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PERSPECTIVE

Pollinators, pests, and predators: Recognizing ecological trade-offs in agroecosystems

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Abstract Ecological interactions between crops and wild animals frequently result in increases or declines in crop yield. Yet, positive and negative interactions have mostly been treated independently, owing partly to disciplinary silos in ecological and agricultural sciences. We advocate a new integrated research paradigm that explicitly recognizes cost-benefit trade-offs among animal activities and acknowledges that these activities occur within social-ecological contexts. Support for this paradigm is presented in an evidence-based conceptual model structured around five evidence statements highlighting emerging trends applicable to sustainable agriculture. The full range of benefits and costs associated with animal activities in agroecosystems cannot be quantified by focusing on single species groups, crops, or systems. Management of productive agroecosystems should sustain cycles of ecological interactions between crops and wild animals, not isolate these cycles from the system. Advancing this paradigm will therefore require integrated studies that determine net returns of animal activity in agroecosystems.

Keywords Agroecology · Ecosystem services · Animal–plant interactions · Sustainable agriculture · Cost-benefit analysis

INTRODUCTION

Ecologically sustainable management of agroecosystems is crucial, given the rapid expansion of cropland to support humanity's increasing demand for food, fiber, and biofuel. While cultivated plants provide these goods for human consumption, wild animals directly and indirectly mediate the quantity and commercial quality of the goods produced via their activity in agroecosystems. Animal activity can have two major outcomes on production: (i) it can inflict costs on growers, for example, through direct damage to crops that cause yield and income losses (e.g., Gebhardt et al. 2011; Murray et al. 2013); and (ii) it can provide benefits via the delivery of ecosystem services (ES) like pollination or predation and parasitism of pests (e.g., Cardinale et al. 2003; Garibaldi et al. 2013). Understanding how to manage these two outcomes for an overall net benefit (where the overall benefits outweigh costs through a trade-off between social, ecological, and economic factors) is critical to sustainable agriculture. While many farm managers recognize this, their on-ground application of ecological practices can be limited by their understanding of ecological processes and the application of the ES concept (Lamarque et al. 2014).

This is not only largely an artifact of disciplinary silos, but also related to the challenges of studying complex interactions. Growers often rely on agricultural scientists for information and resources, rather than ecologists or conservation biologists. Yet, historically, agricultural scientists have primarily focused on documenting the costs of animal activity to agriculture and strategies for reducing these costs, while ecologists have championed ES research that emphasizes the conservation value of nature. Research into the negative impacts of animals in agroecosystems rarely acknowledges the potential benefits also arising from these interactions (e.g., Gebhardt et al. 2011), while studies focused on the positive outcomes of animal activity emphasize benefits (i.e., ES), mostly overlooking potential costs (e.g., Wenny et al. 2011). Biological control by natural enemies is one case where costs and benefits may be

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considered simultaneously, but these discussions are generally within the context of habitat conservation and management to encourage biological control ES (e.g., Chaplin-Kramer et al. 2011; Veres et al. 2013). Yet, the costs and benefits of animal activity generate clear ecological trade-offs for production in agroecosystems, and it is imperative to consider both when developing management practices for sustainable agriculture (Fig. 1). For example, within a given crop, seed set from insect pollination is ultimately traded off against seed damage caused by insect pests (Lundin et al. 2013). Similarly, fruit damage from bird frugivory before harvest is traded off against the benefits of removal of diseased fruit after harvest (Luck 2013). Although these outcomes are acknowledged by many biologists, a practical model that synthesizes ecological and agricultural knowledge to focus on net results of wild animal activity (incorporating both benefits and costs) has not been proposed.

We present an evidence-based conceptual model (Fig. 2) built on five ecological statements to demonstrate how the feeding behavior of bird and insect species positively or negatively affects crop production in space and time. We

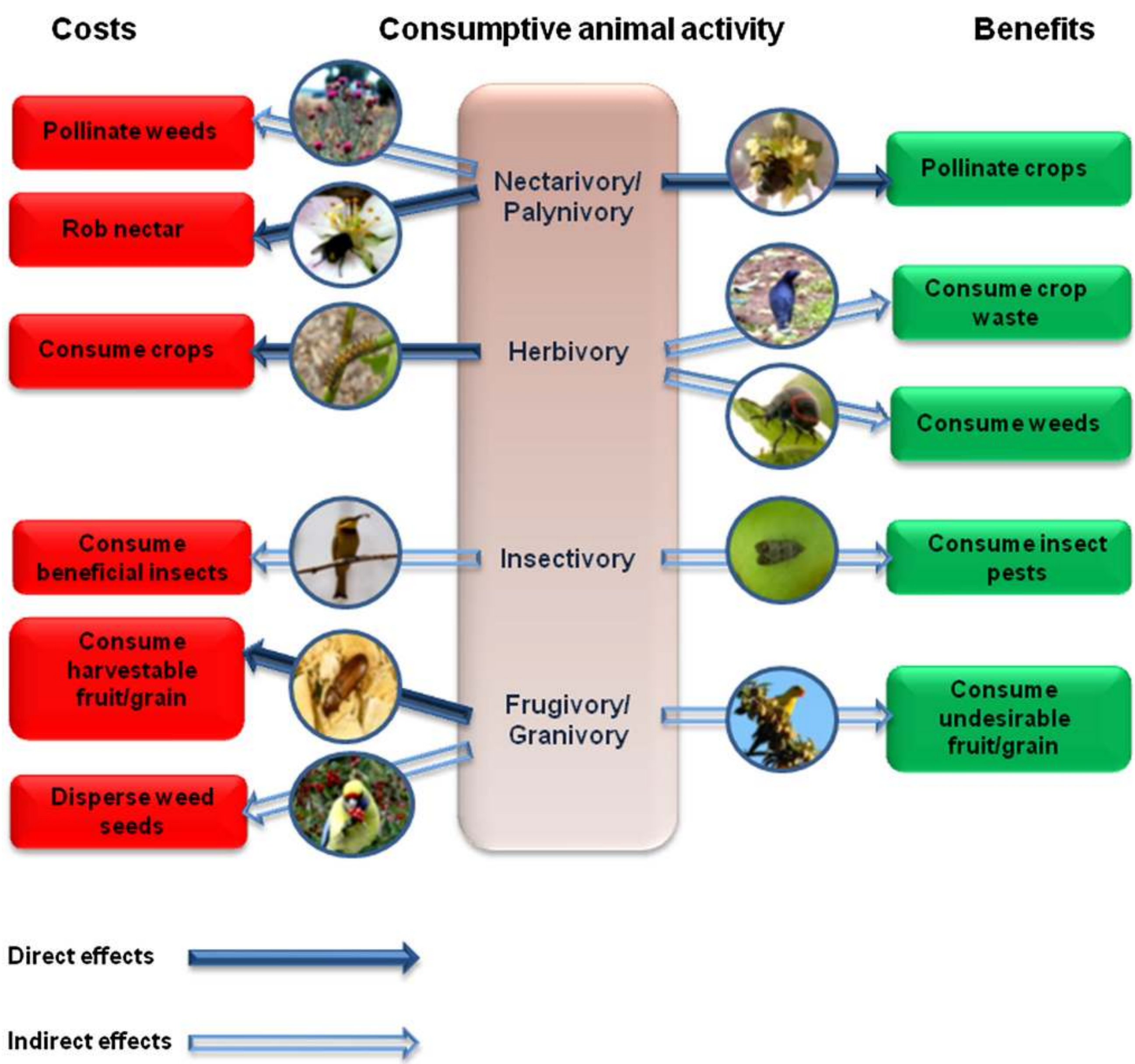

Fig. 1 The activity of animals in agroecosystems can inflict costs or confer benefits on growers through direct or indirect interactions with crop plants. Both outcomes need to be considered to calculate the net outcome of animal activity for production. Note that this simple diagram does not include the hidden costs or benefits associated with social-ecological contexts, which are discussed in Statement 5. Photos: Manu Saunders, Hugh McGregor, David McClenaghan

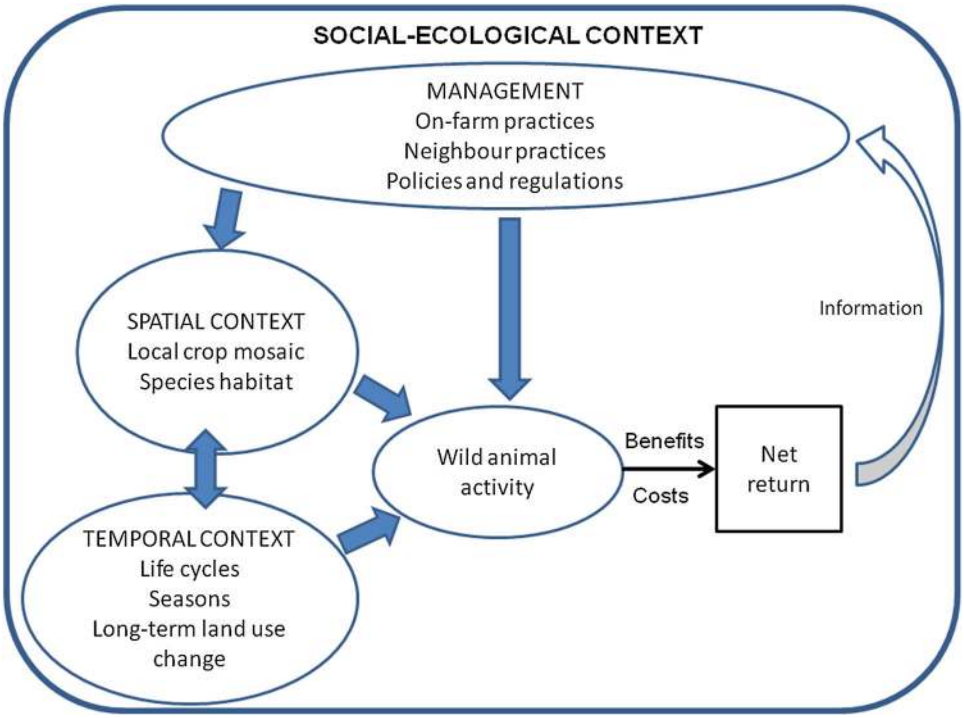

Fig. 2 Evidence-based conceptual model showing how wild animal activity influences crop yields positively (benefits) and negatively (costs) to produce a net return for growers. The value of the net return is a function of the spatial and temporal contexts that influence wild animal activity. Management practices exert a top-down influence on the ecological contexts and the wild animal activities themselves, and these practices can be changed through information feedback via identification of net outcomes

focus on birds and insects because these taxonomic groups not only provide two valuable ES to farmers (pollination and pest control), but can also cause severe damage to crops. Our model integrates evidence from two bodies of literature, agricultural, and ecological sciences, which have traditionally been considered as separate disciplines. To keep our argument focussed, in statements 1–4, we consider costs and benefits primarily in the context of increases or decreases in crop yield, or the income generated from the crop. We consider these to be tangible and meaningful metrics that are often the primary driver of a grower's land management decisions. Also, income (in a monetary sense) is one metric that is commensurate across crops and systems, allowing for cost-benefit trade-offs to be examined in a compatible way in different contexts. However, we acknowledge that costs or benefits can be defined more broadly, in ways that cannot be measured with simple metrics (e.g., in relation to human wellbeing, ecosystem resilience etc.), and that animal interactions within agroecosystems occur within a broader social-ecological context (see statement 5). This evidence calls for a new research and management paradigm that considers net outcomes of animal activity in agroecosystems by recognizing cost-benefit trade-offs among animal activities and environmental contexts. Managing agroecosystems relative to these trade-offs, beyond the limited scope of single species, crop stages, or systems, is fundamental to agricultural sustainability as it supports vital synergies between agricultural production and biodiversity conservation (Altieri 2004; Cunningham et al. 2013). Our approach avoids simplistic classifications of species groups as either 'beneficial' or 'detrimental' and instead shifts the focus to the overall costs and/or benefits of animal activity within a given social-ecological context.

STATEMENTS OF EVIDENCE

Production in a single crop field can be affected positively and negatively by multiple animal species throughout the growing season

Many studies of how animal activities affect crop yield focus on the activities of species relevant to one phenological stage of a crop, such as insect pollinators found in the crop during bloom. Some of these studies also examine interactions among species within a particular functional group during a specific crop stage. For example, pollinator interactions on crop flowers can indirectly affect crop yields because some insect pollinators are more likely to move between flowers (thus potentially increasing pollination efficiency) when other pollinators

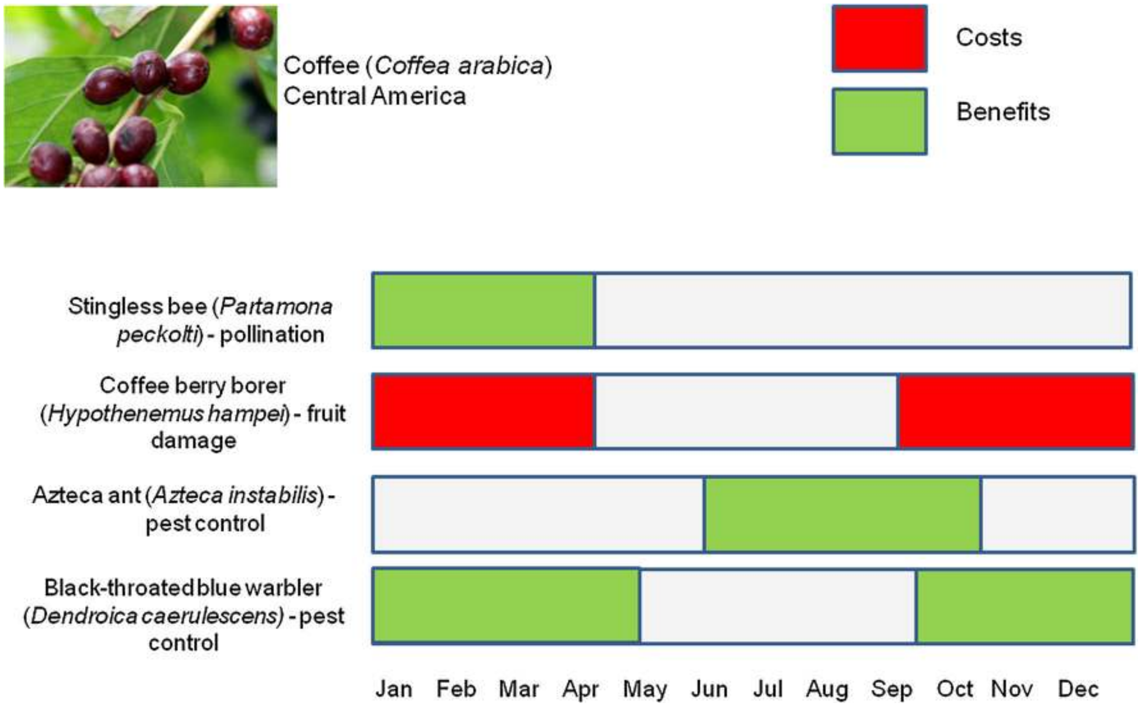

Fig. 3 For a single crop type in a given region, such as *Coffea arabica* grown in Central America, the activity of multiple bird and insect species across the year will have positive and negative effects on production at different crop stages. Other bird and insect species have been recorded in coffee systems in this geographic region; however, this figure is a representation based on the studies we collected that specifically focused on quantifying a cost/benefit. See Supplementary material for references. Photo: M. Martin Vicente

are present (Greenleaf and Kremen 2006; Carvalheiro et al. 2011). Other studies have shown how negative (e.g., pest damage) and positive (e.g., pest predation) effects of animal activity occurring during the fruit/seed development stage of a crop can be managed in combination for an optimal effect on final yields (e.g. Cardinale et al. 2003). While these studies are valuable in determining the impact of animal activity at key crop stages, they generally overlook how interactions among multiple animal species across the crop's life cycle can also affect yields. Many of these interactions have been widely studied in natural systems, but are rarely considered in agroecosystems. For example, the combined action of herbivores and pollinators can have synergistic or additive effects on plant reproduction. Through direct or indirect impacts on floral displays, herbivores can affect the nature, strength, and fitness consequences of the interaction between plants and their pollinators by altering the flower's attractiveness to pollinators (Krupnick et al. 1999; Mothershead and Marquis 2000). Similarly, predatory flower spiders can influence seed production by reducing the frequency and duration of floral visits by pollinating insects (e.g. Suttle 2003). These types of interactions are only now being considered in the context of crop production (Lundin et al. 2013; Classen et al. 2014), and greater attention to these interactions in agroecosystems studies would lead to a more comprehensive picture of how positive and negative activities impact production outcomes.

For example, in Central America and the Caribbean, coffee (*Coffea* sp.) not only is an economically important crop that benefits from insect pollination, but also suffers serious yield losses from the introduced coffee berry borer *Hypothenemus hampei* during fruit development (Fig. 3; see Supplementary material for references). Increased abundance and diversity of pollinators at flowering time can reduce the amount of unmarketable 'peaberries' that develop and enhance coffee berry yield and net revenue for farmers. During fruit development, harvest losses can be significantly reduced if the system supports insectivorous birds and predatory insects that control borer populations. When both flowering and fruiting stages are considered, the independent positive and negative outcomes of all of these activities (pollination, pest damage, predation) can be weighed against each other to identify an overall cost or benefit effect on final yields (e.g. Classen et al. 2014). Similar relationships are likely to be common in other pollinator-dependent crops that are susceptible to animal damage, such as tree fruit (e.g. Luck 2013).

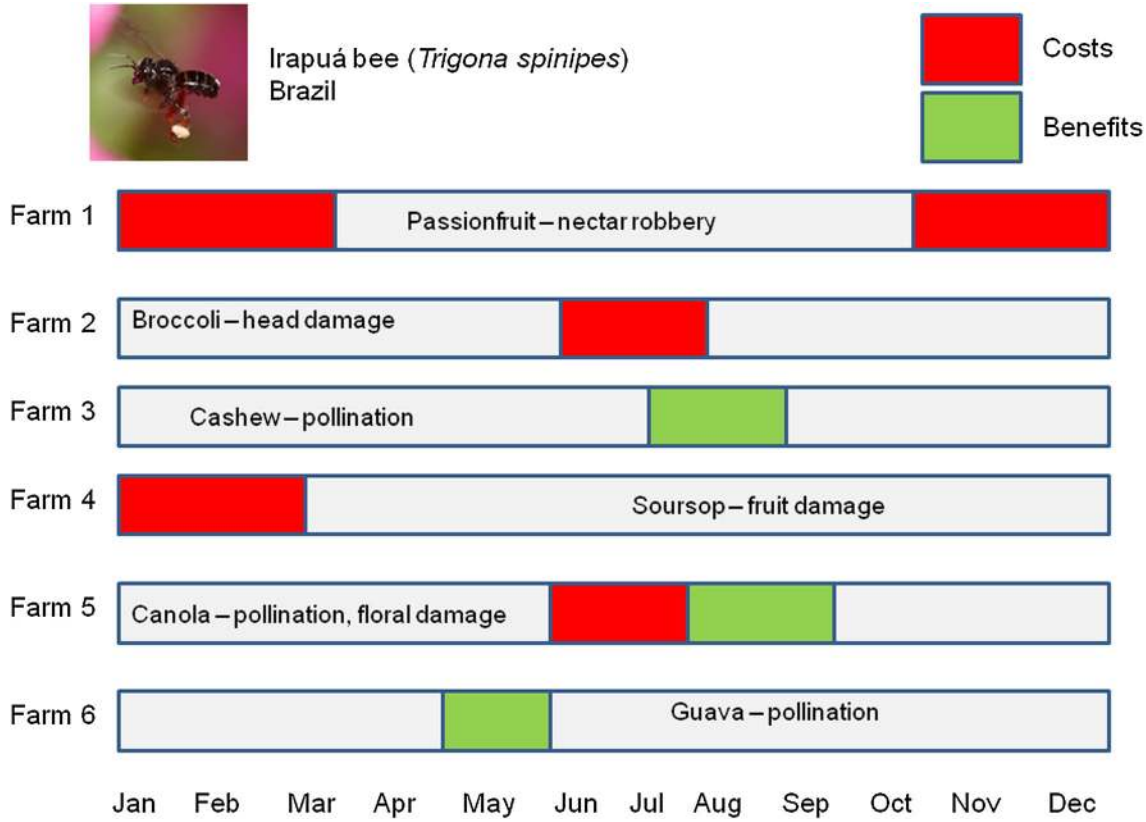

Fig. 4 A single species can have positive and negative outcomes in different crop types across its native range, such as the stingless Irapuá bee in Brazil. See Supplementary material for references. Photo: Chantal Wagner

Production in a single crop field can be affected positively and negatively by the same animal species or functional group at different phenological stages of the crop

The feeding behavior of one functional group may have either positive or negative outcomes for growers depending on the stage of the crop. For example, in south-east Australian almond (*Prunus dulcis*) plantations, granivorous birds can cause losses to farmers by damaging developing fruit on trees before harvest; however, the same bird species may benefit farmers after harvest by removing residual almonds from trees that can harbor diseases and pathogens (Luck 2013). In this example, Luck (2013) demonstrated that the economic value of the benefit outweighed the economic value of the cost, meaning that, when considered across the growing season, the feeding behavior of granivorous birds resulted in a positive net return to growers.

Just as one species can shift from beneficial to detrimental relative to crop phenology, role shifts in an entire functional guild (e.g., insectivorous birds) can also impact crop production. It is well known that insectivorous birds can control insect pests that damage crops, particularly during the fruiting stage of the crop, thus improving yield (Wenny et al. 2011). However, the same insectivorous birds may also consume bees and other beneficial insects during crop flowering, potentially having indirect negative effects on fruit/seed set in pollinator-dependent plants (Meehan et al. 2005). Bee-eater species (Coraciiformes: Meropidae), in particular, are not only common predators of honey bee (*Apis mellifera*) pollinators in the northern hemisphere, but also prey on crop pests (Chakravarthy 1988). The European bee-eater *Merops apiaster* can also spread viable spores of the honey bee hive parasite *Nosema ceranae*, a pest of managed honey bee colonies, through its feces (Valera et al. 2011).

Activity of a single animal species can have different effects on yield in different crops

A single animal species can have positive or negative effects on yields in different crop types. For example, the Brazilian Irapuá bee *Trigona spinipes* is a pest in broccoli (*Brassica oleracea*) and soursop (*Annona muricata*) crops, where it damages fruit, flowers and leaves to gather food and nesting materials, but is also considered an important wild pollinator in guava (*Psidium guajava*) and cashew

(*Anarcadium occidentale*) crops (Fig. 4; see Supplementary material for references). Similarly, natural enemies of crop pests may become a pest themselves when environmental conditions change. The mirid bug *Dicyphus tamaninii* is a polyphagous predator in the Mediterranean that controls a number of damaging pests of vegetable crops in the Mediterranean, but can also damage fruit when insect prey are scarce (Gabarra et al. 1995).

At a global scale, the outcome of a species' activity in crop systems may change when it is introduced to a new country and encounters new resources. In its native range, the European blackbird *Turdus merula* is predominantly an insectivore, generally turning to frugivory when invertebrates are in low supply (Chamberlain et al. 1999). It was introduced to Australia and New Zealand in the late 1800s, where it is now a damaging pest of many fruit crops, particularly grapes (e.g. Tracey and Saunders 2003). Interestingly, the blackbird has also been recorded as beneficial in its introduced range, where it may be a more efficient pollinator of feijoa (*Acca sellowiana*) than European honey bees (Stewart and Craig 1989).

Different life stages of a single animal species can also impact yields of multiple crops in different ways. As adult moths, the hawkmoths *Hippotion celerio* and *Agrius convolvuli* provide pollination services to papaya (*Carica papaya*) growers in Kenya (Martins and Johnson 2009), but during larval stages, they can be pests of other crops throughout Africa and southern Europe (e.g., sweet potato, Nsibande 1999). In contrast, many species of hoverfly (Diptera: Syrphidae) can have positive effects on crop yields at both larval and adult stages. For example, larvae of the European *Eristalis tenax* and marmalade *Episyrphus balteatus* hoverflies suppress aphid pests, while adults are important pollinators in multiple crops (Rader et al. 2012; Raymond et al. 2014).

The activities of multiple animal species across multiple crop systems results in landscape level cost-benefit trade-offs

No farm is an island. Productivity of crops on individual farms is influenced by processes occurring at landscape and regional scales. To our knowledge, no study has examined the net outcomes of animal activities on multiple crop yields across an agricultural landscape. Land-use diversity can promote economic resilience in agricultural landscapes (Abson et al. 2013), so understanding how landscape-scale ecological trade-offs affect production on multiple farms can inform a collaborative, landscape-scale approach to management. The potential for this approach can be explored by looking at individual studies from a single region and considering key interactions between crop and animal phenologies. For example, peak bird and insect activities in New Zealand agroecosystems occur in summer. As a result of this activity, at this time, summer-flowering crops can benefit from insect pollinators, while developing fruit on spring-flowering crops may be affected negatively by pest birds and positively by raptors that suppress pest bird activity (Fig. 5; see Supplementary material for references).

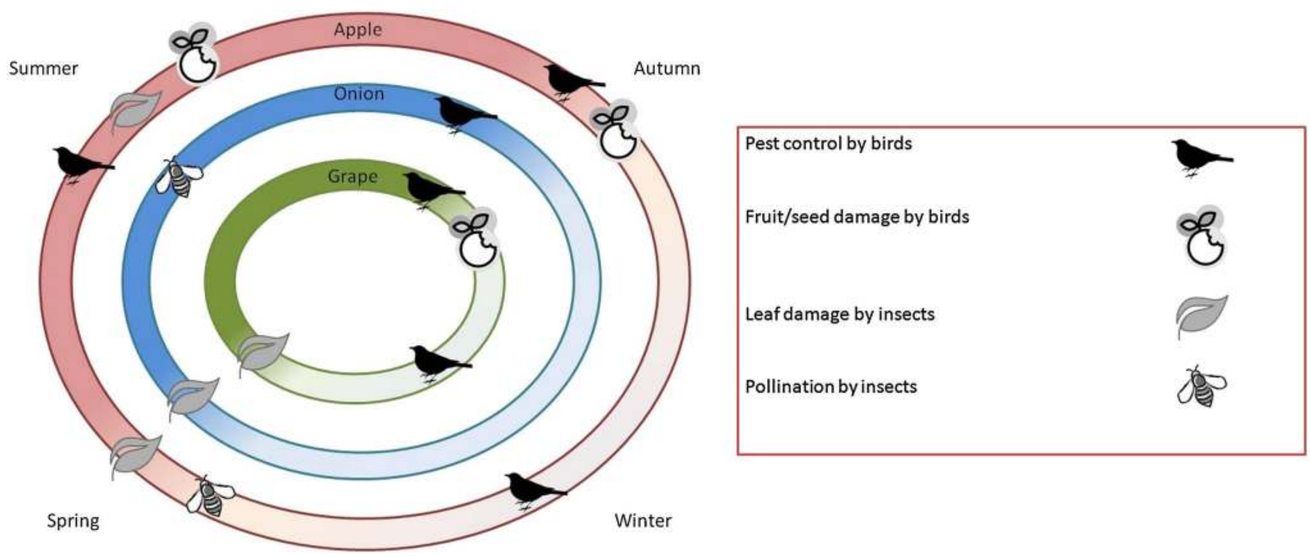

Fig. 5 The relationship between crop phenology and animal activity in a New Zealand agroecosystem. Each *circle* represents the annual cycle of a single crop grown in the region. *Icons* represent when beneficial or detrimental activities by birds and insects may occur in each crop. Taken as a whole, the figure demonstrates the complexity of cost-benefit trade-offs occurring across the entire life-cycle of multiple crops in the same region. See Supplementary material for references

Animal activities, and the magnitude of their overall effects on crop production, are mediated by landscape composition, configuration, and farm management practices. For example, intensification of agroecosystems, via farm management practices and land-use change, is linked to declines in functional diversity of animal species and altered community composition of ES providers (Flynn et al. 2009). Spillover of animal communities across habitat types, especially in systems where resource availability differs for each habitat, may be an important ecological process structuring communities. Remnant vegetation provides vital resources for beneficial insects such as pollinators and natural enemies, including food, nesting, and overwintering sites. Distance to remnant vegetation is often negatively correlated with crop yields, as pollinator diversity and pollination services decline with greater isolation from natural or semi-natural habitats (Taki et al. 2010; Garibaldi et al. 2011). While there is much evidence for spillover from natural habitats to managed areas, little attention has been given to spillover in the opposite direction (Rand et al. 2006; Blitzer et al. 2012; Gaigher et al. 2015). Spillover of insect natural enemies released as management inputs in agroecosystems may also affect prey populations in natural habitat fragments (Blitzer et al. 2012). In particular, high productivity and temporally variable resource abundance in agricultural systems can result in strong spillover effects to natural habitats when agricultural resources are exhausted (Rand et al. 2006). Conversely, natural habitats can provide resources for some species (e.g., foraging and perching sites for frugivorous and granivorous birds), which can lead to greater damage to crops that are adjacent to native vegetation (Bollinger and Caslick 1985; Luck et al. 2013).

The relative densities of the animal species and the crop it interacts with can influence how that activity affects yield (e.g., Cardinale et al. 2003). Mass-flowering crop monocultures can attract pollinators from surrounding habitats during flowering, with obvious benefits for crop yields (Bartomeus and Winfree 2011). Yet, after the brief flowering period is over, the abrupt decline in floral density can reduce pollinator reproduction rates (Jauker et al. 2012), potentially having long-term negative effects on crop production in the local area. Similarly, when flowering crops are temporarily saturated with managed honey bee colonies, the net benefits of fruit set can decline once flower visitation rates surpass an optimal number of visits (Aizen et al. 2014).

Yields often increase on farms where local management practices have incorporated vegetation heterogeneity within the farm (e.g., polycultures, balancing annual, and perennial plant resources). In particular, polyculture practices (e.g., trap crops, intercropping) designed to enhance ES for the farm's primary crop have the added benefit of increasing net revenue through additional yields from the secondary crop (Cavanagh et al. 2010). Species-rich weedy plant communities growing in and around the crop can enhance yields by providing floral resource diversity and connectivity that sustains populations of insect pollinators and predators (e.g., Haaland et al. 2011). Although some weedy herbs can impact crops negatively through direct competition or contamination of harvested yield, they can also provide a high quality, early-flowering source of nectar and pollen that can increase bee numbers in managed honey bee colonies used for crop pollination (e.g., Paterson's Curse *Echium plantagineum*; Keogh et al. 2010). Agricultural intensification (e.g., broad-scale monocultures) may enhance crop yields by removing competition from non-crop vegetation; however, this is likely to be a short-term effect at the expense of long-term agricultural sustainability, as high inputs (e.g. synthetic fertilizer) and negative ecological impacts may eventually cause yield declines and disrupt ecosystem function (e.g., Flynn et al. 2009; Bennett et al. 2012).

Management practices aimed at mediating negative outcomes of wild animal activity can also indirectly affect crop yields. Synthetic chemicals are commonly used in conventional systems to control the negative activity of insect pests that cause yield losses. However, they also indirectly affect crop yields by suppressing the positive effects of bird and insect activity. Pesticides are associated with declines in insectivorous birds (Hallmann et al. 2014), pollinators and natural enemies (Bommarco et al. 2011; Rundlöf et al. 2015), thereby suppressing beneficial animal activities that enhance marketable yields (Bommarco et al. 2011; Gillespie et al. 2014) and affecting ES in the long term (Chagnon et al. 2015).

Complex interrelationships between social and ecological systems influence the net outcomes of animal activity in agroecosystems

The human values (ethical, spiritual, cultural, etc.) of agricultural communities have a profound influence on decision-making and management practices in agroecosystems, which ultimately affects crop-animal interactions. Hence, the most informative analysis of cost-benefit trade-offs is one that considers the whole social-ecological agroecosystem setting. A clear example of this is in situations where the activity of threatened species in agroecosystems inflicts costs on farmers, but control options are restricted by legal or political frameworks. In Africa, large vertebrate crop-raiders (e.g., elephants, primates) not only inflict direct costs on growers by damaging plants, but also create indirect costs for farming families through poor health and wellbeing and disruption of livelihoods (Mackenzie and Ahabyona 2012; Barua et al. 2013). In some cases, managing the ‘pest’ through ecological interactions with other animals can reduce costs and enhance benefits for farmers. For example, elephants avoid African honey bee (*A. mellifera scutellata*) hives, through fear of attack, and King et al. (2011) showed how Kenyan farming communities used a fence of bee hives to keep crop-raiding elephants from damaging their crops, while also enhancing pollination services and gaining additional income from honey harvests.

In many countries, spiritual beliefs and cultural practices have strong ties to the plant–animal interactions that occur in local agroecosystems. Traditional knowledge of animals is often based on their functional roles in the ecosystem rather than, for example, taxonomic groupings (e.g., Gurung 2003). Religious or cultural rituals in agrarian communities can also be designed to enhance crop yields by supporting beneficial animal interactions, particularly biological control (e.g., Ulluwishewa 1992). In cases where complex social-ecological farming systems are replaced with intensive, high-input production models, this can create a negative feedback effect on production, whereby increased pest and disease activity associated with monoculture farming exacerbate social costs, thus increasing farm abandonment and collapse of the social structure supporting the agroecosystem (Altieri 2004; Aragona and Orr 2011).

FUTURE DIRECTIONS

The complexity in these examples demonstrates that ecological interactions between crops, wild animals, and the surrounding environment involve constantly evolving natural processes. Spatial and temporal variation in these processes occurs at multiple scales, from daily fluctuations in animal activity within single fields to annual variation in community structure across regions (e.g., Rader et al. 2012). The magnitude of variations in activity, and subsequent impacts on crop yield, is not constant between seasons or years (e.g., Raymond et al. 2014), as each plant–animal interaction occurs within a broader ecological context that also varies. Thus, quantifying the results of a single species’ activity at one stage of a crop cycle, or in one location, can create either a positive or negative ‘label’ for that species that is not always indicative of its net value to the system. Similarly, a net gain or loss at harvest cannot be linked to a single wild animal species or ecosystem function. To account for ecological variation while producing sustainable crop yields, the current agricultural paradigm needs to move beyond managing agroecosystems based on biological simplification and intensification of production and land use (Weis 2010). This approach to agriculture allows for ease of management but is ecologically unsustainable and can result in long-term yield declines and serious social and environmental consequences (Aragona and Orr 2011; Tscharntke et al. 2012).

It is imperative that future research and management strategies for agroecosystems recognize that cycles of ecological interactions between crops and wild animals are inherent to productive agroecosystems and should be sustained, rather than isolated from the system. Our conceptual model shows how identifying net returns through trade-offs between these interactions can better inform management decisions to benefit biodiversity conservation and food production in agroecosystems (Fig. 2). A first step in the practical implementation of our conceptual approach is for growers to identify the key potential costs and benefits occurring at particular crop stages, and the animal groups delivering these costs and benefits (Table 1). From there, growers should consider the management options available to them to enhance benefits or limit costs, weighed against the social, ecological, and economic implications of a particular management action (e.g., spraying pesticides), and how management at one crop stage may impact interactions at other crop stages. Managers should also be aware that the outcomes of cost-benefit interactions will be mediated by spatial and temporal environmental drivers and social-ecological contexts. An important future challenge is addressing the idea that landscape-scale management approaches can enhance regional food production more than multiple, and potentially opposing, farm-scale approaches (Cunningham et al. 2013). This requires coordination of management activities across multiple private-land holdings. This is also relevant when agricultural industries plan to expand into new landscapes, where novel trophic webs between established animal communities and introduced cultivated plants may arise (Watson et al. 2013).

Recent evidence suggests that investigating net outcomes of multiple ecosystem functions and activity across functional groups within an agroecosystem is feasible (Lundin et al. 2013; Classen et al. 2014), and is often more useful for agricultural sustainability and conservation than identifying effects from a simplified ‘single species, system or ES approach. However, we stress that the detailed ecological and biological information gained from studying these less complex interactions is still valuable, but much more research is needed that identifies net outcomes of animal activity within a given social-ecological context and relates these outcomes to food production.

The future of food and fiber production depends on sustainable management of agroecosystems that enhances yields and reduces environmental costs (Bommarco et al. 2013). Our model approach, integrating ecological and agricultural knowledge, shows this can be achieved by identifying the net outcomes of managed and unmanaged

Table 1 Relationships between critical crop stages/resources and the insect or bird functional groups responsible for inflicting costs or providing benefits. Parasitic species can affect outcomes at all stages by influencing populations of each functional group, but we have not included these interactions here for simplicity

Crop stage	Animal functional group	Cost or benefit
Stems	Stem borers (e.g. Cerambycidae beetles)	(−) Reduce quality of woody material
		(+) Trigger fruit set in some crops
	Probers (e.g. woodpeckers)	(+) Consume borer pests and other insects under bark
	Chewers (e.g. parrots)	(−) Damage to stems by chewing
Buds	Bud borers and feeders (Helicoverpa moths)	(−) Damage buds by boring or chewing
	Bud gleaners and probers (e.g. treecreepers)	(+) Control insect pests on bud surfaces and crevices
Leaves	Leaf chewers (e.g. sawfly larvae)	(−) Stunted plant growth from damaged foliage
	Foliage gleaners (e.g. warblers)	(+) Control insect pests on leaves
Flowers	Pollinators (e.g. bees, honeyeaters)	(+) Pollinate flowers
	Nectar robbers (e.g. some Bombus sp.)	(−) Damage flowers
	Flower feeders (e.g. flower thrips)	(−) Damage/consume flower parts
	Flycatchers (e.g. bee-eaters)	(−) Consume insect pollinators
		(+) Consume insect pests
Fruits/seeds	Frugivores/granivores (e.g. parrots, moth larvae)	(−) Damage/consume fruit and/or seeds
		(+) Consume decaying/diseased fruit
	Insectivores (e.g. gleaning, probing or hawking birds)	(+) Consume insect pests
	Raptors (e.g. falcons, hawks)	(+) Suppress frugivorous bird activity

agroecosystem dynamics. This approach links research and management outcomes by recognizing ecological interactions and trade-offs between multiple wild animal species and understanding how environmental conditions of the system mediate these trade-offs.

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