CHAPTER THREE

Trophic Interaction Networks and Ecosystem Services

Christopher J. Whelan, Diana F. Tomback, Dave Kelly, and Matthew D. Johnson

Thanks to their power of flight, birds live on all continents and even on the most remote oceanic islands. Birds, as a group, function in every trophic category except primary producer and decomposer (although some birds are detritivores). They engage in local trophic interaction networks everywhere they occur. They forage in terrestrial, aquatic, and aerial environments. Through trophic interactions, they participate in antagonistic, mutualistic, and commensal interactions with other inhabitants of their ecosystems. In short, birds play many functional roles in their ecosystems, such as those of carnivore and herbivore, but also those of seed disperser, pollinator, scavenger, and ecosystem engineer.

Borrowing from Darwin, Terborgh et al. (2010) noted that species in ecosystems are engaged in tangled webs of interactions. Even simple food webs encompass a great number of direct and indirect interactions (see below). Using Holt's (1997) concept of the community module—a subset of the entire food web—the basic community module critical for pest control is a three-species food chain: a single species in the third trophic level (e.g., insectivorous bird) consumes a species of the second trophic level (caterpillar), which in turn consumes all or part of a species of the first trophic level (oak tree). The feeding interactions here comprise a trophic cascade, whereby the insectivore reduces the number of herbivores, which increases the biomass of the plant (fig. 3.1E). From the plant's perspective, the enemy (the bird) of its enemy (the caterpillar) is its friend: the bird indirectly benefits the plant by consuming the caterpillar.

A more complex community module consists of a trophic interaction network, in which multiple species at multiple trophic levels are linked. A complete food web consists of many such modules, each represented by an interaction chain or an interaction network. Through their participation in trophic interaction chains and networks, birds provide many ecosystem functions. When those functions benefit humans, birds provide ecosystem services. In fact, birds provide services in each of the four categories of ecosystem services identified by the Millennium Ecosystem Assessment (2003; see Whelan et al. 2008; Wenny et al. 2011).

Types of Trophic Interactions

Direct and Indirect

Interactions between or among species may be classified in the broad sense as direct or indirect. Direct interactions are those in which a given species

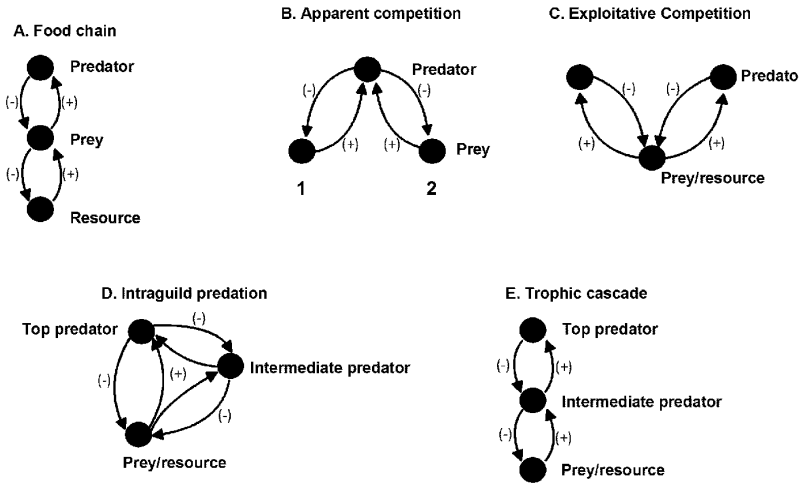

FIGURE 3.1. Examples of trophic interactions (following Holt 2009). Each example represents a community module, a simple subweb drawn from a potentially more complex community food web. Direct interactions are those between species linked by arrows (e.g., A. food chain: secondary consumer, primary consumer, and resource). Indirect interactions are those in which two species are linked via an intermediate species (e.g., B. apparent competition: prey 1 and prey 2 are linked indirectly by a shared predator). In intraguild predation (D.), a top predator both competes with and preys upon an intermediate predator. A trophic cascade (E.) is a food chain in which a top predator suppresses an intermediate predator, thus releasing the prey of the intermediate predator from suppression by the intermediate predator.

influences the behavior, population density, and reproductive success, among other characteristics, of a second species. Examples of direct interactions include predation, herbivory, and pollination. Indirect interactions are those in which species A interacts directly with species B, in turn influencing how species B interacts with species C; indirect effects (in this case between A and C) are the products of two or more direct effects. Examples include exploitative resource competition, apparent competition, and trophic cascades (fig. 3.1).

Top-Down, Bottom-Up

Ecological interactions are also classified by the direction in which their effects flow. With bottom-up interactions, or donor control, effects originate at one trophic level and move up the interaction network. Examples include pulsed inputs to ecosystems from mast crops (e.g., beech nuts, acorns) and insect irruptions (e.g., periodical cicadas) in terrestrial ecosystems, and algal blooms in aquatic systems. With top-down interactions, effects originate at one trophic level and move down the food web. Examples include the direct effects of predation and herbivory, and the indirect effects of trophic cascades.

Ecology of Trophic Interactions and Ecosystem Services

Trophic interactions are feeding relationships: one species consumes another. Trophic interactions that benefit humans represent ecosystem services. For instance, birds of prey may consume rodents, which in turn consume a valuable seed or nut crop. Delivery of ecosystem services through trophic interactions results from both direct and indirect effects and both top-down and bottom-up effects. Many of the ecosystem services provided by birds directly or indirectly result from their foraging interactions (Whelan et al. 2008). Through foraging, birds transfer energy and nutrients both within and among ecosystems (chapter 9), and thus contribute to ecosystem function and resilience (Lundberg and Moberg 2003). In this chapter we examine a variety of ecological contexts in which ecosystem services delivered by birds are the consequence of, and are impacted by, trophic interactions.

The impact of trophic interactions, whether direct or indirect, on other members of a community depends upon the scale at which resources are detected and, thus, the spatial scale of the functional response of the consumer

species (Morgan et al. 1997). Consumers may respond to resources numerically, through population growth or aggregation, or functionally, through changes in foraging behavior (Solomon 1949). For a predator to deliver pest control services, for instance, it must be able to detect and respond to the spatial scale of heterogeneity in variation in pest densities (Schmidt and Whelan 1998). Under these conditions, predators will be able to respond to resources in a density-dependent manner, a condition necessary for a regulating impact on prey populations.

Trophic Cascades

A trophic cascade is an indirect trophic interaction in which a top predator benefits the prey or resource, owing to its consumption of an intermediate predator (fig. 3.1E). Most typically in trophic cascades with birds as the apex predators, insectivorous birds induce the top-down control of herbivorous insects, thereby benefiting the plants that would otherwise be consumed by the herbivores (Şekercioğlu 2006). Birds of prey potentially act as the apex predator in trophic cascades by consuming granivorous or herbivorous rodents, thus benefiting plants whose seeds or foliage would otherwise be consumed. Birds delivering ecosystem services via trophic cascades often serve as pest control agents.

Birds as Pest Control Agents

We broadly define a pest as any organism that decreases fitness, population size, growth rate, or economic value of any resource important to humans. Examples of pests abound: fungal pathogens destroy valuable crops and timber; herbivorous insects consume crops, and arthropods vector disease, to name a few. A biological pest control agent, therefore, is an organism that reduces the effect of a pest species on one or more resources, thus increasing the abundance, growth rate, or economic value of that resource for humans. Birds serve as pest control agents through their consumption of the pest, and pest control arises solely through cascading top-down trophic interactions. In the terminology of the Millennium Ecosystem Assessment (2003), pest control services may be classified as supporting services (Whelan et al. 2008).

Şekercioğlu et al. (2004) and Wenny et al. (2011) classified birds by trophic status, ecosystem services, and vulnerability to extinction. Pest control services potentially can be delivered by species in each of the trophic levels,

with the likely exception of nectarivory, but data demonstrating such services are largely unavailable for most species. The trophic categories with the strongest evidence for pest control services are consumers of terrestrial invertebrates and scavengers. Of the approximately 10,000 species of birds in the world, about 5,706 terrestrial bird species consume invertebrates (Şekercioğlu et al. 2004). Pest control services by members of this trophic category have been documented in both natural and agro-ecosystems (chapter 1; see below). Obligate scavengers (36 species) control pests indirectly by ridding the environment of carrion (Buechley and Şekercioğlu 2016). This important service limits the spread of disease organisms and competing species like rodents and feral dogs that vector diseases to humans. As discussed in depth by Devault et al. (chapter 8), the value of these services were dramatically demonstrated in south Asia following a rapid and massive loss of four obligate scavenging vulture species (Oaks et al. 2004). The loss of scavengers enabled rodent and feral dog populations to increase, which in turn spread disease to humans, their domestic pets and livestock, and, likely, other species.

Natural Ecosystems

Trophic cascades in community modules with birds as the apex predator have been examined in a wide variety of natural ecosystems around the world, including grasslands and boreal, temperate, and tropical forests. The exclosure experiment of Holmes et al. (1979) provided the inspiration for later studies, though Holmes et al. (1979) did not examine the full cascade. Holmes et al. (1979) demonstrated that insectivorous forest birds depress abundances of lepidopteran larvae in forest understory vegetation when those densities are at endemic (nonirruptive) densities. The largest impacts on insect numbers coincided with nestling and fledgling periods of the nest cycle. Because their focus was on the direct effect of birds on insects, Holmes et al. (1979) did not examine the indirect effect of bird predation on herbivory levels or subsequent plant productivity. This study and other early exclosure experiments (Askenmo et al. 1977; Solomon et al. 1977; Joern 1986; Fowler et al. 1991) presented compelling evidence that birds can depress abundance of at least some arthropod prey, in some systems at some times. But they assessed only the predators (birds) and their prey (arthropods, especially herbivorous insects), and not the consequences for vegetation. Insect pest predators need not be insect pest control agents, because reductions in pests may not translate into greater plant productivity (chapter 1).

Subsequent studies expanded to examine all three trophic levels: insectivorous birds, arthropods, and plants. Atlegrim (1989) documented the effect of birds on herbivory: leaf damage to bilberry (*Vaccinium myrtillus*) increased significantly in the absence of birds. Marquis and Whelan (1994) found that excluding birds from sapling white oaks (*Quercus alba*) significantly increased both the density of leaf-damaging insects and leaf damage, which in turn decreased production of new biomass in the subsequent growing season. Marquis and Whelan (1994) included an insecticide treatment. Both birds and insecticide reduced arthropod abundance and leaf damage, and had about equal benefits for subsequent plant biomass production.

Top-down effects of insectivorous birds, including trophic cascades, have now been examined in many natural environments, including northern hardwood forest (Holmes et al. 1979; Strong et al. 2000), mixed grass prairie (Fowler et al. 1991), arid grassland (Bock et al. 1992), temperate oak forest (Marquis and Whelan 1994; Murakami and Nakano 2000; Lichtenburg and Lichtenburg 2002; Böhm et al. 2011), tropical forest (Van Bael et al. 2003), ponderosa pine forest (Mooney 2007), and hybrid cottonwoods (Bridgeland et al. 2010). The majority of these studies demonstrated, minimally, top-down effects of birds on arthropods. Many of them also found that bird predation on insects benefited plants (Whelan et al. 2008; Mäntylä et al. 2011; Wenny et al. 2011; Maas et al. 2015).

Accidental introductions of insects, such as that of the emerald ash borer (*Agrilus planipennis*) to North America, create opportunities to examine the responses of insectivorous birds to spreading and sometimes irruptive novel prey. Woodpeckers and other bark foragers prey upon emerald ash borer (Cappaert et al. 2005b; Duan et al. 2010), and their predation rates have been correlated with emerald ash borer density (Lindell et al. 2008). Some woodpecker species and white-breasted nuthatches (*Sitta carolinensis*) increased in density in regions infested with emerald ash borers (Koenig et al. 2013). Various bark-foraging species increased their use of ash trees in relation to the degree of infestation (Flower et al. 2013), which is indicative of a density-dependent response that could potentially contribute to population control. These results collectively suggest that bark-foraging birds may help slow the spread of this lethal pest in North America. Ecologists should be poised to take advantage of such "natural experiments," as they provide opportunities to examine ecological function at relevant spatial and temporal scales not attainable in manipulative experiments (Whelan et al. 2008; Rogers et al. 2012).

Agro-Ecosystems

The potential role of birds as agents of biological control was investigated by the economic ornithologists of the US Biological Survey from the late 1800s into the early 1900s (chapter 1). These studies, based on field observations and examination of stomach contents, implicated birds as effective pest control agents. Interest in this ecosystem function of birds waned with the advent of chemical insecticides and criticism of the methods employed by economic ornithologists. New investigations over the last decade confirm that, in some situations, birds do serve as effective pest control agents in agro-ecosystems. Many of these studies, like those in natural ecosystems, employ exclusion cages to reveal bird effects from their absence or "subtraction."

Moreover, some investigators employ "addition" manipulations, in which nest boxes are added to increase the density of birds inhabiting the study areas. For instance, Jedlicka et al. (2011) used nest boxes to attract western bluebirds (*Sialia mexicana*) to California (US) vineyards. The nest boxes greatly increased the abundance activity of bluebirds, and thereby increased the removal of larvae deployed in the field as bioassays of avian predation. Total avian abundance increased twofold before fledging, and 2.6-fold after fledging. Mols and Visser (2002) used a combination of nest boxes, to increase the density of great tits (*Parus major*), and exclusion cages to measure the tits' top-down effects in apple orchards, reporting that increased tit density decreased leaf and apple damage, and increased the apple yield by 66%. Bird control of insect pests has been documented in a variety of agricultural systems, including those of corn (Tremblay et al. 2001), apples (Mols and Visser 2002, 2007), broccoli (Hooks et al. 2003), kale (Ndang'ang'a et al. 2013), cacao (Van Bael et al. 2007; Maas et al. 2013), coffee (Kellerman et al. 2008; Johnson et al. 2009, 2010), oil palm (Koh 2008); and grapes (Jedlicka et al. 2011).

Ndang'ang'a et al. (2013) quantified bird diversity and foraging behavior in a Kenyan agroecosystem and found that most species foraged from the ground, consuming primarily seeds, fruits, and flowers of weed species. Ndang'ang'a et al. (2013) also observed two abundant aerial insectivores. The assemblage of observed bird species, in combination with their foraging behaviors, suggests a potential for beneficial pest control services by birds in this area. However, insectivorous birds decline in abundance over time in tropical agricultural ecosystems, in comparison to their rate of decline in tropical forests and agroforests (chapter 11; Şekercioğlu 2012).

Retaining native tree species and forest patches in agricultural areas may maintain higher numbers of insectivorous birds (Skreekar et al. 2013) and reduce crop damage.

A number of studies indicate that deployment of either nest boxes or hunting perches within agricultural systems may attract raptors in agroecosystems. In most cases, the increased density and activity of raptors resulted in decreased population sizes of rodent agricultural pests and, in some cases, decreased damage from those pests.

As reported by Smal et al. (1990), field trials investigating the use of barn owls (*Tyto alba*) as biological control agents of rodents (predominantly Malayan field rats, *Rattus tiomanicus*) in oil palm plantations in peninsular Malaysia began in 1986, at least in part owing to the evolution of resistance to the rodenticide warfarin. Smal et al. (1990) developed computer simulation models indicating that higher owl densities could reduce rat numbers, resulting in economically acceptable damage levels. This could be accomplished with biological control alone, or as part of an integrated pest management program (IPM) that reduces the use of rodenticides. Duckett (1991) recounted the history of natural spread of the barn owl in peninsular Malaysia following development of the oil palm industry, as well as the results of a nest box provisioning program aimed at enhancing barn owl density. This program proved biologically and economically successful, with the collateral benefit of population increases in mammalian predators (common palm civet, *Paradoxurus hermaphroditus*; leopard cat, *Prionailurus bengalensis*; feral house cat, *Felis catus*) which had previously declined owing to unintended consumption of warfarin-laced baits.

More recent work indicates that owl predators are effective biological control agents of rats in maize (Kenya: Ojwang and Oguge 2003), rice (Malaysia: Hafidzi and Na'iM 2003), alfalfa (Israel: Motro 2011), various field crops (wheat, sweet corn, alfalfa, clover, vetch, and oats), and date plantations (Israel: Meyrom et al. 2009), and also of rodents in semiurban (South Africa: Meyer 2008) and urban (Israel: Charter et al. 2007) environments. Nest boxes for barn owls were deployed successfully in Chile to control rodents, the reservoir for hantavirus syndome (Muñoz-Pedreros et al. 2010). Investigations of strategies to recruit raptors for biological control of vertebrate pests should be a priority in applied ecological research worldwide. In a twist on the use of raptors in agroecosystems (Kross et al. 2012), where birds can be both the top predator and the pests, New Zealand falcons (*Falco novaeseelandiae*) introduced into

vineyards decreased the abundance of three species of introduced (Eurasian blackbird, *Turdus merula*; song thrush, *Turdus philomelos*; and starling, *Sturnus vulgaris*) and one native (silvereye, *Zosterops lateralis*) pest bird species, thus reducing grape losses by 95% in comparison to those in vineyards with no falcons.

Cascade Strength

Birds exert top-down trophic cascades in some but not all systems. What underlies this variability? Terborgh, Estes, and Holt (2010) examined ecological theory to investigate factors or relationships producing variability in the magnitude of trophic cascades. They found that trophic cascades will be of greater magnitude (1) in systems with high plant productivity, (2) when intense predation at higher trophic levels is coupled with strong density dependence at those levels, (3) with little intraguild predation and interference, and, (4) with greater predator niche complementarity.

Empirical studies are largely consistent with these expectations. Marquis and Whelan (1994) found cascading effects of bird predation on leaf-chewing insects on biomass production of white oak (*Quercus alba*) in relatively high-productivity oak forest in Missouri. Strong et al. (2000) found that bird predation decreased Lepidoptera abundance and mean size, but did not lead to a significant increase in biomass production of sugar maple (*Acer saccharum*) in less productive northern hardwood forest in New Hampshire. Similarly, Van Bael et al. (2003) found that bird invertebrate consumption decreased leaf herbivory in the more productive canopies of three Neotropical forest species than in the less productive understory. Mooney et al. (2010) found greater cascading effects, due to density dependence, on high-quality trees that enhance caterpillar growth more than did low-quality trees (though they found cascading effects on the latter trees as well). Van Bael et al. (2008) found greater cascading effects from birds in the canopy trees of tropical agroforests than from birds in the understory crop trees, and greater cascading effects when bird diversity was greatest owing to the presence of migratory species. These studies confirm expectations regarding productivity, density dependence, predator diversity, and niche complementarity.

In a meta-analysis of 114 empirical studies from aquatic and terrestrial ecosystems, Borer et al. (2005) reported that cascade strength was not well explained by ecosystem productivity, but was related to taxonomy of the herbivore (invertebrate) and the top predator (mammal or bird). These

conditions apply to systems with insectivorous birds and herbivorous arthropods, which are now fairly widely studied (reviewed by Şekercioğlu 2006; Whelan et al. 2008; Wenny et al. 2011; and in this volume). Many of these investigations found birds effective at inducing strong cascading effects.

Bottom-Up Interaction Chains

Loss of Plants That Are Keystone Mutualists

Delivery of ecosystem services often depends on energy flux from primary producer to bird consumer. Consider the case history of whitebark pine (*Pinus albicaulis*) and Clark's nutcracker (*Nucifraga columbiana*), both discussed in detail by Tomback (chapter 7). The nutcracker is the primary seed disperser for whitebark pine. In this system, an introduced pathogen (*Cronartium ribicola*), which causes blister rust in five-needle white pines, and a natural episodic pest, the mountain pine beetle (*Dendroctonus ponderosae*)—or both—disrupt the seed dispersal services for the pine by the nutcracker in a lethal combination. Both the fungal pathogen and the insect pest may be considered predatory organisms, operating within a community module from high- to mid-level trophic levels down. The disease alone acts more slowly, but peak outbreaks of the beetle kill high proportions of mature cone-bearing trees (Tomback and Achuff 2010; Logan et al. 2010). Both mortality factors drastically reduce whitebark pine cone production. Following reduced cone production, nutcrackers seek higher rates of food rewards elsewhere, altering their use of whitebark pine communities and disrupting the regeneration cycle for whitebark pine. The likelihood of seed dispersal by nutcrackers consequently plummets, as does the likelihood of forest regeneration (McKinney et al. 2009; Barringer et al. 2012). Whitebark pine serves many important ecosystem functions as a foundation and keystone species, including the provision of ecosystem services to humans (chapter 7). These will decline as whitebark pine forests decline.

With growing globalization and increasingly rapid spread of exotic disease, other foundation and keystone species are at risk. For example, oak trees in Europe are succumbing to a previously unknown bacterial pathogen that causes the syndrome referred to as acute oak decline (Brady et al. 2010). In coastal California and Oregon, sudden oak death, caused by a fungal pathogen, has rapidly killed oaks and tanoaks as well as other

plants (Rizzo and Garbelotto 2003). The acorns of oaks and tanoaks are important food sources for jays, which are important seed dispersal mutualists (chapter 7). The loss of these trees affects forest biodiversity and community structure, and disrupts the seed dispersal services of birds.

Intermediate Trophic Position

Predators may disrupt delivery of pollination (chapter 4) and seed dispersal (chapters 5, 6, 7) services by birds. Such disruption is commonly observed on oceanic islands, where endemic birds frequently evolved with no mammalian predators, but human colonists deliberately or inadvertently introduced a diversity of mammalian predators. Introduced mammals are often devastatingly successful predators on adults and young of native birds, reducing populations, sometimes to local or global extinction. Even when not driven to extinction, species may become functionally extinct (Şekercioğlu et al. 2004).

As reviewed by Innes et al. (2010), New Zealand now hosts 33 introduced mammal species, including devastating bird predators like the Pacific rat (*Rattus exulans*), ship rat (*Rattus rattus*), brushtail possum (*Trichosurus vulpecula*), and stoat (*Mustela erminea*). The disruption of ecosystem service delivery, including seed dispersal and pollination, has been particularly well studied in New Zealand (chapter 4). More importantly, New Zealand ecologists have investigated restoring those services.

As on many oceanic islands, birds play important functional roles as seed dispersal agents (for 59% of all tree species, and about 12% of all flora) and pollination agents (30% of trees, 4.5% of total flora) in New Zealand (chapters 5 and 6; Kelly et al. 2010). Delivery of these dispersal and pollination services is disrupted by introduced mammals, many assuming the role of apex predators in trophic interaction chains in which native New Zealand birds now occupy an intermediate trophic position. Predation has reduced some native bird species to functional extinction and reduced the density of others. Such declines end or limit the delivery of ecosystem services. A diversity of introduced mammals in New Zealand combine to prey on native bird species representing different communities, life history characteristics, body sizes, and ecological functions. For instance, stoats prey on many bird species, from yellowhead (*Mohoua ochrocephala*) to blue duck (*Hymenolaimus malacorhynchos*); three species of rat (ship rat; Pacific rat; and Norway rat, *R. norvegicus*) prey

on various smaller adult songbirds, eggs of many species, and nestlings of larger species; brushtail possums prey upon larger species like kaka (*Nestor meridionalis*) and kokako (*Callaeas cinerea*; see Innes et al. 2010).

On the New Zealand mainland, Kelly et al. (2005) experimentally removed stoats from a 400-hectare Broken River site while using the 300-hectare Cheeseman site as a nontreatment area to test whether conservation management can restore bird pollination services for a native mistletoe (*Peraxilla tetrapetala*). Stoat removal rapidly increased bellbird reproductive success and an 85% increase in local densities, but Kelly et al. (2005) detected no significant increase in mistletoe pollination. These results suggest a dismal outcome for other desired projects, such as the restoring of bird pollination of *Rhabdothamnus* on the New Zealand mainland to levels quantified on New Zealand islands. An obvious lesson from this work, and from much else in conservation, is that preserving natural systems is much easier and less expensive than restoring or recreating them once they have been degraded or destroyed through human mismanagement and exploitation.

A dramatic example of loss of bird services (top-down trophic effects) results from the virtually complete extirpation of native forest birds from the Pacific island of Guam, the most southern island in the Mariana Island chain. Inadvertent introduction of the brown tree snake (*Boiga irregularis*) around World War II led to the annihilation of land birds and reductions in many mammals and lizards resident on Guam (Savidge 1987; Wiles et al. 2003; Mortenson et al. 2008). The nonnative snake assumed the role of apex predator while changing the position of insectivorous birds to that of intermediate predator (see fig. 3.1). The consequences of losing the Guam avifauna are (1) a precipitous decline in animal vectors of seed dispersal (Caves et al. 2013), and (2) a tremendous increase in the density of spiders (Rogers et al. 2012). Caves et al. (2013) found widespread seed dispersal by birds on Saipan, another island in the Marianas chain, where the native bird community is still intact, in contrast to the situation on Guam. Similarly, Rogers et al. (2011) found that spider density on Guam was up to 40 times greater than that on Saipan, an island farther to the north which lacks the tree snake. Moreover, to determine whether the loss of birds cascades down to affect plants, Rogers et al. (2011) compared seedling survival on Guam with that on the islands of Saipan, Tinian, and Rota, which all have relatively intact avifauna. For five or six plant species, seedling survival on Guam was equivalent or greater than on islands with birds. This suggests that the increased spider population on Guam in the

absence of birds may control insect herbivores. Given that the extirpation of native birds on Guam occurred between 1945 and 1985, and that the first anecdotal reports of high spider densities were in the 1990s, spiders likely respond to bird loss quickly. Indeed, a meta-analysis of bird exclosure studies showed an increase in spiders after bird exclusion in 75% of the tests (Gunnarsson 2008), thus suggesting that spiders may frequently respond to bird declines or losses. However, the full effects of insectivorous birds is likely to be context-dependent, and too few landscape-level studies exist to make general predictions.

Human-Related Impact on Trophic Interaction Networks and Ecosystem Services

Many bird species known or likely to deliver ecosystem services are under risk of decline and extinction (Şekercioğlu et al. 2004). As discussed by Şekercioğlu and Buechley (chapter 11), human modification of habitats often changes the composition of bird communities, thus impacting the delivery of ecosystem services (see also Ferger et al. 2012). Maintaining services delivered by birds requires preservation of habitats and resources that support the bird species themselves (Whelan et al. 2008; Whelan et al. 2010). Conservation measures that generally enhance avian populations concomitantly strengthen their delivery of ecosystem services (Jedlicka et al. 2012; Barbaro et al. 2013). Increased understanding of the relationships among species richness, ecological function, and ecosystem service delivery will help reveal important consequences for the persistence of ecosystem services in the face of human impact (Philpott et al. 2009). As habitats are disturbed and climates change, species are not lost randomly; agricultural expansion and intensification selectively purge species with a distinct set of traits (Tscharntke et al. 2008). The same functional traits that confer species persistence may simultaneously affect service provision (Zavaleta and Hulvey 2004; Larsen et al. 2005). Dietary generalists survive in highly modified landscapes better than specialists (Lindell et al. 2004; Tscharntke et al. 2008), and they are less extinction-prone in general (Boyles and Storm 2007; Şekercioğlu 2011). Field data and models also indicate that generalists can exert stronger top-down control on their prey than can specialists (Symondson et al. 2002; Bianco Faria et al. 2008). Therefore, dietary generalism may dampen the adverse effects of land use intensification on the ecosystem services provided by avian

trophic interactions. However, the conservation of ecosystem services may also hinge on retaining functionally unique species (Zavaleta and Hulvey 2004)—for example, species that consume a specific insect that is avoided by other insectivores. Because different birds have their own suite of preferred prey and their own foraging niches, the pest control ecosystem service provided by a bird assemblage may be noticeably changed by the functional extinction of a subset of the birds, even if all the common generalist bird species persist. The relationship between dietary specialization and functional uniqueness is uncertain. Understanding how both of those things change with the degree of competition among bird species should be a priority for diet and community research.

Climate Change

Global climate change affects birds around the world (Möller et al. 2010; Wormworth and Şekercioğlu 2011; Şekercioğlu et al. 2012), and, potentially, their delivery of ecosystem services. Global climate change causes shifts in the timing of ecological processes (Bradley et al. 1999; Ellwood et al. 2013), and abundance and distributions of numerous organisms, both animal and plant (Parmesan and Yohe 2003; Wormworth and Şekercioğlu 2011; Şekercioğlu et al. 2012). Changes in abundance and distribution of species are linked to the emergence of disease. The timing of nesting and migration of some bird species, in particular, has already changed (Dunn and Winkler 1999, 2010; Mills 2005; Kobori et al. 2011), and may reduce the ability of insectivorous birds to control populations of plant-eating insects that can influence the productivity of natural and agricultural systems.

Delivery of many ecosystem services may be threatened by global climate change, while others may be enhanced. Birds may even potentially render some ecosystems resilient to some consequences of global climate change. As demonstrated by the sentinel pest experiment of Jedlicka et al. (2011), birds may control agricultural pests that arrive in new areas in response to climate change or from accidental introductions. Indeed, the work of Koenig et al. (2013) and of Flower et al. (2013), as discussed above, indicates that a variety of bark-foraging bird species prey upon the introduced and expanding emerald ash borer in precisely such a manner. Although the expected negative consequences of global climate change often receive greater public attention, some of the changes may be beneficial. A study projecting changes in the range of species suggests that northern Europe may see an increase in diversity of species that provide ecosys-

tem services following global warming, while southern Europe may see a decrease in those same species (Civantos et al. 2012).

Şekercioğlu et al. (2012) investigated the potential effects of climate change for tropical species. They concluded that species living in montane areas, those with no corridors to higher elevations, those living in coastal forests, and those with restricted geographical ranges are most vulnerable to population decline and extinction. Şekercioğlu et al. (2012) suggest that the establishment of new protected areas, or the enhancement of existing areas, must consider future climate change. This includes the development of area networks with extensive topographical diversity, wide elevational ranges, and high connectivity. These networks should be integrated into human-dominated landscapes to mesh with conservation priorities while simultaneously facilitating the delivery of ecosystem services (Tscharntke et al. 2005; Whelan et al. 2010; Woltz et al. 2012).

Şekercioğlu et al. (2012) argue that particular suites of bird species are particularly vulnerable, owing to geography and evolutionary history. For instance, some tropical mountain species living at particular elevations may have restricted ranges because of specialized habitat requirements and/or species interactions. Other species may occupy areas at high risk of increasing global temperatures, but have no ready access to higher elevations to mitigate rising temperatures (e.g., species in the central Amazon basin, far from the Andes). Coastal forest bird species and species with highly restricted geographic ranges (e.g., island species and many endemic species) are especially vulnerable. Some bird species may be especially susceptible to increased seasonality of annual rainfall (both increased and decreased), as such change may affect the abundance and/or timing of resources required for successful reproduction. Many species will also be vulnerable to extreme weather events such as heat waves, cold spells, and tropical cyclones. Birds that experience limited temperature variation and have low basal metabolic rates will be most prone to the physiological effects of warming temperatures and heat waves. Şekercioğlu et al. (2012) conclude by emphasizing the importance of using "various methods to estimate the economic value of ecosystem services delivered by birds and other animals."

Species will not respond to climatic changes uniformly or predictably. Some species may tolerate climate change, and even benefit from it (Civantos et al. 2012), while other species decline. The ecosystem services delivered by the former species will be persistent in the face of climate change, while those of the latter may be reduced, disrupted, and ultimately

lost. However, these responses are likely to be complex, since bird species which persist in an area could change their diet or behaviors in response to the loss of other species from the area, as noted above.

Conclusions and Future Directions

Birds deliver important ecosystem services through a number of complex trophic interactions, with birds sometimes driving the interaction and sometimes under pressure from other trophic levels. These ecosystem services include pest control, seed dispersal, pollination, and scavenging services. Research is needed now to address at least three aspects of ecosystem services:

1. How Can We Mitigate against Human-Caused Disruption of These Services?

We need to identify traits that make some species good providers of ecosystem services, and to determine whether those traits make them more or less susceptible to anthropogenic disturbance such as habitat loss and climate change. With this knowledge, we may be able to target particularly important providers of ecosystem services and improve the conservation of the ecosystems or unique habitats and resources they require for persistence. Establishment and enhancement of networks of protected areas facilitate the ability of species to adjust their ranges in the face of climate change and thereby continue to provide the service. Any public and private actions that reduce human contribution to climate change will help conserve birds and their ecosystem services.

2. How Might We Facilitate and Enhance the Delivery of Ecosystem Services through Exploitation of Natural Interaction Networks?

Careful management of habitat availability, use of nest boxes and hunting perches, and control of invasive species that disrupt delivery of services may enhance birds' ability to deliver ecosystem services. This may even involve an otherwise uncommon species that has suffered from human disturbance, such as the New Zealand falcon, which provides conservation as well as economic benefits in vineyards. Research is needed to elucidate how we can manage or manipulate human-dominated envi-

ronments, particularly urban and agricultural environments, in ways that promote high bird abundance and diversity and, hence, their ecosystem services. For instance, Jones and Sieving (2006) demonstrated that insect-consuming birds attracted to fields of organic vegetable crops with intercropped sunflower (*Helianthus annuus*) resulted in reduction of important crop pests, and, importantly, had no negative consequences for the crops themselves.

3. Can We Better Elucidate the Value of Ecosystem Services Provisioned by Trophic Interactions Involving Birds?

Both economists and ecologists have made conceptual advances in identifying the ethics and values leading to the valuation of ecosystem services (chapter 2), including those provided by birds. Chapter 2 points to various methods for estimating the economic value of ecosystem services delivered by birds and other animals. In the case of trophic cascades involving birds, techniques such as the avoided cost, replacement cost, and factor income methods may allow researchers to estimate the economic value of bird-provisioned services. In addition, because birds are mobile agents of ecosystem services, future research should be aimed at understanding how habitat and landscape composition may affect bird movements and the spatial delivery of their services. For example, Jirinec et al. (2011) found that pest-eating warblers commuted from diurnal foraging home ranges in coffee farms to nocturnal roosting sites in surrounding forests, a behavior which could link the delivery of pest control on farms to the preservation of forest in the landscape and vice versa. While estimating the value of birds' trophic interactions, researchers should be mindful that the commodification of birds' services may reproduce some of the pitfalls of neoclassical market economics (Gómez-Baggethun et al. 2010). The primary purpose for assigning economic value to the ecosystem services provided by birds must be to argue that conservation of birds is not only a matter of ethics and aesthetics, but is also essential for ecosystem function and human livelihood.

Acknowledgments

We thank Joel Brown and his lab group for helpful suggestions on an early draft of this chapter.

References

Askenmo, C., Bromssen, A., von Ekman, J., and Jansson, C. 1977. Impact of some wintering birds on spider abundance in spruce. *Oikos* 28:90–94.

Atlegrim, O. 1989. Exclusion of birds from bilberry stands: Impact on insect larval density and damage to the bilberry. *Oecologia* 79:136–39.

Barbaro, L., Dulaurent, A-M., Payet, K., Blache, S., Vetillard, F., and Battisti, A. 2013. Winter bird numerical responses to a key defoliator in mountain pine forests. *Forest Ecology and Management* 296:90–97.

Barringer, L. E., Tomback, D. F., Wunder, M. B., and McKinney, S. T. 2012. Whitebark pine stand condition, tree abundance, and cone production as predictors of visitation by Clark's nutcracker (*Nucifraga columbiana*). *PLoS ONE* 7(5):e37663.

Bianco Faria, L., Umbanhowar, J. and McCann, K. S. 2008. The long-term and transient implications of multiple predators in biocontrol. *Theoretical Ecology* 1:45–53.

Bock, C. E., Bock, J. H., and Grant, M. C. 1992. Effects of bird predation on grasshopper densities in an Arizona grassland. *Ecology* 73:1706–17.

Böhm S. M., Wells, K., Kalko, E. K. V. 2011. Top-down control of herbivory by birds and bats in the canopy of temperate broad-leaved oaks (*Quercus robur*). *PLoS ONE* 6:e17857.

Borer, E. T., Seabloom, E. W., Shurin, J. B., Anderson, K. E., Blanchette, C. A., Broitman, B., Cooper, S. D. and Halpern, B. S. 2005. What determines the strength of a trophic cascade? *Ecology* 86:528–37.

Boyles, J. G., and Storm, J. J. 2007. The perils of picky eating: Dietary breadth is related to extinction risk in insectivorous bats. *PLoS ONE* 2:e672.

Bradley N. L., Leopold, A. C., Ross, J., and Huffaker, W. 1999. Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences* 96:9701–4.

Brady, C., Denman, S., Kirk, S., Venter, S., Rodríguez-Palenzuela, and Coutinho, T. 2010. Description of *Gibbsiella quercinecans* gen. nov., sp. nov., associated with acute oak decline. *Systematic and Applied Microbiology* 33:444–50.

Buechley, E. R., Şekercioğlu, Ç. H. 2016a. The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. *Biological Conservation*. In press.

Cappaert, D., McCullough, C. G., and Poland, T.M. 2005. The upside of the emerald ash borer catastrophe: A feast for woodpeckers. In *Emerald Ash Borer Research and Technology Development Meeting,* ed. V. Mastro and R. Reardon, 69–70. US Department of Agriculture Forest Service, Washington.

Caves, E. M., Jennings, S. B., Hille Ris Lambers, J., Tewksbury. J. J., and Rogers, H. S. 2013. Natural experiment demonstrates that bird loss leads to cessation of dispersal of native seeds from intact to degraded forests. *PLoS ONE* 8:e65618.

Charter, M., Izhaki, I., Shapira, L. and Leshem, Y. 2007. Diets of urban breeding barn owls (*Tyto alba*) in Tel Aviv, Israel. *Wilson Journal of Ornithology* 119:484–85.

Civantos, E., Thuiller, W., Maiorano, L., Guisan, A., and Araújo, M. B. 2012. Potential impacts of climate change on ecosystem services in Europe: The case of pest control by vertebrates. *BioScience* 62:658–66.

Duan, J. J., Ulyshen, M. D., Bauer, L. S., Gould, J. and Van Driesche, R. 2010. Measuring the impact of biotic factors on populations of immature emerald ash borers (Coleoptera: Buprestidae). *Environmental Entomology* 39:1513–22.

Duckett, J. E. 1991. Management of the barn owl (*Tyto alba javanica*) as a predator of rats in oil palm (*Elaeis quineensis*) plantations in Malaysia. *Birds of Prey Bulletin* 4:11–23.

Dunn, P. O., and Winkler, D. W. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London Biology B* 266:2487–90.

———. 2010. Effects of climate change on timing of breeding and reproductive success in birds. In *Effects of Climate Change on Birds*, ed. A. P. Moller, W. Fiedler, and P. Berthold, 113–28. Oxford University Press, Oxford.

Ellwood, E. R., Temple, S. A., Primack, R. B., Bradley, N. L., and Davis, C. C. 2013. Record-breaking early flowering in the eastern United States. *PLoS ONE* 8:e53788.

Ferger, S. W., Böhning-Gaese, K., Wilcke, W., Oelmann, Y., and Schleuning, M. 2013. Distinct carbon sources indicate strong differentiation between tropical forest and farmland bird communities. *Oecologia* 171:473–86.

Flower, C. E, Long, L., Knight, K. S., Rebbeck, J., Brown, J. S., Gonzalez-Meler, M. A., and Whelan, C. J. 2013. Native bark-foraging birds preferentially forage in infected ash (*Fraxinus* spp.) trees and prove effective predators of the invasive emerald ash borer (*Agrilus planipennis* Fairmaire). *Forest Ecology and Management* 313:300–306.

Fowler, A. C., Knight, R. L., George, T. L., and McEwen, L. C. 1991. Effects of avian predation on grasshopper populations in North Dakota grasslands. *Ecology* 72:1775–81.

Hafidzi, M. N., and Na'iM, M. 2003. The use of the barn owl, *Tyto alba*, to suppress rat damage in rice fields in Malaysia. In *Rats, Mice and People: Rodent Biology and Management*, ed. G. R. Singleton, L. A. Hinds, C. J. Krebs, and D. M. Spratt, 274–77. Australian Centre for International Agricultural Research, Canberra.

Holmes, R, T., Schultz, J. C., and Nothnagle P. 1979. Bird predation on forest insects: An exclosure experiment. *Science* 206:462–63.

Holt, R. D. 1997. Community modules. In *Multitrophic Interactions in Terrestrial Ecosystems*, ed. A. C. Gange and V. K. Brown, 333–49. 36th symposium of the British Ecological Society. Blackwell Science, Oxford.

———. 2009. Predation and community organization. In *The Princeton Guide to Ecology*, ed. S.A. Levin, 274–81. Princeton University Press, Princeton, NJ.

Hooks, C. R., Pandey R. R., and Johnson, M. W. 2003. Impact of avian and arthropod predation on lepidopteran caterpillar densities and plant productivity in an ephemeral agroecosystem. *Ecological Entomology* 28:522–32.

Innes, J., Kelly, D., Overton, J. M., and Gillies, C. 2010. Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology* 34:86–114.

Jedlicka, J. A., Greenberg, R., and Letourneau, D. K. 2011. Avian conservation practices strengthen ecosystem services in California vineyards. *PLoS ONE* 6:e27347.

Joern, A. 1986. Experimental-study of avian predation of coexisting grasshopper populations (Orthoptera, Acrididae) in a sandhills grassland. *Oikos* 46:243–49.

Johnson, M. D., Levy, N. J., Kellermann, J. L., and Robinson, D. E. 2009. Effects of shade and bird exclusion on arthropods and leaf damage on coffee farms in Jamaica's Blue Mountains. *Agroforestry Systems* 76:139–48.

Johnson, M. D., Kellermann, J. L., and Stercho, A. M. 2010. Pest reduction services by birds in shade and sun coffee in Jamaica. *Animal Conservation* 13:140–47.

Jones, G. A., and Sieving, K. E. 2006. Intercropping sunflower in organic vegetables to augment bird predators of arthropods. *Agriculture, Ecosystems & Environment* 117:171–77.

Kellermann, J. L., Johnson, M. D. Stercho, A. M., and Hackett. S. C. 2008. Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. *Conservation Biology* 22:1177–85.

Kelly, D., Brindle, C., Ladley, J. J., Robertson, A. W., Maddigan, F. W., Butler, J., Ward-Smith, T., Murphy, D. J., and Sessions, L. A. 2005. Can stoat (*Mustela erminea*) trapping increase bellbird (*Anthornis melanura*) populations and benefit mistletoe (*Peraxilla tetrapetala*) pollination? *New Zealand Journal of Ecology* 29:69–82.

Kelly, D., Ladley, J. J., Roberston, A., Anderson, S. H. , Wotton, D. M., and Wiser, S. K. 2010. Mutualisms with the wreckage of an avifauna: The status of bird pollination and fruit dispersal in New Zealand. *New Zealand Journal of Ecology* 34:66–85.

Kobori, H., Kamamoto, T., Nomura, H., Oka, K., and Primack, R. 2011. The effects of climate change on the phenology of winter birds in Yokohama, Japan. *Ecological Research* 27:173–80.

Koenig, W. D., Liebhold, A. M., Bonter, D. N., Hochachka, W. M., Dickinson, J. L. 2013. Effects of the emerald ash borer invasion on four species of birds. *Biological Invasions* 15:2095–2103.

Koh, L. P. 2008. Birds defend oil palms from herbivorous insects. *Ecological Applications* 18:821–25.

Kross, S. M., Tylianakis, J. M., and Nelson, X. J. 2012. Effects of introducing threatened falcons into vineyards on abundance of Passeriformes and bird damage to grapes. *Conservation Biology* 6:142–49.

Lindell, C. A., McCullough, D. G., Cappaert, D., Apostolou, N. M., Roth, M. B. 2008. Factors influencing woodpecker predation on emerald ash borer. *American Midland Naturalist* 159:434–44.

Logan, J. A., MacFarlane, W. W., and Willcox, L. 2010. Whitebark pine vulnerability to climate-driver mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecological Applications* 20:895–902.

Lundberg, J., and Moberg, F. 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6:87–98.

Maas, B., Clough, Y., and Tscharntke, T. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecology Letters* 16:1480–87.

Maas, B., Karp, D. S., Bumrungsri, S., Darras, K., Gonthier, D., Huang, C. -C., Lindell, C. A., Maine, J. J., Mestre, L., Michel, N. L., Morrison, E. B., Perfecto, I., Philpott, S. M., Şekercioğlu, Ç. H., Silva R. M., Taylor, P., Tscharntke, T., Van Bael, S. A., Whelan, C. J. and Williams-Guillén, K. 2015. Bird and bat predation services in tropical forests and agroforestry landscapes. *Biological Reviews*. Article first published online 23 July 2015. DOI: 10.1111/brv.12211.

Mäntylä, E., Klemola, T., Laaksonen, T. 2011. Birds help plants: A meta-analysis of top-down trophic cascades caused by avian predators. *Oecologia* 165:143–51.

McKinney, S. T., Fiedler, C. E, and Tomback, D. F. 2009. Invasive pathogen threatens bird-pine mutualism: Implications for sustaining a high-elevation ecosystem. *Ecological Applications* 19:597–607.

Meyer, S. 2008. *Owl as a Control Agent for Rat Populations in Semi-Urban Habitats*. Master's thesis, University of the Witwatersrand, Johannesburg.

Meyrom, K., Motro, Y., Leshem, Y., Aviel, S., Izhaki,I., Argyle, F. and Charter, M. 2009. Nest-box use by the Barn Owl *Tyto alba* in a biological pest control program in the Beit She'an valley, Israel. *Ardea* 97:463–67.

Millennium Ecosystem Assessment. 2003. *Ecosystems and Human Well-Being: A Framework for Assessment*. Island Press, Washington.

Mills, A.M. 2005. Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *Ibis* 147:259–69.

Möller, A. P., Fiedler, W., and Berthold, P. 2010. *Effects of Climate Change on Birds*. Oxford University Press, Oxford.

Mols, C. M. M., and Visser, M. E. 2002. Great tits can reduce caterpillar damage in apple orchards. *Journal of Applied Ecology* 39:888–99.

———. 2007. Great tits (*Parus major*) reduce caterpillar damage in commercial apple orchards. *PLoS ONE* 2:e202.

Mooney, K. A. 2007. Tritrophic effects of birds and ants on a canopy food web, tree growth, and phytochemistry. *Ecology* 88:2005–14.

Mooney, K. A., Halitschke, R. Kessler, A. and Agrawal, A. A. 2010. Evolutionary trade-offs in plants mediate the strength of trophic cascades. *Science* 327:1642–44.

Morgan, R. A., Brown, J. S., and Thorson, J. M. 1997. The effect of spatial scale on the functional response of fox squirrels. *Ecology* 78:1087–97.

Motro, Y. 2011. Economic evaluation of biological rodent control using barn owls *Tyto alba* in alfalfa. 8th European Vertebrate Pest Management Conference, 79–80. DOI: 10.5073/jka.2011.432.040.

Muñoz-Pedreros, A., Gil, C., Yáñez, J. and Rau, J. R. 2010. Raptor habitat management and its implication on the biological control of the Hantavirus. *European Journal of Wildlife Research* 56:703–15.

Murakami, M., and Nakano, S. 2000. Species-specific bird functions in a forest-canopy food web. *Proceeding of the Royal Society of London B*. 267:1597–1601.

Ndang'ang'a, P. K., Njoroge, J. B. M., Ngamau, K., Kariuki, W., Atkinson, P. W., and Vickery, J. 2013. Avian foraging behaviour in relation to provision of ecosystem services in a highland East African agroecosystem. *Bird Study* 60:156–68.

Ndang'ang'a, P. K., Njoroge, J. B. M., and Vickery, J. M. 2013. Quantifying the contribution of birds to the control of arthropod pests on kale, *Brassica oleracea* acephala, a key crop in East African highland farmland, *International Journal of Pest Management* 59:211–16.

Oaks, J. L. et al. 2004. Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature* 427:630–33.

Ojwang, D. O., and Oguge, N. O. 2003. Testing a biological control programme for rodent management in a maize cropping system in Kenya. In *Rats, Mice and People: Rodent Biology and Management*, ed. G. R. Singleton, L. A. Hinds, C. J. Krebs and D. M. Spratt, 251–53. Australian Centre for International Agricultural Research, Canberra.

Parmesan, C., and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.

Philpott, S. M., Soong, O., Lowenstein, J. H., Pulido, A.L., Lopez, D. T., Flynn, D. F. B., and DeClerck, F. 2009. Functional richness and ecosystem services: Bird predation on arthropods in tropical agroecosystems. *Ecological Applications* 19:1858–67.

Rizzo, D. M., and Garbelotto, M. 2003. Sudden oak death: Endangering California and Oregon forest ecosystems. *Frontiers in Ecology and the Environment* 1:197–204.

Rogers, H., Lambers, J. H. R., Miller, R., Tewksbury, J. J. 2011. "Natural experiment" demonstrates top-down control of spiders by birds on a landscape level. *PLoS ONE* 7:e43446.

Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* 68:660–68.

Schmidt, K. A., and Whelan, C. J. 1998. Nest predation on woodland songbirds: When is nest predation density dependent? *Oikos* 87:65–74.

Şekercioğlu, Ç. H. 2006. Ecological significance of bird populations. In *Handbook of the Birds of the World*, ed. J. del Hoyo, A. Elliott, and D. A. Christie, volume 11, 15–51. Lynx Edicions, Barcelona.

———. 2011. Functional extinctions of bird pollinators cause plant declines. *Science* 331:1019–20.

———. 2012. Bird functional diversity in tropical forests, agroforests and open agricultural areas. *Journal of Ornithology* 153:S153–61.

Şekercioğlu, Ç. H., Daily, G. C. and Ehrlich, P. R. 2004. Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences* 101:18042–47.

Şekercioğlu, Ç. H., Primack, R., Wormworth, J. 2012. Effects of climate change on tropical birds. *Biological Conservation* 148:1–18.

Smal, C. M., Halim, A. H. Din Amiruddin, M. 1990. *Predictive Modelling of Rat Populations in Relation to Use of Rodenticides or Predators for Control*. No. 25. Palm Oil Research Institute Malaysia, Kuala Lumpur.

Solomon, M. E. 1949. The natural control of animal populations. *Journal of Animal Ecology* 18:1–35.

Strong, A. M., Sherry, T. W., and Holmes, R. T. 2000. Bird predation on herbivorous insects: Indirect effects on sugar maple saplings. *Oecologia* 125:370–79.

Symondson, W. O. C., K. D. Sunderland, and M. H. Greenstone. 2002. Can generalist predators be effective as biocontrol agents? *Annual Review of Entomology* 47:561–94.

Terborgh, J., Holt R. D., and Estes, J. A. 2010. Trophic cascades: What they are, how they work, and why they matter. In *Trophic Cascades: Predators, Prey and the Changing Dynamics of Nature*, ed. J. Terborgh and J. A. Estes, 1–18. Island Press, Washington.

Tomback, D. F., and P. Achuff. 2010. Blister rust and western forest biodiversity: Ecology, values, and outlook for white pines. *Forest Pathology* 40:186–225.

Tremblay, A., Mineau, P., Stewart, R.K. 2001. Effects of bird predation on some pest insect populations in corn. *Agriculture, Ecosystems and Environment* 83: 143–52.

Tscharntke,T., Klein, A. M., Kruess, A., Ingolf, S.-D. and Thies, C. 2005. Landscape perspectives on agricultural intensification and biodiversity: Ecosystem service management. *Ecology Letters* 8:857–74.

Tscharntke, T., Şekercioğlu, Ç. H., Dietsch, T. V., Sodhi, N. S., Hoehn, P., and Tylianakis, T. M. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* 89:944–51.

Van Bael, S. A., Bichier, P., Greenberg, R. 2007. Bird predation on insects reduces damage to the foliage of cocoa trees (*Theobroma cacao*) in western Panama. *Journal of Tropical Ecology* 23:715–19.

Van Bael, S. A., and Brawn, J. D. 2005. The direct and indirect effects of insectivory by birds in two contrasting Neotropical forests. *Oecologia* 143:106–16.

Van Bael, S. A., Brawn, J. D., and Robinson, S. K. 2003. Birds defend trees from herbivores in a Neotropical forest canopy. *Proceedings of the National Academy of Sciences* 100:8304–07.

Van Bael, S. A., Philpott, S. M., Greenberg, R., Bichier, P., Barber, N. A., Mooney, K. A., and Gruner, D. S. 2008. Birds as predators in tropical agroforestry systems. *Ecology* 89:928–34.

Wenny, D. G., DeVault, T. L., Johnson, M. D., Kelly, D., Şekercioğlu, C. H., Tomback, D. F., and Whelan, C. J. 2011. The need to quantify ecosystem services provided by birds. *Auk* 128:1–14.

Whelan, C. J., Wenny, D. G., and Marquis, R. J. 2008. Ecosystem services provided by birds. *Annals of the New York Academy of Sciences* 1134:25–60.

Wiles, G. J., Bart, J., Beck, R. E. Jr., and Aguon, C. F. 2003. Impacts of the brown tree snake: Patterns of decline and species persistence in Guam's avifauna. *Conservation Biology* 17:1350–60.

Wormworth, J., Şekercioğlu, Ç. H. 2011. *Winged Sentinels: Birds and Climate Change*. Cambridge University Press, New York.

Zavaleta, E. S., and Hulvey. K. B. 2004. Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* 306:1175–77.