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Review

Current status and potential of conservation biological control for agriculture in the developing world

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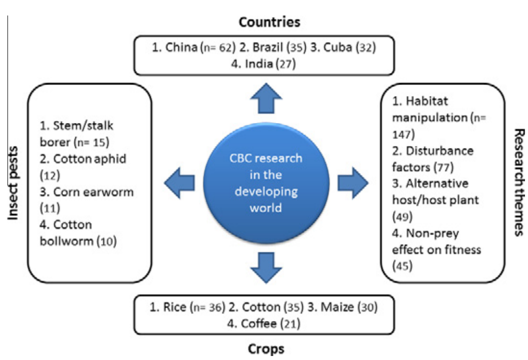
HIGHLIGHTS

- A total of 390 literature records from 53 different crops and 53 nations were found.
- Most research focused on habitat management and changes in disturbance regimes.
- No CBC records were found for several key staple crops and cash crops.
- 70% of pests with high incidence of insecticide resistance have been overlooked.
- Many nations have high insecticide use and import, but little CBC research attention.

GRAPHICAL ABSTRACT



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ABSTRACT

Conservation biological control (CBC), often described as the field of biological control with the greatest potential for use in developing world agriculture, has received only marginal, scattered research attention outside Western Europe or North America. As a consequence, pesticide overuse remains rampant in many cropping systems, while in others, a complete lack of safe, affordable and effective pest control options leaves farmers vulnerable in face of herbivore attack. In this study, we describe the current status of CBC research in a wide variety of agro-production systems outside North America, Australia, New Zealand, Japan and Western Europe. We summarize information on (1) a variety of CBC themes related to natural enemy biology and ecology, (2) factors that either disrupt or enhance natural enemy efficacy, and (3) field evaluation of CBC schemes. A total of 390 CBC-related literature records from 53 different crops were considered. Most records were from China, Brazil, or Cuba, while no CBC references were found from several developing countries. CBC research primarily focused on habitat management, with 71 records on general habitat manipulation and 80 records on the effects of inter-or cover-crops on natural enemy abundance or efficacy. The effects of deliberate modification of disturbance regimes, through alterations in pesticide use or tillage, on natural enemies were well-characterized in many cropping systems. For each of the CBC themes, research progress was assessed and opportunities were identified to translate current findings into practical solutions. On a crop level, most research was targeted at rice,

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maize and cotton. No CBC records were found for key staple crops such as yams, taro, sago or breadfruit; fruits such as papaya, pineapple and avocado; or forage crops. Also, millet, lentils, barley and plantain, all crops grown mainly in the developing world, received limited CBC research attention. CBC research has been done on myriad arthropod pests, including species with high levels of insecticide resistance such as *Chilo suppressalis* (Lepidoptera: Crambidae) and *Helicoverpa armigera* (Lepidoptera: Noctuidae). However, almost 70% of pests with high incidence of insecticide resistance have been overlooked. Lastly, we contrast country-specific CBC research advances with the national level of insecticide use and importation, and identify lucrative opportunities for countries to save funds through targeted research investment. Based upon our delineation of the current status of CBC, we indicate potential for well-orchestrated regional research projects to pursue higher levels of CBC integration into current pest management schemes. This work constitutes a first step in drawing a roadmap for developing-world research that provides local farmers with safe, low-cost means to control damaging insect pests, safeguard harvests and secure their livelihoods.

1. Introduction

Arthropods provide many valuable ecosystem services, including the natural control of agricultural pests (Daily, 1997). In the United States alone, the annual value of these biological control services is estimated at $4.5 up to $17 billion (Pimentel et al., 1997; Losey and Vaughan, 2006), and this value may still be much higher for small-scale agriculture in the developing world. Such natural pest control services are delivered through a diverse community of arthropod predators, parasitoids and entomo-pathogens that are present in the vegetation in or around farm fields. The deliberate manipulation of agro-ecosystems to enhance the survival, fitness, and behavioral performance of these natural enemies, and to improve their resulting pest control action, is termed conservation biological control (CBC) (Barbosa, 1998; Landis et al., 2000). Through vegetation manipulation, CBC can provide control of both primary and secondary pests, while reducing the likelihood of pest outbreaks and resurgences (e.g., Naranjo and Ellsworth, 2009). Also, CBC practices do not lead to the development of insecticide resistance, a process that prevents closure of yield gaps in many developing world crops (Godfray et al., 2010). Lastly, CBC does not bring about human health risks, as compared to many chemically-defined insecticides.

Despite being one of the oldest forms of pest control, with records dating back to 300 BC (see Huang and Yang, 1987), CBC has only received limited attention (Ehler, 1998). With the onset of the pesticide era, chemical insecticides came to replace the action of naturally occurring natural enemies. By displacing natural biological control agents from farm fields, pesticides thus quickly divorced agricultural production from ecology (Robertson and Swinton, 2005). Similarly, the spectacular achievements with importation biological control projects in the 1980s may have reduced interest in CBC. However, the volume of CBC research has steadily increased and some related tactics are being adopted in cropping systems in Europe and North America (e.g., McLeod et al., 2004; Jonsson et al., 2008; Naranjo and Ellsworth, 2009; Nilsson, 2011). Despite these evolutions, the potential for the management of pest insects using CBC has yet to be fully exploited, especially for control of indigenous crop pests that have large natural enemy complexes.

In many parts of the developing world, CBC is believed to be the area of biological control with the greatest scope for pest control in multiple crops (e.g., Waage and Schulthess, 1989; Yaninek and Cock, 1989; Tamo et al., 1997; Gurr et al., 2011). Lower consumer expectations regarding cosmetic standards for harvested produce, relatively diverse agro-ecosystems, and the low resource base supporting local production systems all make CBC an attractive pest management solution for local farmers (Neuenschwander, 2010). In systems where pest losses are high, better pest management through enhancement of biological control services can raise crop yields more than most other types of crop research (Pretty et al., 2011). However, a range of problems impede the development and implementation of CBC in developing countries. Often, adequate ecological information describing the action of indigenous natural enemies and an assessment of ways to exploit them is missing (Yaninek and Cock, 1989; Legg et al., 2003). Also, instead of being seen as an opportunity to advance CBC, the predominance of generalist predators is frequently thought an impediment to effective biological control (Cherry et al., 2003). Consequently, pesticide use in many parts of the developing world remains high and interferes with natural biological control services. In the Latin American horticultural sector, for example, dependence on pesticides is at worrying levels, with the bulk of growers naming insecticides as their sole pest management tool (Nunes et al., 2005; Wyckhuys et al., 2011). In other systems, farmers seem to be falling back into the pesticide treadmill. The classic Peruvian Canete Valley success, in which insecticide applications in cotton fields were reduced from 16 to 2–3 per crop (Doutt and Smith, 1971; Barducci Boza, 1972), had completely degenerated within 30 years, with a return to pesticide-dominated pest control (Way and van Emden, 2000). Even in Southeast Asia, where increased understanding of agro-ecosystem functioning led to far-reaching management and policy changes in the 1990s, pesticide use is increasing and associated pest problems are mounting once again (Bottrell and Schoenly, 2012). For those systems, there is a need to seriously assess the potential of CBC as a complementary or alternative pest management tactic. In other parts of the developing world, such as Sub-Saharan Africa, farmers do not have the financial means to use insecticides and insects continue to cause vast yield losses and imperil food security (Neuenschwander, personal communication). In those systems, CBC could constitute an equally attractive pest management option, representing a low-cost means to promote resident natural enemies and contribute to pest control.

In some countries, such as Cuba, CBC has received a fair amount of research attention and occupies a prominent place in pest management schemes (Vázquez et al., 2008). Also, in a small set of subsistence crops, farmers have historically learned to manage their pests with limited use of insecticides (Jago, 1991; Way and van Emden, 2000; Wyckhuys and O'Neil, 2007a). These cases should be documented to help guide the development of CBC practices for other crops in the tropics and in the developed world.

Agricultural production systems tend to lower the abundance and efficacy of natural enemies through increased levels of disturbance (i.e., pesticide use, tillage), simplification of landscapes, or use of monocultures (Letourneau, 1998). CBC tactics, as tools to correct these problems, have been categorized into those that reduce natural enemy mortality, provide supplementary resources used by natural enemies, control secondary enemies, or manipulate host plant (or habitat) attributes to the benefit of natural enemies (Rabb et al., 1976; van den Bosch and Telford, 1964). Initial literature reviews show that CBC research has been carried out in all of the above areas in the developing world, but to date this information has not been compiled.

Here we review CBC advances in regions outside of North America, Australia, New Zealand, Japan and Western Europe. We describe its current status in a wide variety of agro-production systems, by drawing on less accessible literature and work published in languages other than English, which is less widely known. The resulting information is organized along the following themes (see Fig. 1): (1) elucidation of the role of non-prey foods in sustaining natural enemies; (2) use of artificial food sprays; (3) on-farm habitat manipulation; (4) deliberate modification of disturbance regimes, with emphasis on tillage and pesticide use; (5) identification of alternative host or prey items; (6) characterization of the effect of plant varietal traits on natural enemy performance and survival; and (7) examples of actual use of CBC at the farm or landscape level.

In this exercise, we limited ourselves to records related to arthropod natural enemies, and to their effect in controlling field populations of agricultural pests. No records were included on natural enemy efficacy and life history (when fed prey items), as these do not exclusively support CBC. Although this review is intended to be as complete as possible, we acknowledge that some valuable research may have escaped our attention. Despite its potential limitations, this review should help identify opportunities to promote pest management in the developing world, while providing a basis for a more intensive cross pollination of CBC research globally.

2. Assessment of the effect of non-prey foods on natural enemy fitness

The importance of consumption of plant-based foods by natural enemies was first reported by Thorpe and Caudle (1938), who reported nectar consumption by parasitoids of the pine shoot moth *Rhyacionia buoliana*. Gradually, researchers have come to acknowledge that non-prey foods such as nectar, honeydew or pollen influence many life processes critical to the success of parasitoids and predators alike (Wackers et al., 2005; Lundgren, 2009). These plant compounds may supplement prey diets or act as alternative foods that sustain natural enemies under sub-optimal conditions. For many natural enemies, a diversity of plant-based foods can increase many fitness parameters and consequent biological control efficacy.

A total of 39 records were found in which a comparative assessment was made of natural enemy performance on different plant-based food resources, with the oldest record being work on winter moth *Operophtera brumata* parasitoids in Uzbekistan (Appendix 1; Eremenko, 1971). The majority of studies ($n = 16$) did not specify the cropping system, while systems that received relatively more attention were cassava (5), maize (3), and crucifer vegetables (2). Most records were found for China (9), but Colombia (4) and Egypt (4) were also well represented. A total of 9 studies dealt with braconid wasps, nine with phytoseiid mites and four with earwigs (Forficulidae). The following food sources were tested: mixed flower honey (16), pollen (14), synthetic mono-or polysaccharides (8), floral nectar (7), honeydew (5), and fungal spores (2). One record described the role of other plant-based foods such as maize grains, fruit juice or wetted raisins. Parameters that were computed for

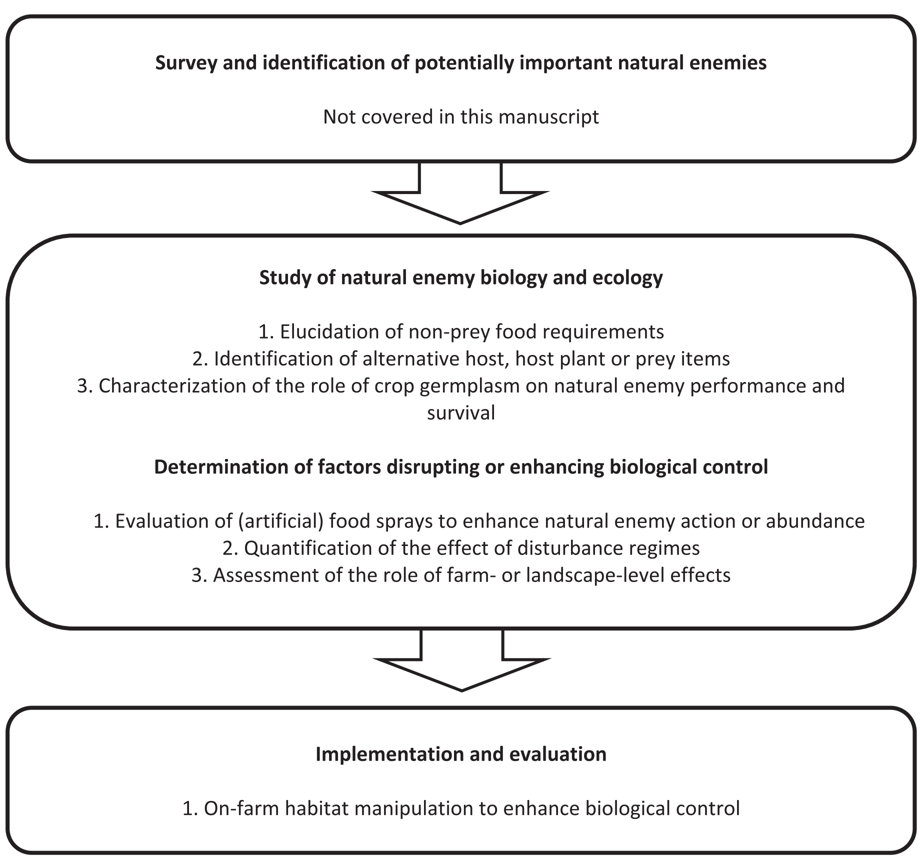

Fig. 1. Focal themes of the manuscript, as identified within different sections of an existing conceptual framework for conservation biological control research (see Naranjo, 2001).

the different food sources were longevity/survival (24), fecundity or reproductive output (11), overall development (8), body nutrient levels (4), parasitism (3), and egg load or maturation (2). Only single records were found for resource consumption level and duration of the oviposition period.

With exception of the work on cassava phytoseiids in Benin, Brazil and Colombia (e.g., Gnanvossou et al., 2005; Onzo et al., 2005), no evidence was found of sustained research on natural enemy nutritional ecology in a particular cropping system. However, the consumption of pollen by earwigs in cereal crops has been researched on separate occasions in Latin America and Africa (e.g., Boukary et al., 1997; Sueldo de Escano and Virla, 2009). Possibly, this work was guided by the high abundance and conspicuousness of these predators in several crops and initial US-based research on pollen-dependence in the earwig *Doru taeniatum* (Jones et al., 1988). Lastly, a multi-country initiative is currently assessing the role of plant-based food sources for natural enemies of several key rice pests in Southeast Asia (Gurr et al., 2011, 2012).

Pollen and carbohydrates are steadily gaining recognition as key food sources for natural enemies. Aside from maize pollen, the relative nutritional value of pollen from several other crop and non-crop plants has been determined (e.g., Pu et al., 1991). While honey has been widely researched as a high-quality food source, isolated initiatives from Chile, China, Turkey, Philippines, and Uzbekistan have also assessed the role of floral nectar. A broad set of flowering plants, such as soybean, *Daucus carota*, *Brassica parachinensis*, *Vicia angustifolia* or wildflowers (e.g., *Solidago altissima*, *Erigeron annuus*) were found to enhance key life history parameters of various parasitoids. Nevertheless, aside from exploratory work in South America on the importance of nectar composition and floral architecture (Chalcoff et al., 2006), much remains to be done to properly select plant species for habitat diversification schemes that benefit natural enemies (e.g., Patt et al., 1997; Wackers, 2004; Fiedler and Landis, 2007). As is well documented in Europe, New Zealand or North America, floral resources not only improve fitness of natural enemies but may also benefit the pest (Baggen et al., 1999; Lavandero et al., 2006; Wackers et al., 2007). This has also been recognized in the developing world. In Brazil, buckwheat *Fagopyrum esculentum* nectar was consumed by the parasitoid *Mirax* sp. (Hymenoptera: Braconidae) but was equally exploited by the coffee leaf miner, *Leucoptera coffeella* (Lepidoptera: Lyonetiidae) (Rosado, 2007). Along the same lines, floral nectar supplied for the benefit of natural enemies favored the wheat armyworm, *Pseudaletia sequax* (Lepidoptera: Noctuidae) (Marchioro and Foerster, 2012).

The effect of extra-floral nectar, an omnipresent food in several cropping systems (Lundgren, 2009; Nicolson et al., 2010), has only recently been assessed for phytoseiids, lacewings, and whitefly parasitoids in Benin, Brazil, and Colombia, respectively. Although some baseline work has been done on cassava extra-floral nectar (e.g., Toko et al., 1994), the nutritional value of this resource from other crops such as pulses has not been determined. A sound appreciation of its role may be essential to manipulate resident natural enemy populations, or help design pest-suppressive polycultures. Overall, insights into the natural enemy's food requirements appear to have been primarily used to fine-tune their (laboratory) mass rearing instead of improving their efficacy under field conditions (Chen et al., 2010). A rare exception is the exemplary way in which insights in earwig nutritional ecology have helped define habitat manipulation schemes in East Africa (Boukary et al., 1997; Koji et al., 2007). In the vast majority of cropping systems, however; laboratory assays wait to be transferred to semi-field trials and management recommendations.

Natural enemy groups such Araneae, Carabidae, Formicidae, Syrphidae or predaceous heteropterans have not received any attention, while other groups such as Coccinellidae, Tachinidae or aphid parasitoids have been frequently investigated. A large literature exists on the interactions between ants and extra-floral nectaries in natural habitats of the tropics (e.g., O'Dowd, 1979; Cuautle and Rico-Gray, 2003). However, this wealth of information, poorly known outside ecology circles, waits to be used for the design of crop diversification schemes that enhance natural control. As a promising development, research in China and Turkey has started to assess the effect of wildflower nectar on the life history of *Trichogramma* spp., undoubtedly one of the most widely used groups of wasps in pest control (Tuncbilek et al., 2010; Guo et al., 2011).

3. Elucidation of associations with alternative hosts, food and prey items

Earliest records on the importance of alternative hosts for natural enemies were by Hardy (1938). Since then, research has been conducted on identifying alternative hosts, prey and food items in many cropping systems (e.g., Agusti et al., 2003; Isaacs et al., 2009). In our literature revision, we encountered a total of 51 references identifying such resources (Appendix 2). A total of 20 studies identified alternative hosts or host plants, while other resources such as non-prey food (10), alternative prey (4) or refuges (3) received less attention. In a total of 12 studies, a broad community of parasitoids was studied, while other natural enemy guilds that received major attention were Coccinellidae (8), Braconidae (5) or pirate bugs (4). In most cases, researchers studied natural enemy associations with plants present in natural habitats, such as common weeds, shrubs or (fruit) trees.

In many studies, high natural enemy abundance was considered indicative of trophic linkages to a given plant species, but relative importance of such linkages was rarely assessed (but see Soroushmehr et al., 2008). No studies were encountered in which nectar consumption on a given plant species was proven, e.g., through use of biochemical assays (e.g., Wyckhuys et al., 2008). Only one record was found where pollen grain analysis was used to identify plant associations for a given natural enemy (Medeiros et al., 2010). A more in-depth elucidation of the nature of those trophic linkages or refuge provision with certain plants could help define appropriate conservation practices.

In a similar way, advances have been made in the identification of alternative host items, with sometimes unexpected results such as the identification of native trees as alternative hosts for parasitoids of the cowpea pod borer *Maruca vitrata* (Tamo et al., 2002). These studies not only pinpoint plants necessary to sustain certain natural enemies, but also plants that provide the pest with refuges from natural enemy action (e.g., Morrill and Almazan, 1990). One critical drawback in many of the studies is the lack of identification of temporal patterns in natural enemy abundance on such alternative host (or food source). Long-term studies from Israel, for example, show that it is essential to understand when alternative host plants such as *Rhamnus* sp. shrubs are important to predatory anthocorids (Shaltiel and Coll, 2004). Similar limitations have been identified for studies on alternative host items. Although the identification of alternative food or host resources constitutes a necessary first step in the research process, long-term focused studies are needed to help guide the definition of CBC schemes and their proper incorporation in cropping systems.

With exception of some Cuban and African studies (e.g., Schulthess et al., 2001; Cherry et al., 2003; Kahuthia-Gathu et al., 2008), many initiatives remain isolated and miss follow-up research. For example, Beingolea (1959) elegantly explored plant associations of several key predators and parasitoids in Peruvian cotton agro-ecosystems, and stressed the importance of taking into account those ecological relationships to define sustainable pest management programs. Fifty-three years after this publication, however, no evidence was found of changes in management practices that derived from this study. In contrast, an identification of alternative host plants for the African gall midge *Orseolia oryzae* led to an evaluation of habitat manipulation schemes, and serves as an example that different approaches are possible (Nwilene et al., 2008). Also, separate research initiatives could easily guide studies in other parts of the developing world. For example, findings from Mexico or Brazil that native fruit trees help conserve fruit fly parasitoids (Figueroa de la Rosa et al., 1998; Carvalho et al., 2010) should constitute a basis for biological control of native fruit flies in Thailand and Malaysia, amongst others (see Chinajariyawong et al., 2000).

4. Determination of the role of artificial food supplements

The potential of artificial food sprays to increase abundance and impact of natural enemies has been recognized for over 40 years (Wade et al., 2008). In our literature revision, a total of 19 references evaluated the effect of artificial food supplements on natural enemy abundance and efficacy, with the oldest record being the mention of yeast sprays to enhance aphid predation by *Chrysopa* sp. (Appendix 3; Trujillo and Altieri, 1990). Even earlier, sugar sprays were briefly mentioned for use in Indian pulse crops (Iswer-an & Sen, 1972). Records were found for a range of crops, with maize (3) and citrus (2) having received the most attention. Crops included principally vegetables and fruits, such as tomato, almond, peppermint or cocoa. In seven cases, target pests were not specified, while homopterans such as aphids, whitefly or membracids were the focal pests of six studies. Ants were studied in a total of 12 studies, while other groups included Chrysopidae (3), Coccinellidae (2), Vespidae (1), Tachinidae (1), Syrphidae (1), Trichogrammatidae (1), Phytoseiid mites (1) or Anthocoridae (1). A diverse range of food supplements were described, covering both carbohydrate (i.e., sucrose solution, molasses, honey) and protein sources (i.e., pollen, protein hydrolysate, milk, powdered fish, intestines). All studies with lacewings evaluated the role of yeast or protein + sugar mixtures. The main effects of the artificial food provision were increased abundance or sustained ant colony presence (9) and reduced tending of homopterans (3). When describing the effect of sugar sprays on ant-hemipteran interactions, no mention was made of increased predation (but see Carabali-Banguero et al., in press).

Although sugar sprays have been shown to boost efficacy of *Trichogramma* spp. under field conditions (Yu and Byers, 1994), their use was only recently reported from Pakistan (Ahmad et al., 2011). Similarly, even though food sprays greatly benefit Coleoptera (Wade et al., 2008), no research has specifically focused on this group. One possible reason for this lack of attention could be concern over the viability of costly broadcast sprays of sucrose solutions, especially for small-scale farmers. Nevertheless, sugar-rich industry waste products such as molasses could be a valuable alternative to refined sugar (see Perfecto and Castiñeiras, 1998; Choate and Drummond, 2011) and make this more affordable. That sugar sprays have potential even for small-scale farmers is exemplified by Colombian research, showing that sugar sprays can be combined with selective insecticides to increase whitefly biological control in cash crops such as tomato (Hernandez et al., unpublished).

In addition to external applications of sugar, two records were found of farmers' intentional infestation of their crop with (non-pestiferous) hemipterans, as sources of sugar-rich honeydew for the predatory ants *Dolichoderus bituberculatus* Mayr and *D. thoracicus* Smith (Graham, 1991; Ho and Khoo, 1997). Through such pest introductions, farmers secure a continuous availability of carbohydrates and a resulting high activity and intensive foraging by predatory ants in cocoa orchards. Lastly, broadcasting of maize pollen as supplemental food in Israeli avocado orchards increased natural enemy abundance and pest control (Maoz et al., 2009). Other promising low-cost approaches to boost predator abundance and action include the deployment of powdered fish bones, as described from work in Uganda (Sekamatte et al., 2001b, 2002). Based upon this experience, an evaluation of similar low-cost protein baits to increase abundance and foraging of other ground-foraging ant predators such as *Solenopsis geminata*, *Wasmannia auropunctata* or *Pheidole* spp. may carry particular promise. Often, literature references mention the use of artificial food supplementation as farmer innovations (e.g., Van Mele and Cuc, 2000; Bentley, 2006), but do not document its effects as result of scientific experimentation. The only exception may be the validation of sugar-sprays and the burying of dead animals, as a farmer innovation, in Honduran and Ugandan small-scale maize fields (Canas and O'Neil, 1998; Sekamatte et al., 2001b). A more formal evaluation of some of these practices could validate artificial food supplementation in various other cropping systems (e.g., Mensah, 1996; Cook et al., 2007; Hazarika et al., 2009).

5. Effects of structural habitat manipulation on resident natural enemies

The agricultural crop itself undoubtedly has the largest direct effect on natural enemy abundance and efficacy. However, it was not until the 1950s that European researchers recognized that the ecological infrastructure of agricultural habitats could be manipulated for the benefit of these natural enemies and biological control (Gyorfi, 1951). Since then, research has come to show that habitat management and plant diversification schemes, such as intercropping or the establishment of flowering plants, can greatly enhance natural enemy abundance (Letourneau et al., 2011). However, recent research shows that the efficacy of those schemes is still tied to landscape complexity (Woltz et al., 2012). While the science of habitat manipulation only became popular in the 1990s (Landis et al., 2000), it has advanced considerably during the past decade, with ecological engineering taking shape as a separate discipline dedicated to its promotion (Gurr et al., 2004). This has resulted in myriad promising technologies such as the use of shelter habitats, beetle banks (McLeod et al., 2004) and wildflower strips (Lavandero et al., 2005; Pfiffner et al., 2009), with some of those approaches increasing pest control in specific cropping systems.

In the developing world, habitat manipulation could easily be incorporated in local agro-production systems, already being an integral feature of Chinese agriculture (Olkowski and Zhang, 1998) and having been widely adopted under the form of polycultures in African and Central American traditional agriculture alike (Morales and Perfecto, 2000; Kfir et al., 2002; Greathead, 2003). Early on, possibilities were discussed to manipulate agricultural habitats to increase natural enemy abundance in Ugandan coffee plantations (Taylor, 1945). Our literature revision found a total of 71 records of habitat manipulation (HM), and an additional 80 studies specifically on the effect of inter- and cover-cropping (ICC) on natural enemy abundance or efficacy (Appendix 4). Cropping systems that received most attention were coffee (9), rice (7), maize and citrus (7), apple, cocoa and wheat (5) and beans (4). For inter- and cover-cropping, great attention was paid to maize (11), cotton (11), apple (5), sweetpotato, bean, tomato and sorghum (4) as focal crops. In most cases, target pests were not specified for HM (44), and ICC (30). In cases where the target pest was mentioned, aphids (5), thrips (3) and corn earworm (3) were common in HM studies, while aphids (14), sweet potato weevil (5) and corn earworm (5) received great attention for ICC. The effect of habitat manipulation was assessed on several natural enemies, such as ants (17), coccinellids (10), spiders (10), hoverflies (6), lacewings

Table 1
Plant species and associated natural enemy guilds, commonly studied as companion plants in inter- and cover-cropping schemes in the developing world.

Plant family	Genus	Species	Common name	# Records	Focal crop	Focal natural enemies
Aliaceae	*Allium*	*ampeloprasum*	Leek	1	Vegetables	NS
		sativum	Garlic	1	Chinese cabbage	Th, Ly
		cepa	Onion	1	Vegetables	NS
Apiaceae	*Coriandrum*	*sativum*	Coriander	4	Tomato, chickpea, safflower	Ar, Ch, Co, Fr, Ic
	Galinsoga	*parviflora*	Gallant soldier	1	Tomato	Ar, Co, Fr
	Pimpinella	*anisum*	Anise	1	Vegetables	NS
Arecaceae	*Cocos*	*nucifera*	Coconut	1	Cocoa	Fr
Asteraceae	*Ageratum*	*conyzoides*	Billy-goat weed	1	Citrus	Ph
		houstonianum	Bluemink	1	Pear	Co, Ph, Ch
	Carthamus	*tinctorius*	Safflower	1	Cotton	Ch
	Lactuca	*sativa*	Lettuce	1	Chinese cabbage	Th, Ly
	Tagetes	*patula*	French marigold	1	Pear	Co, Ph, Ch
Brassicaceae	*Brassica*	*campestris*	Rape	3	Apple, cotton, wheat	NS
		oleraceae	Green cabbage	1	Chinese cabbage	Th, Ly
Commelinaceae	*Commelina*	*diffusa*	Climbing dayflower	1	Coffee	Fr, Br, Ic
	Zebrina	*pendula*	Wandering jew	1	Coffee	Fr, Br, Ic
Cucurbitaceae	*Cucurbita*	*pepo*	Squash	2	Maize	Ch, Fr
	Trichosanthes	*cucumerina*	Snake gourd	1	Tea	Ar
Euphorbiaceae	*Manihot*	*esculenta*	Cassava	1	Maize	Sc
Fabaceae	*Arachis*	*hypogaea*	Peanut	3	Sorghum, maize	Ar, Fr, Tr
		pintoi	Pinto peanut	1	Tea	Ar, Ca
	Cyamopsis	*tetragonoloba*	Cluster bean	1	Cotton	Ar, Co
	Desmodium	*sp.*	Tick clover	1	Maize	Ar
	Glycine	*max*	Soybean	4	Maize, sweetpotato	Ar, Fr, Sc
	Medicago	*sativa*	Alfalfa	5	Apple, cotton	An, Ar, Ca, Ch, Co, Na, Ge, Ch, Br, St, Sy
	Melilotus	*albus*	Honey clover	1	Apple	Ch, Ph
	Neonotonia	*wightii*	Perennial soybean	1	Citrus	Ph
	Phaseolus	*vulgaris*	Kidney bean	6	Cereals, maize, sorghum, sugarcane	Br, Ch, Eu, Fr, Ic, Ph, Ta, Tr
	Pisum	*sativum*	Pea	2	Grape, wheat	Co, Ve, Fr, Br
	Trifolium	*fragiferum*	Strawberry clover	1	Apple,	Ca, St, Co, Na, Ge, An, Ch, Ar, Br
		repens	White clover	1	Apple	Ch, Co, Sy
	Vigna	*radiata*	Mungbean	3	Cowpea, maize, sorghum	An, Ar, Fo, Tr
		unguiculata	Cowpea	3	Cotton, maize, sorghum	Ar, Br, Co, Ic, Sc
Lamiaceae	*Lagopsis*	*supina*	NA	1	Apple	NS
	Melissa	*officinalis*	Lemon balm	1	Vegetables	NS
	Mentha	*haplocalyx*	Mint	1	Pear	Ch, Co, Ph
		x piperita	Peppermint	1	Vegetables	NS
	Ocimum	*basilicum*	Basil	2	Pear	Co, Ph, Ch
	Salvia	*officinale*	Sage	1	Vegetables	NS
	Satureja	*hortensis*	Summer savory	1	Pear	Co, Ph, Ch
Malvaceae	*Gossypium*	*hirsutum*	Cotton	1	Pigeonpea	Sc
	Hibiscus	*sabdariffa*	Roselle	1	Tomato	Br, Ic
Myricaceae	*Myrica*	*rubra*	Waxberry	1	Tea	Ar
Poaceae	*Avena*	*strigosa*	Black oat	1	Grape	Ve, Fr, Co
	Brachiaria	*decumbens*	Suriname grass	1	Banana, plantain	Ar, Ci, Fr, Fo
	Festuca	*arundinaceae*	Fescue	1	Apple	Ca, St, Co, Na, Ge, An, Ch, Ar, Br
	Lolium	*perenne*	Perennial ryegrass	1	Apple	Ch, Co, Sy
	Melinis	*minutiflora*	Molasses grass	1	Maize	Br
	Pennisetum	*glaucum*	Pearl millet	3	Cereals, cowpea, pigeonpea	Br, Eu, Ic, Ta, Tr
		purpureum	Napier	1	Maize	Ar

(*continued on next page*)

Table 1 (*continued*)

Plant family	Genus	Species	Common name	# Records	Focal crop	Focal natural enemies
			grass			
	Sorghum	*bicolor*	Sorghum	6	Blackgram, cereals, cowpea, cotton, pigeonpea	An, Ar, Br, Eu, Ic, Fo, Ta, Tr
	Triticum	*aestivum*	Wheat	1	Cotton	Co, Ar
	Zea	*mays*	Maize	16	Beans, cabbage, cereals, cowpea, cotton, groundnut, pigeonpea, potato, soybean, sweetpotato, tomato	An, Ar, Br, Ca, Co, Ch, Eu, Fo, Fr, Ic, Ly, Ma, Sc, St, Sy, Ta, Tr, Ge
Rutaceae	*Citrus*	*sinensis*	Orange	1	Tea	Ar
Theaceae	*Camellia*	*sinensis*	Tea	1	Citrus	Br, Hy

NS : non-specified.
An: Anthocoridae; Ar: Araneae (spiders, unspecified); Br: Braconidae ; Ca : Carabidae ; Ch : Chrysopidae ; Ci : Chilopoda (centipedes, unspecified) ; Co : Coccinellidae ; Eu : Eulophidae ; Fo : Forficulidae ; Fr : Formicidae ; Ge: Geocordiae; Ic : Ichneumonidae ; Ly : Lycosidae ; Ma : Mantidae ; Na: Nabidae; Ph : Phytoseiidae ; Sc : Scelionidae ; Sy : Syrphidae ; St : Staphylinidae ; Ta : Tachinidae ; Th : Theridiidae ; Tr : Trichogrammatidae ; Ve : Vespidae.

and phytoseiids (3), for HM. For ICC, natural enemies that received most attention were spiders (20), coccinellids (17), ants (12), anthocorids (8) and lacewings (7).

Several HM tactics were tested, with the most common being the use of herbaceous strips in the field plot (21), tolerance of weeds (13), judicious selection of border plants (11), and the establishment of shade trees (7). Flower strips or weed borders were evaluated, using a total of 21 different plant species belonging to 6 families. Members of Poaceae (6), Brassicaceae (5) and Fabaceae (4) were widely used. In four studies, existing weeds were tolerated in some sections of the field plot, instead of intentionally establishing new plants in separate strips. In two studies from India, Sri Lanka and Malaysia, researchers assessed the effect of practices such as partial weeding on the beneficial arthropod fauna (Rickson and Rickson, 1998; Rekha et al., 2009). Tolerance of some weed cover could be a labor-saving approach to help conserve natural enemies (Norris and Kogan, 2000), and merits more intensive research as a tailor-made HM tactic for small-scale farmers. Lastly, six studies on the provision of artificial shelter and nesting resources introduce (possibly) effective, simple and low-cost practices to conserve predatory ants or mites. However, if those tactics actually contribute to pest control waits to be evaluated in many of above cases. In ICC schemes, an equally broad diversity of plant species was evaluated either as cover crops or intercrops (Table 1). A total of 54 different plant species were tested, with various species belonging to Fabaceae (14) or Poaceae (10). A great number of records were found for maize (16), sorghum (6) and alfalfa (5) as companion plans. For Poaceae, the effect of different plant species was primarily quantified on Araneae (5), Coccinellidae (5), Forficulidae, Formicidae or Chrysopidae (3). For Fabaceae, the effect of several species was assessed on Araneae (8), Coccinellidae (6) and Formicidae (4). In the bulk of ICC studies, researchers evaluated the effect of a given practice on natural enemy abundance (43) and to lesser extent on pest pressure (21). No records were found in which the underlying drivers for increased natural enemy abundance were determined. Although limited research has been conducted on proper management of cover- or intercrops, findings from Chinese apple (Du and Yan, 1994), Chinese cotton (Zhang et al., 2000), Chinese chestnut (Lu et al., 2008) and Guadeloupian citrus orchards (Mailloux et al., 2010) indicate this to be a fertile field for future research. However, in many of those systems, with exception of Chinese apple orchards, little evidence exists of widespread adoption of those cover crop management schemes.

In certain systems, clear potential exists for follow-up research on HM or ICC tactics. For example, the effect of grass borders on natural enemies waits to be determined in Latin American bean production (Altieri, 1981). In Central America, in-field abundance of earwigs is directly related to grass cover in neighboring fields, but little attention has been paid to its related potential as HM tactic (Wyckhuys and O'Neil, 2007b). Lastly, Vietnamese citrus growers recognize that pest problems are lower in weedy fields (Van Mele and van Lenteren, 2002), which could point towards effective HM schemes. In other cases, early research has been translated into HM practices and widely adopted, as is the case for the use of *Ageratum conyzoides* cover crops in 135,000 ha of Chinese citrus orchards or the broad adoption of sunflower strips in Cuban small-scale agriculture (Liang and Huang, 1994; Vázquez et al., 2007). Similarly, an exhaustive evaluation of the role of flowering plants in attracting natural enemies has been translated in HM tactics for Tajik cotton and vegetable production (Saidov and Landis, 2008; Saidov et al., 2011).

Although considerable effort has gone into the evaluation of habitat manipulation schemes, little or no attention has been paid to consolidating a mechanistic basis for this research. Instead of simply adding diversity to agro-production systems or evaluating the effect of (a small set of) common crops or N-suppliers on the resident natural enemy community, it may be preferable to a priori identify the 'right kind' of diversity (Landis et al., 2000; Gurr, 2009), or pursue the promotion of healthy ecosystems (J. Lundgren, personal communication). With applied ecological research identified as a necessary step to develop pest-suppressive crop diversification schemes in the Western hemisphere (Barbosa et al., 2009; Letourneau et al., 2011), such work is urgently needed in the developing world. By linking new mechanistic modeling work (e.g., Tixier et al., 2011; Vinatier et al., 2012) to recent advances in natural enemy ecology (e.g., Wackers, 2004; Fiedler and Landis, 2007; Tompkins et al., 2010), such habitat manipulation schemes could be within close reach for certain (perennial) systems in the tropics.

6. Deliberate manipulation of disturbance regimes

Several types of disturbance, such as tillage or weed management, can have far-reaching effects on the detritus food web and consequently on the resident natural enemy community (Wardle, 1995). Also, while insecticide use directly impacts natural enemies, relatively little research has been conducted in the Western hemisphere to make chemical control compatible with (natural) biological control (Naranjo and Ellsworth, 2009). In our literature revision, a total of 77 references were found that describe the effect of disturbances (e.g., pesticide use, tillage, fertilizer application) on arthropod natural enemies (Appendix 5). Research was commonly conducted in major crops such as rice (13), cotton (12), coffee (10) or soybean-corn rotations (5). A total of 25 accounts were from (semi-)perennial systems, while all other references were on short-term crops. Many references evaluated the effect on ants (12), spiders (8), coccinellids (4) and ground beetles (5). A range of disturbance factors were taken into account, with most research focusing on insecticide use frequency or timing (22), use of organic fertilizer or soil amendments (8) and alteration in tillage regimes

(8). Other accounts dealt with practices such as pruning (3), collection of fallen fruits (2), hand weeding (1), modification of fallow regimes (1), overhead irrigation (1), and the use of insectivorous farm animals such as ducks (1). Insecticide use alterations were mostly evaluated on natural enemy abundance (15), but rarely on pest pressure (2) or natural enemy efficacy (3). Organic fertilizer use was commonly evaluated on natural enemy abundance (8), but only once on predation levels and pest pressure. Similarly, alterations in tillage regimes were mostly evaluated on abundance (5) and not on pest pressure. This is surprising, as tillage is frequently mentioned in folk knowledge as an efficient way to reduce pests. For example, among the Tzeltal Maya in present-day Mexico, land preparation is widely seen as a way to expose *Phyllophaga* sp. white grubs to predation by a variety of natural enemies (Gomez et al., 2000). This shows that much research waits to be conducted, and that an exclusive focus on natural enemy abundance may obscure (possibly) stronger effects of certain disturbance factors on biological control efficacy.

Fertilizer use and the addition of organic matter generate bottom-up forces that conserve resident natural enemies in many cropping systems, with tangible increases of foliage-foraging predators such as spiders in Asian rice (Settle et al., 1996), aphid predators in African bean (Karungi et al., 2006) or earwigs in Brazilian maize (Galvao et al., 2001). Similarly, crop residue retention led to a 7- and 15-fold increase in the respective abundance of predatory ants and springtails in Brazilian common bean (Pereira et al., 2010). In several systems, pest outbreaks proved less likely upon addition of organic matter, but its effect on natural enemies was not assessed (Neuenschwander et al., 1990). Given the (relatively) steep and increasing costs of chemical fertilizers for small-scale farmers, there is a need to assess effects of organic fertilizers, manure or crop residue retention schemes on biological control. This work is particularly relevant in light of the rising use of unsustainable practices in various developing world nations, such as straw burning in Indian rice–wheat systems (Gupta et al., 2004).

Along the same lines, research has shown that rational insecticide use can bring about dramatic increases in natural enemy levels. Such practices led to natural enemy increases of 300% in Chinese cotton fields (Xing et al., 1991), or parasitism levels up to 97% in Indian tea plots (Hazarika et al., 2001). In South Africa, native parasitoids exerted sufficient control of the invasive potato tuber moth, even when farmers refrained from insecticides (Kfir, 2003). In the meantime, several commonly-used herbicides and fungicides greatly affect natural enemies, either by causing direct mortality (Chen et al., 1999) or through changes in habitat structure, composition or health (Pereira et al., 2007). Consequently, a reduction of pesticide use in certain crops can boost the contribution of biological control and thus become a valuable pest management approach for resource-poor farmers (e.g., Greathead and Girling, 1981). Classic experiments in Asian rice systems (Kenmore et al., 1984; Settle et al., 1996) or Peruvian cotton (Beingolea, 1959) helped create broad awareness on the side-effects of pesticide over-use and highlighted the potential of biological control. Recent renewed pest outbreaks in several of those systems signal that the time may be ripe to revisit those historic works and use them to re-orient deficient pest management schemes.

7. Germplasm effects on natural enemy performance

Agricultural crops, as highly suitable host plants of arthropod pests, may equally affect natural enemies through multi-trophic interactions (Bottrell et al., 1998). In the Western hemisphere, researchers have come to acknowledge that a sound appreciation of plant–pest–natural enemy evolution can help develop CBC schemes. In our literature search, we found a total of 27 studies that describe crop-mediated influences on natural enemies (Appendix 6). Crops that received most attention were pigeon pea (6), cotton (4) and cassava (4), with a third of studies from India. The effect of crop germplasm was assessed on a diverse range of natural enemy groups, with Phytoseiidae (4), Coccinellidae (3) and Trichogrammatidae (3) commonly studied. Crop attributes that received most importance were leaf pubescence or trichome density (8), pest resistance (4) and varietal-dependent production of volatiles (3).

In some crops, such as cassava, leaf trichomes have been shown to facilitate establishment and presence of certain predators while trapping alternate foods such as pollen (Zundel et al., 2009). As multiple natural enemies readily feed upon cassava extra-floral nectar (Bakker and Klein, 1992; Bruce-Oliver et al., 1996), the potential for CBC by selecting cassava varieties with enhanced nectar secretion or pubescence has been repeatedly identified (Salick, 1983). This characteristic however, in addition to leaf pubescence, has yet to be taken into account in breeding programs (A. Bellotti, personal communication). Along the same lines, several researchers have identified the considerable potential of breeding crops that resist specific pests and simultaneously encourage their antagonists (e.g., Sharma and Yadav, 1993; Lou and Cheng, 2003). Host plant resistance does not necessarily interfere with natural enemy fitness, mobility or host searching ability (Tandon, 2001) and moderate levels of resistance could easily boost natural enemy abundance and efficacy (Kartohardjono and Heinrichs, 1984; Shannag and Obeidat, 2008).

With insecticide- and herbicide-resistant crops steadily adopted in many developing countries, the assessment of their impact on biological control could prove a fertile field of research (Romeis et al., 2006; Lundgren et al., 2009). Herbicide-tolerant crops can lead to substantial losses of in-field vegetational diversity and thus (possibly) interfere with biological control. On the other hand, *Bt*-transgenic varieties can reduce insecticide use and give natural enemies a chance (e.g., Lu et al., 2012). While our study focused on CBC studies related to conventional germplasm, we also found work that dealt with the effect of transgenic crops on resident natural enemies in Indian Bt chickpea (Romeis et al., 2004), Brazilian Bt cotton (Faria et al., 2006), amongst others. The bulk of these studies provide guidelines for pre-release risk assessment of transgenics. However, in most developing countries, laboratory and field trials wait to be conducted that assess compatibility of transgenic crops and natural enemies (Lovei et al., 2009). Although transgenic crops can help promote natural biological control in conventional agriculture in certain countries, they are not suitable for organic production systems.

Above findings show that germplasm research could pave the road towards more pest-suppressive cropping systems. Nevertheless, few breeding programs in the tropics have carried out sustained research on CBC promotion through judicious selection of crop germplasm. In the meantime, CBC researchers in the developing world may need to consider including transgenic crops in their agendas.

8. CBC at the landscape level

In the broader agricultural landscape, the presence of more stable and heterogeneous (non-crop) habitats such as forests, hedgerows, fallows or meadows is thought essential to CBC services (Tscharntke et al., 2008). They provide important resources for natural enemies such as refuge sites, alternative prey, pollen and nectar (e.g., Landis et al., 2000; Cronin and Reeve, 2005; Bianchi et al., 2006). In the Western hemisphere, the importance of landscape-level contributions to biological control was first reviewed half a century ago (van Emden, 1965). In our literature revision, a total of 29 records were found that describe landscape-level effects on biological control (Appendix 7). Amongst those, ten studies describe rice agro-ecosystems, while less attention has gone to cotton (3) and another eight crops. Natural enemy guilds that received most attention were spiders (5) and Trichogrammatidae (3). In the broader agricultural landscape, the effect of surrounding crop fields (8), landscape complexity and diversity (7) and the presence or (relative) cover of natural habitats (9) was assessed.

Despite comparatively little research attention, several promising findings have been reported. In SE Asia, asynchronous rice planting over large areas allowed natural enemies to build up (Way and Heong, 1994; Ives and Settle, 1997). In China, high abundance and efficacy of *Trichogramma* spp. on certain vegetables or (early-season) sweet potato crops has been used to diversify grain-cropping landscapes (Wang et al., 1988; Zhou et al., 1997). Also, landscape mosaics composed of rice and horticultural crops benefited from high natural enemy abundance and increased pest suppression (Zhang et al., 2011). In those systems, biological control can be enhanced either through overall increase of landscape diversity (e.g., Gardiner et al., 2009), or through the provision of habitats that benefit one or more key natural enemies, such as *Trichogramma* spp. Along the same lines, a mosaic of natural habitats at differing stages of succession supports a diverse natural enemy community in Central American small-scale maize production (Wyckhuys and O'Neil, 2007b). It is suspected that shifting agriculture inadvertently preserves the diversity of habitats and biological control services within those systems. Despite these promising findings, much remains to be investigated in this field. More so, in certain regions, such as Africa, virtually nothing is known about the effect of landscape structure on biological control (Neuenschwander et al., 2003).

9. General tendencies in developing world CBC research

Our literature review reported a wide range of CBC-related studies from the developing world, on a total of 53 different focal crops. Research was reported from 16 different fruits, ten vegetables, eight pulses, six cereals, three tuber/root crops and a small set of cash or forage crops. Research effort greatly differed between crop species and crop types. The greatest number of studies was recorded from rice (36), cotton (35), maize (30), coffee (21), citrus (14) and beans (13). The number of records per crop species was highest for cereals (14.33 ± 6.31; mean ± SE) and lowest for fruits (4.75 ± 1.48) and vegetables (2.80 ± 0.94). Although most fruit crops were only covered in one or two publications, citrus, apple and coffee were the focus of more than ten studies each. Similar patterns were found for vegetables, but research effort was more equally distributed between crop species for pulses. CBC research in some important staple crops proved very limited or entirely missing (Fig. 2). For example, only one record was found for banana/plantain production systems, lentils, barley or millet. This is particularly worrisome, as crops such as millet or banana/plantain are grown on 35.1 and 10 million hectares, respectively, and are key staples in many parts of the tropics. Also, comparatively little research effort has been dedicated to CBC in potato (3), groundnut (2) or fava bean (2). For other important staple crops such as yams, taro, sago or breadfruit, we found no references at all. Possibly, the limited research effort to some root or tuber crops could be due to the cryptic nature of (many of) its pests, and associated natural enemies. CBC research could take forward pest management in several of those crops, while crop species that already received certain coverage could benefit from sustained research built upon a meticulous review of actual advances.

Perennial fruit orchards are optimum habitats to promote conservation biological control (e.g., Brown, 1999; Landis et al., 2000; Simon et al., 2010). Nevertheless, it is rather unfortunate to note an absence of sustained research in perennial fruits, with the number of CBC references for major fruits such as mango (2), avocado (1), papaya (0) or pineapple (0) being strikingly low. For minor fruits, the situation is even more critical, with no records found for most crops. In many fruit cropping systems, the current lack of research attention is reflected in an ever more acute proliferation of

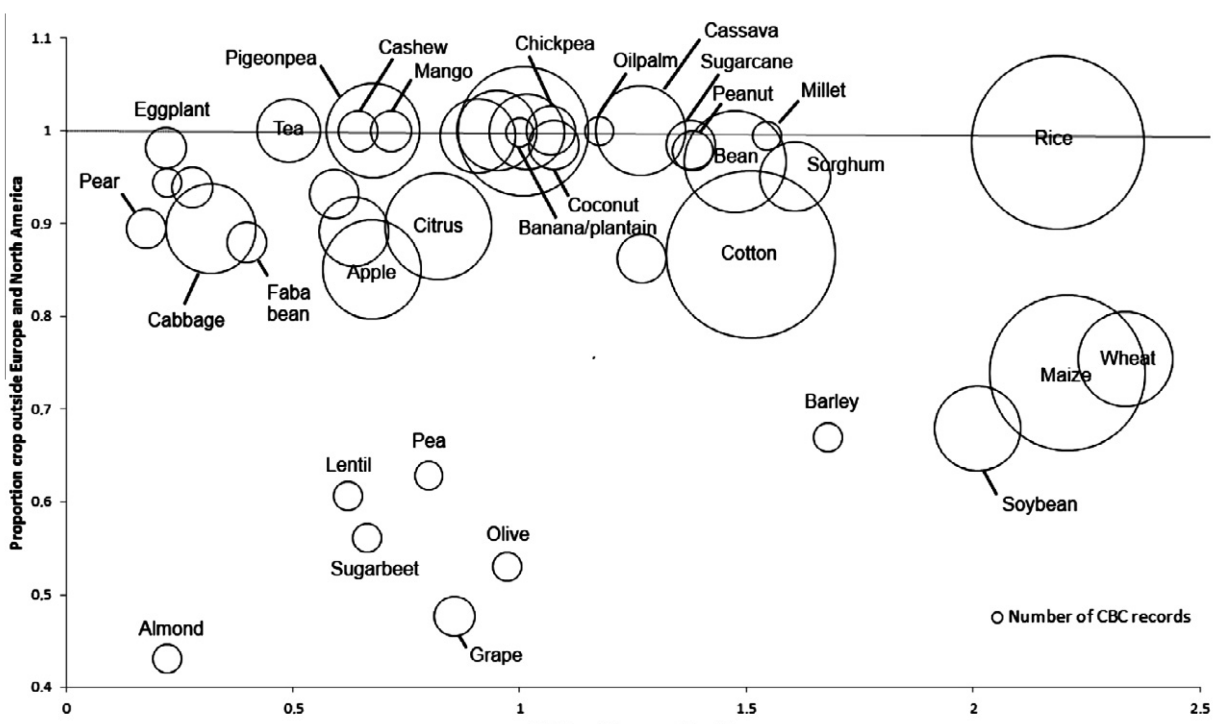

Fig. 2. Number of CBC records per crop, in relation to its 2010 global acreage (log10) and the share of its production outside the European Union and North America. Crop production data were obtained from FAO Stat (http://faostat.fao.org). Selected crops are identified in the figure, while we did not include crops for which no CBC records were found or that did not have reliable global production data.Size of the circles represents the number of CBC records for a given crop.

Table 2
Number of CBC records for a given pest species, as contrasted with its respective number of worldwide records of insecticide resistance. Insecticide resistance records were obtained through the Arthropod Pesticide Resistance Database (www.irac-online.org), and are solely reported for agricultural arthropod pests that are important in the developing world. We included the 30 pest species with highest incidence of insecticide resistance.

Species name	Family	Number of pesticide resistance records	Number of CBC records
Helicoverpa armigera	Noctuidae	640	10
Plutella xylostella	Plutellidae	455	5
Bemisia tabaci	Aleyrodidae	436	9
Myzus persicae	Aphididae	392	1
Tetranychus urticae	Tetranychidae	389	2
Spodoptera exigua	Noctuidae	322	0
Spodoptera litura	Noctuidae	238	2
Panonychus ulmi	Tetranychidae	187	1
Aphis gossypii	Aphididae	160	12
Frankliniella occidentalis	Thripidae	153	0
Nilaparvata lugens	Delphacidae	123	7
Heliothis virescens	Noctuidae	121	0
Delia antiqua	Anthomyiidae	90	0
Thrips tabaci	Thripidae	72	3
Trichoplusia ni	Noctuidae	68	0
Bactrocera dorsalis	Tephritidae	65	0
Earias vittella	Noctuidae	64	0
Pectinophora gossypiella	Gelechiidae	56	2
Chilo suppressalis	Crambidae	51	15
Heliothis assulta	Noctuidae	50	0
Spodoptera littoralis	Noctuidae	50	0
Panonychus citri	Tetranychidae	49	0
Anthonomus grandis	Curculionidae	41	0
Sogatella furcifera	Delhacidae	39	1
Liriomyza trifolii	Agromyzidae	38	0
Spodoptera frugiperda	Noctuidae	29	9
Tetranychus cinnabarinus	Tetranychidae	26	0
Nephotettix cincticeps	Cicadellidae	25	0
Tuta absoluta	Gelechiidae	25	0
Pseudoplusia includens	Noctuidae	23	0

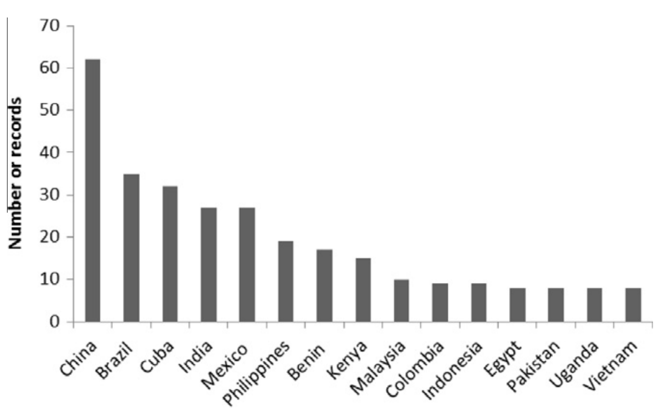

Fig. 3. Number of historical CBC literature records for a subset of the 15 developing countries with highest research output. One single publication can be considered as multiple records, depending upon the number of CBC aspects (as described in this manuscript) that are covered. Publications from the former Soviet Union are not grouped, but reported per member state.

unsustainable practices. In small-scale Colombian passionfruit production for example, >90% of farmers rely on calendar-based insecticide sprays, despite the presence of an abundant and effective natural enemy community (Wyckhuys et al., 2011; Carrero and Wyckhuys, unpublished). Similar patterns can be found in vegetable cropping systems (e.g., Grzywacz et al., 2010), where only tomato (6) and certain crucifers (10) appear to have received sustained CBC research attention. Last but not least, with the sole exception of one study on alfalfa, forage crops have largely been deprived from CBC research. As many of the above crops are grown by smallholders and sustain rural economies, the time might be ripe for a serious appreciation of CBC opportunities in many of those systems.

CBC research covered a wide range of pest insects, with *Busseola fusca* or *Chilo suppresalis* stemborers (15), cotton aphid (12), corn earworm (11) or cotton bollworm (10) receiving most attention. Some of these pests, such as *Chilo suppressalis* and *Helicoverpa armigera*, are suitable targets for CBC research given their high susceptibility to insecticide resistance development. In contrast, other pest insects with high pesticide resistance incidence, such as *Spodoptera exigua*, *Frankliniella occidentalis* or *Heliothis virescens*, have received little or no CBC research attention (Table 2). Strikingly, no CBC records were found for more than half of the 30 agricultural arthropod pests with highest incidence of insecticide resistance. Increased CBC research attention to some of those pests could help slow insecticide resistance development, and contribute to a closure of yield gaps (Godfray et al., 2010). Also, lack of CBC research for certain large-scale cropping systems (e.g., West African cotton) in concert with irrational insecticide use seems to trigger resistance development in other noxious organisms, such as the malaria vector *Anopheles gambiae* (Yadouleton et al., 2011).

Many developing countries invest millions of dollars annually in insecticide imports to fight agricultural pests (Fig. 4). Countries such as Algeria, Thailand or Morocco have comparatively high insecticide imports, but seem not to fully recognize the potential of natural biological control. Similarly, while interest in CBC research steadily grows in countries with high insecticide use such as Colombia, nations such as Bangladesh seem not to explore other cost-saving alternatives such as CBC (Fig. 4). Certain mega-diverse countries, such as Peru, Ecuador or the Philippines possibly have ample resident natural enemies effective against pests that are presently controlled with insecticides. For many of these countries, CBC research could help identify cost-saving pest control tactics and save scarce funds for more pressing development issues.

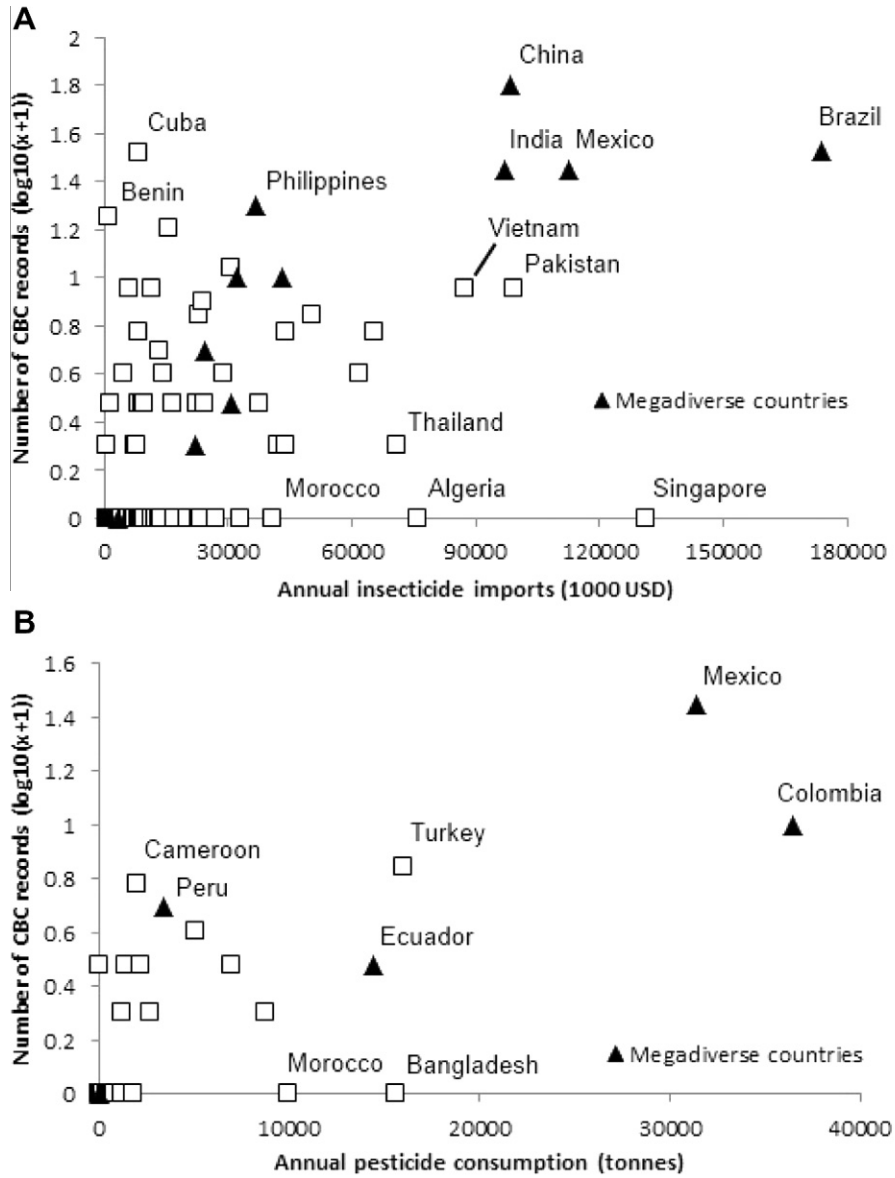

Fig. 4. Number of CBC records from developing countries, in relation to country-specific annual insecticide imports (A) or annual insecticide consumption levels (B). Insecticide use data were obtained for the year 2005, from FAO Stat (http://faostat.fao.org). For many developing countries, no reliable information was available on insecticide consumption or import.

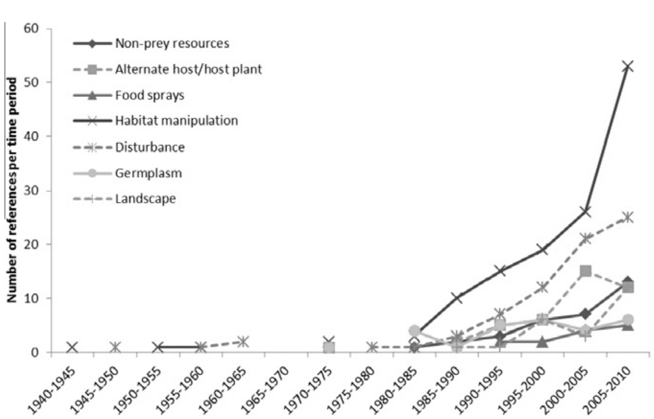

Fig. 5. Temporal patterns in the number of literature references on different aspects of conservation biological control from developing world nations.

Our literature search encountered a total of 390 CBC-related literature records from 53 different nations (Fig. 3), with the greatest number of records from China, Brazil and Cuba. We acknowledge that records from certain countries such as Russia and Middle Eastern nations may be far from complete, as some studies are only reported in the grey literature or local languages. On the other hand, our focused search in the Chinese and Cuban literature could have disproportionately increased the number of records from those countries.

With the earliest records on developing-world CBC research dating from the 1940s, the number of references has steadily increased since the 1980s (Fig. 5). During 2005–2010, a total of 50 studies were found on habitat manipulation and up to 25 on the modification of disturbance regimes. Research attention to crop germplasm or the assessment of alternative host or prey items appears to be diminishing, while food sprays have continued to receive low but constant levels of research over the past 20 years. A promising trend is the mounting number of references on the identification of non-prey food sources for (omnivorous) natural enemies. During 1985–90, only two of 19 studies assessed aspects related to natural enemy nutrition. Since 2010 onwards, a total of 12 (out of 49) studies described plant-based food sources of certain natural enemies. Possibly, this latter tendency can generate much-needed baseline data to take CBC forward in many cropping systems.

Time-held and novel research approaches alike wait to be employed to elucidate ecological particularities of natural enemies in many cropping systems. Ecological experiments, such as addition/exclusion trials, combined with molecular gut content analysis or biochemical assays could help assess the real potential for conservation biological control. Only in a few cases, researchers have moved beyond initial natural enemy surveys, and used exclusion trials, palynology, gut content analysis or feeding studies to assess the role of certain natural enemies or identify plant-natural enemy associations (see Santos-Neto et al., 2010; Jaramillo et al., 2010; Medeiros et al., 2010; Duyck et al., 2011; Narvaez et al., 2012). Such approaches carry considerable potential to help identify resident natural enemies of a variety of (cryptic) pests, determine their nutritional requirements and generate much-needed information to guide habitat modification schemes or artificial food sprays.

Looking at historic patterns in CBC research, we note a particular emphasis on two domains: survey and identification of (potentially) important natural enemies and on-farm evaluation of possible CBC schemes (see Naranjo, 2001). In many developing countries, a wealth of information has been generated through direct observation or (descriptive) population censuses of natural enemies. Observations were primarily carried out in agricultural crops, and a very small share in natural or non-crop areas. In certain systems, natural enemy surveys have spanned several years (Sharma and Agarwal, 2007). In others, natural enemies have only recently been identified (Rao, 2005), or still wait to be described (e.g., Baskaran et al., 1999). Surprisingly, there is a critical lack of natural enemy surveys in certain major staple crops or for key pests, such as whitefly or *Phyllophaga* white grubs (e.g., Legg et al., 2003; Bellotti et al., 2012). Only recently, the predator complex of cassava whitefly has been characterized (Lundgren et al., unpublished) and promising research venues have been identified for cassava whitefly CBC (Ewesi, 2011). For many other crops or pests, sensible CBC practices can only be defined once insights have been gained on the identity, abundance and action of resident natural enemy community.

On the other hand, researchers have gone to great lengths studying effects of disturbance schemes (20% historic records) and evaluating habitat manipulation approaches (38%). For habitat manipulation, companion plants have traditionally been selected based upon their N-fixing capacity or status as food or cash crop, mostly with little insights into their benefits for resident natural enemies. Through time, only a handful of studies have conducted the necessary, sequential set of experiments to successfully develop CBC or habitat manipulation schemes. Poster-child examples of such long term studies to boost natural enemy efficacy or abundance are the work on African stemborers (Ndemah et al., 2001; Kfir et al., 2002), West African cassava mites and mealybugs (e.g., Onzo et al., 2005), Mexican fruit fly parasitoids (Aluja, 1994), SE Asian rice pests (Matteson, 2000), and the recent revival of weaver ant research (van Mele, 2008). Amongst in-field evaluations of CBC tactics, we found few records where the extent of target pest suppression was assessed. By missing this pest angle, these studies also have little relevance to pest management (see Jonsson et al., 2008; Furlong and Zalucki, 2010).

Although we note numerous promising tendencies in CBC research in the developing world, its future may be threatened by agricultural development in several regions. First and foremost may be the rising level of mechanization, intensification and simplification of present-day cropping systems. Although pest severity and related insecticide use in Chinese cotton-wheat intercrops is far lower than in monoculture crops (Lu, personal communication), these systems are gradually disappearing. Amounting to >50% of Chinese cotton acreage at the turn of the century, its proportion has recently dropped to under 15% (Mao, 2010). In Indian rice–wheat cropping systems, field borders have long been valued as a refuge habitat for a broad diversity of natural enemies (Jaipal et al., 2002). With increasing mechanization in major wheat-growing regions (e.g., Punjab), straw burning has risen dramatically in the past decade and its impact on biological control is thought to be devastating (e.g., Gupta et al., 2004). Lastly, global cassava production is rapidly shifting towards large-scale monocultures with little place for on-farm biodiversity. Dropping natural enemy numbers, the appearance of novel pests and more severe outbreaks of existing pests all point to considerable deficiencies in those production systems (Bellotti et al., 2012).

Under these scenarios, CBC may be promoted by capitalizing on human ingenuity, deployed for centuries to solve agricultural challenges (Kiers et al., 2008). In many parts of the developing world, small-scale farmers have acquired an intimate knowledge of (part of) the local pest and natural enemy community (Bentley and Rodriguez, 2001; Wyckhuys and O'Neil, 2007a but see Abate et al., 2000). Based upon this knowledge, many farmers use simple, on-farm experiments to gradually adapt management practices to local farming systems (Scoones and Thompson, 1994; Sumberg and Okali, 1997). Farmer inventions for pest management have been documented from all over the globe, with records as old as written history (Kiritani and Nakasuji, 1977; Peng, 1983). Even though farmer inventions have been derided as a result of inaccurate folk science, a multitude of valuable pest management practices can be documented. For example, Chinese citrus farmers relied on observation to understand key aspects of weaver ant ecology and devise tactics to improve their efficacy in pest control. Many of these inventions have survived the test of time, and have been adopted by generations of farmers worldwide. A systematic documentation of such local CBC innovations and their possible insertion into modern-day farming could carry tremendous potential (see Morales and Perfecto, 2000; Wyckhuys and O'Neil, 2007a; van Mele, 2008). Such approach fits seamlessly within emerging interests for traditional knowledge and practices to help guide ecological engineering processes (Martin et al., 2010).

10. Conclusions

As a practice that is neither self-perpetuating (i.e., as classical biological control) nor benefits from political support or financial backing through vested industry interests, the future of CBC has often been termed as bleak (Ehler, 1998). However, our documentation of 390 CBC-related literature records from 53 different nations and >50 crops shows exactly the opposite. Active research in this field is being conducted, and critical insights in natural enemy ecology and CBC effectiveness are slowly but gradually being generated. Given that past work has mainly been conducted in isolation and long-term, sustained research on a given cropping system is still very much a rarity, we identify vast potential for well-orchestrated regional CBC projects that make strategic use of historic data, carry out additional research and wisely employ (local) knowledge to pursue higher levels of CBC integration into current pest management schemes. Now more than ever, CBC in the developing world is at a crossroads. In times of far-reaching budget cuts in international agricultural research, scientists have become increasingly concerned of focusing on "trendy" issues, such as biotechnology or computational science. However, with pest management improvements causing five times higher multiplicative increases than plant breeding in West African food production (Pretty et al., 2011), a closer look should be taken at present-day research priorities. Our work shows that the time is ripe to broadly recognize the benefits of biological control, and consider it as an integral part of sustainable crop intensification strategies in the developing world (Neuenschwander, 2010). By doing so, one could reduce greenhouse gas emissions, improve human and environmental health, circumvent insecticide resistance development and promote stability in yield gaps (Godfray et al., 2010). To achieve this, we identify an urgent need of funding to conduct fundamental agricultural ecology research, and ensure continuity of emerging initiatives in several cropping systems. While this work may be unfashionable, it could provide vital guidance for the design of cost-effective, environmentally-sound pest management solutions that are tailor-made to small-scale farming systems worldwide.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocontrol.2012.11.010.

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