Ecosystem services in agriculture: understanding the multifunctional role of invertebrates

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The ecosystem services concept was developed in the 1980s-1990s to promote understanding that nature is essential for human survival and well-being (Westman, 1977; Ehrlich & Mooney, 1983; Daily, 1997). Of course, this idea is not new. Humans have appreciated the benefits nature provides for millennia. But incorporating the concept into modern science and developing meaningful ways to quantify and value ecosystem services has been complicated. There are also broad misconceptions about the concept. Although much of the literature on ecosystem services has focused on economics and accounting systems, the concept is not simply about 'putting a price on nature'. As a conceptual framework, it has direct application to basic and applied research on species and systems that interact with humans. Quantifying how species and their interactions provide benefits to humans is a valuable way to inform biodiversity conservation programs and sustainable production systems.

Ecosystem services are particularly relevant to agricultural systems, which provide food, fibre and livelihoods for human communities. Ecologically sustainable management of agroecosystems, i.e. management that balances production of food and fibre with conservation of biodiversity and ecosystem function, is essential to meet the growing needs of humanity. A key challenge in achieving this goal is to understand how plant-animal and animal-animal interactions provide ecosystem services on farms, in terms of increases in yield quality or quantity, or other production benefits.

Wild animals produce ecological costs and benefits daily via their activity and interactions within agroecosystems. Not all of these interactions will affect final yields, and the outcome of many interactions can vary with context. Yet most people associate nearly all wild animal taxa with simplified positive and negative labels, e.g. bees are always beneficial and aphids are always pests. The reality is far more complex (Saunders *et al.*, 2016). Achieving sustainable agriculture goals requires greater collaboration and communication between agricultural scientists, entomologists and ecologists. Unfortunately, knowledge development in these disciplines has traditionally been isolated. In a recent review of studies quantifying the costs and benefits of bird and insect activity in agroecosystems, we found a clear disciplinary divide (Peisley *et al.*, 2015). Studies of wild animals producing costs for growers were more common overall, and were mostly found in the agricultural science literature. In contrast, studies of the benefits wild animals provide were mostly found in the ecology and conservation literature. These disciplinary research silos limit understanding of the trade-offs and synergies that occur between animal activities, and across environmental contexts, and ultimately affect production.

Unmanaged invertebrates provide numerous benefits in agroecosystems, including pollination, biological pest control, soil aeration, waste decomposition and dung removal (Losey & Vaughan, 2006; Nichols *et al.*, 2008; Cross *et al.*, 2015). A large body of literature has examined how farm and landscape management influences beneficial invertebrate communities in agroecosystems (Bianchi *et al.*, 2006; Chaplin-Kramer *et al.*, 2011; Kennedy *et al.*, 2013; Nicholls & Altieri, 2013). Yet we know very little about the direct benefits these species provide in agroecosystems, or the ecological and biological mechanisms underlying these benefits. Pollinators have been the most widely-studied invertebrate ecosystem service providers. This bias in the literature is most likely because pollination seems intuitively easy to quantify with fruit set and crop yields, or because insect pollinators (especially the European honey bee, *Apis mellifera* L.) generally benefit from greater media attention and political interest than other insect taxa (Smith & Saunders, 2016). Historically, there has been a strong focus on managed European honey bees as the key pollinator of most crops. Early studies of crop pollination systems mostly quantify seed or fruit set from honey bee visitation, largely ignoring other insect visitors. The benefits of pollination services from non-*Apis* bee species and diverse wild pollinator communities have since been acknowledged (Garibaldi *et al.*, 2013; Rader *et al.*, 2016), but the distribution and ecology of wild pollinator communities in many agroecosystems, especially outside Europe and North America, are largely unknown (but see Caro *et al.,* 2016; Tangtorwongsakul *et al*., 2017). Understanding drivers of pollinator losses and how to manage agroecosystems for optimal pollination services are key questions for future research (Mayer *et al.*, 2011). Of course, the benefits of pollinators are not always clear-cut. Insects can rob nectar without pollinating, or may facilitate the spread of noxious weeds. In some contexts, bee species may even become 'pests', causing direct costs to growers by damaging fruit or flower parts (Sobrinho *et al.*, 1999; Santos *et al.*, 2012; Aizen *et al.*, 2014).

The biological control of insect pests is another commonly-recognised ecosystem service with a long history in the scientific literature. Surprisingly, relatively few studies have attempted to directly quantify the value of biological control services to crop production (but see Östman *et al*., 2003). Quantifying yield outcomes of biological control is a lot harder to do than measuring pollination services. Fruit/seed set can be measured as a direct outcome of a plant-animal interaction (i.e. pollination), but fruit/seed damage is an indirect outcome of multiple plant-animal and animal-animal interactions. Most systems support a combination of generalist and specialist predators, parasitoids and hyperparasitoids, and are influenced by human activities that also affect pest populations, like pesticide applications and habitat modification. These human influences on the pests present in a study system are often unaccounted for and difficult to analyse. Most studies that attempt to quantify the benefits provided by natural enemies in agroecosystems use indirect measures of their activity, e.g. pest populations as a reverse proxy for natural enemy activity. A key goal in quantifying biological control services in agroecosystems is to directly link unmanaged natural enemy communities with crop yield outcomes via *in situ* parasitism and predation rates. In addition, much of the pest control literature from agroecosystems focuses on insect natural enemies. Insectivorous birds also provide valuable pest control services, a fact widely-acknowledged by the field of economic ornithology in its heyday at the turn of the twentieth century (Kronenberg, 2014). More recently, studies of bird activity in agroecosystems have focused on costs (Peisley *et al.*, 2015) and relatively few studies have considered how birds complement, or interfere with, the pest control services provided by insect natural enemies.

A major limitation of most studies quantifying benefits from invertebrates in agroecosystems is that nearly all are snapshots of the whole system. That is, benefits are measured at the scale of a single crop stage, agroecosystem or taxon. This approach is valuable for understanding particular interactions and processes, but tells us little about how positive and negative interactions trade-off across time and space to influence final yields. Understanding how functional roles change across agroecosystem contexts, and how the net outcome (benefits minus costs) of different activities influences production, is an important avenue for inquiry. For example, Luck (2013) used this approach to identify a net benefit to growers from the activity of granivorous bird species in Australian almond plantations. These birds were considered pests during fruit development, as they damaged developing almond fruits. But the damage was largely concentrated at plantation edges, and the same birds provided a service to growers after harvest by removing residual 'mummy nuts' on trees that can harbour pests and pathogens. Luck calculated trade-offs between the costs and benefits of the bird activity, and management costs, to show that these birds provided a net benefit to growers. A similar approach can also be applied to invertebrate species or functional groups to examine net outcomes across crop production periods (e.g. Saunders & Luck, 2016). A particularly important goal for research is to understand how pollinators, pests and natural enemies interact within a single system. Most studies consider the outcome of pollination and pest control services separately. But crop yield is a net outcome of interactions between multiple pest and beneficial invertebrates, as well as abiotic factors, across multiple seasons (Lundin *et al.*, 2013; Classen *et al.*, 2014; Bartomeus *et al.*, 2015; Saunders & Luck, 2016; Sutter & Albrecht, 2016).

Invertebrates provide myriad other benefits in agroecosystems, most of which have so far been overlooked in the ecosystem services literature. The essential role of soil invertebrates, particularly earthworms, in enhancing soil quality has been long recognised (Darwin, 1881; Russell, 1910; Lavelle *et al.*, 2006), but there have been few attempts to quantify how soil organisms enhance agricultural yields (but see Evans *et al.*, 2011). Invertebrates provide other economic and cultural benefits to humans in agroecosystems, either directly as a food source or indirectly through substances produced by the organisms. An important path of inquiry lies in understanding how managing these useful invertebrates indirectly, by managing the habitat to support them, can provide knock-on benefits for the agroecosystem that enhance overall production. For example, supporting host plants for invertebrates that produce valuable substances, like lac insects, can provide additional benefits for habitat quality and soil health (Saint-Pierre & Bingrong, 1994), while direct harvesting of pests for human consumption can reduce the need for insecticides (Cerritos & Cano-Santana, 2008). Invertebrates also provide services in livestock agroecosystems, many of which are not well-understood, including decomposition or bioconversion of dung (Holter, 1979; Nichols *et al.*, 2008; Wu & Sun, 2010; Li *et al.*, 2011), or removal of carrion wastes (Barton & Evans, 2017). The trophic links between aquatic and terrestrial systems have also been long-recognised (Polis *et al.*, 1997; Knight *et al.*, 2005), but crop production ecosystem services derived from invertebrates that spend all or part of their life cycle in water have only recently been quantified (Stewart *et al.*, 2017).

Clearly the future for applied ecosystem services research is bright. Unmanaged invertebrates are more numerous, more diverse and more active in global agroecosystems compared to wild vertebrates, but the knowledge we have of their distributions, life cycles and interactions is limited relative to our knowledge of vertebrates. Historically, a strong focus on invertebrates as pests, both in agroecosystems and society generally, has left large gaps in knowledge of how interactions between invertebrates benefit human well-being. Understanding how invertebrates enhance agricultural production is essential to inform sustainable management of agroecosystems, and will also go a long way towards enhancing the perception of invertebrates more broadly.

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