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Increasing awareness of avian ecological function

Cagan H. Sekercioglu

Stanford University Center for Conservation Biology, Department of Biological Sciences, Stanford, CA 94305-5020, USA

Birds are one of the most diverse groups of ecosystem service providers, whose ecological functions range from creating soil to shaping primate behavior, Nevertheless, the impression that birds have little influence on ecological processes has been hard to change. Given the ongoing declines in avian functional groups, there is a pressing need to compare avian ecological functions to those of other taxa, to understand how these functions translate to ecosystem services and to estimate the ecological implications of bird declines. Here, I review the ecological functions of birds, link them to ecosystem services and outline research priorities for understanding avian contributions to ecosystem functioning.

Birds as ecological actors

Birds are the best-studied class of organism and various investigations have established their significance as important mobile links (see Glossary) in the dynamics of natural and human-dominated ecosystems (Box 1; Figure 1) [1–6]. Birds also benefit humans by providing important ecosystem services [7], such as: provisioning services via game meat for food, down for garments and guano for fertilizer; regulating services by scavenging carcasses and waste, by controlling populations of invertebrate and vertebrate pests, by pollinating and dispersing the seeds of plants; cultural services, as exemplified by the prominent roles of birds in art and religion [8,9] and by the billions of dollars spent on birdwatching [10]; and supporting services by cycling nutrients [6,11] and by contributing to soil formation [12].

Birds exhibit the most diverse range of ecological functions among vertebrates. Although mammals have comparable roles, birds have twice as many taxa, ten times more flying species and are more resilient to extirpation [13]. Many avian functions either complement those of mostly nocturnal mammals [3,14] or have no other vertebrate equivalents, exemplified by aerial leaf litter gleaners (e.g. checker-throated antwrens *Myrmotherula fulviventris* [15]), cavity drillers (e.g. red-naped sapsuckers *Sphyrapicus nuchalis* [16]), large flying predators (e.g. crowned hawk-eagles *Stephanoaetus coronatus* [17]), obligate scavengers (e.g. long-billed vultures *Gyps indicus* [18], Figure 1c) and upland-nesting marine foragers (e.g. tufted puffins *Fratercula cirrhata* [6], Figure 1b).

Given the ecological significance of birds (Table 1), an overview of their ecological functions and services is overdue and is essential for delineating research priorities. Despite extensive literature on some functions [3,4,19] and increasing interest in less-studied ones [5,6,20–22], important gaps remain, particularly regarding scavengers [9] and birds of prey [23]. Studies of avian contributions toecosystems will benefit from an ecological research framework [24] and the use of efficiency measures that are suitable for ecological investigations (Table 1). The conservation status of avian functional groups and the ecosystem implications of bird declines have been addressed elsewhere [25], thus, I focus here on the ecological functions of birds (Figure 1, 2).

Genetic linkers

A hornbill (Figure 1a) swallowing fruits and defecating viable seeds away from the parent tree and a hummingbird (Figure 2b) pollinating flowers while foraging are important 'genetic information linkers' [1] because they transport plant genetic material via seed dispersal and pollination, respectively. These functions also result in ecosystem services for humans. Birds pollinate dozens of crop species [26] and avian seed dispersal is particularly important for big-seeded tropical tree species [27] [such as avocados (Lauraceae)], some of which provide valuable fruits and timber.

Seed dispersers

Darwin [28] considered birds to be 'highly effective agents in the transportation of seeds' (Figure 2a). Seed dispersal reduces the density-dependent mortality of seeds and seedlings by enabling escape from seed predators [29], herbivores [30], pathogens [31] and competitors [19,32]. Although most seed dispersal mutualisms are no longer considered to be tightly coevolved [33], seed dispersal is integral to the maintenance of plant diversity [2,34]. For

Glossary

Ecosystem engineers: organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials [83].

Ecosystem services: the benefits that humans obtain from ecosystems [7]. If an avian ecological function, such as insect consumption, results in material benefits for humans, such as pest control, it is also considered an ecosystem service.

Functional group: the primary diet-based grouping that parallels the main ecological function of the species (e.g. seed dispersal is the most important function of primarily frugivorous birds) [25].

Mobile link: organisms that actively move in the landscape and connect habitats in space and time [1].

Trophic cascade: changes in the population of an organism at a trophic level that causes significant population changes at another trophic level(s) [78].

Corresponding author: Sekercioglu, C.H. (cagan@stanford.edu).

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Box 1. Birds as mobile links

Birds are mobile links that are crucial for maintaining ecosystem function, memory and resilience [1]. Avian ecological functions encompass all three major linkages: genetic, resource and process. Seed-dispersing frugivores (Figure 2a, main text) and pollinating nectarivores (Figure 2b, main text) are genetic linkers that carry genetic material from one plant to another or to habitat that is suitable for regeneration, respectively. Piscivorous birds (Figures 1b, 2c, main text) are resource linkers whose droppings transport aquatic nutrients to terrestrial environments. Grazers, such as geese (Figure 2d, main text), and predatory birds, such as insectivores (Figure 2e, main text) and raptors (Figure 2f, main text), are trophic process linkers that influence plant, invertebrate and vertebrate prey populations, respectively. Ecosystem engineers, such as woodpeckers (Figure 1d, main text), are non-trophic process linkers that modify their environment by physically transforming materials from one state to another [1,83].

Mobile link categories are not mutually exclusive. Birds, particularly colonial species (e.g. social weavers *Philetairus socius*) and woodpeckers, can modify their environment substantially by constructing nests, which are often used by a variety of other species [16]. Thus, many bird species are both trophic and physical process linkers. Piscivorous bird colonies (Figure 1b, main text) can carry out all of these linkages as these birds can consume fish, deposit nutrients, engineer ecosystems via burrow construction and even disperse seeds that are adhered to their feet [90].

example, in some tropical forests, up to 90% of the tree species can be dispersed by animals [32]; 56% of angiosperms are dispersed by vertebrates, which have increased the diversification rate and dominance of woody angiosperms [35].

Bird and mammal frugivores often target different species [33]. On similar species, birds not only outperform primates in long-distance dispersal [13], but also generally disperse seeds to different areas [14,32]. In tropical forests that have lost their large mammals, avian seed dispersal might be the only option [13]. Consequently, seed dispersal could be the most influential avian ecological function, particularly in the tropics [2,32,36]. More than half of Costa Rican tree and shrub species are bird dispersed [2]. The lowest proportion of these species is in dry deciduous forests (39%), followed by humid lowland (48%–57%) and highland forests (71–77%). Birds become more important with increasing elevation and rainfall, and other comparable neotropical sites exhibit similar percentages [2].

Directed dispersal by birds to suitable establishment and survival sites can be vital, exemplified by Costa Rican three-wattled bellbirds *Procnias tricarunculata*. These birds disperse seeds to gaps under song perches, where seedling mortality is nearly twice as low as that in other areas [37]. Directed dispersal is especially important in regeneration and in arid areas, where the few available trees attract birds and provide favorable microclimates for seedlings. Furthermore, rare events of long-distance dispersal can have evolutionary significance [19]. For example, seed-caching Eurasian jays *Garrulus glandarius* can carry acorns up to 20 km in one go and, as a result of avian dispersal, large-seeded trees have followed glaciers northwards significantly faster than one would expect [32]. Although effective seed dispersal can help counter the genetic effects of reduced pollination caused by fragmentation [38], fragmentation can reduce even generalist frugivore populations, leading to corresponding declines in seed dispersal and recruitment [36].

Perhaps the least appreciated contribution of avian seed dispersers is enabling the colonization and regeneration of barren, deforested, ephemeral, remote, post-glacial, volcanic and other marginal habitats [32,39,40]. For example, seabirds not only visit and colonize volcanic islands, but can also jumpstart ecosystem buildup by simultaneously transferring nutrients and dispersing seeds (e.g. [40]).

Most birds cannot swallow fruits wider than a few centimeters [33,41] and dispersal efficiency declines with seed size [41]. Large seeds often characterize shade-tolerant and late successional tropical tree species with big trunks [27]. Lauraceae, Burseraceae and Sapotaceae [42] are important large-seeded plant families that depend on relatively few large frugivores [33], such as hornbills (Figure 1a), which can disperse seeds over vast areas [13]. Although small frugivores are not necessarily resilient and replaceable [36], bigger size usually means a higher probability of extinction [25,43]. Thus, large frugivore losses are more likely to lead to recruitment

Table 1. Major avian ecosystem services and ways to measure their efficiency[a]

Service type[b]	Service	Primary ecosystem service providers[c]	Efficiency measure(s) [24]	Sample Refs
Regulating	Seed dispersal	Frugivores (1350/1800)	Dispersal distance, recruitment rate, seed and seedling survival	[19,32,36]
	Pollination	Nectarivores (600/350)	Pollen deposition rate, flower ripening rate, seed/fruit set	[48,50]
	Pest control	Invertebrate (5700/1700) and vertebrate (300/1100) feeders	Invertebrate numbers, plant damage, primary productivity	[5,21,22]
	Carcass and waste disposal	Scavengers (40/300)	Rate of disappearance of carcasses and wastes	[9,80]
Supporting	Nutrient deposition	Aquatic birds (950)[d]	Soil, water, and plant nutrient levels; plant abundance and productivity	[6,20,57]
	Ecosystem engineering	Burrow and cavity diggers (1000)[e]	Number of nesting holes, nesting populations of dependent species, process rate[f]	[16,84,85]

[a] Based on [24].

[b] Based on [7].

[c] The approximate number of bird species providing each service is in parentheses ([25] [unpublished data]). Although additional bird species might be involved (e.g. seed dispersal via adhesion or all birds transferring some nutrients in their droppings), groups listed are those that are known to provide the bulk of the service. The first figure is the approximate number of species that are known to feed primarily on that item and the second is the approximate number of other bird species also known to consume it. Given that primary feeders account for most of the ecological function, the first figure reflects the number of species in that functional group.

[d] An aquatic bird is a species whose primary habitat consists of wetlands, rivers or the sea.

[e] Only species that actively dig burrows or cavities are included.

[f] Refers to processes such as erosion [86] that result from digging.

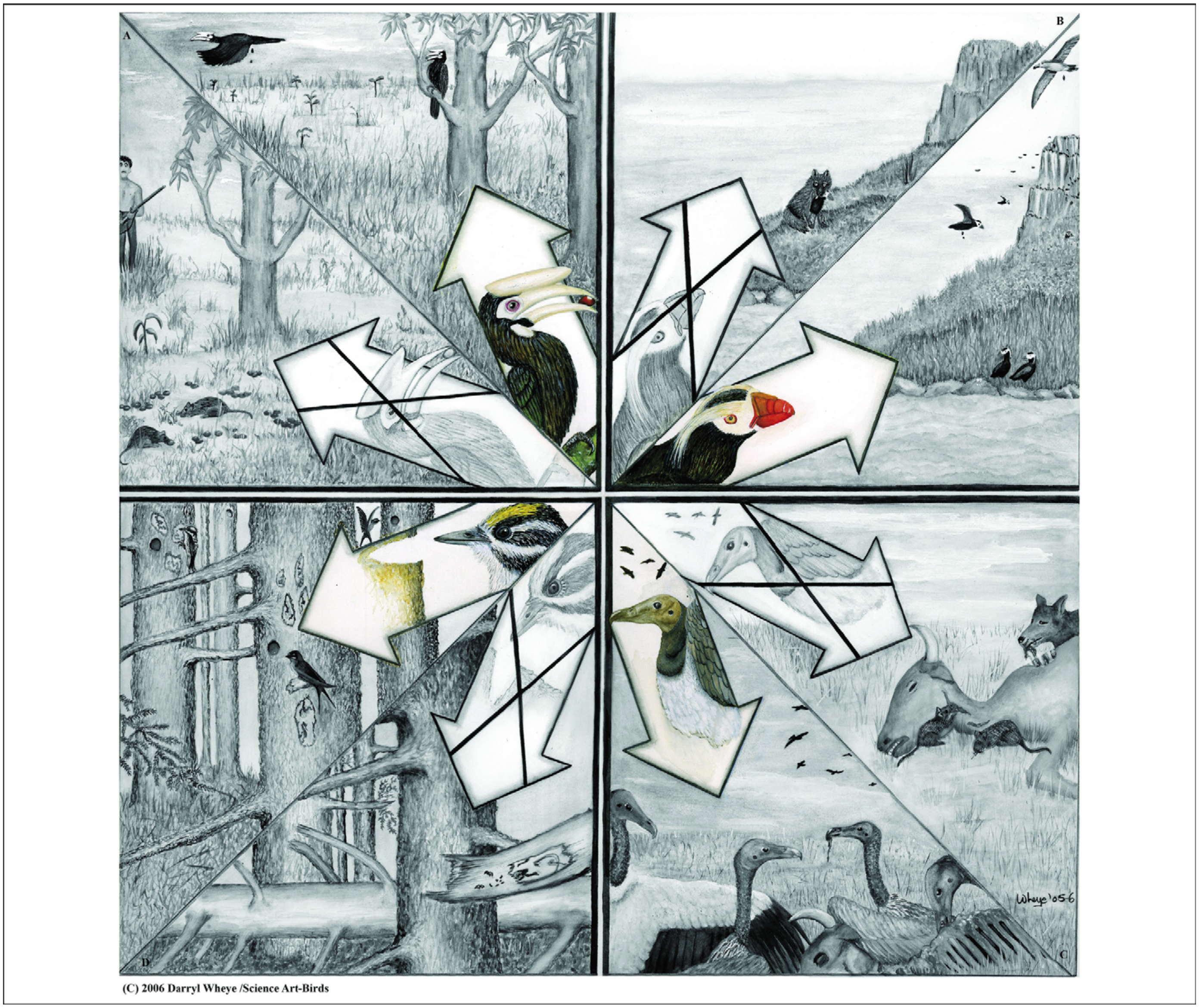

Figure 1. Examples of the four main types of avian mobile links [1] and the potential consequences of their removal. **(a)** Genetic linkers (Box 1): in the Philippines, the loss of seed dispersers, such as Palawan hornbills *Anthracoceros marchei*, can result in most seeds being deposited under the parent tree and being consumed by seed predators [43]. **(b)** Resource linkers: the elimination of Aleutian seabirds, such as tufted puffins *Fratercula cirrhata*, by introduced foxes can lead to reduced nutrient deposition, triggering a shift from grassland to maritime tundra [6]. **(c)** Trophic process linkers: disappearance of scavenging Indian long-billed vultures *Gyps indicus*, can cause increases in the number of rotting carcasses and of attending mammalian scavengers [9]. **(d)** Trophic and non-trophic process linkers: reduced numbers of three-toed woodpeckers *Picoides tridactylus* in forest fragments can cause increases in spruce bark beetles (*Dendroctonus* and *Ips* species) [60] and decreases in nesting holes used by other species [16]. In addition to habitat loss, which affects all avian functional groups, large frugivores are highly susceptible to exploitation, seabirds are threatened by by-catch mortality and introduced species, woodpeckers decline as a result of fragmentation and vultures are particularly sensitive to chemicals. Reproduced with permission from Darryl Wheye/http://birds.stanford.edu.

bottlenecks and extinctions of the species that they disperse [43,44]. Studies of how changes in avian seed-dispersers affect plant communities, particularly of tropical, large-seeded or invasive species, are likely to deliver results of immediate ecological and conservation value.

Pollinators

Although most plants are insect pollinated [3], >900 bird species, mainly hummingbirds (Figure 2b), sunbirds, honeyeaters and other nectarivores, pollinate ~500 of the 13 500 vascular plant genera [26], whereas bats pollinate plants from ~250 genera [45]. To meet their higher energy needs, many birds visit numerous flowers regularly, which increases gene flow among plants [46]. Such birds often provide higher quality pollination than do insects, particularly of self-incompatible flowers with patchy distributions [46].

Most avian pollination occurs in the tropics [3], New Zealand and Australia, and is particularly important in the Austral and Oceanic regions [47–49], where >10% of the flora can be bird pollinated and where there is significant pollen limitation [48]. Some Australian plants are more adapted to avian pollination to make up for reduced insect pollination and limited avian seed dispersal [47]. However, as with seed dispersal, pollinator limitation is more crucial in island ecosystems [48,50] with fewer species, tighter linkages and plant species that are no longer able to self-pollinate [49].

There has been little research on the economic importance of avian pollination, but birds are thought to

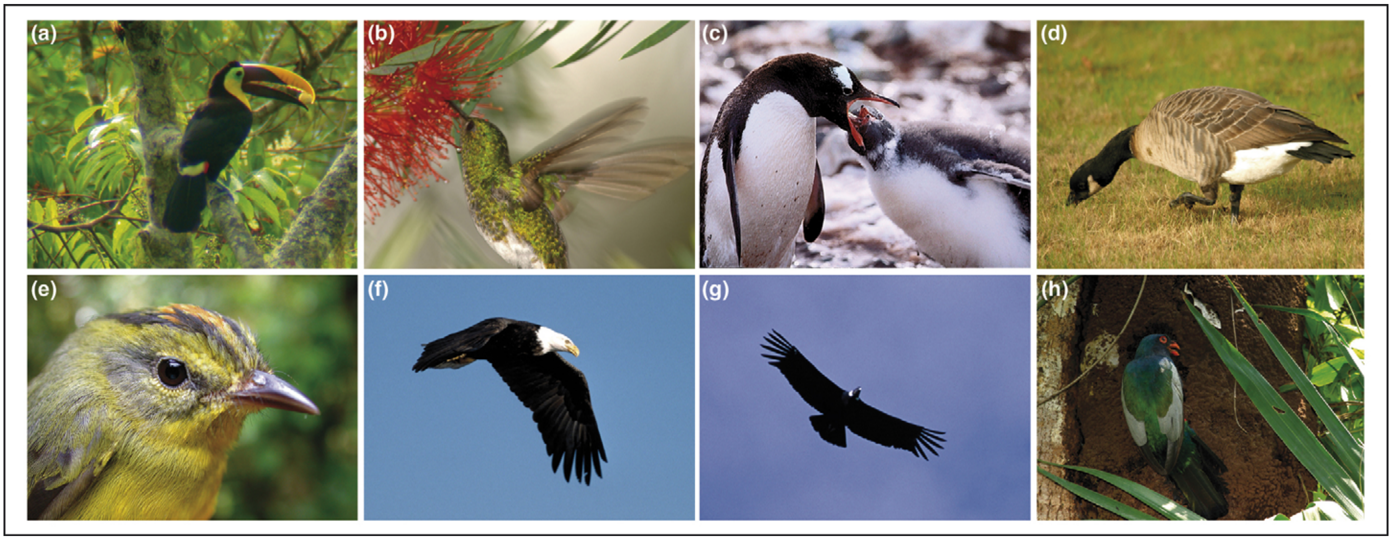

Figure 2. Examples of the eight main types of avian ecosystem service providers. **(a)** Seed disperser: black-mandibled toucan *Ramphastos ambiguus* (Las Cruces, Costa Rica). **(b)** Pollinator: snowy-bellied hummingbird *Amazilia edward* (Las Cruces, Costa Rica). **(c)** Nutrient depositor: Gentoo penguin *Pygoscelis papua* (Port Lockroy, Antarctica). **(d)** Grazer: cackling goose *Branta hutchinsii* (California, USA). **(e)** Insectivore: golden-crowned warbler *Basileuterus culicivorus* (Las Cruces, Costa Rica). **(f)** Raptor: bald eagle *Haliaeetus leucocephalus* (Alaska, USA). **(g)** Scavenger: Andean condor *Vultur gryphus* (Patagonia, Chile). **(h)** Ecosystem engineer: slaty-tailed trogon *Trogon massena* (Pipeline Road, Panama). Reproduced with permission from the author.

pollinate 3.5%–5.4% of >1500 crop species whereas 165 bat species pollinate 6.8%–10.7% [26]. Avian pollination has ecological, economical, evolutionary and conservation significance, especially on islands and in certain species-rich communities, such as tropical forest understorey herbs, Australian sclerophyllous plants and Andean cloud forest shrubs. For example, approximately 1% of Costa Rican tree species and 6%–10% of epiphytes (such as bromeliads) are bird pollinated [2]. Birds are particularly important pollinators for sparsely distributed plant species with isolated populations [47] that suffer from pollen limitation [48]. Declines in avian pollinators could have consequences for rare plants, and this is a little-studied, exciting research frontier in conservation ecology.

Resource linkers

By transporting minerals and nutrients in their guano, birds can be vital resource linkers [1], particularly between marine and terrestrial [6], and between terrestrial and wetland [11] ecosystems. This ecological function provides the ecosystem service of crop fertilization, which can occur thousands of kilometers away from the original source of the nutrients.

Nutrient depositors

Although Murphy [51] estimated that seabird guano transfers annually 10^4–10^5 tons of phosphorous to land, and waterfowl can input 40% of the nitrogen and 75% of the phosphorous entering a wetland [11], avian nutrient transfer received little research interest until the 1990s. Since then, the ecological importance of seabirds has been demonstrated in the natural laboratory of the nutrient-poor Gulf of California islands [20,52,53]. The currents that facilitate spectacular marine productivity, such as California and Humboldt, also create temperature inversions that lead to low productivity deserts on nearby land masses. In such places, the guano and carcasses of seabirds provide crucial external nutrients, especially to coasts and unproductive islands, where birds subsidize terrestrial ecosystems dominated by 'bottom-up' influences [20]. Soil enrichment with nutrient-laden guano can have direct or cascading effects on the populations of plants [52,54], invertebrates [20], rodents [53] and even large mammals [55]. In addition to enriching the soil, seabirds can also create it in polar regions [12].

Seabird colonies can influence plant community composition [20] and evolution [56], sometimes shaping entire ecosystems [6]. Effects on the life histories of island species can be substantial, even increasing the survival of small mammals [57] and the reproductive success of large ones [55]. In the Aleutian Islands, a 60-fold reduction of seabirds by introduced arctic foxes *Alopex lagopus* resulted in a corresponding decrease in nutrient deposition. This led to declines in soil phosphorous, marine-derived nitrogen and plant nitrogen content, triggering a switch from grassland to maritime tundra on affected islands [6,54].

Seabird eliminations by introduced mammals are common and the current dire status of many seabird species [25] needs urgent attention. This also applies to avian nutrient deposition research, presently focused on aquatic and insular communities. Studies of other ecosystems, research on nutrient deposition by terrestrial birds and comparisons of relevant efficiency measures (Table 1) present pressing and stimulating research opportunities.

Trophic process linkers

Birds that are trophic-process linkers connect habitats by serving as primary (Figure 1a, 2a, b, d) or secondary (Figure 1b, c, d; 2c, e, f, g) consumers across habitats [1]. The ecological function of predation is considered an ecosystem service if avian predators reduce agricultural pests and increase yields [5] or if they limit pest activity through fear [23]. Scavengers provide sanitary services, such as carcass disposal, waste recycling, indirect population control of scavenging mammalian disease vectors and even funereal services for some cultures [9].

Insectivores

Early studies focusing on the irruptions of economically important temperate lepidopterans concluded that insectivorous birds exert little control over ecosystem processes [58]. However, increasing evidence from a range of ecosystems (e.g. [5,15,21,22,59–62]) suggests that insectivorous birds are important in controlling the populations, behavior and evolution of their invertebrate prey [58]. Avian control of insect herbivores and consequent reductions in plant damage can also have economic value [5,61,63], as much as US\$1820 km^{-2} y^{-1} [64].

The impacts of insectivorous birds vary temporally and depend on the initial invertebrate population size [58,65]. Birds are more effective at controlling low (40–70% reduction in temperate Lepidoptera [58]) to moderate (20–60% reduction) invertebrate populations, although (with some exceptions [60]), are unable to influence outbreaks (0–10% reduction) [58,65]. Most studies of bird–invertebrate interactions have been done in temperate climates, where seasonality increases the magnitude of insect population fluctuations [66]. In the tropics, where reduced seasonality means fewer and less severe outbreaks, thousands of insectivorous bird species might be more significant year-around control agents, possibly contributing to the typically limited extent of tropical forest outbreaks [66]. Indeed, tropical studies suggest the importance of insectivorous birds, both in agricultural [22,61] and forested [15,21] landscapes.

Insect control services of largely diurnal birds overlap little with those of insectivorous bats. Evidence suggests that invertebrate control by a bird species can also complement predation by other birds [67], invertebrates [62] or parasitoids [63]. Higher species richness of insectivorous birds also increases the probability of having a highly effective insectivorous species (e.g. Figure 2e) [22]. Although avian reductions of insect herbivores do not always lead to reduced plant damage [59], a recent review showed that removals of insectivorous birds often result in increases in herbivores and in plant consumption, sometimes reducing crop yields [5]. Thus, well-designed studies are needed to measure avian control of invertebrates in various ecosystems and to augment this valuable service that might be declining in many tropical areas [68].

Raptors

Recent studies have shown that raptors (e.g. Figure 2f) [69], can be important top predators, especially when indirect effects are considered [17,70]. More mobile than nonflying predators, raptors can respond faster to increases (or decreases) in prey populations. Raptor species that initially appear ecologically similar, such as variable hawks *Buteo polyosoma* and Harris's hawks *Parabuteo unicinctus* in Chile, can have distinct functions, especially in ecosystems with large spatiotemporal fluctuations [71]. Raptors might reduce populations of rodent and avian agricultural pests or indirectly limit their impact [72,73], but research in this front is limited.

Raptors influence prey populations by their very presence. By establishing a 'landscape of fear' [74], avian predators can have indirect effects that are more important than their direct effects [23]. Perceived risk of predation can affect prey behavior [75], stabilize predator–prey dynamics [76] and lead to higher species richness via competitive coexistence [73]. Fear of predation can limit the population size of a prey species by reducing its foraging [72,74] and indirect 'defense' of the nests of other birds by raptors is well documented [77].

Large raptors are ecologically unique, are more sensitive to disturbance and are more threatened than most birds of prey. Declines in large tropical forest raptors, such as Philippine eagles *Pithecophaga jefferyi*, could have significant impacts on the numbers [17] and behavior [74] of their prey, with further changes possible through trophic cascades [78]. Given their potential importance, there is a substantial but mostly unmet need for research on raptors as population control agents, particularly in agricultural and tropical ecosystems.

Scavengers

Scavenging birds (Figure 1c, 2g) recycle carcasses, lead other scavengers to dead animals [79], maintain energy flows higher in food webs [80] and limit the spread of diseases and of undesirable mammalian scavengers [9]. Vultures are the only known obligate vertebrate scavengers (Figure 2g) [18] and, in many ecosystems, are (or were) the main meat-eaters owing to their efficiency in finding and consuming dead animals [79]. Vultures have an impressive ability to resist and possibly detoxify bacterial toxins in rotting flesh. Extremely acidic secretions of the vulture stomach ($pH = 1$) can kill all but the most resistant spores, significantly reducing bacterial sources of infection from consumed carcasses [81].

Although efficient scavengers, vultures are vulnerable to poisoning, persecution, power line collisions, habitat loss and human disturbance [9,79]. Vultures are declining worldwide, particularly in south Asia [9,82], where their consumption of cattle tissue laced with the anti-inflammatory drug diclofenac leads to lethal kidney failure [82]. Vulture declines in India appear to have led to increases in rotting carcasses and in attending mammalian scavengers, especially around human habitations [9]. Population explosions of feral dogs and rats, which are disease-carrying scavengers and/or predators, are likely to have public and wildlife health consequences, and could initiate trophic cascades [78].

Scavengers, especially vultures, provide one of the most important yet underappreciated and little-studied ecosystem services of any avian group. A 'before and after' study comparing carcass decomposition rates would have been valuable in quantifying the ecological and societal effects of the population crash of vultures in the Indian subcontinent [9]. If worldwide vulture declines continue, finding an intact community will be increasingly difficult. Therefore, comparative studies on the ecological significance of this unique group are urgently needed.

Non-trophic process linkers

Birds that are non-trophic process linkers (Figure 1d, 2h) supply or facilitate an essential process that influences 'the physicochemical environment rather than the trophic web' [1] and are analogous to allogenic ecosystem engineers [83]. Such birds can indirectly generate ecosystem services, for example by providing frugivorous and predaceous birds with nesting cavities and nectarivorous birds with food resources [16].

Ecosystem engineers

Perhaps the least appreciated avian ecological contribution is ecosystem engineering, mainly via the construction of cavity and burrow nests (Figure 1d, 2h). In addition to drilling cavities that are also used by secondary cavity-nesting species (Figure 1d), some woodpeckers also control insect outbreaks [60] or make nutritious sap available to other organisms [16]. Colonial social weavers *Philateirus socius* construct the largest avian nests, which, in addition to hosting other organisms, can even bring down trees (personal observation). Burrow-nesting European bee-eaters *Merops apiaster* engineer arid ecosystems by extensively removing soil, by creating nest burrows used by other species and by attracting burrow-using invertebrates consumed by other birds [84]. Other burrow nesters (Figure 2h) engineer in tropical forests [85] or on islands (Figure 1b), where colonial seabirds can impact soil fertility and stability [86].

Possibly the most significant avian ecosystem engineer might also be the least acknowledged. The passenger pigeon *Ectopistes migratorius* is sometimes presented as a superabundant species whose decline from billions during the 19th century to none by 1914 appeared to have no measured effects on its ecosystem [87]. However, passenger pigeons, which reached enormous densities in northern red oak *Quercus rubra* forests in North America, probably had substantial non-trophic effects by generating physical disturbance, tree breakage, increased fuel loads and higher fire frequency [88], as well as non-engineering effects via acorn consumption and nutrient deposition. Furthermore, after passenger pigeons went extinct, the oak crop increase might have augmented the populations of white-footed mouse *Peromyscus leucopus* and black-tailed deer *Odocoileus hemionus*, contributing to the higher frequency of Lyme disease currently observed [89]. Fascinating questions concerning ecosystem engineering by birds present an overlooked field of research in need of investigation by avian ecologists.

Conclusions

Birds are important but ecologically little-known actors in many ecosystems. Avian seed dispersal might be the ecological function that affects the greatest number of species, especially considering its importance for late successional tropical trees with large seeds. Consequently, studies of the botanical implications of large avian frugivore extinctions are sorely needed. Compared with seed dispersal, bird pollination is an order of magnitude less common, but still important in regions such as Australia, Oceania and Andean cloud forests, and for certain plant groups such as tropical understorey herbs. The substitutability of avian pollinators remains a key question.

Empirical and experimental studies have shown that, excepting outbreaks, insectivorous birds can suppress populations of insect herbivores and reduce consequent plant damage, but further research is required to understand how frequently this suppression leads to an increase in plant biomass. Similar to insectivores, the indirect effects of raptors might be equally or more important than their direct effects, but more studies are needed, especially in agricultural and urban ecosystems where these effects can have economic value. We know little about the impacts of avian grazing (Figure 2d), but substantial declines in formerly numerous species, such as Aleutian Canada geese *Branta canadensis leucopareia*, could have top-down effects on plants [54]. Although we are becoming increasingly aware of the importance of nutrient deposition by seabirds and of carcass disposal by scavengers, there is a pressing need for further ecological studies, especially to estimate the consequences of the rapid and recent declines in these groups.

The same need exists for birds in general. Declines in bird populations, especially of more vulnerable large-bodied species that have disproportionate and sometimes irreplaceable ecological functions, can rapidly diminish certain ecosystem processes before we can study the underlying mechanisms. Therefore, long-term, experimental and community-level investigations that compare efficiencies (Table 1) of intact and reduced bird populations are urgently required. We also need studies that simultaneously measure the magnitude of an ecological function (e.g. invertebrate consumption) and that of the consequent ecosystem service benefiting humans (e.g. pest control), hence providing 'exchange rates' between ecological functions and ecosystem services. In addition to generating exciting findings, research on avian ecological functions and ecosystem services could help us predict, prepare for and possibly prevent the ecological and economical consequences of bird population declines worldwide.

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