Ecosystem services provided by Neotropical birds

Nicole L. Michel,¹,* Christopher J. Whelan,²,³,⁴ and Gregory M. Verutes¹,⁵,⁶

¹ National Audubon Society, New York, New York, USA
² Department of Cancer Physiology, Moffitt Cancer Center and Research Institute, Tampa, Florida, USA
³ Department of Biological Sciences, University of Illinois at Chicago, Illinois, USA
⁴ Field Museum, Chicago, Illinois, USA
⁵ Faculty of Political and Social Sciences, Universidade de Santiago de Compostela, Santiago de Compostela, Spain
⁶ Campus Do*Mar - International Campus of Excellence, Vigo, Spain
*Corresponding author: Nicole.L.Michel1@gmail.com

ABSTRACT

The Millennium Ecosystem Assessment described 4 classes of services or functions that ecosystems and their component parts deliver to the benefit of humans: provisioning, regulating, supporting, and cultural services. Birds, including Neotropical birds, provide a diverse array of services in all 4 classes. We review the literature describing ecosystem services provided by Neotropical birds, draw inference from studies of avian services in other regions when Neotropical studies are limited, and identify key information gaps. Neotropical birds provide provisioning services in the form of meat and eggs for food, and feathers for down and ornamentation. Regulating services are among the most valuable services provided by Neotropical birds, including pollination, pest control, seed dispersal, and scavenging. Neotropical birds also provide supporting services in the form of nutrient cycling, such as through the deposition of guano on offshore islands. Finally, Neotropical birds provide cultural services as pets (caged birds), sources of recreation (e.g., birdwatching, hunting), as well as by inspiring art, photography, and religious customs. Much remains to be learned about the ecology and natural history of many Neotropical birds before we can fully assign value—monetary, nonmaterial, or otherwise—to the services they provide. However, what we have learned to date makes it clear that humans benefit from birds through multiple services, including but not limited to pest reduction, pollination of some agricultural plants, and seed dispersal.

Keywords: ecosystem services, Neotropical birds, pest control, pollination, seed dispersal

Servicios ecosistémicos provistos por aves neotropicales

RESUMEN

La Evaluación de los Ecosistemas del Milenio describe cuatro clases de servicios o funciones que los ecosistemas y sus partes componentes proveen para el beneficio de los humanos: servicios de abastecimiento, de regulación, de apoyo y culturales. Las aves, incluyendo las aves neotropicales, proporcionan una amplia gama de servicios en todas las cuatro clases. Revisamos la literatura que describe los servicios ecosistémicos provistos por las aves neotropicales, sacamos inferencias de estudios de servicios de las aves en otras regiones cuando los estudios neotropicales no alcanzaron, e identificamos vacíos claves de información. Las aves neotropicales proveen servicios de abastecimiento en forma de carne y huevos para alimento, y plumas para plumón y ornamentación. Los servicios de regulación están entre los servicios más valiosos provistos por las aves neotropicales, incluyendo polinización, control de plagas, dispersión de semillas y consumo de carroña. Las aves neotropicales también proveen servicios de apoyo en forma de cíclado de nutrientes, por ejemplo, a través de la deposición de guano en islás de alta mar. Finalmente, las aves neotropicales proveen servicios culturales como mascotas (aves en jaula), fuentes de recreación (e.g., avistamiento de aves, cacería), así como inspirando arte, fotografía y costumbres religiosas. Queda mucho por aprender sobre la ecología y la historia natural de muchas aves neotropicales antes de que podamos asignar el valor completo—monetario, inmaterial o de otra manera— a los servicios que ellas proveen. Sin embargo, lo que hemos aprendido a la fecha deja en claro que los humanos se benefician de las aves a través de múltiples servicios, que incluyen, entre otros, reducción de plagas, polinización de algunas plantas agrícolas y dispersión de semillas.

Palabras clave: aves neotropicales, control de plagas, dispersión de semillas, polinización, servicios ecosistémicos
INTRODUCTION

Nature’s Services
We first review what ecosystem services are and how the concept was developed. The demand for ecosystem services information has grown exponentially over the last 20 yr, following the 1997 release of Nature’s Services: Societal Dependence on Natural Ecosystems (Daily 1997). Previous research had evaluated and described concepts such as “environmental services,” “ecological services,” and even “ecosystem services” (Westman 1977, Ehrlich and Ehrlich 1981, Mooney and Ehrlich 1997, Costanza et al. 1997). However, it was Nature’s Services that provided the clearest definition of what ecosystem services are, as “the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life” (Daily 1997, p. 3). This work kicked off 2 decades of research aimed at understanding the mechanisms and magnitude of services that ecosystems and their component parts deliver to the benefit of humans.

Next, the Millennium Ecosystem Assessment (MEA; Millennium Ecosystem Assessment 2005) challenged managers and policymakers to acknowledge recent losses to ecosystem services that communities will continue to experience under a future of business as usual. The MEA groups ecosystem-based benefits into 4 distinct categories: provisioning, regulating, supporting, and cultural services. Provisioning services describe material outputs such as food, water, and medicine; regulating services regulate processes such as herbivory and carbon sequestration; supporting services describe services that support other species or biodiversity (e.g., woodpeckers’ nest cavities used secondarily by other species); and cultural services describe qualitative benefits to humans such as recreation and spiritual experiences. Scientists and economists use ecological production functions to quantify current and future flows of ecosystem services in biophysical and economic terms based on social, political, economic, and technological drivers, along with changes in the distribution and intensity of demand for services by human beneficiaries. Still, the full suite of goods and services that healthy, functional ecosystems provide to people are typically undervalued and misunderstood (Costanza et al. 1997, Guerry et al. 2015).

Ecosystem Services Provided by Birds
Birds provide benefits from all 4 classes of ecosystem services—provisioning, regulating, supporting, and cultural services—to ecosystems and people (Table 1). Where services could fall under more than one category (e.g., seed dispersal may be classified as either a regulating or supporting service), we follow the definitions in the Millennium Ecosystem Assessment (2005). Provisioning services include birds or bird parts used as food, clothing, tools, or ornamentation (Whelan et al. 2016a). Bird-based regulatory services include pollination, pest control, and seed dispersal (Şekercioğlu 2006, Klein et al. 2007, Peisley et al. 2015, Maas et al. 2016, Wenny et al. 2016). Birds also provide services that support life on Earth, such as nutrient cycling (e.g., aquatic fish-eating birds nesting on oceanic islands move phosphorus from ocean to shore) and ecosystem engineering (e.g., cavity-forming birds create habitat for numerous other organisms; Floyd and Martin 2016, Fujita and Kameda 2016). The cultural services supported by birds include recreational opportunities for people such as tourism and wildlife viewing (Belaire et al. 2015). Whelan and colleagues (2008) further organize these services into those that result from bird behavior vs. products.

In the Anthropocene, where humans dominate every flux and cycle of the planet’s ecology and geochemistry (Caro et al. 2012, Kareiva et al. 2012), the ecosystem services of birds are an opportunity to demonstrate that where birds thrive, people can also prosper. Bird-focused tourists flock to areas where they can see rare species or large and diverse communities of birds and the often-pristine habitats that support them (Maple et al. 2010, Wood et al. 2013). By drawing tourists to areas they might not otherwise visit, birds can provide important socioeconomic benefits such as ecotourism (Carver et al. 2009, Lee et al. 2010). This is particularly important in postwar nations of the Neotropics such as Colombia, which supports 20% of all bird species worldwide, and which could benefit from an estimated US$9 million annually in bird-based travel by North Americans alone (Maldonado et al. 2018). In some cases, the protection of natural areas (e.g., parks) for birds and birding tourism may provide additional services (or “co-benefits”) such as scenery, water quality, climate regulation, freshwater availability, and shoreline protection (Outeiro and Villasante 2013, Keeler et al. 2015, Holding and Allen 2016, Verutes et al. 2017). Ecosystem service co-benefits are a lens through which the conservation of birds, and the habitats they rely upon, can illuminate potential options for maintaining or even enhancing a larger suite of services delivered to people now and into the future.

Unique to the Neotropics is the immense diversity of flora and fauna, which is part of a phenomenon known as latitudinal species gradients (Stevens 1989). For example, ~30% of the world’s species of birds occur in the Amazon Basin, and there are more than 1,500 species of breeding birds in Colombia compared with just 195 in New York State (Forsyth and Miyata 1984). This means that ecosystem stocks and services are many and varied in the Neotropics, and that there is great potential for multiple forms of capital (natural, social, political, and others) to interact and generate life- and livelihood-giving services (Daily et al. 2009, Guerry et al. 2015). The Neotropics, with...
TABLE 1. List of notable ecosystem services provided by Neotropical birds, summarized by family (Passeriformes) or order. Common or distinctive ecosystem services are listed for each order or family, rather than a complete listing. As all bird species provide cultural services such as bird-based tourism, contribution to knowledge, and inspiration for art and religion, these services are not listed here except for specific examples included in this article.

| Order               | Families                      | Representative species                      | Ecosystem services                                                                 |
|---------------------|-------------------------------|--------------------------------------------|-----------------------------------------------------------------------------------|
| Rheiformes          | Rheidae                       | Rheas                                      | Food                                                                              |
| Tinamiformes        | Tinamidae                     | Tinamous                                   | Food, seed dispersal, nutrient cycling                                           |
| Anseriformes        | Anatidae, Anhimidae           | Ducks, geese, waterfowl, screamers         | Food, medicine, ornament, nutriment cycling                                       |
| Galliformes         | Cracidae, Numididae, Odontophoriidae, Phasianidae | Guans, curassows, quail, grouse, and allies | Food, medicine, tools, ornament, seed dispersal                                   |
| Phoenicopteriformes | Phoenicopteridae              | Flamingos                                  | Food, ornament, medicine                                                         |
| Podicipediformes    | Podicipedidae                 | Grebes                                     | Food, medicine, ornament, seed dispersal                                          |
| Columbiformes       | Columbidae                    | Pigeons, doves                             | Food, medicine, ornament, pest control                                           |
| Cuculiformes        | Cuculidae                     | Cuckoos                                    | Food                                                                             |
| Caprimulgiformes    | Caprimulgidae, Nyctibiidae, et al. | Nightjars, potoos, oilbird, and allies     | Food, medicine, ornament, pollination, pest control, knowledge                   |
| Apodiformes         | Apodidae, Trochilidae         | Swifts, hummingbirds                       | Knowledge                                                                       |
| Opisthocomiformes   | Opisthocomidae                | Hoatzin                                    | Food, medicine, ecosystem engineering, nutrient cycling                          |
| Gruidiformes        | Rallidae, Helmornithida, Aramidae, Psophidae, Gruidae | Rails, gallinules, coots, limpkin, sungrebe, trumpeters, cranes            | Food, ecosystem engineering, nutrient cycling                                     |
| Charadriiformes     | Charadriidae, Jacanidae, Scolopacidae, Stercorariidae, Alcidae, Laridae, et al. | Shorebirds, jacanas, skuas, jaegers, auks, murrels, puffins, gulls, terns, skimmers | Ecosystem engineering, nutrient cycling                                          |
| Eurypygiformes      | Eurypygidae                   | Sunbittern                                 | Nutrient cycling                                                                 |
| Phaethontiformes    | Phaethontidae                 | Tropicbirds                                | Ornament, nutrient cycling                                                        |
| Gaviiformes         | Gaviidae                      | Loons                                      | Medicine, scavenging, tourism, art, religion, disservices                         |
| Sphenisciformes     | Spheniscidae                  | Penguins                                   | Food, medicine, tools, ornament, scavenging, falconry, art, religion, disservices |
| Procellariiformes   | Diomedeidae, Oceanitidae, Procellariidae, et al. | Albatrosses, storm-petrels, shearwaters, petrels | Medicine, ornament, ecosystem engineering, religion                             |
| Ciconiformes        | Ciconiidae                    | Storks                                     | Food, ornament, seed dispersal, ecosystem engineering, tourism, art, religion     |
| Suliformes          | Fregatidae, Sulidae, Anhingidae, Phalacrocoracidae | Frigatebirds, boobies, gannets, anhingas, cormorants | Food, ornament, ecosystem engineering                                             |
| Pelicaniformes      | Pelecanidae, Ardeidae, Threskiornithidae | Pelicans, herons, egrets, bitterns, ibises, spoonbills | Food, ornament, ecosystem engineering                                             |
| Cathartiformes      | Cathartidae                   | New World vultures                         | Medicine, ornament, ecosystem engineering, tourism, art, religion, disservices   |
| Accipitriformes     | Pandionidae, Accipitridae     | Osprey, hawks, eagles, kites               | Food                                                                               |
| Strigiformes        | Tytonidae, Strigidae          | Owls, barn-owls                            | Medical, ornament, ecosystem engineering                                           |
| Trogoniformes       | Trogonidae                    | Trogons, quetzals                          | Food                                                                               |
| Coraciiformes       | Todidae, Motmotidae, Alcedinidae | Todies, motmots, kingfishers              | Food, ornament, ecosystem engineering, tourism, art, religion                     |
| Galbulifomines      | Buccoidea, Galbulidae         | Puffbirds, jacamars                         | Food, pest control, ecosystem engineering                                         |
| Piciformes          | Capitonidae, Semonornithidae, Ramphastidae, Picidae | New World barbets, toucans, woodpeckers | Food, medicine, ornament, pest control, seed dispersal, ecosystem engineering, disservices |
| Cariamiformes       | Cariamidae                    | Seriemas                                   | Food, medicine, pest control, falcony                                             |
| Falconiformes       | Falconidae                    | Falcons, caracaras                         | Food, medicine, ornament, pollination, seed dispersal, ecosystem engineering, tourism, caged birds, disservices |
| Psittaciformes      | Psittacidae                   | New World and African parrots              | Food                                                                               |
**TABLE 1.** Ecosystem services provided by Neotropical birds

| Order         | Families               | Representative species                                      | Ecosystem services                                      |
|---------------|------------------------|------------------------------------------------------------|----------------------------------------------------------|
| Passeriformes | Thamnophilidae         | Suboscine and oscine perching birds                        | Pest control                                             |
|               | Conopophagidae         | Typical antbirds                                           | Pest control                                             |
|               | Grallariidae           | Gnateaters                                                 | Pest control                                             |
|               | Rhinocryptidae         | Antpittas                                                  | Pest control                                             |
|               | Formicariidae          | Anthrushes                                                 | Pest control                                             |
|               | Furnariidae            | Ovenbirds, woodcreepers                                    | Pest control                                             |
|               | Tyrannidae             | Tyrant flycatchers                                         | Pest control                                             |
|               | Pipridae               | Manakins                                                   | Pest control                                             |
|               | Cotingidae             | Cotingas                                                   | Pest control                                             |
|               | Tityridae              | Tityras and allies                                         | Pest control                                             |
|               | Laniidae               | Shrikes                                                    | Pest control                                             |
|               | Vireonidae             | Vireos and allies                                          | Pest control                                             |
|               | Corvidae               | Crows, jays, magpies                                       | Medicine, pest control                                    |
|               | Hirundinidae           | Swallows                                                   | Medicine, pest control                                    |
|               | Paridae                | Titmice, chickadees                                        | Pest control                                             |
|               | Troglodytidae          | Wrens                                                      | Pest control                                             |
|               | Polioptilidae          | Gnatcatchers                                              | Pest control                                             |
|               | Turdidae               | Thrushes and allies                                        | Pollination, pest control, seed dispersal               |
|               | Mimidae                | Mockingbirds, thrashers                                    | Pest control                                             |
|               | Motacilidae            | Wagtails, pipits                                          | Pollination, pest control, seed dispersal               |
|               | Fringillidae           | Finches, euphonias                                         | Food, ornament, pollination, seed dispersal             |
|               | Passerellidae          | New World sparrows                                        | Ornament, pest control, seed dispersal, disservices      |
|               | Icteridae              | Blackbirds, orioles, caciques and allies                   | Food, medicine, ornament, pollination, pest control, seed dispersal, disservices |
|               | Parulidae              | New World warblers                                         | Food, ornament, pollination, seed dispersal             |
|               | Cardinalidae           | Cardinals and allies                                       | Ornament, pollination, pest control, seed dispersal      |
|               | Thraupidae             | Tanagers and allies                                        | Food, ornament, pollination, seed dispersal             |
|               | Passeridae             | Old World sparrows                                         |                                                         |

*Only selected families of Passeriformes are presented, including families that are particularly diverse, abundant, and/or provide substantial or unique ecosystem services.*
its rich natural capital, including high biodiversity as well as rare, threatened, and endemic birds, offers the opportunity to put ecosystem services science into practice for improved management and policy.

**ECOSYSTEM SERVICES PROVIDED BY NEOTROPICAL BIRDS**

**Provisioning Services**

**Food.** Large Neotropical birds such as curassows, guans, and chachalacas (Craciidae), tinamous (Tinamidae), woodquails (Odontophorus spp.), and trumpeters (Psophia spp.) provide important food resources for humans. In the tri-frontier region of Brazil, Peru, and Colombia, 11% of rural residents had consumed bushmeat the previous day, with birds accounting for 26% of bushmeat taxa (Van Vliet et al. 2014). Andean Flamingos (Phoenicopterus andinus) were hunted extensively throughout their range during the 1980s and 1990s, resulting in an estimated population loss of 50,000–100,000 individuals; and reduced hunting still continues to threaten flamingo populations today (U.S. Fish and Wildlife Service 2010). Low-income rural residents of Brazilian Amazonia traditionally hunted and consumed an estimated 23 to 56 million wild birds annually, totaling 145,000 to 356,000 tons of avian biomass (Peres 2000). Birds have been an important part of the diets of native tribes in the Amazon basin, where subsistence hunters killed an average of 0.9 guans (Penelope spp.) and toucans (Ramphastos spp.) per hunter per year (Redford and Robinson 1987). In Colombia, the Maraca Indians hunted an estimated 51 species of birds for food, including 10 species of hummingbirds (Table 1; Ruddle 1970). Non-native hunters kill fewer birds than sustainable hunters in the Neotropics (Redford 1992), yet large birds such as tinamous and curassows are among the first species to disappear from forests with legal or illegal hunting in regions ranging from remote Amazonian villages (Peres 2001) to the Panamanian Canal zone (Robinson et al. 2000).

Bird eggs also provide a source of food for people in the Neotropics. Eggs collected from wild birds accounted for 0.2% of the diet of a Machiguenga tribe studied in Peru (Kaplan and Kopischke 1999), and were frequently eaten by the Maraca Indians (Ruddle 1970). Rhea (Rhea americana) eggs have been an important seasonal food for the Sirionó of Bolivia (Stearman 1999). Eggs of Andean, Chilean (Phoenicopterus chilensis), and James Flamingos (P. jamesi) have long been collected for food across their range, and this activity continues to threaten populations today (U.S. Fish and Wildlife Service 2010). Villagers near the Salinas and Aguada Blanca Nature Reserve in southern Peru have an ample protein supply from llama and alpaca husbandry, yet collected flamingo eggs due in part to a lack of awareness that these are protected species (Ugarte-Núñez and Mosaurieta-Echegaray 2000).

**Tools.** Bird bones are used by native tribes to produce tools such as awls, needles, drills, punches, tubes, and multi-function tools. Bird bones were preferred over mammal bones for awls and punches by tribes in southern California (Breitborde 1983). The reason for this preference is not clear, but bird bone awls—which are rare elsewhere—appeared early in southern Californian islands, where mammals were limited, spread across southern California, and persisted through the historic period (Meighan 1959). Bird bone tools have been found at archaeological sites across the Neotropics, including Mexico (Teeter 2013), southern Patagonia (Scheinsohn 2013), and Los Toldos, Argentina (Miotti and Marchionni 2013). Feathers were also used to produce tools such as arrows, whisks, and fans (Castello Yturvide 1993).

**Clothing and ornamentation.** Feathers were traditionally used to produce, decorate, and ornament clothing in Mexico, Central and South America, and were still used into the late 20th century to produce huipils (traditional Yucatecan women’s dress) and costumes for traditional dances (González-Hontoria de Álvarez Romero 1973, Stark 1974, Rowe 1984). Feathers from a wide range of taxa were used, particularly brightly colored birds such as parrots, trogons (including quetzals), cotingas, motmots, oropendolas, egrets, eagles, grosbeaks, spoonbills, honeycreepers, cuckoos, and hummingbirds (Castello Yturvide 1993). Feathers were highly valued in Mesoamerica due to their perceived magical properties in bringing luck.

**Medicine.** Birds feature in traditional folk medicine across the Neotropics. At least 48 bird species in 19 families are used in traditional Mexican folk medicine (Table 1; Alonso-Castro 2014). Birds are primarily used for magical-religious practices, including 62% of all bird species and all owls (Strigidae), which are believed to be messengers warning that something bad is about to happen. However, the meat or eggs of at least 20 species are consumed to treat illnesses such as epilepsy or injuries such as snakebites (Guerrero-Ortiz 2013). In other cases, fat, bile, or excrement is rubbed on the skin to treat pain, infection, or dandruff (Corona-Martinez 2008, Alonso-Castro et al. 2011). Feathers of Turkey Vultures (Cathartes aura) are burned, with the smoke inhaled to treat asthma and diabetes, and the ashes used to treat burns (Jacobo-Salcedo et al. 2011, Serrano-González et al. 2011). Similarly, Andean Flamingo meat, blood, and feathers are used medicinally in incense or oil form (U.S. Fish and Wildlife 2010). In lab studies, extracts from the body tissues and eggs of Common Raven (Corvus corax), Wild Turkey (Meleagris gallopavo), and Domestic Chicken (Gallus gallus domesticus) showed antimicrobial activity against pathogenic bacteria (Shaharabany et al. 1999, Wellman-Labadie et al. 2008), and extracts from Turkey Vulture (Cathartes aura) meat showed cytotoxic effects against human cancer cells (Jacobo-Salcedo et al. 2013).

**Feathers were tradition-
Mayans raised birds for feathers as well as food, and Aztecs used feathers to decorate ceremonial shields, doublets, and ceremonial garments. The Purépecha of Mexico used feather-decorated pieces of wood to declare war, and buried soldiers killed in war with feathers (Castello Yturbe 1993). Andean Flamingo feathers have long been used for adornment and ritualistic purposes (U.S. Fish and Wildlife Service 2010). Bird bones were also used by Neotropical tribes to create beads and other jewelry pieces (McCafferty and McCafferty 2009).

Regulating Services

Pollination. Pollination is critical for successful reproduction of flowering plants. Worldwide, animal vectors pollinate ~78% of flowering plants, and that increases to ~94% in the tropics (Ollerton et al. 2011). Arthropods (mostly insects in the orders Lepidoptera, Hymenoptera, and Coleoptera) are the most important pollinators relative to the number of flowering plant species they pollinate. Although long considered rare and localized to specific geographical regions and a few bird taxa, research over recent decades has revealed that bird pollination is considerably more common than previously thought (Anderson et al. 2016, M. Betts personal communication). Bird pollination services range from highly specialized interactions between certain bird and flower species, to more opportunistic interactions of low specificity. Recent work has documented the importance of bird pollination by evaluating how the absence of bird pollinators affects pollination success (Anderson et al. 2016). We will provide a brief overview of what major bird taxa and plant growth forms are involved in pollination services, where these services are most frequently found geographically, how these services benefit the functioning of ecosystems, and how they benefit humans.

Worldwide, nearly 1,200 bird species are involved with pollination services in some way (Anderson et al. 2016). Of these, the most important families are the hummingbirds (Trochilidae, 330 species, Neotropical endemics), the honeyeaters (Meliphagidae, 176 species), and the sunbirds (Nectariniidae, 130 species). Anderson et al. (2016) classified bird taxa that provide pollination services along a continuum of specialization based on inclusion of nectar in the diet, and morphological traits like a brush tongue and hovering flight. Three of the 11 major groups of flower-visiting birds named are found in the Neotropics, and only the Neotropical Trochilidae are highly specialized. One Neotropical group, Thraupidae (honeycreepers), was classified as highly specialized, and the remaining Neotropical group, Icteridae (blackbirds), was classified as having low specialization for pollination.

Information on the number of plant species pollinated by birds is even more incomplete. Estimates range from 2.1 to 3.4% of flora at sites in Costa Rica (Sekercioglu 2006), 1.7–2.4% of trees on Barro Colorado Island, Panama (Bush and Riviera 2001), 2% of woody plants in Cerrado forest of central Brazil (Martins and Batalha 2006), and are likely similar elsewhere in the Neotropics. Across the Neotropics, at least 20 species of lianas (woody vines) are pollinated by birds (Michel et al. 2014a). These pollination rates are lower than those reported elsewhere, which
range up to 10% on some islands (Kato and Kawakita 2004, Whelan et al. 2008), and 15% in Australia (Armstrong 1979, Keighery 1982, Johnson 2013, each cited in Anderson et al. 2016). Kelly et al. (2010) reported flowers of 85 plant species (5% of flora) were visited by birds in New Zealand. Bird pollination varies with plant growth form, with trees most represented in the Paleotropics and Australasia (Anderson et al. 2016), and shrubs and epiphytes most represented in the Neotropics (Whelan et al. 2008).

Bird pollination of agricultural crops in the tropics is apparently minor. Pantropical estimates of agricultural crop pollination by birds ranges between 4.3% of 1,330 crop plants (Roubik 1995) and 5.4% of 960 crop plants (Anderson et al. 2016). In the Neotropics, birds pollinate an estimated 6.4% of 422 economically important crop plants (Roubik 1995). Nonetheless, examples of economically important plant species whose primary pollinators are birds do exist, including (Figure 1):

- Feijoa, aka pineapple guava (Acca sellowiana), native to South America, is grown commercially and ornamentally in the Neotropics and beyond. Although the plants contain no nectar, petal-consumming bird species in the families Turdidae and Thraupidae are responsible for pollination in South America (Ramirez and Kallarackal 2017), which occurs when they eat the rolled petals that resemble berries (Westerkamp and Gottsberger 2000, Anderson et al. 2016).
- Papaya (Carica papaya) is grown commercially for fruit production in the Neotropics. It is pollinated by a variety of bird and insect pollinators, including the Cinnamon Hummingbird (Amazilia rutila) and Canivet’s Emerald (Chlorostilbon canivetii) in Mexico’s Yucatan Peninsula (Badillo-Montaño et al. 2018).
- Hummingbirds are the primary pollinators of wild pineapple (Ananas comosus). Because pollination reduces fruit quality, the importation of hummingbirds into Hawaii, a major fruit production region, is forbidden. However, pollination is necessary for seed production, and cultivated pineapples are strictly hand-pollinated (Westerkamp and Gottsberger 2000).

An important consideration is that bird pollination may be underestimated in general, and in agricultural crops in particular, for 2 reasons: (1) many agricultural plants have flowers with morphologies that do not fit the notion of “ornithophilous” flowers. Ornithophilous flowers tend to be red or orange, with long corolla tubes, and sucrose-rich, dilute nectar (Cronk and Ojeda 2008). Although most bird-pollinated plant species possess ornithophilous flowers, birds are known to pollinate some plants with non-ornithophilous flowers (Anderson et al. 2016), and these may include some agricultural plants; and (2) bird pollination may be more effective than that of insects like bees, which tend to move from flower to flower within a plant, and which tend not to move long distances (but see Janzen 1971). By traveling long distances, birds may increase outcrossing rates relative to insect pollinators. This is especially true in tropical forests, in which many plant species occur at low density and at considerable distances from each other. Birds are also active throughout the year and under a wider range of weather conditions, making them more reliable and consistent pollinators than insects (Triplet et al. 2012). Bird pollination in both natural and agroecosystems deserves greater research emphasis.

**Pest control.** Birds provide an important ecosystem service by suppressing insect pests. Arthropod pests damage 8–15% of global wheat, rice, maize, potato, soybean, and cotton crops; without biological control and pesticides, 9–37% of crops would be lost (Oerke 2006). In the United States, arthropod pests reduce crop production by 13%, at a cost of US$33 billion (Pimentel et al. 2005). Insectivorous birds consume a wide variety of arthropod prey, including herbivorous and frugivorous insects that stunt plant growth and reduce crop yield (Whelan et al. 2016b). As a result, insectivores, including insectivorous birds, impact the evolution, abundance, and behavior of their arthropod prey (Holmes 1990). These ecosystem services are particularly important in the tropics, including the Neotropics, where insectivorous bird diversity reaches its peak (Maas et al. 2016, Sherry et al. 2020). Insectivores account for nearly half of the world’s ~10,700 known bird species, but over 60% of the ~4,000 known Neotropical bird species (Şekercioğlu et al. 2004, Wilman et al. 2014, Maas et al. 2016). Insectivorous birds are most dominant in forests, where they comprise nearly 70% of bird species worldwide, but account for over half of the bird species found in agricultural and mixed forest-agricultural ecosystems in the Neotropics and globally (Şekercioğlu 2012, Maas et al. 2016).

Insectivorous birds suppress arthropods and thereby indirectly benefit plants, including crops, in what is known as a trophic cascade (reviewed in Whelan et al. 2016b). Trophic cascades occur in tropical, temperate, and boreal ecosystems in the western and eastern hemispheres alike with similar effect sizes (Mooney et al. 2010, Mântylä et al. 2011, Morrison and Lindell 2012). Exclusion experiments show that insectivorous birds in natural Neotropical habitats effectively control arthropod herbivores at sub-outbreak levels and reduce leaf damage, increase plant growth, and/or increase fruit yield (reviewed in Maas et al. 2016; note that insectivorous bats also contribute to arthropod and herbivory suppression). Insectivorous birds may even limit the extent of herbivore outbreaks in Neotropical forest (Van Bael et al. 2004). The suppression of arthropods and herbivory has been documented in communities with the
following characteristics (all studies cited below were conducted partially or entirely in Neotropical forests and/or agroecosystems):

- higher bird species and functional richness (Philpott et al. 2009, Michel 2012);
- more generalist predators (Karp et al. 2013);
- higher seasonality and leaf turnover (Van Bael and Brawn 2005);
- higher plant quality (Michel et al. 2014b);
- larger arthropods (Greenberg et al. 2000b);
- lower herbivorous arthropod diversity (Schmitz et al. 2000, Van Bael and Brawn 2005);
- more arthropod predators and greater intraguild predation (i.e. bird consumption of arthropod predators; Mooney et al. 2010).

Twenty-four bird species have provided documented benefits to agroecosystems in Central America and the Caribbean (Peisley et al. 2015), and many more species contribute via indirect effects. Trophic cascade strength is similar in natural and agricultural environments globally (Mäntylä et al. 2011) and in the Neo- and Paleotropics (Van Bael et al. 2008, Maas et al. 2016). Insectivorous birds suppress arthropod herbivores and plant damage in Neotropical agroforestry systems including coffee (shaded and unshaded mono- and polycultures), cacao, and Inga spp. (reviewed in Van Bael et al. 2008, Maas et al. 2016). Birds are particularly effective at suppressing arthropods and herbivory during boreal winter, when Neotropical agroforests experience influxes of Nearctic–Neotropical migrant birds (Greenberg et al. 2000a, Williams-Guillen et al. 2008). Birds significantly reduced leaf damage across 7 Neotropical exclosure experiments (Van Bael et al. 2008). Birds also contribute to increasing coffee yield by consuming coffee berry borers, saving US$44–310 ha$^{-1}$ in Jamaican and Costa Rican coffee plantations (Kellermann et al. 2008, Johnson et al. 2010, Karp et al. 2013).

Neotropical rainforest understory insectivorous birds, including species that may provide pest control services in agroforestry environments, have experienced significant population declines and extirpations (Şekercioğlu et al. 2002, 2004, Stratford and Robinson 2005, Sigel et al. 2010, Visco et al. 2015, Martinez et al. 2020). The loss of understory insectivorous birds in the Neotropics could have dramatic ecosystem-wide consequences in both natural and agricultural environments via herbivorous arthropod release unless other insectivores are able to compensate or efforts are undertaken to bolster insectivorous bird abundance (Şekercioğlu et al. 2004, Şekercioğlu 2006, Whelan et al. 2008). Increasing forest cover within or adjacent to agricultural fields and increasing habitat complexity at the landscape scale have been shown to increase pest control and crop yields in Neotropical systems (Bianchi et al. 2006, Chaplin-Kramer et al. 2011, Karp et al. 2013; but see Tscharntke et al. 2016). Crop type also influences pest control service provision (Tscharntke et al. 2016) (e.g., insectivorous bird suppression of arthropods, herbivory, and yield loss is greater in sun than shade coffee in the Neotropics; Greenberg et al. 2000b, Johnson et al. 2009). In addition to increasing pest control and crop yields, insectivorous birds may help reduce pesticide use and provide cultural services in the form of birdwatching and ecotourism (Lindell et al. 2018).

Habitat structure also influences insectivorous bird abundance and provision of ecosystem services. In natural forests, lianas (i.e. woody vines) provide important food resources, nesting and roosting sites, and protection of predators to birds, including 148 insectivorous bird species (Michel et al. 2014a). Abundance of several Neotropical insectivorous bird species increases with increasing liana density and cover (Michel et al. 2015), and one of these species (Checker-throated Antwren [Epinecrophylla fulviventris]) suppressed arthropod abundance by 44% in forest understory (Gradwohl and Greenberg 1982). Therefore, maintaining lianas, which are often viewed as detrimental to Neotropical forests (reviewed in Michel et al. 2014a), in agroforests or adjacent forest patches, may contribute to increased pest control services.

**Seed dispersal.** Seed dispersal is the movement away from the mother plant of her seeds; mechanisms include ballistic projection, wind, water, or animal vectors. Bird-vectored seed dispersal is widely viewed as a diffuse mutualism; many bird species consume the fruit of multiple plant species. Likewise, most fruit-producing plant species have their fruits consumed by multiple bird species. The birds gain nutrients and energy, while the plant’s seeds escape pathogens, predators, and competitors. Wenny et al. (2016) provide a recent and comprehensive review. The multiplicity of fruiting plant species and bird disperser species often forms complex interaction networks. In some specialized cases, however, bird species have evolved closer dispersal interactions with particular plant species; these often involve members of the Corvidae (see a comprehensive review in Tomback 2016). Seed dispersal may be the paramount ecosystem service provided by birds, and the importance of seed dispersal by birds is much greater in the tropics than elsewhere (Wenny et al. 2016).

Estimates of the number of bird species and the number of plant species involved in dispersal networks is still incomplete and in need of further research. Over 4,000 bird species (~40% of all bird species on the planet) are reported to include fruit as part of their diet (Wenny et al. 2016, Carlo et al. 2020). For most of these species, fruit constitutes >30% of the diet. In the Neotropics, ~539 bird species consume >50% fruit in their diet, and an estimated
additional 1,106 species consume up to 50% fruit in their diet (Wenny et al. 2016). On Barro Colorado Island in Panama, 79 species of birds consume seeds and/or fruits (Willis 1980), and ~30% (lianas) to >80% (midsstory, understory, and shrub) plant species are primarily dispersed by birds (Muller-Landau and Hardesty 2005). Overall, birds consume and disperse an estimated 16 kg ha⁻¹ of seeds on Barro Colorado Island (Muller-Landau and Hardesty 2005). Wenny et al. (2016) reported that almost 69,000 plant species in over 1,500 genera and over 240 families (including gymnosperms, basil angiosperms, monocots, and eudicots; ~25% of total seed-producing plant species and ~50% of all plant families) are known or suspected to be dispersed by birds. Bird seed dispersal is common in tropical and temperate latitudes, and in terrestrial and aquatic ecosystems. Green et al. (2016) provide a comprehensive review of seed dispersal by aquatic birds.

In the tropics, plant communities are dominated by woody plant species, and, regionally, birds disperse the seeds of 65–75% of tree species and 40–60% of the shrub species (Wenny et al. 2016). Which fruits are consumed by birds is constrained by maximum gape size, which determines how wide they can open their bills. Consequently, owing to gape size variation among bird species, most bird-dispersed fruits worldwide are small (mean diameter ≤12 mm; Wenny et al. 2016). Less than 2% of a sample of 376 bird species with known gape size had gapes exceeding 34 mm. Because a greater proportion of these larger bird dispersers tend to be at risk of extinction than the smaller dispersers, their dispersal services are also more at risk of disruption. Most of these large species occur in the tropics, with curassows and guans (Cracidae) and toucans (Ramphastidae) living in the Neotropics. Nonetheless, many small bird species also disperse some fruits, and declining populations owing to forest fragmentation and other threats also put their dispersal services at risk (Cordeiro and Howe 2003).

As discussed by Wenny et al. (2011 and 2016), determining the economic value of seed dispersal is difficult for multiple reasons: the benefits accrue only after many decades for forest trees, and many of those benefits (e.g., carbon sequestration, habitat for other organisms, timber production) impact humans indirectly. In tropical forests, up to 59% of the genera and up to 47% of timber volume comes from tree species who depend upon animal seed dispersal (Wenny et al. 2016). Tropical tree genera with bird seed dispersal include timber species (e.g., Aniba, Beilschmiedia, Guaiacum, Guarea, Nectandra, Ocotea, Protium, Ocotea, Scheffera, Simarouba, Terminalia, Trichilia, and Virola), edible species (including some spices; e.g., Cinnamomum, Euterpe, Malpighia, Myristica, Erythroxylon, Ilex, Paulinia, Plinia, Psidium, Solanum, Stenocereus, and Vaccinium), species with medicinal uses (e.g., Bursera, Clusia, Drimys, Ephedra, Erythroxylum, Ocotea, Paulinia, and Virola), ornamentals (e.g., Bursera, Cecropia, Coccoloba, Coccolithax, Diefenbachia, Monstera, Philodendron, Roystonea, and Schinus), and those with other uses (Bixa). Most of these species are not propagated commercially and rely instead on natural seed dispersal.

Many efforts to estimate the economic value of bird dispersal services have calculated the replacement cost of those services with human labor (see Tomback 2016 for examples and an itemization of one such example). To date, these economic valuations have used examples from temperate systems. The results are eye-opening: the cost of replacing the dispersal service of a single pair of Eurasian Jays (Garrulus glandarius) to maintain oak forest in a Swedish park ranges from ~US$5,000 to over US$22,000. Similar calculations have estimated the value of seed dispersal services of whitebark pine (Pinus albicaulis) by Clark's Nutcracker (Nucifraga columbiana) at ~US$2,000 ha⁻¹. Replacing those services across the 5,770,000-ha range of whitebark pine would cost from US$11.425 billion to US$13.877 billion (Tomback 2016).

We know of no similar examples of estimates of replacement costs of natural bird seed dispersal services yet from the tropics. Neotropical plants often rely on multiple species or guilds of dispersers (e.g., birds and mammals or wind), and the higher diversity of both bird, mammalian, and insect dispersers in the Neotropics relative to temperate regions reduces dependence on any given bird species. For example, 60% of Barro Colorado Island’s plant species are dispersed by multiple animal guilds (Muller-Landau and Hardesty 2005). Yet avian seed dispersal benefits many plants by increasing the probability of germination (Traveset and Verdú 2002), and dispersing seeds far from parent trees in a more scattered fashion than other dispersal modes, where they can escape predation and disease pressure (Howe 1989). Additionally, directed dispersal of seeds to gaps, where seedlings have better odds of recruitment, by gap-dwelling species such as bellbirds, benefits many tree species (Wenny and Levey 1998, Dalling and Hubbell 2002). Indeed, a 10-yr seed trap study on Barro Colorado Island found that seed dispersal, through its effects on seedling recruitment, was essential for maintaining tropical tree biodiversity (Hubbell et al. 1999). Therefore, given the large number of plant species in the tropics that depend upon natural bird seed dispersal, and the crucial benefits birds provide for both individual plant species and community-level biodiversity, the costs of replacing lost avian seed dispersal services in the Neotropics could be astronomical.

Scavenging. The importance of carrion consumption by scavenging birds became dramatically evident following the rapid and catastrophic population declines of 5 vulture
species in South Asia in the late 20th century (Green et al. 2004; Oaks et al. 2004; see a comprehensive review of avian scavenging services in DeVault et al. 2016). Avian scavengers play critical roles in regulating disease (regulating services: DeVault et al. 2016), nutrient transport (supporting services: DeVault et al. 2003, Ogada et al. 2012), and, more recently, they have become attractions for ecotourism (cultural services: Moleón et al. 2014). Interactions of vultures with species of homo have been traced to the Plio/Pleistocene transition (Moleón et al. 2014). Inclusion of vultures in human spiritual rituals may date to 200,000 yr ago (Moleón et al. 2014). The vulture declines in South Asia during the transition from the 20th to the 21st century disrupted the sky burial tradition of the Parsi and Tibbetan Buddhists, in which human corpses are presented to vultures for purification (DeVault et al. 2016). Both New World and Old World vultures have been incorporated in cultural rituals in many human societies (DeVault et al. 2016).

Buechley and Şekercioğlu (2016) analyzed the population and conservation status of obligate scavenger bird species (New and Old World vultures), and facultative scavenger bird species globally. Based on inclusion of ≥10% carrion in the diet, they identified a total of 106 bird species as scavengers. Of these species, the 22 obligate scavenger vulture species face dire conservation threats, with 9 species critically endangered, 3 species endangered, and 4 species near-threatened. Of the 7 species of New World vultures, the Andean Condor (Vultur gryphus) is near-threatened, and the remaining 5 species found within the Neotropics are all of least concern (Buechley and Şekercioğlu 2016). Threats to vultures are most severe in the Old World, including tropical areas in South Asia and sub-Saharan Africa, where threats include deliberate poisoning and secondary poisoning from the veterinary drug, diclofenac. Fortunately, a rapid ban of the use of diclofenac in South Asia has led to a stabilization of the vultures of this region (Prakash et al. 2012), although they remain in critical conservation status. Threats to New World vultures include lead poisoning (California Condor [Gymnogyps californianus]) and forest fragmentation within the Neotropics (Buechley and Şekercioğlu 2016).

The decline in vultures in South Asia, and the current decline in sub-Saharan Africa, clearly demonstrate the economic contribution of their scavenging services and indicate the critical role they likely play in Neotropical ecosystems as well. Reduced vulture populations in South Asia led to reduced scavenging services, which in turn sparked an increase in rats and feral dogs (facultative scavengers), which serve as reservoirs and vectors of diseases like canine distemper virus, canine parvovirus, Leptospira spp. bacteria, and rabies (Pain et al. 2003, Prakash et al. 2003, Markandya et al. 2008). Increased rates of transmission of these and other diseases to humans and domesticated and natural animal populations may have caused an additional 48,000 rabies deaths at a cost of US$34 billion from 1993 to 2006. Until vulture populations recover, costs will continue to escalate. Similar costs of vulture decline in Africa are mounting.

As with estimating the economic value of seed dispersal, calculations of replacement costs with human labor of vulture scavenging services indicate their great economic value. For instance, replacing the scavenging services of vultures and other facultatively scavenging species in Spain could cost up to US$50 million, while concomitantly releasing up to 77,344 metric tons of CO2 equivalent to the atmosphere, an indirect externality. When considered together with the medical costs associated with vulture declines, vulture ecosystem services are valuable, even while they are greatly underappreciated. Because the greatest threats to vulture species worldwide are anthropogenically sourced dietary toxins, generally from pesticides, regulation or outright bans of their use are needed to reverse population declines of threatened and vulnerable species.

**Supporting Services**

**Ecosystem engineering.** Ecosystem engineers are species that transform a part of their physical environment in a way that creates resources for other species with which they coexist (Jones et al. 1994). Bird ecosystem engineering, as considered here, consists primarily of the excavation of nesting or roosting cavities in trees or burrows in soil, along with construction of nest structures like open-cup, domed, and mud nests of passerines, and platform nests of raptors (Whelan et al. 2008). Cavities, burrows, cup and platform nests are all often used after the birds that constructed them are no longer doing so. For instance, open-cup and domed nests are often colonized by small mammals (Gates and Gates 1975), overwintering spiders (Otzen and Schaefer 1980), bumblebees (Dame et al. 2002), and ants (C. J. Whelan personal observation). Beetles, social wasps, rodents, lizards, snakes, frogs, and other bird species take over domed nests of tropical ovenbirds (Furnariidae; Remsen 2003). Woodpecker cavities, perhaps the best studied of engineered bird excavations, are often used only once by the individuals who excavated them but may subsequently be used for multiple decades by other taxa (Blanc and Martin 2012), including other birds, various mammals, amphibians, and arthropods (Connor et al. 1997, Neubig and Smallwood 1999, Montrubio-Rico and Escalante-Pliego 2006), who use their cavities after the excavators abandon them. While most bird ecological functions have been poorly characterized from the perspective of ecosystem services, bird nest engineering is possibly the least studied. The engineers are keystone species that help to maintain diversity (Daily et al. 1993, Connor et al. 1997, Duncan 2003). Hence, their benefits to
humans accrue primarily indirectly and may be difficult to quantify economically. Floyd and Martin (2016) provide a comprehensive review of cavity engineering in birds.

Found nearly worldwide, except in Antarctica, Australia, Madagascar, New Guinea, and far northern areas, woodpeckers, sapsuckers, wrynecks, and piculets (Piciformes, Picidae) are the most well-studied group of cavity-excavating birds. The 35 genera of ~254 species range in size from ~10 g (e.g., the Speckled Piculet \( \text{Picumnus inomnunatus} \)) to over 500 g (e.g., the Imperial Woodpecker \( \text{Campephilus imperialis} \)). Cavity size varies by species. The number of tree-cavity nesting bird species is greater in the Neotropics than any other biogeographic region, with 678 species of primary and secondary nesting species (van der Hoek et al. 2017).

Many species in a variety of orders are also excavators, but these species burrow into the earth or into termitaria. Burrows are excavated by penguins (Sphenisciformes), various seabirds (Procellariiformes, Charadriiformes), parrots (Psittaciformes), owls (Strigiformes), kingfishers (Coraciiformes), and songbirds (Passeriformes). The key excavators of burrow nests in the Neotropics include species of todies (Todidae), motmots (Momotidae), kingfishers (Alcedinidae), jacamars (Galbulidae), puffbirds (Bucconidae), parrots and parakeets (Psittacidae), and miners and leaf-tossers (Furnariidae). As with woodpecker cavities, often these burrows are later inhabited by other species. Burrows excavated by the European Bee-eater \( \text{(Merops apiaster)} \), for instance, were later used by 19 vertebrate species (12 birds, 2 snakes, 4 mammals, and 1 amphibian; Casas-Crivillé and Valera 2005). Abandoned cavity nests of the Citreoline Trogon \( \text{(Trogon citerolus)} \) in arboreal termitaria have been found occupied by several species of arthropods and mammals (Valdivia-Hoeflich et al. 2005).

Woodpeckers, through their foraging excavations, often leave wood “shrapnel” on the ground near the base of the tree on which they are drilling or probing for insects. Floyd and Martin (2016, p. 302) note that, “Observations of other birds, such as chickadees and nuthatches, foraging among the feeding excavations of the Pileated Woodpecker \( \text{(Hylatoma pileatus)} \); Bull and Jackson 2011) and American Three-toed Woodpecker \( \text{(Picoides dorsalis)} \); Tremblay et al. 2018), suggest that the feeding activity of woodpeckers might open up a source of food normally available only to species with sturdy beaks capable of digging into bark or heartwood.”

Ecosystem services provided by the excavation of nesting cavities and burrows are largely supporting services. These include providing nesting and roosting habitat for many additional species, which helps maintain biodiversity. Burrowing into soil results in bioturbation that can alter nutrient dynamics and provide regeneration opportunities for some plant species. Like other supporting services, humans benefit only indirectly from them. The foraging of woodpeckers, on the other hand, as a regulating service resulting in pest control, may benefit timber production, thus benefiting humans more directly. To date, the economic valuation of neither type of service has been estimated.

Several species of woodpeckers, especially sapsuckers (\( \text{Sphyrapicus sp.} \)), feed at sap wells that they excavate into the sapwood of shrubs and trees. In the Neotropics, this behavior has been reported for the Magellanic Woodpecker \( \text{(Campephilus magellanica)} \); Schlatter and Vergara 2005) and the White-headed Woodpecker \( \text{(Picoideos albolarvatus)} \); Kozma 2010). Numerous species of both vertebrates and invertebrates are known to feed at sapsucker wells (Ehrlich and Daily 1988, Rissler et al. 1995). In the Chaco region and Monte Desert of Argentina, sap wells created by White-fronted Woodpeckers \( \text{(Melanerpes cactorum)} \) were used by >12 species of birds (Blendinger 1999, Montellano et al. 2013). Hence, like cavities and burrows, sap wells represent supporting services that may help maintain diversity where they are created.

**Nutrient cycling.** Nutrient cycling is the movement of mineral and organic nutrients through both the living and nonliving components within the boundaries of an ecosystem, and nutrient flux is the movement of nutrients across the boundaries of an ecosystem (Holmes and Likens 2016). The contribution of birds to nutrient cycling and nutrient fluxes is highly context-dependent. Because bird species differ in social structure, often seasonally, the role of birds in such biogeochemical processes is highly variable in both space and time. Fujita and Kameda (2016) provide a comprehensive review of these regulating and supporting services of birds.

Many seabirds nest in large concentrations on remote oceanic islands and have done so for thousands of years or more. These colonial nesting congregations are often associated with oceanic upwelling that creates nutrient-rich waters and abundant fisheries. Under these conditions, large accumulations of excreta, or guano, build up in massive quantities. Some of the best known of these guano islands occur along the west coast of South America (the Chinchia Islands, Peru), and others are found in the Caribbean Sea. These guano deposits represent the transport of nutrients, most importantly nitrogen and phosphorus, from the ocean to land. In the 19th century, guano deposits were valuable because their rich, concentrated nitrates and phosphates were important additions to agricultural fertilizer and gunpowder and were important to the explosives and chemical industries (Wilkinson 1984, see Whelan et al. 2008). Disputes over key islands spawned the Guano Wars among Peru, Bolivia, and Chile (Skaggs 1994, Hollett 2008), and even led the United States Congress to pass the Guano Islands Act of 1856, which allowed...
U.S. citizens to claim uninhabited oceanic islands for the mining of guano.

By contrast, many species, particularly passerines during the breeding season, live in relatively low densities, many in intraspecifically defended territories used exclusively by a mated pair. Two now classic studies, Wiens (1973) in shrub-steppe-grassland habitat, and Holmes and Sturges (1975) in northern hardwoods forest habitat, both in the United States, found a negligible contribution of birds to energy and nutrient transport in each of these 2 biomes. We know of no similar studies conducted within tropical forest or grassland communities. Terborgh et al. (1990) reported about 5 times the avian biomass/ha at Cocha Cashu, Peru, compared with the Hubbard Brook site of Holmes and Sturges (1975). The greater avian biomass, it would seem, should contribute more to energy and nutrient transport at Cocha Cashu than that measured at Hubbard Brook. Evidence that tropical forest birds (and mammals) affect soil phosphorus turnover comes from an exclosure study in rainforest in Ivory Coast (Dunham 2008). Excluding understory birds (and mammals) revealed a 4-level cascade of effects in which vertebrate predators depressed spider densities, which increased microbiworms, which in turn positively affected inorganic soil phosphorus levels (Dunham 2008). These sorts of ecosystem services represent supporting services, and their benefits to humans will therefore be indirect and likely hard to quantify economically.

Cultural Services

**Bird-based tourism.** Birdwatching is a popular hobby that provides important economic benefits. As of February 2020, >389,000 eBird checklists were submitted in Mexico, >771,000 were submitted in Central America (including >300,000 in Costa Rica alone), and >1,125,000 in South America (eBird 2020). In the United States, bird viewing and photography is the most steadily growing recreational activity, growing 287% from 1982 to 2009 (Cordell et al. 2009). In 2011, some 52 million Americans spent an estimated US$4.07 billion on bird feed, and another US$970 million on nest boxes, birdhouses, feeders, and baths (U.S. Fish and Wildlife Service 2012). Bird feeding is also popular in some tropical countries, such as Brazil, where many people put out nectar feeders for hummingbirds, fruit for tanagers and other frugivores, and seed for granivores (E. Dias de Oliveira personal communication), but we are unaware of estimates of the economic value of those activities in tropical countries.

Bird-based tourism is an economic boon for Neotropical countries. Birders flock to areas with birds that are desired target species (e.g., Monteverde Cloud Forest Reserve, Costa Rica, for the Resplendent Quetzal [Pharomachrus mocinno]) or in large aggregations (e.g., American Flamingo [Phoenicopterus ruber] at Reserva de la Biosfera Rio Lagartos in Mexico). An estimated 3 million international trips are taken globally each year for the purpose of birdwatching (Acorn Consulting Partnership 2008). In Peru in 2010, 19% of international tourists—over 400,000—included birdwatching among their motivations for travel (Puhakka et al. 2011), and a single macaw visiting a clay lick can generate up to US$4,700 annually and US$165,000 in tourism receipts in its lifetime due to its long lifespan, charismatic nature, and frequent, reliable return to the clay lick for viewing (Munn 1992). In Costa Rica, an estimated 41% of the US$1 billion tourism income in 1999 was from birding tourists (Şekercioğlu 2003), and bird guiding can provide a significant source of income for local guides (Şekercioğlu 2002). Tourism revenue contributes to 64% of the support for conservation of threatened and endangered birds worldwide, with the largest contributions in South America and Africa (Steven et al. 2013).

**Caged birds.** Caged birds are kept by hundreds of millions of people worldwide (Whelan et al. 2016a). In the Neotropics, cage bird trapping is among the primary threats to Psittacidae, including the Yellow-naped Amazon (Amazona auropalliata), Hyacinth Macaw (Anodorhynchus hyacinthinus), Great Green Macaw (Ara ambigua), and Scarlet Macaw (Ara macao; Snyder et al. 2000). However, captive-bred birds displayed at zoos or used in educational programs can educate the public about the importance of bird conservation. In a few cases, cage bird breeders have been recruited to contribute to conservation programs (Whelan et al. 2016a).

**Falconry.** Falconry as a sport dates back to at least 2,000 Before the Common Era, when it originated in Mesopotamia (Whelan et al. 2016a). Falconry was brought to the Neotropics by the Spanish conquistadores in the 16th century, who reportedly taught Moctezuma to hunt small birds with a “sparrow hawk” (Carnie 2013). Common Neotropical falconry birds include the Peregrine Falcon (Falco peregrinus) and Harris’s Hawk (Parabuteo unicinctus). Today, there are ~600 falconers in Mexico who practice primarily for hunting and commercial pest control (Rojo 2017). In South America, the International Association for Falconry has affiliates in a number of countries in the Neotropics, including Argentina, Brazil, Columbia, El Salvador, Ecuador, Mexico, Paraguay, Peru, Uruguay, and Venezuela. The Brazilian Falconers and Raptor Preservation Association enlists falconers to conduct environmental education raising awareness about raptors and conservation of natural resources (International Association for Falconry 2016).

**Art and heraldry.** Birds are frequent subjects of Neotropical art works. Frida Kahlo often painted portraits of herself with animals, including parrots (My Parrots and I, 1941; Self Portrait with Monkey and Parrot, 1942), and was photographed with a falcon. Birds were common subjects of Mesoamerican art, perhaps most famously depictions of the Golden Eagle (Aquila chrysaetos) eating a snake that...
led the Aztecs to Tenochtitlan, current-day Mexico City (Miller 2012). Birds continued to feature in traditional and current folk art of Mexico and other Neotropical countries. Many folk songs feature birds, e.g., “La pajarita pintita” (The spotted bird) by Maria Elena Walsh. Birds also feature on many national flags and coats of arms. The Guatemalan flag features the resplendent quetzal, which also lends its name to their currency (the quetzal). Birds of prey feature prominently: the harpy eagle (Harpia harpyja) is on the Panamanian coat of arms, the Andean Condor (Vultur gryphus) is featured prominently on Ecuador’s coat of arms and flag, and a Golden Eagle graps a snake on Mexico’s coat of arms and flag.

Religion. Birds serve as symbols in traditional and modern-day religious traditions in the Neotropical region. Birds cross between Earth and the underground spiritual realm in religious works of the Inca and Tiwanaku tribes (Smith 2011). In the central Andes, the mythical chullumpi bird passes between the worlds and transforms itself into the shape of a llama (Dransart 2002). The Toltec god Quetzalcoatl is depicted as a serpent covered in quetzal feathers, and the Aztec god Huitzilopochtli is associated with hummingbirds and depicted with feathered plumage and an eagle shield (Castillo Yturbe 1993). Aztec priests wore featherwork, and feathers continue to feature prominently in ceremonial clothing to this day. Feathers of Scarlet Macaws were so prized as spiritual emblems that the birds were farmed in northern Mexico and the US Southwest from about 900 to 1,200 Common Era (George et al. 2018). In Aztec and Mayan cultures, birds such as owls were revered as divine messengers (Alonso-Castro 2014).

Knowledge. Birds have long featured prominently in science and knowledge (reviewed in Whelan et al. 2016a). Aristotle first speculated on the migratory movements of birds. The study of birds has contributed to advances in aerodynamics, navigation, ecology, evolution, and physiology, among other fields. Metabolic studies of birds have provided unique insights into the relationships between diet, oxidative capacity, and endurance physiology (e.g., Maillot and Weber 2007, Cooper-Mullin and McWilliams 2016). Neotropical hummingbirds have been used in studies aimed at improving helicopter technology (Kruyt et al. 2014). Studies seeking to explain the high diversity and endemism of Neotropical birds have helped inform our understanding of the processes of evolution and biogeography (Smith et al. 2014, Oliveira et al. 2017). The enigmatic Hoatzin (Opisthocomus hoazin), in particular, has contributed to our understanding of the origin of avian flight (Chatterjee and Templin 2012), digestive physiology (Grajal et al. 1989), and challenged phylogeneticists to improve our understanding of avian evolution and speciation (Prum et al. 2015). As charismatic animals that are easy to observe, birds have been the subject of long-running surveys such as the National Audubon Society’s Christmas Bird Count that shed light on trends of biodiversity decline (Soykan et al. 2016). Birds continue to be harbingers of ongoing threats such as climate change to natural and human communities (Pearce-Higgins and Green 2014).

Ecosystem Disservices

No discussion of bird ecosystem services is complete without also considering bird disservices. Bird disservices include birds or bird behaviors that directly or indirectly harm human activities, human structures, or humans themselves. Bird disservices include the spread of disease or invasive species, reduction or damage to agricultural crops, damaging buildings and homes, nutrient loading (eutrophication), and collisions with aircraft. An increasing number of efforts aim to simultaneously examine the positive and negative effects of birds in certain contexts in terms of net effects; specifically, how do the positive services tradeoff with the negative disservices (Triplett et al. 2012, Peisley et al. 2016, Şekercioğlu et al. 2016)?

Birds are often believed to cause significant damage to agricultural crops, although perceived losses often exceed actual losses (see Whelan et al. 2016a, pp. 18–19). Various grain crops are generally thought to suffer the most from bird losses, followed by various fruit crops. When actual crop yield is quantified or estimated, however, losses may be negligible, sometimes <1% total yield (Red-winged Blackbird [Agelaius phoeniceus] in Canada: Weatherhead et al. 1982; Dickcissel [Spiza americana] in Venezuela: Basili and Temple 1999; but see Lindell et al. 2016). By contrast, Elser et al. (2019) found that grower perceptions and field estimates of bird damage to wine grapes and sweet cherries were similar, although growers perceived greater bird damage to “Honeycrisp” apples than found in field estimates.

Peisley et al. (2016) examined net bird effects in Australian apple orchards and reported that birds provided orchard growers with net benefits. Similar studies could be conducted in crops typical of Neotropical agriculture, such as coffee and cacao. Existing studies have found that birds using these crops for foraging boost yields (see Pest control section), but to our knowledge, net effects have yet to be determined. Birds may also increase agricultural costs preying on beneficial insects (Galeotti and Inglis 2001). Large raptors may also prey on livestock, such as Black-and-Chestnut Eagle (Spizaetus isidori) preying on domestic fowl in the eastern Andes of Colombia (Zuluaga and Echeverry-Galvis 2016). The relative costs and benefits of raptor predation are difficult to determine, however, because birds often feed on either dead, or alive but ill, animals (Triplett et al. 2012).
Birds serve as reservoirs for some zoonotic diseases, such as West Nile virus, avian influenza, salmonellosis, and psittacosis. Although each of these diseases can be serious, prevention is not difficult with proper application of sanitary precautions, such as handwashing, or through actions to minimize mosquito bites. Birds have also been implicated in the transmission of some plant viral diseases through activities such as moving plant materials in the process of nest construction, or while foraging within vegetation. According to Peters et al. (2012), bird transmission of plant viruses is not likely an effective mechanism of virus spread, but it could be an effective mechanism of introduction into previously uninfected areas. This is an area of bird disservices that requires additional research.

Woodpeckers and a few other tree-nesting bird species such as Monk Parakeets (Myopsitta monachus) may become pests under some circumstances. Pileated Woodpeckers (Dryocopus pileatus), for instance, often target wooden utility poles as foraging or nesting sites. Many homeowners are all too familiar with woodpeckers drilling into wooden siding, but these problems are not likely common throughout much of the tropical areas of the world, including the Neotropics.

Some bird species are attracted to airports owing to large expanses of open area. Birds using these areas can pose grave risks from collisions with aircraft during both taking off and landing. These collisions inevitably cause the death of the birds or other wildlife (mammals, reptiles) that collided with the aircraft. The prevalence worldwide is poorly known owing to how such events are recorded and itemized by the industry. Estimates indicate that, considering global air travel, costs may exceed US$1.2 billion in damage and delays to commercial airlines annually (Allan and Orosz 2001). Brazil implemented a wildlife management program at 10 Brazilian airports, Fauna in Brazilian Airports, in 2010. Over the first 5 yr of the program, 2,592 wildlife strikes were recorded, of which 92% were of birds or bats, with the remaining 8% mammals and reptiles (Novaes et al. 2016). Bird and wildlife strikes have been quantified at the Kotoka International Airport in Accra, Ghana, with the aim of identifying bird species at risk and devising mitigation measures (Holbech et al. 2015). Clearly, research into effective means to prevent collisions of aircraft with birds and other wildlife will be mutually beneficial to the airline industry and to the many animal species attracted to airports. More detailed data may suggest effective strategies to minimize wildlife-aircraft collisions (Washburn et al. 2014). These may include fencing (Novaes et al. 2016), and management of surface water and grass height on airport properties (Holbech et al. 2015). Other measures may include dog patrols (Holbech et al. 2015), flights of trained falcons (Kelley 2005), and “bird migration reports,” which are currently used by the Israeli air force to avoid areas of high bird concentrations (Pearce 2004), and further experimentation to help devise additional nonlethal means to discourage birds and other wildlife from concentrating around and on airport properties.

**Economics of Neotropical Bird Ecosystem Services and Future Directions**

The ecological economics community has designed approaches that utilize spatially explicit information to map, measure, and value the supply of, and demand for, benefits provided by ecosystems to people (Boyd and Banzhaf 2007, Tallis et al. 2012). New science and tools have been developed to quantify these flows and make more explicit the synergies and tradeoffs associated with maintaining critical services (Goldstein et al. 2012, Bhagabati et al. 2014, Arkema et al. 2015). However, birds are not usually included in ecosystem service models (e.g., Kareiva et al. 2011) because, as reviewed above, many services provided by birds are indirect. Moreover, those efforts that have incorporated birds in ecosystem service models focused on temperate regions where the ecology, natural history, and functional roles of birds are well understood. By contrast, in the Neotropics, much remains to be learned about basic natural history, functional roles, distributions, and the community composition of birds before their contributions to ecosystem services can be valued.

Framing the need for conservation in terms of economic valuation is controversial for a variety of reasons (reviewed in Johnson and Hackett 2016). First, assigning economic value to birds and their habitats implies that their primary or sole value is their usefulness to humans, which undermines their intrinsic value and may ultimately undermine their conservation (Ludwig 2000, Gómez-Baggethun and Ruiz-Pérez 2011). Critics also argue that reducing birds and their functional roles to economic terms implies that birds or their services can easily be replaced or compensated for, e.g., through the use of pesticides to counteract reduced pest control services following declines or extirpations of insectivorous birds (Johnson and Hackett 2016). The movement towards justifying conservation through economic valuation has led to intense ethical debates among conservation scientists that still rage on (e.g., McCauley 2006, Kareiva and Marvier 2012, Doak et al. 2014).

However, understanding the value of ecosystem services provided by birds can lead to better management of land and other natural resources. Ecosystem services information can support strategies for climate change adaptation, identifying alternative livelihoods where traditional uses are becoming increasingly unsustainable, and additional economic opportunities that improve community well-being. By assessing the response of ecosystem services and biodiversity to different policy and management options through monitoring, rapid assessment, and reporting.
(Pereira et al. 2013, Geijzendörffer et al. 2016, Neugarten et al. 2016), nations will be more likely to meet key targets such as Sustainable Development Goals, the Convention on Biological Diversity, and the recent Paris Accord. At the local scale, a more detailed understanding of ecosystem service synergies and tradeoffs based on future drivers of change can guide planners and managers in balancing multiple objectives for birds and people.

Given the wide array of ecosystem services provided by Neotropical birds, researchers in the Neotropics are well positioned to contribute to the ecosystem services knowledge base and fill in science gaps to inform management and policy that considers how birds matter to ecosystems and people (Şekercioğlu et al. 2004, 2016, Wenny et al. 2011). By appealing to people’s wallets as well as their hearts and minds, we can best ensure conservation of birds and their habitats for generations to come.

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