



## The functional roles of mammals in ecosystems

THOMAS E. LACHER, JR.,\* ANA D. DAVIDSON, THEODORE H. FLEMING, EMMA P. GÓMEZ-RUIZ, GARY F. MCCrackEN, NORMAN OWEN-SMITH, CARLOS A. PERES, AND STEPHEN B. VANDER WALL

Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA (TEL)

Global Wildlife Conservation, P.O. Box 129, Austin, TX 78767-0129, USA (TEL)

Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA (ADD)

Colorado Natural Heritage Program, Colorado State University, Fort Collins, CO 80523, USA (ADD)

Emeritus, Department of Biology, University of Miami, Coral Gables, FL 33124, USA (THF)

Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, San Nicolás de los Garza, Nuevo León, México (EPG)

Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA (GFM)

Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits 2050, South Africa (NO-S)

School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom (CAP)

Department of Biology and the Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV 89557, USA (SBVW)

\* Correspondent: [tlacher@tamu.edu](mailto:tlacher@tamu.edu)

The diverse functional roles of over 6,000 species of extant mammals that range in body size across eight orders of magnitude, from blue whales (*Balaenoptera musculus*) to tiny Etruscan shrews (*Suncus etruscus*), contribute to shaping Earth's ecosystems. Large mammalian herbivores (e.g., African elephants [*Loxodonta africana*], American bison [*Bison bison*], hippopotamuses [*Hippopotamus amphibius*]) and carnivores (e.g., wolves [*Canis lupus*], pumas [*Puma concolor*], sea otters [*Enhydra lutris*]) often have significant effects on primary producers in terrestrial, aquatic, and marine systems through nutrient cycling, energy flow, and the exertion of bottom-up and top-down processes. Small mammals, like bats, are important pollinators, dispersers of fruits, and consumers of arthropods, and others, especially rodents and primates, are important predators and dispersers of seeds. Many of these mammal-mediated processes occur simultaneously in the same ecosystem, and have significant effects on community structure of primary producers that in turn alter communities of other vertebrates and invertebrates. Many mammals also are ecosystem engineers (e.g., elephants, American beavers [*Castor canadensis*], porcupines [*Erethizon dorsatum*], prairie dogs [*Cynomys* spp.]) that create, significantly modify, or destroy habitat, and by doing so, they alter ecosystem structure and function and increase habitat heterogeneity and biodiversity. The extensive influence mammals have on ecosystems results in important services that contribute to human well-being, such as pollination, insect pest control, and bioturbation of soils. The rapid declines in abundance of many mammal populations and the associated increase in extinction risk raise conservation concerns for mammals. To maintain mammalian diversity and the critical ecosystem processes they provide, scientists need to mobilize concern for their status and strive for more effective and comprehensive conservation action. We provide insights and synthesis on the ecological role of mammals and highlight key research questions and future directions for their conservation.

Los diversos roles funcionales de las más de 6,000 especies de mamíferos existentes—que varían en peso corporal de hasta eight órdenes de magnitud entre si, desde las ballenas azules (*Balaenoptera musculus*) hasta las diminutas musarañas etruscas (*Suncus etruscus*) desempeñan un papel importante en la formación de los ecosistemas del planeta. Los grandes mamíferos herbívoros (elefantes [*Loxodonta africana*], bisontes [*Bison bison*], hipopótamos [*Hippopotamus amphibius*]) y carnívoros (lobos [*Canis lupus*], pumas [*Puma concolor*], nutrias marinas [*Enhydra lutris*]) a menudo tienen efectos significantes en los productores primarios de los ecosistemas terrestres, acuáticos

y marinos, a través del ciclo de nutrientes, flujo de energía, y de los procesos ecológicos de abajo hacia arriba y de arriba hacia abajo. Mientras que los pequeños mamíferos como los murciélagos son importantes polinizadores, dispersores de frutas, y consumidores de artrópodos; los roedores y primates, son también importantes depredadores y dispersores de semillas. Muchos de estos procesos mediados por mamíferos ocurren simultáneamente en el mismo ecosistema y tienen efectos significantes en la estructura de comunidades de productores primarios que a su vez modifican las comunidades de otros vertebrados e invertebrados. Muchos mamíferos son también ingenieros del ecosistema (elefantes, castores [*Castor canadensis*], puerco espín [*Erethizon dorsatum*], perritos de pradera [*Cynomys* spp.]) que crean, modifican significativamente, o destruyen el hábitat alterando la estructura y función del ecosistema, e incrementando de este modo la heterogeneidad del hábitat y su biodiversidad. La extensa influencia que los mamíferos ejercen en los ecosistemas, resulta en servicios importantes que contribuyen al bienestar humano, como la polinización, el control de plagas, y la bioturbación de suelos. La disminución rápida de la abundancia de muchas poblaciones de mamíferos y el consecuente aumento del riesgo de extinción, son consideraciones alarmantes en cuanto a la conservación de mamíferos. Los científicos deberían de ocuparse del estado actual de los mamíferos y aunar esfuerzos para su conservación, de modo a mantener la biodiversidad de mamíferos y los procesos cruciales que ellos proporcionan a los ecosistemas. Con este trabajo se proveen varias ideas y una sinopsis acerca del papel ecológico de los mamíferos y se enfatizan preguntas claves para las futuras investigaciones para la conservación de mamíferos.

Key words: ecosystem engineers, ecosystem function, ecosystem services, energetics, nutrient cycling, pest control, pollination, seed dispersal

Lee R. Dice presented an annotated list of the mammals of southeastern Washington State in the first issue of the *Journal of Mammalogy* (Dice 1919). In this article, he addressed the relationship of a number of mammal species with the landscape and associated plant communities, with other species of mammals, and with humans. He observed the role that American beavers play, noting “they are even of some value to the agriculturist in helping to stop with sticks and mud the leaks in brush dams commonly placed in the river to divert water for irrigating ditches.” The language at the time of publication was informal, more like popular natural history writing, but it showed an appreciation of the roles of mammals in an ecosystem, and even the services that they provide to humans.

The concept of the ecosystem grew out of the work of such early natural historians, as they began to explore the complex interactions revealed by detailed natural history studies. Contemporary ecosystem ecology seeks to describe the patterns of species structure in ecosystems and the mechanisms or processes associated with these patterns (Hooper et al. 2005), and show how various biotic and abiotic components interact in driving large-scale processes. Research activities include detailed investigations of subsystems, focused on topics like competition, food webs, and predator-prey relations, to gain insights into mechanistic aspects that underlie ecosystem function, processes that occur in a temporal and spatial continuum within ecosystems (Ricklefs 2008).

Ecosystem ecologists seek to understand the contributions of species to ecosystem processes. Ecologists frame function in terms of emergent properties of interacting species and the physical and chemical components of systems that generate large-scale processes like net primary productivity, nutrient cycling, and hydrological dynamics. The contributions of individual species are categorized through the assignment of functional traits related to their ecological role, and assessment of how these traits govern ecosystem

function, including the redundancy of functions within a system (Loreau et al. 2001).

The critical role of mammals in mediating ecosystem processes has emerged from recent research. We understand the importance of biodiversity to ecosystem function (Kinzig et al. 2002), and the significant role that mammals play in ecosystems (Estes et al. 2011; Davidson et al. 2012; Ripple and Beschta 2012). We attribute much of this to the diversity of form and function of mammals. Mammals range from small (< 2 g, Etruscan shrew) to large (nearly 140,000 kg, blue whale) and may be short- (< 1 year for many shrews) or long-lived (over 200 years for bowhead whales, *Balaena mysticetus*). Some are highly restricted habitat specialists, like the Chachalero viscacha rat (*Tympanoctomys loschchalerorum*), which is limited to shrublands bordering a small complex of salt flats in Argentina, while the geographic ranges of others, like the puma, extend across multiple continents. The largest mammalian herbivores and carnivores are energy-intensive organisms, and are among the most conspicuous animals in terrestrial and marine ecosystems. Gaining clarity about how community structure shapes ecosystem processes (Morris et al. 1989) has helped to better implement management and conservation actions in the face of the anthropogenic degradation of landscapes (Hoffmann et al. 2010).

Mammals are severely affected by habitat loss, overexploitation, and invasive species (Schipper et al. 2008), and now increasingly by the threat of climate change (Pacifi et al. 2017). Current trends in the decline of mammalian populations (Ceballos et al. 2017), dramatic losses in range and population size of primates (Estrada et al. 2017), and the ongoing worldwide collapse of carnivore (Ripple et al. 2014a) and herbivore (Ripple et al. 2015) populations, all elevate the risk of extinction of many species of mammals. This decline also compromises the functions that they perform and the valuable ecosystem services that they provide. The *Millennium Ecosystem Assessment*

(2005) report defines ecosystem services as “the benefits people obtain from ecosystems.” It is impossible to discuss the role of mammals as key to ecosystem processes without being aware of the conservation challenges associated with preserving these services for human benefit.

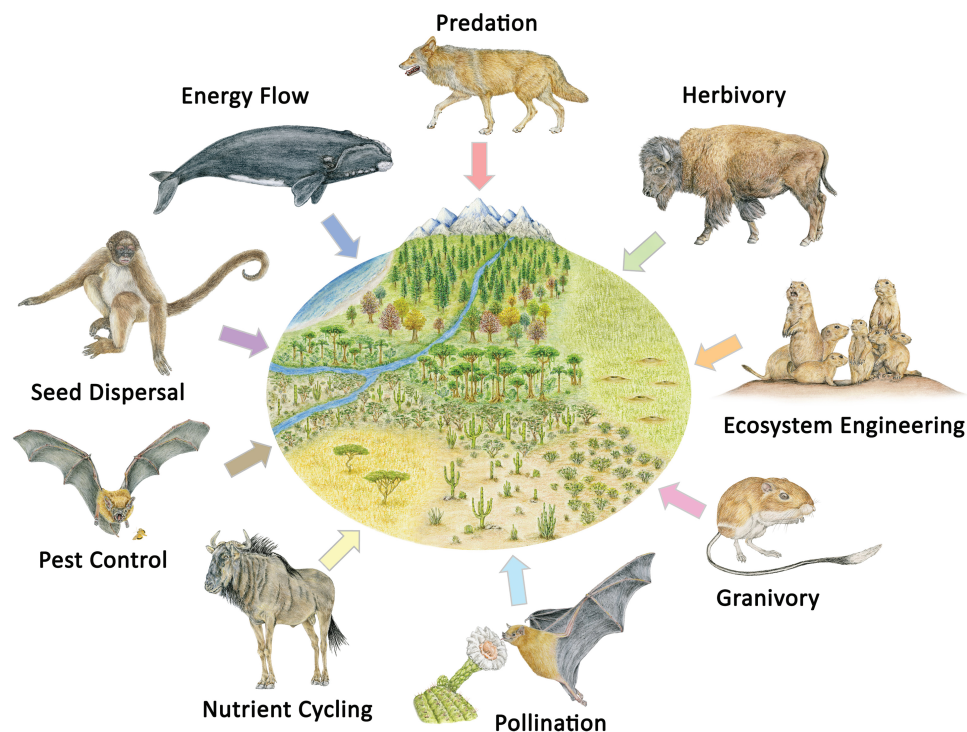
Here, we discuss the critical roles of mammals from an ecological perspective, focusing on key components of ecosystem functioning. Although these differ among regions and across terrestrial, marine, and aquatic systems, our emphasis is primarily terrestrial. We highlight examples and case studies for which years of research have illuminated the ecological roles of mammals, including cases where they act as keystone species, transforming landscapes and ecosystem-scale processes. Finally, we discuss the emerging conservation emphasis on the provisioning of ecosystem services and the role of mammalian conservation in preserving those processes. Using insights derived from a review of current literature, we highlight critical research needs and propose future research directions that will improve understanding of the functional role of mammals in ecosystem processes.

### FOOD-WEB DYNAMICS, ECOSYSTEM ENGINEERS, AND KEYSTONE SPECIES

Many species of mammals transform and shape the ecosystems in which they occur through a diversity of ecological pathways (Fig. 1). Mammalian predators and herbivores influence ecosystem structure and functioning through the consumption of prey (Ripple et al. 2014b, 2015). Mammalian ecosystem

engineers physically modify their environment, such as through the construction of burrows, digging of soil pits, or creation of dams (Jones et al. 1994). The trophic or engineering effects of some of mammal species are so large that they are considered keystone species whose effects are not only disproportionately large relative to their abundance, but are functionally irreplaceable (Power et al. 1996).

*Alteration of food-web dynamics.*—Apex predators, such as wolves, pumas, and sea otters, are among the best-studied predators whose activities affect all trophic levels (Beschta and Ripple 2009; Eisenberg 2010; Ripple et al. 2014a, 2014b). Research from the Greater Yellowstone Ecosystem illustrates how wolves, removed in the late 1800s and then reintroduced, regulate the abundance of elk (*Cervus elaphus*) populations, and consequently reduce herbivory on riparian vegetation. This regulatory role is important for maintaining riparian vegetation, such as willows (*Salix* spp.), aspens (*Populus tremuloides*), and cottonwoods (*Populus* spp.), that American beavers use for building dams and that riparian birds and other animals use for habitat or forage (Ripple and Beschta 2012; Beschta and Ripple 2016). Although reintroduction of wolves has reduced elk populations with consequent increases in woody plants and herbaceous forage that benefits American beavers, American black bears (*Ursus americanus*), and American bison, Yellowstone ecosystem recovery remains in the early stages (Ripple and Beschta 2012; Ripple et al. 2014b; Stier et al. 2016). Similar findings characterize the cascading effects of pumas on riparian ecosystems (Ripple and Beschta 2006). Apex marine predators also play important roles in regulating the abundance of



**Fig. 1.**—Mammals play important roles in all ecosystems performing a broad range of critical functions. The decline in abundance, local extirpation, or global extinction of mammals will have negative effects on ecosystem processes and will limit the number and amount of services these systems provide to human populations. (Drawings by Sharyn Davidson.)



their herbivorous prey (Steneck 2012; McCauley et al. 2015; Estes et al. 2016). Overharvesting of sea otters in California for fur resulted in dramatic increases in sea urchins, their primary prey, which overgrazed kelp forests (Estes et al. 2016). Loss of these kelp forests resulted in declines in many species that rely on them for habitat with consequent shifts in prey available for predators (Estes et al. 2016). Where kelp forests have been lost, seabird diets shift from fish to macroinvertebrates, and bald eagles (*Haliaeetus leucocephalus*) rely more heavily on seabirds as prey (Anthony et al. 2008; Estes et al. 2016). The restoration of sea otter populations has helped restore kelp forest ecosystems (Estes et al. 2016).

Large herbivores also affect ecosystems through consumption and trampling of vegetation, and by acting as key prey for apex predators (Frank et al. 1998; Ripple et al. 2015; Hobbs 2016). They play especially important roles in maintaining and creating grassland landscapes by preventing the encroachment of shrubs and trees (Frank et al. 1998; Goheen et al. 2010; Asner et al. 2016). Through their grazing, large herbivorous mammals create a low mat of vegetation characterized by grazing-tolerant species, and increase nutrient cycling rates (McNaughton 1984; Hobbs 2016). These grazing lawns occur in patches across the larger landscape, increasing heterogeneity, reducing fuel load and fire frequency, and providing habitat for animals that prefer shortgrass landscapes, including many species of mesoherbivores (Frank et al. 1998; Pringle 2008; Waldram et al. 2008). For example, grazing by white rhinoceroses (*Ceratotherium simium*) maintains patches of short grass that provide preferred habitat for blue wildebeests (*Connochaetes taurinus*) and zebras (*Equus* spp.—Waldram et al. 2008). African elephants play important roles in converting woodland to shrubland, which provides browsing habitat for impalas (*Aepyceros melampus*) and black rhinoceros (*Diceros bicornis*), facilitates predation by apex predators, and provides structural habitat for lizards (de Boer et al. 2015; Hobbs 2016). Similarly, American bison expand and maintain grasslands in North America, creating preferred open grassland habitat and higher quality forage for animals like prairie dogs (Knapp et al. 1999). The heterogeneous patches of grazed habitat alter fire regimes and structure grasshopper communities (Sinclair 1975). In addition, American bison wallows create small ponds across the grassland landscape that provide important habitat for amphibians and arthropods (Knapp et al. 1999; Gerlanc and Kaufman 2003; Joern 2005). Following the reestablishment of locally extirpated large herbivores within savanna grasslands in Kruger National Park, white rhinoceros grazing increased the presence of grazing lawns by up to 20-fold (Cromsigt and te Beest 2014). Experimental exclusion of large African herbivores revealed a breakdown of a critical ant-*Acacia* tree mutualism by reducing the carbohydrate rewards to protective ants, which resulted in reduced growth and survival of *Acacia* trees central to African savanna ecosystems (Palmer et al. 2008).

**Impacts of burrowing mammals.**—Many small- to medium-sized burrowing mammals influence the structure and functioning of ecosystems through herbivory, ecosystem engineering (mound building, burrowing, digging, and clipping

of vegetation), and serving as important prey for predators (Davidson et al. 2012; Root-Bernstein and Ebensperger 2013). Burrowing mammals range from solely fossorial to semifossorial (Supplementary Data SD1). Burrowing mammals occur in most terrestrial ecosystems, and are especially ubiquitous in grassland and desert ecosystems. Their burrow mounds dot landscapes, and range in size and shape from open areas surrounding pika (*Ochotona* spp.) burrows ( $\leq 0.5 \text{ m}^2$ ), to aboveground soil mounds of  $\leq 0.5\text{--}3 \text{ m}^2$  around prairie dog, marmot (*Marmota* spp.), and ground squirrel (*Ammospermophilus*, *Spermophilus*, *Uroditellus* spp.) burrows, to  $15\text{--}65 \text{ m}^2$  soil mounds created by wombats (*Vombatus ursinus* and *Lasiorhinus* spp.) and bettongs (*Bettongia lesueuri*), and plains vizcacha (*Lagostomus maximus*) mounds that are  $300\text{--}700 \text{ m}^2$  with up to 100 burrow entrances (Davidson et al. 2012; see Supplementary Data SD1). A common feature of burrow mounds is that vegetation and soil properties on or immediately surrounding them differs in composition and structure from adjacent areas (Davidson et al. 2012; Clark et al. 2016) which increases habitat heterogeneity and provides unique habitat for animals (Davidson and Lightfoot 2006; Yoshihara et al. 2009, 2010). Burrows provide key three-dimensional habitat, especially lacking in grasslands, and serve as critical homes and belowground shelter for numerous vertebrates and invertebrates (Davidson et al. 2012; Root-Bernstein and Ebensperger 2013; Šklíba et al. 2016). Although many burrowing mammals are herbivores and are key prey for predators, others are omnivores or carnivores, and lack the direct impacts of herbivory. However, these species (e.g., badgers [Melinae and Taxideinae], aardvarks [*Orycteropus afer*], and numerous species of foxes and armadillos) similarly alter landscapes through the construction of their burrows and mounds (Whittington-Jones 2007; Desbiez and Kluyber 2013; Root-Bernstein and Ebensperger 2013; Kurek et al. 2014). Excavations made by giant armadillos (*Priodontes maximus*) in the Brazilian Pantanal wetland create resources benefiting 24 other vertebrate species (Desbiez and Kluyber 2013).

Some burrowing mammals are solitary, like kangaroo rats (*Dipodomys* spp.), whereas others are highly social and live in large colonies, such as prairie dogs, plains vizcachas, and plateau pikas (*Ochotona curzoniae*; Supplementary Data SD1). Black-tailed prairie dogs (*Cynomys ludovicianus*) in North America's central grasslands are probably the best-studied semifossorial, colonial rodent, and provide a good example of the ecological impacts of burrowing, colonial rodents (Whicker and Detling 1998; Kotliar et al. 2006; Davidson et al. 2012). Black-tailed prairie dog colonies represent islands of open grassland habitat dotted with mounds that attract grassland animals that prefer open grassland habitat (e.g., mountain plovers, *Charadrius montanus*) and utilize burrows for homes or shelter (e.g., burrowing owls, *Athene cunicularia*—Davidson et al. 2012; Ray et al. 2016). Prairie dogs maintain grasslands by clipping shrubs and consuming their seedlings (Ceballos et al. 2010; Ponce-Guevara et al. 2016). Their activities also increase water infiltration rates, ground water recharge, soil stability, and soil carbon storage within colonies (Martínez-Estévez et al. 2013). Prairie dogs provide high density, localized, and reliable

prey for numerous predators, such as badgers, kit and swift foxes (*Vulpes macrotis* and *V. velox*), coyotes (*Canis latrans*), black-footed ferrets (*Mustela nigripes*), and numerous raptors (Kotliar et al. 2006; Davidson et al. 2012). The role of prairie dogs, especially black-tailed prairie dogs, in shaping grassland ecosystems in North America is so significant that they are considered keystone species (Kotliar et al. 2006; Davidson et al. 2012). The decline of black-tailed prairie dogs by about 98% across their range is due to sylvatic plague (introduced from Asia), poisoning and shooting to reduce their purported competition with livestock, and widespread habitat loss. This decline has resulted in cascading losses in populations of animals that associate with them and in shrub encroachment into grasslands (Kotliar et al. 2006; Eads and Biggins 2015; Ponce-Guevara et al. 2016). Similarly, poisoning of plateau pikas has resulted in dramatic declines in species that use their burrows and colonies for habitat or that rely on plateau pikas as prey, as well as in ecosystem services, such as large-scale reductions in water infiltration with likely impacts on watershed hydrological regimes (Lai and Smith 2003; Wilson and Smith 2014).

*Habitat modification in wetlands.*—American and Eurasian beavers (*Castor fiber*) are important ecosystem engineers (Wright et al. 2002; Bouwes et al. 2016). Beavers are semi-aquatic herbivorous rodents and are keystone species of riparian ecosystems (Janiszewski et al. 2014; Nummi and Holopainen 2014). They create wetland habitat by building dams that flood upstream areas, dramatically altering community structure and ecosystem functioning of ponds, streams, and surrounding riparian habitat (Naiman et al. 1988; Hood and Larson 2015). Through their herbivory, felling, and flooding of woody vegetation, beavers transform the riparian forest communities (Wright et al. 2002). The ponds they create increase habitat complexity, providing many animals with a greater diversity of habitats for breeding, rearing offspring, foraging, resting, and avoiding predation (Smith and Mather 2013; Nummi and Holopainen 2014; Zero and Murphy 2016). Because beaver ponds provide habitat that differs from the surrounding landscape, they support distinct communities of plants and animals, increasing beta and gamma biodiversity across the greater landscape (Wright et al. 2002). Beavers were extirpated throughout much of North America and Eurasia by the early 1900s, but their populations have been recovering, with cascading effects on riparian ecosystems (Bouwes et al. 2016).

Because ecosystem engineers and keystone species play such large roles in ecosystems, their restoration often lies at the core of conservation efforts (Davidson et al. 2018). Restoring mammals that play critical ecological roles, whether as top predators like wolves or ecosystem engineers like American beavers, has the benefit of restoring entire suites of associated species and ecosystem functions (Ripple and Beschta 2012; Beschta and Ripple 2016; Bouwes et al. 2016). However, because of their large, transformative ecological roles, keystone mammals are also often in conflict with humans, especially large predators that increasingly come into contact with humans who chose to live in exurban areas and suburbs that encroach on natural habitats. Consequently, many of their populations have

declined dramatically and their restoration often faces extreme resistance. Finding ways for mammals with especially important ecological roles to coexist with humans is one of the biggest challenges facing ecosystem restoration and conservation. Research is needed to uncover novel strategies for addressing the complex socio-ecological challenges in human–wildlife conflict that are at play across the globe.

## LANDSCAPE DYNAMICS OF MAMMALIAN MEGAFaUNA

Mammalian herbivores, carnivores, and plankton feeders are the largest extant animals, and often dominate various ecosystem-level processes, including energy flow, nutrient cycling, and vegetation dynamics because of their energy demands. However, in most parts of the world the mammalian megafauna is greatly impoverished compared to pre-Anthropocene faunas (Ripple et al. 2014a, 2014b). The best terrestrial examples of intact mammalian megafauna are found in savanna and woodland ecosystems of Africa, but the number and size of such locations decline each year (Hanks and Charlton 2003). These few systems testify to the impacts of large mammal communities mostly unaffected by recent extinctions, and provide insights on the functions lost because of Pleistocene or more recent extinctions and local extirpations, especially of mega-herbivores exceeding 1,000 kg in adult body mass.

*Functional roles of mammals across large landscapes.*—Some of the greatest impacts on landscape dynamics are driven by dispersal and migration of large mammals. Migratory herds of African elephants, American bison, buffalo (*Syncerus caffer*), and other bovids on land, and pinnipeds and cetaceans in the ocean, transfer nutrients and biomass across continents and oceans, and this movement shapes landscapes, seascapes, and freshwater environments.

Large herbivores play important functional roles through their dispersal and migration by transporting macronutrients across landscapes and fertilizing otherwise nutrient-poor habitats. In faunally intact communities, their movements operate as a landscape-scale pump for otherwise limiting nutrients (e.g., phosphorus, calcium, sodium) dispersed across sharp nutrient gradients, such as those between floodplains and inland areas (Doughty et al. 2016a). For example, hippopotamuses transfer significant inputs of dissolved organic carbon, nitrogen, and phosphorus, from savanna grassland ecosystems to rivers in sub-Saharan Africa (Subalusky et al. 2015). Estimated increases in nutrients in a segment of a river with hippopotamus populations compared to upstream sites were 670% for coarse particulate organic matter, 15% for dissolved organic carbon, and 25% for total nitrogen and total phosphorus. In the southern boreal forests on Isle Royale, moose (*Alces alces*) play a similar role, moving nutrients from freshwater to terrestrial ecosystems. They transfer large amounts of nitrogen from rivers to the surrounding terrestrial environment, which enhances nitrogen availability to riparian forests (Bump et al. 2009).

Whales move nutrients throughout the oceans by two different pathways: laterally during their migrations between

breeding and feeding areas, and vertically by moving nutrients from deep water to the surface, where they release them via feces and urine (Doughty et al. 2016b). Declines in abundance of some marine mammals between 66% and 99% in the past several hundred years have resulted in a loss of nutrient transport (Doughty et al. 2016b). Lateral transfer has declined dramatically, down to 14% of historical values in the North Atlantic and 2% in southern oceans. Vertical nutrient transport induced by once-abundant great whales also moves otherwise unavailable nutrients such as dietary iron from water columns into the oligotrophic photic zone where it can be metabolized by phytoplankton (Roman et al. 2014). Collapse of this nutrient pump following the decimation of large whales by the whaling industry likely has had severe consequences for the productivity of shallow marine waters (Roman et al. 2014). Declines in phosphorous transport are globally estimated at 23% of historical values and range from 28% in the North Atlantic to 16% in southern oceans (Doughty et al. 2016b).

Boreal forests and the arctic retain high densities of large mammalian herbivores, such as caribou (*Rangifer tarandus*) that graze and browse vegetation throughout their summer and winter ranges. Caribou can digest lichens and bryophytes, and these are essential resources during the winter; they shift to vascular plants and graminoids in the summer (Bernes et al. 2015). Grazing by large migratory caribou herds can shift the dominant vegetation from lichen-bryophyte communities to those dominated by grasses and sedges (Bernes et al. 2015). For example, grazing and trampling by caribou in the Rivière George herd of approximately 650,000 individuals in Québec and Labrador reduced plant productivity and shrub biomass on the summer range (Manseau et al. 1996). Lichen productivity on grazed summer range was only 6% of that on comparable ungrazed sites, and vascular plant productivity was suppressed by 25% on grazed sites.

Landscape-level effects of large herbivores change in concert with climatic variation and warming trends. Shrub biomass in the Arctic is increasing with warming. The functional role of mammalian herbivores, in this case caribou, is interacting with functional traits of different species of expanding shrub populations. Caribou forage heavily on more-palatable shrub species like willow (*Salix glauca*) and non-resinous birch (*Betula nana* ssp. *nana*) and avoid alder (*Alnus viridis*), a resinous birch (*Betula nana* ssp. *exilis*), and a number of palatable evergreen species that have more effective chemical defenses (Christie et al. 2015). Differential foraging impacts ultimately influence which shrub species dominate across the arctic tundra (Christie et al. 2015). Additionally, sea ice loss caused by climate warming has caused local warming in adjacent terrestrial areas, increasing plant biomass across the summer ranges of caribou and promoting shrub expansion (Fauchald et al. 2017). Caribou abundance has declined in parts of their summer ranges where a decline in high-quality forage has occurred, associated with the expansion of less-palatable shrubs (Fauchald et al. 2017).

Many plant–herbivore interactions and processes over large landscapes will change in potentially unforeseen fashions, especially for large migrations that interact with vegetation

over large spatial scales. Future research is needed to increase our predictive understanding of the interactions between climate change, plant productivity, landscape dynamics, and large herbivores.

*Functional roles of large mammals in African savannas.*—The most distinctive feature of Africa's large mammal fauna is the abundance and richness of grazing ruminants (Owen-Smith 2013). This is related to the prevalence of grassy savanna ecosystems in the seasonally dry environments that predominate over much of Africa. These savannas include iconic megaherbivores, such as African elephants, white and black rhinoceroses, hippopotamus, and comparatively smaller herbivores such as blue wildebeest, plains zebra (*Equus burchellii*), and Thomson's gazelle (*Gazella thomsonii*—Owen-Smith 1988). They play important roles in moving nutrients across the landscape.

The largest amount of vegetation consumed by large herbivores in Africa's savannas occurs in two circumstances. One is in places characterized by a high abundance of browsing (African elephant) and grazing (hippopotamus or white rhinoceros) megaherbivores, along with numerous smaller grazing ruminants (e.g., Queen Elizabeth and Murchison Falls National Parks in Uganda, or Hluhluwe-iMfolozi Park in southeastern South Africa; Supplementary Data SD2). The other circumstance is in places with high abundances of smaller migratory grazers such as blue wildebeest, plains zebra, and Thomson's gazelle. The Serengeti ecosystem (28,000 km<sup>2</sup>) in Tanzania is a prime example, with 1.3 million migratory blue wildebeest, 200,000 plains zebra, 300,000 Thomson's gazelle, as well as numerous other antelopes and buffalo, but with relatively few African elephants and hippopotamuses because of the lack of major rivers and lakes (Hanks and Charlton 2003).

Large herbivores in savanna ecosystems like the Serengeti play a key role in nutrient cycling of plant biomass, processed through their gut. Bacterial fermentation within the rumen or colon of a large herbivore occurs more rapidly than does decomposition by soil organisms, and continues year-round without being depressed by cold or dry conditions. This enhances rates of nitrogen and phosphorus release back into the soil via dung and urine to promote further plant growth across the savanna landscape. Large and small herbivores have different relative contributions to energy flow and nutrient recycling as a consequence of mass-specific metabolic rates. Large herbivores, like African elephants and hippopotamuses, have slower metabolic rates and lower rates of consumption compared to smaller herbivores like Thompson's gazelles that have faster metabolic rates. The relative amount of food consumed per unit of biomass diminishes with body mass according to a power relationship with an exponent of  $-0.25$ . As a consequence, small antelopes consume about 3.5% of their body mass per day, whereas African elephants consume daily only ~1% of their body mass as dry body mass relative to live weight body mass (Owen-Smith 1988). This allometric relationship can be used to transform herbivore biomass into the resultant uptake of plant biomass by grazers versus browsers or megaherbivores versus smaller ungulates, and localities can be thus compared if the local fauna has remained relatively intact.



To estimate the effect of consumption by assemblages of large herbivores on nutrient cycling at larger scales, consumption needs to be related to annual production of vegetation. Annual production of aboveground grass typically amounts to 500–1,000 kg km<sup>-2</sup> per mm of annual rainfall in African savanna ecosystems (Deshmuck 1984). Combined levels of offtake by large herbivores in the most densely occupied ecosystems total less than 20% of total annual aboveground production by grass. However, within short-grass lawns that mega-grazers such as white rhinoceroses and hippopotamuses cultivate, almost all grass is cropped, so most nutrients there are cycled locally via dung and urine. Browsers consume a much smaller fraction of foliage production by trees because much of it remains out of reach of herbivores and most African savanna trees shed their leaves during the dry season. In systems with strongly seasonal growth of vegetation, the mean proportion of vegetation consumed is not a meaningful annual indicator of nutrient cycling, since most of the available vegetation is consumed by the late dry season and only grass stubble prevails over vast areas. Thus, estimates of nutrient cycling based upon consumption must consider the relative contributions of various functional groups as well as variation in primary production throughout the year.

Fire is an ecologically important process in savannas, and locally high levels of consumption of vegetation suppress the spread of fires (Owen-Smith 1988; Waldram et al. 2008). Within the Serengeti, growth of the migratory blue wildebeest population has reduced the extent of the landscape that is burned annually from  $\geq 90\%$  to  $< 50\%$  (Eby et al. 2015). Grass incinerated by fire loses some nitrogen content to the atmosphere, whereas this nitrogen is retained when processed through herbivore guts (De Mazancourt et al. 1998). By breaking branches or felling trees, African elephants contribute to the cycling of the mineral nutrients contained in these plants parts. However, these impacts on nutrient cycling are not evenly distributed in space. Similarly, hippopotamuses concentrate most of their grazing near rivers or lakes where they seek refuge during the day (Lock 1972). African elephants and water-dependent grazers become restricted to the proximity of perennial water sources during the dry season. Fires remain the major agent recycling vegetation biomass in regions remote from perennial surface water, and the combination of these processes results in complex patterns of nutrient cycling across the landscape.

We lack data on the relationship between soil properties and herbivore function. We need to enhance our understanding of the role that soil fertility (governed by geological parent material and leaching) plays in the rate of nutrient cycling by grazing herbivores. There is a strong interaction between soil nutrient status and rainfall in controlling plant growth, and for a given level of precipitation, soils with high nutrient availability can support about 20 times the biomass of large grazing ungulates (Fritz and Duncan 1994). Clay particles can retain cations against leaching, but phosphorus is the most widely limiting nutrient for animal production in African savannas (Pellegrini 2016); it is less available in coarse sedimentary deposits than in basic igneous rocks. Sodium is especially attractive to

herbivores because of its deficiency in most plants (Seagle and McNaughton 1992). Finer-textured soils that allow less water infiltration, and hence greater evaporation, retain more sodium than do coarse-grained sands. How changing climate through increased temperature (and drought) and alterations in the pattern and amount of precipitation will alter the availability of soil micronutrients affecting plant nutritional quality and herbivore diversity and abundance is a critical area of research.

If wild herbivores are missing or depauperate in diversity or abundance across large landscapes, this will impact energy flow and nutrient cycling. This is currently the case in northern Eurasia or the Americas, where all megaherbivores and most grazers have been eliminated. The biomass attained by free-ranging domestic herbivores where native megaherbivores have been extirpated matches that exhibited by diverse wild ungulate assemblages in Africa only where mean annual rainfall approaches 1,000 mm (Fritz and Duncan 1994). The role of mammalian herbivores in nutrient cycling and subsequent restructuring of vegetation and their cascading impacts is quite large. Loss of large herbivores on other continents and their replacement by domestic livestock has likely also resulted in major shifts in ecosystem structure and function, resulting in the altered communities that we see today. To understand the large-scale processes of nutrient cycling across much of the planet, we need to develop a new research paradigm where agropastoral systems are considered the major ecological drivers.

## REGULATION OF INSECT PEST POPULATIONS

Bats are voracious feeders of night-flying insects. High mass-specific metabolic rates put large energetic demands on bats during their active periods (Speakman and Thomas 2003). Field studies of feeding rates and daily energy budgets suggest that individual bats typically consume the equivalent of 1/4 to 2/3 of their body mass in insects each night, with these demands peaking during reproduction (Kunz et al. 1995). Extrapolation from numbers of bats feeding over landscapes has led to impressive estimates of the numbers (billions of individuals) and mass of insects (1,000s of tons) eaten nightly by large populations of bats (Lee and McCracken 2005; Leelapaibul et al. 2005). We now have a clearer understanding of the diets of insectivorous bats and whether this might affect pest insect populations, or associated ecosystem services.

The first anecdotal attributions that feeding by bats might reduce insect populations and protect crops date from nearly a century ago (Allen 1939:78–82). Visual inspection of insect fragments in feces has informed us on what bats eat; however, the approach is labor-intensive, has limited taxonomic resolution, and is biased against recovery of rare, very small, or soft-bodied insects (Whitaker et al. 2009). Difficulty of identification is increased because bats often cull the hardest and most diagnostic parts of insects before consuming them (Gardner 1977). By counting body parts recovered in fecal pellets, Whitaker (1995) estimated that between April and October, a colony of 150 big brown bats (*Eptesicus fuscus*) in Illinois would consume about 600,000 cucumber beetles (*Diabrotica*

spp.) and presented this as evidence that *E. fuscus* is an important biological control agent for cucumber beetles and other crop pests; it is unclear if this level of consumption regulates cucumber beetle populations. Analyses of stomach contents can reveal detailed information on diet but is lethal and not recommended (Whitaker et al. 2009). More recent studies of bat diets have utilized polymerase chain reaction (PCR) to amplify insect gene sequences to identify prey from fecal DNA. This approach has vastly improved taxonomic resolution. Clare et al. (2009) matched DNA sequences amplified from the culled body parts of insects to identify a total of 127 arthropod species in the diet of red bats (*Lasiurus borealis*). Automated meta-barcoding techniques now employ mass extraction of DNA from guano samples to reveal the incredible diversity in the diets of bats; they typically identify 100s of species of prey belonging to diverse arthropod taxa (e.g., Zeale et al. 2011; Clare et al. 2014). PCR primers were developed for the mitochondrial cytochrome oxidase (COI) gene for meta-barcoding studies of bat diets (Zeale et al. 2011). This allows for the identification of insects in the diet and provides data on numbers of sequence reads for each identified food item. Recent work argues that relative sequence reads can provide information on proportional abundance of dietary items (Deagle et al. 2018). Nonetheless, quantitative interpretation of how many or what proportion of an animal's diet comprises any particular prey species has been elusive in molecular studies (Deagle et al. 2018), including alternative approaches employing quantitative PCR to amplify targeted pest species (McCracken et al. 2012). Both traditional and molecular studies of bat diets show that bats are opportunistic consumers. Diets differ among species (Whitaker 1995; Clare et al. 2014), the diet of a particular species can differ markedly in time and space (Whitaker et al. 1996; Lee and McCracken 2005; Clare et al. 2013), and different cohorts of bats within populations may eat different types of insects (Johnston and Fenton 2001; Mata et al. 2016). These studies concur that insectivorous bats are generalist predators and that variation in diet reflects prey availability and differences among bats in foraging behaviors rather than in food specialization per se.

It is uncertain if insectivorous bats can exert sufficient predation pressure to regulate (control or suppress) insect populations. Favored agents for biocontrol of insect populations are specialist predators and parasitoids, and generalist feeders are thought to be ineffective in suppressing pest populations (i.e., as pest numbers decline, the predator will shift attention to more abundant prey—Knippling 1979). Nonetheless, insect-eating bats have been shown to provide significant services by reducing the impacts of insect pests on agricultural production and costs of pest control (Kunz et al. 2011; Boyles et al. 2013). As examples, Cleveland et al. (2006) estimated that Mexican free-tailed bats (*Tadarida brasiliensis*) provided services valued at \$121,000 to \$1,725,000 USD annually in limiting damage and costs of insecticides on cotton in an eight-county region in south-central Texas, and Federico et al. (2008) demonstrated that the agronomic impact of bats persists with the adoption of transgenic (*Bacillus thuringiensis*, Bt) cotton. Extrapolating

these services, the annual value of bats to all agriculture across the continental United States was estimated at between \$3.7 and \$53 billion USD (Boyles et al. 2011). In addition to estimates of avoided cost, replicated field experiments demonstrate that exclusion of bats from agricultural plots results in greater damage to crops by insects (Williams-Guillén et al. 2008; Böhm et al. 2011). Excluding bats from cornfields results in losses of more than \$1 billion USD globally for this crop alone (Maine and Boyles 2015). Worldwide, insect-eating bats make huge contributions with regard to increased crop yields (Leelapaibul et al. 2005; Maas et al. 2013; Puig-Montserrat et al. 2015), reduced need for pesticides and enhanced ecosystem integrity (Maas et al. 2013; Puig-Montserrat et al. 2015), and increased food security (Wanger et al. 2014). In addition, the value of these contributions changes in space and time in response to market forces and shifting agricultural practices (López-Hoffman et al. 2014). The services that insectivorous bats provide are cogent arguments for bat conservation (Wiederholt et al. 2014; Maine and Boyles 2015).

Generalist predators can be effective as biological control agents if they 1) persist on alternative prey when pest numbers decline, and 2) recruit rapidly to exploit resurgent pest numbers (Symondson et al. 2002). Their dietary opportunism, high metabolic demands, ability to swiftly travel long distances, and longevity (Wilkinson and South 2002) suggest that bats fulfill these requirements. Despite assertions that bats might affect vectors of West Nile or Zika viruses, with the exception of reducing fungal infections in corn (Maine and Boyles 2015), no evidence conclusively documents that bats mitigate insect-borne diseases or regulate or control populations of any insect species. However, the apparent threat of foraging bats may reduce oviposition in mosquitoes (Reiskind and Wund 2009), and recent molecular analysis of the diet of little brown bats (*Myotis lucifugus*) reveals higher prevalence of mosquitoes in their diet than previously documented, including consumption of nine species of mosquitoes known to be vectors of West Nile virus (Wray et al. 2018). Carefully designed studies of the impacts of bats on insect-borne diseases are an important emerging area of research, especially in light of climate change and the expansion of certain tropical diseases.

## MAMMAL–PLANT INTERACTIONS

*Pollination services.*—Most flowering plants (angiosperms) rely on animals as pollinators to maintain fitness and genetic diversity and improve resilience to environmental change through enhanced gene flow. Animals pollinate 78% of plant species within temperate-zone communities and up to 94% in tropical communities (Ollerton et al. 2011). Animals that pollinate plants include insects, birds, and mammals, and they serve as mobile links among plant populations, sometimes facilitating pollen and gene flow over considerable distances. A total of 355 mammal species have been reported to visit flowers to feed on nectar and pollen, either as their main diet source or in an opportunistic manner (Fleming and Kress 2013; Regan et al. 2015).



Morphologically and behaviorally specialized nectar-feeding mammals occur in only two orders, representing three of the 154 families and 64 species of terrestrial mammals listed by Wilson (2009). Of the 64 species, most are bats (Table 1). Additional species of pteropodid, phyllostomid, and vespertilionid bats (e.g., species of *Pteropus* spp., *Artibeus* spp., and *Antrozous pallidus*, respectively) can be effective pollinators despite being opportunistic flower visitors (reviewed in Fleming and Kress 2013; Frick et al. 2013; Aliperti et al. 2017). Nonflying mammals such as marsupials, primates, rodents, and small carnivores also visit flowers (Fleming and Kress 2013). Nonetheless, pollination effectiveness (i.e., sufficient transfer of pollen to receptive stigmas) of many of these species is still questionable because these mammals often damage flowers as they feed (Fleming and Sosa 1994).

Plants have evolved flower traits called pollination syndromes that reflect convergent adaptation for pollination by particular types of animals (Fenster et al. 2004). Nectar-feeding mammals generally select large flowers with large nutritional rewards. A well-documented pollination syndrome, chiropterophily, involves the adaptation of flowers to attract bats, which are the most common nectar-feeding mammals that effectively pollinate plants (Tschapka and Dressler 2002).

The evolution of bat pollination in tropical and subtropical plants from a phylogenetic and biogeographical perspective for both plants and bats was reviewed by Fleming et al. (2009). Pollination and nectar-feeding are common in only two of the 20 currently recognized families of bats: Pteropodidae (megabats), which occur throughout tropical and subtropical regions of Africa, including Madagascar, Asia including Indonesia, Australia, Papua New Guinea, and Pacific islands; and Phyllostomidae, which inhabit tropical and subtropical regions of the Americas. Flower-visiting phyllostomid species occur in two closely related subfamilies: Glossophaginae and Lonchophyllinae (Supplementary Data SD3). Only six genera and 11 species in Pteropodidae are morphologically specialized for flower visiting, and they represent three clades (two in Asia and one in Africa—Giannini and Simmons 2005; Supplementary Data SD3). Specialized nectar-feeding bats in these families share a common set of morphological features, including an elongated rostrum, dentition that is reduced in size and number of teeth, and a long tongue that is tipped with hair-like papillae, which are used to collect nectar rapidly during brief flower visits. Flower-visiting pteropodids lack echolocation, and differ from phyllostomids with respect to body size (pteropodids are larger), rostral and tongue lengths relative to

**Table 1.**—Summary of mammal groups documented to visit flowers. Families with specialized nectar-feeding species are shown in bold font. Data from Fleming and Kress (2013), Frick et al. (2013), and Regan et al. (2015). Threatened species include IUCN Red List categories: Critically Endangered, Endangered, and Vulnerable (IUCN et al. 2008).

Order	Family	Genera	Species	Threatened species ( <i>n</i> )
Carnivora	Procyonidae	3	3	0
	Viverridae	1	1	0
	Cetartiodactyla	1	1	0
Chiroptera	Mystacinidae	1	1	0
	Pteropodidae (part)	15	105	28
	<b>Pteropodidae (part)</b>	6	12	12
	Phyllostomidae (part)	14	79	6
	<b>Phyllostomidae (part)</b>	19	51	6
	Vespertilionidae	1	1	0
	Dasyuridae	5	12	3
Dasyuromorphia	Didelphidae	4	6	0
Didelphimorphia	Acrobatidae	1	1	0
Diprotodontia	Burramyidae	2	5	1
	Petauridae	1	3	1
	Phalangeridae	1	3	0
	Pseudocheiridae	1	1	0
	<b>Tarsipedidae</b>	1	1	0
	Macroselididae	1	2	0
	Macroselidae	1	2	0
Primates	Aotidae	1	2	1
	Atelidae	3	3	2
	Callithricidae	2	2	1
	Cebidae	4	9	2
	Cercopithecidae	6	9	2
	Cheirogaleidae	4	7	0
	Daubentoniidae	1	1	0
	Galagidae	1	1	0
	Lemuridae	2	6	4
	Lorisidae	2	2	1
	Cricetidae	3	3	0
	Gliridae	1	1	0
	Muridae	9	11	0
Rodentia	Platacanthomyidae	1	1	1
	Sciuridae	5	7	0
	Scandentia	2	2	0
		125	355	71
TOTAL				

overall size (greater in phyllostomids), and foraging behavior when approaching flowers for feeding (phyllostomids typically hover, whereas pteropodids usually land on flowers before feeding—[Fleming et al. 2009](#)). These two families have different evolutionary histories ([Supplementary Data SD3](#)).

One nonvolant mammal is a specialized flower visitor, the Australian honey possum (*Tarsipes rostratus*). It is an important pollinator of *Banksia* spp. (Proteaceae), a common tree in on the southern coast of Western Australia ([Wooller et al. 1993](#)). Although not specialized flower visitors, several murid rodents in South Africa (e.g., *Acomys subspinosus* and *Micaelamys namaquensis*) are dedicated flower visitors and likely are effective pollinators (e.g., [Johnson et al. 2001](#); [Kleizen et al. 2008](#)).

Pollination is a regulating service and can have a significant economic impact. Because the definition of ecosystem services implies benefits for people, the main aspects of pollination that have been considered are those related to crop production. A global initiative, the Economics of Ecosystems and Biodiversity (TEEB), presented estimates of the importance of pollination services to people and indicated that about 70% of the world's crop plants, as well as many plants that are sources for pharmaceuticals, rely on pollination by animal vectors, especially bees ([TEEB 2010](#)). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) report emphasized the need for focused conservation initiatives on plant–pollinator complexes ([IPBES 2016](#)).

The role of mammals as pollinators has been recognized widely, but the link to its economic value has seldom been studied in detail (e.g., [Fujita and Tuttle 1991](#); [Bumrungsri et al. 2009](#)). As a first step, it is necessary to understand the geographic distribution of nectar-feeding mammals worldwide

to identify links to the potential services that they provide within agricultural landscapes. Specialized nectar-feeding mammals, primarily bats, are important pollinators of several tropical crops ([Table 2](#)). Human-valued plants with chiropterophilous flower traits occur in the Agavaceae, Bignoniaceae, Bromeliaceae, Cactaceae, Fabaceae, Gesneriaceae, Malvaceae, Musaceae, Myrtaceae, Sapotaceae, and Solanaceae ([Kunz et al. 2011](#)). Nonetheless, estimates of the economic value of pollination services provided by mammals to species in these families are difficult to quantify for two main reasons: 1) lack of information about the economic value of many crops, and 2) lack of detailed knowledge about the actual contribution of mammals to the pollination of crops with economic value. In addition to direct economic benefits, mammalian pollinators also provide indirect ecological services whenever they help to maintain plant populations that are often important species within ecosystems. Those plants contribute to ecosystem functionality, as they are a food source for herbivores, especially during times of scarce resources.

Given the importance of bat-mediated pollination, a number of conservation concerns are related to specialized nectar-feeding bats. Some bats migrate annually between a series of landscapes and over considerable distances (e.g., some *Leptonycteris* migrate > 1,200 km, one-way), and these movements are driven by the availability of flower resources ([Fleming and Kress 2013](#); [Gomez-Ruiz and Lacher 2017](#)). These kinds of seasonal movements are known for glossophagine bats in Mexico, the United States, and Costa Rica. In pteropodids, migratory species occur in lowland Malaysia and in the eucalypt forests of eastern and northern Australia ([Kunz et al. 2011](#)). The conservation concern is that most of the foraging areas along

**Table 2.**—Examples of economically and ecologically important plants that are pollinated by bats. Data from [Kunz et al. \(2011\)](#) and [Fleming and Kress \(2013\)](#).

Family or subfamily	Taxon	Comments
Economically important plants		
Agavaceae	<i>Agave</i> , subgenus <i>Agave</i>	Paniculate agaves such as <i>A. tequilana</i> are used to make tequila, mescal, and bacanora with high economic value; leaf fibers are used as sisal
Cactaceae	Many genera in tribe Pachycereeae, subfamily Cactoideae	Native populations in the southwestern United States 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
Caryocaraceae	<i>Caryocar</i>	Many species have seeds that are oil sources in tropical America; inner bark of <i>C. glabrum</i> (soapwood) used for washing
Fabaceae, Mimosoidae	<i>Parkia speciosa</i>	Commercially important fruit species in Southeast Asia
Malvaceae, Bombacoideae	<i>Ceiba</i>	Fibers from fruits of <i>C. pentandra</i> and other congeners are used to make kapok
Malvaceae	<i>Ochroma</i>	Balsa, world's lightest commercial timber
Malvaceae, Helicteroideae	<i>Durio</i>	<i>Durio zibethinus</i> (durian) and several other congeners are cultivated for edible fruits and seeds in Southeast Asia and elsewhere in the tropics
Musaceae	<i>Musa</i>	Bananas, pteropodid bats pollinate flowers of wild bananas. Cultivated bananas have high economic value
Ecologically important plants		
Agavaceae	<i>Agave</i>	Many species of paniculate agaves are conspicuous members of arid upland habitats in the Neotropics
Cactaceae, Cactoideae	Many columnar cacti in several tribes of this subfamily	Columnar cacti are keystone species in many arid habitats of the Neotropics
Malvaceae, Bombacoideae	<i>Adansonia</i> , <i>Bombax</i> , <i>Ceiba</i> , <i>Pachira</i> , <i>Pseudobombax</i> , etc.	Trees are often dominant (in terms of basal area) members of tropical forests worldwide
Proteaceae	<i>Banksia</i>	Common tree on the southern coast of Western Australia, pollinated by honey possums ( <i>Tarsipes</i> spp.)

migration routes are not protected, and conservation strategies must entail multinational collaboration as these bats often move across international borders. Regan et al. (2015) studied global trends in the status of bird and mammal pollinators based on the Red List Index (Butchart et al. 2004) using data from 1996 and 2008, and suggested that mammalian pollinators are declining in status, with more species moving toward extinction than away from it. In the most recent mammal risk assessment (IUCN et al. 2008), a total of 71 flower-visiting mammal species are endangered, including 18 (28%) of the specialized nectar-feeding mammal species (Table 1). We need to support studies that clarify the impact of the declines in pollinator species on reductions in genetic diversity in ecologically and economically important plants and reduced climate resilience of plant populations.

**Frugivory and seed dispersal.**—Frugivory and associated seed dispersal are the major mutualistic interactions that mammals have with their food plants. In this mutualism, plants provide fleshy fruits to attract frugivores, which provide dispersal of seeds. Unlike most mammalian nectar-feeders and pollinators, which are generally small, frugivores span the entire size range of terrestrial mammals, from 0.005-kg phyllostomid bats (e.g., *Ectophylla alba*) to 7,500-kg African elephants. Although many mammals, including some carnivores, eat fruit and disperse seeds, mammals whose diets are especially rich in fruits are mostly tropical in distribution and include at least 10 orders, 14 families, and about 600 species (Fleming and Kress 2013). The order Primates is notable because frugivory occurs in most of its species (Gómez and Verdú 2012). Primates play a critical role in the dispersal of the seeds of large fruits, yet are under increasing risk of extinction through severe population declines driven by habitat loss and overexploitation (Estrada et al. 2017). Frugivory is also common in two families of bats: Phyllostomidae (> 70 fruit-eating species), and Pteropodidae (> 160 fruit-eating species). Moreover, frugivory is primarily a tropical phenomenon because a majority of plant species there produce fleshy fruits whose seeds are dispersed by a wide variety of birds and mammals.

Angiosperms began to evolve fleshy fruits and to rely on vertebrates to disperse their seeds about 80 Ma (Eriksson 2016). After the extinction of multituberculate mammals in the Paleocene and Eocene, angiosperm fruit and seed size increased sharply and eutherians such as rodents and primates (both plesiadapiforms and euprimates) became important seed dispersers (e.g., Sussman et al. 2013). By mid-Miocene, essentially modern guilds of frugivorous birds and mammals, including bats, had evolved in concert with a diverse array of fruit types and sizes that occur throughout angiosperm phylogeny (Fleming and Kress 2013).

Fruit and seed size has played an important role in the coevolution of angiosperms and their interactions with fruit-eating seed dispersers. Cretaceous angiosperm plants, fruits, and seeds were small and thought to have been dispersed abiotically. Fruit and seed size diversity increased substantially during the early Paleogene, as angiosperms formed closed-canopy forests, which often favor the evolution of large seeds (Eriksson

2008). Single-seeded drupes were apparently more common than multi-seeded berries in these forests. The seeds of drupes are generally larger than those of berries (Leishman et al. 2000) and their prevalence in basal tropical forest angiosperms in the Paleocene and Eocene implies that relatively large-sized frugivorous mammals were in these forests because the body sizes of frugivorous birds and mammals are correlated positively with average size and size range of their fruit (Fleming and Kress 2013).

Fruit and seed size vary predictably as a function of successional stage and forest stratum in contemporary habitats. Early successional plants generally produce smaller fruits and seeds compared to plants associated with late successional stages, and canopy trees generally produce larger fruits and seeds (and a greater variety of propagule sizes) compared to understory plants (Leishman et al. 2000). Small-seeded fruits can be ingested easily by many frugivores of a wide range of body sizes, which gives such seeds a high degree of dispersability. In contrast, large-seeded fruits are most easily eaten by a more limited range of (large) body sizes, which gives such seeds more limited dispersability.

Contemporary assemblages of fruit-eating tropical mammals occur in three broad categories: 1) terrestrial species that are typically large, including species of caviomorph rodents (in the Neotropics), browsing ungulates (e.g., cervids, tragulids), gorillas, elephants, tapirs (*Tapirus* spp.), and rhinoceroses; 2) scansorial-arboreal species that are typically intermediate in size, including squirrels and primates; and 3) small bat species (Table 1). In general, Old World frugivores in each of these groups are larger than their New World counterparts (Table 3; Fleming et al. 1987). Currently, the terrestrial megafauna of mammals weighing > 1,000 kg is depauperate in the Neotropics compared to the Paleotropics, but this has not always been the case. For example, the megafauna in the Pleistocene of Central and South America included horses, gomphotheres, and ground sloths that were important dispersers of seeds found in large fruits of many plant families (Janzen and Martin 1982; Guimarães et al. 2008).

The diet breadths of mammalian frugivores generally are correlated with body size, and the diets of large species often include more fruit species than do those of small species. African and Asian elephants (*Elephas maximus*), for instance, have diets that include at least 350 and 100 fruit species, respectively (Harich et al. 2016), and certain large-seeded species in Africa such as *Balanites wilsoniana* (Zygophyllaceae; seeds are 8.8 cm long) and *Sacoglottis gabonensis* (Humiriaceae; seeds are 4 cm long) rely exclusively on African elephants for dispersal. No such exclusive relationship is yet known for Asian elephants (Harich et al. 2016). Similarly, the diets of eight species of primates in the Lope Reserve of Gabon contain 20–114 species of fruit, with western lowland gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*) eating many more fruit species than smaller cercopithecines (Tutin et al. 1997). In contrast, two well-studied species of phyllostomid bats with broad geographic distributions, *Carollia perspicillata* (18 g) and *Artibeus jamaicensis* (45 g), eat 13–24 and 10–16 species



**Table 3.**—Major mammalian families containing fruit-eating species in three tropical regions. Data from [Fleming and Kress \(2013\)](#) and [Nowak \(1991\)](#). Sc-Arb = scansorial-arboreal; Terr = terrestrial; Vol = volant. Number of species indicates number of fruit-eating species.

Region	Order and family	Foraging zone	Number of species	Range of body mass (kg)
Neotropics	Carnivora, Procyonidae	Sc-Arb	14	0.80–12.0
	Chiroptera, Phyllostomidae	Vol	70	0.005–0.090
	Perissodactyla, Tapiridae	Terr	3	180–320
	Primates, Aotidae	Sc-Arb	24	0.95–1.1
	Primates, Atelidae	Sc-Arb	24	8.0–12.1
	Primates, Cebidae	Sc-Arb	56	0.10–5.0
	Primates, Pitheciidae	Sc-Arb	10	2.0–3.0
	Rodentia, Dasyproctidae	Terr	13	1.3–12.0
	Rodentia, Echimyidae	Sc-Arb	90	0.039–0.700
African Tropics	Artiodactyla, Tragulidae	Terr	1	9.7–12.0
	Carnivora, Viverridae	Sc-Arb	1	2.1–5.0
	Chiroptera, Pteropodidae	Vol	25	0.020–0.42
	Perissodactyla, Rhinocerotidae	Terr	2	1,400–3,600
	Proboscidea, Elephantidae	Terr	2	To 7,500
	Primates, Cheirogalidae	Sc-Arb	21	0.098–0.60
	Primates, Loridae	Sc-Arb	11	0.125–2.0
	Primates, Lemuridae	Sc-Arb	19	2.5–4.5
	Primates, Indriidae	Sc-Arb	11	1.2–10.0
	Primates, Cercopithecidae	Sc-Arb	41	1.23–41.0
	Primates, Hominidae	Terr-Arb	4	50–275
	Rodentia, Anomaluridae	Sc-Arb	7	0.018–1.10
	Rodentia, Gliridae	Sc-Arb	14	0.018–0.030
	Artiodactyla, Tragulidae	Terr	3	0.7–0.8
	Carnivora, Viverridae	Sc-Arb	7	1.5–14.0
	Chiroptera, Pteropodidae	Vol	160	0.012–1.60
	Dermoptera, Cynocephalidae	Sc-Arb	3	1.0–1.8
Asian Tropics	Perissodactyla, Tapiridae	Terr	1	180–320
	Perissodactyla, Rhinocerotidae	Terr	3	1,000–2,200
	Primates, Loridae	Sc-Arb	3	0.085–2.0
	Primates, Cercopithecidae	Sc-Arb	16	2.50–15.0
	Primates, Hylobatidae	Sc-Arb	14	8.0–13.0
	Primates, Hominidae	Sc-Arb	1	50–90
	Proboscidea, Elephantidae	Terr	1	To 5,400
	Scandentia, Tupaiidae	Sc-Arb	19	0.060–0.35

of fruit, respectively, at localities throughout their ranges ([Fleming 1986](#)).

Despite typically broad diets, most mammalian (and avian) frugivores concentrate on particular core fruit families for the bulk of their diets. In the tropics, these families generally have long fruiting seasons, are species-rich, and are abundant in many habitats ([Fleming 1986](#)). Well-known core families for frugivorous phyllostomids include Piperaceae, Solanaceae, and Moraceae. Neotropical monkeys forage on Myristicaceae and Sapotaceae; African monkeys forage on Ebenaceae and Fabaceae; and African elephants forage on Euphorbiaceae and Rubiaceae (see [Fleming and Kress 2013](#) for a more extensive list of core plant families).

Although mammals eat many kinds of fruit, the issue remains about the effectiveness of different groups of frugivores as seed dispersers. In their review of the effects of mammalian mutualists on the reproductive success of their food plants, [Fleming and Sosa \(1994\)](#) noted that frugivores can affect plant reproductive success by allowing seeds to escape pre- and post-dispersal predators, by affecting the recruitment rate of new seedlings, and by enabling plants to colonize new habitats. This highlights three additional questions concerning frugivores and seed dispersal: 1) Are particular frugivores legitimate dispersers and do they treat seeds in germinable fashion? 2) Are frugivores efficient in depositing many seeds in good germination sites?

and 3) Are frugivores effective by accounting for most of the seedlings that become established?

The answer to the first question generally is yes. Experimental studies using many kinds of fruit-eating mammals (e.g., bats, primates, elephants) indicate that most species regurgitate or defecate seeds in germinable condition (e.g., [Heer et al. 2010](#); [Fuzessy et al. 2016](#); [Harich et al. 2016](#)). In fact, ingestion by mammals generally enhances germination success and germination rates.

For the second question, it is difficult to determine the fate of most seeds that are dispersed by mammals (e.g., [Fleming 1988](#); [Russo and Augspurger 2004](#)). Although the fate of most consumed seeds is death, a sufficient number survive because of the sheer numbers being dispersed across different sites by multiple species. Consequently, dispersal by mammals is beneficial for many plants. Certain phyllostomid bats, which are generally common in disturbed habitats, are especially important dispersers of seeds of colonizing plants in the Neotropics ([Muscarella and Fleming 2007](#)). As a result, these bats play an especially important role in regeneration of Neotropical forests. Bats could be an important tool for accelerating natural regeneration of degraded tropical forest by drawing them to roosts scented with essential fruit oils ([Bianconi et al. 2010](#)).

Regarding the third question, determining which dispersers are responsible for the recruitment of particular plant seedlings

is difficult. Nonetheless, natural experiments and computer simulations indicate that seed dispersal by mammals is important because in its absence, seedling recruitment rates of their food plants will decrease and plant community composition will change (e.g., Webb and Peart 2001; Muller-Landau 2007). Where hunters have reduced the abundance of large mammals, few seeds are dispersed, leading to a recruitment bottleneck in large-seeded plants (Howe et al. 1985; Wright et al. 2000). In persistently hunted Amazonian forests, where large primates are severely reduced in numbers, the probability of effective dispersal of large-seeded plants that are ingested primarily by these frugivores can decline by > 60% (Peres and van Roosmalen 2002). This can lead to large-scale disruptions of ecosystem services, including the intrinsic capacity of tropical forests to maintain carbon stocks, as shown for the Brazilian Atlantic Forest (Bello et al. 2015) and the Amazon (Peres et al. 2016). In a comparison of effects of medium-to-large primates at three unhunted and three hunted forest sites in lowland Peru, species richness decreased by 46% and the frequency of seedlings of abiotically dispersed species increased by 284% in the hunted sites (Nuñez-Iturri et al. 2008). Similar results have been reported elsewhere in the Neotropics and in the Afrotropics (e.g., Effiom et al. 2013; Rosin and Poulsen 2016).

Increased mobility of propagules (pollen and seeds) is perhaps the most important reason why angiosperms have evolved mutualisms with many animals. In the case of frugivory, movement of seeds away from the immediate vicinity of parent plants can result in increased seed survival and seedling recruitment rates, particularly in the tropics (reviewed by Carson et al. 2008). Some seed dispersal is nearly always better than none (Howe and Miriti 2004). Although seed dispersal probabilities away from parent plants decrease rapidly with distance in most systems, frugivorous birds and mammals are especially important for producing dispersal curves with long tails. For example, given their long gut retention times and long daily movements, African and Asian elephants can disperse seeds dozens of kilometers before defecating them (Harich et al. 2016). Most other mammals, however, including many primates and bats, provide much more modest maximum dispersal distances of only a few kilometers (reviewed in Fleming 1988; Fleming and Kress 2013). Nonetheless, even these dispersal distances are sufficient to maintain tropical plant populations and to provide the occasional colonization of new or recently disturbed habitats (e.g., Muscarella and Fleming 2007; Heymann et al. 2017).

Finally, the fate of many large-bodied frugivorous birds and mammals in the tropics, including pteropodids on oceanic islands, currently hangs in the balance because of overhunting and habitat fragmentation (Peres and Palacios 2007; Wiles and Brooke 2009). As populations of these species decline, so does the effective dispersal of their food plants in two respects: 1) overall seed rain away from parent plants is reduced, and 2) maximum dispersal distances are shortened. As a result, large-seeded plants that rely on large-bodied birds and mammals for dispersal will suffer reduced recruitment rates, as well as a decline in abundance with a concomitant increase in the abundance of small-seeded plants that are dispersed either

abiotically or by small-bodied vertebrates. Current fruit–mammalian frugivore interactions are the products of at least 65 million years of evolution. Unless efforts to protect valuable mammalian mutualists increase throughout the tropics, the extinction of many of these interactions will likely occur within a few human generations.

*Scatter hoarding and seed dispersal.*—Mammals and especially rodents are important predators of seeds (e.g., Brown et al. 1979; Hulme and Benkman 2002). Their impact on seed populations is rivaled only by that of a large variety of seed-eating insects. Seeds are nutritious, often containing high proportions of proteins and lipids; therefore, many granivorous rodents have evolved to exploit this rich resource. Rodent communities can have important impacts on plant population dynamics by consuming seeds and disturbing the soil, thereby affecting biodiversity and changing the structure of vegetation (e.g., Heske et al. 1993). But when rodents store seeds, they can have overall positive impacts on plant populations despite the fact that they consume most of the seeds (Jansen and Forget 2001). This net positive effect arises because scatter hoarding can be an effective means of seed dispersal (e.g., Price and Jenkins 1986).

When the American Society of Mammalogists first met in 1919, scatter hoarding of seeds by animals and its effect on seed dispersal was in the realm of natural history. Early ecologists were aware that squirrels (*Sciurus* spp.) and corvids (e.g., jays) buried nuts in the fall as a winter food, and it was generally believed that those nuts that were not retrieved germinated in the spring. Our understanding of the scatter hoarding–seed dispersal syndrome has expanded to include a much wider variety of propagules (see Supplementary Data SD4).

Unlike other seed dispersal syndromes, propagules dispersed by scatter-hoarding animals are sometimes described as not having any obvious adaptations for seed dispersal. For example, some plant species dispersed in this way were initially described as having unassisted seed dispersal. This incorrect impression largely arose because, prior to the 1970s, the adaptive nature of these seeds and nuts was not well understood. Before that time, a coevolutionary perspective was not pervasive. Adaptations to attract dispersers include being relatively large, spherical, richly colored in various brownish hues (i.e., conspicuous), very nutritious (e.g., rich in fats), and poorly defended chemically (acorns are an exception). Additionally, some seeds fall to the ground at maturity so that they can be gathered by ground-foraging rodents (Jansen and Forget 2001; Steele et al. 2001; Vander Wall 2001). Nuts and seeds are typically encased in an inedible protective husk, but in some cases, the outer covering is edible (Beck and Vander Wall 2011). This indicates that primary dispersal might be by a different vector (e.g., frugivores) (Vander Wall and Longland 2004). Masting, the synchronous production of large seed crops over a large region, separated by one or more years of small seed crops, helps to satiate seed predators and increase the effectiveness of dispersal (Sork 1983; Vander Wall 2002). Scatter hoarding is regarded as a nearly global seed dispersal syndrome, occurs

on all continents in temperate and tropical environments, and includes broad-leaved forests, coniferous forests, deserts, and other habitats (Supplementary Data SD5).

Understanding of the dynamics and fates of stored seeds and nuts has increased with the development of new methods to track individual propagules. Larger nuts with metal objects inserted into the interior of the seed have been tracked using a metal detector (Sork 1984) and seeds with rare earth magnets detected with a magnetometer (Borchert 2004). Colored threads, ribbons, or fine wires have been attached to large nuts with small numbered tags (Forget 1992). Relatively small seeds have been numbered and tracked with radioisotopes (e.g., Vander Wall 1994, 2008). Large nuts of *Astrocaryum standleyanum* have been equipped with tiny transmitters and tracked by radiotelemetry in conjunction with camera traps to monitor which rodent recovered the nuts (Jansen et al. 2012). These studies have allowed researchers to follow the fates of individual seeds and nuts, greatly increasing our understanding of the spatial and temporal dynamics of cached foods.

The impact of rodent and corvid seed scatter hoarders on plant communities can be tremendous. In some plant communities, seed caching accounts for most of the plant biomass. For example, Jeffrey pine (*Pinus jeffreyi*) forests essentially form monocultures in lower elevations of the Sierra Nevada and Cascade Mountains of western North America. Virtually all of these trees are thought to be established by scatter-hoarding rodents and corvids (Vander Wall 2008), accounting for > 95% of plant biomass. Further, the dominant understory shrubs (antelope bitterbrush, *Purshia tridentate*—Vander Wall 1994; Sierra bush chinquapin, *Castanopsis sempervirens*—Roth and Vander Wall 2005; and green-leaf manzanita, *Arctostaphylos patula*—Moore and Vander Wall 2015) are all dispersed by seed-caching rodents. Similar claims could be made for oak-hickory (*Quercus*–*Carya*) forests of the eastern United States (Sork 1983; Steele et al. 2001) and the single-leaf pinyon–Utah juniper (*Pinus monophylla*–*Juniperus osteosperma*) woodlands of Nevada (Vander Wall 1997; Dimitri et al. 2017).

New seed-tracking methods suggest that pilfering and re-caching is frequent (e.g., Vander Wall 2008; Jansen et al. 2012) as many rodent species are proficient at detecting and excavating hidden seeds and nuts. In some environments, seeds move from site to site on nearly a daily basis, resulting in a spatially and temporally dynamic stored food resource. An individual that does not pilfer quickly loses control of the stored food resource, resulting in strong selection for pilfering ability. Some species of rodents, such as yellow-pine chipmunks (*Tamias amoenus*—Vander Wall 2000), Merriam's kangaroo rats (*Dipodomys merriami*—Murray et al. 2006), and agoutis (*Dasyprocta* spp.—Jansen and Forget 2001; Jansen et al. 2012) have evolved to be effective seed pilferers, enabling them to secure a larger portion of stored food resources. High levels of pilfering have important implications for the coexistence of competing rodent species (Leaver and Daly 2001). Instead of competing for seeds at the source (e.g., Brown et al. 1979), species compete for seeds buried in the soil. This could mean that a species that is an inferior competitor at the food source

might avoid competitive exclusion from a community if it is a superior pilferer of scatter-hoarded seeds.

When stored food being pilfered and re-cached is a seed, pilfering and re-caching have important consequences for plants. Seed dispersal by scatter-hoarding animals does not involve a single step of movement from a source plant to a cache site, but incorporates numerous subsequent movements (secondary dispersal). Each time a stored seed is handled, there is a small probability that it could be eaten, but most seeds are moved a short distance and restored. Approximately half of these secondary movements are away from the source plant, increasing maximum dispersal distances. Each time seeds are re-cached, maximum dispersal distances increase. This “relay dispersal” could significantly increase the dispersibility of nuts beyond what is normally considered likely for propagules cached by rodents and corvids (e.g., Jansen et al. 2012), which could increase plant migration rates following disturbance (e.g., deglaciation) or increase a plant's ability to colonize new habitats.

In many situations, levels of pilfering are so high (> 5% per day—Vander Wall and Jenkins 2003) that it is unlikely that individuals that initially store seeds consume them months later. The evolution of scatter-hoarding behavior might have a different explanation than that proposed by Andersson and Krebs (1978), who theorized that a scatter hoarder had to benefit from *its own* caches more than would any other individual. This view emerged at a time when it was thought that cached foods were relatively static. Indeed, this may be the case for many bird species such as chickadees and tits (Paridae). But many individual rodents, including members of different species that scatter-hoard seeds in a similar way, engage in “cache exchanges,” in which the seeds that are eventually consumed are not necessarily those initially stored by that individual (Vander Wall and Jenkins 2003; Price and Mittler 2006). If future studies confirm these findings, new theories must be developed to account for the evolution and maintenance of scatter-hoarding behavior in rodents.

## INTERACTIONS BETWEEN HUMANS AND OTHER MAMMALS

Interactions between humans and other mammals generate significant economic benefit. Many of the terrestrial-based protein sources in the human diet are from domesticated mammals. Hunting in the United States creates more than 700,000 jobs with a nationwide economic impact of about \$61 billion/year, supporting nearly 1% of the entire civilian labor force across all sectors of the American economy (LaBarbera 2003). Over 20 million hunters in the United States spend about half a billion days afield in pursuit of mammalian game, and fees levied to game hunters finance a vast acreage of conservation land in many countries where hunting is regulated (Warren 1997). Mammals also contribute to local and regional economies as natural predators that control agricultural pests (such as bats) and as bushmeat for subsistence hunters in many developing countries.



The land-use revenue value of ecotourism with the primary focus on wild mammals is also significant in many countries. For example, jaguar-*(Panthera onca)* centric ecotourism in the world's largest wetland (Brazilian Pantanal) was valued three times higher per unit area than the crude land-use revenue from cattle ranching, the only alternative economic activity in this region (Tortato et al. 2017). Financial losses induced by African elephant and African forest elephant (*Loxodonta cyclotis*) poaching that would otherwise be accrued to African countries via ecotourism amount to ~USD \$25 million annually, and these lost benefits far exceed the required anti-poaching costs to stop elephant declines across the continent (Naidoo et al. 2016). The colony of Mexican free-tailed bats living under the Congress St. bridge in Austin, Texas is a major ecotourism draw, generating over 3 million US dollars per year in revenue (Kunz et al. 2011).

Large mammals also can benefit humans by indirectly suppressing the abundance of competent reservoirs of human pathogens, thereby suppressing the risk of infectious diseases (Civitello et al. 2015). A negative relationship exists between mammal diversity, or biomass, and disease prevalence (Civitello et al. 2015), in which hosts in high-diversity systems have lower average competence for a particular pathogen or parasite, thereby reducing transmission and community-level prevalence for those causal agents. This is referred to as the dilution effect. As a consequence of this relationship, mammalian defaunation through human disturbance can systematically benefit some parasites and pathogens associated with human zoonoses having important impacts on public health (Civitello et al. 2015; Young et al. 2016). A widely cited example of the dilution effect was reported by Ostfeld and Keesing (2000) regarding Lyme disease in the eastern United States. The numerically dominant white-footed mouse (*Peromyscus leucopus*) is also an effective host for the bacteria via the vector tick *Ixodes scapularis*. White-footed mice are generalists that can tolerate disturbance and become quite abundant with the decline of more specialist species of rodents. Many of these species have lower competence as reservoirs for the Lyme disease bacteria; higher diversity can therefore dilute the prevalence of infection in the vector. A similar situation has been observed in the transmission of hantavirus, where transmission is primarily host-to-host contact. In more diverse rodent communities, some species act as dead-end hosts. High species richness can therefore dilute the prevalence of the virus (Mills 2006).

Although the generality, magnitude, and mechanism of the dilution effect are still under investigation, systematic compensatory increases in rodent abundance following competitive release from declines of large mammalian herbivores can augment rodent-borne diseases (Young et al. 2014). Hyperabundance of mammalian mesopredators following local extinctions of apex predators driven by habitat fragmentation can also artificially inflate populations of competent hosts (Levi et al. 2016). In fact, increases in disease prevalence may be consistently associated with large mammal extirpations inducing systematic losses in low-competence hosts, which may release competent hosts from competition (Joseph et al. 2013).

## CONSERVATION OF MAMMALS AND THEIR FUNCTIONAL ROLES

Discussion of the functional role of mammals would not be complete without including humans. *Homo sapiens* is a “hyper-keystone” species (Worm and Paine 2016), having transformed the land, water, atmosphere, and biodiversity of the planet (Barnosky et al. 2012). We have been especially successful because of our ability to capture extra-metabolic energy, mostly from fossil fuels, that has supported the development of industrial agriculture, roads, and cities, and culminating in a highly interconnected, global civilization supported by massive infrastructure. Our impacts have been so profound that many scientists argue that the Earth has entered a new geological epoch, the Anthropocene (Lacher and Pyare 2018).

Our pervasive impacts are altering the Earth's biogeochemical cycles. Our use of fertilizers for agriculture has created oxygen-depleted “dead zones” across freshwater and ocean ecosystems (Watson 2016). Our combustion of fossil fuels and burning of fields for agriculture are warming the planet and acidifying the world's oceans, with increased CO<sub>2</sub> levels that have not been present since the early Pliocene (3.5–5 MA—Hoegh-Guldberg and Bruno 2010). Indeed, we have converted about 43% of the Earth's land surface to near homogenous urban or agricultural landscapes, with much of the remaining landscapes dissected by roads (Barnosky et al. 2012). Our activities are defaunating the planet and driving the Earth's sixth mass extinction (Dirzo et al. 2014; McCauley et al. 2015). As a super predator, we harvest terrestrial carnivores and top predators at median rates 4–10 times higher than do other species; and 11–15 times greater in marine than in terrestrial ecosystems (Darimont et al. 2015). Because humans often target top predators and other keystone species, we are functionally reducing or eliminating the regulatory keystone roles these other species have on ecosystems (Estes et al. 2011; Worm and Paine 2016).

About one-quarter of all mammals are now in danger of extinction, and more than half of all mammal populations are in decline (Schipper et al. 2008). Twenty-five of the world's largest mammalian herbivore species currently occupy an average of only 19% of their historical ranges (Ripple et al. 2015), and local extinctions of mammal populations are occurring at a much faster rate than the background extinction rate (Ceballos et al. 2017). In a recent analysis of 177 mammal species, all had lost at least 30% of their geographic ranges and > 40% of the species had experienced > 80% range shrinkage between 1900 and 2015 (Ceballos et al. 2017). In many parts of the world, healthy populations of large mammals are entirely restricted to protected areas, and overhunting can severely depress mammal biomass, even in sparsely settled areas. A comparative analysis of 101 forest sites censused throughout the Amazon Basin and Guiana Shield revealed that the mean aggregate population biomass of the 12 most harvest-sensitive species (most of which are mammals) was reduced almost 11-fold from 979.8 kg/km<sup>2</sup> in unhunted sites to only 89.2 kg/km<sup>2</sup> in moderately to heavily hunted sites (Peres and Palacios 2007). Illicit poaching and trafficking continue to thwart conservation efforts, and

overexploitation is the driving force of population depletion in 301 of all 1,169 terrestrial mammal species listed as threatened from the 4,556 species assessed by the International Union for Conservation of Nature (IUCN—[Ripple et al. 2016](#)). This goes far beyond iconic mammals, such as tigers (*Panthera tigris*), elephants, and rhinoceroses, and includes many lesser-known species (e.g., pangolins, large primates) facing intense pressures for survival. Mammals also dominate global illegal wildlife trade, with elephant ivory and rhinoceros horn representing over 50% of all wildlife seizures in 2013 ([SDG 2017](#)). As a consequence, mammal-defaunated seascapes and landscapes no longer exercise their full ecological, biogeochemical, or structural potential.

The IUCN Red List of Threatened Species is the global standard for the assessment of threatened species, used to guide conservation priorities. Although habitat loss and overexploitation remain the greatest threats, climate change is a rapidly emerging threat. The IUCN recently released a new document so that species vulnerability to climate change can be assessed more effectively ([Foden and Young 2016](#)). In addition to assessments of extinction risk, many IUCN specialist groups are defining both priority species and regions based upon analyses of the revised data (e.g., see [Lacher et al. 2017](#)). A more complete picture of global mammal conservation priorities will be available with the reassessment of all mammals in 2018, providing needed guidance on current mammalian research needs and conservation investment.

The priorities developed by IUCN Species Survival Commission Specialist Groups need to be developed into action plans that can be used by the Convention on Biological Diversity (CBD) member states for the development of National Biodiversity Strategies and Action Plans (NBSAPs; [www.cbd.int/nbsap/](http://www.cbd.int/nbsap/)). The 196 United Nations (UN) member states and the European Union (the only UN member not to ratify the CBD is the United States) must develop NBSAPs to guarantee that the various agencies responsible for aspects of conservation mitigate impacts on biodiversity. To date, many NBSAPs have been developed using disaggregated global data sets that often align poorly with nationally derived data sets ([Han et al. 2017](#)). In order for national conservation plans for mammals to be implemented, countries need to generate more national-level data specific to their conservation goals, and funding needs to be provided to facilitate the collection of these data. Research priorities at the national level should include the conservation of mammals known to have important ecological impacts.

The most critical immediate actions required to conserve ecosystem functions that are mediated by mammals are to mitigate habitat loss and overexploitation, and address the impending threats of climate change. As human populations and consumption grow in tandem, less and less land remains to conserve biodiversity ([Aukema et al. 2017](#)). What protected areas exist will be under growing pressure to be converted to working landscapes (e.g., see [www.paddtracker.org](http://www.paddtracker.org)), providing growing challenges to efforts to conserve large-scale ecosystem processes and associated services. Declining populations of large mammals ([Ripple et al. 2015](#); [Estrada et al. 2017](#)), increasing fragmentation with threshold levels of losses

in specialist species and collapsing communities ([Pardini et al. 2010](#)), and the threat of rapid climate change ([Heller and Zavaleta 2009](#)) necessitate urgent social, political, and scientific action. Additionally, we may be moving toward a world of novel community assemblages, presenting new challenges in monitoring and protecting community processes ([Williams and Jackson 2007](#)). The barriers for research funding and collaboration that exist between academic institutions and conservation nongovernmental organizations (NGOs) need to be dissolved. Academics must take a more active role in translating their research results to conservation action and NGO researchers need to seek engagement with universities that have the facilities and laboratories to generate ecological and genetic information that is critically needed for conservation, but that is beyond the scope of NGO science programs ([Lacher et al. 2012](#)).

The work of other IUCN Commissions, like the World Commission on Protected Areas (WCPA), develops innovative approaches to the protection of ecosystems beyond traditional fortress conservation approaches. The collaboration of the WCPA with the Commission on Ecosystem Management on the Red List of Ecosystems is an excellent example ([Keith et al. 2013](#)). This initiative will prioritize conservation efforts on those systems deemed most at threat based upon a set of quantitative criteria, much like the Red List. New ways to view protected areas, like the development of Key Biodiversity Areas based on the model of Important Bird Areas of BirdLife International ([Eken et al. 2004](#); [IUCN 2016](#)), the Alliance for Zero Extinction initiative (<http://www.zeroextinction.org/>), the EDGE of Existence Programme (<https://www.edgeofexistence.org/>), and community-based conservation that more effectively shares conservation benefits ([Berkes 2007](#)), have gained significant traction in the conservation world. The emphasis of the service value of ecosystem processes has encouraged more joint management of protected areas with a diverse group of stakeholders with the expectation of more effective management of these areas. We need to have the continued development of these and other novel approaches to effectively protect critical ecological processes.

The development of a number of policy mechanisms linked to international conventions requires science-based decision-making to meet the targets of these conventions. Linking these efforts to sustainable development and more recently ecosystem services has shifted some of the conservation effort to human–environment linkages and benefits. The IPBES was established to provide science-based information on the relationship between biodiversity and ecosystem services of value to society ([Diaz et al. 2015](#)). IPBES currently draws upon the expertise of over 1,000 scientists worldwide. Much like the concerns in applying global data to NBSAPs, similar concerns exist for IPBES, where the scale of data sets needs to match regional and national conservation actions. There are many opportunities during the IPBES consultation process for input on data needs and necessary additional research ([www.ipbes.net](http://www.ipbes.net)). There are great opportunities for mammalogists to raise the profile of the functional roles of mammals relevant to ecosystem process and associated services. There has never been a

more opportune time to provide science-based information on the critical role of mammals in ecosystem processes, functions, and services to landscapes and human societies.

Understanding of the functional role of mammals in ecosystems has advanced far beyond the musings of Lee R. Dice in 1919. We understand ecosystem functioning from both an empirical and theoretical perspective, and have clarified the benefits and services that ecosystems provide to human well-being through the application of science to the actions of numerous international agencies and conventions. Yet, we face the threat of the collapse of marine, freshwater, and terrestrial processes due to severe human-driven degradation. Our prior 100 years of research on mammals has provided the basis to begin to address these threats, and this will be our 100-year challenge for the future.

### ACKNOWLEDGMENTS

All authors contributed significantly to the development of the manuscript. We thank S. Davidson for the drawings in Fig. 1, and anonymous reviewers for their helpful comments that improved our manuscript. Thanks to Dr. M. Mora-Zacharias for the Spanish abstract.

### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Type of burrowing behavior for species with potential ecosystem-level effects (information from ADD, this paper).

**Supplementary Data SD2.**—Projected annual consumption of vegetation by African large herbivores partitioned among feeding guilds. Uganda = Queen Elizabeth + Murchison Falls National Parks; Sereng = Serengeti ecosystem in Tanzania; HiP = Hluhluwe-iMfolozi Park in South Africa; KrRuChHw = amalgamation of Kruger (South Africa), Ruaha (Tanzania), Chobe (Botswana), and Hwange (Zimbabwe) National Parks; CoBoKa = composite of Comoe (Ivory Coast), Bouba Njida (Cameroon), and Kasungu (Malawi) National Parks. Sources of data: Laws et al. (1975); Eltringham and Din (1977); Van Lavieren and Esser (1980); Bell (1981); Barnes and Douglas-Hamilton (1982); Steinhauer-Burkart (1987); Sinclair et al. (2008); Chamaillé-Jammes et al. (2009); Skarpe et al. (2015); Le Roux et al. (2017); and South African National Parks (unpublished).

**Supplementary Data SD3.**—Evolutionary radiation of the two families of bats with a summary of pollinating species.

**Supplementary Data SD4.**—Studies of propagules involved in scatter hoarding and seed dispersal syndromes.

**Supplementary Data SD5.**—History and geography of scatter-hoarding studies, in chronological order of their progression.

### LITERATURE CITED

- ALIPERTI, J. R., D. A. KELT, P. A. HEADY, AND W. F. FRICK. 2017. Using behavioral and stable isotope data to quantify rare dietary plasticity in a temperate bat. *Journal of Mammalogy* 98:340–349.
- ALLEN, G. M. 1939. *Bats*. Harvard University Press, Cambridge, Massachusetts.
- ANDERSSON, M., AND J. KREBS. 1978. On the evolution of hoarding behaviour. *Animal Behaviour* 26:707–711.
- ANTHONY, R. G., J. A. ESTES, M. A. RICCA, A. K. MILES, AND E. D. FORSMAN. 2008. Bald eagles and sea otters in the Aleutian Archipelago: indirect effects of trophic cascades. *Ecology* 89:2725–2735.
- ASNER, G. P., N. VAUGHN, I. P. J. SMIT, AND S. LEVICK. 2016. Ecosystem-scale effects of megafauna in African savannas. *Ecography* 39:240–252.
- AUKEMA, J. E., N. G. PRICOPE, G. J. HUSAK, AND D. LOPEZ-CARR. 2017. Biodiversity areas under threat: overlap of climate change and population pressures on the world's biodiversity priorities. 12:e0170615.
- BARNOSKY, A. D., ET AL. 2012. Approaching a state shift in Earth's biosphere. *Nature* 486:52–58.
- BECK, M. J., AND S. B. VANDER WALL. 2011. Diplochory in western chokecherry: you can't judge a fruit by its mesocarp. *Oecologia* 165:131–141.
- BELLO, C., ET AL. 2015. Defaunation affects carbon storage in tropical forests. *Science Advances* 1:e1501105.
- BERKES, F. 2007. Community-based conservation in a globalized world. *Proceedings of the National Academy of Sciences of the United States of America* 104:15188–15193.
- BERNES, C., K. A. BRATHEN, B. C. FORBES, J. D. M. SPEED, AND J. MOEN. 2015. What are the impacts of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A systematic review. *Environmental Evidence* 4:4.
- BESCHTA, R. L., AND W. J. RIPPLE. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142:2401–2414.
- BESCHTA, R. L., AND W. J. RIPPLE. 2016. Riparian vegetation recovery in Yellowstone: the first two decades after wolf reintroduction. *Biological Conservation* 198:93–103.
- BIANCONI, G. V., U. M. S. SUCKOW, A. P. CRUZ-NETO, AND S. B. MIKICH. 2010. Use of essential fruit oils to assist forest regeneration by bats. *Restoration Ecology* 20:211–217.
- BÖHM, S. M., K. WELLS, AND E. K. KALKO. 2011. Top-down control of herbivory by birds and bats in the canopy of temperate broad-leaved oaks (*Quercus robur*). *PLoS One* 6:e17857.
- BORCHERT, M. 2004. Vertebrate seed dispersal of *Marah macrocarpus* (Cucurbitaceae) after fire in the Western Transverse Ranges of California. *Ecoscience* 11:463–471.
- BOUWES, N., ET AL. 2016. Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). *Scientific Reports* 6:28581.
- BOYLES, J. G., P. M. CRYAN, G. F. MCCracken, AND T. H. KUNZ. 2011. Conservation. Economic importance of bats in agriculture. *Science* 332:41–42.
- BOYLES, J. G., C. L. SOLE, P. M. CRYAN, AND G. F. MCCracken. 2013. On estimating the economic value of insectivorous bats: prospects and priorities for biologists. Pp. 501–515 in *Bat evolution, ecology, and conservation* (R. A. ADAMS and S. C. PEDERSON, eds.). Springer, New York.
- BROWN, J. H., O. J. REICHMAN, AND D. W. DAVIDSON. 1979. Granivory in desert ecosystems. *Annual Review of Ecology and Systematics* 10:201–227.
- BUMP, J. K., K. B. TISCHLER, A. J. SCHRANK, R. O. PETERSON, AND J. A. VUCETICH. 2009. Large herbivores and aquatic-terrestrial links in southern boreal forests. *The Journal of Animal Ecology* 78:338–345.



- BUMRUNGSRI, S., E. SRIPAORAYA, T. CHONGSRI, K. SRIDITH, AND P. A. RACEY. 2009. The pollination ecology of durian (*Durio zibethinus*, Bombacaceae) in southern Thailand. *Journal of Tropical Ecology* 25:85–92.
- BUTCHART, S. H., ET AL. 2004. Measuring global trends in the status of biodiversity: Red List Indices for birds. *PLoS Biology* 2:e383.
- CARSON, W. P., J. T. ANDERSON, E. G. LEIGH, AND S. A. SCHNITZER. 2008. Challenges associated with testing and falsifying the Janzen-Connell hypothesis: a review and critique. Pp. 210–241 in *Tropical forest community ecology* (W. P. CARSON AND S. A. SCHNITZER, eds.). Wiley-Blackwell, Oxford, United Kingdom.
- CEBALLOS, G., ET AL. 2010. Rapid decline of a grassland system and its ecological and conservation implications. *PLoS One* 5:e8562.
- CEBALLOS, G., P. R. EHRLICH, AND R. DIRZO. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the United States of America* 114:E6089–E6096.
- CHRISTIE, K. S., J. P. BRYANY, L. GOUGH, V. T. RAVOLAINEN, R. W. RUESS, AND K. D. TAPE. 2015. The role of vertebrate herbivores in regulating shrub expansion in the Arctic: a synthesis. *BioScience* 65:1123–1133.
- CIVITELLO, D. J., ET AL. 2015. Biodiversity inhibits parasites: broad evidence for the dilution effect. *Proceedings of the National Academy of Science of the United States of America* 112:8667–8671.
- CLARE, E. L., ET AL. 2013. The diet of *Myotis lucifugus* across Canada: assessing foraging quality and diet variability. *Molecular Ecology* 23:3618–3632.
- CLARE, E. L., E. E. FRASER, H. E. BRAID, M. B. FENTON, AND P. D. HEBERT. 2009. Species on the menu of a generalist predator, the eastern red bat (*Lasiurus borealis*): using a molecular approach to detect arthropod prey. *Molecular Ecology* 18:2532–2542.
- CLARE, E. L., W. O. SYMONDSON, AND M. B. FENTON. 2014. An inordinate fondness for beetles? Variation in seasonal dietary preferences of night-roosting big brown bats (*Eptesicus fuscus*). *Molecular Ecology* 23:3633–3647.
- CLARK, K. L., L. C. BRANCH, J. L. HIERRO, AND D. VILLARREAL. 2016. Burrowing herbivores alter soil carbon and nitrogen dynamics in a semi-arid ecosystem, Argentina. *Soil Biology and Biochemistry* 103:253–261.
- CLEVELAND, C. J., ET AL. 2006. Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Frontiers in Ecology and the Environment* 4:238–243.
- CROMSIGHT, J. P. G. M., AND M. TE BEEST. 2014. Restoration of a mega-herbivore: landscape-level impacts of white rhinoceros in Kruger National Park, South Africa. *Journal of Ecology* 102:566–575.
- DARIMONT, C. T., C. H. FOX, H. M. BRYAN, AND T. E. REIMCHEN. 2015. Human impacts. The unique ecology of human predators. *Science* 349:858–860.
- DAVIDSON, A. D., J. K. DETLING, AND J. H. BROWN. 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment* 10:477–486.
- DAVIDSON, A. D., AND D. C. LIGHTFOOT. 2006. Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography* 29:755–765.
- DAVIDSON, A. D., ET AL. 2018. Reintroducing a keystone burrowing rodent to restore an arid North American grassland: challenges and successes. *Restoration Ecology* 26:909–920.
- DE BOER, W. F., J. W. A. VAN OORT, M. GROVER, AND M. J. S. PEEL. 2015. Elephant-mediated habitat modifications and changes in herbivore species assemblages in Sabi Sand, South Africa. *European Journal of Wildlife Research* 61:491–503.
- DE MAZANCOURT, C., M. LOREAU, AND L. ABBADIE. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology* 79:2242–2252.
- DEAGLE, B. E., ET AL. 2018. Counting with DNA in metabarcoding studies: how should we covert sequence reads to dietary data? *Molecular Ecology* 2018:1–16.
- DESBIEZ, A. L. J., AND D. KLUYBER. 2013. The role of giant armadillos (*Priodontes maximus*) as physical ecosystem engineers. *Biotropica* 45:537–540.
- DESHMUCK, I. 1984. A common relationship between precipitation and grassland peak biomass for east and southern Africa. *African Journal of Ecology* 22:181–186.
- DIAZ, S., ET AL. 2015. The IPBES conceptual framework – connecting nature and people. *Current Opinion in Environmental Sustainability* 14:1–16.
- DICE, L. R. 1919. The mammals of southeastern Washington. *Journal of Mammalogy* 1:10–22.
- DIMITRI, L., W. LONGLAND, AND S. B. VANDER WALL. 2017. Cone and seed traits of two *Juniperus* species influence roles of frugivores and scatter-hoarding rodents as seed dispersal agents. *Acta Oecologia* 85:93–103.
- DIRZO, R., H. S. YOUNG, M. GALETTI, G. CEBALLOS, N. J. ISAAC, AND B. COLLEN. 2014. Defaunation in the Anthropocene. *Science* 345:401–406.
- DOUGHTY, C. E., A. WOLF, C. BARALOTO, AND Y. MALHI. 2016a. Interdependency of plants and animals in controlling the sodium balance of ecosystems and the impacts of global defaunation. *Ecography* 39:204–212.
- DOUGHTY, C. E., ET AL. 2016b. Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences of the United States of America* 113:868–873.
- EADS, D. A., AND D. E. BIGGINS. 2015. Plague bacterium as a transformer species in prairie dogs and the grasslands of western North America. *Conservation Biology* 29:1086–1093.
- EBY, S., J. DEMPEWOLF, R. M. HOLDO, AND K. L. METZGER. 2015. Fire in the Serengeti ecosystem: history, drivers, and consequences. Pp. 73–104 in *Serengeti IV* (A. R. E. SINCLAIR, K. L. METZGER, S. A. R. MDUMA, AND J. M. FRYXELL, eds.). University of Chicago Press, Chicago, Illinois.
- EFFIOM, E. O., G. NUÑEZ-ITURRI, H. G. SMITH, U. OTTOSSON, AND O. OLSSON. 2013. Bushmeat hunting changes regeneration of African rainforests. *Proceedings of the Royal Society of London, B. Biological Sciences* 280:20130246.
- EISENBERG, C. 2010. *The wolf's tooth: keystone predators, trophic cascades, and biodiversity*. Island Press, Washington, D.C.
- EKEN, G., ET AL. 2004. Key biodiversity areas as site conservation targets. *BioScience* 54:1110–1118.
- ERIKSSON, O. 2008. Evolution of seed size and biotic seed dispersal in angiosperms: paleoecological and neoecological evidence. *International Journal of Plant Sciences* 169:863–870.
- ERIKSSON, O. 2016. Evolution of angiosperm seed disperser mutualisms: the timing of origins and their consequences for coevolutionary interactions between angiosperms and frugivores. *Biological Reviews of the Cambridge Philosophical Society* 91:168–186.
- ESTES, J. A., ET AL. 2011. Trophic downgrading of planet Earth. *Science* 333:301–306.
- ESTES, J. A., M. HEITHAUS, D. J. MCCAULEY, D. B. RASHER, AND B. WORM. 2016. Megafaunal impacts on structure and function of

- ocean ecosystems. *Annual Review of Environment and Resources* 41:83–116.
- ESTRADA, A., ET AL. 2017. Impending extinction crisis of the world's primates: why primates matter. *Science Advances* 3:e1600946.
- FAUCHALD, P., T. PARK, H. TØMMERVIK, R. MYNENI, AND V. H. HAUSNER. 2017. Arctic greening from warming promotes declines in caribou populations. *Science Advances* 3:e1601365.
- FEDERICO, P., ET AL. 2008. Brazilian free-tailed bats as insect pest regulators in transgenic and conventional cotton crops. *Ecological Applications* 18:826–837.
- FENSTER, C. B., W. S. ARMBRUSTER, P. WILSON, M. R. DUDASH, AND J. D. THOMSON. 2004. Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics* 35:375–403.
- FLEMING, T. H. 1986. Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. Pp. 105–118 in *Frugivores and seed dispersal* (A. ESTRADA and T. H. FLEMING, eds.). Dr. W. Junk Publishers, Dordrecht, The Netherlands.
- FLEMING, T. H. 1988. The short-tailed fruit bat, a study in plant-animal interactions. University of Chicago Press, Chicago, Illinois.
- FLEMING, T. H., R. L. BREITWISCH, AND G. W. WHITESIDES. 1987. Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics* 18:91–109.
- FLEMING, T. H., C. GEISELMAN, AND W. J. KRESS. 2009. The evolution of bat pollination: a phylogenetic perspective. *Annals of Botany* 104:1017–1043.
- FLEMING, T. H., AND W. J. KRESS. 2013. The ornaments of life: co-evolution and conservation in the tropics. University of Chicago Press, Chicago, Illinois.
- FLEMING, T. H., AND V. J. SOSA. 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. *Journal of Mammalogy* 75:845–851.
- FODEN, W. B., AND B. E. YOUNG (eds.). 2016. IUCN SSC guidelines for assessing species' vulnerability to climate change. Version 1.0. Occasional Paper of the IUCN Species Survival Commission No. 59. IUCN Species Survival Commission, Cambridge, United Kingdom and Gland, Switzerland.
- FORGET, P.-M. 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica* 24:408–414.
- FRANK, D. A., S. J. MCNAUGHTON, AND B. F. TRACY. 1998. The ecology of the Earth's grazing ecosystems. *BioScience* 48:513–521.
- FRICK, W. F., R. D. PRICE, P. A. HEADY, AND K. M. KAY. 2013. Insectivorous bat pollinates columnar cactus more effectively per visit than specialized nectar bat. *The American Naturalist* 181:137–144.
- FRITZ, H., AND P. DUNCAN. 1994. On the carrying capacity for large ungulates of African savanna ecosystems. *Proceedings of the Royal Society of London, B. Biological Sciences* 256:77–82.
- FUJITA, M. S., AND M. D. TUTTLE. 1991. Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. *Conservation Biology* 5:455–463.
- FUZESSY, L. F., T. G. CORNELISSEN, C. JANSON, AND F. A. O. SILVEIRA. 2016. How do primates affect seed germination? A meta-analysis of gut passage effects on neotropical plants. *Oikos* 125:1069–1080.
- GARDNER, A. L. 1977. Feeding habits. Pp. 293–350 in *Biology of bats of the New World family Phyllostomatidae, part II* (R. J. BAKER, J. K. JONES, Jr., and D. C. CARTER, eds.). Special Publications of the Museum Texas Tech University, Lubbock.
- GERLANC, N. M., AND G. A. KAUFMAN. 2003. Use of bison wallows by Anurans on Konza Prairie. *The American Midland Naturalist* 150:158–168.
- GIANNINI, N. P., AND N. B. SIMMONS. 2005. Conflict and congruence in a combined DNA-morphology analysis of megachiropteran bat relationships (Mammalia: Chiroptera: Pteropodidae). *Cladistics* 21:411–437.
- GOHEEN, J. R., T. M. PALMER, F. KEESING, C. RIGINOS, AND T. P. YOUNG. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *The Journal of Animal Ecology* 79:372–382.
- GÓMEZ, J. M., AND M. VERDÚ. 2012. Mutualism with plants drives primate diversification. *Systematic Biology* 61:567–577.
- GÓMEZ-RUIZ, E. P., AND T. E. LACHER. 2017. Modelling the potential geographic distribution of an endangered pollination corridor in Mexico and the United States. *Diversity and Distributions* 23:67–78.
- GUIMARÃES, P. R., M. GALETTI, AND P. JORDANO. 2008. Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS One* 3:e1745.
- HAN, X., C. JOSSE, B. E. YOUNG, R. L. SMYTH, H. H. HAMILTON, AND N. BOWLES-NEWARK. 2017. Monitoring national conservation progress with indicators derived from global and national datasets. *Biological Conservation* 213:325–334.
- HANKS, J., AND S. CHARLTON. 2003. African plains game. Pp. 111–121 in *Wildlife spectacles* (R. A. MITTERMEIER, et al., eds.). CEMEX, Agrupación Sierra Madre, Conservation International, Mexico City, Mexico.
- HARICH, F. K., ET AL. 2016. Seed dispersal potential of Asian elephants. *Acta Oecologica* 77:144–151.
- HEER, K., L. ALBRECHT, AND E. K. KALKO. 2010. Effects of ingestion by neotropical bats on germination parameters of native free-standing and strangler figs (*Ficus* sp., Moraceae). *Oecologia* 163:425–435.
- HELLER, N. E., AND E. S. ZAVALA. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation* 142:14–32.
- HESKE, E. J., J. H. BROWN, AND Q. GUO. 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan desert. *Oecologia* 95:520–524.
- HEYMANN, E. W., ET AL. 2017. Long-term consistency in spatial patterns of primate seed dispersal. *Ecology and Evolution* 7:1435–1441.
- HOBBS, N. T. 2016. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695–713.
- HOEGH-GULDBERG, O., AND J. F. BRUNO. 2010. The impact of climate change on the world's marine ecosystems. *Science* 328:1523–1528.
- HOFFMANN, M., ET AL. 2010. The impact of conservation on the status of the world's vertebrates. *Science* 330:1503–1509.
- HOOD, G. A., AND D. G. LARSON. 2015. Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. *Freshwater Biology* 60:198–208.
- HOOPER, D. U., ET AL. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- HOWE, H. F., AND M. N. MIRITI. 2004. When seed dispersal matters. *Bioscience* 54:651–660.
- HOWE, H. F., E. W. SCHUPP, AND L. C. WESTLEY. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66:781–791.
- HULME, P. E., AND C. W. BENKMAN. 2002. Granivory. Pp. 132–154 in *Plant-animal interactions: an evolutionary approach* (C. M. HERRERA and O. PELLMYR, eds.). Blackwell Science, Padstow, United Kingdom.

- IPBES. 2016. Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.
- IUCN. 2016. A global standard for the identification of key biodiversity areas, version 1.0. 1st ed. IUCN, Gland, Switzerland.
- IUCN, CONSERVATION INTERNATIONAL, ARIZONA STATE UNIVERSITY, TEXAS A&M UNIVERSITY, UNIVERSITY OF ROME, UNIVERSITY OF VIRGINIA, ZOOLOGICAL SOCIETY OF LONDON. 2008. An analysis of mammals on the 2008 IUCN Red List. [www.iucnredlist.org/mammals](http://www.iucnredlist.org/mammals). Accessed 11 June 2017.
- JANISZEWSKI, P., V. HANZAL, AND W. MISIUKIEWICZ. 2014. The Eurasian beaver (*Castor fiber*) as a keystone species - a literature review. *Baltic Forestry* 20:277–286.
- JANSEN, P. A., AND P.-M. FORGET. 2001. Scatterhoarding rodents and tree regeneration. Pp. 275–288 in *Nouragues: dynamics and plant-animal interactions in a neotropical rainforest* (F. BONGERS, P. CHARLES-DOMINIQUE, P.-M. FORGET, and M. THÉRY, eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.
- JANSEN, P. A., B. T. HIRSCH, W.-T. EMSENS, V. ZAMORA-GUTIERREZ, M. WIKELSKI, AND R. KAYS. 2012. Thieving rodents as substitute dispersers of magafaunal seeds. *Proceedings of the National Academy of Sciences of the United States of America* 109:12610–12615.
- JANZEN, D. H., AND P. S. MARTIN. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. *Science* 215:19–27.
- JOERN, A. 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology* 86:861–873.
- JOHNSON, S. D., A. PAUW, AND J. MIDGLEY. 2001. Rodent pollination in the African lily *Massonia depressa* (Hyacinthaceae). *American Journal of Botany* 88:1768–1773.
- JOHNSTON, D. S., AND M. B. FENTON. 2001. Individual and population-level variability in diets of pallid bats (*Antrozous pallidus*). *Journal of Mammalogy* 82:362–373.
- JONES, C. G., J. H. LAWTON, AND M. SHACHAK. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–386.
- JOSEPH, M. B., J. R. MIHALJEVIC, S. A. ORLOFSKE, AND S. H. PAULL. 2013. Does life history mediate changing disease risk when communities disassemble? *Ecology Letters* 16:1405–1412.
- KEITH, D. A., ET AL. 2013. Scientific foundations for an IUCN Red List of ecosystems. *PLoS One* 8:e62111.
- KINZIG, A. P., S. W. PACALA, AND D. TILMAN (eds.). 2002. *The functional consequences of biodiversity: empirical progress and theoretical extensions*. Princeton University Press, Princeton, New Jersey.
- KLEIZEN, C., J. MIDGLEY, AND S. D. JOHNSON. 2008. Pollination systems of *Colchicum* (Colchicaceae) in Southern Africa: evidence for rodent pollination. *Annals of Botany* 102:747–755.
- KNAPP, A. K., ET AL. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* 49:39.
- KNIPLING, E. F. 1979. *The basic principles of insect population suppression and management*. United States Department of Agriculture, Washington, D.C.
- KOTLIAR, N. B., B. J. MILLER, R. P. READING, AND T. W. CLARK. 2006. The prairie dog as a keystone species. Pp. 53–64 in *Conservation of the black-tailed prairie dog: saving North America's western grasslands* (J. L. HOOGLAND, ed.). Island Press, Washington, D.C.
- KUNZ, T. H., E. BRAUN DE TORREZ, D. BAUER, T. LOBOVA, AND T. H. FLEMING. 2011. Ecosystem services provided by bats. *Annals of the New York Academy of Sciences* 1223:1–38.
- KUNZ, T. H., J. O. WHITAKER, AND M. D. WADANOLI. 1995. Dietary energetics of the insectivorous Mexican free-tailed bat (*Tadarida brasiliensis*) during pregnancy and lactation. *Oecologia* 101:407–415.
- KUREK, P., P. KAPUSTA, AND J. HOLEKSA. 2014. Burrowing by badgers (*Meles meles*) and foxes (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest. *Ecological Research* 29:1–11.
- LABARBERA, M. 2003. *Economic importance of hunting in America*. International Association of Fish and Wildlife Agencies, Washington, D.C.
- LACHER, T. E., JR., L. BOITANI, AND G. A. B. DA FONSECA. 2012. The IUCN global assessments: partnerships, collaboration and data sharing for biodiversity science and policy. *Conservation Letters* 5:327–333.
- LACHER, T. E., JR., AND S. PYARE (eds.). 2018. *Biodiversity*, vol. 3, the encyclopedia of the Anthropocene. Elsevier, Oxford, United Kingdom.
- LACHER, T. E., JR., R. P. YOUNG, R. KENNERLEY, N. S. ROACH, S. MCCAY, AND S. T. TURVEY. 2017. Conserving the biodiversity of the largest order of mammals: priorities and actions for the Rodentia. Pp. 15–22 in *Handbook of mammals of the world*. Vol. 7. Rodents 2 (D. E. WILSON, T. E. LACHER, JR., AND R. A. MITTERMEIER, eds.). Lynx Editions, Barcelona, Spain.
- LAI, C. H., AND A. T. SMITH. 2003. Keystone status of plateau pikas (*Ochotona curzoniae*): effect of control on biodiversity of native birds. *Biodiversity and Conservation* 12:1901–1912.
- LEAVER, L. A., AND M. DALY. 2001. Food caching and differential cache pilferage: a field study of coexistence of sympatric kangaroo rats and pocket mice. *Oecologia* 128:577–584.
- LEE, Y.-F., AND G. F. MCCracken. 2005. Dietary variation of Brazilian free-tailed bats links to migratory populations of pest insects. *Journal of Mammalogy* 86:67–76.
- LEELAPAIBUL, W., S. BUMRUNGSI, AND A. PATTANAWIBOON. 2005. Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchanan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. *Acta Chiropterologica* 7:111–119.
- LEISHMAN, M. R., I. J. WRIGHT, A. T. MOLES, AND M. WESTOBY. 2000. The evolutionary ecology of seed size. Pp. 31–57 in *Seeds, the ecology of regeneration in plant communities* (M. FENNER, ed.). CABI Publishing, Wallingford, United Kingdom.
- LEVI, T., A. L. MASSEY, R. D. HOLT, F. KEESING, R. S. OSTFELD, AND C. A. PERES. 2016. Does biodiversity protect humans against infectious disease? *Comment. Ecology* 97:536–542.
- LOCK, J. M. 1972. The effect of hippopotamus grazing in grasslands. *Journal of Ecology* 60:445–467.
- LÓPEZ-HOFFMAN, L., ET AL. 2014. Market forces and technological substitutes cause fluctuations in the value of bat pest-control services for cotton. *PLoS One* 9:e87912.
- LOREAU, M., ET AL. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808.
- MAAS, B., Y. CLOUGH, AND T. TSCHARNTKE. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecology Letters* 16:1480–1487.
- MAINE, J. J., AND J. G. BOYLES. 2015. Bats initiate vital agroecological interactions in corn. *Proceedings of the National Academy of Sciences of the United States of America* 112:12438–12443.
- MANSEAU, M., J. HUOT, AND M. CRÊTE. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. *Journal of Ecology* 84:503–513.
- MARTÍNEZ-ESTÉVEZ, L., P. BALVANERA, J. PACHECO, AND G. CEBALLOS. 2013. Prairie dog decline reduces the supply of



- ecosystem services and leads to desertification of semiarid grasslands. *PLoS One* 8:e75229.
- MATA, V. A., F. AMORIM, M. F. CORLEY, G. F. MCCracken, H. REBELO, AND P. BEJA. 2016. Female dietary bias towards large migratory moths in the European free-tailed bat (*Tadarida teniotis*). *Biology Letters* 12:20150988.
- MCCAULEY, D. J., M. L. PINSKY, S. R. PALUMBI, J. A. ESTES, F. H. JOYCE, AND R. R. WARNER. 2015. Marine defaunation: animal loss in the global ocean. *Science* 347:1255641.
- MCCRACKEN, G. F., J. K. WESTBROOK, V. A. BROWN, M. ELDRIDGE, P. FEDERICO, AND T. H. KUNZ. 2012. Bats track and exploit changes in insect pest populations. *PLoS One* 7:e43839.
- MCAUGHTON, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *The American Naturalist* 124:863–886.
- MILLENNIUM ECOSYSTEM ASSESSMENT. 2005. Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, D.C.
- MILLS, J. N. 2006. Biodiversity loss and emerging infectious disease: an example from the rodent-borne hemorrhagic fevers. *Biodiversity* 7:9–17.
- MOORE, C. M., AND S. B. VANDER WALL. 2015. Scatter-hoarding rodents disperse seeds to safe sites in a fire-prone ecosystem. *Plant Ecology* 216:1137–1153.
- MORRIS, D. W., Z. ABRAMSKY, B. J. FOX, AND M. R. WILLIG. 1989. Patterns in the structure of mammalian communities. Texas Tech University Press, Lubbock.
- MULLER-LANDAU, H. C. 2007. Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica* 39:372–384.
- MURRAY, A. L., A. M. BARBER, S. H. JENKINS, AND W. S. LONGLAND. 2006. Competitive environment affects food-hoarding behavior of Merriam's kangaroo rats (*Dipodomys merriami*). *Journal of Mammalogy* 87:571–578.
- MUSCARELLA, R., AND T. H. FLEMING. 2007. The role of frugivorous bats in tropical forest succession. *Biological Reviews of the Cambridge Philosophical Society* 82:573–590.
- NAIDOO, R., B. FISHER, A. MANICA, AND A. BALMFORD. 2016. Estimating economic losses to tourism in Africa from the illegal killing of elephants. *Nature Communications* 7:13379.
- NAIMAN, R. J., C. A. JOHNSTON, AND J. C. KELLEY. 1988. Alteration of North American stream by beaver. *BioScience* 38:753–762.
- NOWAK, R. M. 1991. Walker's mammals of the world, vol. 1–2. Johns Hopkins University Press, Baltimore, Maryland.
- NUMMI, P., AND S. HOLOPAINEN. 2014. Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24:623–633.
- NUÑEZ-ITURRI, G., O. OLSSON, AND H. F. HOWE. 2008. Hunting reduces recruitment of primate-dispersed trees in Amazonian Peru. *Biological Conservation* 141:1536–1546.
- OLLERTON, J., R. WINFREE, AND S. TARRANT. 2011. How many flowering plants are pollinated by animals? *Oikos* 120:321–326.
- OSTFELD, R. S., AND F. KEESING. 2000. Biodiversity and disease risk: the case of Lyme disease. *Conservation Biology* 14:1–7.
- OWEN-SMITH, R. N. 1988. Megaherbivores. The influence of very large body size on ecology. Cambridge Studies in Ecology. Cambridge University Press, Cambridge, United Kingdom.
- OWEN-SMITH, N. 2013. Contrasts in the large herbivore faunas of the southern continents in the late Pleistocene and the ecological implications for human origins. *Journal of Biogeography* 40:1215–1224.
- PACIFICI, M., P. VISCONTI, AND C. RONDININI. 2017. A framework for the identification of hotspots of climate change risk for mammals. *Global Change Biology* 24:1626–1636.
- PALMER, T. M., M. L. STANTON, T. P. YOUNG, J. R. GOHEEN, R. M. PRINGLE, AND R. KARBAN. 2008. Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African savanna. *Science* 319:192–195.
- PARDINI, R., A. DE ARRUDA BUENO, T. A. GARDNER, P. I. PRADO, AND J. P. METZGER. 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS One* 5:e13666.
- PELLEGRINI, A. F. 2016. Nutrient limitation in tropical savannas across multiple scales and mechanisms. *Ecology* 97:313–324.
- PERES, C. A., T. EMILIO, J. SCHIETTI, S. J. M. DESMOULIÈRE, AND T. LEVI. 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America* 113:892–897.
- PERES, C. A., AND E. PALACIOS. 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* 39:304–315.
- PERES, C. A., AND M. VAN ROOSMALEN. 2002. Patterns of primate frugivory in Amazonia and the Guianan shield: implications to the demography of large-seeded plants in overhunted tropical forests. Pp. 407–423 in *Seed dispersal and frugivory: ecology, evolution and conservation* (D. LEVEY, W. SILVA, and M. GALETTI, eds.). CABI International, Oxford, United Kingdom.
- PONCE-GUEVARA, E., A. DAVIDSON, R. SIERRA-CORONA, AND G. CEBALLOS. 2016. Interactive effects of black-tailed prairie dogs and cattle on shrub encroachment in a desert grassland ecosystem. *PLoS One* 11:e0154748.
- POWER, M. E., ET AL. 1996. Challenges in the quest for keystones: identifying keystone species is difficult—but essential to understanding how loss of species will effect ecosystems. *BioScience* 46:609–620.
- PRICE, M. V., AND S. H. JENKINS. 1986. Rodents as seed consumers and dispersers. Pp. 191–235 in *Seed dispersal* (D. R. MURRAY, ed.). Academic Press, Sydney, New South Wales, Australia.
- PRICE, M. V., AND J. E. MITTLER. 2006. Cachers, scavengers, and thieves: a novel mechanism for desert rodent coexistence. *The American Naturalist* 168:194–206.
- PRINGLE, R. M. 2008. Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology* 89:26–33.
- PUIG-MONTERRAT, X., ET AL. 2015. Pest control service provided by bats in Mediterranean rice paddies: linking agroecosystems structure to ecological functions. *Mammalian Biology* 80:237–245.
- RAY, J. D., N. E. MCINTYRE, M. C. WALLACE, A. P. TEASCHNER, AND M. G. SCHOENHALS. 2016. Factors influencing burrowing owl abundance in prairie dog colonies on the southern high plains of Texas. *Journal of Raptor Research* 50:185–193.
- REGAN, E. C., ET AL. 2015. Global trends in the status of bird and mammal pollinators. *Conservation Letters* 8:397–403.
- REISKIND, M. H., AND M. A. WUND. 2009. Experimental assessment of the impacts of northern long-eared bats on ovipositing *Culex* (Diptera: Culicidae) mosquitoes. *Journal of Medical Entomology* 46:1037–1044.
- RICKLEFS, R. E. 2008. Disintegration of the ecological community. *The American Naturalist* 172:741–750.

- RIPPLE, W. J., ET AL. 2014a. Status and ecological effects of the world's largest carnivores. *Science* 343:1241484.
- RIPPLE, W. J., ET AL. 2015. Collapse of the world's largest herbivores. *Science Advances* 1:e1400103.
- RIPPLE, W. J., AND R. L. BESCHTA. 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation* 133:397–408.
- RIPPLE, W. J., AND R. L. BESCHTA. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation* 145:205–213.
- RIPPLE, W. J., R. L. BESCHTA, J. K. FORTIN, AND C. T. ROBBINS. 2014b. Trophic cascades from wolves to grizzly bears in Yellowstone. *The Journal of Animal Ecology* 83:223–233.
- RIPPLE, W. J., ET AL. 2016. Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science* 3:160498.
- ROMAN, R. J. A., ET AL. 2014. Whales as marine ecosystem engineers. *Frontiers in Ecology and Environment* 12:377–385.
- ROOT-BERNSTEIN, M., AND L. A. EBENSBERGER. 2013. Meta-analysis of the effects of small mammal disturbances on species diversity, richness and plant biomass. *Austral Ecology* 38:289–299.
- ROSIN, C., AND J. R. POULSEN. 2016. Hunting-induced defaunation drives increased seed predation and decreased seedling establishment of commercially important tree species in an Afrotropical forest. *Forest Ecology and Management* 382:206–213.
- ROTH, J. K., AND S. B. VANDER WALL. 2005. Primary and secondary seed dispersal of bush chinquapin (Fagaceae) by scatterhoarding rodents. *Ecology* 86:2428–2439.
- RUSSO, S. E., AND C. K. AUGSPURGER. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Viola calophylla*. *Ecology Letters* 7:1058–1067.
- SCHIPPER, J., ET AL. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322:225–230.
- SDG. 2017. The sustainable development goals report. United Nations, New York. <https://unstats.un.org/sdgs/files/report/2017/TheSustainableDevelopmentGoalsReport2017.pdf>. Accessed 20 July 2017.
- SEAGLE, S. W., AND S. J. McNAUGHTON. 1992. Spatial variation in forage nutrient concentrations and the distribution of Serengeti ungulates. *Landscape Ecology* 7:229–241.
- SINCLAIR, A. R. E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. *Journal of Animal Ecology* 44:497–520.
- ŠKLÍBA, J., M. JIRK, AND R. ŠUMBERA. 2016. Burrow systems of mole-rats as refuges for frogs in the miombo woodlands of south-east Africa. *Journal of Tropical Ecology* 32:158–161.
- SMITH, J. M., AND M. E. MATHER. 2013. Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. *Freshwater Biology* 58:1523–1538.
- SORK, V. L. 1983. Mast-fruiting in hickories and availability of nuts. *American Midland Naturalist* 109:81–88.
- SORK, V. L. 1984. Examination of seed dispersal and survival in red oak, *Quercus rubra* (Fagaceae), using metal-tagged acorns. *Ecology* 65:1020–1022.
- SPEAKMAN, J. R., AND D. W. THOMAS. 2003. Physiological ecology. Pp. 430–480 in *Bat ecology* (T. H. KUNZ AND M. B. FENTON, eds.). University of Chicago Press, Chicago, Illinois.
- STEELE, M. A., P. D. SMALLWOOD, A. SPUNAR, AND E. NELSEN. 2001. The proximate basis of the oak dispersal syndrome: detection of seed dormancy by rodents. *American Zoologist* 41:852–864.
- STENECK, R. S. 2012. Apex predators and trophic cascades in large marine ecosystems: learning from serendipity. *Proceedings of the National Academy of Sciences of the United States of America* 109:7953–7954.
- STIER, A. C., ET AL. 2016. Ecosystem context and historical contingency in apex predator recoveries. *Science Advances* 2:e1501769.
- SUBALUSKY, A. L., C. L. DUTTON, E. J. ROSI-MARSHALL, AND D. M. POST. 2015. The hippopotamus conveyor belt: vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa. *Freshwater Biology* 60:512–525.
- SUSSMAN, R. W., D. TAB RASMUSSEN, AND P. H. RAVEN. 2013. Rethinking primate origins again. *American Journal of Primatology* 75:95–106.
- SYMONDSON, W. O., K. D. SUNDERLAND, AND M. H. GREENSTONE. 2002. Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47:561–594.
- TEEB. 2010. The economics of ecosystems and biodiversity, ecological and economic foundations (P. KUMAR, ed.). Earthscan, London, United Kingdom and Washington, D.C.
- TORTATO, F. R., T. J. IZZO, R. HOOGESTEIJN, AND C. A. PERES. 2017. The numbers of the beast: valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. *Global Ecology and Conservation* 11:106–114.
- TSCHAPKA, M., AND S. DRESSLER. 2002. Chiropterophily: on bat-flowers and flower-bats. *Curtis's Botanical Magazine* 19:114–125.
- TUTIN, C. E., R. M. HAM, L. J. WHITE, AND M. J. HARRISON. 1997. The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology* 42:1–24.
- VANDER WALL, S. B. 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. *Ecology* 75:1911–1926.
- VANDER WALL, S. B. 1997. Dispersal of singleleaf pinon pine (*Pinus monophylla*) by seed-caching rodents. *Journal of Mammalogy* 78:191.
- VANDER WALL, S. B. 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology* 11:544–549.
- VANDER WALL, S. B. 2001. The evolutionary ecology of nut dispersal. *Botanical Review* 67:74–117.
- VANDER WALL, S. B. 2002. Masting in animal-dispersed pine facilitates seed dispersal. *Ecology* 83:3508–3516.
- VANDER WALL, S. B. 2008. On the relative contributions of wind vs. animals to seed dispersal of four Sierra Nevada pines. *Ecology* 89:1837–1849.
- VANDER WALL, S. B., AND S. H. JENKINS. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology* 14:656–667.
- VANDER WALL, S. B., AND W. S. LONGLAND. 2004. Diplochory: are two seed dispersers better than one? *Trends in Ecology & Evolution* 19:155–161.
- WALDRAM, M. S., W. J. BOND, AND W. D. STOCK. 2008. Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems* 11:101–112.
- WANGER, T. C., K. DARRAS, S. BUMRUNGSRI, T. TSCHARNTKE, AND A. M. KLEIN. 2014. Bat pest control contributes to food security in Thailand. *Biological Conservation* 171:220–223.
- WARREN, L. S. 1997. *The hunter's game: poachers and conservationists in twentieth-century America*. Yale University Press, New Haven, Connecticut.
- WATSON, A. J. 2016. Oceans on the edge of anoxia. *Science* 354:1529–1530.

- WEBB, C. O., AND D. R. PEART. 2001. High seed dispersal rates in faunally intact tropical rain forest: theoretical and conservation implications. *Ecology Letters* 4:491–499.
- WHICKER, A. D., AND J. K. DETLING. 1998. Ecological consequences of prairie dog disturbances. *BioScience* 38:778–785.
- WHITAKER, J. O. 1995. Food of the big brown bat *Eptesicus fuscus* from maternity colonies in Indiana and Illinois. *The American Midland Naturalist* 134:346–360.
- WHITAKER, J. O., JR., G. F. MCCracken, AND B. M. SIEMERS. 2009. Food habits analysis of insectivorous bats. Pp. 565–592 in *Ecological and behavioral methods for the study of bats* (T. H. KUNZ AND S. PARSONS, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.
- WHITAKER, J. O., C. NEEFUS, AND T. H. KUNZ. 1996. Dietary variation in the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). *Journal of Mammalogy* 77:716–724.
- WHITTINGTON-JONES, G. M. 2007. The role of aardvarks (*Orycteropus afer*) as ecosystem engineers in arid and semi-arid landscapes of South Africa. M.Sc. thesis, Rhodes University, Grahamstown, South Africa.
- WIEDERHOLT, R., ET AL. 2014. Optimizing conservation strategies for Mexican free-tailed bats: a population viability and ecosystem services approach. *Biodiversity and Conservation* 24:63–82.
- WILES, G. J., AND A. P. BROOKE. 2009. Conservation threats to bats in the Pacific islands and insular Southeast Asia. Pp. 405–459 in *Island bats: evolution, ecology, and conservation* (T. H. FLEMING AND P. A. RACEY, eds.). University of Chicago Press, Chicago, Illinois.
- WILKINSON, G. S., AND J. M. SOUTH. 2002. Life history, ecology and longevity in bats. *Aging Cell* 1:124–131.
- WILLIAMS, J. W., AND S. T. JACKSON. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.
- WILLIAMS-GUILLÉN, K., I. PERFECTO, AND J. VANDERMEER. 2008. Bats limit insects in a neotropical agroforestry system. *Science* 320:70.
- WILSON, D. E. 2009. Class mammalia (Mammals). Pp. 17–47 in *Handbook of the mammals of the world* (D. E. WILSON AND R. A. MITTERMEIER, eds.). Lynx Edicions, Barcelona, Spain.
- WILSON, M. C., AND A. T. SMITH. 2014. The pika and the watershed: the impact of small mammal poisoning on the ecohydrology of the Qinghai-Tibetan Plateau. *Ambio* 44:16–22.
- WOOLLER, R. D., K. C. RICHARDSON, AND B. G. COLLINS. 1993. The relationship between nectar supply and the rate of capture of a nectar-dependent small marsupial *Tarsipes rostratus*. *Journal of Zoology* 229:651–658.
- WORM, B., AND R. T. PAINE. 2016. Humans as a hyperkeystone species. *Trends in Ecology & Evolution* 31:600–607.
- WRAY, A. K., ET AL. 2018. Incidence and taxonomic richness of mosquitoes in the diets of little brown and big brown bats. *Journal of Mammalogy* 99:668–674.
- WRIGHT, J. P., C. G. JONES, AND A. S. FLECKER. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101.
- WRIGHT, S. J., H. ZEBALLOS, I. DOMINGUEZ, M. M. GALLARDO, M. C. MORENO, AND R. IBÁÑEZ. 2000. Poachers alter mammal abundance, seed dispersal and seed predation in a Neotropical forest. *Conservation Biology* 14:227–239.
- YOSHIHARA, Y., T. OHKURO, B. BAYARBAATAR, AND K. TAKEUCHI. 2009. Effects of disturbance by Siberian marmots (*Marmota sibirica*) on spatial heterogeneity of vegetation at multiple spatial scales. *Grassland Science* 55:89–95.
- YOSHIHARA, Y., T. OHKURO, B. BUUVEIBAATAR, J. UNDARMAA, AND K. TAKEUCHI. 2010. Pollinators are attracted to mounds created by burrowing animals (marmots) in a Mongolian grassland. *Journal of Arid Environments* 74:159–163.
- YOUNG, H. S., ET AL. 2014. Declines in large wildlife increase landscape-level prevalence of rodent-borne disease in Africa. *Proceedings of the National Academy of Sciences of the United States of America* 111:7036–7041.
- YOUNG, H. S., ET AL. 2016. Large wildlife removal drives immune defense increases in rodents. *Functional Ecology* 30:799–807.
- ZEALE, M. R., R. K. BUTLIN, G. L. BARKER, D. C. LEES, AND G. JONES. 2011. Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. *Molecular Ecology Resources* 11:236–244.
- ZERO, V. H., AND M. A. MURPHY. 2016. An amphibian species of concern prefers breeding in active beaver ponds. *Ecosphere* 7:1–13.

Submitted 30 January 2018. Accepted 3 January 2019.

Special Issue Editor was Michael R. Willig.