



Ecosystem services by birds and bees to coffee in a changing climate: A review of coffee berry borer control and pollination

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ABSTRACT

Coffee is one of the most important tropical crops on earth, considering both its gross production value and the number of families that depend on it for their livelihoods. Coffee also grows within some of the world's most biodiverse habitats, in areas predicted to experience severe climate change impacts. Like many other crops, coffee benefits from several ecosystem services (ES) that provide important inputs or conditions for production. Given coffee's strong interactions with conservation, livelihoods, and climate change, it is important to understand the roles of biodiversity-regulated ES to coffee and how they are likely to change under future climates. Here we review the available literature on the provision of two essential and interacting ES that regulate coffee production: control of a beetle pest by birds and pollination by bees. Studies show that bird and bee communities provide pest control and pollination services that improve coffee quantity and quality, benefiting coffee farmers whose livelihoods depend on this crop. The literature also shows that a variety of plot, farm, and landscape management practices that support resources for bees and birds can enhance these ES. We also evaluate how these ES and their interactions may change under future climate change. Several studies have estimated likely climate impacts on coffee per se, but few have investigated climate vulnerability of pollination and pest control ES. Even less studies have quantified interactions between these ES. Although evidence is incomplete, managing coffee farms as diversified agroforestry systems could improve climate resilience of coffee cropping and communities of birds and bees, and therefore help farming families adapt to their changing environment. Based on our review, we identify six critical research priorities in this active area of study. Filling knowledge gaps would advance our understanding of interactions among landscapes, ES, and climate change, and would support climate adaptation for the millions of households whose livelihoods depend on coffee.

1. Introduction

Coffee is one of the most important tropical crops on earth. Coffee production occupies almost 11 million ha (Fig. 1) of the 1.59 billion ha dedicated to permanent crops worldwide (FAO, 2016). The gross value of production of raw coffee in 2015 exceeded US\$16 billion, and its export value reached US\$24 billion in 2012 (FAO, 2015). Approximately 70% of the world's coffee is produced on farms smaller than 10 ha (Jha et al., 2011). There are an estimated 20–25 million coffee growing households worldwide that depend on its production for their livelihoods (Vega et al., 2003, 2009; Eakin et al., 2009; Jha et al., 2011), not to mention millions more harvesters, processors, and

industry workers.

In recent decades, coffee cultivation has intensified dramatically. While global cultivated coffee area decreased by 9% between 1990–2010, coffee production increased by 36% during that same period (Jha et al., 2014). Coffee farmers have shifted from original shaded cultivation practices towards a shade free production, based on a debated assumption that shade trees lower coffee yield and increase diseases in coffee plants (Perfecto et al., 1996; Lin et al., 2008; Jha et al., 2014; Avelino et al., 2015). According to Jha et al. (2014), by 2010 the global area of coffee under traditional shade cultivation was approximately 20% lower than in 1996. Increased use of synthetic agrochemicals (e.g., pesticides, fungicides, herbicides, fertilizers)

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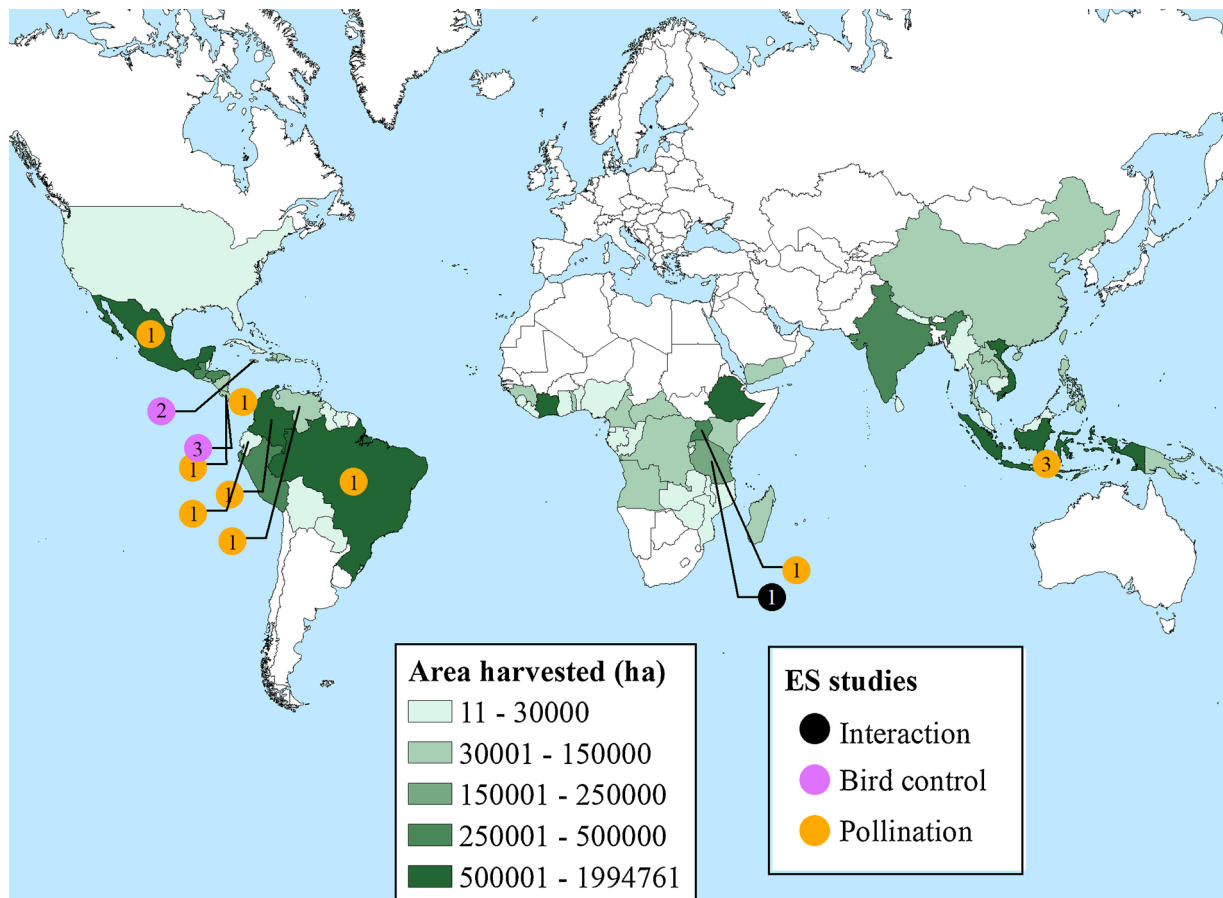


Fig. 1. Distribution of coffee production and location of reviewed studies. Countries are shaded to indicate total area harvested (ha) according to data from [FAO \(2016\)](#). United States data corresponds to coffee harvested in Hawaii. Dots indicate the location of studies that have focused on ecosystem services to coffee: coffee berry borer control by birds (pink dots), pollination by bees (orange dots), and their interaction (black dots). The number within the dots indicates the number of studies conducted in each country. More detail on these studies is given in [Table 1](#).

usually accompany reduced shade cover ([Perfecto and Vandermeer, 2008](#); [Haggar et al., 2011](#); [Jha et al., 2014](#)). Agrochemicals including endosulfan, chlorpyrifos and copper sulfate are sprayed to control insect pests and fungal diseases ([Donald, 2004](#); [Jaramillo et al., 2006](#); [De la Mora et al., 2015](#); [Infante, 2018](#)). Endosulfan and chlorpyrifos are highly toxic and a threat to the environment, the farmers who use them, and the communities living adjacent to treated coffee farms ([Baker et al., 2002](#); [Donald, 2004](#); [Infante, 2018](#)), moreover there is evidence that CBB is capable of developing resistance to this highly toxic insecticide ([Brun et al., 1989](#)).

Coffee is cultivated within some of the most biodiverse habitats on earth ([Hardner and Rice, 2002](#)), and its cultivation intensification has threatened biodiversity ([Perfecto et al., 1996](#); [Moguel and Toledo, 1999](#); [Jha et al., 2014](#); [Hipólito et al., 2018](#)). Intensification of coffee cultivation is also likely to reduce the provision of ecosystem services (hereafter, ‘ES’) in these landscapes ([De Beenhouwer et al., 2013](#); [Jha et al., 2014](#)). Two services in particular – pollination by bees and pest control by birds – are provided by communities of mobile organisms ([Kremen et al., 2007](#); [Kellermann et al., 2008](#); [Martínez-Salinas et al., 2016](#)). Because mobile organisms respond strongly to landscape composition and configuration ([Perfecto et al., 2003](#); [Ricketts, 2004](#); [Karp et al., 2013a](#); [Boesing et al., 2017](#)), these services are especially vulnerable to changes in landscape and farm management. Several studies have established the critical role that coffee cultivation in the form of shaded coffee systems play for biodiversity conservation, particularly in comparison with simplified coffee agroecosystems characterized by lower diversity of shade trees and more chemically intensive cultivation ([Perfecto et al., 1996, 2003](#); [Greenberg et al., 1997a, 1997b](#); [Donald,](#)

[2004](#); [Philpott et al., 2008](#); [Perfecto and Vandermeer, 2008](#); [Tscharnkte et al., 2011](#); [De Beenhouwer et al., 2013](#); [Jha et al., 2014](#)). Coffee agroforestry systems are defined as the biological interaction between coffee plants and at least one woody perennial species ([Somarriba, 1992](#)). Potential combinations between coffee plants and woody perennials provide a wide array of spatial arrangements and shade typologies, from one-on-one interactions to more complex coffee agroforestry systems where the coffee plant interacts with multiple woody perennial species (hereafter, ‘shaded coffee systems’).

Significant challenges for coffee farmers worldwide include market volatility, diseases and pests, and climate change ([Jha et al., 2014](#)). The price of coffee is highly unstable, and abrupt changes in coffee prices can generate significant shocks to coffee producers ([Brown and Gibson, 2006](#); [Eakin et al., 2009](#)), affecting incomes, livelihoods, food security, and production strategies, especially for smallholders ([Brown and Gibson, 2006](#); [Eakin et al., 2014](#)). Coffee is affected by a range of fungal diseases and insect pests. Among insect pests, coffee berry borer (*Hypothenemus hampei* Ferrari) (Coleoptera: Curculionidae: Scolytinae) is the most devastating species affecting coffee production worldwide ([Vega et al., 2009](#)). It is broadly distributed across all dominant coffee producing regions ([Damon, 2000](#); [Jaramillo et al., 2006](#); [Vega et al., 2009](#); [Infante, 2018](#)) and causes worldwide annual losses estimated to surpass US\$500 million ([Vega et al., 2017](#)). In Brazil alone, annual losses caused by coffee berry borer (hereafter, ‘CBB’) have been estimated at US\$215–358 million ([Oliveira et al., 2013](#)). Climate change is also expected to impact coffee cultivation, by decreasing climatic suitability at lower altitudes and higher latitudes ([Adhikari et al., 2015](#); [Bunn et al., 2015b](#); [Magrath and Ghazoul, 2015](#); [Ovalle-Rivera et al.,](#)

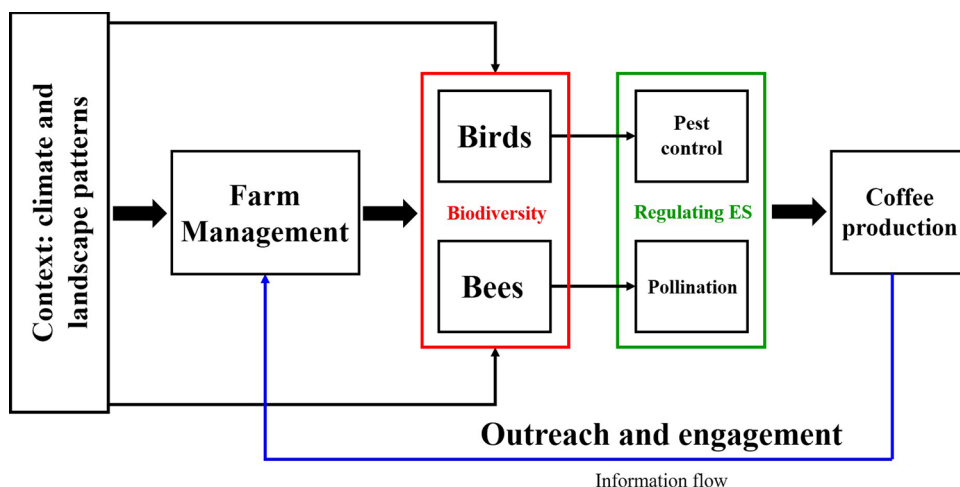


Fig. 2. Relationships among factors affecting bird and bee communities and the ecosystem services (ES) they provide to coffee farms. From left to right: contextual factors such as climate (which affects temperature and precipitation) and landscape patterns (which shapes species distribution and composition) directly influence farm management decisions. Management decisions in turn influence biodiversity, particularly birds and bees, which provide ES such as pest control and pollination to coffee. These services can increase coffee production (and quality). Lastly, the blue arrow from right to left indicates how knowledge about these interactions can inform management decisions and contribute to biodiversity conservation by improving habitat. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

2015; Schroth et al., 2015; Chemura et al., 2016), by affecting flowering and fruiting stages (Gay et al., 2006; Villers et al., 2009), and by increasing pressure from pests and diseases (Cleveland et al., 2006; Avelino et al., 2015).

Given the economic importance of coffee growing systems, their potential effects on native biodiversity, and their vulnerability to climate change, it is important to understand the roles of biodiversity-regulated ES in coffee growing landscapes and how they are likely to change under future climates. Here we review the available literature on the provision of two ES that support coffee production: control of CBB by birds and pollination by bees (Fig. 2). We focus on these two ES specifically because they are both provided by diverse communities of mobile organisms (Kremen et al., 2007), which are likely to respond strongly to changes in land use and land management (Fig. 2). Because ecological and economic interactions among ES are likely common but seldom studied, we highlight evidence for these interactions. Because coffee, birds, and bees have all been shown to be sensitive to climate change (e.g., Grunewald, 2010; Şekerioğlu et al., 2012; Giannini et al., 2012; Ovalle-Rivera et al., 2015; Bunn et al., 2015b; Imbach et al., 2017), we pay particular attention to evidence of climate impacts on these ES and their interactions. By understanding how changes in land use and climate are likely to affect important ES to coffee, we can improve the management of coffee farms and surrounding landscapes. This paper synthesizes knowledge to date and identifies research priorities to fill essential gaps in that knowledge.

2. Coffee, biodiversity and ecosystem services

Biodiversity conservation is crucial for supporting ecosystem functioning and the provision of ES (Tilman, 1997; Cardinale et al., 2012). In particular, agricultural ecosystems benefit from many ecological processes that provide ES that are fundamental to food production and farm management (Zhang et al., 2007; Garbach et al., 2014). Agricultural ecosystems can hold important levels of biodiversity, depending on management practices and intensities (DeClerck et al., 2010). In particular, shaded coffee systems have been shown to support greater levels of native biodiversity compared to other crops and other coffee management systems (Greenberg et al., 1997a, 1997b; Komar, 2006; Jha and Dick, 2010; Tscharnke et al., 2011; Jha et al., 2011, 2014; Frishkoff et al., 2014; Buechley et al., 2015). Coffee farms can also help link forest fragments, increasing landscape connectivity and providing important pathways for resident and migratory species movement (Jha et al., 2014). Roles of individual species as well as interactions among species may affect the type and strength of ES delivered (Zavaleta et al., 2010; Mouillot et al., 2013). Understanding species roles in the provision of specific services is necessary to

maximize the positive impacts of biodiversity conservation in agriculture-dominated landscapes.

In coffee systems, in particular, available literature about ES provisioning is biased towards shaded coffee systems given the interactions between the crop (i.e., coffee) and a wide variety of tree species that provide diverse habitats for native animal species (Perfecto et al., 1996; Moguel and Toledo, 1999; Philpott et al., 2008), and because shaded coffee systems, even though naturally grown under the forest canopy, are nowadays emerging as a promising climate adaptation practice that seeks to take advantage of existing ecological processes and biological diversity more than other technological solutions. There are multiple examples of ES provided in shaded coffee systems, such as carbon sequestration (Albrecht and Kandji, 2003; Tumwebaze and Byakagaba, 2016), maintenance of nutrient cycling and soil fertility (Beer et al., 1998; Cerda et al., 2017), reduction of soil erosion (Gómez-Delgado et al., 2011; Cerdán et al., 2012), food provision (Rice, 2011), wood and timber (Bacon et al., 2008), regulation of diseases (Schroth et al., 2000; Soto-Pinto et al., 2002), reduction or control of weeds (Muschler, 1997; Beer et al., 1998), pollination (Kremen et al., 2007; Klein et al., 2007, 2008), and pest control (Philpott et al., 2004; Wenny et al., 2011; Milligan et al., 2016). A few studies have also shown that shaded coffee systems usually benefit from the provision of important ES in comparison with sun coffee systems (Cerda et al., 2017; Jezeer et al., 2017; Meylan et al., 2017). While the majority of evidence is for shaded coffee systems, sun coffee systems can also support species and ecosystem services from several taxa (Saturni et al., 2016; Boesing et al., 2017; Librán-Embid et al., 2017; Barrios et al., 2018; Aristizábal and Metzger, 2019) perhaps as a result of surrounding forested land uses exerting positive spillover effects (Van Bael et al., 2008; Johnson et al., 2009). Although there is a growing number of studies focusing on the evaluation of ES in coffee systems, there are still very few that are focused on understanding the trade-offs and synergies between ES that are critical for coffee production sustainability (but see Classen et al., 2014; Allinne et al., 2016; Cerda et al., 2017). Exploring the synergies and trade-offs between critical ES is thus necessary to inform farm management and promote biodiversity conservation (Bennett et al., 2009; Fig. 2). In this section, we will review and discuss existing knowledge on the importance of birds and bees in the delivery of CBB control and pollination services, and their interaction (Table 1), considering the landscape context and the economic relevance of these ES to coffee farmers.

2.1. Pest control by birds

Birds are important insect predators in coffee systems and play essential roles in pest control (Greenberg et al., 2000; Perfecto et al.,

Table 1
 Reviewed studies on coffee berry borer (CBB) control by birds (CBB control), pollination by bees (pollination) and their interaction (CBB × pollination) in coffee systems worldwide. ELEV: Elevation; AR: annual rainfall, MAT: mean annual temperature. Studies of CBB control by birds, pollination by bees and their interaction are shown separated and listed in chronological order from newest at the top to oldest at the bottom.

ES	Reference	Country	Size and number of study sites	Elevation and climate	Coffee variety	Coffee shade	Farm management	Response variable (s)	Study design	Other factor(s) assessed	Economic value assessed
CBB control	Martínez-Salinas et al. (2016)	Costa Rica	1 farm: 1036 ha; coffee area: 85 ha; 10 sites	ELEV: 600 m a.s.l.; AR: 2636 mm; MAT: 22 °C	<i>Coffea arabica</i> var. <i>catarra</i>	Simplified agroforestry systems with <i>Erythrina poeppigiana</i> (seasonal canopy cover 0–80%)	Conventional management by applying herbicides and insecticides (once a year application of endosulfan)	Number of CBB infested berries	10 bird-proof enclosures (1 plant each). 1 control plant (access to foraging birds) for each bird-proof enclosure	Bird species richness, abundance, functional composition, and functional diversity	No
CBB control	Karp et al. (2014)	Costa Rica	See Karp et al., 2013a,b	See Karp et al., 2013a,b	See Karp et al., 2013a,b	See Karp et al., 2013a,b	See Karp et al., 2013a,b	Coffee berry borer DNA from faecal samples of collected birds	3 mist-netting stations at each plantation. 3 visits per year/station		No
CBB control	Karp et al. (2013a, 2013b)	Costa Rica	2 plantations: 30 ha family owned, 250 ha certified commercial operation	ELEV: ~1100 m a.s.l.; AR: 3600 mm; MAT: 17–24 °C	<i>Coffea arabica</i>	Sun coffee (seasonal canopy cover 25 ± 6%)	Year-round application of fertilizer, herbicide, and fungicide; post-harvest removal of unharvested and fallen berries for CBB management. In the 250 ha plantation: application of low doses of endosulfan and use of CBB traps	Number of CBB infested berries	36 bird-proof enclosures (4 plants each) in the 30 ha plantation. 60 bird-proof enclosures (1 plant each) in the 250 ha plantation. 1 control (access to foraging birds) for each bird-proof enclosure	Forest cover, elevation	Yes
CBB control	Johnson et al. (2010)	Jamaica	1 farm: 17.7 ha		<i>Coffea arabica</i> var. <i>typica</i>	Farm: 70% shade, 30% sun coffee	Yearly application of endosulfan; removal of overripe unharvested berries	Number of CBB infested berries	4 bird-proof enclosures (3 plants each) in shade coffee. 4 bird-proof enclosures (3 plants each) in sun coffee. 3 control plants (access to foraging birds) for each bird-proof enclosure	Shade	Yes
CBB control	Kellermann et al. (2008)	Jamaica	4 farms: 34 ha, 22 ha, 6 ha, 6 ha	ELEV: 864–1316 m a.s.l	<i>Coffea arabica</i> var. <i>typica</i>	Native tree species mixed with some non-native species	3 farms with yearly application of endosulfan; 1 certified organic farm not sprayed	Number of CBB infested berries, depth of borer penetration	30 bird-proof enclosures (1 plant each). 1 control plant (access to foraging birds) for each bird-proof enclosure	Vegetation complexity, agricultural intensification	Yes
Pollination	Bravo-Monroy et al. (2015)	Colombia	12 farms	ELEV: 1577–1919 m a.s.l	<i>Coffea arabica</i>	6 certified organic and 6 conventional farms		Initial fruit set, final fruit set, final fruit retention, number of peaberries	112 plants. 2 branches per plant. 1 wind + self pollination branch, 1 open pollination branch	Proximity to forest, farm management	Yes
Pollination	Munyuli (2014)	Uganda	26 study sites. 30 coffee fields (0.25–15 ha)		<i>Coffea canephora</i>	4 banana-coffee agroforests: complex, home gardens, simple shaded, simple sunny	9 organic, 14 conventional, and 7 commercial fields	Early fruit set, potential proportional yield of coffee, proportional bee contribution to fruit set, proportional pollination limitation	5 plants per coffee field. 3 branches per plant, one for each pollination treatment: open pollination, cross-pollination by hand, self-pollination	Blooming season, site, number of trees per site	No
Pollination	Vergara and Badano (2009)	Mexico	16 plantations	ELEV: 1040–1245 m a.s.l	<i>Coffea arabica</i>	4 systems: rustic shaded coffee, commercial	Gradient of shade types with different	Fruit set rate	4 sites per shade category. 4 coffee plants per site. 2 branches per plant. 1 branch with bee-	Management type	No

(continued on next page)

Table 1 (continued)

ES	Reference	Country	Size and number of study sites	Elevation and climate	Coffee variety	Coffee shade	Farm management	Response variable (s)	Study design	Other factor(s) assessed	Economic value assessed
Pollination	Bos et al., (2007)	Ecuador	22 plantations		<i>Coffea arabica</i> var. <i>catuira</i>	polyculture, specialized shaded coffee, and sun coffee	impacts on natural ecosystems	Initial fruit set, final fruit set, fruit abortion	prof enclosure; 1 open pollination branch 4 plants per plantation. 3 inflorescences per plant, one for each pollination treatment: self-pollination, wind pollination, open pollination		No
Pollination	De Marco and Coelho (2004)	Brazil	6 farms	ELEV: 649 m a.s.l	<i>Coffea arabica</i> var. <i>catuai</i>	3 different systems: monoculture with native vegetation, agrosilvicultural system, monoculture without native vegetation	No fertilizers or other chemical inputs used	Fruit set	15 plants per farm. 4 branches per plant. 1 branch with pollinator proof enclosure (allowing pollen grains passage).	Shade type, distance to forest	No
Pollination	Ricketts et al. (2004)	Costa Rica	1 farm: 1065 ha; 12 sites		<i>Coffea arabica</i> var. <i>catuira</i>	<i>Eucalyptus deglupta</i> shade	Homogenous farm management regarding weed and pest control, planting and harvest practices, and shade tree species and density	Seed mass; fruit set, peaberry frequency	5 plants per site. 4 branches per plant. 2 cross-pollination by hand branches, 2 open pollination branches	Distance to forest, density of weed and shade flowers, canopy cover	Yes
Pollination	Klein et al. (2003a)	Indonesia	24 sites		<i>Coffea arabica</i>	Agroforestry coffee fields differing in the amount of shade		Fruit set	3 pollination treatments per site: open pollination, cross-pollination by hand, self-pollination by hand. 4 plants per treatment. 3 branches per plant.	Diversity and abundance of bees, number of plant species, pollen and nectar availability, light intensity, distance to forest	No
Pollination	Klein et al. (2003b)	Indonesia	15 sites	ELEV: 1224-1299 m a.s.l	<i>Coffea canephora</i>	Agroforestry coffee fields differing in the amount of shade		Fruit set	2 pollination treatments per site: cross-pollination by hand, open pollination. 4 coffee plants per treatment. 2 branches per plant	Distance to forest, pollen and nectar availability, light intensity	No
Pollination	Klein et al. (2003c)	Indonesia	24 coffee fields	ELEV: 1000-1200 m a.s.l	<i>Coffea canephora</i> syn. <i>Coffea robusta</i> ; <i>Coffea arabica</i>	Agroforestry coffee fields differing in the amount of shade		Fruit set	6 pollination treatments: open pollination, wind + self-pollination, cross-pollination by hand, self-pollination by hand (pollen of the same plant), self-pollination by hand (pollen of the same flower), self-pollination. 4 plants per treatment. 6 branches per plant	Distance to forest, pollen and nectar availability, light intensity	No
Pollination	Manrique and Thimann (2002)	Venezuela	2 plots: 7 ha each	ELEV: 1400 m a.s.l; AR: 1400 mm; MAT: 17 °C	<i>Coffea arabica</i> var. <i>catimor</i>	Adult <i>Inga</i> spp. trees		Number of flowers blooming, number of mature grains, weight of wet/dry grains	60 plants divided into 3 treatments: 20 uncovered branches, 20 branches enclosed with bee hive, 20 uncovered branches in a no hive-containing plot	Presence of Africanized honeybee colonies	No
Pollination	Roubik (2002)	Panama						Number of ripe berries, weight of ripe berries	50 plants. Branches in 2 pollination treatments: open pollination and bagged		No

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Table 1 (continued)

ES	Reference	Country	Size and number of study sites	Elevation and climate	Coffee variety	Coffee shade	Farm management	Response variable (s)	Study design	Other factor(s) assessed	Economic value assessed
CBB × pollination	Classen et al. (2014)	Tanzania	12 sites	ELEV: 1120 - 1660 m a.s.l	Coffea arabica	3 systems: traditionally managed home gardens (canopy cover ~80%), shaded coffee plantations (canopy cover ~30%) and sun coffee plantations	All systems: pruning once per harvest season, sprinkle irrigation during dry season. Home gardens: water channel for irrigation, irregular application of insecticides and fungicides, hand weeding. Shaded and sun coffee: regular, intensive pesticide and fungicide spraying, manual weeding or control with herbicides or grass cutting	Early fruit set, late fruit set, fruit retention rate, fruit weight, CBB infestation rates	3 shade categories. 4 sites per shade category. 3 clusters of 4 coffee plants per site. Each plant assigned to 1 of 4 treatments: open control, pollinator exclusion, vertebrate exclusion, combined pollinator and vertebrate exclusion	Land use intensity	Yes

* Endosulfan is an organochlorine insecticide.

** Early or initial fruit set correspond to the percentage of flowers developing fruits (i.e., proportion of flowers that were successfully pollinated); final fruit set is the percentage of flowers that resulted in mature fruits; coffee fruit retention is calculated as the ratio between the number of mature fruits and the number of initial fruits; peaberries correspond to berries harvested with only one developed ovule; fruit abortion is the proportion of fruits that was lost between initial and final fruit set.

2004; Philpott et al., 2004, 2008; Kellermann et al., 2008; Van Bael et al., 2008; Johnson et al., 2010; Wenny et al., 2011; Karp et al., 2013a; Martínez-Salinas et al., 2016; Milligan et al., 2016; Sherry et al., 2016; Nyffeler et al., 2018). This suggests that coffee farmers could substantially benefit from reduced pest losses if their farms and surrounding landscapes provide sufficient habitat for key predator species (Lindell et al., 2018).

The coffee berry borer (CBB) is the primary insect pest affecting coffee production worldwide. Its control, either by chemical or natural means, is extremely difficult because the majority of its life cycle occurs inside coffee berries (Damon, 2000; Jaramillo et al., 2006; Vega et al., 2009; Infante, 2018). Studies on CBB control in Jamaica (Kellermann et al., 2008; Johnson et al., 2010) and Costa Rica (Karp et al., 2013a, 2014; Martínez-Salinas et al., 2016) have demonstrated that both resident and migratory bird species are effective predators of CBB. Birds lowered infestation rates as much as 50% in simplified and intensively managed agroforestry coffee farms (Martínez-Salinas et al., 2016) and as much as 58% in sun coffee farms (Johnson et al., 2010). Although birds are key predators of CBB, it is important to highlight that other species might also contribute to the suppression of this pest. For example, there is growing evidence that different species of ground-and-coffee foraging ants contribute to CBB control (Philpott and Armbrrecht, 2006; Armbrrecht and Gallego, 2007; Larsen and Philpott, 2010; Gonthier et al., 2013; De la Mora et al., 2015; Morris and Perfecto, 2016; Morris et al., 2018; Aristizábal and Metzger, 2019) and that insectivorous bats might also play a role in the suppression of the beetle (Karp et al., 2013a), however their relevance in controlling CBB needs further examination.

Agricultural intensification can have negative effects on bird communities thus hindering their contribution to pest control. The presence and richness of pest-regulating bird species are dependent on landscape configuration (Boesing et al., 2017; Lindell et al., 2018). Forested landscapes, for instance, contribute to the persistence of insectivorous species that benefit even sun coffee farms (Karp et al., 2013a; Sherry et al., 2016). Percent canopy cover and tree diversity in shaded coffee systems have been shown to be positively correlated with insect removal (Perfecto et al., 2004; Van Bael et al., 2008; Milligan et al., 2016); and particularly with CBB removal (Railsback and Johnson, 2014). However, there is also evidence that birds can provide the service in sun coffee (Johnson et al., 2010), perhaps supported by surrounding habitats (Karp et al., 2013a,b). This is also supported by other studies that have shown positive correlations between pest removal and proximity to adjacent forest fragments (Milligan et al., 2016; Boesing et al., 2017). Furthermore, Karp et al. (2013a) found that CBB-consuming birds increased in abundance and exerted stronger control on CBB populations on coffee farms with higher forest cover, observing less severe CBB infestation on coffee farms showing greater forest elements. Finally, Avelino et al. (2012) proposed fragmenting coffee farms with forest corridors to reduce CBB movements between plots. Incorporating both shade trees within the farm and small forest patches on farm edges could support bird species delivering crucial pest control services (Railsback and Johnson, 2014). However, additional studies are needed to understand the effects of landscape context and farm management (i.e., shade and agronomic management) on provision of this service (Fig. 2). For instance, recent findings by Karp et al. (2018) show that CBB control depends on surrounding landscape composition, demonstrating that maintaining small areas of natural habitat in otherwise agriculture-dominated landscapes might not be enough to increase pest control.

Birds make significant, global, but rarely quantified contributions to our economies, mostly because methods to quantify avian services and their values are poorly developed (Wenny et al., 2011; Whelan et al., 2015). ES provided by birds are mostly supporting and regulating services which are the most difficult to quantify (Wenny et al., 2011). These ES are mainly indirect and support or enhance other services (Şekerciöglü, 2006), so neither bird nor their services are generally

included in ecosystem-valuation models (but see Letourneau et al., 2015). In coffee systems only Kellermann et al. (2008); Johnson et al. (2010) and Karp et al. (2013a) have assessed the economic value of pest control services provided by birds. Kellermann et al. (2008), in high-elevation Jamaican farms, estimated 1–14% lower infestation rates of CBB and a greater quantity of marketable fruits in plants foraged by birds that had a market value of US\$44–\$105/ha/year. Johnson et al. (2010), in a Jamaican mid-elevation farm, also estimated the economic value of CBB control by birds to be US\$310/ha/year. In Costa Rica, Karp et al. (2013a) estimated that pest control by birds prevents US\$75–310 ha/year in damage related to CBB. These studies indicate that birds can control CBB in a variety of settings and contribute substantial benefits to coffee farmers as a result.

2.2. Pollination by bees

Coffee production benefits from native and non-native bee visits, which increase fruit set, berry size, and overall yield (Olschewski et al., 2006; Klein et al., 2008; Veddeler et al., 2008; Ngo et al., 2011; Boreux et al., 2013; Bravo-Monroy et al., 2015). There is strong evidence that honeybees (*Apis mellifera* L.) are important coffee pollinators throughout the ranges of its various cultivars and greater fruit set and fruit weight are observed with increased visits (Roubik, 2002; Manrique and Thimann, 2002; Klein et al., 2003b; Ricketts et al., 2004; Ngo et al., 2011; Boreux et al., 2013). Roubik (2002) suggests that a substantial increase in Latin American coffee yield partly coincides with the establishment of honeybees in those countries. However, although sometimes disregarded, native bees enhance and increase pollination services to coffee as well. Visits by a range of native wild bees have been shown to increase coffee fruit set and yield (Klein et al., 2003a, 2003b; Ricketts et al., 2004; Veddeler et al., 2008; Munyuli, 2014).

Pollinator diversity has also been shown to affect fruit set and yield in coffee (Klein et al., 2003a, 2003b; Vergara and Badano, 2009), although studies are fewer than those for visitation rate or bee abundance. Other studies have evaluated pollination by bees from a functional diversity perspective. Klein et al. (2008) suggested that pollinator species diversity increases the number of functional types in the community, and diversity of functional traits correlates with increased pollination success. A broader knowledge of ecosystem functions helps connect the implicit link between biodiversity and provision of ecosystem services (Swift et al., 2004). The functional trait approach is a growing field and bees functional traits that have been studied include sociality, tongue length and body size (Klein et al., 2003a; Munyuli, 2014).

A global study in 33 different pollinator-dependent crops (including coffee), in Africa, Asia, and Latin America found that yield gaps (i.e. the difference in crop yield between high- and low-yielding farms of a given crop system), could be closed by a median of 24% in small farms (< 2 ha) through increased flower-visitor density (Garibaldi et al., 2016). However, across the globe, agricultural intensification jeopardizes wild bee communities and their pollination services (Klein et al., 2007; Grunewald, 2010). Pollinator diversity and visitation rate respond to landscape context (e.g., distance to the forest) and farm management (e.g., shade and agronomic management intensification) (Steffan-Dewenter and Tscharnitke, 1999; Klein et al., 2003a, 2003b; Ricketts, 2004; Ricketts et al., 2008; Klein, 2009; Vergara and Badano, 2009; Jha and Vandermeer, 2010; Garibaldi et al., 2011; Munyuli, 2011; Hipólito et al., 2018). Coffee near intact rainforest receive visits from diverse pollinators, which results in more stable visitation rates (Ricketts, 2004) and more consistent fruit set than coffee further from forest which receives few or even a single species of pollinator (Ricketts, 2004; Klein, 2009). Moreover, crop proximity to forests increases coffee yields (Roubik, 2002; Ricketts et al., 2004), fruit set, and berry weight (Olschewski et al., 2006). Landscape and management planning can therefore improve crop yields (Priess et al., 2007). For example, flower visitation can be improved by sowing flower strips and

planting hedgerows, providing nesting resources, and decreasing exposure to pesticides and parasites (e.g. targeted use of pesticides) and/or restoration of adjacent seminatural and natural areas (Garibaldi et al., 2016).

Even with growing evidence that pollination services can improve coffee production, the potential economic benefits of these services often remain obscure to farmers. However, in comparison to pest control by birds, the value of the pollination ecosystem service has been more extensively addressed at local, regional and global scales (Hanley et al., 2015). In Costa Rican coffee systems, Ricketts et al. (2004) estimated that forest patches contributed US\$62,000/year to farms (within 1 km), via increased pollination and resulting fruit set and seed mass. De Marco and Coelho (2004), in Brazil, estimated that coffee close to native forests increased production value by US\$1860 ha/year. At a national level in Brazil, Giannini et al. (2015a) estimated the contribution of pollinators to coffee production as US\$1.9 billion/year. In Colombia, Bravo-Monroy et al. (2015) found that a reduction of native bees (i.e., stingless bees) could result in revenue losses of around US\$16.5/ha (1.7% of farmer's net revenue) and a reduction in honeybees could result in US\$129.6/ha (3.7% of farmer's net revenue). In Ecuador, Veddeler et al. (2008) also found higher coffee yield due to increased pollination generated higher net revenues per hectare. In particular, a fourfold increase in bee density was associated with an 816% increase in net revenues. In Indonesia, net revenues decreased from 100 US\$/ha near forest fragments to 53 US\$/ha in sites 1.5 km away (a 47% decline) (Olschewski et al., 2006). Also in Indonesia, pollination services were valued at approximately 52.7 US\$/ha, and using different future land use scenarios predicted coffee yields to decrease as much as 18% and net revenues per hectare as much as 14% (Priess et al., 2007).

2.3. Interaction between pest control and pollination

Since management actions toward the improvement of one ecosystem service may affect the provision of others, it is crucial to understand the relationships among different ecosystem services (Bennett et al., 2009). Generally, pollination and pest control services have been studied in isolation, but in recent years studies have begun to explore the interactions and synergies between these two critical services on crop yield (Garibaldi et al., 2018).

To our knowledge, only one study on the interaction between pest control and pollination has been conducted in coffee systems. Using an experimental enclosure approach in Mount Kilimanjaro, Classen et al. (2014) demonstrated that pest predators and pollinators both contribute to coffee production, but do so independently by affecting different yield parameters. The enclosure of predators resulted in ca. 9% reduction in fruit set, while pollinators significantly increased fruit weight by 7.4% (Classen et al., 2014). The effect of pollination on fruit weight was independent of the impact of pest control on fruit set. Thus, results indicated that while pest control and pollination services do not act in synergy (i.e., positive interactions), they complement each other in coffee production (i.e., additive effects).

Studies on the interaction of these two ecosystem services have been conducted in other crops, involving different pest and predators, and six studies (including Classen et al., 2014) are reviewed in Garibaldi et al. (2018). Most of these studies consist of factorial field or pot experiments with different levels of pest regulation and pollination (e.g., via exclusion treatments), but some relied on correlative approaches (e.g., measures across several agricultural fields) (Garibaldi et al., 2018). For example, studies have found synergistic effects of pollination and pest control on yields of red clover (Lundin et al., 2013) and oilseed rape (Sutter and Albrecht, 2016). These findings indicate that the gain in yield when simultaneously increasing pollination and pest control exceeded the sum of gains obtained when increasing each service separately. In contrast, in cacao (Forbes and Northfield, 2017) and cucumber (Barber et al., 2012), no interactions between these two

ecosystem services were found, suggesting that pollinator and pest control effects operate independently. Only one study (Bartomeus et al., 2015) found a negative interaction between pollination and pest control in oilseed rape crops. However, this negative interaction should be interpreted with care since pest number and pollinator abundance are weakly correlated (see Bartomeus et al., 2015). Interestingly, this study was the only observational study over broad scales. Across all crops, evidence for negative interactions between pollination and pest regulation services is scarce (Garibaldi et al., 2018).

While evidence to date is mixed, the studies above indicate that the synergistic effects of pollination and pest control can lead to greater economic benefits than predicted from independent effects. For example, Sutter and Albrecht (2016) demonstrated that combined effects of pollination and pest control could have an economic benefit on winter oilseed rape that is 1.8 times greater than the individual contributions of these two ecosystem services. When they do occur, therefore, synergies can be ecologically significant and economically highly valuable. Additional studies are important to understand the conditions under which such positive interactions are likely so that they can be managed together.

3. Effects of climate change on coffee production, pest control and pollination, and economic repercussions

Altered patterns of temperature and precipitation due to climate change, present challenges to agriculture and food supplies in many regions worldwide (Lin et al., 2008; Wheeler and von Braun, 2013; Myers et al., 2017; IPCC, 2018). Greater precipitation shortages and heat stress (Ramirez-Villegas and Challinor, 2012), reduced crop quality (Ahmed and Stepp, 2016) and increased pressures of pests and diseases will present severe challenges for agriculture (Fischlin et al., 2007; Myers et al., 2017). Moreover, management intensification (Lin et al., 2008) and habitat loss (Brown and Paxton, 2009) may exacerbate climate change effects. Although climate fluctuations are already occurring, few studies have focused on the sensitivity of coffee systems to temperature and precipitation changes (Lin et al., 2008) and its impacts on coffee production.

3.1. Effects of climate change on coffee

The current distribution of coffee lands is expected to shift due to climatic change. In general, a range of modeling studies indicate that higher temperatures and changes in precipitation are likely to move the climates suitable for coffee growth upwards in altitude (Schroth et al., 2009, 2015; Jha et al., 2011; Davis et al., 2012; Baca et al., 2014; Adhikari et al., 2015; Bunn et al., 2015b; Magrath and Ghazoul, 2015; Ovalle-Rivera et al., 2015; Chemura et al., 2016). Predicted changes in optimal coffee producing elevations vary by region and climate scenario, but areas currently growing Arabica coffee (*Coffea arabica* L.) within 5°–10° of the Equator at elevations less than 1000–1200 m a.s.l. are likely to become unsuitable due to higher temperatures (Schroth et al., 2009; Ovalle-Rivera et al., 2015; Bunn et al., 2015b; Läderach et al., 2017). As suitable areas are located at higher altitudes, less land will be available at those higher elevations, leading to an overall reduction in suitable area for coffee production across coffee-growing regions worldwide (Schroth et al., 2009, 2015; Davis et al., 2012; Bunn et al., 2015a, 2015b; Magrath and Ghazoul, 2015; Ovalle-Rivera et al., 2015; Chemura et al., 2016; Ranjitkar et al., 2016; Imbach et al., 2017; Läderach et al., 2017; Moat et al., 2017; Fain et al., 2018; Tavares et al., 2018). The predicted magnitude of these reductions varies among studies, regions, and scenarios, but all estimates are substantial. For example, by 2050 under high warming scenarios (RCP 8.5), suitable area for Arabica coffee has been predicted to decline up to 88% for Latin America (Imbach et al., 2017), with regions like Brazil showing substantial declines in suitability (Bunn et al., 2015b; Magrath and Ghazoul, 2015; Ovalle-Rivera et al., 2015); up to 85% for South East

Asia (Bunn et al., 2015b); up to 63% for East Africa (Bunn et al., 2015b; Magrath and Ghazoul, 2015); and up to 30% for the Asian and Pacific Islands (Bunn et al., 2015b).

Climatic change will not only affect the future spatial distribution of coffee. Rising temperatures and decreasing or irregular rainfall patterns are also expected to negatively affect coffee production (Gay et al., 2006; Schroth et al., 2009; Craparo et al., 2015; Rahn et al., 2018; Tavares et al., 2018), quality (Gay et al., 2006; Schroth et al., 2009; dos Santos et al., 2015; Läderach et al., 2017), flowering, and fruiting (Gay et al., 2006; Lin et al., 2008; Schroth et al., 2009; Villers et al., 2009). Higher temperatures are related to lower coffee yields (Gay et al., 2006; Schroth et al., 2009; Craparo et al., 2015; Läderach et al., 2017; Rahn et al., 2018; Tavares et al., 2018), and coffee beans with low acidity and flavor (Läderach et al., 2017). Higher temperatures also result in faster and shorter ripening of the berries which translates into poorer bean quality (Vaast et al., 2006; dos Santos et al., 2015). The phenology of coffee is strongly dependent on rainfall distribution over the year (Gay et al., 2006; Lin et al., 2008; Schroth et al., 2009; Villers et al., 2009). For example, blooming takes place just after the first rains of spring after a “relative drought”. If a persistent dry spell occurs, flowers are not produced, and so neither are fruits. On the contrary, if heavy rains occur, flowers and fruit can drop from the shrubs (Gay et al., 2006; Schroth et al., 2009; Villers et al., 2009). Finally, sporadic rains during the flowering season (e.g., many small rain showers instead of a few larger events) can lead to erratic flowering and fruit ripening which may result in inefficient harvest and fewer, smaller beans of lower quality (Damatta et al., 2007; Craparo et al., 2015). Thus, under predicted future climate scenarios, coffee production faces multiple impacts from increasing temperatures and shifting precipitation regimes.

3.2. Effects of climate change on birds and coffee berry borer control

Climate change will impact bird species in a wide variety of forms. Some of the most significant impacts of climate change on bird populations will be related to changes in patterns of species distribution (Anciães and Peterson, 2006) and changes in species composition of avian communities (Brawn et al., 2017) in response to changing temperature and rainfall patterns. For instance, based on a meta-analysis, Chen et al. (2011) indicated that bird communities would shift across their latitudinal and altitudinal ranges as a result of climate change. Similarly, Freeman et al. (2018) highlighted extirpation risks for mountaintop tropical bird species which are shifting its current distributions due to climate change induce temperature increases. Additionally, Lawler et al. (2009) showed that even lower emission scenarios provide evidence that climate change will have a significant impact on bird species turnover, suggesting that future communities will little resemble current ones. Climate change will also impact bird breeding patterns as a response to changes in phenology of plant species on which avian species depend (Crick, 2004; Senapathi et al., 2011).

Furthermore, Şekercioğlu, et al. (2008) showed that climate change-related pressures coupled with continuing habitat loss would increase extinction probabilities of hundreds of bird species across the globe with only 21% of the species predicted to become extinct being currently considered as threatened with extinction. Similarly, Newbold (2018) showed that climate and land use change will likely become a major pressure on biodiversity, with combined effects of up to 37.9% losses of vertebrate species, while Şekercioğlu et al. (2012) found that in tropical areas of the world, where coffee is produced, climate change and habitat loss will increase extinctions of land bird species dramatically. However, it is important to highlight that bird species providing pest control services in agricultural-dominated landscapes may not be as vulnerable as those dependent on large tracts of forests or those restricted to mountaintops, as these species rely more heavily on the composition and spatial arrangement of different agricultural landscape elements, i.e. “landscape-moderated” species (Tscharntke et al., 2012). Finally, in most cases, authors point out that the lack of basic

information regarding tropical bird species current geographical distributions hinders prediction efforts on the effects of climate and land use change.

Changes in temperature and rainfall patterns will also augment diseases and pests related pressures on coffee (Ziska et al., 2018). For CBB specifically, the beetle today causes little damage above 1500 m a.s.l., likely due to temperature constraints on reproduction rates (Damon, 2000; Jaramillo et al., 2009; Vega et al., 2009). CBB optimal development thermal range is estimated to be between 14.9 and 32 °C (Jaramillo et al., 2009), suggesting that climate change induce temperature increases will likely benefit CBB range expansion creating additional pressures to coffee production at higher elevations (Gay et al., 2006; Avelino et al., 2015). CBB is a highly specialized herbivore whose distribution is restricted by both temperature and the availability of coffee host plants, so it is likely to follow the shifting distribution of coffee production (Jaramillo et al., 2009; Thomson et al., 2010). Recent data from Uganda and Indonesia show that CBB has already expanded its altitudinal distribution range and is now attacking coffee farms at sites as high as 1864 m a.s.l. (Jaramillo et al., 2009). Jaramillo et al. (2011) have further predicted that by 2050 CBB would be particularly damaging in current areas of high-quality *C. arabica* production in East Africa, in medium to higher altitudes ranging from 1200 to 1800 m a.s.l. Moreover, Jaramillo et al. (2011) predicted that the number of CBB generations per year will increase with rising temperatures such that areas currently considered as marginally suitable for CBB will become favorable for population persistence in the future. Increased and more widespread losses in production due to CBB may increase the area required to produce the same amounts of coffee. According to findings by Magrach and Ghazoul (2015), CBB is projected to expand its distribution under different climate trajectories, potentially affecting $77.8 \pm 1.7\%$ of Arabica and up to $93.02 \pm 1.3\%$ of Robusta, as compared to ca. 57% and 50% of coffee suitable areas respectively that are currently exposed.

While most studies have focused on temperature effects on CBB, shifting precipitation regimes may also have strong effects. For instance, CBB is highly dependent on precipitation stimuli to trigger dispersal and colonization of new coffee berries (Damon, 2000). Shifting rainfall patterns will have a direct effect on humidity levels which can have positive and negative effects on CBB survival (Damon, 2000). For instance, higher humidity levels favors infestation of CBB by allowing coffee berries to maintain optimal humidity thresholds, a key factor for CBB survival especially during the inter-harvest period (Barradas and Fanjul, 1986; Damon, 2000). Lower humidity levels combined with high temperatures can affect survival of CBB by inducing desiccation of the coffee berries and forcing CBB to abandon the fruits as a response of the beetle sensitivity to humidity, abandoning berries at moments of low fruit availability can result in mortality due to starvation or predation (Damon, 2000). Further impacts of changes in precipitation regimes relates to the effects on the physiology of the coffee plant. Continued exposure, throughout the year, of coffee shrubs to precipitation will induce several flowering events (Beer et al., 1998) which in turn will guarantee availability of fruits for CBB to infest at different periods of the year, allowing survival of the pest for longer periods of time (Damon, 2000; Vega et al., 2009).

Climate change is not only expected to affect the distribution of crops and agricultural pests but is also likely to generate diverse effects on natural enemies of pest species, with possible impacts on pest control (Thomson et al., 2010). Still, there is no information about impacts of climate change on birds capacity to deliver important ecosystem services such as pest control.

3.3. Climate change effects on bees and pollination

There is clear evidence that climate change has affected various groups of pollinators through shifts and reductions in geographical range, declines in local abundances, and extinctions (Abrol, 2012; Potts

et al., 2016; Settele et al., 2016). In North America and Europe, observations and model predictions report declines in abundance, diversity, and distribution of managed honey bees and wild bees (e.g., Biesmeijer et al., 2006; Potts et al., 2010; Cameron et al., 2011; Bartomeus et al., 2013a; Burkle et al., 2013; Kerr et al., 2015; Koh et al., 2016; Settele et al., 2016; Marshall et al., 2018). Evidence in tropical regions is more sparse (Vanbergen, 2013), but declines in bee abundance and diversity and changes in their spatial distributions have also been observed (e.g., Giannini et al., 2012, 2015b, 2017; Martins et al., 2015; Nemésio et al., 2016; Elias et al., 2017; Imbach et al., 2017). In general, increases in temperatures, decreases in water supply, and changes in seasonality are all likely to negatively affect bee populations. These changes can alter bees' emerging dates, foraging and breeding seasons and can change their current distributions by shifting them to more favorable areas. Ultimately, climate change can result in the extinction of locally adapted bee species and limit bee abundance and diversity by indirectly affecting the access of pollinators to food resources (e.g., Grünewald, 2010; Giannini et al., 2012, 2017; Classen et al., 2015; Kerr et al., 2015; Martins et al., 2015; Imbach et al., 2017; Ogilvie et al., 2017). While studies of climate change impacts on coffee pollinators specifically are rare, observed changes in pollinator abundance, diversity, and distribution patterns in other systems suggest potential shifts in pollination services to crops (Abrol, 2012; Potts et al., 2016; Settele et al., 2016). Plants and their pollinators both appear to respond phenologically (e.g., advanced flowering date of plants and seasonal pollinator flight activity) to changes in mean global temperatures (Mommott et al., 2007; Hegland et al., 2009; Bartomeus et al., 2011; Willmer, 2012; Abrol, 2012; Pyke et al., 2016). If plants and pollinators respond differently to temperature changes, spatial and temporal mismatches can occur whereby pollinators are not present when needed for pollination or food resources for pollinators are not met. These mismatches mainly affect specialist pollinators such as many native bees (Biesmeijer et al., 2006; Mommott et al., 2007; Hegland et al., 2009; Grünewald, 2010; Abrol, 2012; Burkle et al., 2013; González-Varo et al., 2013; Miller-Struttman et al., 2015; Pyke et al., 2016; Settele et al., 2016; Ogilvie et al., 2017). For example, declines in both specialist pollinators and their plant mutualists have been observed in Europe (Biesmeijer et al., 2006), indicating that pollinators that specialize on a few plants may decline the most.

For coffee specifically, there is some evidence that shifts in precipitation affect flowering phenology (Lin et al., 2008), which can in turn influence richness of visiting bee species and resulting fruit set (Peters and Carroll, 2012). Expected changes in the spatial distributions of coffee and bees under climate change also suggest that coffee farms could suffer pollinator deficits in the future (Giannini et al., 2015b; Imbach et al., 2017). Complementarity offered by high diversity levels of wild bees can help stabilize pollination services in the face of climate change by increasing the response diversity of pollinators to climatic fluctuations (Bartomeus et al., 2013b; Brittain et al., 2013; Rader et al., 2013). Overall, the more generalist the relationships (i.e., multiple pollinator species for a plant or broad diet in pollinators), the more resilient the interactions are under climate change (González-Varo et al., 2013; Settele et al., 2016). Climate change effects on animal-mediated pollination are exacerbated by other global change pressures such as landscape alteration, agricultural intensification, non-native species, and spread of pathogens (Grünewald, 2010; Potts et al., 2010, 2016; González-Varo et al., 2013; Vanbergen, 2013; Cariveau and Winfree, 2015; Nemésio et al., 2016; Settele et al., 2016; Marshall et al., 2018). Thus, isolating the potential effects of climate change on bee and pollination services remains challenging.

3.4. Adaptation strategies to climate change in coffee farms

Imminent threats from global climate change on agriculture require adaptation strategies. Coffee will not only suffer changes in its current distribution due to climate change, but coffee production and quality

are expected to be negatively affected by increases in temperature and changes in rainfall patterns (e.g., Gay et al., 2006; Ovalle-Rivera et al., 2015; Bunn et al., 2015b; see other references cited in Section 3.1). Although reduced coffee production may not threaten food security *per se*, many farmers depend on this crop for their livelihoods (Lin et al., 2008; Schroth et al., 2009) and already report experiences with climate change and its impacts on production (e.g., Frank et al., 2011; Eakin et al., 2014; Harvey et al., 2018). Climate vulnerability of producers differs among regions of coffee production (Baca et al., 2014), however, impoverished smallholders, which account for a considerable proportion of coffee cultivation, are highly vulnerable to the impacts of climate change (Eakin et al., 2014; Gross, 2014; Harvey et al., 2018).

Several strategies have been proposed or are already being implemented to increase the resilience of coffee systems to climate change impacts. One common strategy is to diversify crops and income sources for farmers, to reduce exposure to failure in any one crop including coffee. For example, environmental services payments for forest conservation and restoration, sustainable forest management, and diversified cropping systems would provide income under variable weather conditions and grow demand for coffee produced via sustainable land use and forest conservation (Schroth et al., 2009; Jha et al., 2011; Lin, 2011; Baca et al., 2014; Eakin et al., 2014; Rahn et al., 2014). Other strategies at farm and plot level include crop insurance programs for smallholders (Schroth et al., 2009; Rahn et al., 2014), and management practices including managing shade to reduce temperature stress (Beer et al., 1998; Lin et al., 2008; Schroth et al., 2009; Jha et al., 2011; Baca et al., 2014; Rahn et al., 2014); increasing water efficiency through investments in irrigation infrastructure and technologies, using coffee varieties tolerant to temperature and drought stress, and adopting soil conservation practices to improve moisture content (Lin et al., 2008; Schroth et al., 2009; Baca et al., 2014; Eakin et al., 2014; Rahn et al., 2014); use of coffee varieties with higher tolerance to pests (Schroth et al., 2009); and other ecosystem-based adaptation strategies (Vignola et al., 2015; Harvey et al., 2017, 2018).

Some of these adaptation strategies for coffee will also help to increase the climate resilience of pollination and pest control services, while additional practices can be added to focus specifically on these ES. For example, diverse shade canopies can provide nesting and foraging habitats for both bees and birds, increasing richness and abundance (Greenberg et al., 1997a, 1997b; Klein et al., 2003c; Philpott et al., 2008; Jha et al., 2014; Frishkoff et al., 2014; Imbach et al., 2017). Increasing crop and overall plant diversity within fields and field margins, edges, pathways, and live fences can benefit both bees and birds, since allowing non-crop plant and weed species to grow and flower on farms can provide forage resources to complement the brief and intense flushes of coffee flowers themselves (Wunderle and Latta, 1998; Klein et al., 2003b, 2003c; Perfecto et al., 2004; Komar, 2006; Grünwald, 2010; Bakermans et al., 2012; Nicholls and Altieri, 2013; Caudill et al., 2016; Potts et al., 2016; Fisher et al., 2017; Liere et al., 2017). Organic farming practices and integrated pest management practices, i.e., reduced or controlled use of chemical pesticides and herbicides, can also maintain bee and bird populations (Klein et al., 2003c; Smith et al., 2010; Grünwald, 2010; Potts et al., 2016; Liere et al., 2017; Goded et al., 2018). Creating dense shade canopies can reduce rates of CBB reproduction rates by reducing temperatures, and fully harvesting all ripe berries can help remove refuge habitats for CBB between harvest seasons (Vega et al., 2009; Jaramillo et al., 2009, 2013; Mariño et al., 2016; Infante, 2018).

Several adaptation strategies for pollination and pest control involve maintaining diversity in the birds and bees that provide these services. In general, diverse communities are likely to show higher diversity in species responses to environmental change (Tilman and Downing, 1994; Klein et al., 2008; Philpott et al., 2009; Mori et al., 2013; Karp et al., 2013b; Martins et al., 2015). This response diversity can confer resilience to climate change, especially if the nature of future change is uncertain. Several studies have shown that proximity to

natural or semi-natural habitats increases bee diversity and pollination services (e.g., Steffan-Dewenter and Tscharntke, 1999; Klein et al., 2003a, 2003b, 2003c; Ricketts, 2004; Priess et al., 2007; Ricketts et al., 2008; Klein, 2009; Garibaldi et al., 2011; Munyuli, 2011; Hipólito et al., 2018) and bird diversity and pest control services (e.g., Perfecto et al., 2004; Van Bael et al., 2008; Karp et al., 2013a; Railsback and Johnson, 2014; Milligan et al., 2016; Sherry et al., 2016; Boesing et al., 2017; Lindell et al., 2018). Maintaining heterogeneous agricultural landscapes around farms can, therefore, be an important adaptation strategy, in which forest patches and other semi-natural areas (e.g., forest fallows, live fences, home gardens) help maintain the diversity of service-providing species and improve the stability and resilience of ecosystem services.

While evidence is far from complete, studies to date suggest that shaded coffee systems could be an effective strategy to improve climate resilience of coffee, birds, and bees and therefore help farmers and families adapt to their changing environment. First, shaded coffee systems could improve resilience of coffee crops themselves to extreme climate events, by reducing ambient surface temperatures, decreasing runoff and erosion, protecting plants from high solar radiation, wind, heavy rain and pest attacks (Beer et al., 1998; Perfecto et al., 2004; Lin, 2007, 2011; Lin et al., 2008; Schroth et al., 2009; Jaramillo et al., 2009, 2011, 2013; Siles et al., 2010; Cannavo et al., 2011; Gross, 2014; Rahn et al., 2014; Harvey et al., 2017; Fain et al., 2018). Second, shaded coffee systems offer habitat for diverse species, among them birds and bees that provide ecosystem services to coffee and other crops (Perfecto et al., 1996; Moguel and Toledo, 1999; Philpott et al., 2008). Third, in comparison to reduced shade systems, shaded coffee systems typically use fewer synthetic agrochemicals (Perfecto and Vandermeer, 2008; Haggard et al., 2011; Jha et al., 2014) that could negatively impact these service-providing species. Fourth, shaded coffee systems can provide varied income streams that reduce farmers' exposure to weather-related failures in any one crop (Lin et al., 2008; Schroth et al., 2009; Baca et al., 2014; Gross, 2014). Implementation of shaded coffee systems, therefore, is a promising approach for adapting to changing conditions and reducing the ecological and economic vulnerability of rural farmers. The adoption of shaded coffee systems would not be difficult to implement, as it can be based on a return to a more traditional, diverse farming methods that were common before intensification and monoculture were adopted (Moguel and Toledo, 1999; Baca et al., 2014).

4. Future research priorities

This paper has reviewed research to date on two important and interacting ES to coffee, and how the provision of these two services may change under future climate change. This is an active and exciting area of research. Studies have already demonstrated that bird and bee communities provide pest control and pollination services that improve coffee quantity and quality, measurably benefitting coffee farmers whose livelihoods depend on this crop. The existing literature also shows that these ES are improved under certain plot, farm, and landscape management practices that support resources for birds and bees. Several research gaps remain, however, and next we identify several of the most important ones:

- Quantify ecological and economic synergies or trade-offs in managing landscapes for bird and bee communities. When is the same management practice beneficial to both? Do the two ES affect yields in additive or synergistic or antagonistic ways?
- Understand the effects of landscape context on the provision of pest control and pollination services. How are changes in the landscape surrounding coffee crops affecting birds, bees, services and interactions between them? Do these relationships respond differently when measured at different scales?
- Develop rigorous analyses of return on investment for management practices to enhance ES and climate resilience on coffee farms. Are

the expected returns worth the costs? What are the thresholds of investment that produce positive returns?

- Implement field experiments explicitly testing interacting ES with climate change, either by taking advantage of natural climate gradients or by conducting long-term monitoring. How will changes in temperature and precipitation affect coffee pollination by bees and pest control by birds?
- Quantify the role of functional diversity, ecological redundancy, and complementarity in the provision of ecosystem services. How does the presence or absence of particular species traits impact ecosystem services? How many functional groups are needed to provide pollination and pest control services?
- Investigate the ecological importance and economic value of other service-providing taxa and the benefits they provide to coffee systems (e.g., soil communities for soil fertility, shade plants for carbon storage and water regulation). How strong are synergies or trade-offs among multiple ecosystem services? How well can a given management practice enhance multiple ecosystem services?

Declarations of interest

None.

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