Ecosystem consequences of bird declines

Çağan H. Şekercioğlu*, Gretchen C. Daily, and Paul R. Ehrlich

Center for Conservation Biology, Department of Biological Sciences, Stanford University, 371 Serra Mall, Stanford, CA 94305-5020

Contributed by Paul R. Ehrlich, October 28, 2004

We present a general framework for characterizing the ecological and societal consequences of biodiversity loss and applying it to the global avifauna. To investigate the potential ecological consequences of avian declines, we developed comprehensive databases of the status and functional roles of birds and a stochastic model for forecasting change. Overall, 21% of bird species are currently extinction-prone and 6.5% are functionally extinct, contributing negligibly to ecosystem processes. We show that a quarter or more of frugivorous and omnivorous species and one-third or more of herbivorous, piscivorous, and scavenger species are extinction-prone. Furthermore, our projections indicate that by 2100, 6–14% of all bird species will be extinct, and 7–25% (28–56% on oceanic islands) will be functionally extinct. Important ecosystem processes, particularly decomposition, pollination, and seed dispersal, will likely decline as a result.

ecosystem services | functional extinctions | trophic cascades | community disassembly | ecological redundancy

The accelerating extinction of species (1) is the tip of the iceberg of global wildlife declines (2–5) that threaten to disrupt vital ecosystem processes and services (6). Although patterns of biodiversity loss have been explored extensively (7), their ecological implications have been the subject of few studies. These studies have been largely limited to temperate plants, microbes, and invertebrates (8). Yet ongoing reductions in vertebrate abundance and species richness are also likely to have far-reaching consequences, with diverse societal impacts, including plant extinctions , the loss of agricultural pest control, and the spread of disease. Birds are the best known major group of organisms (9), and the conservation status of all bird species have been assessed twice (1). Even though only 1.3% of bird species have gone extinct since 1500 (10), the global number of individual birds is estimated to have experienced a 20–25% reduction during the same period (5), indicating that avian populations and dependent ecosystem services are declining faster than species extinctions would indicate.

We compiled and analyzed a database of the conservation status, distribution, and life histories of all extant (9,787) and historically extinct (129) bird species. We synthesized, in a second database, studies of the ecological roles of birds and outlined their contributions to the functioning of diverse natural and human-dominated ecosystems (Table 1, and Table 2, which is published as supporting information on the PNAS web site). To assess the potential effects of bird population declines and extinctions on ecosystem processes and services, we compare the current distribution of threatened birds across various functional groups, habitats, and regions to the distributions forecasted for 2100 based on three scenarios. The scenarios are projections based on the past and present distributions of threatened and nonthreatened birds. Our objective here is to address the ecological implications of the current and future distribution of extinction-prone bird species among major ecological and geographical groupings, not to examine correlates of extinction threat in detail (for pertinent references, see Table 3, which is published as supporting information on the PNAS web site).

Methods

Scenarios. We entered available data on the conservation, distribution, ecology, and life history of all extant (9,787) and historically extinct (129) bird species of the world from 248 sources into a database with >600,000 entries. Our scenarios (Fig. 3, which is published as supporting information on the PNAS web site) are based on the extinction probabilities for threatened species used by International Union for Conservation of Nature and Natural Resources (IUCN). These probabilities are as follows: 50% chance of extinction in the next 10 years for critically endangered species, 20% chance of extinction in the next 20 years for endangered species, and 10% chance of extinction in the next 100 years for vulnerable species. We report the averages of 10,000 simulations run for each decade from 2010 to 2100.

For scenario 1 (best case), we assume that conservation measures will be sufficient to prevent any more bird species from becoming threatened but will be unable to reduce the extinction likelihood of threatened species during this century. Restricted range species and wide-ranging species are treated equally. For scenario 2 (intermediate case), we compared threatened bird lists of 1994–2003 (1, 11) to calculate the probability (0.0111) that a nonthreatened bird species (including "near threatened" species) will become threatened after a decade. We assume that nonthreatened species will continue to become threatened at this rate and that newly threatened species are randomly distributed among three threat categories based on the current percentage of threatened species in each threat category. For scenario 3 (worst case), we assume that the probability of a nonthreatened species becoming threatened will increase by a conservative 1% per decade (1.11% in 2010, 2.11% in 2020, and so on) and that threatened species will go extinct at the rates given above. These assumptions are conservative because it is estimated that every year, natural habitats and dependent vertebrate populations decrease by an average of 1.1% (ref. 12 and *Supporting Methods and Materials*, which is published as supporting information on the PNAS web site).

Because some species are more likely to become threatened and to go extinct than others in the same threat category, for scenarios 2 and 3, we examined various criteria and indices for weighting the probabilities of becoming threatened and going extinct. In agreement with the IUCN's most important criteria (1, 10), population size class ($r^2 = 0.54$, $P < 0.0001$) and range size class ($r^2 = 0.27$, $P < 0.0001$) explain the greatest amount of variance in conservation status. However, we had to choose a variable that was available for all of the species in our database. Restricted range status (global range <50,000 km^2) has the next highest correlation ($r^2 = 0.23$, $P < 0.0001$) and has the added advantage of being straightforward to incorporate into our models. Primary diet does not have a high correlation with threat status ($r^2 = 0.011$, $P < 0.001$), and was not used in weighting the model. This finding also means our reasoning is not circular, because we use extinction likelihoods based on population and range sizes to predict the distribution of species across functional groups based on primary diet. Therefore, in scenarios 2 and 3, species with restricted ranges have higher probabilities of becoming threatened and going extinct (Fig. 3), and these proba-

Abbreviation: IUCN, International Union for Conservation of Nature and Natural Resources.

*To whom correspondence should be addressed. E-mail: cagan@stanford.edu.

bilities are calculated by using the ratio of threatened restricted range species to threatened wide-ranging species in their respective categories during the previous time step. Further details can be found in *Supporting Materials and Methods*; a bibliography of all of the database sources is in *References for Global Bird Database*, which is published as supporting information on the PNAS web site; and a sample of the database is Data Set 1, which is published as supporting information on the PNAS web site.

Some caveats should be considered when interpreting our results. The IUCN extinction probabilities normally pertain only to the quantitative analysis criterion of the IUCN Red List. However, given the lack of data on bird extinction likelihoods, that these probabilities have been used in the past to estimate future bird extinctions (10, 13), and that even our worst-case scenario is conservative compared with actual rates of habitat loss (12), these numbers provide realistic lower bounds.

For some species, such as those with long generation times, the extinction probabilities may be lower than the IUCN estimates. On the other hand, species with long generation times often have low reproductive rates and are particularly sensitive to adult mortality, as can be seen in the rapidly worsening plight of albatrosses and vultures (9). In addition, the extinction probabilities of many species may increase if sources of threat such as exploitation, habitat clearance, and accidental mortality persist or increase in intensity.

To calculate the rate of becoming threatened, we do not exclude 305 recently described species (Table 2) that are significantly more likely to be threatened (35%) than birds in general (12%). As molecular techniques become widespread, more and more subspecies are raised to species status, and this trend will continue during this century. Excluding them would seriously underestimate the percentage of species becoming threatened in the future. In fact, given that birds' ecological contributions are related to the size and number of their populations, status of subspecies, rather than species, is a better estimate of the percentage of threatened bird populations and avian ecosystem services, but most bird subspecies have not been evaluated.

Functional Extinction and Deficiency. Forty-three percent of threatened bird species are endangered, critically endangered, or extinct in the wild. Combined with extinct species, these birds comprise 7% of all historic bird species, whereas they make up 0.025% of the global bird population and contribute little to ecosystem processes compared with the rest of the avifauna. In addition, 72% of these birds have global populations of $<$2,500 individuals, 90% of those populations are declining, and 40% are in rapid, continuous decline (50–80% population reduction in three generations). Therefore, we define birds that are endangered, critically endangered, or extinct in the wild as "functionally extinct." We define as functionally deficient bird species that have undergone recent and substantial declines in abundance, and/or extent or occupancy of geographic range, in places where some semblance of their habitat (and potential function) remains. We then use the IUCN category of vulnerable species as an imperfect means of identifying those species that are functionally deficient. Some vulnerable species that have experienced significant habitat losses may yet occur at predisturbance densities in remaining habitat, and 162 species are classified as vulnerable only based on their naturally very small population (IUCN Criterion D1) and/or global range (IUCN Criterion D2). Both of these types of vulnerable species inflate our estimate of the number of functionally deficient species. To offset this inflation, we exclude all 731 near threatened species from our estimates of functionally deficient species, although many near threatened species doubtlessly meet the definition (10). However, uncertainties regarding many near threatened species and the impossibility of estimating the number and extinction rate of near threatened species in future scenarios provide further support for their exclusion, although it makes our estimates conservative. By definition, extinct species are also functionally extinct, and functionally extinct species are also functionally deficient.

Results

Based on the criteria used by the IUCN (1), 21% of 9,916 historic bird species (all species that survived past A.D. 1500) are extinction-prone, a category that includes species that are extinct (1.3%), threatened with extinction in the next 10–100 years (12%), and close to qualifying or likely to qualify for a threatened category in the near future (7.4%, near threatened). Extinction-prone birds are not randomly distributed across different functional groups (based on primary diet; Fig. 1*a*) or guilds (based on diet and order of food preference; Fig. 4*a*, which is published as supporting information on the PNAS web site). Even though primary diet is not a good predictor of threat status ($r^2 = 0.011$), some functional groups have more extinction-prone species than average: frugivores ($\chi^2 = 31.0$; $P < 0.0001$), herbivores (consumers of nonreproductive plant parts; $\chi^2 = 31.6$; $P < 0.0001$), omnivores ($\chi^2 = 44.9$; $P < 0.0001$), piscivores ($\chi^2 = 52.2$; $P < 0.0001$), and scavengers ($\chi^2 = 22.2$; $P < 0.005$). Insectivores ($\chi^2 = 24.0$; $P < 0.005$) have slightly fewer extinction-prone species than average. Increased specialization is highly correlated with increased likelihood of extinction (Fig. 1*b*), and 41% of bird species limited to one habitat type are extinction-prone.

Higher concentrations of extinction-prone birds in certain groups may lead to community disassembly and to more pronounced ecological consequences than one would expect from global aggregated extinction probabilities. There are significant differences in the distribution of extinction-prone species among categories other than diet, such as habitat, region, altitudinal distribution, body mass, clutch size, and evolutionary uniqueness (Fig. 1 and Tables 3 and 4, which are published as supporting information on the PNAS web site). Island birds are particularly at risk, although this is due to their small global ranges rather than an "island effect" (14); in our stepwise regression model with forward selection (4,515 species), compared with "range size" alone ($r^2 = 0.274$), addition of "island status" was a negligible improvement ($r^2 = 0.275$).

When distinct ecosystems, such as forests or wetlands, are destroyed, the ecological roles of birds often disappear with them. In many cases, however, bird declines occur independent of habitat loss; exploitation, introduced species, pathogens, fragmentation, and other factors (9) eliminate birds and their services from ecosystems (6). In fact, half of threatened species are threatened by a factor besides habitat loss. This result is particularly the case for scavengers (100%), piscivores (80%), herbivores (78%), omnivores (76%), granivores (56%), frugivores (53%), and birds that weigh $>$100 g (73%), all of which, except granivores, are groups significantly more threatened than average.

Given the momentum of climate change, widespread habitat loss, and increasing numbers of invasive species, avian declines and extinctions are predicted to continue unabated in the near future (9). The results of our scenarios for 2100 support this view and reinforce previous estimates (13). By 2100, we expect 6–14% of all historic bird species to be extinct, 7–25% to be functionally extinct, and 13–52% to be functionally deficient (Fig. 2). We project greater-than-average extinction rates for frugivores, herbivores, nectarivores, piscivores, and scavengers (Fig. 2*a*). Some guilds may lose up to 46% of their species (Fig. 4*b*). Specialists are predicted to have more extinctions than average (Fig. 2*b*). This estimate is also the case for monospecific genera (9–16% of species projected extinct) and bird families with five or fewer species (11–20% of species projected extinct). Forest, marine, and wetland habitats (Fig. 2*c*), and regions with large numbers of island birds, are projected to experience the highest propor-

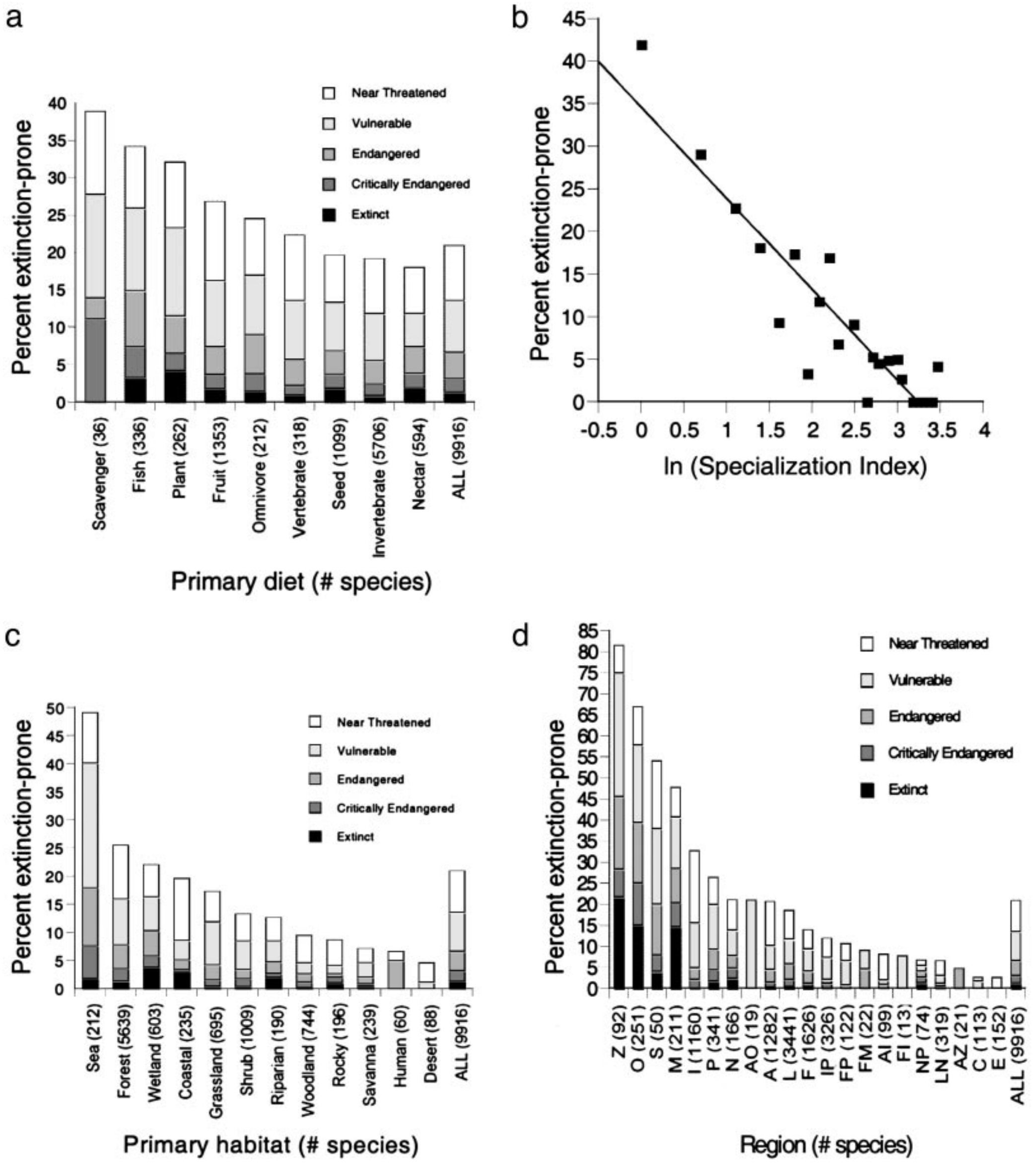

Fig. 1. Current conservation status of bird species. Number of species in each group is in parentheses. Species that are endangered or more threatened are considered functionally extinct and those that are vulnerable or more threatened are considered functionally deficient. (*a*) Distribution of extinction-prone species based on primary diet. If omnivores are reclassified based on first diet choice, percentages do not change except for scavengers (32%). (*b*) More specialization increases extinction risk; $r^2 = 0.851$. Specialization index is the product of habitats used and food types consumed. Higher numbers indicate less specialization. Species with an index of 32 or more have been pooled because of small sample sizes. (*c*) The likelihood of extinction based on primary habitat. Human, human-dominated habitats such as farms, plantations, and towns. If forest birds are taken out, global average drops to 16%. (*d*) Regional distribution of extinction-prone species. Regions displayed in Fig. 5, which is published as supporting information on the PNAS web site, are as follows: A, Austral; C, Cosmopolitan; E, Eastern Hemisphere; F, Afrotropical; I, Indomalayan; M, Malagasy; N, Nearctic; L, Neotropical; O, Oceania; P, Palearctic; S, South Polar; and Z, New Zealand. Each bird is placed in only one region. Two letters indicate combination regions (e.g., NP includes all bird species found in both Nearctic and Palearctic regions).

tion of real and functional extinctions with Malagasy, New Zealand, and Oceanic regions forecasted to lose 26–48% of their species (Fig. 2*d*).

Discussion

Bird extinctions and population reductions (5) in the 21st century may disrupt ecosystem processes and services of potential importance to society (15, 16). Declines in bird species that are important for a particular ecosystem process/service may not necessarily mean a decline in that process/service if the populations of other functionally equivalent species increase in response (17). On the other hand, many bird species, such as the southern cassowary *Casuarius casuarius* (18) and the three-wattled bellbird *Procnias tricarunculata* (19), have irreplaceable roles in ecosystems despite initial impressions to the contrary (19). Even generalist species may not be replaceable (20). In addition, avian dispersers and pollinators for some plant communities, including Cape fynbos and tropical lowland humid forest, have low equivalence, resulting in a high risk of plant extinctions from lost mutualisms (21). Because highly specialized and evolutionarily unique species are more likely to go extinct, the probability of others taking their place is reduced. Paralleling the estimated decrease in the numbers of individual birds (5), a quarter of all European (22) and North American (23) bird

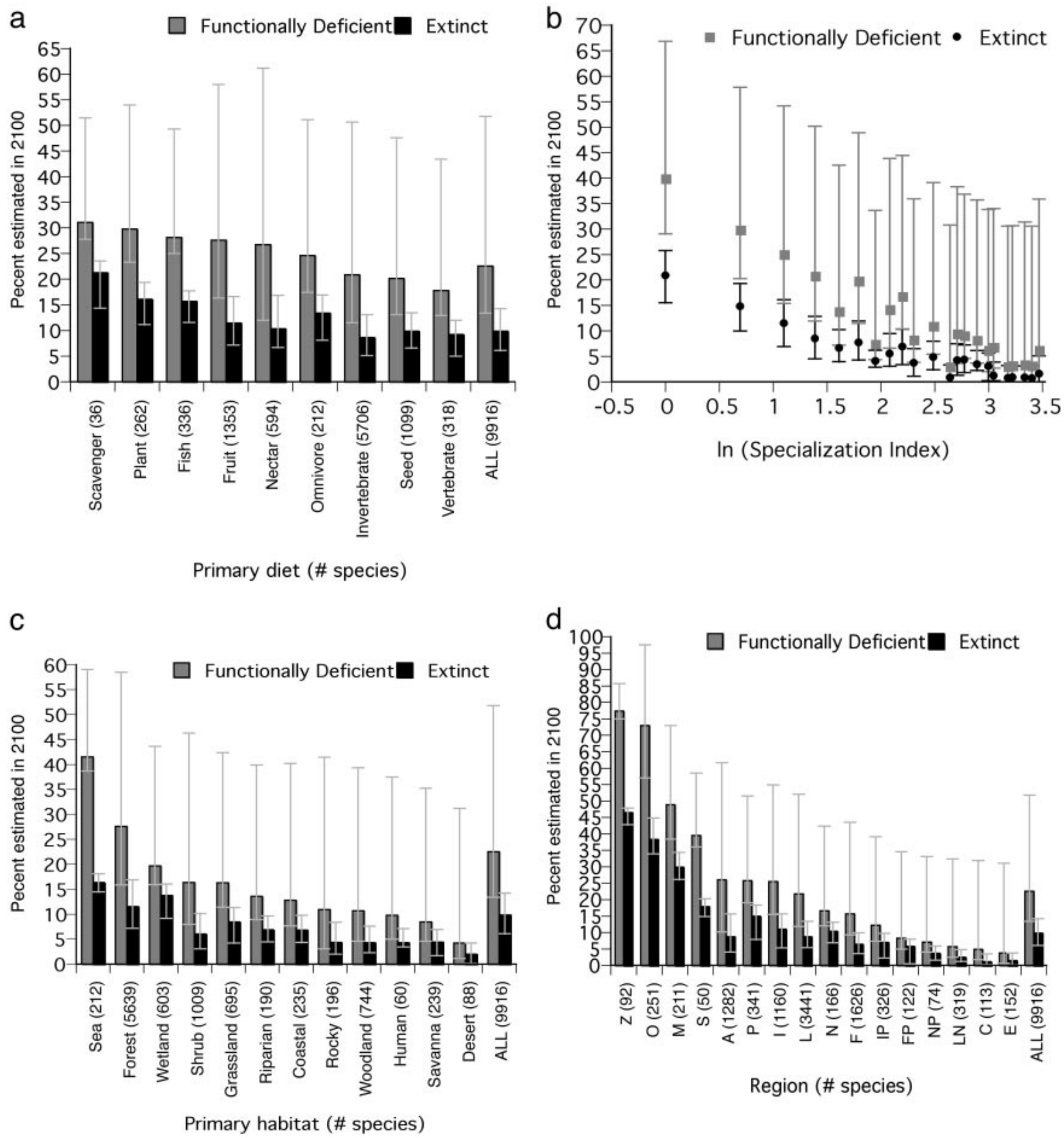

Fig. 2. Predicted percentages of extinct and functionally deficient bird species for 2100 based on scenario 2 (intermediate). Threatened and extinct species are considered functionally deficient. Error bars, not used in a conventional sense, indicate averages of 10,000 simulations of scenarios 1 (best case) and 3 (worst case). See Fig. 1 for category details. (*a*) Distribution based on primary diet. (*b*) Specialized species are more likely to be extinct ($r^2 = 0.894$) and functionally deficient ($r^2 = 0.879$). (*c*) Distribution based on primary habitat. (*d*) Distribution among biogeographic regions. Some combination regions were excluded for the sake of clarity.

species have significantly declined in the past three decades and, globally, 78% of threatened bird species have continuously diminishing populations. Such widespread declines mean that the losses of sensitive species are not, overall, being compensated by increases in other bird species.

Among the bird functional groups that are expected to have more extinctions than average, nectarivores pollinate many plant species and frugivores are important seed dispersers, both of which have important consequences for plant populations and community dynamics (Table 1). Declines in pollination (24) and seed dispersal (20) as a result of bird extinctions may lead to extinctions of dependent plant species (25). The former is particularly important in the Austral, New Zealand, and Oceanic regions, where the proportion of bird-pollinated plants is higher than other parts of the world (26), and, in the case of the latter two regions, most of the presettlement avifauna is already extinct (27). Even though there has been little research on the economic importance of avian pollination and seed dispersal, our survey of the literature (Table 1) reveals that bird pollination and dispersal of a number of economically important species have been demonstrated in Indomalayan, Neotropical, and Palearctic regions, and avian seed dispersal is important in reducing the cost of restoring degraded lands.

Little is known about the potential consequences of widespread disappearance of fish eating and scavenging bird species. There is an urgent need to investigate whether ongoing declines in seabird populations may have unanticipated top-down or bottom-up consequences as a result of trophic cascades or significant reductions in nutrient deposition (Table 1). Because most scavenging birds are highly specialized to rapidly dispose of

Table 1. Ecological and economical contributions of avian functional groups

Functional group	Ecological process	Ecosystem service and economical benefits	Negative consequences of loss of functional group
Frugivores	Seed dispersal	Removal of seeds from parent tree; escape from seed predators; improved germination; increased economical yield; increased gene flow; recolonization and restoration of disturbed ecosystems	Disruption of dispersal mutualisms; reduced seed removal; clumping of seeds under parent tree; increased seed predation; reduced recruitment; reduced gene flow and germination; reduction or extinction of dependent species
Nectarivores	Pollination	Outbreeding of dependent and/or economically important species	Pollinator limitation; inbreeding and reduced fruit yield; evolutionary consequences; extinction
Scavengers	Consumption of carrion	Removal of carcasses; leading other scavengers to carcasses; nutrient recycling; sanitation	Slower decomposition; increases in carcasses; increases in undesirable species; disease outbreaks; changes in cultural practices
Insectivores	Predation on invertebrates	Control of insect populations; reduced plant damage; alternative to pesticides	Loss of natural pest control; pest outbreaks; crop losses; trophic cascades
Piscivores	Predation on fishes and invertebrates and production of guano	Controlling unwanted species; nutrient deposition around rookeries; soil formation in polar environments; indicators of fish stocks; environmental monitors	Loss of guano and associated nutrients; impoverishment of associated communities; loss of socioeconomic resources and environmental monitors; trophic cascades
Raptors	Predation on vertebrates	Regulation of rodent populations; secondary dispersal	Rodent pest outbreaks; trophic cascades; indirect effects
All species	Miscellaneous	Environmental monitoring; indirect effects; birdwatching tourism; reduction of agricultural residue; cultural and economic uses	Losses of socioeconomic resources and environmental monitors; unpredictable consequences

Table annotated with source references is available as Table 2, which is published as supporting information on the PNAS web site.

the bodies of large animals, these birds are important in the recycling of nutrients, leading other scavengers to dead animals, and limiting the spread of diseases to human communities as a result of slowly decomposing carcasses. In South Asia, the combination of extremely rapid crash of vulture populations (28, 29), highly virulent diseases, and high human population density may cause increases in incidences of anthrax, bubonic plague, and rabies (28), but this potentially crucial interaction has not been studied. In 1997, >30,000 of the world's 35,000–50,000 rabies deaths took place in India (30) where feral dog and rat populations have exploded after the decline of vultures (28).

Although less threatened than average, insectivorous birds include more extinction-prone species than any other group. Because of their high ecological specialization (31), many tropical forest insectivores are highly sensitive to habitat fragmentation (32), and 26% of these species are extinction-prone. Exclusions of insectivorous birds from apple trees, coffee shrubs, oak trees, and other plants have resulted in significant increases in insect pests and consequent plant damage (Table 1). Natural pest-control services are increasing in importance as invertebrate pests develop resistance to chemicals, and pesticide use is curbed by environmental regulations and consumer trends (33). Extreme specializations of many insectivorous birds, especially in the tropics, make it unlikely that other taxa can replace these birds' ecosystem services.

The societal importance of ecosystem services is often appreciated only during their loss. Important avian guilds are in rapid decline and consequent reductions in ecosystem processes are likely. Disconcertingly, avian declines may in fact portray a best case scenario because fish, amphibians, reptiles, and mammals are 1.7–2.5 times more threatened (10). Invertebrates, much less known but far more speciose and arguably of greater ecological significance, may also be disappearing faster (34). Investments in understanding and preventing declines in populations of birds and other organisms will pay off only while there is still time to act.

We thank Burak Över for entering the data of thousands of bird species; Francisco Barron, Manuel Jemente, Athelie LaGuierre, Elizabeth Micks, Robin Phelps, and Doğan Şekercioğlu for dedicated assistance with data entry; BirdLife International (particularly Mark Balman and Martin Sneary), Thomas Brooks, Adrian Craig, John Dunning, Raymond Paynter, Adam Riley, and Don Roberson for data sources and advice; Ragıp Akbaş, Utkan Demirci, and Gökhan İnalhan for assistance with running the models; John Fay and Ann McMillan for help with the figures; and Reşit Akçakaya, Carol Boggs, Sandra Diaz, Jianguo Liu, Harold Mooney, Henrique Pereira, and Peter Vitousek for providing valuable comments and suggestions to improve the manuscript. This work was supported by Dr. Walter Loewenstern, the Gifford Undergraduate Fund, and the Koret, Moore, and Winslow foundations.

1. International Union for Conservation of Nature and Natural Resources (2003) *2003 IUCN Red List of Threatened Species*; www.redlist.org.
2. Hughes, J. B., Daily, G. C. & Ehrlich, P. R. (1997) *Science* **278,** 689–692.
3. Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., *et al*. (2001) *Science* **293,** 629–637.
4. Ceballos, G. & Ehrlich, P. R. (2002) *Science* **296,** 904–907.
5. Gaston, K. J., Blackburn, T. M. & Goldewijk, K. K. (2003) *Proc. R. Soc. London Ser. B* **270,** 1293–1300.
6. Redford, K. H. (1992) *Bioscience* **42,** 412–422.
7. Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., *et al*. (2000) *Science* **287,** 1770–1774.
8. Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., *et al*. (2001) *Science* **294,** 804–808.
9. BirdLife International (2004) *State of the World's Birds 2004: Indicators for Our Changing World* (BirdLife International, Cambridge, U.K.).
10. BirdLife International (2000) *Threatened Birds of the World* (Lynx Edicions and BirdLife International, Barcelona and Cambridge, U.K.).

11. Collar, N. J., Crosby, M. J. & Stattersfield, A. J. (1994) *Birds to Watch 2: The World List of Threatened Birds* (BirdLife International, Cambridge, U.K.).
12. Jenkins, M., Green, R. E. & Madden, J. (2003) *Conserv. Biol.* **17,** 20–23.
13. Crosby, M. J., Stattersfield, A. J., Collar, N. J. & Bibby, C. (1994) *Biodivers. Lett.* **2,** 182–185.
14. Manne, L. L., Brooks, T. M. & Pimm, S. L. (1999) *Nature* **399,** 258–261.
15. Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., *et al*. (2000) *Nature* **405**, 234–242.
16. Luck, G. W., Daily, G. C. & Ehrlich, P. R. (2003) *Trends Ecol. Evol.* **18,** 331–336.
17. Walker, B. H. (1992) *Conserv. Biol.* **6,** 18–23.
18. Stocker, G. C. & Irvine, A. K. (1983) *Biotropica* **15,** 170–176.
19. Wenny, D. G. & Levey, D. J. (1998) *Proc. Natl. Acad. Sci. USA* **95,** 6204–6207.
20. Cordeiro, N. J. & Howe, H. F. (2003) *Proc. Natl. Acad. Sci. USA* **100,** 14052–14056.
21. Bond, W. J. (1994) *Philos. Trans. R. Soc. London B* **344,** 83–90.
22. Heath, M. F., Borggreve, C., Peet, N. & Hagemeijer, W. J. M. (2000) *European Bird Populations: Estimates and Trends* (BirdLife International, Cambridge, U.K.).
23. Sauer, J. R., Hines, J. E. & Fallon, J. (2004) *The North American Breeding Bird Survey, Results, and Analysis* 1966–2003 (USGS Patuxent Wildlife Research Center, Laurel, MD), Version 2004.1, www.mbr-pwrc.usgs.gov/bbs.
24. Robertson, A. W., Kelly, D., Ladley, J. J. & Sparrow, A. D. (1999) *Conserv. Biol.* **13,** 499–508.
25. Cardoso da Silva, J. M. & Tabarelli, M. (2000) *Nature* **404,** 72–74.
26. Ford, H. A. (1985) *Proc. Ecol. Soc. Aust.* **14,** 153–158.
27. Steadman, D. W. (1995) *Science* **267,** 1123–1131.
28. Pain, D. J., Cunningham, A. A., Donald, P. F., Duckworth, J. W., Houston, D. C., Katzner, T., Parry-Jones, J., Poole, C., Prakash, V., Round, P., *et al*. (2003) *Conserv. Biol.* **17,** 661–671.
29. Oaks, J. L., Gilbert, M., Virani, M. Z., Watson, R. T., Meteyer, C. U., Rideout, B. A., Shivaprasad, H. L., Ahmed, S., Chaudhry, M. J. L., Arshad, M., *et al*. (2004) *Nature* **427,** 630–633.
30. Public Health Agency of Canada (2000) *World Survey of Rabies, 1997* (Canada Communicable Disease Report) **26–02,** 13–16; http://www.phac-aspc.gc.ca/publicat/ccdr-rmtc/00vol26/dr2602eb.html.
31. Sherry, T. W. (1984) *Ecol. Monogr.* **54,** 313–338.
32. Şekercioğlu, Ç. H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D. & Sandi, R. F. (2002) *Proc. Natl. Acad. Sci. USA* **99,** 263–267.
33. Naylor, R. & Ehrlich, P. R. (1997) in *Nature's Services: Societal Dependence on Natural Ecosystems*, ed. Daily, G. C. (Island Press, Washington, D.C.), pp. 151–174.
34. Thomas, J. A., Telfer, M. G., Roy, D. B., Preston, C. D., Greenwood, J. J. D., Asher, J., Fox, R., Clarke, R. T. & Lawton, J. H. (2004) *Science* **303,** 1879–1881.