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Issue: *The Year in Ecology and Conservation Biology***Ecosystem services provided by bats**Thomas H. Kunz,¹ Elizabeth Braun de Torrez,¹ Dana Bauer,² Tatyana Lobova,³ and Theodore H. Fleming⁴¹Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, Massachusetts.²Department of Geography, Boston University, Boston, Massachusetts. ³Department of Biology, Old Dominion University, Norfolk, Virginia. ⁴Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona

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Ecosystem services are the benefits obtained from the environment that increase human well-being. Economic valuation is conducted by measuring the human welfare gains or losses that result from changes in the provision of ecosystem services. Bats have long been postulated to play important roles in arthropod suppression, seed dispersal, and pollination; however, only recently have these ecosystem services begun to be thoroughly evaluated. Here, we review the available literature on the ecological and economic impact of ecosystem services provided by bats. We describe dietary preferences, foraging behaviors, adaptations, and phylogenetic histories of insectivorous, frugivorous, and nectarivorous bats worldwide in the context of their respective ecosystem services. For each trophic ensemble, we discuss the consequences of these ecological interactions on both natural and agricultural systems. Throughout this review, we highlight the research needed to fully determine the ecosystem services in question. Finally, we provide a comprehensive overview of economic valuation of ecosystem services. Unfortunately, few studies estimating the economic value of ecosystem services provided by bats have been conducted to date; however, we outline a framework that could be used in future studies to more fully address this question. Consumptive goods provided by bats, such as food and guano, are often exchanged in markets where the market price indicates an economic value. Nonmarket valuation methods can be used to estimate the economic value of nonconsumptive services, including inputs to agricultural production and recreational activities. Information on the ecological and economic value of ecosystem services provided by bats can be used to inform decisions regarding where and when to protect or restore bat populations and associated habitats, as well as to improve public perception of bats.

Keywords: arthropod suppression; biological pest control; ecosystem valuation; insectivory; pesticide reduction; pollination; seed dispersal; sustainable agriculture

Introduction

Ecosystems consist of living organisms and their interactions with the abiotic environment (both physical and chemical). Terrestrial ecosystems include forests, grasslands, deserts, wetlands, and caves. Aquatic ecosystems include rivers, streams, lakes, ponds, estuaries, and oceans. For thousands of years, both terrestrial and aquatic ecosystems have been subject to human alterations, including conversion of natural ecosystems to agricultural ecosystems that were needed to sustain increasing human population growth. Natural ecosystems throughout

the world have become increasingly threatened by human-generated or anthropogenic factors such as urbanization, mining, deforestation, chemical and light pollution, and invasive species. Healthy ecosystems are especially important in providing various regulatory processes (e.g., insect suppression, pollination, seed dispersal, purification of water and air, stabilization of soils, decomposition of wastes, binding of toxic substances, mitigation of diseases, mitigation of floods, and regulation of climate, etc.); products or provisions (e.g., food, fuel, fiber, and medicines); supporting processes (e.g., nutrient cycling, soil formation, and primary production); and

cultural benefits (e.g., aesthetic, spiritual, educational, and recreational) that improve human well-being.¹ These processes and products are commonly referred to as *ecosystem services*^{2,3} and have been duly recognized by the United Nations Millennium Ecosystem Assessment.^{4,5} Ecosystem services vary depending on the ecosystems and the organisms that they constitute. In this paper, we consider the role of bats in providing ecosystem services, focusing primarily on those that both regulate and provide services needed to sustain humankind, with brief references to supporting and cultural services. One of the grand challenges that society faces is how best to identify, protect, and conserve services that are critical for human and ecosystem health.^{1,6}

In their present form, bats have been on Earth for over 52 million years⁷ and during this period have diversified into at least 1,232 extant species.^{8,9} Bats have evolved an incredibly rich diversity of behavioral, roosting, and feeding habits.^{10,11} By day, many species occupy caves and cave-like structures, such as tombs and mines;¹² others roost in tree cavities and foliage,¹³ sometimes modifying foliage into unique tent-like structures.^{14–16} By night, bats fill the skies to forage on a diversity of food items ranging from insects, nectar, and fruit, to seeds, frogs, fish, small mammals, and even blood.

Unfortunately, many threats face bats today. Bats in western cultures have long been subjects of disdain and persecution and have often been depicted in the popular media as rampant vectors of disease, blood-sucking demons, ingredients of witches brew, and, at times, associated with the dark side of some religious practices.¹⁷ Common myths include that bats are attracted to and become caught in women's hair, are associated with the devil, and that extracts from the skin of bats can cure baldness.^{18,19} As with many myths and folklore, there may be some elements of truth, yet the vast majority of real or imagined images of bats often portrayed in art, poetry, books, movies, television, and the press convey them as having little redeeming value except to frighten for the sake of corporate or personal profit. By contrast, in many eastern cultures, especially those that prevailed during the middle and late Qing Dynasty (1644–1911) in China, bats were considered to be symbols of good fortune, such as long life, health, wealth, virtue, and serenity of mind.^{18,19} Today, these cultural symbols persist, but appear to be less important to modern Chinese society.²⁰

Since their evolutionary origin, some species of bats have become locally extirpated or regionally extinct, mostly for unknown reasons.²¹ In recent years, increased evidence of anthropogenic activities such as depletion or destruction of forests and other terrestrial ecosystems, disturbances to caves, depletion of food resources, overhunting for bush meat,²² increased use of pesticides,^{11,23} and the proliferation and operation of utility-scale wind energy facilities^{20,24–26} have contributed to unintended and, in some cases, unprecedented mortality of bats. Bats that roost in caves, for example, are often disturbed by unsuspecting visitors either during maternity periods or hibernation, which can lead to death or abandonment. Bats known to roost in buildings are sometimes excluded or even exterminated for perceived or real threats to human health, and sometimes simply from unfounded fear stirred by the media.

Increased human populations and associated habitat degradation have been linked to the decline of many fruit-eating and nectar-feeding species, especially of endemic taxa and certain tropical species that evolved on remote islands.²⁷ Increased human pressures by indigenous cultures in Asia, Africa, and the Pacific Islands for bush meat have also led to the local or regional extirpation of some species. The recent decline of the little brown myotis, *Myotis lucifugus*, one of the most common and widespread species in North America, has been attributed to white-nose syndrome,²⁸ an emerging disease associated with the putative fungal pathogen, *Geomyces destructans*,^{29,30} which may have been introduced from Europe.^{31,32}

Bat biologists are often asked, “Why should we care about bats?” The simple answer is that scientists care about the fate of animals and as a consequence have invested their careers in studying and, perhaps more importantly, protecting these marvelous flying mammals. Benefits that humans inadvertently and unsuspectingly derive from bats will be forever lost or severely diminished, causing both known and unknown consequences to the ecosystems in which they have evolved.

The rich diversity of dietary habits of bats, ranging from species that feed on insects and other arthropods to those that feed on fruit, nectar, and flowers,^{10,11} provide valuable ecosystem services and, thus, are the subjects of this paper, although other species that feed on seeds, frogs, fish, small

mammals, and even blood also assume important roles in ecosystems as predators or prey in sustainable ecosystems. Bats provide value to ecosystems as primary, secondary, and tertiary consumers that support and sustain both natural and human dominated ecosystems ranging from the simple to the complex. In this review, we describe the ecosystem services provided by bats that feed on insects and other arthropods, on nectar and pollen, and on fruit. Insectivorous species, largely feeding on airborne insects and other arthropods, suppress both naturally occurring and anthropogenically-generated insect populations (such as agricultural pest species and insects that annoy or transmit specific pathogens to humans and other mammals) and contribute to the maintenance of ecosystem stability. Frugivorous bats help maintain the diversity of forests by dispersing seeds across different ecosystems, often introducing novel plant species into previously disturbed landscapes³³ and to oceanic islands.³⁴ Similarly, nectarivorous bats that visit flowers provide valued ecosystem services by pollinating plants, dispersing pollen, and, thus, helping to maintain genetic diversity of flowering plants. In addition to suppressing insect populations, pollinating flowers, and dispersing seeds, insectivorous, nectarivorous, and frugivorous species may redistribute nutrients and energy through their guano to sustain terrestrial, aquatic, and cave ecosystems. Lastly, where data are available, we consider the economic value of bats to terrestrial ecosystems. While data on the economic value of bats to ecosystems are limited, we present a framework that is needed to make such assessments and to examine why the diverse forms of this group of mammals deserve respect, protection, and conservation.

The role of bats in arthropod suppression

Among the estimated 1,232 extant bat species,⁸ over two thirds are either obligate or facultative insectivores (Table 1). They include species that glean insects from vegetation and water in cluttered forests to those that feed in open space above forests, grasslands, and agricultural landscapes (Fig. 1). Although popular literature commonly recognizes bats for their voracious appetites for nocturnal and crepuscular insects,³⁵ the degree to which they play a role in herbivorous arthropod suppression is not well documented. In this section, we review the available literature on the predator–prey interactions between



Figure 1. Brazilian free-tailed bat (*Tadarida brasiliensis*) flying with a moth in its mouth (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org).

bats and arthropod pests—including the magnitude of arthropod consumption by bats, the responses of prey to threats of predation, and the quantitative impacts of bats on arthropod populations—and discuss the various methods used to obtain these data. This type of information could ultimately be used to estimate the ecological and economic value of bats in both natural and agricultural systems, a topic that we discuss in detail in the section on economic valuation of ecosystem services.

Dietary considerations: what's on the menu?

Foraging modes. Insectivorous bats use various methods for capturing and consuming insect prey (Table 1). Aerial hawking bats hunt prey on the fly, often scooping insects from the air with their wing or tail membrane and transferring them to their mouths.^{36–38} Gleaning bats, those that take prey from surfaces, generally forage in cluttered environments (e.g., dense foliage) where background echoes can mask echoes from insects.^{38,39} Some gleaners are able to finely discriminate targets using low-intensity, broadband echolocation calls,^{40,41} whereas others passively listen for prey-generated sounds or use vision and/or olfaction.³⁸ Trawling bats glean insects off the surface of water using their long feet and/or tail membrane. Fly-catching and perch-hunting bats hang from perches and wait for aerial and ground-dwelling prey, respectively. These foraging modes, however, are not mutually exclusive, and it is often difficult to categorize a given species.

General insect consumption. Studies of dietary habits of insectivorous bats date back many

Table 1. An ecological classification of bats, Order Chiroptera. Taxonomy follows Wilson and Reeder.²⁴¹

Family (common name)	Number of genera, species	Distribution	Diet and foraging modes
Pteropodidae (Old World fruit bats)	42, 186	Old World tropics and subtropics	Plant visitors that feed nearly exclusively on nectar and fruit; most species feed in forest canopies, but a few feed in forest understories
Rhinolophidae (horseshoe bats)	1, 77	Old World tropics and subtropics	Insectivorous: use aerial hawking, gleaning, fly catching, perch hunting; many forage very close to the ground, hover in place, and pluck prey from spider webs
Hipposideridae (Old World leaf-nosed bats)	9, 81	Old World tropics and subtropics	Insectivorous: use aerial hawking, gleaning, fly catching, perch hunting; fly close to the ground
Megadermatidae (false vampire and yellow-winged bats)	4, 5	Old World tropics	Both insectivorous and carnivorous: primarily use perch hunting; consume arthropods and small vertebrates (e.g., fish, frogs, lizards, birds, mice, or other bats)
Rhinopomatidae (mouse-tailed or long-tailed bats)	1, 4	Old World tropics	Insectivorous: little information on foraging behavior; fly at least 6–9 m above ground; slit-like nostrils that can exclude sand and dust
Craseonycteridae (Kitti's hog-nosed bat)	1, 1	Thailand	Insectivorous: use aerial hawking, gleaning; glean insects and spiders from tree-top foliage and can hover
Emballonuridae (sac-winged, sheath-tailed, and ghost bats)	13, 51	Pantropical	Insectivorous: use primarily aerial hawking; have long narrow wings for swift flight; occasionally eat fruit
Nycteridae (slit-faced or hollow-faced bats)	1, 16	Old World tropics	Primarily insectivorous: consume insects, spiders, small scorpions; one species specializes on vertebrates (e.g., frogs, small birds); forage close to surfaces
Myzopodidae (Old World sucker-footed bat)	1, 1	Madagascar	Insectivorous: little is known about its foraging behavior
Mystacinidae (New Zealand short-tailed bats)	1, 2	New Zealand	Primarily insectivorous: use aerial hawking but well adapted to hunting arthropods on the ground; also pollinate certain terrestrial flowers and eat fruit

Continued

Table 1. Continued

Family (common name)	Number of genera, species	Distribution	Diet and foraging modes
Phyllostomidae (New World leaf-nosed bats)	55, 160	Neotropics	Diverse foraging and feeding habits, including gleaning and aerial insectivores, carnivores, blood-feeders, nectar-feeders, and fruit-eaters. Plant-visiting species forage in forest understory and canopy
Mormoopidae (ghost-faced bats, moustached bats, and naked-backed bats)	2, 10	Neotropics	Insectivorous: primarily feed on insects close to or on surfaces of water
Noctilionidae (bull dog bats)	1, 2	Neotropics	Both species capture insects in or from the surface of water; <i>Noctilio leporinus</i> eats fish, frogs, and crustaceans by trawling its long feet and claws through the water
Furipteridae (smoky bats and thumbless bats)	2, 2	Neotropics	Insectivorous: may specialize on moths and butterflies
Thyropteridae (disc-winged bats)	1, 3	Neotropics	Insectivorous: characterized by fluttery, moth-like flight; consume small insects
Natalidae (funnel-eared bats)	3, 8	Neotropics	Insectivorous: characterized by fluttery, moth-like flight; consume small insects
Molossidae (free-tailed bats)	16, 100	Cosmopolitan in tropics and subtropics	Insectivores: use aerial hawking; most species forage in open areas and are swift, straight fliers
Vespertilionidae (evening and vesper bats)	48, 407	Cosmopolitan	Primarily insectivorous: diverse foraging modes including aerial hawking (often using their tail membrane as a scoop), gleaning, trawling; a few species eat scorpions, fish, and small birds

years,^{42–49} but few have assessed the potential impacts of prey consumption on human health or natural and agricultural systems. Although it is beyond the scope of this review, there has been considerable debate as to the degree of prey selection by bats.^{38,50} While some studies have shown individuals to actively select among available prey,^{51–54} others have concluded that insectivorous bats are generalist predators, feeding on a wide diversity of taxonomic groups and opportunistically consuming appropriately sized prey according to its avail-

ability within a preferred habitat.^{48,50,55} Insectivorous bat activity and diversity are strongly correlated with arthropod abundance,^{56–58} suggesting that bats seek out areas of concentrated prey sources. Although there is considerable variation in the relative proportions consumed by different species, most insectivorous bats eat large quantities of lepidopterans (moths), coleopterans (beetles), dipterans (flies), homopterans (cicadas, leaf hoppers), and hemipterans (true bugs).^{44,47,59–63} Some species also eat unusual prey items such as scorpions and

spiders.⁶⁴ Prey size can vary from as small as 1 mm (midges and mosquitoes) to as large as 50 mm long (beetles and large moths), depending on the species of bat.^{52,59,60,65–68} Bats often forage throughout the night, returning to their roosts to nurse young and to rest during periods of low insect activity.^{59,69,70}

The magnitude of arthropod consumption by a bat varies considerably by species, season, and reproductive cycle. On average, insectivorous bats maintained in captivity have been estimated to consume up to 25% of their body mass in insects each night (*Myotis lucifugus* and *Eptesicus fuscus*,⁴⁶ *M. lucifugus* and *M. thysanodes*,⁷¹ *Lasiurus cinereus*,⁷² *Lasiorycteris noctivagans*⁷³). Under natural conditions, these estimates increase, most likely due to higher energy demands. Using field metabolic rates based on turnover of doubly labeled water, Kurta *et al.*⁷⁴ estimated that at the peak night of lactation, a 7.9 g little brown bat (*M. lucifugus*) needs to consume 9.9 g of insects (over 100% of its body mass) to account for the marked increase in energy expenditures due to this costly stage of the reproductive cycle.⁷⁵ At peak lactation, a female Brazilian free-tailed bat (*Tadarida brasiliensis*) can consume up to 70% of her body mass in insects each night; furthermore, she frequently culls her prey, consuming only the nutrient-rich abdomen of moths while discarding the wings, head, and appendages, which greatly increases feeding efficiency and hence the quantity of insects consumed.⁶¹ To put this in perspective, an average maternity colony of one million Brazilian free-tailed bats weighing 12 g each could consume up to 8.4 metric tons of insects in a single night. These studies hint at the immense capability of nightly insect consumption and at the potential role of bats in top-down suppression of arthropod populations.

Agricultural pests and pesticide use. Herbivorous arthropods destroy approximately 25–50% of crops worldwide.^{76,77} The response to these threats by modern agriculture has been predominantly through the application of synthetic pesticides, a practice that has led to many unintended consequences including human health risks, degradation of ecosystem function, evolved toxicity resistance by pests, and severe alterations of the dynamics of agribusiness.^{76,78–80} The World Resources Institute estimates that over 400 pest species have evolved resistance to one or more pesticides,

and that despite an increase in pesticide use, the proportion of crops destroyed by insect pests in the United States has doubled (to 13%) since the 1940s.⁸¹ By eliminating beneficial invertebrate and vertebrate predators through indiscriminate use of broad-spectrum insecticides, insect species that are not normally considered pests are often elevated to pest status.^{80,82} Efforts to curb the widespread and indiscriminate use of chemical pesticides include the promotion of biological controls.⁸³ An estimated 99% of potential crop pests are limited by natural ecosystems,^{80,84} of which some fraction can be attributed to predation by bats. Naylor and Ehrlich⁸⁰ estimated that the value of the global pest control ecosystem service ranges between \$54 billion and \$1 trillion, an estimate that includes reductions in both crop losses due to pests and direct/indirect costs of pesticide use. Pimentel *et al.*⁷⁷ concluded that a 50% reduction in pesticide use could be achieved with only a 0.6% increase in the cost of purchased food, provided that biological, cultural, and environmental pest control technologies are used.

Consumption of specific agricultural pests by bats. Various species of prominent agricultural insect pests have been found in the diets of bats based on identification of insect fragments in fecal samples and stomach contents. These insects include, but are not limited to, June beetles (Scarabidae), click beetles (Elateridae), leafhoppers (Cicadellidae), planthoppers (Delphacidae), the spotted cucumber beetle, (*Diabrotica undecimpunctata*, Chrysomelidae), the Asiatic oak weevil (*Cyrtopistomus castaneus*, Curculionidae), and the green stinkbug (*Acrosternum hilare*, Pentatomidae) (Table 2 and Appendix A).

Based on the dietary composition, minimum number of total insects per guano pellet, number of specific agricultural pest species in each pellet, and the number of active foraging days per year, Whitaker⁸⁵ calculated that a colony of 150 big brown bats (*Eptesicus fuscus*) in the midwestern United States annually consumes approximately 600,000 cucumber beetles, 194,000 June beetles, 158,000 leafhoppers, and 335,000 stinkbugs. Subsequently, assuming that each female cucumber beetle lays 110 eggs,⁸⁶ this average-sized bat colony could prevent the production of 33,000,000 cucumber beetle larvae (corn rootworms), which are severe crop pests (Appendix A). While these calculations include a

large number of assumptions and ignore various sources of natural variation, this study took the extra step of translating ecological data into a form more readily appreciated by the public. With the addition of data on corn rootworm damage to crops in the study area, an economic value for this colony could be estimated.

A common challenge in these investigations is the overwhelming lack of basic ecological information regarding foraging behavior and diet for many species of bats. For example, traditional dietary analyses through fecal or stomach contents have historically only identified arthropod fragments to the ordinal or familial level, rather than to species,^{46,60,69,87} and in cases where species identification is possible, it has typically been restricted to hard-bodied insects, such as beetles, that remain partially undigested. Recently, novel molecular techniques have allowed detection and species identification of both hard- and soft-bodied insects, such as lepidopterans, within guano collected from bats.^{88–93} Whitaker *et al.*⁹⁰ described the development of quantitative polymerase chain reaction (qPCR), coupled with controlled feedings of known insects to captive bats, as an approach to estimate the number or percent volume of specific insects consumed by wild bats. qPCR has been used to document consumption of the corn earworm moth (*Helicoverpa zea*) and the beet armyworm (*Spodoptera exigua*), both major pests of corn, cotton, and other crops throughout the United States, by Brazilian free-tailed bats, *Tadarida brasiliensis*, in south-central Texas.^{88,90,92} Brown⁹¹ used qPCR to identify the pecan nut casebearer moth (*Acrobasis nuxvorella*), the hickory shuckworm moth (*Cydia caryana*), and *H. zea* moths in the diet of Brazilian free-tailed bats from guano collected beneath bat houses located in organic pecan orchards. This author also identified the southern green stink bug (*Nezara viridula*) by sequencing insect fragments found in the guano (see Appendix A).

To date, Clare *et al.*⁸⁹ conducted the most comprehensive dietary analysis of an insectivorous bat. These authors extracted DNA from insect fragments found in fecal samples and used a polymerase chain reaction (PCR) coupled with a sequence-based technique to assess the diet of the eastern red bat, *Lasiurus borealis*, in Canada. Through comparison of fecal DNA sequences to a reference database, they were able to identify 127 prey species (5 orders, 16 families

of lepidopterans), some of which were notable agricultural, forest, and orchard/garden pests including gypsy moths (*Lymantria dispar*), tent caterpillars (*Malacosoma sp.*), coneworms (*Dioryctria sp.*), cutworms (*Noctua pronuba*), snout moths (*Acrobasis sp.*), and tortrix moths (*Cydia sp.*) (see Table 2 and Appendix A). All bats were captured in a provincial park that was adjacent to agricultural land. Although this study provides unprecedented detail regarding the diversity of insects consumed by the eastern red bat, the techniques used did not allow for quantification of pest consumption, and the authors did not have sufficient data to estimate the ecological or economic value of these bats to any particular ecosystem.

Direct and indirect impacts of insectivorous bats

Understanding complexities of predator–prey interactions. The studies reviewed in the previous sections document the consumption of herbivorous arthropods by bats; however, few studies have measured their actual impacts on natural or agroecosystems. Top- and midlevel predators can have direct effects on herbivore communities and indirect effects on plant communities through both density-mediated (consumption) and trait-mediated (behavioral) interactions.⁹⁴ The following sections address the research that has begun to document these interactions between insectivorous bats and their prey.

A pioneering study by Buckner dating back to the 1960s, which examined the role of vertebrate predators in the biological control of forest insects,⁹⁵ illustrates the complexities involved with assigning a value to natural predators and may serve as a template for the assessment of the ecosystem services provided by bats. Buckner asserted that three basic measurements must be made to understand a predator–prey system: density of the prey, density of the predators, and the extent of destruction of prey by the predators. Few studies have thoroughly evaluated these seemingly simple questions. Equally fundamental, but perhaps more ecologically complex, is the evaluation of an individual predator species in relation to its local ecological community. What is the predator's capacity for consumption of the prey? What are the effects of the density of prey or the presence of alternative prey on the predator's density and/or rate of consumption? What defense

Table 2. Examples of studies found in the literature documenting the consumption of agricultural insect pests by different species of bats, analytical methods used for dietary analysis, and estimated quantity of consumption^a

Pest species	Species of bat predator	Analysis	Estimate of consumption (%)
Coleoptera			
June beetles (Scarabidae)	Cave myotis, <i>Myotis velifer</i> ⁵⁹	Stomach content	15.9 of Coleoptera
	Brazilian free-tailed bat, <i>Tadarida brasiliensis</i> ⁶⁶	Fecal dissection	19.7 of Coleoptera
	Eastern red bat, <i>Lasiurus borealis</i> ²⁴²	Fecal dissection	11.2
	Northern long-eared myotis, <i>M. septentrionalis</i> ²⁴²	Fecal dissection	5.5
	Big brown bat, <i>Eptesicus fuscus</i> ^{45, 85, 242*243}	Fecal dissection	29.6
Click beetles or wire worm (Elateridae)	Big brown bat, <i>E. fuscus</i> ²⁴³	Fecal dissection	31.2
Spotted cucumber beetle, <i>Diabrotica undecimpunctata</i> (Chrysomelidae)	Big brown bat, <i>E. fuscus</i> ^{45, 85*242}	Fecal dissection	28.2
	Brazilian free-tailed bat, <i>T. brasiliensis</i> ⁶⁶	Fecal dissection	Unreported
	Evening bat, <i>Nycticeius humeralis</i> ²⁴⁴	Fecal dissection	23.5
	Indiana myotis, <i>Myotis sodalis</i> ²⁴⁵	Fecal dissection	1.1 (3.9 by frequency)
Asiatic oak weevil, <i>Cyrtopistomus castaneus</i> , (Curculionidae)	Little brown myotis, <i>Myotis lucifugus</i> ²⁴²	Fecal dissection	5.3
	Indiana myotis, <i>Myotis sodalis</i> ^{245*242}	Fecal dissection	7.7 (23.2 by frequency)
	Eastern red bat, <i>Lasiurus borealis</i> ²⁴²	Fecal dissection	29
	Big brown bat, <i>Eptesicus fuscus</i> ²⁴²	Fecal dissection	13.9
Homoptera			
Leaf hoppers (Homoptera: Cicadellidae)	Cave myotis, <i>M. velifer</i> ⁵⁹	Stomach content	17.4 of Homoptera
	Big brown bat, <i>E. fuscus</i> ^{45, 85}	Fecal dissection	8.2
	Brazilian free-tailed bat, <i>T. brasiliensis</i> ⁶⁶	Fecal dissection	37.3 of Homoptera
	Big free-tailed bat, <i>Nyctinomops macrotis</i> ²⁴⁶	Fecal dissection	26.7 (58.9 by frequency)
	Eastern pipistrelle, <i>Perimyotis subflavus</i> ²⁴²	Fecal dissection	14.5
White-backed planthopper, <i>Sogatella sp.</i> (Delphacidae)	Indiana myotis, <i>M. sodalis</i> ²⁴²	Fecal dissection	1.8 (17.9 by frequency)
	Wrinkled-lipped bats, <i>Tadarida plicata</i> ⁶³	Fecal dissection	25.3 by frequency**

Continued

Table 2. Continued

Pest species	Species of bat predator	Analysis	Estimate of consumption (%)
Hemiptera			
Stink bugs (Pentatomidae)	Brazilian free-tailed bat, <i>T. brasiliensis</i> ⁶⁶	Fecal dissection	26.8
Green stink bug, <i>Acrosternum hilare</i>	Indiana myotis, <i>Myotis sodalis</i> ²⁴⁵	Fecal dissection	0.1 (1.4 by frequency)
	Hoary bat, <i>Lasiurus cinereus</i> ²⁴²	Fecal dissection	43.8
	Eastern red bat, <i>Lasiurus borealis</i> ²⁴²	Fecal dissection	2.1
	Big brown bat, <i>E. fuscus</i> ^{45,85,242,243*}	Fecal dissection	18.3
Brown stink bug, <i>Euschistus servus</i>	Big brown bat, <i>E. fuscus</i> ²⁴²	Fecal dissection	2.5
	Northern long eared myotis, <i>M. septentrionalis</i> ²⁴²	Fecal dissection	1.0
Lepidoptera			
Corn earworm moth, <i>Helicoverpa zea</i> (Noctuidae)	Brazilian free-tailed bat, <i>T. brasiliensis</i> ^{88,92}	Molecular: qPCR	N/A
Gypsy moths, <i>Lymantria dispar</i> (Lymantriidae)	Eastern red bat, <i>Lasiurus borealis</i> ⁸⁹	Molecular: sequence based	N/A
Cutworms, <i>Noctua pronuba</i> (Noctuidae)			
Coneworms, <i>Dioryctria spp.</i> (Pyralidae)			
Tent caterpillars, <i>Malacosoma spp.</i> (Lasiocampidae)			
Tortrix moths, <i>Cydia sp.</i> (Tortricidae)			
Diptera			
Mosquitos (Culicidae)	Indiana myotis, <i>M. sodalis</i> ²⁴⁵	Fecal dissection	1.0 (4.3 by frequency)
Hessian fly, <i>Mayetoila destructor</i>	Indiana myotis, <i>M. sodalis</i> ²⁴⁵	Fecal dissection	<0.1 (0.4 by frequency)

^aEstimates of consumption are in percent volume of the total diet unless otherwise specified. See Appendix A for descriptions of pest species.

*The study from which estimates of consumption are taken if more than one.

**Estimate refers to Homoptera: “most” were *Sogatella sp.*

mechanism does the prey have and use against the predator? Buckner argued that until these aspects are studied thoroughly, the understanding of predation as a biological control factor will be incomplete. Researchers investigating invertebrate and aquatic systems have begun to do this (reviewed in Refs. 96 and 97), but few if any studies of vertebrate predators have fully addressed these important questions.

Ecosystem services of the Brazilian free-tailed bat: a case study. Of the approximately 900 insectivorous bat species, the Brazilian free-tailed bat, *Tadarida brasiliensis*, provides one of the most impressive examples of continental-scale natural pest suppression in the world.⁹⁸ Several studies have attempted to document the nightly foraging behavior and prey consumption patterns in this species



Figure 2. Brazilian free-tailed bats (*Tadarida brasiliensis*) dispersing over agricultural landscapes from a maternity roost in south-central Texas (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org).

to better understand its ecosystem service.^{62,66,99,100} Millions of Brazilian free-tailed bats migrate northward each year in the spring from Mexico to form enormous maternity colonies in limestone caves and bridges throughout the southwestern United States.^{43,101} Each evening, large numbers of bats emerge from these roosts (Fig. 2) and disperse across natural and agricultural landscapes in high enough densities to be detected by NEXRAD WSR-88D Doppler weather radars.⁹⁹ As recently as the 1950s and early 1960s, midsummer colonies of Brazilian free-tailed bats in 17 caves in the southwestern United States were estimated to total about 150 million individuals.¹⁰² However, recent estimates, based on improved census methods using thermal infrared imaging and computer detection and tracking algorithms, conclude that these same caves now house closer to nine million bats, indicating either a marked population decline or an overestimation in past observations.¹⁰³ The likelihood of historic overestimates is supported by further quantitative assessments of colony dynamics and emergence behavior of Brazilian free-tailed bats that roost in Carlsbad Caverns, New Mexico.¹⁰⁴

Although Brazilian free-tails are known to consume a wide variety of prey items (12 orders, 35 families), numerous studies indicate that moths (Lepidoptera) are their primary food source,^{61,62,66,105} including devastating agricultural pests such as the corn earworm or cotton bollworm moth (*Helicoverpa zea*) and the tobacco budworm moth (*Heliothis virescens*).^{88,98} Studies have found that the proportion of moths consumed by Brazilian free-tailed bats increases markedly during their early morning for-

aging bouts in comparison to evening foraging bouts from May to the end of June,^{66,105} a time period that coincides with the immigration of swarms of corn earworm moths and fall armyworms, *Spodoptera exigua*, into Texas from northern Mexico on prevailing winds.^{106,107} In a study on the foraging activity of these bats at high altitudes, McCracken *et al.*¹⁰⁰ documented that echolocation search calls and feeding buzzes were most abundant at ground level and at 400–500 m above ground level, the latter of which corresponds with the low-elevation southerly wind jet, a major aeroecological corridor for the nocturnal dispersal of corn earworm moths, fall armyworms, and other insects. Des Marais *et al.*¹⁰⁸ used stable isotope ratios of carbon from bat guano to estimate that more than one-half of all insects eaten by Brazilian free-tailed bats that roost in Carlsbad Caverns fed on crops, based on landscape data showing that 90% of the crops surrounding the cave were C3 plants while the majority of the native plants were C4. Similarly, Mizutani *et al.*¹⁰⁹ estimated that two-thirds of the guano sampled from a cave housing several million Brazilian free-tailed bats in Arizona included insects or other arthropods that fed on C3 crops (cotton and alfalfa) in an area dominated by native C4 vegetation.

These studies strongly suggest that Brazilian free-tailed bats opportunistically forage over agricultural fields that both produce and attract large insect populations. Research suggests that after initial arrival into Texas from northern Mexico, corn earworm and tobacco budworm moths and their progeny undergo an annual migration northward through the southern and central croplands of the United States.^{106,107} Thus, the benefits conferred to agriculture by consumption of these moths by bats may not be limited to their local foraging areas (e.g., in Texas and New Mexico) but may extend to agricultural landscapes hundreds of kilometers away. Several recent studies have estimated the economic value of the pest suppression service provided by Brazilian free-tailed bats^{98,103,110,111} and are further discussed in the section on valuation of ecosystem services.

Density-mediated direct and indirect effects: consumption. Research evaluating ecosystem services of other insectivorous bat species fall far behind that of the Brazilian free-tailed bat; however, several recent studies have provided compelling evidence that

bats can limit insect populations in both agricultural and natural systems.

For example, Williams-Guillén *et al.*¹¹² and Kalka *et al.*¹¹³ separated the effects of insectivorous birds and bats on pest suppression by conducting predator enclosure experiments in a coffee plantation in Mexico and a lowland tropical forest in Panama, respectively. Both studies placed agricultural netting around individual plants to exclude bats at night and birds during the day. Previous studies using predator enclosures attributed any results of arthropod suppression to bird predation,^{114,115} ignoring bats as potential contributors. Williams-Guillén *et al.*¹¹² found that, by excluding bats, total arthropod densities increased by 84% per coffee plant in the wet season but were not affected in the dry season. They attributed the seasonal difference to the increased abundance, reproductive activity, and hence energy demands of bats during the wet season. In both seasons, bats and birds together had the highest impact on arthropod densities, suggesting an additive effect. Although there was a clear direct effect of bats and birds on herbivorous arthropods, the authors did not find a significant indirect effect on leaf damage for any of the treatments. By contrast, Kalka *et al.*¹¹³ demonstrated that the exclusion of bats from five common tropical understory plants significantly increased both arthropod densities (by 65%) and leaf damage (by 68%) relative to control treatments. They also found that bats consistently had a higher impact on insect populations than birds. These authors emphasize that their estimates of direct and indirect impacts of both groups are likely conservative due to predation by aerial insectivores outside of the enclosures, the exclusion of large arthropods along with bats and birds, the presence of predatory arthropods in the enclosures, and their focus on understory plants rather than the more-productive forest canopy. For both of these studies, a list of insect orders that were suppressed is available in their supporting online material; however, neither study identified pests to the species level, nor did they attempt to estimate the economic value of bats in these systems.

Reiskind and Wund⁶⁷ provided compelling evidence that northern long-eared bats (*Myotis septentrionalis*) suppress mosquito (*Culex spp.*) populations through direct predation. Although bats are commonly credited for their role in mosquito control, this is the first study documenting a quanti-

tative impact on mosquito populations. Predator enclosures were erected in the field that contained artificial oviposition sites and allowed passage of naturally occurring mosquitoes. These researchers released wild-captured northern long-eared bats into the enclosures to forage for a total of nine nights. They found that nightly oviposition by mosquitoes was reduced by 32% in enclosures that contained bats when compared to control enclosures with no bats. Based on their finding of no difference between control enclosures and unenclosed artificial oviposition sites adjacent to bat enclosures, they concluded that these effects were due to predation rather than the alteration of mosquito behavior.

Enclosure and enclosure studies, such as those described above, have the potential to provide valuable information on the direct and indirect effects of bats as arthropod predators; however, results should be interpreted with caution. Enclosures effectively exclude bats that glean insects directly from vegetation but most likely have a limited effect on aerial insectivores that capture insects on the fly often far from the plant of interest. Enclosures, on the other hand, may inflate estimates of prey suppression due to unnatural conditions such as an elevated density of bats or limited availability of other suitable prey items within the enclosures.

Trait-mediated indirect interactions: ecology of fear. Predator-prey interactions are central features in all ecological communities, yet traditional models of predator-prey dynamics treat individuals as unresponsive units and do not consider the prey's physical or behavioral response to the presence of a predator.¹¹⁶ In a fear-driven system, prey enact an inducible defense in response to the presence or threat of a predator in order to reduce the risk of consumption by altering such behaviors as predator vigilance, foraging decisions, and mate attraction.^{97,116} This behavioral plasticity may have significant impacts on species interactions, community structure, and ecosystem function.^{97,117}

The threat of predation by bats has led to the evolution of both physical and behavioral defense mechanisms in many species of moths, including aposematic signaling,^{118,119} the production of ultrasonic jamming clicks,¹²⁰ and evasive flight maneuvers¹²¹ to avoid consumption. In an agricultural setting, the presence of bats may alter the behavior

and/or population dynamics of moth pests within that system. Belton and Kempster¹²² found that the infestation rate of sweet corn (maize) by the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Pyralidae), was reduced by over 50% in test plots that were exposed to ultrasound broadcast at frequencies, amplitudes, and pulse rates characteristic of bat calls. This result provides an excellent example of the ecology of fear; however, the sample size of the study was very small (only two replicates over one season), the broadcasts may not have represented natural levels of bat activity, and possible changes in predation due to bat responses to the broadcast were not accounted for. In a laboratory study, the true armyworm, *Pseudaletia umpuncta* (Lepidoptera: Noctuidae), and the European corn borer, altered their mating behavior in response to high levels of simulated predation risk (ultrasonic bat calls) by reducing their mate-seeking behavior, pheromone production, and mating calls.¹²³ Huang *et al.*^{124,125} documented that when exposed to ultrasound in the laboratory, female Indian meal moths, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) received fewer spermatophores from males, produced fewer and smaller larvae, reduced mate calling, and reduced the length of mating time when compared to female moths not exposed to ultrasound. These studies suggest that the mere presence of bats, whether foraging due to high prey availability or being attracted to roosting opportunities, may aid in reducing damaging activities or disrupting population dynamics of insect pests in a given agricultural landscape.

Conclusions, future directions, and management of arthropod suppression services

The studies reviewed in this section hint at the immense potential for bats to provide pest suppression services in both natural and agroecosystems; however, more research is needed to adequately document the extent to which bats interact with and limit insect pest populations across the geographical landscape and over time. Some of the authors have attempted to address one or all of the three basic measurements outlined in Buckner:⁹⁵ density of predator, density of prey, and capacity of destruction of prey; however, uncertainties lie in each of these parameters. Determining the degree of spatial and temporal overlap between predator and prey, how

the densities of the predator and prey are affected by third party effects, such as alternative prey sources or competition, and how crop production affects these relationships are all examples of sources of variation and uncertainty. This information is essential in models predicting the ecological and economic value of a predator.

Unfortunately, small-scale temporal and spatial variation in the diet is often difficult to detect through traditional methods and requires extensive fieldwork. The findings by Whitaker *et al.*¹⁰⁵ and Lee and McCracken,⁶⁶ that dietary composition is markedly different between the evening and morning foraging bouts of female Brazilian free-tailed bats living in caves near major agricultural regions, illustrate the importance of taking into consideration temporal variation when characterizing the diet of a species as well as assessing any potential ecosystem service. Other studies have shown temporal variation in the diet of bats by season,^{126,127} year,^{60,128} and age class.^{129,130} Dietary variation also exists between co-occurring species and geographically within a given species.^{48,60,131–133} Additionally, many frugivorous and nectarivorous bat species (e.g., *Glossophaga soricina*;^{134,135} *Phyllostomus discolor* and *Phylloderma stenops*¹³⁶) include insects in their diets as a supplement to their dominant food sources. For example, among the 39 species of bats captured in an agricultural mosaic in Mexico, 22 were classified as omnivorous (i.e., consuming insects in addition to fruit, nectar, or meat).¹³⁷ These species are not typically considered when evaluating potential pest suppression yet undoubtedly contribute to the overall service. Findings from these studies highlight the importance of encouraging high bat diversity (not only species richness, but also reproductive class and functional diversity) in a given area to maintain ecosystem function.

A detailed resolution of dietary composition across bat species, in which identification of prey items is to species rather than only to the familial or ordinal level, is needed to track patterns of consumption of agricultural pests spatially, seasonally, and relative to other benign insects. Molecular techniques used by McCracken *et al.*^{88,92} and Clare *et al.*⁸⁹ have the potential to yield this scale of resolution and offer exciting new avenues for research in mapping food webs and trophic cascades; however, studies on quantifiable effects of bats on crop yields and damage should be coupled with

these dietary analyses to avoid making assumptions of impact based purely on evidence of consumption. Similarly, studies investigating the biology of bat populations within specific agroecosystems—roosting dynamics, habitat selection, and estimates of density—are critical for a complete evaluation of the role of bats in pest suppression, leading ultimately to an estimate of the economic value of this service.

Beyond the studies reviewed here, there have been many other studies investigating habitat use by insectivorous bats in agricultural systems that have not specifically addressed the effects of bats on pest suppression (e.g., organic farms in the United Kingdom,^{56,57} shade cacao plantations in Brazil,¹³⁸ olive orchards in Greece,¹³⁹ Midwestern agricultural land,¹⁴⁰ cereal crops in England,¹⁴¹ arboreal crops in Mexico,¹³⁷ and agricultural riparian areas¹⁴²). These, and other agroecosystems where high bat activity has been documented, are ideal candidates for further research investigating the potential ecosystem service provided by insectivorous bats.

Incorporating the results of ecosystem service studies into integrated pest management (IPM) programs designed to restore the natural predator–pest balance⁸³ has the potential to lead to beneficial results for both farmers and bats. Natural predators may not control 100% of forest and agricultural pests, but a combination of factors can keep populations, and therefore crop losses, in check. With white-nose syndrome causing massive declines of up to 90% and expected regional extinctions of insectivorous bat populations in the eastern and midwestern United States,²⁸ the loss of this important regulating service may severely impact agricultural production in affected areas.¹⁴³ Identification and measurement of the magnitude and value of this natural pest control service can be an effective tool in influencing public support, policy, and private land management toward conservation of natural ecosystems; however, due to the complexities and large scale at which natural pest control acts, cross-disciplinary approaches, collaboration, and creativity are essential.

Pollination and seed dispersal

In addition to insect suppression through predation, some bat species also play important roles as pollinators and seed dispersers in tropical and subtropical habitats throughout the world. These ecosystem ser-

vices are provided primarily by bats in two families, Pteropodidae in the Old World and Phyllostomidae in the New World (Table 1). These two families are distantly related and differ in evolutionary age. Current information suggests that Pteropodidae evolved in Asia about 56 mya (million years ago), whereas Phyllostomidae evolved in the northern Neotropics about 35 mya.¹⁴⁴ Because feeding on nectar and pollen requires relatively specialized morphology (e.g., elongated snouts and tongues), relatively few members of these families are obligate (or nearly so) pollinators. Only 15 species in six genera are morphologically specialized nectar-feeders in the Pteropodidae; other members of this family are primarily fruit-eaters, although species in genera such as *Cynopterus*, *Epomophorus*, and *Pteropus* also visit flowers opportunistically (Fig. 3). The Phyllostomidae contains a diverse array of feeding adaptations (Table 1), but over one half of its species are plant-visitors. About 38 species in 16 genera are specialized nectar-feeders; 90 species in 22 genera are primarily frugivorous, although a number of these in genera such as *Artibeus*, *Carollia*, and *Phyllostomus* also visit flowers (Fig. 4).

Unlike predation, which is an antagonistic population interaction, pollination and seed dispersal are mutualistic population interactions in which plants provide a nutritional reward (nectar, pollen, and fruit pulp) for a beneficial service: pollen and seed dispersal. Bats, along with many other flower-visiting and fruit-eating animals, provide important mobility for plant gametes and propagules. As a result, there has been extensive coevolution between plants and their pollinators and seed dispersers.



Figure 3. Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) approaching a baobab flower of which it pollinates (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org).

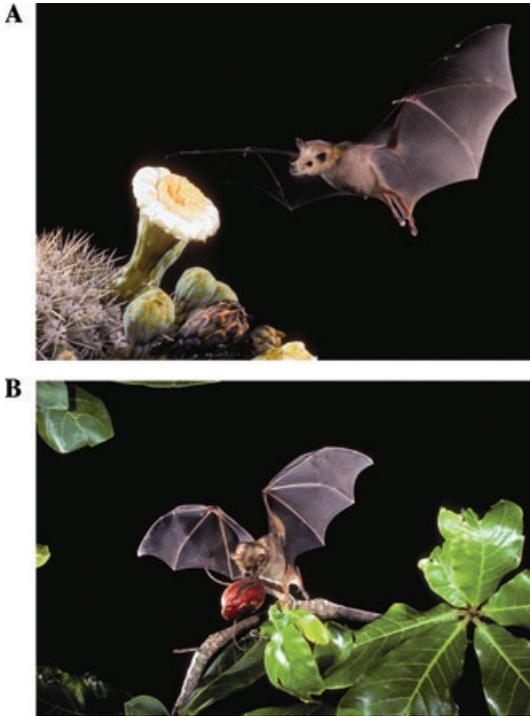


Figure 4. (A) Lesser long-nosed bat (*Leptonycteris curasoae*) approaching a Saguaro cactus flower of which it pollinates (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org). (B) Jamaican fruit bat (*Artibeus jamaicensis*) removing a ripe tropical almond fruit (*Terminalia catappa*) before taking off in flight (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org).

Bat pollination occurs in about 528 species in 67 families and 28 orders of angiosperms worldwide (Fig. 4). Pteropodid bats are known to pollinate flowers of about 168 species in 100 genera and 41 families; phyllostomid bats pollinate flowers of about 360 species in 159 genera and 44 families.¹⁴⁵ Most of the plants pollinated by pteropodid

bats, which are substantially larger than phyllostomids, are canopy trees or shrubs, whereas those pollinated by the smaller phyllostomids are epiphytes and lianas as well as trees and shrubs.¹⁴⁶ The fruit diets of phyllostomids are much better known than those of pteropodids. A total of at least 549 species in 191 genera and 62 families are dispersed by bats in the Neotropics.¹⁴⁷ Pteropodid bats are known to eat fruit from at least 139 genera in 58 families.¹⁴⁸ As in the case of flowers, most fruits eaten by pteropodid bats are produced by trees or shrubs, whereas those eaten by phyllostomids include fruits produced by epiphytes and vines as well as trees and shrubs.

Major plant families (in terms of number of genera) containing species either pollinated or dispersed by the two families of bats are listed in Table 3. Reflecting the independent evolution of bat–plant interactions in Old and New World plant lineages, only a few families are common in the diets of both bat families. For flowers, these include Fabaceae, Malvaceae (especially subfamily Bombacoideae, formerly known as Bombacaceae), and Bignoniaceae (in which bat flowers occur in different clades in the Old and New Worlds). For fruits, these include Araceae (palms) and Sapotaceae. Although only represented by a few genera in the diets of bats, a few additional families are notable for containing many species of bat-pollinated flowers or bat-dispersed fruit. In the New World, these include flowers (Campanulaceae and Marcgraviaceae) and fruit (Araceae, Cecropiaceae, Clusiaceae, Piperaceae, and Solanaceae). In the Old World, these include fruit (Moraceae). Figs (Moraceae) are very important in the diets of both pteropodid and phyllostomid bats worldwide (Fig. 5).

The evolution and ecology of bat–plant interactions are discussed in detail in Fleming,¹⁴⁹ Fleming

Table 3. Examples of the most important angiosperm families (in terms of number of plant genera, in parentheses) whose flowers are pollinated and/or seeds dispersed by pteropodid and phyllostomid bats^a

Bat family	Pollination	Seed dispersal
Pteropodidae	Bignoniaceae (10), Fabaceae (11), Malvaceae (7), Myrtaceae (8), Sapotaceae (7)	Anacardiaceae (8), Araceae (7), Meliaceae (8), Rubiaceae (7), Sapotaceae (10)
Phyllostomidae	Cactaceae (26), Fabaceae (23), Malvaceae (18), Solanaceae (7), Bignoniaceae, Bromeliaceae, Gesneriaceae (6)	Araceae (15), Cactaceae (11), Moraceae (10), Myrtaceae (10), Sapotaceae (6)

^aSources of data: work by Fleming *et al.*;¹⁴⁵ Lobova *et al.*;¹⁴⁷ and Mickleburgh *et al.*¹⁴⁸



Figure 5. Gambian epauletted fruit bat (*Epomophorus gambianus*) taking flight after plucking a fig infructescence (photo by Merlin D. Tuttle, Bat Conservation International, www.batcon.org).

and Kress,¹⁵⁰ Fleming and Muchhala,¹⁴⁶ Fleming *et al.*,¹⁴⁵ Lobova *et al.*,¹⁴⁷ and Muscarella and Fleming.¹⁵¹ Here, we discuss these interactions in terms of the ecosystem services that provide direct and indirect benefits to humans.

Services providing direct benefits to humans

Although bat pollination is relatively uncommon compared with bird or insect pollination in angiosperms, it involves an impressive number of economically and/or ecologically important plants (Table 4). In arid habitats in the New World, two families, Agavaceae and Cactaceae, have enormous economic and ecological value. Many species of paniculate *Agave* rely heavily on phyllostomid bats for pollination, and many of these same bats are also major pollinators and seed dispersers of columnar cacti.¹⁵² Three species of *Leptonycteris* bats are especially important in this regard in the southwestern United States, Mexico, and northern South America (Fig. 4). The bat-pollinated *A. tequilana* is the source of commercial tequila, a multimillion dollar industry in Mexico; other species of *Agave* are used locally to produce similar alcoholic beverages such as pulque, mescal, and bacanora. Agaves are also important sources of sisal fiber in many tropical localities. Although bats are not the exclusive pollinators of most species of *Agave*, they are critically important pollinators in tropical latitudes in the New World.¹⁵³ This is also true of bats pollinating columnar cacti. For example, bats are minor pollinators of the two northernmost columnar cacti, *Carnegiea gigantea* and *Stenocereus thurbei*, in the Sonoran Desert, but they are the nearly exclu-

sive pollinators of columnar cacti in south-central Mexico and northern Venezuela.¹⁵²

Large-scale cash crops produced by plants either (originally) pollinated or dispersed by bats include nonnative bananas and mangos in the New World and native bananas, breadfruits, durians, mangos, and petai (*Parkia speciosa*) in the Old World (Table 4). Of these, only durians and petai currently rely on bats (among other animals) for pollination. The same is true for trees such as *Ceiba pentandra*, the kapok tree, and *Ochroma lagopus*, the balsa tree. Other bat-fruits that are harvested and sold locally include sapodilla and organ pipe cactus (*Stenocereus*) in the New World and the shea butter tree (*Vitellaria (Butyrospermum) parkii*) in Africa.^{154–156} Many other species are listed in Table 4. Placing a dollar value on the economic services of plant-visiting bats is important but is beyond the scope of this paper for at least two reasons: lack of readily accessible information about the economic value of many crops, especially ones that are sold locally, and, more importantly, lack of detailed knowledge about the actual contribution of bats to the pollination and/or seed dispersal of many of these plants. In the case of cultivated plants, bats are no longer needed to pollinate their flowers or disperse their seeds. But the ecological services these bats provide for their wild relatives are important for preserving genetic diversity in these plants.

In India, the Mahwa tree (*Madhuca indica*), also called the honey tree, sugar tree, or Indian butter tree, is pollinated by *Pteropus giganteus*, *Rousettus leschenaulti*, and *Cynopterus sphinx*.¹⁵⁷ These pollination services highlight one of the highly valued ecosystem services provided by plant-visiting bats both culturally and economically. The timber of this tree is used for making wagon wheels in India. The flowers, also called honey flowers, are used as food and for preparing a distilled spirit (matkom duhli). Sun-dried fruits are directly consumed by humans, and the oil extracted from flowers and seeds, known locally as *mahwa*, *mowrah butter*, or *yallah*, is incorporated into soaps, candles, cosmetics (e.g., lipstick, lotions), and lubricants, and used medicinally as an emetic, an antirheumatic, and in the treatment of leprosy. Extracts from the fruits are also thought to prevent wrinkles and restore skin flexibility.^{158,159} Seedcakes made from *M. indica* are used as food for cattle and goats^{160–163} and are known to increase their milk production.¹⁶⁴

Table 4. Examples of economically and ecologically important plants that are either pollinated (P) or dispersed (D) by bats^a

Plant family and subfamily	Taxon	Service	Comments
Economically important plants			
Anacardiaceae	<i>Anacardium occidentale</i>	D	Cashew, yields three major global and local economic products: cashew (seed), cashew apple (hypocarp), and cashew nutshell liquid (mesocarp resin) ^{262,263}
	<i>Mangifera indica</i>	D	Mango, commercial crop globally and locally ¹⁴⁷
	<i>Spondias</i>	D	<i>S. cytherea</i> , <i>S. mombin</i> , and <i>S. purpurea</i> fruits are important locally in tropical America and consumed fresh or preserved ¹⁴⁷
Annonaceae	<i>Annona</i>	D	<i>A. muricata</i> (soursop), <i>A. reticulata</i> (custard apple), <i>A. squamosa</i> (sweetsop) with edible syncarps are locally important in tropical America ¹⁴⁷
Araceae	<i>Anthurium</i> , <i>Philodendron</i>	D	Commonly cultivated as ornamental plants ¹⁴⁷
Araliaceae	<i>Dendropanax arboreus</i>	D	Cultivated ornamental and timber plant in tropical America ^{135,264,265}
Arecaceae	<i>Acrocomia</i> , <i>Astrocaryum</i> , <i>Bactris</i> , <i>Euterpe</i> , <i>Prestoea</i> , <i>Roystonea</i> , <i>Sabal</i> , <i>Socratea</i>	D	Used as source of “palm-hearts,” especially <i>Euterpe edulis</i> and <i>E. oleraceae</i> ¹⁴⁷
	<i>Euterpe edulis</i>	D	Source of popular açai fruits ²⁶⁶
	<i>Phoenix dactylifera</i>	D	Date palm, commercial crop and staple food for Arabia and North Africa; leaves for matting and thatch ^{135,267,268}
	<i>Roystonea regia</i>	D	Royal palm, commonly cultivated ^{267,269}
	<i>Sabal palmetto</i>	D	Leaves are commercially important source of fibers and thatch; stems used for furniture and wharf-piles ²⁶⁷
Agavaceae	<i>Socratea exorrhiza</i>	D	Wood used for construction ^{135,147,262,270–272}
	<i>Agave</i> , subgenus <i>Agave</i>	P	Paniculate agaves such as <i>A. tequilana</i> are used to make tequila, mescal, bacanora, etc., with high economic value; leaf fiber is used as sisal ^{153,273}
Boraginaceae	<i>Cordia dodecandra</i>	D	Cultivated for edible fruits and fine timber in tropical America ¹³⁵
Cactaceae	Many genera in tribe Pachycereeae, subfamily Cactoideae	P, D	Native populations in the southwestern U.S. and Latin America harvest fruits of bat-pollinated cactus species in genera such as <i>Carnegiea</i> , <i>Pachycereus</i> , and <i>Stenocereus</i> . Some species of <i>Stenocereus</i> are grown commercially for their fruits ^{152,156}

Continued

Table 4. Continued

Plant family and subfamily	Taxon	Service	Comments
Caricaceae	<i>Carica papaya</i>	D	Papaya, widely cultivated in tropics for fruits and as a source of papain used in culinary and medical products ¹⁴⁷
Caryocaraceae	<i>Caryocar</i>	P, D	Many species have seeds that are oil source in tropical America; <i>C. glabrum</i> (soapwood) inner bark used for washing ^{135,274,275}
Cecropiaceae	<i>Cecropia peltata</i>	D	Wood used for pulp, also cultivated as ornamental in tropical America ¹⁴⁷
Chrysobalanaceae	<i>Chrysobalanus icaco</i>	D	Grown for edible fruits; seed oil used for candles in West Africa ¹⁴⁷
Clusiaceae	<i>Clusia, Symphonia, Vismia</i>	D	Resins are locally medicinal in South America ¹⁴⁷
Combretaceae	<i>Terminalia catappa</i>	D	Tropical almond, source of valuable timber, edible seeds, tannins for dye, bark extract for medicine in Indomalaya ¹⁴⁷
Cyclanthaceae	<i>Carludovica palmata</i>	D	Panama hat palm, grown for hat manufacture, important export plant for Ecuador, also used for mats and baskets in tropical America ^{135,136,149,276}
Ebenaceae	<i>Diospyros digyna, D. kaki</i>	D	Grown for edible fruits (black sapote, Japanese persimmon) in Central America and Asia ¹⁴⁷
Fabaceae	<i>Dipteryx odorata</i>	D	Fragrant seeds used for scenting tobacco and snuff ¹⁴⁷
Faboideae	<i>Andira inermis</i>	D	Valuable timber, bark used for medicine, planted for shelter belts in West Indies (cabbage-tree) ¹⁴⁷
Fabaceae, Mimosoideae	<i>Inga vera</i>	D	Guaba, widely grown in South America for edible fruit pulp, timber, shade, medicine, and alcoholic beverage cachiri ^{277,278}
	<i>Parkia speciosa</i>	P	Commercially important fruit species in Southeast Asia ¹⁵⁴
Lecythidaceae	<i>Lecythis pisonis</i>	D	Paradise nuts, cultivated in South America for edible seeds ^{147,279}
Malpighiaceae	<i>Malpighia glabra</i>	D	Barbados cherry, edible fruits high in vitamin C, also ornamental in tropical America ^{135,262,280}
Malvaceae, Bombacoideae	<i>Ceiba</i>	P	Fibers from fruits of <i>C. pentandra</i> and other species of <i>Ceiba</i> are used to make kapok ¹⁵⁴
Malvaceae	<i>Ochroma</i>	P	Balsa, world's lightest commercial timber ¹³⁵

Continued

Table 4. Continued

Plant family and subfamily	Taxon	Service	Comments
Malvaceae, Helicteroideae	<i>Durio</i>	P	<i>D. zibethinus</i> (durian) and several other species of <i>Durio</i> are cultivated widely for edible fruits and seeds in Southeast Asia and elsewhere in the tropics ^{135,154}
Moraceae	<i>Artocarpus</i>	D	<i>A. altilis</i> (breadfruit) and other species are cultivated and sold commercially throughout tropical Asia and Australasia as a source of starch-rich infructescences ¹⁴⁷
	<i>Brosimum alicastrum</i>	D	Breadnut, seeds are edible and valuable source of fiber, vitamins, and microelements; leaves used for fodder; latex and wood are also utilized ¹⁴⁷
	<i>Ficus</i>	D	Numerous species of fig used for rubber, fibers, paper, timber, medicine, and as ornamentals throughout the world tropics ¹⁴⁷
Muntingiaceae	<i>Muntingia calabura</i>	D	Firewood crop in tropical America ¹⁴⁷
Musaceae	<i>Musa</i>	P, D	Bananas, pteropodid bats both pollinate flowers and disperse seeds of wild bananas. Cultivated bananas have very high economic value ¹⁴⁷
Myrtaceae	<i>Ananomis umbellulifera</i>	D	Edible fruits in West Indies ^{135,262,280}
	<i>Psidium guajava</i>	D	Guava, cultivated for edible fruits, commercial crop in tropical America ¹⁴⁷
	<i>Syzygium cumini</i> , <i>S. jambos</i> , <i>S. malaccensis</i>	D	Rose apple, cultivated for edible fruits in Old World tropics ¹⁴⁷
Passifloraceae	<i>Passiflora</i>	D	Passionfruit, important edible tropical fruits ¹⁴⁷
Piperaceae	<i>Piper aduncum</i>	D	Fruits edible in Puerto Rico ¹⁴⁷
Polygonaceae	<i>Coccoloba uvifera</i>	D	Seaside grape, cultivated for edible fruits in tropical America ¹⁴⁷
Rhamnaceae	<i>Hovenia dulcis</i>	D	Japanese raisin tree, swollen, fleshy pedicels are sweet and edible; also used in medicine and for timber in Asia ²⁸¹
Rosaceae	<i>Eriobotrya japonica</i>	D	Loquat, native to Asia but widely cultivated throughout world tropics for edible fruits ¹⁴⁷
Rubiaceae	<i>Coffea arabica</i>	D	Coffee, native to Old World but cultivated for seeds as source of coffee throughout the world ²⁶⁷
Rutaceae	<i>Casimiroa edulis</i>	D	White sapote, cultivated for edible fruits in Central America ¹³⁵
Salicaceae	<i>Flacourtia indica</i>	D	Fruits edible and medicinal in Old World tropics ^{135,262,280}
Sapindaceae	<i>Melicoccus bijugatus</i>	D	Mamoncillo, edible fruits in tropical America ¹⁴⁷

Continued

Table 4. Continued

Plant family and subfamily	Taxon	Service	Comments
	<i>Sapindus saponaria</i>	D	Soapberry, fruits used as soap substitutes in tropical America ^{135,149,280}
Sapotaceae	<i>Chrysophyllum cainito</i>	D	Star-apple, cultivated for edible fruits in tropical America ¹⁴⁷
	<i>Manilkara</i>	D	Species of <i>Manilkara</i> , including <i>M. zapota</i> (sapodilla), produce commercially valuable fruits ¹⁴⁷
	<i>Mimusops elengi</i>	D	Cultivated for fragrant flowers throughout tropics ^{135,262,280}
	<i>Pouteria</i>	D	<i>P. sapota</i> (sapote) is important Caribbean fruit; <i>P. campechiana</i> is also a source of edible fruits in Central America ¹⁴⁷
Sterculiaceae	<i>Guazuma ulmifolia</i>	D	Light timber for boats, barrels, and fuelwood in tropical America ^{263,267}
Ulmaceae	<i>Trema micrantha</i>	D	Used for pre-Hispanic barkcloth in tropical America; soft timber for matches and chests; also used in shade coffee plantations ^{265,282,283}
Vitaceae	<i>Vitis vinifera</i>	D	Grape vine, source of edible fruits and alcoholic beverages, native probably to Asia, broadly cultivated throughout the world ^{135,280,284}
Ecologically important plants			
Agavaceae	<i>Agave</i>	P	Many species of paniculate agaves are conspicuous members of arid upland habitats in the Neotropics ^{153,273}
Arecaceae	Many New and Old World genera	D	Palms are common elements of many tropical forests, especially in the Neotropics ^{147,148}
Cactaceae, Cactoideae	Many columnar cacti in several tribes of this subfamily	P, D	Columnar cacti are keystone species in many arid Neotropical habitats ^{152,156}
Cecropiaceae	<i>Cecropia</i>	D	Species of <i>Cecropia</i> are important pioneer trees throughout the Neotropics ^{151,285}
Clusiaceae	<i>Vismia</i>	D	<i>Vismia</i> shrubs are important pioneer species in the Neotropics ¹⁵¹
Malvaceae, Bombacoideae	<i>Adansonia</i> , <i>Bombax</i> , <i>Ceiba</i> , <i>Pachira</i> , <i>Pseudobombax</i> , etc.	P	Trees of this subfamily are often dominant (in terms of basal area) members of tropical forests worldwide ^{135,286,287}
Moraceae	<i>Ficus</i>	D	Fig trees are often keystone members of tropical forests worldwide ¹⁶⁹
Piperaceae	<i>Piper</i>	D	<i>Piper</i> shrubs are pioneer plants and common members of Neotropical forest understories ²⁸⁸

Continued

Table 4. Continued

Plant family and subfamily	Taxon	Service	Comments
Solanaceae	<i>Solanum</i>	D	<i>Solanum</i> shrubs are pioneer plants and common members of Neotropical forest understories, particularly at mid-elevations ²⁸⁹
Ulmaceae	<i>Trema micrantha</i>	D	Fast-growing pioneer tree ^{265,282,283}

^aSource of commercial uses of these plants comes from work by Mabberley,¹⁵⁵ unless noted. In cases when there are more than three references of a particular bat–plant interaction, a reference to the appendices of the review, by Lobova *et al.*,¹⁴⁷ is given. Please note that for most of these plants, the precise quantitative role that bats play as pollinators and dispersers is unknown.

Throughout much of India, there appears to be a social taboo against cutting *M. indica*, probably due to its recognized value in tribal regions. However, in the North Karanpura Valley, this is one of the most threatened species, where it is being destroyed by the thousands in coal mining regions.¹⁶⁵ The economic importance of pollination by fruit bats and the products derived from species such as the Mahwa tree extend well beyond the borders of India. Increased efforts are needed to educate government agencies, industries, international corporations, and the general public about the ecological and economic value of plant-visiting bats to this species and other native flowering and fruit-bearing trees.¹⁶⁶

The tropical almond tree, *Terminalia catappa* (Combretaceae) of Indomalaya, is an example of a bat-dispersed tree with many human uses. This tree is dispersed by *Cynopterus* bats throughout Asia. In India, it is important in coastal communities where it provides shade, fuel-wood, and edible nuts.¹⁶⁴ The timber derived from almond trees makes a decorative general-purpose hardwood and is well suited for making furniture and for interior building timbers. Tannin is extracted from the bark, leaves, roots, and the fruit shell. The large leaves are also used as wrapping material and have many medicinal uses, including diaphoretic, antiindigestion, and antidysentery. Young leaves are used to cure headaches and colic. A black dye is obtained from the bark, fruit, and foliage. Its leaves and bark have a wide range of other medicinal uses. Children sometimes consume the outer flesh of agreeable fruit types. In the Philippines, a wine is made by fermentation of mature fruits. The nuts may be consumed fresh after ex-

tracted from the shell or preserved by drying or smoking and consumed up to a year later. Sun-dried kernels yield 38–54% of bland, yellow oil that is edible. The bark is used as an astringent for dysentery and thrush.^{167,168}

Services providing indirect benefits to humans

Over and above the economic value of their pollination and seed dispersal services, plant-visiting bats provide important ecological services by facilitating the reproductive success of their food plants, including seed set and the recruitment of new seedlings and saplings. Many of these plants are among the most important species in terms of biomass in their habitats (Table 4). In the New World, bat-pollinated columnar cacti and agaves are dominant vegetation elements in arid and semiarid habitats as are various species of Bombacoideae in dry and wet tropical forests throughout the world. Bat-dispersed palms and figs are also common in many tropical forests worldwide. Because they are also eaten by many birds and mammals, figs often act as keystone species (i.e., species whose ecological impact often exceeds their biomass) in tropical forests.¹⁶⁹ Figs are important bat-fruits throughout the tropics. Bat-dispersed, soft-fruited species of *Cecropia*, *Piper*, *Solanum*, and *Vismia* are critically important early pioneer species that are among the most abundant plants during early primary and secondary succession in the Neotropics.¹⁵¹ Fruit-eating phyllostomid bats thus play an extremely important role in forest regeneration in the New World. This is not necessarily true in the Paleotropics, where most early successional plants are bird dispersed. Pteropodid

bats play a more important role in the dispersal of later successional trees than in the dispersal of pioneer species.¹⁵¹ Some of these plants, such as species of *Pouteria* and *Plaquium* (both Sapotaceae) in Asia and *Milicia* (*Chlorophora*) *excelsa* and *Antiaris africana* (both Moraceae) in Africa, are important timber trees.¹⁷⁰ An exception to this is the dispersal of seeds of pioneer species of *Ficus* in the Old World. During the recolonization of Krakatau, for example, bird- and bat-dispersed figs were early colonists and attracted frugivores that brought in seeds of other plant taxa.¹⁷¹ Thus, bat-dispersed figs likely “jump-started” forest regeneration on these islands.

One of the most important ecological services that bats provide for their food plants is long-distance dispersal of pollen and seeds. This is especially true in arid New World habitats where *Lep- tonycteris* species visiting the flowers of columnar cacti have a large foraging area.¹⁷² Flower-visiting phyllostomid and pteropodid bats forage in both continuous forest and forest fragments and, thus, help to maintain genetic connections among fragmented plant populations. For example, phyllostomid bats pollinating *Hymenaea courbaril* trees in tropical dry forest fragments in Puerto Rico often move pollen 600–800 m between individuals.²²⁶ In Brazil, *Phyllostomus* species are known to move the pollen of *Hymenaea courbaril* trees 18 km between individuals in riverine forest.¹⁷³ Glossophagine bats regularly move pollen between individuals of the canopy tree *Ceiba pentandra* within continuous forest and between forest trees and isolated pasture trees in western Mexico.¹⁷⁴ The Australian pteropodid *Syconycteris australis* usually moves pollen < 200 m between *Syzygium cormiflorum* trees but also moves pollen up to about six km between individuals in different habitat patches.¹⁷⁵

Most seed dispersal systems, including those involving vertebrates, produce leptokurtic dispersal distributions. That is, most seeds are dispersed close to parent plants with only a few being dispersed 100s to 1,000s of meters away. Seeds dispersed by frugivorous bats undoubtedly conform to this pattern, but bats can also provide relatively long seed-dispersal distances for their food plants. For example, in central Panama the Jamaican fruit bat *Artibeus jamaicensis* carries single fig fruits 100–250 m away from fruiting plants before beginning to feed in a night roost; it often feeds at several

trees located a kilometer or more apart in a single night.¹⁷⁶ Similarly, *Cynopterus sphinx*, the Asian pteropodid ecological analogue of the Neotropical *A. jamaicensis*, is known to forage on more than one island in the Krakatau group in a single night.¹⁷¹ Although it is generally a short-distance seed disperser, the phyllostomid *Carollia perspicillata* is known to move 1–2 km between foraging areas and frequently moves seeds between habitats.^{149,177} In contrast to forest-dwelling frugivorous birds, phyllostomid and pteropodid bats readily fly over open areas and defecate seeds in flight. As a result, phyllostomid bats eating the small seeds of pioneer plant species provide substantial mobility for their seeds and help them to quickly colonize forest treefall gaps and disturbed areas such as abandoned pastures and logged forests.¹⁵¹

We close this section with a brief discussion of an important conservation concern associated with plant-visiting bats. Many species of nectar- or fruit-eating bats annually migrate between a series of landscapes, and these movements are driven by seasonal fluctuations in the availability of flower or fruit resources. In western Mexico, for example, many individuals of the lesser long-nosed bat, *L. yerbabuena*, spend the fall and winter in tropical dry forest where they mate. Here, they feed on the flowers and fruit of dry tropical forest trees and shrubs. In the spring, many females migrate up to 1,000 km north to form maternity colonies in the Sonoran Desert where they feed on flowers and fruit of columnar cacti. In late summer and early fall, females and their offspring move into upland areas of southern Arizona and Sonora, Mexico, where they feed at flowers of paniculate agaves before migrating south again.¹⁷⁸ Seasonal movements among landscapes by flower-visiting bats are also known to occur in northeastern Costa Rica, lowland Malaysia, and in the eucalypt forests of eastern and northern Australia.^{179–181} Similarly, some frugivorous phyllostomid and pteropodid bats undergo altitudinal or latitudinal movements.^{182,183} For example, populations of the African pteropodid *Eidolon helvum* migrate over 1,000 km annually from the Democratic Republic of Congo to central Zambia.¹⁸⁴ Most of the foraging areas along the migration route are not protected by conservation legislation.

Because they often move across international borders, as well as among habitats that often do not have state or federal protection, migratory species

are of special conservation concern.¹⁸³ This is especially true of vertebrate pollinators and seed dispersers whose movements and survivorship are of critical importance for the reproductive success of their food plants. Protection of migratory pathways and critical feeding areas of migrants must be major conservation goals worldwide.

Finally, some of the greatest conservation concerns in bats involve island-dwelling species, including nectar- and fruit-eaters.^{185,186} Because of their remoteness, oceanic islands usually have reduced biodiversity and disharmonic (unbalanced) faunas in which bats play an especially important role in the pollination and dispersal biology of trees, vines, and shrubs.¹⁸⁷ As a result of overhunting, persecution, and habitat destruction, many island bats are critically endangered, and their conservation is of substantial concern to bat biologists and ecologists.^{183,188,189}

Provisioning and cultural services

Bats provide additional provisioning and cultural ecosystem services beyond the regulatory services (i.e., arthropod suppression, pollination, and seed dispersal) that we have emphasized throughout this paper. In this section, we briefly discuss these underappreciated benefits to humans provided by bats and then revisit them in the section on valuation of ecosystem services.

Redistribution of nutrients from guano

Guano from bats has long been mined from caves for use as fertilizer on agricultural crops due to the high concentrations of nitrogen and phosphorous, the primary limiting nutrients of most plant life.^{190,191} Although the benefits of nitrogen to plants are well known, most of the evidence supporting bat guano as fertilizer is anecdotal, and few studies have explicitly measured its effects on plant growth parameters.¹⁹² Because bats regularly or occasionally roost in caves, they are thought to provide the primary organic input to cave ecosystems, which are inherently devoid of primary productivity.^{193–196} Cave-dwelling salamander and fish populations and invertebrate communities, for example, are highly dependent upon the nutrients from bat guano.^{197,198}

Several researchers have begun to investigate the potential ecological role of guano in nutrient redistribution over the landscape via the “pepper-shaker effect.”^{191,192,199,200} Because insectivorous bats con-

sume energy rich prey, experience rapid digestion during flight, and forage significant distances over heterogeneous habitat types, it is expected that guano is sprinkled over the landscape throughout the night.²⁰¹ Thus, bats contribute to nutrient redistribution from nutrient-rich sources (e.g., lakes and rivers) to nutrient-poor regions (e.g., arid or upland landscapes). However, to date, no studies have explicitly tested this prediction. Reichard¹⁹² estimated that a colony of one million Brazilian free-tailed bats, *Tadarida brasiliensis*, in Texas could contribute 3,600,000 kJ/day of energy and 22,000 g of nitrogen in the form of guano. He also demonstrated that moderate applications of guano in a controlled greenhouse experiment promoted growth in a grass species native to Texas (Indian grass, *Sorghastrum nutans*), but reduced root/stem ratio and had a neutral effect on two other native species: little bluestem, *Schizachyrium scoparium*, and prairie coneflowers, *Ratibida columnifera*, respectively. He further speculated that guano deposition may have species-specific effects on plant communities and thus emphasize the need for more in-depth experimental and field studies. Other trophic ensembles (e.g., nectarivorous, frugivorous, carnivorous bats) may similarly contribute to nutrient cycling through guano redistribution; however, we were not able to find any studies investigating this potential service.

Bats in medicine and culture

As described in the introduction, bats have long been feared in a diversity of human cultures. Although it is beyond the scope of this paper to provide a full treatment of this topic, it is important to also note the value of bats to ancient and contemporary religions and cultures worldwide. Bat symbols appear in priceless artifacts, such as wall paintings in Egyptian tombs from 2000 B.C., Chinese bowls carved of white jade, Japanese prints, and ancient temple paintings of the Mayan bat god.¹⁸ In fact, the Mayan “Zotzil,” the bat people, continue to live in southern Mexico and Guatemala in cities with the same name: “Tzinacantan,” or the Bat City. These and other cultural heirlooms are not only symbolically cherished for their historical significance but also generate direct revenue for the countries and museums that display them to curious tourists.

Bats have also long been used for food and medicine.^{18,22} Witches and sorcerers used bats in ancient magic to induce desire and drive away sleep.

Shamans and physicians used bats to treat ailments of patients ranging from baldness to paralysis.^{18,202} Some of these traditions continue today, though bats are now consumed primarily as meat.²² One exception is the anticoagulant compound that is found in the saliva of the common vampire bat, *Desmodus rotundus*. This compound, *Desmodus rotundus* salivary plasminogen activator (DSPA), has drawn considerable attention from the medical community as a potential treatment for strokes because, unlike the alternatives, it can be administered much later after a stroke has occurred and still be effective.²⁰³

Today, bats provide aesthetic value through cave visits, nocturnal tours in national parks, and educational nature programs. These activities provide adventure and life memories for the public and revenue for the communities and companies involved.²⁰⁴ Bats also commonly appear as symbols or logos in popular movies (e.g., *Batman*), products (e.g., Bacardi rum), and holidays (e.g., Halloween), all major revenue-generating endeavors.²⁰⁵ Finally, the study of bat echolocation and locomotion has provided inspiration for novel technological advances in such fields as sonar systems, biomedical ultrasound, sensors for autonomous systems, wireless communication, and BATMAVs (bat-like motorized aerial vehicles).^{206,207} Although extremely difficult to quantify, it is important to recognize the extraordinary value of bats to ancient and contemporary traditions and science.

Valuation of ecosystem services provided by bats

As described in the preceding sections, bats provide a variety of ecosystem services that improve human well-being. To date, few studies have attempted to place an economic value on these ecosystem services. This section describes various methods that could be used to value ecosystem services provided by bats and then reviews the available studies that have attempted to do so. Although some of these services provide direct benefits to humans (e.g., food, fuel, fiber, and fertilizer), most ecosystem services offer indirect benefits (e.g., pest suppression, seed dispersal, and pollination). Often times, little attention is paid to the “free” (i.e., nonmarketed) services provided by ecosystems either because the benefits of the services are not fully understood by decision

makers or because the benefits accrue to nonowners of the ecosystem providing the service. Moreover, little consideration has been given to the role of bats in supporting entire cave ecosystems by providing essential organic input that supports assemblages of endemic cave flora and fauna. Information on non-market values of ecosystem services can be used to inform decisions regarding whether to protect existing ecosystem services, improve the current provision of ecosystem services, or restore previously lost ecosystem services.^{4,208}

The economic approach to valuation

Traditionally, economic valuation is the process of measuring the human welfare gains or losses that result from changes in the provision of ecosystem services. The purpose of economic valuation is to provide a common metric with which to compare the impacts of alternative management or policy decisions among ecosystem services and other market-based goods and services.⁴ Consumer surplus and producer surplus are the welfare measures commonly used in economic valuation.^{208,209} Consumer surplus is the amount that consumers would be willing to pay for a good or service above the amount that they actually pay, while producer surplus is the amount that producers receive for a good or service less what it costs them to produce it. Consumer and producer surplus can be measured for market-based goods (e.g., food) by direct estimation of demand and supply functions. For nonmarketed goods and services, including most ecosystem services, alternative valuation methods have been developed.^{208,209} These methods fall into two broad categories. Revealed preference approaches value of ecosystem services through observing consumer or producer behavior for related goods and services.²¹⁰ For example, crop production often uses a variety of ecosystem services as inputs.²¹¹ However, it is not always possible to directly observe consumption or production of ecosystem services. In addition, some ecosystem services have nonuse or existence values. In these cases, stated preference methods of valuation, whereby individuals state their individual willingness to pay for ecosystem services, can be used.²¹² While a complete assessment of valuation methods is beyond the scope of this paper, Appendix B provides brief descriptions for the various methods that could be used to value the ecosystem services provided by bats.

Applying economic valuation to ecosystem services provided by bats

Few studies have attempted to value the ecosystem services provided by bats. In this section, we highlight those that have been published. We also discuss a small number of nonbat studies that describe an interesting approach or present results that might be similar to those used to value bats.

Regulating services. As described earlier, bats provide a number of regulating services including pest suppression, seed dispersal, and pollination within both agricultural and natural ecosystems. Determining the economic value of regulating services provided by bats to natural ecosystems is extremely challenging and no studies were found. Thus, we focus here on studies where the ecosystem service is provided directly to the production of goods and services consumed by humans.

One early study describing the economic importance of bats is that of Fujita and Tuttle,¹⁵⁴ in which the authors identify 289 Old World tropical plant species that rely on the pollination and seed dispersal services of bats for their propagation (see also Table 4). These plants, in turn, contribute to the production of 448 bat-dependent products in a variety of categories, including timber and other wood products (23%); food, drinks, and fresh fruit (19%); medicines (15%); dyes, fiber, animal fodder, fuel wood, ornamental plants, and others. Fujita and Tuttle¹⁵⁴ describe the economic value of some of these products; for example, fiber produced from kapok trees is reported to be worth \$4.5 million. However, because bat-provided services represent one input within a multi-input production process, only a portion of the total value of the end product can be attributed to bats. The primary contribution of this study is in highlighting the expansive role that bats play in the production of goods that contribute to human well-being.

More recently, three studies assess the economic importance of pollination services provided to world agriculture.^{213–215} In each study, the contribution of animal pollinators, including bats, to global primary crop production is assessed. In an extensive literature review, Klein *et al.*²¹³ evaluate the dependence on animal pollinators of primary agricultural crops. Dependence categories are based on the percentage of crop production that would be lost without animal-mediated pollination, a damage

function type of analysis but without an economic component. Their results show that while 87 primary crop species depend to some degree on animal pollination, these crops account for only 35% of global production. Of the crops directly consumed by humans, pollinators were found to be essential for 13, highly dependent for 30, moderately dependent for 27, slightly dependent for 21, unimportant for 7, and of unknown significance for 9. The majority of these crops are pollinated by bees; however, birds, bats, and other insects also contribute to the pollination of the world's leading crops.²¹⁶ In particular, bats are important pollinators of durian (*Durio zibethinus*), star apple (*Chrysophyllum cainito*), and velvet bean (*Mucuna pruriens*). Production data for these bat-dependent crops are not reported separately but rather appear in aggregated crop groupings, so there is no way to extract the specific value of bat pollination services from this study or other studies that use Klein *et al.*'s dependence values.

Gallai *et al.*²¹⁴ combine pollination dependence ratios with regional measures of crop production and prices in an economic valuation of the pollination services provided to 100 world food crops. Of these, 46 crops depend to some degree on animal pollinators (6 essentially dependent, 13 highly dependent, 13 moderately dependent, and 14 slightly dependent), accounting for 39% of world production value. The economic value of the portion of crop production due to animal-dependent pollination is calculated by multiplying the total production value of each crop by its pollinator dependence ratio, a damage function approach to valuation. Summing over all crops, the total economic value of global pollination services is estimated to be €153 billion (~\$200 billion), representing 9.5% of the value of world food crop production in 2005. A small portion of this total is due to bat pollination services. Using rough approximations for demand functions, Gallai *et al.* also estimate consumer surplus values for pollination services to be between €191 and €310 billion (\$250 and \$405 billion), indicating that the damage function approach may underestimate the true economic value for pollination services.

Bauer and Sue Wing²¹⁵ develop a multiregion, multisector model of global agricultural production and trade that incorporates Klein *et al.*'s²¹³ pollinator dependence ratios as exogenous neutral shocks

to four broad crop sectors. Pollinator loss scenarios are implemented as catastrophic shocks to each regional economy, with the services of animal pollinators being completely lost and the productivity of pollinator-dependent crops declining by the corresponding dependence ratio. This general equilibrium analysis estimates the crop sector losses to be \$10.5 billion globally, but total economy-wide losses that account for price effects on downstream sectors (e.g., processed foods) and households to be \$334.1 billion, an order of magnitude greater. Once again, a small portion of this amount is due to bat pollination services.

We found no studies that estimated the economic value of seed dispersal services provided by bats. However, multiple studies describe the ecological relationship between bat-mediated seed dispersal and timber volume for economically important tree species.^{151,217} To estimate the economic value of the seed dispersal service due to bats, the quantitative relationship between the seed dispersal contribution of bats and the volume of marketable timber by species, similar to Klein *et al.*'s²¹³ pollinator dependence ratio, would first need to be established. This information could then be fed into economic analyses similar to those described earlier for pollination services.

One study estimating the economic value of seed dispersal services provided by the Eurasian jay to regeneration of giant oak in a Stockholm National Urban Park in Sweden²¹⁸ mentions that bats do reside in the park, but it is unlikely that insectivorous bats (the only bat feeding ensemble present in Sweden) would contribute to seed dispersal. Notwithstanding, the study uses a replacement cost approach that could be used to estimate the economic value of seed dispersing bats. By first quantifying the number of oaks that are due to jays, the authors then estimate the costs associated with two different types of manual replacement, seeding acorns, or planting saplings. The value of seed dispersal services per pair of jays was estimated at SEK 35,000 (\$4,935) for seeding acorns and SEK 160,000 (\$22,560) for planting saplings, which aggregates up to between SEK 1.5 million and SEK 6.7 million (\$212,000 and \$945,000). The authors acknowledge Shabman and Batie's²¹⁹ three conditions for use of the replacement cost approach and argue that the first two conditions are met by their study but concede uncertainty whether the third condition is met, although

they contend that public support for preservation of giant oak is great.

Three related studies approximate the economic value of pest suppression services provided by Brazilian free-tailed bats to the production of cotton in Texas.^{98,103,110} In the first study, Cleveland *et al.*⁹⁸ employed both damage function and replacement cost approaches in approximating the economic value of bats' pest control service across a 4,000 Ha region. The damage function approach required a detailed assessment of the ecological relationships between Brazilian free-tailed bats, cotton bollworm adults, cotton bollworm larvae, and cotton crops detailing how these relationships vary over the course of the growing season. The value of the avoided damage to cotton is approximately \$0.02 per bat per night in mid-June (dropping to zero by August) for a total annual value of \$638,000. The replacement cost approach was based on an estimated reduction of at least one pesticide application early in the growing season due to high bat predation rates keeping the number of cotton bollworm larvae below the economic threshold for pesticide use. The value of pesticides not used (i.e., replaced by the bat service) is approximately \$100,000 per year across the region. Betke *et al.*¹⁰³ used data collected with thermal imaging technology to update the estimate of bat population across this same cotton-producing region. Feeding this information into the pesticide allocation model used by Cleveland *et al.*,⁹⁸ Betke *et al.* present an updated measure for the pesticide replacement cost of \$500,000 annually.

The Cleveland *et al.*⁹⁸ study, using values from Pimentel *et al.*,⁷⁷ also estimates the reduction in external environmental costs resulting from lower pesticide use at \$3,000 per year. These external costs are those nonprivate costs incurred by society including loss of natural enemies, loss of wild pollinators, groundwater and stream contamination, and the impact on local bird and fish populations.

Federico *et al.*¹¹⁰ develop a more detailed dynamic model of the bat–bollworm–cotton agroecosystem, which includes multiple life stages for both bats and bollworm and compares conventional and transgenic cotton crops. Once again, the pest control services provided by bats are approximated through estimates of crop damage avoided and number of pesticide applications reduced. Four different crop–pesticide scenarios were assessed,

resulting in a range of per-hectare values for bat pest suppression services: (i) \$86 for conventional-spray, (ii) \$757 for conventional-no spray, (iii) \$46 for transgenic-spray, and (iv) \$214 for transgenic-no spray. By combining two valuation methods, both Cleveland *et al.*⁹⁸ and Federico *et al.*¹¹⁰ go beyond the basic damage function approach by allowing producers to vary a second production input (pesticide applications) in their simulations. This use of the replacement cost method seems appropriate as it is based on the economic pest threshold concept that cotton producers use in their decision-making process for pesticide applications.

In an unrelated study, Gándara Fierro *et al.*¹¹¹ estimate the economic value of a population of Brazilian free-tailed bats in Nuevo León, Mexico to range from 6.5 to 16.5 million Mexican pesos (\$479,000–1.2 million) with an average value of 260 pesos (\$19) per hectare. The authors use a simple replacement cost method, basing their estimate on the identification of potential insect pests in the guano of a large colony of bats, surveys of 101 local farmers attesting to the cost and use of pesticides and the presence or absence of bats in different crops, and estimates by Federico *et al.*^{220,221} that bats reduce crop damage by 25–50%.

Rather than valuing the direct contribution of regulating services to agricultural production, some studies value the indirect contribution that natural landscapes make by providing forage and nesting habitat for pollinators, seed dispersers, and natural enemies.^{222,223} In this case, crop production is a function of the quantity of nearby natural habitat. While these studies have predominantly focused on coffee production, which is bee-pollinated, the same methods could be applied to bat-serviced crops resulting in values for conservation of natural habitat used by bats.

Provisioning services. Bats provide a direct source of food in many countries.²² Although no studies were found estimating market demand or supply of bat bushmeat, several studies reported anecdotal pricing information for local consumption of bats (\$2.50–3.50 per bat in Malaysia and \$10 per bat in Jakarta for *Pteropus vampyrus* and *P. hypomelanus*);¹⁵⁴ (65 Naira [\$0.43] per kg for *Eidolon helvum*);²²⁴ (\$0.50–1.25 for *P. vampyrus natunae*;²²⁵ [\$0.50–1.50 for *P. rufus*]²²⁶). In an analysis of several types of bushmeat for vitamin and mineral

composition, bats were found to have the highest value (i.e., lowest cost per kilogram) of protein.²²⁴

Several studies have reported on the overhunting of bat bushmeat, indicating a need for further conservation efforts including recommendations for the establishment of protected areas.^{186,225,227,228} However, a note of caution may be in order, as Fa *et al.*²²⁹ reported a negative relationship between the quantity of bushmeat harvested and the distance between settlements and national parks for many species, although bats were a very small percentage of the total bushmeat harvested in their study area.

Bats also provide another marketable product, bat guano, which is used as a natural fertilizer. Once again, we were not able to find any formal studies estimating market demand and supply of guano. However, an Internet search (keywords: *bat guano price*) conducted in September of 2010 revealed more than 950 bat guano products, clearly indicating a market for the product. Prices for bat guano organic fertilizer varied between \$1.25 and \$12.00 per pound, depending on the size of the package (larger packages have lower per-unit prices) and the mix of ingredients.

Cultural services. Although perhaps not as widely practiced as bird watching or whale watching, bat watching is a growing recreational activity. The majority of bat viewing takes place at cave entrances where nightly emergences can be viewed. Many sites charge small fees ranging from \$5 to \$12 per visitor, which can be interpreted as an individual's minimum willingness to pay to view bats.²³⁰ The 5th Annual Austin Bat Fest reportedly drew over 40,000 participants to the area surrounding the Congress Avenue Bridge, a roosting site for an estimated 1.5 million Brazilian free-tailed bats.²³¹ Tickets to the day-long event cost \$7.00 and included a number of band performances, crafts exhibits, and educational displays. The bridge is home to one of the largest urban bat colonies in the United States, and bat viewing at the bridge is typically free. A fiscal impact study of bat-watching visitors estimated tourist bat-related expenditures of \$3 million per year, with one third of the visitors coming from outside of Texas.²³² Ecotourism clearly is one way to support bat conservation.²³³

In terms of general conservation or existence values for bats, one recent contingent valuation study included one species of bat (*Myotis emarginata*) in

its assessment of willingness to pay for biodiversity conservation in a national park in Spain.²³⁴ Through a photo questionnaire, bats (along with snakes and spiders) were valued five times less than other species (lynx and eagle) due in part to a lack of understanding regarding their ecological role as well as a potential aversion factor. This study highlights the need for further public education on the ecosystem services provided by bats.

Challenges associated with valuation of ecosystem services

It is not possible within this paper to fully describe the process involved in economic valuation of ecosystem services. The National Research Council (NRC)²⁰⁸ provides a book-length treatment of the subject, and Appendix C offers a five-step summary of guidelines. Here, we describe the major challenges one might encounter when conducting a valuation study.

The fundamental challenge of valuing ecosystem services lies in providing an explicit description and adequate assessment of the links between the structures and functions of natural systems, the benefits (i.e., goods and services) derived by humanity, and their subsequent values. (NRC 2005, p. 2)²⁰⁸

As can be seen in the studies by Klein *et al.*,²¹³ Cleveland *et al.*,⁹⁸ and others, development of detailed descriptions of ecological production functions that quantitatively articulate relationships between bats and the marketed output requires much effort at great cost. But these details are necessary in order to estimate the economic value of the pollination, seed dispersal, and pest suppression services provided by bats to agricultural and natural systems. It is tempting to try to use values from previous studies in new applications, a practice known as benefits transfer. However, great care should be taken when applying benefits transfer or when conducting original studies that might be used in later studies.^{235,236} Similar care should be taken when scaling up results from field- or farm-level analyses to regional or global analyses, as it is possible that stakeholder values will vary at different spatial scales.²³⁷ It is also important to clearly define the change (increase or decrease) in the ecosystem service that is being valued.²³⁸

As noted above, direct estimation of supply or cost functions is difficult due to lack of data that in-

cludes measurements of the ecological entities (e.g., bats and bollworms). Efforts should be made to collect these types of data, at least for important crop systems. This includes getting information on other inputs into the production process and assessing producer decision making when various inputs change. It is likely that many agricultural producers are unaware of the services that bats provide because much of this activity occurs at night. Producer surveys could be used to provide education as well as elicit information on producer decision making.

The majority of valuation studies of ecosystem services focus on a single service. Additional challenges exist when attempting to measure values for multiple ecosystem services because double-counting of services is possible and tradeoffs between services may exist.^{238–240}

Summary and conservation considerations

Ecosystem services are the benefits that humans obtain from ecosystems that enhance their well-being. As reviewed here, bats provide many ecosystem services. Humans derive direct benefits from bats as food, guano for fertilizer, and through contributions to medicine and culture. Perhaps more significantly, yet much more difficult to quantify, humans derive indirect benefits from bats through arthropod suppression, forest regeneration, and maintenance via seed dispersal and pollination of a wide variety of ecologically and economically important plants. In turn, the contribution of these services by bats to healthy, functioning ecosystems provides additional benefits to humans by supporting vital regulatory processes such as climate regulation, nutrient cycling, water filtration, and erosion control. Unfortunately, many misconceptions about bats persist, especially in the neotropics, where humans regularly have negative interactions with vampire bats;²⁰⁵ thus, conservation efforts often fall short. Assigning values to the different ecosystem services provided by bats is one way of positively influencing the public's perception of these beneficial mammals; however, economic valuation of these services remains in its nascency. Here, we have reviewed most of the existing literature on the three primary ecosystem services provided by bats and highlighted areas of research that deserve further attention. We have also outlined both market and nonmarket valuation methods that either have been or could be used to estimate the economic value of these ecosystem

services. As was noted by the few published studies, these values can be quite substantial. However, a distinct challenge exists in that most of these efforts require detailed descriptions of ecological production functions (e.g., Klein *et al.*'s²¹³ pollinator dependence ratios) or consumer surveys of households in developing countries that require substantial time and monetary investments. Nevertheless, at a time when critical threats face bat populations (e.g., white-nose syndrome) and biodiversity as a whole is rapidly declining worldwide, the development of alternative conservation strategies—such as the valuation of ecosystem services—should become a priority.

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Appendix A:

Examples of economic and ecological damage caused by insect pests consumed by bats

June beetles. Adults are herbivorous and have the potential to defoliate trees in large numbers; their larvae, white grubworms, attack the roots of grasses and various crops such as corn, wheat, oats, barley, sugarbeets, soybeans, and potatoes.^{247,248}

Wireworms/Click beetles. Wireworms, click beetle larvae, cause several million dollars worth of damage annually, and no crop is known to be entirely immune.²⁴⁹

Leafhoppers and planthoppers. These true bugs are vectors of plant pathogens such as the rice dwarf and the maize mosaic viruses, as well as phytoplasmas and bacteria.²⁵⁰ The brown planthopper has resulted in cumulative losses of rice estimated in the hundreds of millions of dollars, and other species act as serious agricultural pests to potatoes, grapes, almonds, citrus, and row crops.²⁵¹

Spotted cucumber beetles (*Diabrotica undecimpunctata*). Serious pests of corn, spinach, and various cucurbit vines.⁸⁶ In their larval stages, *Diabrotica spp.* (referred to as corn rootworms) decimate corn crops, costing farmers in the United States an estimated \$1 billion annually in crop yields and costs of pesticide applications. The United States Department of Agriculture (www.usda.gov) reports that more hectares of cropland are treated with insecticide to control corn rootworm than any other pest in the United States.

Stinkbugs. Serious pests of various crops including apples, pecans, soybeans, cotton, field corn, grain sorghum, peaches, and vegetables.²⁵² Stinkbugs pierce plant tissues with their mandibular and maxillary stylets to extract plant fluids, which results in staining of the seed, deformation and abortion of the seed and fruiting structures, delayed plant maturation, and the predisposition to colonization by pathogenic organisms.

Gypsy moths. Serious pests of several hundred species of trees, bushes, and shrubs, both hardwood and conifer, and can lead to the complete defoliation when in high enough densities.²⁵³ Introduced into North America in the late 1800s, their range has continually expanded westward and now threatens temperate forested ecosystems throughout the northeast.²⁵⁴

Tent caterpillars. Have irruptive population dynamics, generally advancing to pest status every year in some regions of the United States and causing considerable defoliation of trees over extensive areas.²⁵⁵

Coneworms. Larvae feed within cones on cone scales and seeds of various species of firs and western pines,²⁵⁶ and can cause significant damage to fertilized conifer plantations and loblolly pine seed orchards.^{257,258}

Cutworms. Destructive garden pests, causing fatal damage to nearly any type of vegetable, fruit, or flower.²⁵⁹

Tortrix moths. Many moths of the genus *Cydia* are economically important due to the damage they inflict on fruit and nut crops, and include notable pests such as the codling moth, pear moth, alfalfa moth, and hickory shuckworm moth.

Snout moths. Members of the genus *Acrobasis* feed on a wide variety of shoots, nuts, and fruits

including alders, birches, hickories, pecans, and cranberries.

Corn earworm and tobacco budworm moths. Rank among the top pests in the United States in damage caused to crops and number of insecticides applied to crops to control them.²⁶⁰ In Texas, corn earworms are present in an estimated 98% of cornfields. Each female corn earworm moth potentially lays over 1,000 eggs in her lifetime,²⁶¹ which then develop into larvae that infest corn, cotton, or other crops.

Appendix B:

Methods for the valuation of ecosystem services

Revealed preference methods of valuation

Ecosystem services such as pest suppression, seed dispersal, and pollination are often inputs into the production of agricultural crops.²¹¹ A *production function* approach to valuation can be used to compare the levels of agricultural production with and without the ecosystem service or with a reduction in the service.²⁹⁰ In these situations, the ecosystem service input appears as an argument in the supply or cost function along with other inputs to production such as labor, capital, and materials (e.g., fertilizers). Estimation of consumer and producer surplus welfare measures using a production function approach often requires substantial time-series or cross-sectional panel data that include, among other things, measurements of the ecosystem service input (e.g., the number of bats feeding in each farm across several farms across multiple growing seasons). Because there is often a lack of sufficient data, a *damage function* approach to valuation is sometimes used.²⁹⁰ This approximation is based on the idea that arthropod predators, seed dispersers, and pollinators reduce the loss of agricultural crops that would otherwise result without the associated ecosystem service. It is an approximation rather than a true estimate, because it assumes that use of all other inputs to the production process remain constant, and that the price of the agricultural output does not change. Although fewer data are required with the damage function approach, challenges with establishing clear ecological relationships between the ecosystem service and agricultural output remain.

A related valuation method is the *replacement cost* method in which the value of the ecosystem service

is estimated by what it would cost to replace the service using an alternative approach. For example, pest suppression services may be estimated by the cost of the chemical pesticides that would be required to provide the same level of production output. However, caution must be exercised when using replacement costs as they do not reflect actual consumer or producer behavior and, thus, are not true welfare measures.²⁰⁸ For example, farmers might not be willing to pay the full amount for equivalent pest control. Shabman and Batie²¹⁹ describe three conditions that should be met when using replacement costs in valuations of ecosystem services: the alternative must provide the same level of service, the alternative must be the least-cost alternative, and there should be substantial evidence that individuals would be willing to pay for the alternative if the ecosystem service were eliminated. It is this last criterion that is typically difficult to ascertain.

Another revealed preference method for valuation of ecosystem services is the *hedonic pricing* method in which property values reflect a number of characteristics of a parcel of land including any ecosystem services provided from within the parcel itself or from neighboring parcels. The price of a parcel can be broken down into a set of implicit prices for each of the characteristics. This method is commonly used for valuing air and water quality or open space amenities, but could potentially be used to value ecosystem services provided by bats.

A fifth revealed preference valuation technique is the *travel cost* method, which estimates the recreation values associated with ecosystem services. Using the opportunity cost of time and actual costs incurred with traveling to a particular recreation site, the demand for recreation can be estimated. Expanding the analysis to multiple sites with varying levels of ecosystems services can elicit values for particular services. Travel cost studies are often used to assess ecotourism or sport hunting values.²¹⁰

Food, fuel, and other goods are often harvested directly from the ecosystem rather than being purchased through markets. For example, bats are hunted for local consumption in many developing countries.²² In these situations, *time allocation* models can be used to estimate the time invested in hunting and gathering versus other household activities. These studies are typically conducted through household surveys although a researcher may directly observe the behavior.

Stated preference methods of valuation

Stated preference methods of valuation such as *contingent valuation* and *conjoint analysis* involve surveys that contain hypothetical scenarios of ecosystem services and elicit individual willingness to pay for well-defined changes to one or more ecosystem service.²¹² Despite some early concern over the use of stated preference surveys, the techniques have improved considerably over the past two decades and are commonly accepted methods for eliciting non-market values.^{4,208} Stated preference surveys are the only economic valuation method available for assessing existence values.

Appendix C:

Steps used in the valuation of ecosystem services

There is no one-size-fits-all process for valuing ecosystem services. Each valuation study has its own policy context, within which is an associated set of ecosystem services. The following five steps, adapted from work by Hein *et al.*,²³⁷ NRC,²⁰⁸ and MEA,⁴ are offered as valuation guidelines. For each step, a set of qualifying questions is provided.

Step 1. Identify the policy or decision context for the valuation exercise:

- What is the purpose and how will the results be used?
- Which ecosystem services will be included?
- What is the appropriate geographic scale?
- How is the valuation question framed?

Step 2. Assess the underlying ecology (structure, functions, processes):

- How well understood is the ecosystem of interest?
- Are important dynamics understood?
- Are important nonlinearities and thresholds understood?
- Are the complexities of the system understood?
- Are the linkages between policy alternatives and ecological responses understood?

Step 3. Translate ecological functions to ecosystem services:

- Can the outputs from the ecological models be used as inputs to the economic models?

- Are all direct and indirect linkages between ecological functions and ecosystem services understood?

Step 4. Translate ecosystem services to values:

- What valuation methods are appropriate?
- What data are available?
- How will aggregation of values across individuals, services, and time be handled?
- How will double-counting be avoided?

Step 5. Assess the level of uncertainty:

- What are the primary sources of uncertainty?
- What methods will be used to address uncertainty?
- Are there important gaps in our knowledge?
- Are there important potential irreversibilities?

Conflicts of interest

The authors declare no conflicts of interest.

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