to be a statistically significant factor on total yield, ripe yield, berry drop, and shatter.

Although certainly not conclusive, based on the results of this study producers may consider limiting the establishment of late flowering clones to enhance bloom and harvest synchronization, should this even be possible as lowbush blueberry is not a cultivated crop. However, with the potential of hard late-spring frosts, the presence of late flowering clones may provide a form of insurance against early set fruit loss and still provide farmers with a modest harvest should early set fruit experience unfavourable weather conditions. Consequently, gaining a more nuanced understanding clone phenology, including how it influences total production and how to actively manage for clonal diversity (if that indeed is possible) is therefore another important research area that could provide significant insight into maximizing yield.

3.5 A Final Word on Ecosystem Services and Disservices

What ecologists call “human disturbance” agriculturalists call “management.” But farmers who manage those ecosystems influence flows of many ecosystem services, whether they think about it or not (Swinton, 2008, p. 28).

This quotation, also presented in Chapter 1, serves as an excellent foundation to the discussion of ecosystem services versus disservices presented in this thesis. The definition of ecosystem services, defined as “the benefits people obtain from ecosystems” (MEA, 2005, p.V), firmly and clearly places humans as the recipient subject of nature’s functions – functions that would, presumably, continue uninterrupted in the absence of humans. In other words, fruiting plants would continue to produce fruit, pollinators would continue to pollinate flowers, and so on. Certainly, humans derive considerable benefits from these ecosystem functions, but they are ecosystem services in that *we as humans label them as such*.

While ecosystem *services* point to the *positive* effects that ecosystems provide human well-being, ecosystem *disservices* refer to the *negative* effects that ecosystems have *on humans* (Zhang et al. 2007; Lyytimaki et al. 2008; Dunn, 2010; Döhren & Haase, 2015). In agro-ecosystems in particular, these disservices typically inhibit human welfare and economic growth by reducing productivity and/or increasing production costs (Zhang et al. 2007). Previous studies identifying ecosystem disservices in agro-ecosystems highlight problems such as pest damage, competition for water from other ecosystems, and competition for pollination (Zhang et al. 2007), as well as sedimentation of waterways and increases to greenhouse gas emissions (Power, 2010). What is particularly interesting from this literature is that both services and disservices are easily identified, such as regulation of water quality but also nutrient runoff and sedimentation of waterways, and so on. It appears that what can be positive in one particular context may

perhaps be quite negative in another – or via a change in circumstance. In certain cases, I therefore observe the potential of a *sliding scale of service to disservice*. Furthermore, the recent increase in land devoted to pollinator-dependent crops (Aizen et al. 2008) has consequently placed an increased importance on pollinator services; that we are placing high value onto pollinator services today does not necessarily mean that high value will be placed on pollinator services indefinitely.

Using pollination in lowbush blueberry as a study system, this thesis research questioned whether early season pollination could be an ecosystem disservice to agricultural production – a stance that is comparatively far less represented. However, I want to make it very clear that this uncommon viewpoint *is not synonymous* with a view that early season pollinators themselves are inherently ‘bad’ or ‘unhelpful’. Instead, pollinators as a potential ecosystem disservice speaks directly to agricultural management choices that do not suitably align the managed agro-ecosystem in question with unmanaged, external ecosystem functions. Clear examples of this misalignment, specifically with regards to pollination, are becoming more numerous. For example, excess pollination in fruit trees can reduce both fruit quality and the production of leaves for photosynthesis (Klein et al. 2015), and often requires producers to thin fruitlets in order to increase fruit size, value, and quality at harvest (Free, 1993; Jackson, 1989; Klein et al. 2015). Given these misalignments, it is therefore especially interesting that this thesis research did not find early season pollination to present an ecosystem disservice, despite the temporal mismatch between the unique ‘wild’ developmental characteristics of this crop with management practices that are regulated, mechanized, and conclude with a singular harvest.

3.6 Conclusion

Recently, both academic literature and news media have identified pollination as a positive ecosystem service and important input to maintaining ongoing food security. Yet in managed agro-ecosystems, not all variables can be controlled. Thus, in this thesis, I explored the impacts of early (wild) season pollination versus late (wild and managed) season pollination on lowbush blueberry production in Atlantic Canada in order to test whether pollination can shift from ecosystem service to disservice, depending on the agro-ecosystem context and management practices employed. Specifically, I tested whether early season pollination may result in premature berry ripening and pre-harvest berry drop, and/or reduce berry sweetness should the production of early-season berries reduce plant resources available to late-season berries. Ultimately, however, the results reject this hypothesis. Instead, results indicate that where saleable *ripe* berries are considered, the benefits of excluding all early season pollination were small and only occurred in clones that flowered early. Remarkably, early season pollination plots produced over 70% of the total production per m² than was produced by late season pollination plots. These early season pollination plots also retained their berries just as well as late season pollination plots, and did not exhibit relatively higher levels of shatter (ripe berry drop at harvest), despite having significantly heavier individual berries. Sugar content analysis revealed consistent results across pollination treatment and flowering time. Instead of presenting an ecosystem disservice, my results highlight the contribution and value of early season, wild pollinators to lowbush blueberry production.

Furthermore, while early season pollination did not present a disservice, I did find that clonal flowering time (early clone versus late clone) affected total yield, ripe yield, berry drop, and shatter significantly, with early flowering clones setting more fruit than

late flowering clones. Finally, the importance of yield loss via shatter was highlighted herein, emphasizing the need for continued research on effective harvest methodologies.

Finally, although a pollination timing ecosystem disservice was not identified regarding lowbush blueberry, this thesis also explored ecosystem services versus disservices more broadly in managed agro-ecosystems. Although not as popular or well-established as the ecosystem services literature, this thesis argued that ecosystem disservices can, and do, arise as a consequence of agricultural management decisions, which can alter the flow of service to disservice. It is hoped that this thesis prompts other industries to critically evaluate the alignment (or misalignment) of pollination and harvest that may inadvertently lead to disservice and decreased yields.

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