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An Appraisal of Bird-Mediated Ecological Functions in a Changing World

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Abstract

Birds perform several ecological roles for ecosystem functioning and generate great benefits for human population in some circumstances. However, environmental disturbances, mostly due to anthropogenic actions, have caused a decrease of bird diversity and can lead to the loss of their functions in the remaining habitats. Here, we conducted a scientific literature review to understand the general trends on the ecosystem functions executed by birds and the possible effects of environmental disturbances on them. Our research was conducted in September 2016 in Google Scholar, Scopus, and Web of Science databases, which returned 154 papers that targeted the importance of birds to the ecosystems' maintenance. Among the studies ($n = 99$) that effectively assessed the ecological role of bird species, most were conducted in natural habitats ($n = 63$), and the most evaluated function was invertebrate population control ($n = 70$). About 58% of the publications related some environmental characteristic to the ecological function, but patch and landscape-scaled factors were poorly investigated. Furthermore, 52% of the papers showed that the ecological function of birds can arise from a cascade effect on other trophic levels, though this may depend on the environmental characteristics. Despite the numerous studies in the ornithology field, the ecological roles of birds in several ecosystems are still poorly understood. Future research should consider others ecological functions mediated by birds, such as disease control, and must take different spatial scales and human modification of habitats into consideration, enabling generalizations based on ecosystem type and landscape composition variation.

Keywords

Avian function, disturbance, ecosystem services, human-altered landscape, insectivory, trophic cascade

Introduction

Birds are an important and a well-studied group of vertebrates due to their conspicuousness, morphological diversity, and wide distribution (Stotz, Fitzpatrick, Parker, & Moskovits, 1996; Wiens, 1992). In the last decades, many studies have assessed an array of ecosystem functions mediated by birds, such as pollination (Anderson, Kelly, Ladley, Molloy, & Terry, 2011), control of insect populations (Sanz, 2001; Van Bael et al., 2008), and diseases (Swaddle & Calos, 2008), in different ecosystems throughout the world. In many cases, it was found that the ecological roles played by specific groups of birds is critical to assure ecosystem integrity, thus generating direct and indirect benefits to human (Sekercioglu, Wenny, & Whelan, 2016; Wenny et al., 2011; Whelan, Serkercioglu, & Wenny, 2015; Whelan, Wenny, & Marquis, 2008). For example, the predation of agricultural pests by insectivorous birds can cause an increase in crop productivity (Maas, Clough, & Tscharntke, 2013; Martin, Reineking, Seo, & Steffan-Dewenter, 2013), highlighting their importance in food security. However, environmental disturbances, mostly due to anthropogenic action, have caused a decrease in bird diversity, thus raising the question to the extent to which such changes could impair their functions in the remaining habitats (Sekercioglu, 2006; Whelan, Wenny,

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& Marquis, 2010). Currently, most of the biota is present in human-altered landscapes, in which historical deforestation has reduced large natural habitats that were once continuous into a myriad of small patches that are often isolated from one another by other human-altered land uses (Fahrig, 1997; Haddad et al., 2015). The negative effects of habitat loss and fragmentation on biodiversity are therefore well understood (Haddad et al., 2015). Thus, if bird diversity declines with these processes, functions performed by them are also likely to be lost.

Due to their high mobility, birds have large metabolic demands. Allied to this characteristic, the spatial and temporal variation in resource availability compels many species to move throughout landscapes, exploring a vast array of different habitat types (Whelan et al., 2008). Hence, bird assemblages can connect a variety of habitats in space and time, a crucial process linked with the maintenance of functions and stability of ecosystems (Lundberg & Moberg, 2003; Sekercioglu, 2006). However, fragmentation negatively affects ecosystem functions flows by interrupting movement of organisms across landscapes (Mitchell et al., 2015). This includes the daily movements of birds like pollinators and insect predators across human-altered landscapes. Furthermore, even when certain species are present in remaining patches, their low density may cause a functional extinction before the species itself suffers extinct or extirpation (Galetti et al., 2013; Tobias, Sekercioglu, & Vargas, 2013). The disappearance of frugivorous birds is a well-documented process leading to changes in seed dispersal patterns that ultimately affect forest structure (Garcia, Zamora, & Amico, 2009; Silva & Tabarelli, 2000). Similarly, a decline of bird pollinators and their services may reduce genetic diversity of the corresponding plant community, which may then be more susceptible to stochastic extinctions (Anderson et al., 2011).

In addition, the actual extirpation of bird species, or even changes in their numerical representation, may exert a cascade effect on other trophic levels (Mäntylä, Klemola, & Laaksonen, 2011). Trophic cascades result in alternate patterns of abundance or biomass across more than one trophic link in a food web (Paine, 1980). For a three-level food chain, abundant top predators result in lower abundances of midlevel consumers and higher abundance of basal producers (Pace, Cole, Carpenter, & Kitchell, 1999). Several studies have examined the effect of bird predation on herbivores insect cascading down to plants (e.g., Mäntylä et al., 2011; Marquis & Whelan, 1994) because the herbivory process may affect growth and survival of plant species (Guimarães, Viana, & Cornelissen, 2014) and possibly modify the plant community composition (Hulme, 1996). However, landscape changes may result in the disruption of these ecological interactions (Morante-Filho, Arroyo-Rodríguez, Lohbeck, Tscharntke, & Faria, 2016) because the diversity and abundance of insectivorous birds can be reduced in human-altered landscapes (see Morante-Filho, Faria, Mariano-Neto, & Rhodes, 2015).

Despite the ecological importance of birds, the effects of species extinctions or extirpations to ecosystem functioning and ecosystem services provided by them are poorly understood (Sekercioglu, 2006). It is necessary to quantify ecosystem functions at different scales and investigate what features of landscape structure and composition can be used to improve our ability to manage landscapes for ecosystem services (Mitchell et al., 2015; Whittingham, 2011). In this context, more research needs to move away from simply quantifying of ecological groups of birds and toward identifying locations of service demand and potential pathways of service flow (Bagstad, Johnson, Voigt, & Villa, 2013). Moreover, some studies show the necessity of combining information from different ecosystem functions performed by birds and develop a metric to assess how services can be maximized in several land use contexts (Geijzendorffer & Roche, 2013; Wenny et al., 2011). This information will be useful for the economic valuation of environmental services and are fundamental for the development of effective policy mechanisms.

Facing the growing need to understand how bird communities can contribute to natural and anthropogenic ecosystem functioning, in this study, we aimed to search for general trends in the scientific literature on the ecosystem functions of birds and the possible effects of environmental disturbances on them. Therefore, we investigated which were the main functions and environments (natural and/or anthropic) studied, and what environmental factors, both at local and broad scales, were related to performed functions. In addition, we quantified how many studies have evaluated the cascade effect of birds, and whether environmental characteristics are commonly associated with the results. Overall, we assessed the current understanding of how environmental changes affect ecosystem function and services provided by birds and identified gaps in knowledge that may guide future studies.

Methods

We conducted an extensive review in the Scopus, Web of Science, and Google Scholar databases for original papers without restricting publication year, containing in the title, abstract, or keywords the following search term: (bird OR avian) AND (''ecosystem service'' OR ''ecological function'' OR ''trophic cascade'' OR ''top-down'' OR ''bottom-up'') AND (''land use'' OR ''habitat loss'' OR ''fragmentation'' OR ''disturbance'' OR ''perturbation''). In this review, carried out in September 2016, we considered the studies that focused on the bird species or community and those which, directly or indirectly, assessed the ecological role performed by this group. After selecting the publications that fitted the scope, we conducted exploratory analyses to identify general patterns of how birds' functional role is evaluated by the scientific community.

From each publication, we gathered information on the following: (a) continent (Africa, America, Asia, Europe, and Oceania) and climatic region of the study area, according to Köppen-Geiger's classification, 1954), (b) habitat type (natural, agroforestry, or agricultural systems) where the study was conducted, and (c) scales of the assessed explanatory variables (local, patch, or landscape). We defined the variable scale as local when vegetation characteristics were measured to investigate their effect on bird ecological function. When metrics were related to habitat remnants, such as size or isolation, and characteristics of landscape structure and composition, we classified the variables, respectively, as patch and landscape scales.

We reported studies assessing the ecological role directly played by a species or a group of birds as mutualists or antagonists, and the functions derived from their interactions within trophic cascades. We considered Paine's (1980) definition of the trophic cascade, that is, when changes in a species population's size lead to alterations in the populations of lower levels of the food chain. Although many studies used the term *trophic cascade*, most have quantified only two levels of the food chain. For example, several authors measured the top-down control exerted by birds only on arthropod populations, and therefore, these studies were not classified here as the trophic cascade. Finally, we verified the studies that directly quantified the economic benefits of ecosystem services provided by birds.

Overview

We found 154 publications reporting the importance of birds as vectors performing one or more ecological functions for ecosystem maintenance (Table S1 in supplementary material, Figure 1). However, 36% of the studies ($n = 56$) did not directly measure bird ecological roles. For example, many studies mention only that a decrease

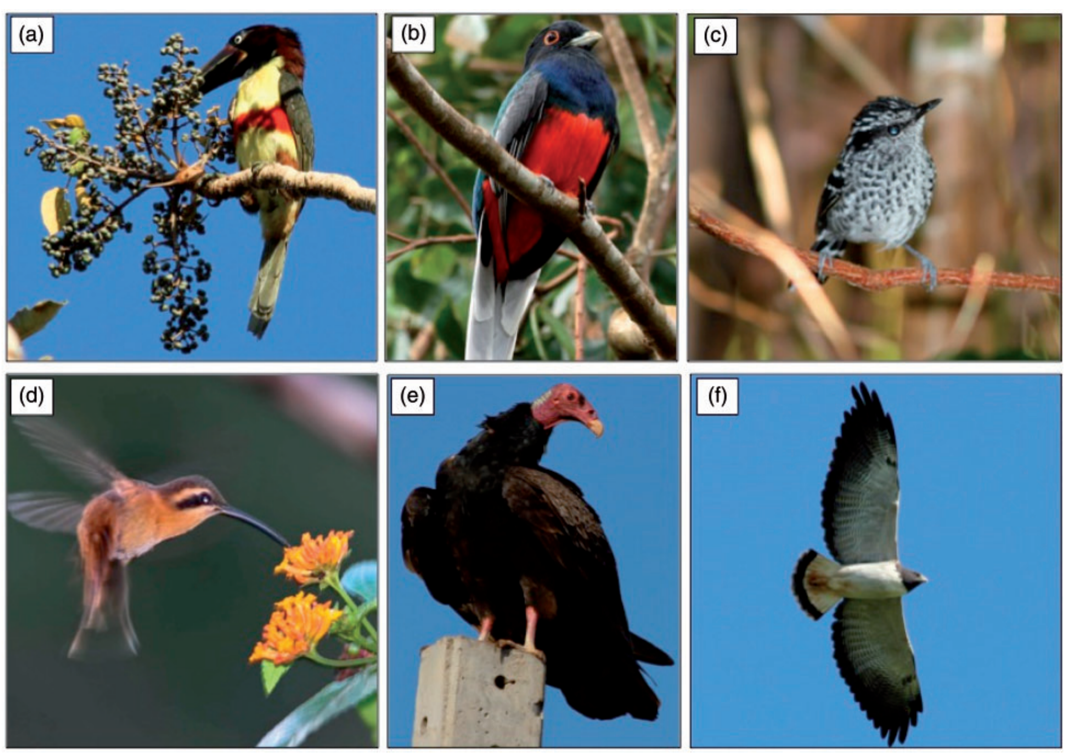

Figure 1. Examples of birds that perform different ecological functions. (A) *Pteroglossus castanotis*, large frugivore that disperses seeds of several tree species. (B) *Trogon surrucura,* species considered an ecosystem engineer because it builds cavities to nest in arboreal termite nests and abandoned hornet nests. The cavities are later used by other species of birds and small mammals. (C) *Drymophila squamata,* insectivorous bird that consumes arthropods in the forest understory. (D) *Phaethornis ruber* acts as pollinator of many plants. (E) *Cathartes aura*, obligate scavenger that consumes carcasses and can assist in disease regulation and transport of nutrients. (F) *Geranoaetus albicaudatus*, controls vertebrate populations, such as birds and small rodents, in agricultural systems. Source: Photos: J. C. Morante Filho.

in bird diversity cause a simplification of ecological roles, with eventual breakdown of interactions in cascade systems (Estes et al., 2011). This has been happening constantly due to changes in natural habitats (Mendenhall, Karp, Meyer, Hadly, & Daily, 2014), such as agricultural intensification throughout the world (Gavier-Pizarro et al., 2012; Muñoz et al., 2013; Sekercioglu, 2012). Other studies focused only on understanding what environmental conditions favor the maintenance of the guilds of birds that can perform important ecosystem services in altered-human landscapes, such as insectivorous birds that control the agricultural pests (Jirinec, Campos, & Johnson, 2011) or frugivorous species performing seed dispersal (Moran & Catterall, 2014). Although the loss of key ecological groups of birds, such as those habitat-specialists, can affect the services provided, evaluating only the abundance and species richness may be inadequate given that both diversity metrics do not consider the biological variations within ecological groups. Quite often population declines drive functional extinction because of behavioral and ecological changes of the remaining individuals and species (Anderson et al., 2011). For instance, flock formation in some bird species, a feature highly associated with the capacity to assess different habitats and resources, is highly dependent on the presence and abundance of other species (Diamond, 1987). This suggests that a more profound knowledge of the strength of interactions among species is the key to more adequately link species diversity changes to the predicted loss of their ecological function (McConkey & O'Farrill, 2015). Such studies provide evidence that, even for those species remaining after disturbances, their functional role can be lost as a consequence of significant changes in their local abundance as well as due to the demise of other key interacting species (McConkey & O'Farrill, 2015).

Bird-Mediated Ecological Functions

From the total, 99 publications (64%) effectively assessed the ecological role of a species or a group of birds (Table S1, Figure 2). Empirical studies comprised 85% of all analyzed papers, and reviews and meta-analyzes totalized 15% (Table S1). Publication years ranged from 1995 to 2016, with a large increase in number of publications from 2005 (92% of the studies were published after this year) (Figure 3). This temporal trend may be a consequence of the influential United Nations report, the Millennium Ecosystem Assessment (2005), which besides compiling a significant proportion of existing information, also standardized and categorized the ecological functions of species in four classes of ecosystem services (see Table 1): provisioning, regulating, cultural, and supporting. Birds may contribute to all four types of ecosystem services (see Sekercioglu, Wenny, & Whelan, 2016; Whelan et al., 2008, 2015). However, an ecological function is considered an ecosystem service only if it brings benefits to the human population (Whelan et al., 2008), for example, if pollination by birds results in an increasing crop yield. After the Millennium Ecosystem Assessment (2005), many debates were held to evaluate how birds' ecosystem services should

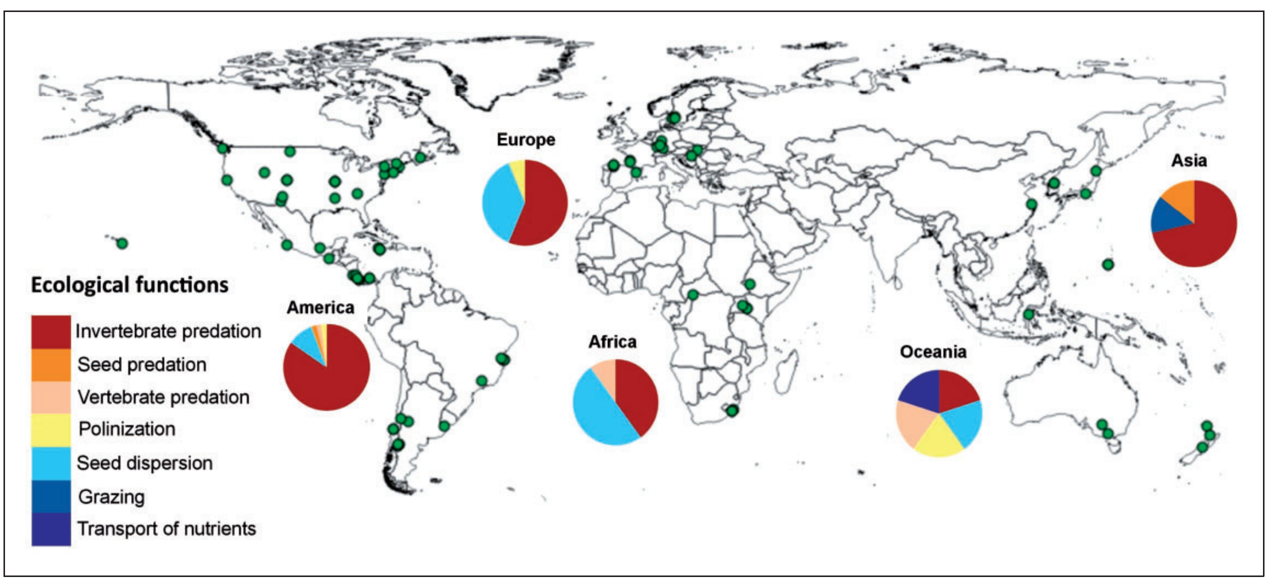

Figure 2. Location (green dots) of empirical studies (see Table S1) that effectively evaluated ecological functions performed by birds: America ($n = 50$ studies), Africa ($n = 9$ studies), Europe ($n = 15$ studies), Asia ($n = 7$ studies), and Oceania ($n = 5$ studies). Pie charts indicate the proportional number of ecological functions evaluated at each continent.

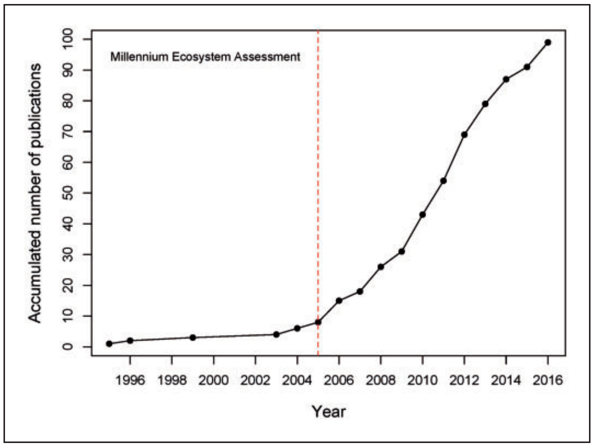

Figure 3. Accumulated number of publications ($n = 99$) up to September 2016 that effectively evaluated ecological functions performed by birds. Dashed line indicates the year of publication of the United Nations report.

Table 1. Ecosystem Services According to the Millennium Ecosystem Assessment (2005).

Ecosystem services	Characteristics
Provisioning	Services related to production of natural compounds involved in human needs, such as food production, fuel, and water purification.
Regulating	Services obtained through ecosystem processes, such as regulation of agricultural pests, removal of carcasses, seed dispersal, and diseases control.
Cultural	Services related to aesthetic, spiritual, recreational enrichment, and inspiration for art and music.
Supporting	Services related to other processes that support ecosystem functioning, such as soil formation, nutrient cycling, biomass, and atmospheric oxygen production.

Table 2. Attributes and Categories Used to Classify the Publications ($n = 99$) from Google Scholar, Web of Science, and Scopus Databases That Effectively Evaluated Ecological Functions Performed by Birds Investigated in This Study.

Attributes	Categories	Number of publications
Climatic region	Tropical	41
	Temperate	29
	Continental	7
	Dry	6
	Polar	2
	Do not apply[a]	12
Ecosystem	Natural	63
	Agriculture	27
	Agroforestry	17
	Do not apply[a]	6
Ecological function	Invertebrate predation	70
	Seed dispersion	15
	Seed predation	5
	Vertebrate predation	3
	Polinization	3
	Transport of nutrients	2
	Grazing	1
	Disease and pest control	1
	Various[b]	6
Value of ecological function	No	88
	Yes	11
Approach scale	Local	48
	Landscape	19
	Patch	5
	Not evaluated[c]	42
Trophic cascade	No	48
	Yes	51

[a]Review studies that do not fit any category.
[b]Review studies that discussed several ecological functions.
[c]Studies that did not correlate any environmental variable with ecological function.

be quantified and valued (Sekercioglu 2006; Sekercioglu et al., 2016; Wenny et al., 2011; Whelan et al., 2008).

Most studies found in the search were conducted in the Americas ($n = 52$), whereas only five were performed in Asia (Figure 2). Studies were mainly from tropical and temperate climate zones (Table 2), with 41 and 29 published papers, respectively. Furthermore, studies were mostly held in natural habitats ($n = 63$), such as forests, and agricultural systems ($n = 27$). Few studies were conducted in agroforestry systems ($n = 17$), although these managed habitats contribute significantly to biodiversity conservation in tropical human-altered landscapes (Pardini et al., 2009; Poch & Simonetti, 2013a). Compared with most agricultural systems, agroforests harbor more biodiversity due to its vertical complexity (Faria, Laps, Baumgarten, & Cetra, 2006; Perfecto, Rice, Greenberg, & Van der Voort, 1996) and shade tree composition that usually encompasses native species that provide shelter and resources for the local biota (Faria et al., 2006). The extent to which agroforests sustain bird diversity depends largely on how species or functional groups are affected by specific disturbance. For instance, understory birds are more directly affected due to the complete replacement of the native species by the coffee or cacao shrubs (Faria et al., 2006), while canopy omnivores and nectarivores are usually well represented (Perfecto et al., 1996; Rice & Greenberg, 2000). Nevertheless, several studies have shown that these agroforests may act as additional or secondary habitats for many bird species, including some forest-specialists in Costa Rica (Harvey & Villalobos, 2007) and Brazil (Faria et al., 2006; Pardini et al., 2009). In Panama, migratory birds heavily rely on shade plantations (Van Bael, Bichier, & Greenberg, 2007), and in Brazil, the recent described bird species (*Acrobatornis fonsecai*) was discovered and still solely reported in the cocoa plantations (Pacheco, Whitney, & Gonzaga, 1996). Thus, although structurally complex agroforests are not surrogates of native habitats, they are certainly important reservoirs of bird species. In this case, they are contributing to the maintenance of the functioning of natural and anthropogenic habitats that compose the landscape (Beenhouwer, Aerts, & Honnay, 2013).

The most analyzed ecological function was the control exerted by birds on invertebrate populations ($n = 70$), mainly in studies carried out in the Americas (Figure 2). Migratory birds are particularly important to decrease arthropod abundance and biomass. For instance, in Central America, the seasonal influx of large number of Nearctic migrant as insectivorous birds, significantly deplete arthropod biomass, as the local bird population often doubles (Van Bael et al., 2008). Similarly, winter predation by insectivorous birds also suppress insect herbivory in temperate forests (Barber & Wouk, 2012). However, most of the knowledge attributing the role of birds in reducing arthropod population comes from exclosure experiments, where the observed rates of herbivory and arthropod richness and abundance are compared by preventing the access of foraging birds while allowing arthropods freely reach treatment plants (Maas et al., 2016). Birds can perform this function on both natural and agricultural systems, controlling pest populations and, indirectly, reducing crop damages (Johnson, Natalee, Kellermann, & Robinson, 2009; Mäntylä et al., 2011). Consequently, this service may result in an increase in the productivity of various crops (Kellermann, Johnson, Stercho, & Hackett, 2008; Mols & Visser, 2007). Nevertheless, part of the arthropod changes originally attributed to birds can be partially exerted by other sympatric predators, such as bats and even insectivorous arthropods (Böhm, Wells, & Kalko, 2011; Kunz, Braun de Torrez, Bauer, Lobova, & Fleming, 2011; Maas et al., 2016). In addition, results from exclosure experiments, considering only bids or also encompassing other predators, are limited to evaluate the effect of those foliage-gleaning predators, thus underestimating the predation pressure of the aerial insectivores (Maas et al., 2016).

Other relevant functions such as pollination and seed dispersal have been scarcely investigated in the studies, probably due to the difficulty of measuring and assessing these ecological processes. For example, seed dispersal effectiveness, defined as the contribution a disperser makes to the future reproduction of the plant (Schupp, Jordano, & Gómez, 2010), is determined by two components: number of seeds dispersed and the probability that dispersed seeds become a new adult plant components (Schupp et al., 2010). However, it has been difficult to obtain data for both components in disperser birds and involved plant species (Mokotjomela, Downs, Esler, & Knight, 2016), particularly due to the overlap with seed-dispersing mammals and incomplete knowledge of many habitats (Wenny et al., 2011). Thus, many studies link the loss this ecological process with a decay in species richness of frugivorous birds and the loss of functional traits (see Moran & Catterall, 2014; Newbold et al., 2013), although the seed dispersal per se is not measured.

Nevertheless, seed dispersal is arguably the most important ecosystem function provided by birds, especially in tropical forests (Sekercioglu, 2006). Loss of avian seed dispersers can affect large-scale processes such as the regeneration of natural habitats but also the specific phenotypic and genetic characteristics of plants species (Galetti et al., 2013; Sekercioglu, 2006). For example, defaunated areas for several decades in Brazilian Atlantic forest showed a phenotypic selection of smaller seeds of palm, *Euterpe Edulis*, than non-defaunated forests, due to large avian frugivores loss, specially toucans and large cotingas (Galetti et al., 2013).

About 58% of the studies evaluated the effect of environmental variables on ecological functions performed by birds. Studies ($n = 48$) assessing factors at local scale, such as vegetation structure, were predominant, while patch and landscape scale factors were poorly investigated (Table 2). Overall, several studies highlight that anthropogenic disturbances leading to simplification of the local structure of habitat, decrease the diversity of different ecological groups of birds, consequently affecting the functions performed by the species. For example, Poch and Simonetti (2013a) support the hypothesis that structural complexity of vegetation is correlated with the ecological function of insect control. Thus, it could be expected a higher insectivory rate as a consequence of a greater abundance of insectivores in more complex habitats (see Bereczki, Ódor, Csóka, Mag, & Báldi, 2014; Johnson et al., 2009). By contrast, few studies have assessed environmental variables at large spatial scales, that is, landscape or region. For example, Breitbach, Laube, Steffan-Dewenter, and Böhning-Gaese (2010) emphasize that knowledge on the relationship between intensity of land use and seed dispersal rates is scarce, with previous studies evaluating the dispersal rate among isolated trees within agricultural areas and within forest fragments (Kirika, Bleher, Böhning-Gaese, Chira, & Farwig, 2008). Nevertheless, an experiment conducted in the Brazilian Atlantic forest, Menezes, Cazetta, Morante-Filho, and Faria (2016) observed a reduction in fruit consumption by birds within forest patches inserted in more deforested landscapes. This result may indicate less efficient seed dispersal, both in numbers of seeds dispersed and in the likelihood of seeds being moved long distances (Menezes et al., 2016). Therefore, it is especially important to study the relationship between land use intensity and seed dispersal because this process is crucial for plant migration in fragmented landscape.

These results highlight knowledge gaps because several studies demonstrate that processes operating at large spatial scales are highly important for biodiversity and ecosystem function maintenance (Östman, Ekbom, & Bengtsson, 2001). For example, fragmentation of forests resulting from logging, road construction, agricultural, and urban expansion can alter plant species composition and growth, negatively affecting animal species (Ewers & Didham, 2006). Simultaneously, this process can improve forest access to human activities, further increasing the likelihood of timber harvesting, hunting, and fire events. Thus, by altering the arrangement and local structure of remaining patches, fragmentation can modify the functional role played by a species (Skórka, Magdalena, Moron, & Tryjanowski, 2013; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). To propose and achieve effective conservation practices designed for birds, their habitats, and especially their functions, it is necessary to understand how land use may interfere in the ecological role of species (Maas et al., 2013; Skórka et al., 2013). This approach can be used to estimate the economic value of native vegetation remnants within agricultural landscapes and provide estimates of ecosystem services under different land use scenarios (Wenny et al., 2011; Winqvist, Ahnstrom, & Bengtsson, 2012).

Most of the studies ($n = 51$) found that the ecological function of a bird species or assemblage can arise from a cascade effect on other trophic levels. For example, the extinction of bird pollinators in New Zealand has reduced pollination, seed production, and density of the endemic shrub, *Rhabdothamnus solandri* (Anderson et al., 2011). Mainly, three levels of the food chain were evaluated, the interaction among birds, arthropods, and plant being the most commonly reported by the studies (e.g., Marquis & Whelan, 1994). Several studies indicate that birds, besides reducing herbivorous insect populations, may also increase plants productivity and biomass (Barber & Marquis, 2011; Mäntylä et al., 2011). Nevertheless, even when herbivory levels are mediated by bird predation, it does not necessarily affect plants reproductive success (De La Vega, Grez, & Simonetti, 2012), a process that is likely to be determined by other factors, such as environmental characteristics (Barber & Wouk, 2012; Giffard, Corcket, Barbaro, & Jactel, 2012).

In 32 studies, the trophic cascade effect was related to some environmental variable. Most were categorical studies that assessed cascades in two or more ecosystems (e.g., different forest types and comparisons between forests and agricultural systems) or studies that measured vegetation structure on sampling sites (Kellermann et al., 2008; Poch & Simonetti, 2013b). For instance, herbivory caused by insects is determined by resource availability, antiherbivore defenses, abundance of predators, and herbivorous, features that are expected to vary across sites depending on the habitat structure (Guimarães et al., 2014). Therefore, disturbed habitats may show increased herbivory not only because of the increased abundance of herbivorous insects (Morante-Filho, Arroyo-Rodríguez, Lohbeck, et al., 2016) but also because of reduced natural enemies of insects, as insectivorous birds (Karp et al., 2013).

On the other hand, few studies have quantified the effects of patch and landscape-scaled factors on trophic cascade. These studies show that complex landscapes can facilitate biological control performed by birds and indirectly contribute to an increase in crop productivity (Martin et al., 2013). Thus, agricultural areas with low land use intensity allied to natural habitats may sustain bird diversity, facilitate the provision of services, and be an important theoretical framework for large-scale conservation programs (Tscharntke et al., 2005). In a study conducted in Indonesia, Maas et al. (2013) found that cocoa productivity decreases in 31% with the reduction of shade tree cover and increase in distance between primary forests and crops. These factors increase the diversity of predatory birds and bats, which regulate herbivorous insect's abundance (Maas et al., 2013). Similar result was found in study conducted in Costa Rica; borer-consuming birds increased in abundance and exerted stronger control on borer populations on coffee plantations with higher surrounding forest cover (Karp et al., 2013). In contrast, De La Vega et al. (2012) found that fragmentation process does not influence the functional role of insectivorous birds. According to the authors, bird density directly affects leaf damage in *Aristotelia chilensis* via insect control, but this process is similar between patches and continuous forests.

As the ecosystem functioning is dependent on the regional species' pool, which is closely related to the landscape characteristics (Whittingham, 2011; Winqvist et al., 2012), changes in landscapes composition and structure, such as reduced size and increased isolation of natural habitats, and decreased environmental heterogeneity, may cause biodiversity decline and loss of different ecological functions (Tscharntke et al., 2005). Furthermore, changes in abiotic conditions and primarily changes in local densities can modify trophic interactions by the exclusion of higher level species, which consequently affect basal level species (Komonen, Penttilae, Lindgren, & Hanski, 2000; Taylor & Marriam, 1995).

Economic Benefits of Birds

We found only 11 studies that economically valued the ecosystem services provided by birds. From these, six are empirical studies, being pest control in agricultural systems the most evaluated service. A large number of the studies evaluating the economic benefits provided by birds started after the seminal publication of Costanza et al. (1997), that for the first time estimated the massive global value of ecosystem services. In most cases, birds are effective vectors depressing economical losses due to predation of arthropods and pathogenetic pests, ultimately increasing the productivity of various crops (Kellermann et al., 2008; Mols & Visser, 2007). In particular, in a study conducted in coffee plantations in Jamaica, the predation by insectivorous birds on arthropods reduced the infestation of fruits by 1% to 14%, increasing the production value by US$44 to $105/ha (Kellermann et al., 2008). Other study reported that pest control mediated by birds prevented $75 to $310 ha year^{-1} in damage in the coffee plantations of Costa Rica (Karp et al., 2013). In Indonesia, where cacao agroforests have a major economic importance, the release of predation pressure of birds and bats is estimated to result in a 31% decreasing of crop yield, or $730 ha year^{-1} (Maas et al., 2013).

The introduction of falcons in crop areas to remove avian pests could potentially result in savings of $234/ha for the Sauvignon Blanc variety of grapes and $326/ha for Pinot Noir variety of grapes, according to a study conducted in the United States (Kross, Tylianakis, & Nelson, 2011). Therefore, because of the economic benefits of birds to society, more research should be conducted to value to the supplied services and generate information to justify bird conservation allied to the preservation of their natural habitats (Wenny et al., 2011).

Concluding Remarks

Although birds are well-studied organisms, the ecological roles performed by species in many ecosystems are still poorly understood. Future studies should analyze the relationship between diversity components, such as taxonomic and phylogenetic diversity, and different ecological functions, and not only focus on the aspects of biodiversity per se. Once the level of functional redundancy among bird species is not evident, it is necessary to understand the implications of bird diversity decline on the loss of ecological functions (Firbank, Bradbury, McCracken, & Stoate, 2013). Although the actual species demise may compromise important aspects of the ecosystem maintenance, we need additional information from species behavior and the strength of interactions with other players in order to fully understand ecosystem function and its consequences to the stability of natural and anthropogenic systems (McConkey & O'Farrill, 2015). Furthermore, the loss of disturbance sensitive species can be numerically compensated for by the proliferation of disturbance-adapted species (i.e., habitat generalist birds) in altered-human landscapes (see Morante-Filho, Arroyo-Rodríguez, & Faria, 2016). Indeed, rather than changes in raw diversity metrics such as overall species richness or abundance, the most characteristic signature of disturbance is the reassembly of local communities with habitat specialists being replaced by generalists (Supp & Ernest, 2014). However, the extent to which species turnover reverberates on the ecological functions (De Coster, Banks-Leite, & Metzger, 2015) depends largely on the level of functional redundancy among the remaining species. Species carrying similar functional traits are expected perform similar roles in a community (Olden, Poff, Douglas, Douglas, & Fausch, 2004), but their functional contribution is also likely to vary according to its abundance (Winfree, Fox, Williams, Neilly, & Cariveau, 2015). Hence, depending on the level of similarity or discrepancy of existing traits within a community, this could result in functional homogenization (Olden et al., 2004) and high functional redundancy, with loss of ecological functions performed by birds in remaining habitats (Sekercioglu, 2006).

This study revealed several gaps in our knowledge about the ecological functions performed by birds. First, our results showed a lack of studies evaluating the ecological role played by birds in urban environments. Several studies highlight the contrasting effects of urbanization on bird species, which the variation of habitat quality of city environments may affect population shifts so that some populations grow, some decline, and others remain stable (see more details in Snep et al., 2016). However, in a recent study, Alberti et al. (2017) has shown that urbanization can lead to phenotypic changes in animal populations, thus affecting the remaining ecosystem functioning in urban landscapes. Thus, it is vital that future studies assess how bird diversity and their ecological functions can be maintained in urban landscapes.

More research should evaluate other important functions to the ecosystem maintenance, being necessary to understand the different benefits that the bird community may bring to the human population, such as disease control. Moreover, future studies must investigate scavenger bird ecology to assess the role of this guild for pest control and nutrients transport between ecosystems (Ogada, Torchin, Kinnaird, & Ezenwa, 2012; Sekercioglu, 2006). These information are especially needed because the extinction of this guild may cause serious problems to human and animal health (see Prakash et al., 2003). For instance, Ogada et al. (2012) reported not only a significant rise on decomposition time of carcasses in the absence of vultures but also a significant increase in the presence of mammalian species scavenging on rotting carcasses, enhancing the chances of disease transmission among African carnivores in Kenya. Therefore, studies in India (Prakash et al., 2003) and Africa (Ogada et al., 2012) support the assertion that the local extinctions or the drastic populational decline of specialized scavengers lead to detectable changes in different ecosystems. Of particular importance is the information gap regarding the role played by birds as seed predators, mainly to understand how such function can affect the recruitment of several plant species, ultimately shaping the habitat structure (Marone, Casenave, Milesi, & Cueto, 2008). In addition, more studies are required for our better understanding of importance of raptors on the population control of vertebrates that affect crop productivity and its economic impacts (Gavier-Pizarro et al., 2012).

Another important neglected issue is that ecological functions mediated by birds largely depend on environmental factors acting on different scales. Pollination is a good example because it can be affected by both the local vegetation structure, which maintains the diversity of pollinating birds, the distance between habitats and matrix characteristics. Therefore, different spatial scales need to be incorporated in future research (Geijzendorffer & Roche, 2013; Tscharntke et al., 2005), so that generalizations can be made based in ecosystems type and landscape characteristics (Winqvist et al., 2012). This information may help to understand the influence of current landscapes dominated by human activities on the ecological role played by birds and, consequently, on the ecosystem functioning (Geijzendorffer & Roche, 2013).

Overall, it is necessary to evaluate the extent of provided services in the trophic cascades (Terborgh & Estes, 2010). Even the most assessed function, which is predation of invertebrates by birds, is scarcely addressed in a trophic cascade approach, with a small number of studies evaluating the effects of environmental disturbances on species interactions. Thus, it is necessary to assess how bird can affect the interaction network existent in the ecosystems (Sekercioglu, 2012), and the relative importance of birds and other interacting species to the observed outcomes. Finally, it is critical that future studies quantify the economic value of services provided by birds in different land use contexts (Wenny et al., 2011). There is a dire need to apply this information to technically support biodiversity policies allying conservation and productive agricultural systems.

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