

# Net Effects of Birds in Agroecosystems

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*Incorporating both ecosystem services and disservices into land-use decisions is essential for meeting conservation and livelihood goals. We discuss the merits and challenges of this concept, termed net effects, for birds in agroecosystems. Although birds have widely documented impacts on agriculture (e.g., pest control, crop damage), the net effects of such activities are rarely quantified. This could be attributed to the complexity of measuring direct and indirect trophic interactions, and the necessity of cross-disciplinary collaboration to value biophysical outcomes in economic and other relevant terms. We suggest that the direction and magnitude of net effects is driven by biotic, farm-level and landscape factors. These factors, some within and others beyond farmer control, interact in potentially predictable ways. We propose a framework for making policy decisions about farming practices and land-use planning informed by net effects to help farmers and society achieve positive outcomes for biodiversity and agricultural production.*

*Keywords: ecosystem services and disservices, farmland birds, nature's contributions to people, sustainable agriculture, trophic interactions*

**E**cosystem services and disservices are aspects of the natural world that have positive or negative effects on human well-being (Shapiro and Baldi 2014). Considering both ecosystem services and disservices, or nature's contributions to people, is critical to achieving conservation and livelihood goals (Dunn 2010, Schaubroeck 2017, Diaz et al. 2018). Therefore, land-use policy and practice should explicitly incorporate both the benefits and the costs of biodiversity to recipients (Zhang et al. 2007), while also acknowledging that this balance will be highly context dependent (Saunders and Luck 2016).

Adopting a decision-making framework that integrates services and disservices is particularly appropriate for the large proportion of all bird species globally that use agricultural habitats (Sekercioglu et al. 2016). Despite the diverse functions they provide, the costs incurred and benefits conferred by birds are rarely quantified and incorporated into agricultural practice and policy (Whelan et al. 2015). However, advancing understanding of the role of birds and other biota in agroecosystems could help conserve biodiversity and meet the needs of a human population growing in size and wealth (Triplett et al. 2012).

Birds matter to science and society because they can induce strong cascading effects on vertebrates (Kross et al. 2012), herbivorous insects, and plants (Mäntylä et al. 2011), thereby providing important services such as pest control (Karp et al. 2013), seed dispersal, and pollination (Sekercioglu et al. 2016). Through bird watching and hunting, birds also provide

a substantial source of revenue, pleasure, mental health, and subsistence to landowners and communities (e.g., Belaire et al. 2015, Cox et al. 2017). However, birds can also be the source of ecosystem disservices. Many species inflict damage directly through granivory or frugivory (Schäckeremann et al. 2014), or indirectly by consuming natural enemies of pests (intraguild predation; Martin et al. 2013), with economic costs for producers. There is also increasing concern about birds transmitting food-borne diseases (Carlson et al. 2011), which has led some farmers to reduce bird habitat and bird access to farms (Karp et al. 2015). Other byproducts of bird habitat use, such as nutrient deposition, and the predation or dispersal of weed seeds, could either enrich or degrade agricultural systems (Gillespie and Wratten 2017).

Understanding the net outcomes of bird-mediated services and disservices ("net effects") for landowners and communities could help them design and manage agroecosystems to improve habitat for biodiversity while also increasing the net positive flow of bird-mediated services to farmers and society (Ekroos et al. 2014; figure 1). The appreciation of net effects may differ in magnitude and direction depending on the recipient group, because some services contribute to private goods (pest control) or costs (crop damage) and others to public goods (bird watching) or negative externalities (zoonoses). Measuring and acknowledging net effects is therefore important for avoiding policies and management interventions that deliberately or inadvertently ignore bird activities and therefore increase one service at the expense of others,



**Figure 1.** Birds provide ecosystem services such as pest and weed control (a and c) and disservices such as intraguild predation and crop damage (b and d) in agroecosystems. This panel of images illustrates (a) an Eurasian hoopoe (*Upupa epops*) carrying a mole cricket, a potential crop pest; (b) an eastern bluebird (*Sialia sialis*) with a spider, demonstrating intraguild predation; (c) a twite (*Carduelis flavirostris*) feeding on weed seeds; and (d) a juvenile Lewis's woodpecker (*Melanerpes lewis*) consuming an apple and causing crop damage. Photographs: (a) Matthias Tschumi, (b) Brian Lasenby/Shutterstock.com, (c) Pettery Hytönen, and (d) Megan Miller.

or even escalate disservices (Bennett et al. 2009). Excluding birds from apple orchards may, for example, protect apples damaged by birds. However, without additional chemical inputs, excluding birds may also increase apple damage by pest insects, likely resulting in a net cost to orchard growers, as well as the loss of bird habitat (Peisley et al. 2016).

Understanding net effects could also be critical for increasing resilience to climate change. Climate change is expected to result in shifts in the composition of biotic communities, which could significantly alter the structure or function of agroecosystems (Civantos et al. 2012). Bird, insect and plant abundance or distribution may change as a direct response to altered temperature or precipitation, or indirectly because of land-use changes as farmers adapt to new climate conditions. For example, future crops may be differentially vulnerable to bird damage, or the pest pressure that birds help reduce may change. Without understanding net effects of birds in today's human-dominated systems, it will be difficult to predict whether and under what circumstances future climate change

could tip net positive to net negative (or vice versa) outcomes for producers (Rasmussen et al. 2017). Advancing understanding of net effects under current and changing conditions could help identify interventions that could increase resilience to global change.

Despite their potential importance, net effects of birds in agriculture are rarely measured, and few practices and policies explicitly incorporate services and disservices into land-use decisions (Sekercioglu et al. 2016). Of a recent review of all studies that measured the costs or benefits of bird activity on crop yield, only five investigated both in the same agroecosystem (Peisley et al. 2015). More often, studies were geographically and temporally segregated, with those in north temperate regions mostly assessing costs, and those in equatorial regions mostly evaluating benefits. Studies in perennial crops appear more likely to report net benefits from bird activity. For example, Borkhataria and colleagues (2006) and Karp and Daily (2014) both found that birds in coffee farms have positive effects on pest control; birds reduce pests and don't interfere with top-down control by arthropod predators. Similarly, birds in apple orchards inflict little direct damage (Mangan et al. 2017) and can provide pest control services with net benefits to producers (Peisley et al. 2016). In contrast, studies of bird activity in annual crops have shown mixed results, with net effects tending to

be neutral or negative. For example, red-winged blackbirds both damage rice and provide pest control (Borkhataria et al. 2012), with no significant effect on yield, and bird predation in wheat and oats disrupted pest control by mesopredators (spiders), with potential net negative effects for producers (Grass et al. 2017).

In this synthesis, we focus on birds and their trophic interactions to (a) offer reasons why net effects are rarely measured, and (b) summarize the diverse and interacting factors that could influence the provision of bird-mediated services and disservices. We then (c) propose a research agenda for net effects research, outline a framework for policy and practice, and (d) highlight emerging tools that could provide new insights into bird-mediated services and disservices in agroecosystems. Finally, we discuss the promise and limitations of the net effects approach for implementing policies and practices to support birds and the services they provide. Our intention is not to provide a comprehensive synthesis of the large body of literature on the trophic effects of birds

in agroecosystems (e.g., Tscharrntke et al. 2008). Rather, we hope to stimulate discussion of the compelling reasons for, and associated challenges with, advancing the science and practice of managing farms, landscapes and bird communities through the lens of net effects.

### Why are net effects rarely measured?

Disservices are often direct effects of bird activity, whereas services are often indirect. Measuring the net effects of bird activity almost always demands an understanding of the nature and magnitude of interspecific interactions across three or more trophic levels (e.g., crop, pest, bird; Kross et al. 2012). Bird activities that affect crops directly usually result in disservices, which are readily observed and more likely to be quantified in biophysical and economic terms relative to services (Shapiro and Baldi 2014, Peisley et al. 2015, Buij et al. 2017). However, most services and some disservices are indirect, and therefore more likely to be overlooked. For example, reduction of crop damage by consumption of crop pests, or disruption of pest control through intraguild predation cannot be observed directly (Martin et al. 2013).

Stakeholders tend to focus on either services or disservices. For example, while producers and agricultural scientists tend to focus on identifying and mitigating crop damage by birds, conservation biologists often seek win-win situations—that is, cases in which birds provide benefits to producers and the producers provide habitat for birds. Both approaches have value but can be problematic in isolation (Saunders et al. 2016). Conservation biologists may be more likely to publish success stories or to select study systems in which high biodiversity is a priori harbored and in which birds are more likely to provide benefits (e.g., shade grown coffee). In contrast, producer perceptions of crop damage by birds are often greater than the actual loss (Luck 2013), and the presence of birds does not necessarily result in measurable impacts on crop yield (Borkhataria et al. 2012, Lindell et al. 2012).

Furthermore, measuring net effects requires a multidisciplinary approach. To assess the effects of bird activity in terms meaningful to producers and society, it is often useful to translate biophysical metrics (e.g., the disservice of the percentage of crop damaged or the service of damage avoided by pest control by birds) into economic terms. These values can then be compared with the cost of mitigating disservices (e.g., netting) or replacement cost of services (e.g., chemical pesticides) using ecological-economic modeling to consider all services and disservices as well as potential substitute inputs (Wätzold et al. 2006). However, some services such as human health benefits from reduced use of pesticides, and many cultural values, might be better assessed in non-economic terms (Diaz et al. 2018). To fully assess the effect of bird activity on stakeholders at local, national and global scales, ecological investigators may need to work collaboratively with their agronomist, economist and social science colleagues to assess both market and nonmarket values. For example, similar bird communities could be predominantly associated with either services or disservices depending on

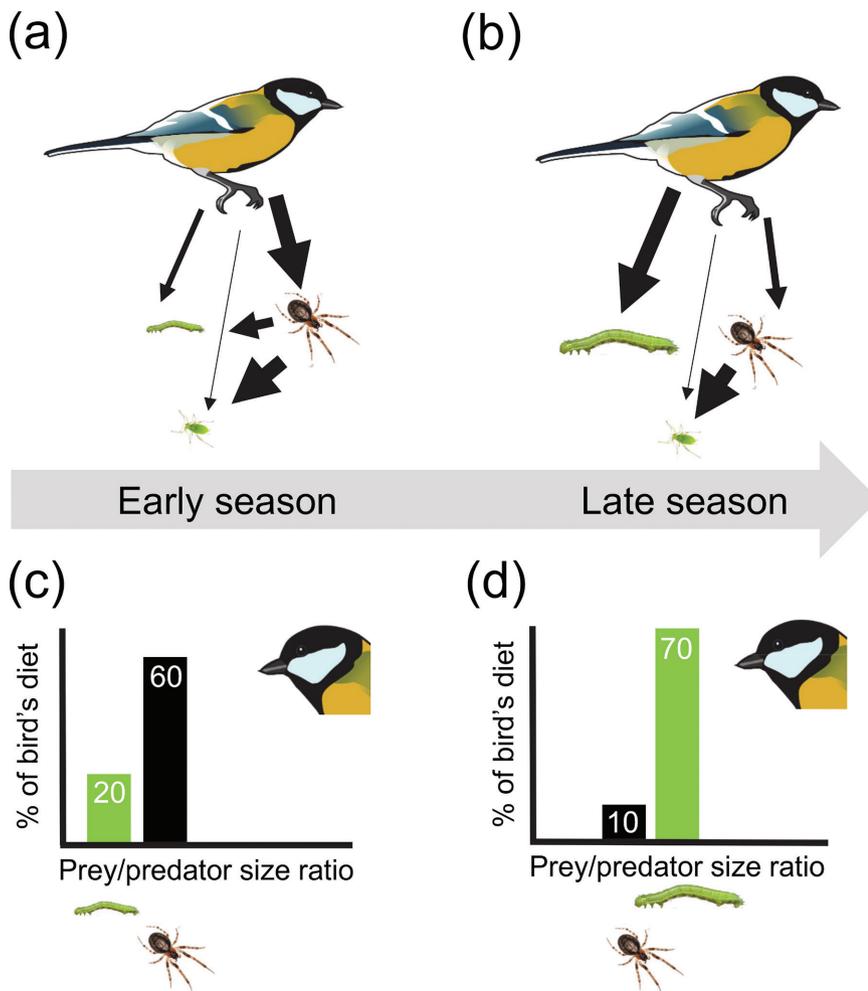
farmers' perceptions, which are partly linked to the farming system (Kross et al. 2018). Furthermore, the scale of economic analysis must be made explicit (e.g., to distinguish among net effects to producers and the welfare of consumers; Hein 2009, Hanley et al. 2015).

The benefits and costs of birds in agroecosystems may also accrue differently across time and space. For example birds may provide net costs during the breeding season in one region (e.g., crop damage during the growing season), and then net benefits (e.g., weed control post harvest) during migration, posing management challenges. Similarly, birds that provide ecosystem services or disservices locally may, because they are mobile, also affect ecosystem services on neighboring properties and beyond. Finally, although small-scale experiments are often used to evaluate net effects (e.g., exclosures), scaling up local effects to farm or landscape levels is crucial for policy and management interventions, but this requires making assumptions that are frequently untested (Muiruri et al. 2016).

### Characteristics that influence net effects across scales

In a given agroecosystem, native plants, crops grown, the traits of the dominant arthropods associated with each crop, and the bird community could all influence net effects (Isaac et al. 2009). Bird body size is a central trait in food webs (Woodward et al. 2005), with predators generally favoring prey of a certain size relative to themselves (Brose et al. 2008). Because of higher metabolic rates relative to body size, the decline of common small European birds is expected to result in a disproportionate loss of pest control services (Inger et al. 2015). This trait and others could therefore be used to predict the strength of interactions among species (Schneider et al. 2012), the net effect of birds on pests, and thereby on crop production.

As an illustration, in systems in which herbivorous insects escape predation by birds because of their small size (e.g., aphids), songbird predation on larger arthropod predators (e.g., spiders) may lead to a predictable and consistent negative indirect effect (i.e., more crop pests). In contrast, the same bird community may be beneficial in another system in which average pest size is larger (e.g., caterpillars in orchards). These effects could also change in predictable but context-dependent ways. For example, Great Tits switch from predating on spiders to predating on caterpillars when these reach a certain size (Naef-Daenzer et al. 2000; figure 2). However, predictability may be limited where crops are affected by a range of pests that fluctuate in relative importance over time (e.g., Maas et al. 2013, Gras et al. 2016), and these relationships could be mediated by other traits such as palatability of the mesopredators, camouflage, and warning coloration in the pests (Philpott et al. 2009, Lichter-Marck et al. 2015). Many ecosystem services provided by birds are a function of their foraging behavior (Sekercioglu et al. 2016). Particularly during the breeding season, birds are central-place foragers that depend on landscapes containing



**Figure 2.** Net effects of birds can be context dependent, as is illustrated in the present figure with temporal changes in trophic interactions. Great tits (*Parus major*) predate on spiders (mesopredators of pest caterpillars) early in the season until caterpillars become large (a, b; Naef-Daenzer et al. 2000). In this case, small prey items (herbivorous pests such as early stage caterpillars, aphids) are a small part of the diet as shown by the thin arrow (a, b), despite high abundances. Therefore, the role of the bird as an ecosystem service provider can be dependent on the relative size and abundance of prey and mesopredators (c, d). Images: the spider image *Zygiella x-notata* is based on a photograph by F. Geller Grimm, CC BY-SA 3.0; the bird image is based on public domain artwork by pegasa, openclipart.org; the aphid and caterpillar are by Y. Clough.

nest sites, roosting sites and foraging habitats (Ydenberg 2007), all of which could affect how management practices in agricultural landscapes alter ecosystem services provided by birds. Pest control is generally higher in landscapes with higher native habitat cover, greater habitat heterogeneity, and in agricultural patches in close proximity to native habitats (Boesing et al. 2017; figure 3). However, complex landscapes can also increase the importance of mesopredators, which serve as natural enemies to insect pests (Landis et al. 2000), and birds can disrupt pest control through predation (Martin et al. 2013, Tscharrntke et al. 2016).

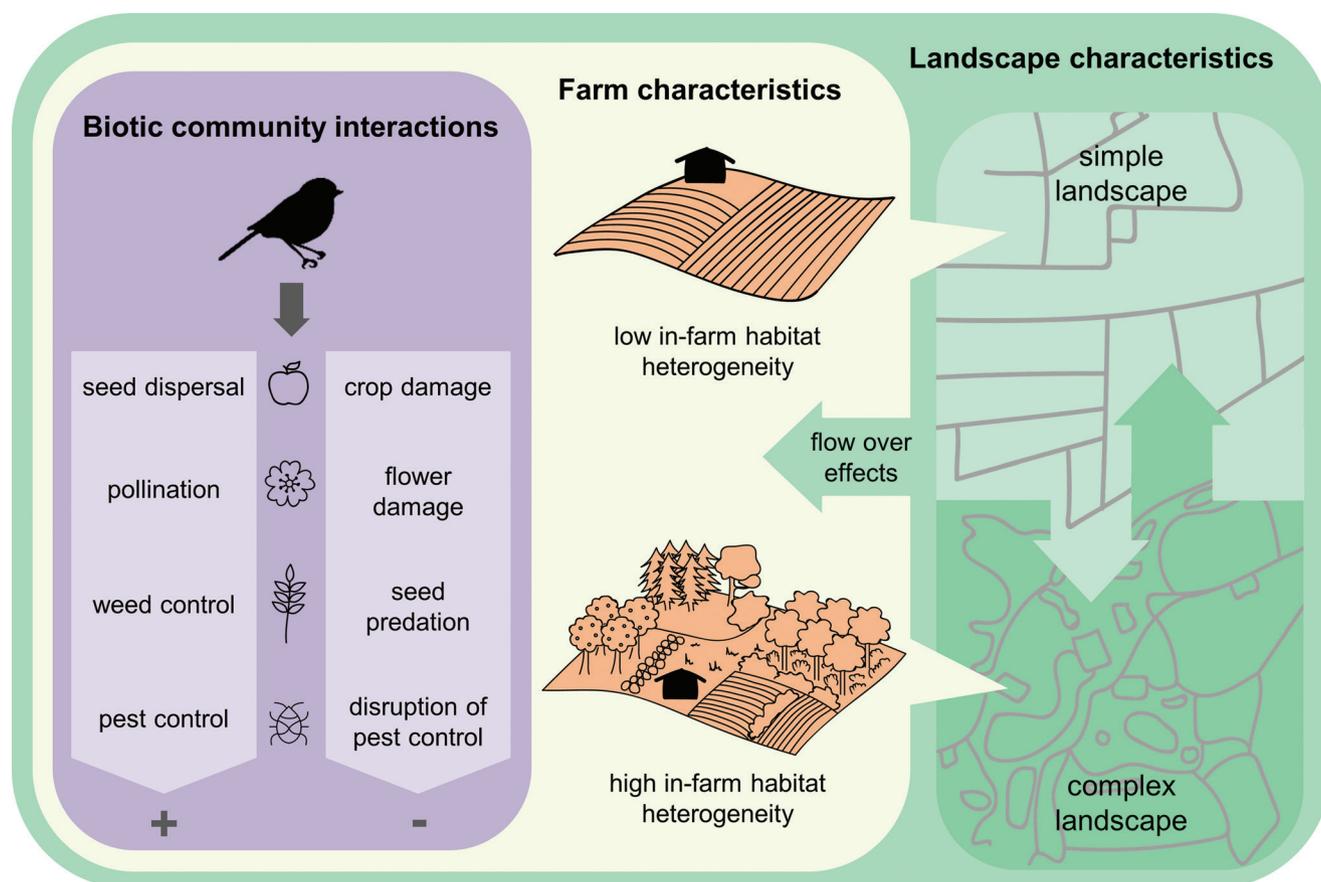
nesting birds with generalist diets (e.g., corvids; McGowan 2001) are more likely to be subject to net negative effects, because large aggregations of these urban birds may spillover into agricultural areas and cause crop damage (Pereira-Peixoto et al. 2014). These scenarios would lead to net negative effects if the costs associated with crop damage outweigh any indirect benefits of pest control by these generalist birds.

In contrast, we predict that farms embedded in a mosaic of remnant natural habitat that support diverse bird and arthropod communities will be associated with net positive effects of bird activity. Natural habitat in and adjacent

The landscape-moderated biodiversity versus ecosystem service management hypothesis (Tscharrntke et al. 2012) predicts that fragmented landscapes are more likely to optimize movement of habitat generalists from natural habitats to agriculture (Boesing et al. 2018), enhancing ecosystem services. However, habitat specialists (often of conservation concern) tend to thrive in landscapes with contiguous and high quality natural habitat (Smith et al. 2014), which suggests there may be fundamental trade-offs in achieving positive net effects from bird activities, and protecting habitat for sensitive species (figure 4). Because many of these hypotheses have yet to be tested in diverse ecoregions, we argue that in addition to documenting the effects of farm-scale practices on biodiversity-mediated ecosystem services, research should be focused on landscape-moderated effects on birds.

#### Predictions and questions to advance science and practice

Given current knowledge of bird-mediated ecosystem services in agriculture, we predict the following factors will be associated with net positive or negative effects of bird activity on individual farms. We expect that net negative effects are more likely on farms embedded in simple landscapes so transformed by intensive agriculture that bird species and functional diversity is extremely low. These landscapes may be more susceptible to midsize to large generalists that can travel far and in large flocks to feed opportunistically on seeds, seedlings or fruits, because granivores more readily thrive in intensive agriculture relative to insectivores (Frishkoff et al. 2014). Similarly, we expect that farms within reach of large urban centers that host high densities of



**Figure 3.** The net effects of bird-mediated services and disservices depend on the abundance of key species and on the structure of bird assemblages. Biotic communities, embedded in farms and landscapes, are affected by practices and interventions at the level of individual farms, but also on the properties of surrounding landscapes, which provide resources for birds foraging at large spatial scales. These large-scale processes will have spillover effects that are less readily managed on the scale of individual farms.

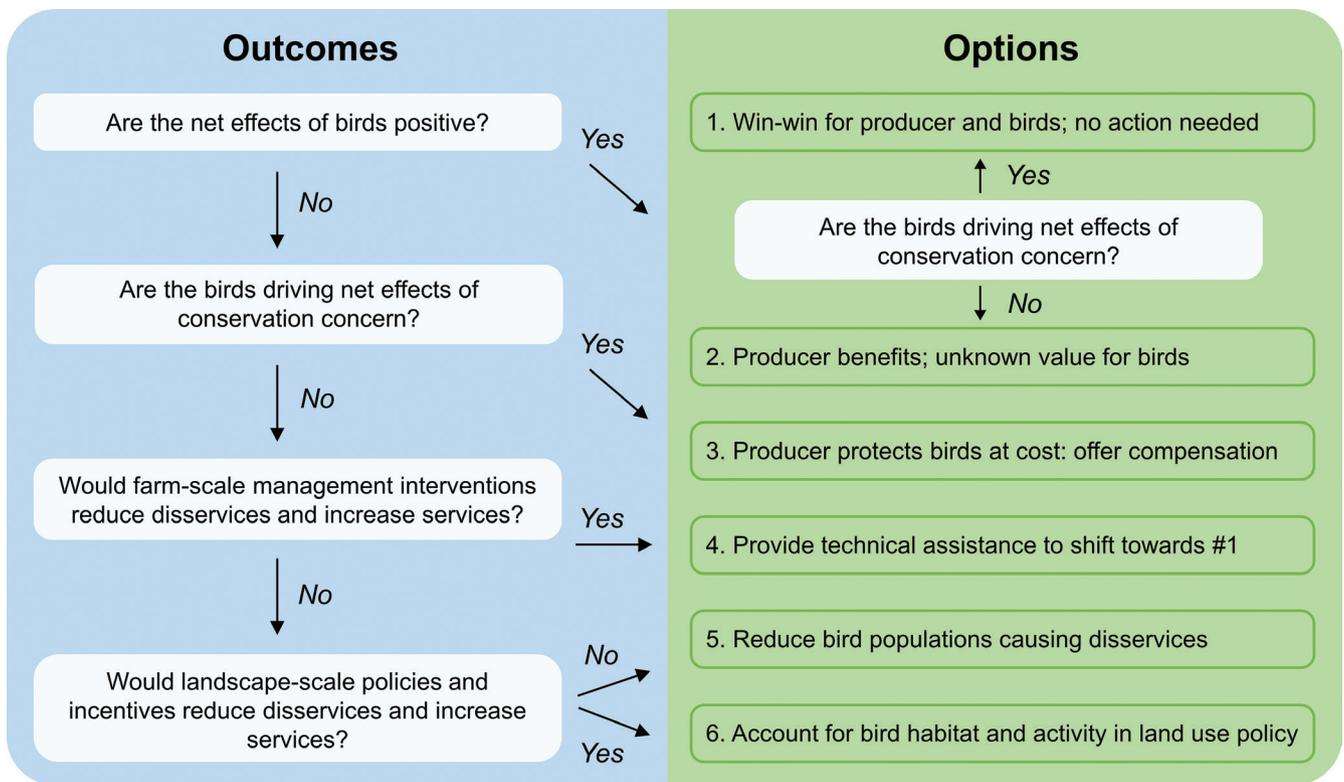
to crops can attract avian insectivores that consume crop pests. Therefore, we expect farms with natural habitat to experience net positive effects of bird activity if crops harbor sufficiently high densities of pest prey such that there is a higher probability of bird predation on pest rather than beneficial arthropods and if natural habitat provides shelter and nesting sites for insectivorous birds, and harbors fewer insect pests than adjacent croplands do. However, in some cases birds can also detract from pest control through suppressing intraguild predation and natural habitat can also harbor crop pests (Tschardt et al. 2016). Furthermore, net positive effects of bird activity in heterogeneous farms and landscapes may in some cases be dependent on whether trees near or within crop fields serve as crucial breeding or roosting habitat for granivorous birds that depredate crop seeds (Schäcker mann et al. 2014).

In light of our predictions that local and large-scale biota, habitat complexity, and landscape context will influence net effects (figure 3), clarifying which factors are within and beyond the control of individual producers will be critical to determining practices and policies that

benefit biodiversity and production. We suggest that the following factors are within at least partial control of individual producers: within-farm habitat heterogeneity, crop type and diversity, the level of inputs used to substitute for bird-mediated ecosystem services (e.g., pesticides), and the actions taken to exclude (nets) or enhance (nest boxes, hedges) local bird populations (Jedlicka et al. 2011).

In contrast, individual producers have little or no short-term control over the following factors, each of which also could play a strong role in shaping bird communities and determining the net effects of birds to farmers and society: landscape composition, configuration and connectivity (e.g., proportion of natural habitat or urban sprawl), the average farm size, spillover effects from the actions of neighboring farms, and the nature and amount of external subsidies provided to enhance or mitigate biodiversity driven services and disservices (e.g., pesticides versus vegetated buffers; cf. Prager et al. 2012).

Given these predictions, we suggest that the net effects research agenda should include the following critical questions: First, at what threshold of complexity do landscapes



**Figure 4.** Strategic policies and management recommendations for managing biodiversity in agroecosystems rely on understanding the direction and magnitude of net effects, the subset of the bird community driving services and disservices, and the farm and landscape level characteristics that influence bird habitat use and activity. This decision framework could help guide policymakers and managers seeking to conserve birds of conservation concern while also increasing the flow of bird-mediated services to producers.

become sufficiently “simple” to experience net disservices from birds? Second, at what distance from urban centers are farms released from disservices associated with the potential spillover effects of human-adapted species that cause crop damage? Third, are there predictable circumstances (crop type, climate, proximity to and extent of natural habitat) under which the bird-mediated benefits of embedded natural habitat (e.g., pest control) exceed the potential costs (e.g., crop damage and land loss to production)? Fourth, can functional traits of predators and prey, and changes in their relative abundance within season (figure 2), be used to predict patterns of pest-suppression by bird communities across ecosystems? Fifth, what is the functional relationship between the relative abundance of bird species, services and disservices (Gaston et al. 2018) in agroecosystems, and what thresholds are optimal for sustaining diverse human-sensitive bird communities and achieving net benefits for producers? Finally, to what extent can bird-mediated services and disservices to crop production be managed at the farm level, and alternatively, when is farmer collaboration or agricultural policies critical to achieving positive outcomes?

Given the objective of improving conditions for biodiversity, and the welfare of individual producers and society, we propose a net effects decision-making framework. This framework offers pathways for evidence-based decisions that also account for the factors within and beyond the control of single producers (figure 4). For example, if the net effects of birds in an agroecosystem are positive and those species are also of conservation concern, then this outcome represents a win–win outcome for conservation and production and no action may be warranted. However, if net effects are negative and birds causing damage are of conservation priority, then producers are providing bird habitat at a cost and could be compensated to continue to provide this service. We suggest that through individual and collective action both producers and society have a strong role to play in applying the outcomes of net effects studies to land-use policy and practice.

#### The net effects toolbox

We highlight two of many existing and emerging tools for advancing a net effects research agenda. First, because the relationship between crop production, natural habitat and the

delivery of ecosystem services and disservices by birds is complex, simulation models informed by well-designed experiments in real systems could be an important tool for testing alternative predictions. For example, Railsback and Johnson (2014) used a spatial simulation model calibrated to field observations to evaluate how bird-mediated pest control affects the outcomes of land-sparing and land-sharing approaches to coffee production and bird conservation in Jamaica. They show that because of bird pest control, coffee farms with shade trees were more likely to benefit birds and coffee than were spatially segregating sun coffee and forest. Such modeling exercises can also identify important gaps in understanding to focus empirical research (e.g., where birds that consume pests roost and how far they will travel from roosting sites to forage in farm fields; Railsback and Johnson 2014).

The field of genomics also offers increasingly sophisticated tools for addressing net effects questions. By characterizing the diets of entire bird communities in agroecosystems, individual bird species can be classified as pest predators, pests, or both. Advances in DNA sequencing of gut contents or feces are being applied to identify which species provide pest control services or act as pests themselves (e.g., Jedlicka et al. 2013, Karp et al. 2014). Once producers know which bird species are beneficial, which are detrimental, and which can be both (depending on context), more species-specific management programs could be developed.

We emphasize that well-designed ecological field studies on net effects in diverse contexts are also warranted, and will be critical to the effective use of simulation modeling and genomics. Together with socioecological research, field studies, DNA barcoding, and modeling approaches are all promising pathways for producing new insights to guide science, practice and policy that incorporates net effects.

## Conclusions

We may have been quick to measure disservices in the past (Shapiro and Baldi 2014), but overemphasizing services (Schaubroeck 2017) is equally unproductive for gaining trust and credibility with the agricultural community, and will not ultimately meet the goal of sustaining both biodiversity and human well-being. Using a net effects approach, there may be opportunities to simultaneously reduce disservices, enhance services and conserve biodiversity, with the objective of sustaining current and future human well-being within ecological limits. Informed by net effects, evidence-based policies and practices could be applied at the farm or landscape scale (Landis 2017; figure 4).

We note, however, that practices and policies adopted in response to bird-mediated net effects could conflict with services provided by other groups of species, or conservation of those groups, or exacerbate disservices. For example, adding natural habitat (e.g., trees and shrubs) within or adjacent to crops could enhance habitat for birds that provide pest control services, but could also provide nesting or roosting habitat for granivores and frugivores that depredate crop

seeds and fruits. Furthermore, in some contexts growing crops in close proximity to natural habitat increases the risk of crop damage and risk to human health from mammals such as wild pigs and primates (Hill 1997). Considering the net effects of multiple taxa is not trivial but may be critical, especially when there is reason to believe that a group provides a strong service or disservice, or that management interventions for one group will negatively affect another.

Although measuring net effects could reveal undiscovered synergies between conservation, production and human well-being, in other cases there may not be obvious win-win outcomes. Practices that benefit birds providing services and reduce the abundance of birds causing damage may not always be compatible with conservation objectives. The majority of bird-mediated services, for example, may be provided by only a small subset of relatively common bird species (Ekroos et al. 2014). In contexts in which policies to ensure bird conservation result in unavoidable net negative effects on producers, schemes to compensate landowners for crops lost in service to society may be warranted.

We anticipate a fundamental change in how we value bird-mediated services and disservices in a future in which clean air and water become increasingly scarce (Schewe et al. 2014). If pesticide use becomes more regulated or if the costs of externalities associated with pesticide and herbicide use are incorporated into their market prices (e.g., through pesticide taxes), natural pest and weed control may necessarily become an integral part of farm-level management and landscape scale policies. Wherever feasible, this approach of considering both positive and negative effects of biodiversity on human well-being should be incorporated into science and practice. During an era marked by increased division between scientists and society, net effects is a transparent and balanced approach to evidence-based decision-making, and an important first step in bringing conservationists and producers into productive dialogue.

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## References cited

- Belaire JA, Westphal LM, Whelan CJ, Minor ES. 2015. Urban resident's perceptions of birds in the neighborhood: Biodiversity, cultural ecosystem services, and disservices. *Condor* 117: 192–202.
- Bennett EM, Peterson GD, Gordon LJ. 2009. Understanding relationships between multiple ecosystem services. *Ecology Letters* 12: 1394–1404.
- Boeing AL, Nichols E, Metzger JP. 2017. Effects of landscape structure on avian-mediated insect pest control services: A review. *Landscape Ecology* 32: 931–944.

- Boesing AL, Nichols E, Metzger JP. 2018. Land use type, forest cover, and forest edges modulate avian cross-habitat spillover. *Journal of Applied Ecology* 55: 1252–1264.
- Borkhataria RR, Collazo J, Groom MJ. 2006. Additive effects of vertebrate predators on insects in a Puerto Rican coffee plantation. *Ecological Applications* 16: 696–703.
- Borkhataria RR, Nuessly GS, Pearlstone E, Cherry RH. 2012. Effects of black-birds (*Agelaius phoeniceus*) on stink bug (Hemiptera: Pentatomidae) populations, damage, and yield in Florida rice. *Florida Entomologist* 95: 143–149.
- Brose U, Ehnes RB, Rall RC, Vucic-Pestic O, Berlow EL, Scheu S. 2008. Foraging theory predicts predator–prey energy fluxes. *Journal of Animal Ecology* 77: 1072–1078.
- Buij R, Melman TCP, Loonen MJ, Fox AD. 2017. Balancing ecosystem function, services and disservices resulting from expanding goose populations. *Ambio* 46: 301–318.
- Carlson JC, Franklin AB, Hyatt DR, Pettit SE, Linz GM. 2011. The role of starlings in the spread of *Salmonella* within concentrated animal feeding operations. *Journal of Animal Ecology* 48: 479–486.
- Civantos E, Thuiller W, Maiorano L, Guisan A, Araujo MB. 2012. Potential impacts of climate change on ecosystem services in Europe: The case of pest control by vertebrates. *BioScience* 62: 658–666.
- Cox LTC, Shanahan DF, Hudson HL, Plummer KE, Siriwardena CM, Fuller RA, Anderson K, Hancock S, Gaston KJ. 2017. Doses of neighborhood nature: The benefits for mental health of living with nature. *BioScience* 67: 147–155.
- Diaz S, et al. 2018. Assessing nature's contributions to people. *Science* 359: 270–272.
- Dunn RR. 2010. Global mapping of ecosystem disservices: The unspoken reality that nature sometimes kills us. *Biotropica* 42: 555–557.
- Frishkoff LO, Karp DS, M'Gonigle LK, Mendenhall CD, Zook J, Kremen C, Hadly EA, Daily GC. 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. *Science* 12: 1343–1346.
- Ekroos J, Olsson O, Rundlöf M, Wätzold F, Smith HG. 2014. Optimizing agri-environment schemes for biodiversity, ecosystem services or both? *Biological Conservation* 172: 65–71.
- Gaston KJ, Cox DTC, Canavelli SB, Garcia D, Hughes B, Maas B, Martinez D, Ogada D, Inger R. 2018. Population abundance and ecosystem service provision: The case of birds. *BioScience* 68: 264–272.
- Gillespie MAK, Wratten SD. 2017. The Role of ecosystem disservices in pest management. Pages 175–194 in Coll M, Wajnberg E (eds). *Environmental Pest Management: Challenges for Agronomists, Ecologists, Economists, and Policymakers*. Wiley.
- Gras P, Tschardt T, Maas B, Tjoa A, Hafsa A, Clough Y. 2016. How ants, birds and bats affect crop yield along shade gradients in tropical cacao agroforestry. *Journal of Applied Ecology* 53: 953–963.
- Grass I, Lehmann K, Thies C, Tschardt T. 2017. Insectivorous birds disrupt biological control of cereal aphids. *Ecology* 98: 1583–1590.
- Hanley N, Breeze TD, Ellis C, Goulson D. 2015. Measuring the economic value of pollination services: Principles, evidence and knowledge gaps. *Ecosystem Services* 14: 124–132.
- Hein L. 2009. The economic value of the pollination service, a review across scales. *The Open Ecology Journal* 2: 74–82.
- Hill CM. 1997. Crop-raiding by wild vertebrates: The farmer's perspective in an agricultural community in western Uganda. *International Journal of Pest Management* 43: 77–84.
- Inger R, Gregory R, Duffy JP, Stott I, Vorisek P, Gaston KJ. 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecology Letters* 18: 28–36.
- Isaac, R, Tuell J, Fiedler A, Gardiner M, Landis D. 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: The role of native plants. *Frontiers in Ecology and the Environment* 7: 196–203.
- Jedlicka JA, Greenberg R, Letourneau DK. 2011. Avian conservation practices strengthen ecosystem services in California vineyards. *PLOS ONE* 6 (art. e27347).
- Jedlicka JA, Sharma AM, Almeida, RPP. 2013. Molecular tools reveal diets of insectivorous birds from predator fecal matter. *Conservation Genetics Resources* 5: 879–885
- Karp DS, Mendenhall CD, Figueroa Sandi R, Chaumont N, Ehrlich PR, Hadly EA, Daily GC. 2013. Forest bolsters bird abundance, pest control and coffee yield. *Ecology Letters* 16: 1339–1347.
- Karp DS, Daily GC. 2014. Cascading effects of insectivorous birds and bats in tropical coffee plantations. *Ecology* 95: 1065–1074
- Karp DS, Judson S, Daily, GC, Hadly EA. 2014. Molecular diagnosis of bird-mediated pest consumption in tropical farmland. *Springerplus* 3: 1–8.
- Karp DS, Baur P, Atwill ER, Master KDE, Gennet S, Iles A, Nelson JL, Sciligo AR, Kremen C. 2015. The unintended ecological and social impacts of food safety regulations in California's Central Coast region. *BioScience* 65: 1173–1183.
- Kross SM, Tylianakis JM, Nelson XJ. 2012. Effects of introducing threatened falcons into vineyards on abundance of Passeriformes and bird damage to grapes. *Conservation Biology* 6: 142–149.
- Kross, SM, Ingram KP, Long, RF, Niles, MT. 2018. Farmer perceptions and behaviors related to wildlife and on-farm conservation actions. *Conservation Letters* 11: e12364.
- Landis DA, Warren SD, Gurr GM. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual review of entomology* 45: 175–201.
- Landis DA. 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology* 18: 1–12.
- Lichter-Marck IH, Wylde M, Aaron E, Oliver JC, Singer MS. 2015. The struggle for safety: Effectiveness of caterpillar defenses against bird predation. *Oikos* 124: 525–533.
- Lindell CA, Eaton RA, Lizotte EM, Rothwell NL. 2012. Bird consumption of sweet and tart cherries. *Human-wildlife Interactions* 6: 283–290.
- Luck GW. 2013. The net return from animal activity in agro-ecosystems: Trading off benefits from ecosystem services against costs from crop damage. *F1000 Research* 2: 239.
- Maas B, Clough Y, Tschardt T. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecology Letters* 16: 1480–1487.
- Mangan AM, Pejchar L, Werner S. 2017. Bird use of organic apple orchards in Colorado: Frugivory, pest control and implications for production. *PLOS ONE* 12 (art. e0183405).
- Mäntylä E, Klemola T, Laaksonen T. 2011. Birds help plants: A meta-analysis of top-down trophic cascades caused by avian predators. *Oecologia* 165: 143–151.
- Martin EA, Reineking B, Seo B, Steffan-Dewenter I. 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences* 110: 5534–5539.
- McGowan KJ. 2001. Demographic and behavioral comparisons of suburban and rural American Crows. Pages 365–381 in Marzluff JM, Bowman R, Donnelly R (eds.). *Avian Ecology and Conservation in an Urbanizing World*. Springer.
- Muiruri EW, Rainio K, Koricheva J. 2016. Do birds see the forest for the trees? Scale-dependent effects of tree diversity on avian predation of artificial larvae. *Oecologia* 180: 619–630.
- Naef-Daenzer L, Naef-Daenzer B, Nager RG. 2000. Prey selection and foraging performance of breeding Great Tits *Parus major* in relation to food availability. *Journal of Avian Biology* 31: 206–214.
- Peisley RK, Saunders ME, Luck GW. 2015. A systematic review of the benefits and costs of bird and insect activity in agroecosystems. *Springer Science Reviews* 3: 113–125.
- Peisley RK, Saunders ME, Luck GW. 2016. Cost-benefit trade-offs of bird activity in apple orchards. *PeerJ* 4: e2179.
- Pereira-Peixoto MH, Pufal G, Martins CF, Klein AM. 2014. Spillover of trap-nesting bees and wasps in an urban–rural interface. *Journal of insect conservation* 18: 815–826.
- Philpott SM., Soong O, Lowenstein JH, Pulido AL, Lopez DT, Flynn DF, DeClerck F. 2009. Functional richness and ecosystem services: Bird predation on arthropods in tropical agroecosystems. *Ecological Applications* 19: 1858–1867.

- Prager K, Reed M, Scott A. 2012. Encouraging collaboration for the provision of ecosystem services at a landscape scale: Rethinking agri-environmental payments. *Land Use Policy* 29: 244–249.
- Railsback SF, Johnson MD. 2014. Effects of land use on bird populations and pest control services on coffee farms. *Proceedings of the National Academy of Sciences* 111: 6109–6114.
- Rasmussen LV, Christensen AE, Danielsen F, Dawson N, Martin A, Mertz O, Sikor T, Thongmanivong S, Xaydongvanh P. 2017. From food to pest: Conversion factors determine switches between ecosystem services and disservices. *Ambio* 46: 173–183.
- Saunders ME, Luck GW. 2016. Limitations of the ecosystem services versus disservices dichotomy. *Conservation Biology* 30: 1363–1365.
- Saunders ME, Peisley RK, Rader R, Luck GW. 2016. Pollinators, pests, and predators: Recognizing ecological trade-offs in agroecosystems. *Ambio* 45: 4–14.
- Schäckermann J, Weiss N, Von Wehredren H, Klein AM. 2014. High trees increase sunflower seed predation by birds in an agricultural landscape of Israel. *Frontiers in Ecology and Evolution* 2: 35.
- Schaubroeck T. 2017. A need for equal consideration of ecosystem disservices and services when valuing nature: Countering arguments against disservices. *Ecosystem Services* 26: 95–97.
- Schewe J, et al. 2014. Multimodel assessment of water scarcity under climate change. *Proceedings of the National Academy of Sciences* 111: 3245–3250.
- Schneider FD, Scheu S, Brose U. 2012. Body mass constraints on feeding rates determine the consequences of predator loss. *Ecology Letters* 15: 436–443.
- Sekercioglu C, Wenny DG, Whelan CJ, eds. 2016. *Why Birds Matter*. University of Chicago Press.
- Shapiro J, Baldi A. 2014. Accurate accounting: How to balance ecosystem services and disservices. *Ecosystem Services* 7: 201–202.
- Smith HG, Birkhofer K, Clough Y, Ekroos J, Olsson O, Rundlof M. 2014. Beyond dispersal: The role of animal movement in modern agricultural landscapes. Pages 51–70 in Hansson L-A, Åkesson S, (eds). *Animal Movement across Scales*. Oxford University Press.
- Triplett S, Luck GW, Spooner P. 2012. The importance of managing the costs and benefits of bird activity for agricultural sustainability. *International Journal of Agricultural Sustainability* 10: 268–288.
- Tscharntke T, Sekercioglu CH, Dietsch TV, Sodhi, NS, Hoehn P, Tylianakis JM. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* 89: 944–951.
- Tscharntke T, et al. 2012. Landscape moderation of biodiversity patterns and processes: Eight hypotheses. *Biological Reviews* 87: 661–685.
- Tscharntke T, et al. 2016. When natural habitat fails to enhance biological pest control: Five hypotheses. *Biological Conservation* 204: 449–458.
- Wätzold F, et al. 2006. Ecological-economic modeling for biodiversity management: Potential, pitfalls, and prospects. *Conservation Biology* 20: 1034–1041.
- Whelan CJ, Sekercioglu, CH, Wenny DG. 2015. Why birds matter: From economic ornithology to ecosystem services. *Journal of Ornithology* 156: 227–238.
- Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH. 2005. Body size in ecological networks. *Trends in Ecology and Evolution* 20: 402–409.
- Ydenberg RC. 2007. Provisioning. Pages 273–304 in Stephens DW, Brown JS, Ydenberg RC, (eds). *Foraging: Behavior and Ecology*. The University of Chicago Press.
- Zhang, W, Ricketts TH, Kremen C, Carney K, Swinton SM. 2007. Ecosystem services and dis-services to agriculture. *Ecological Economics* 64: 253–260.

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