Patterns, Causes, and Consequences of Anthropocene Defaunation

Hillary S. Young,[1] Douglas J. McCauley,[1]
Mauro Galetti,[2] and Rodolfo Dirzo[3]

[1]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106

[2]Departamento de Ecologia, Universidade Estadual Paulista (UNESP), 13506–900 Rio Claro, São Paulo, Brazil

[3]Department of Biology, Stanford University, Stanford, California 94305; email: rdirzo@stanford.edu

Annu. Rev. Ecol. Evol. Syst. 2016. 47:333–58

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev-ecolsys-112414-054142

Keywords

animal conservation, defaunation cascades, animal overexploitation, terrestrial fauna, marine fauna, freshwater fauna

Abstract

Anthropocene defaunation, the global extinction of faunal species and populations and the decline in abundance of individuals within populations, has been predominantly documented in terrestrial ecosystems, but indicators suggest defaunation has been more severe in freshwater ecosystems. Marine defaunation is in a more incipient stage, yet pronounced effects are already apparent and its rapid acceleration seems likely. Defaunation now impacts the planet's wildlife with profound cascading consequences, ranging from local to global coextinctions of interacting species to the loss of ecological services critical for humanity. Slowing defaunation will require aggressively reducing animal overexploitation and habitat destruction; mitigating climate disruption; and stabilizing the impacts of human population growth and uneven resource consumption. Given its omnipresence, defaunation should receive status of major global environmental change and should be addressed with the same urgency as deforestation, pollution, and climatic change. Global action is needed to prevent defaunation's current trajectory from catalyzing the planet's sixth major extinction.

1. INTRODUCTION

The term defaunation was first given a conservation biology connotation when it was used to describe the impact of human activities on mammal communities and its subsequent cascading effects on tropical forests (Dirzo & Miranda 1991). Since then, the term has become an increasingly visible concept in conservation science, initially associated with the motif of the empty forest (Redford 1992) and ultimately amplified by a series of directed studies and syntheses (Dirzo et al. 2014, Galetti & Dirzo 2013, McCauley et al. 2015b, Stoner et al. 2007).

Understanding the scale and consequences of defaunation is now a growing priority for ecologists, wildlife managers, and conservation biologists. In this review, we synthesize the global state of both vertebrate and invertebrate animal life in the Anthropocene, focusing on the salient patterns, causes, and consequences of the contemporary pulse of defaunation. Although the world's ecosystems were deeply influenced by massive Pleistocene losses of megafauna (at least partially activated by humans; see Malhi et al. 2016), our review concentrates on more contemporary defaunation. We conclude with a discussion of research gaps and actions that need to be undertaken to prevent the current momentum of defaunation from propelling us into the sixth major extinction in the Phanerozoic.

2. THE CONTEMPORARY DIVERSITY OF ANIMAL LIFE

Despite five major pulses of extinction, animal life has exhibited a relentless diversification throughout the Phanerozoic, peaking in diversity in contemporary times. Estimates of the contemporary faunal diversity on the planet vary widely. Approximately one million animal species have already been described, and predictions suggest that as many as seven times more animal species are yet to be described (IUCN 2015, Mora et al. 2011). Our sustained ignorance of the tree of animal life is well reflected in discovery rates such as those documented in the Amazon region, where during the period 1999–2009, 257 new species of fish, 216 amphibians, 55 reptiles, 16 birds, 39 mammals, and several thousand invertebrates, mostly insects, were discovered (Thompson & WWF 2010). New discoveries include such ecologically or evolutionarily distinctive species as an herbivorous piranha (Andrade et al. 2013); the smallest tetrapods known to Earth, salamanders in the genus *Thorius*, which are only 2.3 cm long (Hanken & Wake 1994); and a new order of Insecta, Mantophasmatodea, which is the only new order discovered since 1914 (Klass et al. 2002). Even within mammals, one of the best-studied animal groups, discoveries include, remarkably, a new 110-kg tapir (Cozzuol et al. 2013).

Animal diversity is clearly substantially higher on land than in the oceans (Costello 2015, Mora et al. 2011), despite the fact that terrestrial ecosystems compose only 30% of the Earth's surface and were colonized much later. We, however, know far less about animal diversity in the oceans. Ten new species of cetaceans were described in recent decades, and in the last several years new animal phyla (e.g., Xenacoelomorpha) have been proposed. Yet as much as 92% of marine fauna still await description (Just et al. 2014, Philippe et al. 2011).

Freshwater ecosystems harbor the least total number of species, likely due to this realm's smaller proportional size (Dudgeon et al. 2006). For certain freshwater taxa, however, global species richness is not dissimilar from that of marine ecosystems. The number of ray-finned fishes, for example, is roughly similar in both the oceans and freshwater systems (Vega & Wiens 2012).

However, the exuberant animal diversity known to date and the rates of new discoveries need to be seen against the alarming trends of defaunation we are beginning to uncover, as we describe in the next section.

3. CHARACTERIZING DEFAUNATION

3.1. Scales of Defaunation

The modern process of defaunation can be alarmingly obvious or surprisingly cryptic, depending on the scale examined. It is thus important to distinguish three interrelated spatial scales of defaunation.

3.1.1. Global extinction. At a global scale, human-associated extinction of animal life on the planet is profound. Modern rates of vertebrate extinctions have been estimated to be up to 100 times greater than the most conservative background rates of ∼2 vertebrate extinctions per million species per year (Ceballos et al. 2015). Although most of the extinctions to date have been documented in terrestrial ecosystems (e.g., 338 vertebrates since the year 1500) (IUCN 2015), the highest proportion of extinctions has been recorded in freshwater ecosystems (Collen et al. 2014). Marine ecosystems, by comparison, lag much further behind, with only ∼15 marine animal extinctions recorded during this same time period (McCauley et al. 2015b).

Regarding invertebrates, information on global extinctions (or defaunation in general) is very limited (**Supplemental Figure 1;** follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**), but recent efforts on the levels of threat to species in the International Union for Conservation of Nature (IUCN) Red List (Collen et al. 2012) provide some insights. Of the 3,623 terrestrial invertebrate species assessed on the Red List, 42% are classified as threatened with extinction. Of the 1,306 species of marine invertebrates on the Red List, close to 25% are threatened with extinction. Finally, of the 7,784 species of freshwater invertebrates on the Red List, 34% are listed as threatened, but the Red List includes 131 species classified as extinct. Invertebrates, however, are the least well-evaluated faunal groups within the IUCN database, making it challenging to determine precisely the risks faced by data-deficient and unreviewed species (Dirzo et al. 2014, McCauley et al. 2015b).

Supplemental Material

3.1.2. Population extinctions and range contractions. Anthropogenic disturbance has eradicated many animal populations. In some cases such populations are genetically unique, frequently showing phenotypic differences as marked as those between different species. However, our understanding of animal population extinctions is still very limited, and estimations are largely based on assessments of species range contractions. A study using a sample of 86 species (Hughes et al. 1997) suggested that, assuming population extinction is a linear function of habitat loss, as many as 16 million populations (including many animal species populations) are destroyed annually in tropical forests alone. Another study of 173 mammalian species suggests an average loss of approximately 50% of their historic ranges (Ceballos & Ehrlich 2002). Likewise, a study of 25 of the world's largest herbivores found they currently occupy on average only 19% of their historical range (Ripple et al. 2015). Although a large number of species in certain marine faunal assemblages (e.g., large pelagic fishes) have experienced range declines, the median sizes of such contractions are generally smaller in the oceans than those observed on land (McCauley et al. 2015b).

3.1.3. Local declines in abundance. A third major component of defaunation is the decline in individuals within populations. Among vertebrates, the most recent data indicate a mean decline of 52% of individuals (ranging from 39% in terrestrial and marine animals to 76% in freshwater animals) in just the past four decades (McLellan et al. 2014). Although invertebrate biodiversity has been poorly tracked, available evidence suggests that invertebrates have fared no better. For instance, long-term monitoring data on a sample of 452 terrestrial invertebrate species show an overall 45% decline in abundance since 1970 (Dirzo et al. 2014).

Although marine fauna are sometimes buffered from localized declines in abundance because of their increased dispersal potential, pronounced declines in local abundance have been widely observed. Shark species along the US eastern seaboard have declined by more than 90% (Myers et al. 2007), certain great whale species frequenting the North Pacific Ocean by 80–90% (Springer et al. 2003), and Coho salmon populations in California by 90% (Brown et al. 1994). Similarly large declines have been observed in certain marine invertebrates. Reef-building corals are the only group of invertebrate fauna (land or sea) to have been comprehensively assessed by the IUCN, and they are experiencing some of the most extreme declines of any taxa: Approximately one third were determined to be threatened with extinction (Carpenter et al. 2008, IUCN 2015).

3.2. Chronology of Defaunation

In many cases, a general three-phase process of defaunation is observable (McCauley et al. 2015b). In the first phase humans harvest animals directly from ecosystems using simple technologies, and basic animal products (e.g., meat, hides) are directly consumed. In the second phase humans adopt more sophisticated harvest technologies (e.g., firearms, powered fishing nets), facilitating higher faunal biomass yields that are often traded in national and international markets. A third stage typically involves a shift to aggressively harvesting or making use of the animal communities' ecological space. This includes such activities as usurping habitats for urban or agricultural expansion and excavation of land/seabed for mineral or energy products. All three phases can profoundly influence animal populations. Low-tech artisanal hunting was involved in multiple continent-wide megafaunal extinctions during the Pleistocene (Koch & Barnosky 2006), whereas industrial-scale, higher-tech hunting drove some of the planet's most prolific species (e.g., passenger pigeon) to extinction. However, the third phase, habitat change, is often regarded as the most broadly impactful stage of defaunation (Dirzo et al. 2014, Pimm et al. 2014).

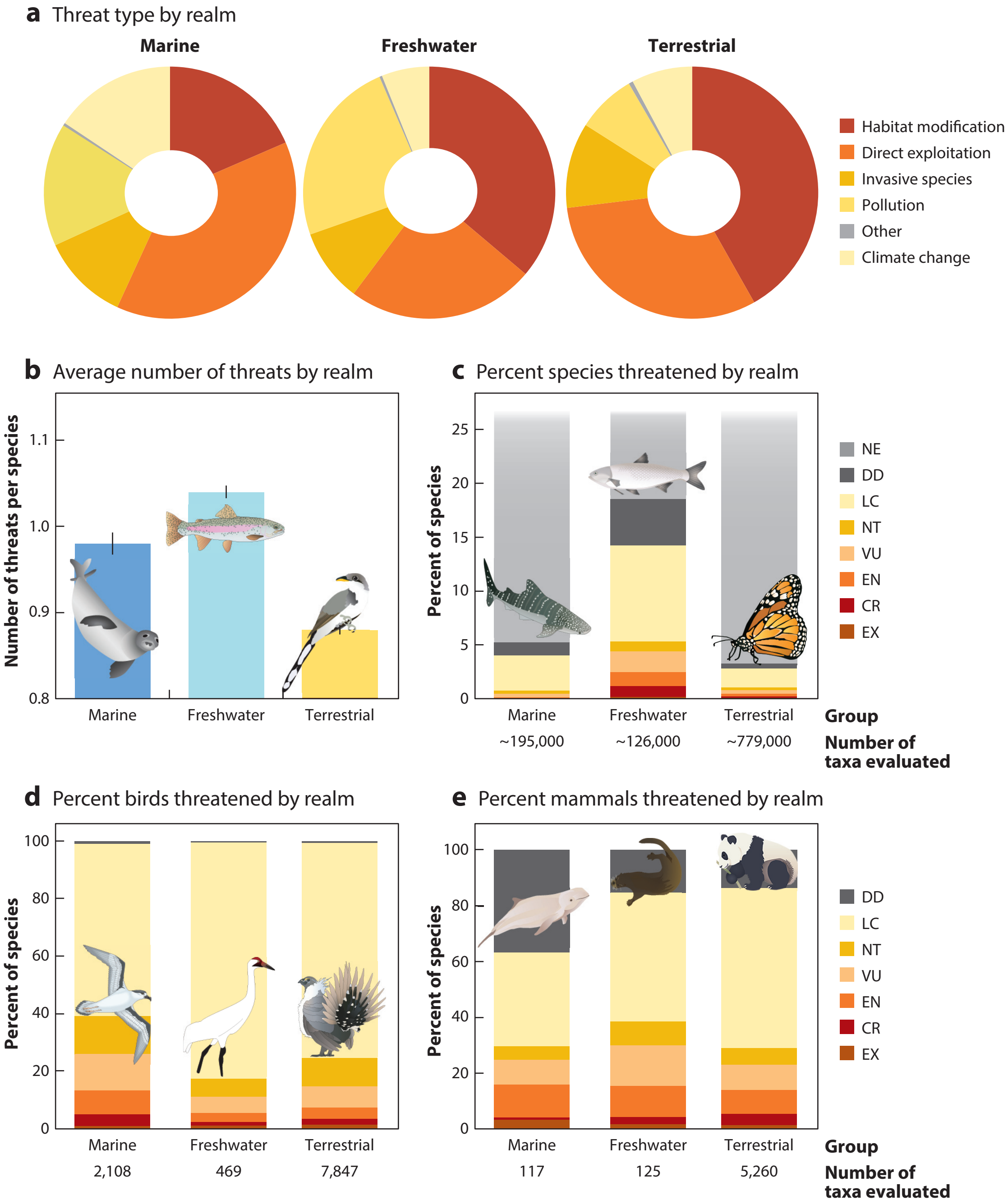
Observations across realms suggest that this three-stage defaunation chronology is more advanced in terrestrial and freshwater ecosystems than in marine ecosystems. Although there has been a deep history of artisanal defaunation in the oceans, by most views marine defaunation appears to have only entered the second phase of animal loss 50 to 100 years ago, when industrial harvest technologies (e.g., sonar, high-powered diesel engines) came online. Direct harvest (e.g., overfishing) is cited as the most prominent contemporary driver of defaunation in the global oceans (**Figure 1*a***) (Jackson et al. 2001). Terrestrial and freshwater realms, where habitat alteration is the most prominent defaunation driver (**Figure 1*a***), entered into the third phase centuries ago during the Industrial Revolution, when space and resources were needed for the expansion of cities and industry. Some of these same kinds of habitat-altering changes have deeply influenced fauna in highly

Figure 1

The threats to animals across the marine, terrestrial, and freshwater realms. (*a*) The relative importance of various threats, as defined by the International Union for Conservation of Nature (IUCN), differs by realm. (*b*) Only species in freshwater ecosystems have, on average, more than one stressor reported per species. (*c*) The freshwater realm also has the highest proportion of animal species listed as threatened, although this may be partially due to having a higher proportion of species evaluated. This pattern is not apparent when using only (*d*) birds and (*e*) mammals, which are both well-evaluated taxa and occur in all three realms. Abbreviations for IUCN categories: NE, not evaluated; DD, data deficient; LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; and EX, extinct (we also include species that are extinct in the wild). Numbers below bars on panels *c* to *e* indicate the number of taxa evaluated. Details on data compilation are provided in the **Supplemental Material Section 1**.

Supplemental Material

accessible coastal marine ecosystems (e.g., mangroves, estuaries, and seagrass beds) that neighbor coastal settlements where a large proportion of the human population lives (Small & Nicholls 2003). We are, however, only now beginning to build technological capacity to significantly modify offshore marine habitats via activities like aquaculture, bottom trawling, and marine mining.



3.3. Patterns of Modern Defaunation

Anthropogenic impacts are already affecting most groups of organisms; in this section we examine patterns of differential geographic and life history susceptibility to defaunation.

3.3.1. Geographic and biome-level patterns of defaunation.

Numerous efforts to map the geography of past and future threats to animal biodiversity have been made. Analyses that focus on the number of species declining find that defaunation is greatest in tropical regions (e.g., moist tropical forests), because of their elevated faunal diversity (Dirzo et al. 2014, Jenkins et al. 2013). However, even when controlling for species richness patterns, all maps of risk for terrestrial vertebrates include hot spots in Southeast Asia, South America, and central Africa. Our ability to make such maps for the marine realm lags behind. Preliminary efforts suggest that human impacts are greatest on the continental shelf/slope and are especially elevated in the North Sea, South and East China Seas, and the eastern seaboard of the United States (Halpern et al. 2008). Freshwater hot spots of faunal diversity and elevated risk include the Mekong, Congo, and Amazon River basins (Dudgeon et al. 2006, Winemiller et al. 2016). Fauna in freshwater ecosystems are experiencing the highest rates of defaunation by most metrics (**Figure 1*b*,*c***). For example, nine times more bony fishes are threatened with extinction in freshwater than marine biomes; additionally, whereas in the last 515 years 65 freshwater bony fish species have gone extinct, none has been documented as extinct in the marine realm (IUCN 2015). In North America, extinction rates for freshwater fauna are predicted to be five times higher than those for the continent's terrestrial fauna (Ricciardi & Rasmussen 1999). Global analyses suggest that freshwater species have declined 76% since 1970, nearly twice the rate observed for marine or terrestrial species (McLellan et al. 2014). The disproportionately high risk observed for freshwater fauna can be partially explained because, unlike oceans, many freshwater ecosystems are embedded near centers of human population activity. As such, freshwater fauna are often exposed to multiple stressors (**Figure 1*b***), including heavy physical modification, extensive water extraction, high rates of species invasions, and highly concentrated exposure to pollutants (Dudgeon et al. 2006).

Insular defaunation is prominent; examples include the loss and threat of faunas from islands in the ocean (Manne et al. 1999, Tershy et al. 2015) as well as the threat of faunas inhabiting other types of isolated ecosystems (e.g., lakes, mountaintops). A recent analysis of birds (White & Bennett 2015) found that species with high elevation requirements (e.g., those living on altitudinal islands) are more likely to be threatened. Many freshwater ecosystems (e.g., lakes, vernal pools) act as aquatic islands, further explaining their observed vulnerability (Collen et al. 2014).

Species that use multiple ecosystems or are extremely wide ranging are also experiencing an elevated threat (McCauley et al. 2015b). For example, seabirds, which use both terrestrial and marine habitats, have shown a 70% decline in abundance over the last 60 years (Paleczny et al. 2015), with the largest declines shown in families containing wide-ranging pelagic species.

3.3.2. Life history patterns of loss.

Several important conclusions emerge from the rich literature that has attempted to identify predictors of faunal extinction. First, life history predictors of extinction clearly vary strongly across taxa (Cardillo et al. 2008, Purvis et al. 2000b), and frequently the best predictors are highly taxon specific. Nevertheless, consistently identified predictors of extinction vulnerability include (*a*) fecundity (Cardillo 2003); (*b*) home range size (Purvis et al. 2000b); (*c*) activity/diet patterns (Liow et al. 2009); (*d*) trophic level (Purvis et al. 2000b); (*e*) specialization and relative brain size (Shultz et al. 2005); (*f*) body size (Cardillo 2003); and (*g*) population size (Cardillo et al. 2005). As anthropogenic climate disruption advances, thermal tolerance will likely be a key addition to this list (Frishkoff et al. 2015).

Identifying predictors of population declines, even within a taxonomic group, has been less commonly attempted and has found fewer generalities than assessing extinction risk. At a global scale, an analysis of risk factors across mammals found intrinsic biological traits to have low ability to predict declines (Collen et al. 2011). At a local scale, however, Newbold et al. (2013) found life history traits in tropical forest birds to accurately predict abundance changes. Pocock (2011) was similarly able to identify traits of passerine birds within a landscape that predicted population declines; however, the important traits varied locally, such that they had little overall predictive capacity. The biological correlates of population decline have also been found to vary substantially based on the type of threat observed in a range of other taxa (e.g., Isaac & Cowlishaw 2004). Thus, predictive capacity for decline seems to be much more taxon and locality specific. For instance, Sirot et al. (2015) found that in fish, spawning season, order, maximum salinity, width of salinity range, and oocyte size were the important correlates of fish population declines.

Our inability to resolve a consistent set of universal predictors of defaunation, particularly on local scales, makes intuitive sense. Century-long attempts to identify traits that integrate across large spatial scales and broad taxonomic groups may obscure the dynamism of the ever-changing defaunation risk landscape.

4. DRIVERS OF DEFAUNATION

The drivers of defaunation range from threats that operate at global scales, such as climate change and ocean pollution, to those that are more local, including direct harvest and habitat conversion. The relative importance of each threat varies by region and habitat type and also changes over time. In this section, we separately address the predominant drivers of defaunation but emphasize that they often interact in complex, synergized ways (Peres 2001).

4.1. Legal and Illegal Direct Harvest and Overexploitation

One of the most prominent drivers of defaunation is direct harvesting, whether for food, medicine, animal objects, or the pet trade. The relative importance of these motivators varies, and they are frequently interrelated. Estimates of harvest rates are often extremely high—for example, 5 million tons of bushmeat are harvested annually across Afrotropical rainforests (Fa et al. 2002) (see **Supplemental Figure 2**). Such harvest data, however, typically include only large- and medium-sized species that are used for food (Galetti & Dirzo 2013), and we often lack information on the magnitude of defaunation for traditional medicine and live animal trade (but see McClenachan et al. 2016).

Supplemental Material

Although information on illegal trading is limited, we have compiled data from 14 independent studies (see details and references in **Supplemental Material Section 2**) in which local inhabitants provided information about the purpose of their hunting. These studies reveal that in most localities hunting is practiced primarily, if not exclusively, for commercial value (**Figure 2*a***). By contrast, in only two of the sites, Serengeti National Park, Tanzania, and Manu National Park, Peru, was hunting predominantly for subsistence. At Manu National Park, an area inhabited by an indigenous group where no guns are used, recent work (Levi et al. 2009) shows that such hunting of the spider monkey population can be continued sustainably. However, our review indicates that such traditional subsistence hunting practices are globally rare.

A synthesis of seizure data (a proxy for data on illegal trading) from 2010 to 2015 (derived from *Traffic Bulletin*; see details in **Supplemental Material Section 2**) revealed a total of 1,300 registered seizures worldwide, representing 81 million kg of animal biomass. Approximately 73% of the biomass originated in Africa, with Asia being the destination for 60% of the biomass.

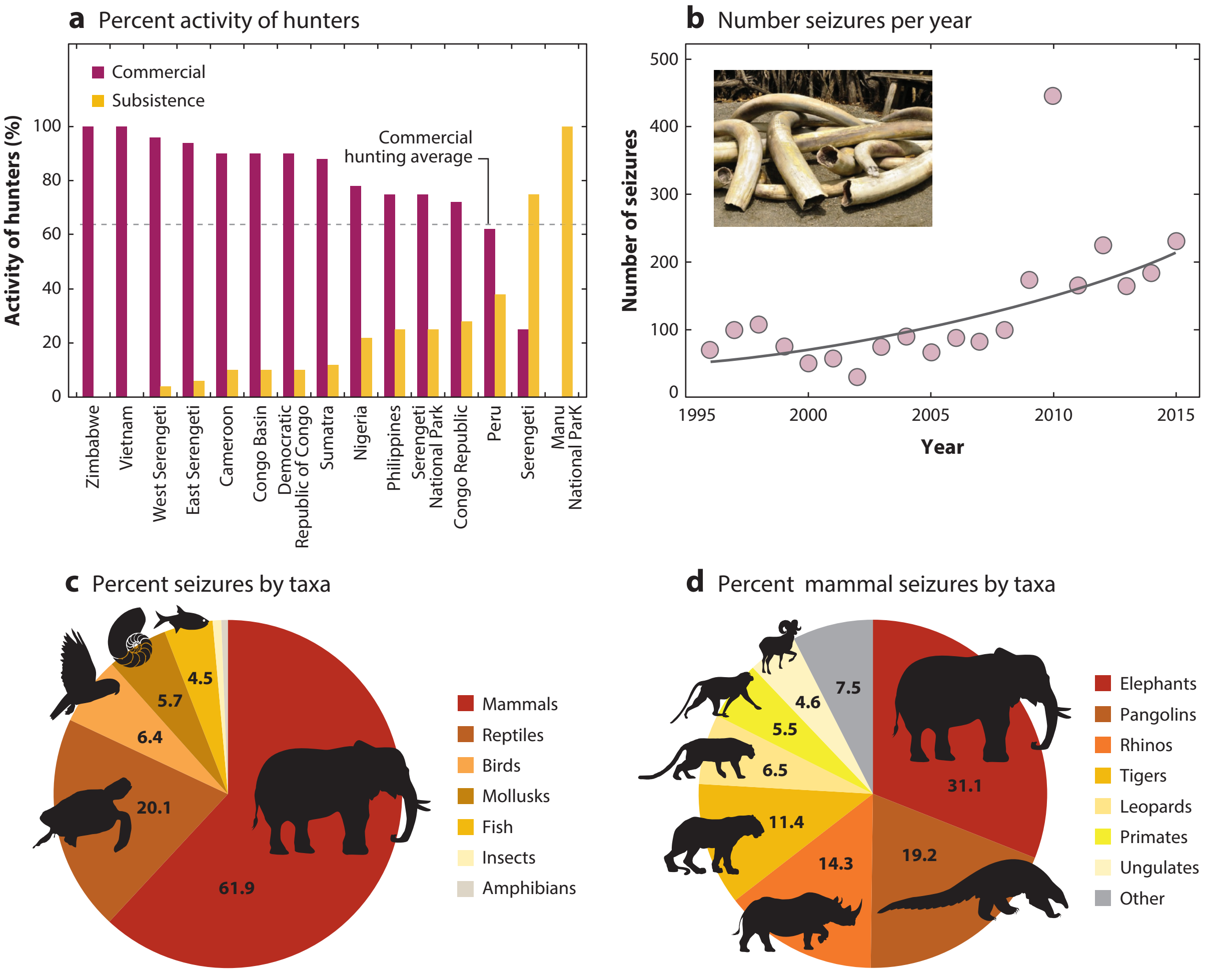


Figure 2

Data from a suite of 14 hunting studies from a range of sites (see references in **Supplemental Material Section 2**). (*a*) These data show the dominance of commercial as compared with subsistence hunting at most sites. (*b*) Data about the number of annual seizures of trafficked wildlife products show a pattern of increasing seizures over time, which is likely indicative of increases in the trade of wildlife products. (*c*) Most products seized originate from mammals. (*d*) Among mammals, elephants followed by pangolins represent the most frequently seized species.

Supplemental Material

Nine Asian nations and the Congo (a likely transit point for ivory) represent the top destination countries, followed by the United States. China alone accounts for 64% of all seizures, and illegal trading does not show evidence of decline or stabilization (**Figure 2*b***), although it remains to be seen if and to what extent this is influenced by an increased effort to detect illegal trading, an aspect that warrants further research. In monetary terms, estimates of the amount of illegal trade as a proportion of total animal trade ranged from 25% to 70% ($13.2 to $37 billion) in 2014. Mammals are the most trafficked group, followed by reptiles (**Figure 2*c***). Elephant trading dominates, followed by pangolins (**Figure 2*d***), which are used for putatively medicinal purposes. Pangolins are now regarded as the most traded terrestrial wild animal, despite the fact that their trade is illegal according to international law.

Wild marine animals are some of the most widely, legally traded food commodities in the world (FAO 2014). The United States, for example, obtains $5 billion in revenue annually from the sale of meat from wild marine fauna, provides more than half a billion dollars a year in government subsidies to foster the capture of marine wildlife, and designs maximum sustainable yield policies intended to explicitly reduce many marine animal populations by up to 50–75% (NOAA 2013, Sharp & Sumaila 2009, Worm et al. 2009). Although this trade in marine wildlife provides highly nutritious food to poor and rich countries alike, the dichotomous ways by which societies view global trade in marine and terrestrial wildlife are striking: Wild marine fishes from Peru or Kenya are a staple in supermarkets of the global north, but wild forest fauna would not be tolerated in this area.

Another major difference in direct harvest patterns in the oceans is that marine faunal harvest is more taxonomically and trophically comprehensive. Humans still actively hunt some of the largest animals in the ocean (e.g., cetaceans, pinnipeds, tuna), but we also heavily target (and actively deplete) faunal subjects whose terrestrial analogs are largely ignored: We aggressively harvest krill (~180,000 tons/year globally) and anchovies (an ~US$1.7 billion/year industry in Peru) but do not, for example, industrially harvest and internationally trade grasshoppers and rodents (Christensen et al. 2014, FAO 2012).

Illegal harvest of wildlife is also equally severe in the oceans and freshwater biomes. Some of the world's most endangered freshwater fauna, such as new world and old world sturgeon, are critically threatened by illegal harvest (Cohen 1997). In the oceans, illegal fishing amounts to a multibillion-dollar trade annually and involves millions of tons of faunal biomass (Agnew et al. 2009). The black market trade in marine fauna is fostered by a lack of capacity to transparently identify and track fishing vessels and their landed product, by seafood mislabeling, and, as on land and freshwater realms, by the involvement of organized crime syndicates (Brashares et al. 2014). Nontarget mortality is also a major issue in the form of the unintended or unwanted bycatch of animals that often have little or no commercial value (e.g., sea turtles, marine mammals, seabirds) (Lewison et al. 2014).

4.2. Habitat Loss and Modification

Habitat loss and modification (e.g., agricultural/aquaculture development, urbanization, road development, logging, and terrestrial and marine mining) is consistently cited as a dominant driver of defaunation, at least in terrestrial contexts (Collen et al. 2014). It is estimated that ~40% of the Earth's land surface is now used as cropland and pasture (Foley et al. 2005), 64 million km of roads now crisscross the world's ecosystems (Laurance et al. 2014), and 129 million ha of global forest have been lost since 1990 (FAO 2015). Only 12% of the world's dense tropical forests are sufficiently far from roads, rivers, or settlements to be assumed to experience low defaunation rates (Potapov et al. 2008). This number is particularly relevant given that deforestation rates of tropical dense forests continue to be high: 74,400 km^2/year, or ~0.45%/year (Hansen et al. 2013).

Aquatic ecosystems are equally or more susceptible to consequences of fragmentation. Ecologically vital connectivity in rivers that may reach across continents can be severed by installations like dams (Revenga et al. 2005). Less than 40% of large rivers in the world are estimated to still be free flowing, and dozens of new dams threaten the world's most faunally rich river basins (Winemiller et al. 2016). Rates of modification of freshwater habitats are predicted to only increase as climate change advances, and new modifications are required to protect water security in a more climatically dynamic future (Strayer & Dudgeon 2010).

Increases in human infrastructure also promote diverse forms of collision-associated mortality. In the United States alone, Loss et al. (2015) estimated that bird collisions with buildings and vehicles totaled 445 and 1,338 million animals/year, respectively. Animal roadkill in particular is projected to only increase with the planned installation of 25 million km of new roads by 2050, mostly in areas rich in biodiversity, such as developing countries (Laurance et al. 2014). Even marine fauna are susceptible to collisions with vessel traffic. Vessel strikes are an important source of mortality to a variety of whale species, and the total annual number of whale strikes has increased dramatically in the past several decades (McCauley et al. 2015b).

4.3. Invasive Species, Including Diseases

Of all extinct animals for which the cause of extinction has been determined, 54% included effects of invasive species (Clavero & García-Berthou 2005). In particular, the introduction of new predatory species into isolated ecosystems can be devastating to native consumers. For example, human introduction of foxes to Arctic islands caused near total eradication of many seabird species, dramatically transforming those ecosystems (Maron et al. 2006). Likewise, rat introductions have decimated many taxa, including a wide range of birds (Jones et al. 2008). In continental systems, invasive, feral cats are currently the largest source of direct mortality of birds in the United States (Loss et al. 2015). Invertebrate introductions, such as the yellow crazy ant (O'Dowd et al. 2003), have also caused the decline of many native invertebrate (and vertebrate) taxa.

One of the most devastating groups of invasive species to faunal health is that of parasites and pathogens. The introduction of avian malaria to Hawaii was a major driver of the collapse of the native avifauna (van Riper et al. 1986). Rinderpest introductions to East Africa in the 1890s caused catastrophic declines (50–90%) in sub-Saharan Africa wild artiodactyls, with cascading ecosystem-level consequences (Dobson et al. 1991). A suite of fungal pathogens has recently caused global- or continental-scale epidemic declines in frogs and bats, and now an emerging pathogen threatens salamanders (Fisher et al. 2012).

4.4. Pollution

The spread of environmental contaminants can be a critical and cryptic driver of defaunation. DDT-driven avian declines stimulated some of the earliest global dialogues on defaunation. Similar cases of pollution-induced defaunation in terrestrial ecosystems are widespread—for example, native pollinators have declined at least in part because of increased pesticide exposure (Potts et al. 2010). Aquatic animals may be at elevated risk to pollution (**Figure 1*a***) as they directly respire, drink, and absorb pollutants that concentrate in aquatic ecosystems. Also, 98% of threatened freshwater crabs are at risk because of pollution (Collen et al. 2014), many frog species appear to be demasculinized by herbicide exposure (Hayes et al. 2002), and pollution appears to have extirpated fish from 5% of the overall length of Chinese rivers (Dudgeon 1999).

Despite the vast volume of the ocean (~1.3 sextillion L) and its associated capacity to dilute contaminants, pollution is an important driver of marine defaunation. For instance, oxygen-depleted dead zones, often caused by runoff of excess fertilizers, have increased exponentially since the 1960s and have been reported in more than 400 systems (Diaz & Rosenberg 2008). Oil spills generate a significant pulsed source of mortality to marine fauna (e.g., seabirds, sea turtles) (Antonio et al. 2011). Since 2000, more than 1,500 spill incidents have occurred, releasing more than 1.5 billion L of oil and fuel into the ocean (NOAA 2015). Plastics are also a growing source of marine pollution and cause of marine animal mortality (Derraik 2002, Gregory 2009). It is estimated that by 2050, 99% of seabirds will have ingested plastic during their life cycle and that the weight of plastics in oceans may exceed fish biomass (WEF 2016, Wilcox et al. 2015).

4.5. Anthropogenic Climate Disruption

Climate change is poised to be the next major driver of defaunation. This is unsurprising, given that a review of mass defaunation events in the fossil record identifies the effects of climate change to be a common causative agent in historical animal species loss (Harnik et al. 2012).

First-generation climate science brought awareness of how changing conditions can reshape range boundaries of species, alter the timing of life cycles (e.g., migration, hibernation), and accelerate extinctions of species (Thomas et al. 2004, Walther et al. 2002). Impacts for polar fauna are well known; however, evidence indicates that tropical fauna could be at an even higher risk to climate change because they are more physiologically specialized to a narrower band of tropical temperatures (Deutsch et al. 2008).

In freshwater ecosystems, climate change has caused increases in water temperature, altered periods of ice cover, and changed the rate and timing of water delivery to these ecosystems. Freshwater fauna are particularly vulnerable to climate change as their capacity to spatially track climate shifts is highly constrained (e.g., overheated lacustrine fish typically cannot relocate to cooler lakes).

Already, climate change is having diverse effects on the oceans by promoting acidification, increasing temperatures, and increasing rates of deoxygenation. Reef-forming animals (e.g., corals, oysters) are especially susceptible to climate change given the sensitivity of their calcium carbonate structures to acidification (Hofmann et al. 2010). This susceptibility is of great significance to defaunation, as coral reefs likely host approximately one third of all marine life (Fisher et al. 2015). Climate change also has great potential to influence phytoplankton and zooplankton (Bednaršek et al. 2014), foundational energy for higher fauna. This pathway is one of the hypothesized mechanisms preventing the recovery of iconic cod populations in the northeast United States (Pershing et al. 2015). Additional pathways of climate change impacts on marine fauna include deleterious effects on their behavior, sensory function, and homing ability (Caprio et al. 2014, Munday et al. 2009).

5. CONSEQUENCES OF DEFAUNATION

5.1. Effect on Community Composition

Defaunation rarely acts to simply delete species from ecosystems, with ecosystems becoming less diverse and wildlife less abundant. We facilitate species invasion, promote species naturalization, and alter species ranges, with the net effect that, on average, local α-diversity has not decreased over time, even in highly disturbed communities. In some instances, patterns of disturbance have even increased local diversity. The overarching global story is one of high turnover in community composition in the most defaunated habitats, resulting in widespread biotic homogenization and reduced β- and γ-diversity (Randall Hughes et al. 2007) and changes in functional and phylogenetic diversity.

5.1.1. Phylogenetic diversity. Growing evidence shows that human disturbance tends to drive declines in local and regional animal phylogenetic diversity (PD) and the evolutionary history it represents. In Costa Rica, forest systems support 300 to 600 million more years of evolutionary history of birds than neighboring agricultural systems (Frishkoff et al. 2014). Notably, this pattern seems to be true even in systems where α-level species richness does not decline or declines only moderately (D'agata et al. 2014, Frishkoff et al. 2014). For instance, in a system where coral reef fishes showed an average 11.7% decline in species richness along a fishing gradient, a decline of 35.8% in PD was observed (D'agata et al. 2014). These relationships are due to the disproportionate loss of phylogenetically rare species following disturbance.

Globally, losses of PD are greater than could be expected by species diversity loss alone. This difference is at least partially explained by the clumped nature of extinctions, which often knock out entire branches of faunal trees, focusing on species-poor lineages (Purvis et al. 2000a).

5.1.2. Functional diversity. PD and functional diversity (FD) are often, but not always, closely correlated (Safi et al. 2011). Thus, FD of animals also tends to decline in disturbed communities. As with PD, anthropogenic change generally tends to cause higher FD loss than species loss, and high functional loss may be observed even without loss in α-diversity (D'agata et al. 2014, Meynard et al. 2011). However, this relationship is not universal, and other studies have found little to no changes in FD under some types of disturbances, even when strong changes in species diversity are observed (e.g., Edwards et al. 2013).

Differences in patterns of defaunation, when viewed from functional, phylogenetic, and species-level perspectives, are likely to lead to strong differences in conservation priorities to limit defaunation. A global analysis of fish diversity found that there is much higher functional redundancy in the tropics than in temperate zones, such that defaunation of any given species will likely have stronger impacts in temperate zones (Stuart-Smith et al. 2013). Coarse relationships between PD and FD may not be helpful if the functional traits that are not captured by PD are disproportionately important for ecosystem function. For instance, we know that large-bodied animals often have unique, and disproportionately important, functional roles in ecosystems (McCauley et al. 2014), yet body size variation in mammals is not well captured by PD in this group (Fritz & Purvis 2010).

5.2. Behavioral and Physiological Consequences

Defaunation can have strong effects on the behavior of residual species. For instance, the systematic decline of large predatory fish is thought to change the foraging behavior of smaller fish, including the distance and time they will forage away from shelter (McCauley et al. 2010, 2012b). The decline in larger seed predators (and the predators of such seed predators) causes a shift in dietary niche in rainforest rodents (Galetti et al. 2015). Loss of large predators even appears to have the capacity to redefine the basic behavioral boundaries between day and night. Small nocturnal reef fish, for example, become more abundant during the day when large predators are depleted (McCauley et al. 2012b). These types of behavioral shifts can accumulate, causing landscape-scale ecological consequences, as seen in the change of algae and reef distribution (Madin et al. 2011), and the alteration of long-term patterns of coral recruitment and large-scale coral algal dynamics (McCauley et al. 2010).

Defaunation also appears to have the capacity to induce diverse shifts in the physiology of both target species and their community associates. For instance, across a fishing gradient at the Line Islands, prey species tend to have higher body condition indices, including higher liver mass, perhaps as a response to changes in foraging restrictions placed by predators that are selectively removed in fishing (Walsh et al. 2012). Elsewhere, protogynous fishes were found to change sex at larger sizes when large predators were less abundant (DeMartini et al. 2005). In African savannas, the selective loss of large herbivores leads to changes in immune function in small rodents, likely partially as a response to the higher-density conditions in which they live (Young et al. 2016).

5.3. Ecological Consequences

The ecological consequences of defaunation include cascading effects on abundance, composition, and ecology of other fauna and flora as well as effects on ecological functions performed by the affected taxa, including impacts on ecosystem services.

5.3.1. Cascading effects on other taxa. Animals exist in complex ecological networks, such that declines in a single species are rarely isolated. Interspecific interactions can be so strong that the loss or decline of one species can lead to the loss of its interacting counterpart. Thus, mutualist, commensal, parasitic, and highly specialized species are all likely to be even more vulnerable to coextinctions than are host species and species without such close relationships (Colwell et al. 2012). However, the cascading effects of animal declines are not restricted to such highly specialized associations. Indeed, one recent review suggests that 80% of all extinctions in a network occur not to the species whose mortality is directly impacted by some form of a disturbance but instead to interacting species (Säterberg et al. 2013). Such coextinctions can be very reticulate, indirect, and challenging to anticipate without intimate knowledge of ecological network dynamics. For example, the extinction of the Stellar's sea cow in the 1700s has been hypothesized to be partially caused by the loss of sea otters in the regions. Overhunting of sea otters is known to release their herbivorous sea urchin prey, therefore depressing or eliminating local kelp abundance, the critical food resource for sea cows (Estes et al. 2016).

Coextinction can also trigger ecological or evolutionary consequences. The rate and shape of coextinction events (and the resulting ecological cascades) depend strongly on the structure of individual ecosystems and the pattern in which species are lost (Rezende et al. 2007). However, much empirical work is needed to improve our predictive capacity of which systems are likely to be most vulnerable to defaunation and which species losses are most likely to trigger collapse.

Defaunation can also allow the increase or release of other species, and some taxonomic groups appear to profit from the accelerating pace of defaunation. The loss of large predators, for example, often allows the release of smaller mesopredators, as in the release of baboons following large predator declines in Africa (Taylor et al. 2016). Similarly, the loss of megafaunal herbivores tends to cause systematic increases in abundance of small rodent herbivores and granivores (Dirzo et al. 2007, McCauley et al. 2006). These systematic releases often have cascading effects on ecosystem functions and services. Both baboons and rodents are seed predators, seed dispersers, and avid consumers of other resources. From a human perspective, these and other expanding mesopredators are important crop pests and disease vectors, thus likely causing negative effects on human populations in these defaunated landscapes.

5.3.2. Consequences to ecosystem functions and services. Any ecological function performed by an animal is potentially imperiled by defaunation. The extinction of ecological interactions, functions, and services often occurs long before extinctions of a population or species (Valiente-Banuet et al. 2015). Meta-analyses suggest that even moderate biodiversity loss can cause impacts on ecosystem function comparable with those from other, more widely recognized major drivers of global change (Hooper et al. 2012).

Defaunation degrades or wholly eliminates myriad vital ecosystem functions, such as rates and patterns of pollination, seed predation, seed dispersal, trampling, bioerosion, nutrient movement, herbivory, and predation (see review in Dirzo et al. 2014). These functions often are not limited to the system where the affected animal primarily resides but have effects that cross ecosystem boundaries and cause entire state changes in secondary ecosystems—for example, by dramatically changing levels of nutrient subsidies or physical structure in systems normally linked by mobile animals (McCauley et al. 2012a).

A comprehensive review of the ecological functions affected by defaunation is beyond the scope of this review. Instead, we focus on a select subset of functions that both critically influence human well-being (i.e., ecosystem services) and shape ecosystem functioning.

5.3.2.1. Nutrient cycling. Animals often play key roles in determining how nutrients move both within and across ecosystems. These roles include direct impacts, such as the movement of nitrogen or other core nutrients through excretion, erosion, respiration, or bodily decomposition. The loss of seabirds from Arctic islands caused transformation of grassland to tundra ecosystems (Maron et al. 2006). Similarly, the loss of salmon from riparian ecosystems causes long-term shifts in nutrient delivery that affect invertebrate abundance, riparian plant communities, and even abundance of terrestrial megafauna (Gende et al. 2002). The great whales are thought to be responsible for moving dietary iron and nitrogen to the surface and also for moving nitrogen from rich temperate feeding grounds to oligotrophic calving grounds. Their recent declines may have fundamentally altered patterns of nutrient movement and net primary productivity in the global oceans (Roman et al. 2014).

The indirect effects of animals on nutrient cycles, through their impacts on plants, microbial communities, and disturbance frequency, among other mechanisms, are often more profound than these direct effects. Megaherbivores in the Arctic are critical in maintaining permafrost-covered grasslands through trampling and grazing. As these megaherbivores decline, the peat may also decay, potentially causing increases in emissions equal to those of both China and the United States (Zimov et al. 2009). Similarly, the loss of wildebeest by Rinderpest in the Serengeti likely caused dramatic releases in CO_2 through changes in fire regimes (Holdo et al. 2009). The loss of sea otters in the North Pacific likely drove dramatic declines in coastal productivity and alteration in carbon flows, due to the otters' cascading trophic effects on kelp forests (Wilmers et al. 2012). Additionally, the extirpation of large frugivores in the Brazilian Atlantic forest has prevented the recruitment of large trees, which may in turn erode long-term carbon storage in these forests (Bello et al. 2015, Peres et al. 2016).

5.3.2.2. Food and water provisioning. Animals impact food production both through indirect effects, including their aforementioned influence on nutrient cycles, and more directly via other pathways such as their influence on pollination and fruit set and crop pest regulation.

More than three-quarters of the world's food crops, roughly $215 billion in annual value (Gallai et al. 2009), is dependent on animal pollination for successful fruit set. Wild pollinators appear to be particularly important in maximizing food yield. A recent global review of 41 worldwide crop systems found universal increases in fruit set with the presence of wild pollinators, compared with only 14% showing increases following visitation by domestic honeybees (Garibaldi et al. 2013). Thus, domesticated pollinators are unlikely to be able to compensate for the services of any loss in their wild counterparts. Yet wild pollinators, and the complex pollination networks they support, are globally collapsing owing to combined anthropogenic stressors of pesticides, introduced parasites, and lack of flower resources (Goulson et al. 2015). Such declines have obvious effects on global economics and food harvest and translate into worrisome increases in human disease burden (Smith et al. 2015).

Many bird and bat species vulnerable to defaunation are critical at controlling pests in both temperate and tropical ecosystems. Recent work shows that the presence of intact bird and bat communities prevented 30% loss in cacao crop yield; the cacao crop represents a billion dollar/year industry (Maas et al. 2013). One common species of bat in Thailand is thought to prevent the loss of approximately 2,900 tons of rice per year (Wanger et al. 2014). Invertebrates also are important in pest control: Beneficial insects provide an estimated $4.5 billion in annual pest control in the United States alone (Losey & Vaughan 2006).

Wildlife may also guard the provisioning services of other fauna or ecosystems. The hippopotamus, for example, appears to help physically engineer fish nursery habitats into wetlands (Mosepele et al. 2009) and provision freshwater ecosystems with terrestrially derived nutrients that are used by other ecologically important freshwater fauna (McCauley et al. 2015a).

Defaunation may also cause negative impacts on quality and quantity of water available. For example, the dramatic recent declines in amphibians may cause negative effects on water quality, nitrogen cycling, and whole stream respiration in Neotropical streams (Rantala et al. 2015). Likewise, experimental removals of large predatory fish have been shown to initiate trophic cascades that cause producers' blooms and sometimes eutrophication (Carpenter et al. 2001).

5.3.2.3. Human disease. Parasites and pathogens are a dominant and healthy component of natural and intact ecosystems (Kuris et al. 2008). As with all other branches of animal life, they are highly vulnerable to patterns of anthropogenic change. As discussed previously, because of their dependent life cycles, they are likely experiencing higher rates of loss than free-living species (Lafferty 2012). However, a growing body of literature suggests that defaunation and other types of biodiversity loss may systematically benefit some parasites and pathogens, including some causal agents of human zoonoses (Civitello et al. 2015, Young et al. 2016). The generality and magnitude of this effect are still under active debate (Civitello et al. 2015, Salkeld et al. 2015), and there is widespread agreement that no universal relationship links defaunation and disease (Johnson et al. 2015). Yet, some forms of defaunation do appear likely to cause strong increases in disease prevalence. For instance, systematic increases in rodent abundance following losses of large mammals tend to cause increases in rodent-borne diseases (Young et al. 2014). Indeed, whenever defaunation causes systematic losses in low-competence hosts, or releases groups of competent hosts, we should expect to see increases in prevalence of disease (Joseph et al. 2013). There are also other potential pathways through which defaunation may cause systematic increases in human disease risk—for example, through behavioral (Dizney & Dearing 2016) or physiological changes in remaining hosts (Young et al. 2016) or through changes in host phylogeny (Suzán et al. 2015).

5.4. Evolutionary Consequences: The Downsizing Effect

Human overexploitation of animals is not homogeneous regarding body size. Size-selective harvesting, targeting the largest animals (within and among species), is a prominent trend with important ecological and evolutionary consequences.

5.4.1. Size selection of the largest individuals. Size-selective harvesting, in which humans target the largest individuals and, once these are depleted, shift to smaller prey, is a ubiquitous human behavior (**Figure 3**). It has been recorded in prehistoric shell middens (Erlandson et al. 2011) and is still observed in hunting and fishing. Harvesting of large individuals within a population not only is responsible for decreases in mean body size of the species but also, more cryptically, can destabilize social structures, alter social behavior, and cause demographic and life history changes (Fenberg & Roy 2008, Milner et al. 2007). All these processes may ultimately lead to the local extinction of the harvested population.

Size-selective harvesting is widespread in both aquatic and terrestrial habitats. At least 108 species of fish, invertebrates, and terrestrial vertebrates have experienced size-selective harvesting (Fenberg & Roy 2008). This pattern can clearly impact key ecological processes. For instance,

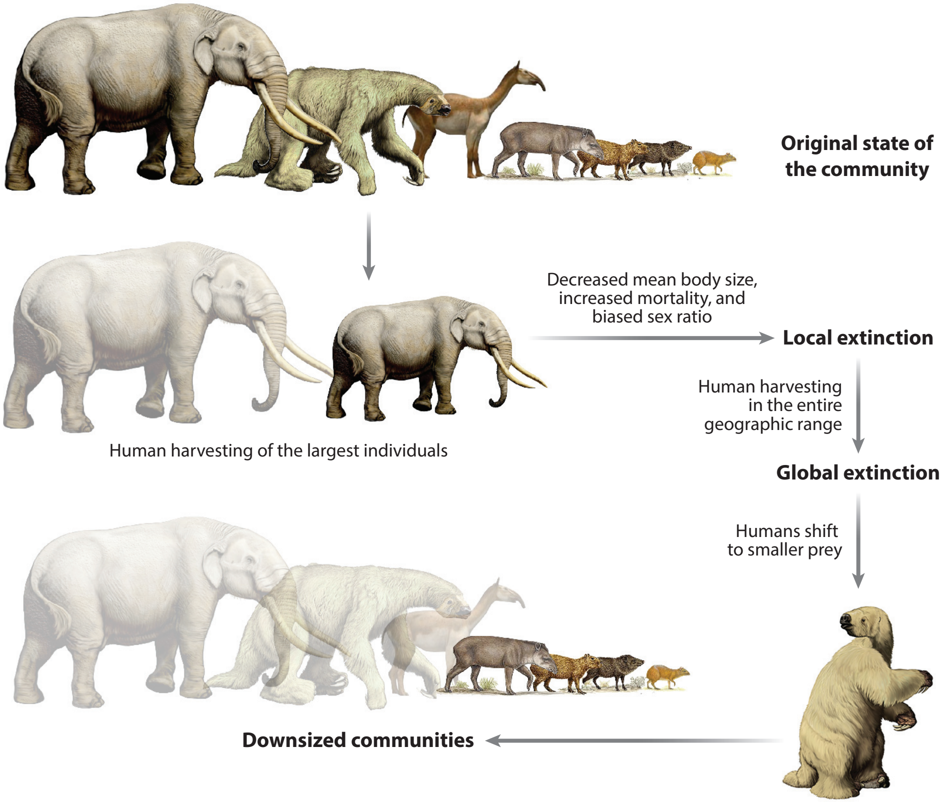


Figure 3

Disproportionate impacts of human harvesting of the largest individuals and the largest species in a community first. Such harvesting causes local declines in abundance of the largest individuals, inducing population-scale downsizing and many population-scale impacts. This decline often proceeds to local extinction of populations of large-sized species. Replicated across regions, this local extinction often progresses to global extinction, such that large body size is a leading predictor of global extinction risk. Megafauna images copyright and courtesy of Fiona A. Reid.

the loss of large fruit-eating fish from tropical rivers may ultimately cause the collapse of trees that rely on fish for dispersal (Costa-Pereira & Galetti 2015). Similarly, Pérez-Méndez et al. (2015) documented a marked decline and eventual collapse of seedling recruitment resulting from a downsizing trend of frugivorous lizards. Also, the size-selective harvesting of large individuals of parrotfish, a critical reef herbivore, may cause severe consequences for the dynamics and regeneration of coral reefs (Lokrantz et al. 2008).

5.4.2. Size selection of the largest species.

Humans also often select the largest species to maximize their yield or gain social capital (Robinson 2000), sequentially targeting smaller species as large ones become rare. This selection has resulted in skewed body mass distributions between extinct and extant mammals (Dirzo et al. 2014, Lyons et al. 2004) (**Figure 3**) and is likely a partial cause of historical reductions in body size of the mammal assemblages in Egypt (Yeakel et al. 2014) and China (Turvey et al. 2015). Such shifts have important ecological and evolutionary consequences (Malhi et al. 2016). For instance, the sequential extinction of large-bodied frugivores from tropical forests due to hunting or fragmentation has led to the lack of dispersal of large seeds, ultimately changing seed size within populations over a few generations (Galetti et al. 2013).

6. WAYS FORWARD

6.1. Research Needs

We cannot effectively slow defaunation without a sufficiently robust scientific understanding of the taxonomy, ecology, and conservation status of the fauna themselves, and our understanding of each domain is now woefully inadequate. Recent ambitious programs to catalog animal species on the planet have given us a needed boost in the race to describe animal fauna before they become extinct, but a great deal of work remains [Costello et al. 2013; see also the World Register of Marine Species (WoRMS) registry at **http://www.marinespecies.org/**]. Research efforts that focus on maintaining FD and PD (Jetz et al. 2014) are even further behind but are critically necessary.

Our understanding of the basic ecology of invertebrates and smaller vertebrates is highly inadequate, despite the fact that many such taxa exhibit comparable declines and geographic contractions as larger vertebrates (Dirzo et al. 2014). However, gaping holes also exist in our understanding of the ecology of some of the world's largest and most charismatic animals: We guess at why white sharks aggregate in the mid-Pacific Ocean and have no good estimates of the home range size of hippopotamuses. In addition to sustained traditional research, novel initiatives that enlist the aid of citizen scientists and employ new analytical tools to synthesize crowdsourced big data can play an increasingly important role in bridging some of these knowledge gaps.

Deficiencies of ecological information on fauna are worst in the tropics. For example, the most severely understudied large herbivores occur in developing nations (Ripple et al. 2015). Given that the tropics are biodiversity hot spots (high faunal endemic diversity and high risk of extinction due to massive habitat destruction) (Myers et al. 2000), these geographic biases must be remedied immediately. Lastly, we must aggressively accelerate the work of reviewing the conservation status of our global fauna. The preponderance of data gaps and data deficiency in the IUCN database cannot be sustained if we are to intelligently understand and strategically respond to defaunation.

It should, however, be stressed that research on understanding diversity and identifying patterns of its decline must not come at the expense of either advancing research on drivers of this decline or actively taking forward solutions to address these challenges. The rapidity by which defaunation is proceeding globally necessitates that we proactively work to address this global threat even in the face of data insufficiencies.

6.1.1. Reversing defaunation. Inspiring successes have emerged from efforts to reverse local extinction of one single species at a time in marine (e.g., northern elephant seals, southern sea otters), freshwater (e.g., Shasta River chinook salmon, Oregon chub), and terrestrial (e.g., North American wolves, American crocodile, golden lion tamarin) realms. More than 485 animal species (mostly birds and mammals) have been reintroduced to their former distributions, but scientists are still learning the best strategies and techniques for achieving successful reintroductions (Seddon et al. 2014). Critically, beyond individual reintroductions, we need to advance in the development of strategies directed to restore interactions and ecosystem functioning.

One clear lesson learned in such efforts is the necessity of investing local stakeholders financially or intangibly in the success of faunal restoration (Andrade & Rhodes 2012). Next-generation refaunation efforts must expand from these principles to embrace the more complex, but also more important, job of restoring multispecies animal complexes, interactions, and functions (Hansen et al. 2010, Seddon et al. 2014).

6.2. Policy Implementation Needs

Recent global and local political decisions suggest reason to be optimistic that climate change could eventually be brought under some degree of control (UNFCCC 2015). The observed capacity of some animal species to adapt to climate stress (Palumbi et al. 2014) provides hope that, if properly implemented, these new climate policies can help avert the most disastrous amplifying effects of climate change on global defaunation.

The establishment of protected areas has been unquestionably important to slowing defaunation, but thus far only a meager proportion of land has been set aside for faunal protection (∼17%), and the situation is much worse in the oceans (∼3.5%) (Lubchenco & Grorud-Colvert 2015). Four important steps should be taken to increase the ability of reserves to safeguard faunal futures: Reserves need to become larger, better connected, more intelligently designed to accommodate climate change, and adequately managed according to stated goals.

Protected areas, however, will only ever be a partial solution to defaunation, and there is a great need to address faunal losses in the vast, unprotected portions of the terrestrial and aquatic world. We must develop policies that adequately address the legal but irresponsible and unsustainable harvest of fauna, particularly in the context of marine fisheries and the large-scale animal use by traditional medicine. Large-scale illegal harvests of fauna in all biomes must be slowed by linked measures that combat corruption, study and address the complex behavioral dynamics of demand, address poaching at its source, adopt next-generation technologies to monitor and share data on illegal trade, and make enforcement smarter and effective. Even more broadly, we must challenge ourselves to responsibly stabilize and manage the effect of the growth of our own populations and to address high and uneven rates of consumption among societal groups—imbalances that add considerable momentum to defaunation.

Large-scale habitat conversion activities already underway (e.g., widespread oil palm expansions) or now being launched (e.g., seabed and land mining and dams) need to be more responsibly planned, such that they spare biodiverse regions and their ecosystem services, alleviating proximate and longer-term threats to fauna, respectively. Management of marine animal diversity in the 64% of oceans that lie beyond national jurisdiction is an urgent policy problem without precedent on land and requires revision to avoid tragedy of the common outcomes for high-seas fauna (Druel & Gjerde 2014).

6.3. What Is at Stake?

There are profound and diverse consequences for failing to address defaunation immediately. Ecological and extinction cascades will make it increasingly difficult to arrest the momentum of defaunation. Left unchecked, defaunation will impoverish our planet by severely reducing its faunal diversity—ultimately undoing the work of millions of years of evolution. The tragedy of such losses is obvious in the case of the extinction of charismatic animals like African elephants, California condors, or Hawaiian monk seals, to which we have a strong aesthetic and cultural connection, but losses are equally significant for biologically intricate and evolutionarily unique mesofauna and microfauna. Reversing defaunation is, however, also a deeply selfish enterprise. The stability of our food systems, economies, and health depends in myriad ways on the sustained health of faunal communities.

Although precedence exists for developing and moving forward cohesive national and international dialogues on deforestation, little such precedence exists for initiating the kind of synchronized momentum that will be needed to address the equally insidious and impactful problem of global defaunation. As we illustrate in this review, the causes and consequences of defaunation are in many ways more diverse and complex than those of deforestation. Defaunation is arguably a more challenging problem to face, but the costs of failing to do so are large. Unified action must be boldly undertaken by all sectors of society to prevent defaunation from accelerating to the point that it initiates a full-blown, human-caused, sixth mass extinction, an event that would be catastrophic to both global biodiversity and humanity.

DISCLOSURE STATMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Symphony Yu, Benjamin Boyce, Ana Guerra, Arturo Dirzo, and Meredith McClintock for intellectual contributions to this review. Pedro Jordano and an anonymous reviewer provided comments that improved a previous draft. Financial support was provided to M.G. by the Fundação de Amparo ‘a Pesquisa do Estado de São Paulo (FAPESP) and the Conselho Nacional de Desenvolvimento Científico (CNPq) and to D.J.M. by the Alfred P. Sloan Foundation and the Benioff Ocean Initiative.

LITERATURE CITED

Agnew DJ, Pearce J, Pramod G, Peatman T, Watson R, et al. 2009. Estimating the worldwide extent of illegal fishing. *PLOS ONE* 4:e4570

Andrade GS, Rhodes JR. 2012. Protected areas and local communities: an inevitable partnership toward successful conservation strategies? *Ecol. Soc.* 17:14

Andrade MC, Giarrizzo T, Jegu M. 2013. *Tometes camunani* (Characiformes: Serrasalmidae), a new species of phytophagous fish from the Guiana Shield, rio Trombetas basin, Brazil. *Neotropical Ichthyol.* 11:297–306

Antonio FJ, Mendes RS, Thomaz SM. 2011. Identifying and modeling patterns of tetrapod vertebrate mortality rates in the Gulf of Mexico oil spill. *Aquat. Toxicol.* 105:177–79

Bednaršek N, Feely R, Reum J, Peterson B, Menkel J, et al. 2014. *Limacina helicina* shell dissolution as an indicator of declining habitat suitability owing to ocean acidification in the California Current Ecosystem. *Proc. R. Soc. B* 281:20140123

Bello C, Galetti M, Pizo MA, Magnago LFS, Rocha MF, et al. 2015. Defaunation affects carbon storage in tropical forests. *Sci. Adv.* 1:e1501105

Brashares JS, Abrahms B, Fiorella KJ, Golden CD, Hojnowski CE, et al. 2014. Wildlife decline and social conflict. *Science* 345:376–78

Brown LR, Moyle PB, Yoshiyama RM. 1994. Historical decline and current status of coho salmon in California. *North Am. J. Fish. Manag.* 14:237–61

Caprio J, Shimohara M, Marui T, Harada S, Kiyohara S. 2014. Marine teleost locates live prey through pH sensing. *Science* 344:1154–56

Cardillo M. 2003. Biological determinants of extinction risk: Why are smaller species less vulnerable? *Anim. Conserv.* 6:63–69

Cardillo M, Mace GM, Gittleman JL, Jones KE, Bielby J, Purvis A. 2008. The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. B* 275:1441–48

Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds OR, et al. 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–41

Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, et al. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321:560–63

Carpenter SR, Cole JJ, Hodgson JR, Kitchell JF, Pace ML, et al. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecol. Monogr.* 71:163–86

Ceballos G, Ehrlich PR. 2002. Mammal population losses and the extinction crisis. *Science* 296:904–7

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. *Sci. Adv.* 1:e1400253

Christensen V, de la Puente S, Sueiro JC, Steenbeek J, Majluf P. 2014. Valuing seafood: the Peruvian fisheries sector. *Mar. Policy* 44:302–11

Civitello DJ, Cohen J, Fatima H, Halstead NT, Liriano J, et al. 2015. Biodiversity inhibits parasites: broad evidence for the dilution effect. *PNAS* 112:8667–71

Clavero M, García-Berthou E. 2005. Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol.* 20:110

Cohen A. 1997. Sturgeon poaching and black market caviar: a case study. *Environ. Biol. Fishes* 48:423–26

Collen B, Böhm M, Kemp R, Baillie JEM. 2012. *Spineless: Status and Trends of the World's Invertebrates*. London: Zool. Soc. Lond.

Collen B, McRae L, Deinet S, De Palma A, Carranza T, et al. 2011. Predicting how populations decline to extinction. *Philos. Trans. R. Soc. B* 366:2577–86

Collen B, Whitton F, Dyer EE, Baillie JE, Cumberlidge N, et al. 2014. Global patterns of freshwater species diversity, threat and endemism. *Glob. Ecol. Biogeogr.* 23:40–51

Colwell RK, Dunn RR, Harris NC. 2012. Coextinction and persistence of dependent species in a changing world. *Annu. Rev. Ecol. Evol. Syst.* 43:183–203

Costa-Pereira R, Galetti M. 2015. Frugivore downsizing and the collapse of seed dispersal by fish. *Biol. Conserv.* 191:809

Costello MJ. 2015. Biodiversity: the known, unknown, and rates of extinction. *Curr. Biol.* 25:R368–71

Costello MJ, May RM, Stork NE. 2013. Can we name Earth's species before they go extinct? *Science* 339:413–16

Cozzuol MA, Clozato CL, Holanda EC, Rodrigues FH, Nienow S, et al. 2013. A new species of tapir from the Amazon. *J. Mammal.* 94:1331–45

D'agata S, Mouillot D, Kulbicki M, Andréfouët S, Bellwood DR, et al. 2014. Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Curr. Biol.* 24:555–60

DeMartini EE, Friedlander AM, Holzwarth SR. 2005. Size at sex change in protogynous labroids, prey body size distributions, and apex predator densities at NW Hawaiian atolls. *Mar. Ecol. Prog. Ser.* 297:259–71

Derraik JG. 2002. The pollution of the marine environment by plastic debris: a review. *Mar. Pollut. Bull.* 44:842–52

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS* 105:6668–72

Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–29

Dirzo R, Mendoza E, Ortíz P. 2007. Size-related differential seed predation in a heavily defaunated neotropical rain forest. *Biotropica* 39:355–62

Dirzo R, Miranda A. 1991. Altered patterns of herbivory and diversity in the forest understory: A case study of the possible consequences of contemporary defaunation. In *Plant-Animal Interactions: Evolutionary Ecology*, ed. PW Price, TM Lewinshon, GW Fernandes, WW Benson, pp. 273–87. New York: Wiley

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJ, Collen B. 2014. Defaunation in the Anthropocene. *Science* 345:401–6

Dizney L, Dearing MD. 2016. Behavioural differences: a link between biodiversity and pathogen transmission. *Anim. Behav.* 111:341–47

Dobson A, Holdo R, Holt R. 1991. *Rinderpest*. Berkeley: Univ. Calif. Press

Druel E, Gjerde KM. 2014. Sustaining marine life beyond boundaries: options for an implementing agreement for marine biodiversity beyond national jurisdiction under the United Nations Convention on the Law of the Sea. *Mar. Policy* 49:90–97

Dudgeon D. 1999. *Tropical Asian Streams: Zoobenthos, Ecology and Conservation*. Hong Kong: Hong Kong Univ. Press

Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, et al. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81:163–82

Edwards FA, Edwards DP, Hamer KC, Davies RG. 2013. Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. *Ibis* 155:313–26

Erlandson JM, Braje TJ, Rick TC, Jew NP, Kennett DJ, et al. 2011. 10,000 years of human predation and size changes in the owl limpet (*Lottia gigantea*) on San Miguel Island, California. *J. Archaeol. Sci.* 38:1127–34

Estes JA, Burdin A, Doak DF. 2016. Sea otters, kelp forests, and the extinction of Steller's sea cow. *PNAS* 113: 880–85

Fa JE, Peres CA, Meeuwig J. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conserv. Biol.* 16:232–37

FAO (Food Agric. Org.). 2012. *Fishstat Plus—universal software for fishery statistical time series*. **http://www.fao.org/fishery/statistics/software/fishstat/en**

FAO (Food Agric. Org.). 2014. *The State of World Fisheries and Aquaculture*. Rome: FAO

FAO (Food Agric. Org.). 2015. *The Global Forest Resources Assessment*. Rome: FAO

Fenberg PB, Roy K. 2008. Ecological and evolutionary consequences of size-selective harvesting: How much do we know? *Mol. Ecol.* 17:209–20

Fisher MC, Henk DA, Briggs CJ, Brownstein JS, Madoff LC, et al. 2012. Emerging fungal threats to animal, plant and ecosystem health. *Nature* 484:186–94

Fisher R, O'Leary RA, Low-Choy S, Mengersen K, Knowlton N, et al. 2015. Species richness on coral reefs and the pursuit of convergent global estimates. *Curr. Biol.* 25:500–5

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, et al. 2005. Global consequences of land use. *Science* 309:570–74

Frishkoff LO, Hadly EA, Daily GC. 2015. Thermal niche predicts tolerance to habitat conversion in tropical amphibians and reptiles. *Glob. Change Biol.* 21:3901–16

Frishkoff LO, Karp DS, M'Gonigle LK, Mendenhall CD, Zook J, et al. 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. *Science* 345:1343–46

Fritz SA, Purvis A. 2010. Phylogenetic diversity does not capture body size variation at risk in the world's mammals. *Proc. R. Soc. B* 277:2435–41

Galetti M, Dirzo R. 2013. Ecological and evolutionary consequences of living in a defaunated world. *Biol. Conserv.* 163:1–6

Galetti M, Guevara R, Côrtes MC, Fadini R, Von Matter S, et al. 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340:1086–90

Galetti M, Guevara R, Galbiati LA, Neves CL, Rodarte RR, Mendes CP. 2015. Seed predation by rodents and implications for plant recruitment in defaunated Atlantic forests. *Biotropica* 47:521–25

Gallai N, Salles J-M, Settele J, Vaissière BE. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* 68:810–21

Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339:1608–11

Gende SM, Edwards RT, Willson MF, Wipfli MS. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *Bioscience* 52:917–28

Goulson D, Nicholls E, Botías C, Rotheray EL. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347:1255957

Gregory MR. 2009. Environmental implications of plastic debris in marine settings—entanglement, ingestion, smothering, hangers-on, hitch-hiking and alien invasions. *Philos. Trans. R. Soc. B* 364:2013–25

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, et al. 2008. A global map of human impact on marine ecosystems. *Science* 319:948–52

Hanken J, Wake DB. 1994. Five new species of minute salamanders, genus *Thorius* (Caudata: Plethodontidae), from northern Oaxaca, Mexico. *Copeia* 3:573–90

Hansen DM, Donlan CJ, Griffiths CJ, Campbell KJ. 2010. Ecological history and latent conservation potential: large and giant tortoises as a model for taxon substitutions. *Ecography* 33:272–84

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova S, et al. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342:850–53

Harnik PG, Lotze HK, Anderson SC, Finkel ZV, Finnegan S, et al. 2012. Extinctions in ancient and modern seas. *Trends Ecol. Evol.* 27:608–17

Hayes TB, Collins A, Lee M, Mendoza M, Noriega N, et al. 2002. Hermaphroditic, demasculinized frogs after exposure to the herbicide atrazine at low ecologically relevant doses. *PNAS* 99:5476–80

Hofmann GE, Barry JP, Edmunds PJ, Gates RD, Hutchins DA, et al. 2010. The effect of ocean acidification on calcifying organisms in marine ecosystems: an organism-to-ecosystem perspective. *Annu. Rev. Ecol. Evol. Syst.* 41:127–47

Holdo RM, Sinclair AR, Dobson AP, Metzger KL, Bolker BM, et al. 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLOS Biol.* 7:e1000210

Hooper DU, Adair EC, Cardinale BJ, Byrnes JE, Hungate BA, et al. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–8

Hughes JB, Daily GC, Ehrlich PR. 1997. Population diversity: its extent and extinction. *Science* 278:689–92

Isaac NJ, Cowlishaw G. 2004. How species respond to multiple extinction threats. *Proc. R. Soc. B* 271:1135–41

IUCN (Int. Union Conserv. Nat.). 2015. *The IUCN Red List of Threatened Species*. Version 2014.3. **http://www.iucnredlist.org**

Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–37

Jenkins CN, Pimm SL, Joppa LN. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *PNAS* 110:E2602–10

Jetz W, Thomas GH, Joy JB, Redding DW, Hartmann K, Mooers AO. 2014. Global distribution and conservation of evolutionary distinctness in birds. *Curr. Biol.* 24:919–30

Johnson PT, Ostfeld RS, Keesing F. 2015. Frontiers in research on biodiversity and disease. *Ecol. Lett.* 18:1119–33

Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, et al. 2008. Severity of the effects of invasive rats on seabirds: a global review. *Conserv. Biol.* 22:16–26

Joseph MB, Mihaljevic JR, Orlofske SA, Paull SH. 2013. Does life history mediate changing disease risk when communities disassemble? *Ecol. Lett.* 16:1405–12

Just J, Kristensen RM, Olesen J. 2014. *Dendrogramma*, new genus, with two new non-bilaterian species from the marine bathyal of southeastern Australia (Animalia, Metazoa *incertae sedis*)—with similarities to some medusoids from the Precambrian Ediacara. *PLOS ONE* 9:e102976

Klass K-D, Zompro O, Kristensen NP, Adis J. 2002. Mantophasmatodea: a new insect order with extant members in the Afrotropics. *Science* 296:1456–59

Koch PL, Barnosky AD. 2006. Late quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Evol. Syst.* 37:215–50

Kuris AM, Hechinger RF, Shaw JC, Whitney KL, Aguirre-Macedo L, et al. 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* 454:515–18

Lafferty KD. 2012. Biodiversity loss decreases parasite diversity: theory and patterns. *Philos. Trans. R. Soc. B* 367:2814–27

Laurance WF, Clements GR, Sloan S, O'Connell CS, Mueller ND, et al. 2014. A global strategy for road building. *Nature* 513:229–32

Levi T, Shepard GH Jr., Ohl-Schacherer J, Peres CA, Yu DW. 2009. Modelling the long-term sustainability of indigenous hunting in Manu National Park, Peru: landscape-scale management implications for Amazonia. *J. Appl. Ecol.* 46:804–14

Lewison RL, Crowder LB, Wallace BP, Moore JE, Cox T, et al. 2014. Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. *PNAS* 111:5271–76

Liow LH, Fortelius M, Lintulaakso K, Mannila H, Stenseth NC. 2009. Lower extinction risk in sleep-or-hide mammals. *Am. Nat.* 173:264–72

Lokrantz J, Nyström M, Thyresson M, Johansson C. 2008. The non-linear relationship between body size and function in parrotfishes. *Coral Reefs* 27:967–74

Losey JE, Vaughan M. 2006. The economic value of ecological services provided by insects. *Bioscience* 56:311–23

Loss SR, Will T, Marra PP. 2015. Direct mortality of birds from anthropogenic causes. *Annu. Rev. Ecol. Evol. Syst.* 46:99–120

Lubchenco J, Grorud-Colvert K. 2015. Making waves: the science and politics of ocean protection. *Science* 340:382–83

Lyons SK, Smith FA, Brown JH. 2004. Of mice, mastodons and men: human-mediated extinctions on four continents. *Evol. Ecol. Res.* 6:339–58

Maas B, Clough Y, Tscharntke T. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecol. Lett.* 16:1480–87

Madin EM, Madin JS, Booth DJ. 2011. Landscape of fear visible from space. *Sci. Rep.* 1:1–3

Malhi Y, Doughty CE, Galetti M, Smith FA, Svenning JC, Terborgh JW. 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *PNAS* 113:838–46

Manne LL, Brooks TM, Pimm SL. 1999. Relative risk of extinction of passerine birds on continents and islands. *Nature* 399:258–61

Maron JL, Estes JA, Croll DA, Danner EM, Elmendorf SC, Buckelew SL. 2006. An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. *Ecol. Monogr.* 76:3–24

McCauley DJ, Dawson TE, Power ME, Finlay JC, Ogada M, et al. 2015a. Carbon stable isotopes suggest that hippopotamus-vectored nutrients subsidize aquatic consumers in an East African river. *Ecosphere* 6:1–11

McCauley DJ, DeSalles PA, Young HS, Dunbar RB, Dirzo R, et al. 2012a. From wing to wing: the persistence of long ecological interaction chains in less-disturbed ecosystems. *Sci. Rep.* 2:1–5

McCauley DJ, Hoffmann E, Young HS, Micheli F. 2012b. Night shift: expansion of temporal niche use following reductions in predator density. *PLOS ONE* 7:e38871

McCauley DJ, Keesing F, Young TP, Allan BF, Pringle RM. 2006. Indirect effects of large herbivores on snakes in an African savanna. *Ecology* 87:2657–63

McCauley DJ, Micheli F, Young HS, Tittensor DP, Brumbaugh DR, et al. 2010. Acute effects of removing large fish from a near-pristine coral reef. *Mar. Biol.* 157:2739–50

McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR. 2015b. Marine defaunation: animal loss in the global ocean. *Science* 347:1255641

McCauley DJ, Young HS, Guevara R, Williams GJ, Power EA, et al. 2014. Positive and negative effects of a threatened parrotfish on reef ecosystems. *Conserv. Biol.* 28:1312–21

McClenachan L, Cooper AB, Dulvy NK. 2016. Rethinking trade-driven extinction risk in marine and terrestrial megafauna. *Curr. Biol.* 26:1640–46

McLellan R, Iyengar L, Jeffries B, Oerlemans N, eds. 2014. *Living planet report 2014: species and spaces, people and places*. WWF Int., Gland, Switz.

Meynard CN, Devictor V, Mouillot D, Thuiller W, Jiguet F, Mouquet N. 2011. Beyond taxonomic diversity patterns: How do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Glob. Ecol. Biogeogr.* 20:893–903

Milner JM, Nilsen EB, Andreassen HP. 2007. Demographic side effects of selective hunting in ungulates and carnivores. *Conserv. Biol.* 21:36–47

Mora C, Tittensor DP, Adl S, Simpson AG, Worm B. 2011. How many species are there on Earth and in the ocean? *PLOS Biol.* 9:e1001127

Mosepele K, Moyle PB, Merron GS, Purkey DR, Mosepele B. 2009. Fish, floods, and ecosystem engineers: aquatic conservation in the Okavango Delta, Botswana. *Bioscience* 59:53–64

Munday PL, Dixson DL, Donelson JM, Jones GP, Pratchett MS, et al. 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *PNAS* 106:1848–52

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–58

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846–50

Newbold T, Scharlemann JP, Butchart SH, Şekercioğlu ÇH, Alkemade R, et al. 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proc. R. Soc. B* 280:20122131

NOAA (Nat. Ocean. Atmos. Admin.). 2013. *Fisheries economics of the United States*. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS-F/SPO-159, Oct. 2015

NOAA (Nat. Ocean. Atmos. Admin.). 2015. Raw incident data. *IncidentNews*. **http://incidentnews.noaa.gov/raw/index**

O'Dowd DJ, Green PT, Lake PS. 2003. Invasional 'meltdown' on an oceanic island. *Ecol. Lett.* 6:812–17

Paleczny M, Hammill E, Karpouzi V, Pauly D. 2015. Population trend of the world's monitored seabirds, 1950–2010. *PLOS ONE* 10:e0129342

Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA. 2014. Mechanisms of reef coral resistance to future climate change. *Science* 344:895–98

Peres CA. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conserv. Biol.* 15:1490–505

Peres CA, Emilio T, Schietti J, Desmoulière S, Levi T. 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *PNAS* 113:892–97

Pérez-Méndez N, Jordano P, Valido A. 2015. Downsized mutualisms: consequences of seed dispersers' body-size reduction for early plant recruitment. *Perspect. Plant Ecol. Evol. Syst.* 17:151–59

Pershing AJ, Alexander MA, Hernandez CM, Kerr LA, Le Bris A, et al. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350:809–12

Philippe H, Brinkmann H, Copley RR, Moroz LL, Nakano H, et al. 2011. Acoelomorph flatworms are deuterostomes related to *Xenoturbella*. *Nature* 470:255–58

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, et al. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344:1246752

Pocock MJ. 2011. Can traits predict species' vulnerability? A test with farmland passerines in two continents. *Proc. R. Soc. B* 278:1532–38

Potapov P, Yaroshenko A, Turubanova S, Dubinin M, Laestadius L, et al. 2008. Mapping the world's intact forest landscapes by remote sensing. *Ecol. Soc.* 13:51

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25:345–53

Purvis A, Agapow P-M, Gittleman JL, Mace GM. 2000a. Nonrandom extinction and the loss of evolutionary history. *Science* 288:328–30

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000b. Predicting extinction risk in declining species. *Proc. R. Soc. B* 267:1947–52

Randall Hughes A, Byrnes JE, Kimbro DL, Stachowicz JJ. 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecol. Lett.* 10:849–64

Rantala HM, Nelson AM, Fulgoni JN, Whiles MR, Hall RO, et al. 2015. Long-term changes in structure and function of a tropical headwater stream following a disease-driven amphibian decline. *Freshw. Biol.* 60:575–89

Redford KH. 1992. The empty forest. *Bioscience* 42:412–22

Revenga C, Campbell I, Abell R, De Villiers P, Bryer M. 2005. Prospects for monitoring freshwater ecosystems towards the 2010 targets. *Philos. Trans. R. Soc. B* 360:397–413

Rezende EL, Lavabre JE, Guimarães PR, Jordano P, Bascompte J. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448:925–28

Ricciardi A, Rasmussen JB. 1999. Extinction rates of North American freshwater fauna. *Conserv. Biol.* 13:1220–22

Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, et al. 2015. Collapse of the world's largest herbivores. *Sci. Adv.* 1:e1400103

Robinson JG. 2000. Calculating maximum sustainable harvests and percentage offtakes. In *Hunting Sustainability in Tropical Forests*, ed. JG Robinson, EL Bennett, pp. 521–24. New York: Columbia Univ. Press

Roman J, Estes JA, Morissette L, Smith C, Costa D, et al. 2014. Whales as marine ecosystem engineers. *Front. Ecol. Environ.* 12:377–85

Safi K, Cianciaruso MV, Loyola RD, Brito D, Armour-Marshall K, Diniz-Filho JAF. 2011. Understanding global patterns of mammalian functional and phylogenetic diversity. *Philos. Trans. R. Soc. B* 366:2536–44

Salkeld DJ, Padgett KA, Jones JH, Antolin MF. 2015. Public health perspective on patterns of biodiversity and zoonotic disease. *PNAS* 112:E6261

Säterberg T, Sellman S, Ebenman B. 2013. High frequency of functional extinctions in ecological networks. *Nature* 499:468–70

Seddon PJ, Griffiths CJ, Soorae PS, Armstrong DP. 2014. Reversing defaunation: restoring species in a changing world. *Science* 345:406–12

Sharp R, Sumaila UR. 2009. Quantification of US marine fisheries subsidies. *North Am. J. Fish. Manag.* 29:18–32

Shultz S, Bradbury RB, Evans KL, Gregory RD, Blackburn TM. 2005. Brain size and resource specialization predict long-term population trends in British birds. *Proc. R. Soc. B* 272:2305–11

Sirot C, Villéger S, Mouillot D, Darnaude A, Ramos-Miranda J, et al. 2015. Combinations of biological attributes predict temporal dynamics of fish species in response to environmental changes. *Ecol. Indic.* 48:147–56

Small C, Nicholls RJ. 2003. A global analysis of human settlement in coastal zones. *J. Coast. Res.* 1:584–99

Smith MR, Singh GM, Mozaffarian D, Myers SS. 2015. Effects of decreases of animal pollinators on human nutrition and global health: a modelling analysis. *Lancet* 386:1964–72

Springer AM, Estes J, Van Vliet G, Williams T, Doak D, et al. 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *PNAS* 100:12223–28

Stoner KE, Vulinec K, Wright SJ, Peres CA. 2007. Hunting and plant community dynamics in tropical forests: a synthesis and future directions. *Biotropica* 39:385–92

Strayer DL, Dudgeon D. 2010. Freshwater biodiversity conservation: recent progress and future challenges. *J. North Am. Benthol. Soc.* 29:344–58

Stuart-Smith RD, Bates AE, Lefcheck JS, Duffy JE, Baker SC, et al. 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501:539–42

Suzán G, García-Peña GE, Castro-Arellano I, Rico O, Rubio AV, et al. 2015. Metacommunity and phylogenetic structure determine wildlife and zoonotic infectious disease patterns in time and space. *Ecol. Evol.* 5:865–73

Taylor RA, Ryan SJ, Brashares JS, Johnson LR. 2016. Hunting, food subsidies, and mesopredator release: the dynamics of crop-raiding baboons in a managed landscape. *Ecology* 97:951–60

Tershy BR, Shen KW, Newton KM, Holmes ND, Croll DA. 2015. The importance of islands for the protection of biological and linguistic diversity. *BioScience* 65:592–97

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, et al. 2004. Extinction risk from climate change. *Nature* 427:145–48

Thompson C, WWF. 2010. *Amazon Alive: A Decade of Discovery 1999–2009*. Washington, DC: WWF Living Amazon Initiat.

Turvey ST, Crees JJ, Di Fonzo MMI. 2015. Historical data as a baseline for conservation: reconstructing long-term faunal extinction dynamics in Late Imperial–modern China. *Proc. R. Soc. B* 282:1–9

UNFCCC (U.N. Framew. Conv. Clim. Change). 2015. *Adoption of the Paris agreement*. FCCC/CP/2015/L.9/Rev.1, Paris

Valiente-Banuet A, Aizen MA, Alcántara JM, Arroyo J, Cocucci A, et al. 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.* 29:299–307

van Riper C III, van Riper SG, Goff ML, Laird M. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56:327–44

Vega GC, Wiens JJ. 2012. Why are there so few fish in the sea? *Proc. R. Soc. B* 283:1–7

Walsh S, Hamilton S, Ruttenberg B, Donovan M, Sandin S. 2012. Fishing top predators indirectly affects condition and reproduction in a reef-fish community. *J. Fish Biol.* 80:519–37

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, et al. 2002. Ecological responses to recent climate change. *Nature* 416:389–95

Wanger TC, Darras K, Bumrungsri S, Tscharntke T, Klein A-M. 2014. Bat pest control contributes to food security in Thailand. *Biol. Conserv.* 171:220–23

WEF (World Econ. Forum). 2016. *The new plastics economy: rethinking the future of plastics*. World Econ. Forum, Geneva, Switz. **http://wef.ch/plasticseconomy**

White RL, Bennett PM. 2015. Elevational distribution and extinction risk in birds. *PLOS ONE* 10:e0121849

Wilcox C, Van Sebille E, Hardesty BD. 2015. Threat of plastic pollution to seabirds is global, pervasive, and increasing. *PNAS* 112:11899–904

Wilmers CC, Estes JA, Edwards M, Laidre KL, Konar B. 2012. Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Front. Ecol. Environ.* 10:409–15

Winemiller K, McIntyre P, Castello L, Fluet-Chouinard E, Giarrizzo T, et al. 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* 351:128–29

Worm B, Hilborn R, Baum JK, Branch TA, Collie JS, et al. 2009. Rebuilding global fisheries. *Science* 325:578–85

Yeakel JD, Pires MM, Rudolf L, Dominy NJ, Koch PL, et al. 2014. Collapse of an ecological network in Ancient Egypt. *PNAS* 111:14472–77

Young HS, Dirzo R, Helgen KM, McCauley DJ, Billeter SA, et al. 2014. Declines in large wildlife increase landscape-level prevalence of rodent-borne disease in Africa. *PNAS* 111:7036–41

Young HS, Dirzo R, Helgen KM, McCauley DJ, Nunn CL, et al. 2016. Large wildlife removal drives immune defense increases in rodents. *Funct. Ecol.* 30:799–807

Zimov NS, Zimov SA, Zimova AE, Zimova GM, Chuprynin VI, Chapin III FS. 2009. Carbon storage in permafrost and soils of the mammoth tundra-steppe biome: role in the global carbon budget. *Geophys. Res. Lett.* 36:1–6

Annu. Rev. Ecol. Evol. Syst. 2016.47:333-358. Downloaded from www.annualreviews.org
Access provided by University of Wisconsin - Madison on 01/29/18. For personal use only.

ANNUAL REVIEWS
Connect With Our Experts

ONLINE NOW!

New From Annual Reviews:

Annual Review of Cancer Biology
cancerbio.annualreviews.org • Volume 1 • March 2017

Co-Editors: **Tyler Jacks**, *Massachusetts Institute of Technology*
Charles L. Sawyers, *Memorial Sloan Kettering Cancer Center*

The *Annual Review of Cancer Biology* reviews a range of subjects representing important and emerging areas in the field of cancer research. The *Annual Review of Cancer Biology* includes three broad themes: Cancer Cell Biology, Tumorigenesis and Cancer Progression, and Translational Cancer Science.

TABLE OF CONTENTS FOR VOLUME 1:

- ***How Tumor Virology Evolved into Cancer Biology and Transformed Oncology***, Harold Varmus
- ***The Role of Autophagy in Cancer***, Naiara Santana-Codina, Joseph D. Mancias, Alec C. Kimmelman
- ***Cell Cycle–Targeted Cancer Therapies***, Charles J. Sherr, Jiri Bartek
- ***Ubiquitin in Cell-Cycle Regulation and Dysregulation in Cancer***, Natalie A. Borg, Vishva M. Dixit
- ***The Two Faces of Reactive Oxygen Species in Cancer***, Colleen R. Reczek, Navdeep S. Chandel
- ***Analyzing Tumor Metabolism In Vivo***, Brandon Faubert, Ralph J. DeBerardinis
- ***Stress-Induced Mutagenesis: Implications in Cancer and Drug Resistance***, Devon M. Fitzgerald, P.J. Hastings, Susan M. Rosenberg
- ***Synthetic Lethality in Cancer Therapeutics***, Roderick L. Beijersbergen, Lodewyk F.A. Wessels, René Bernards
- ***Noncoding RNAs in Cancer Development***, Chao-Po Lin, Lin He
- ***p53: Multiple Facets of a Rubik's Cube***, Yun Zhang, Guillermina Lozano
- ***Resisting Resistance***, Ivana Bozic, Martin A. Nowak
- ***Deciphering Genetic Intratumor Heterogeneity and Its Impact on Cancer Evolution***, Rachel Rosenthal, Nicholas McGranahan, Javier Herrero, Charles Swanton
- ***Immune-Suppressing Cellular Elements of the Tumor Microenvironment***, Douglas T. Fearon
- ***Overcoming On-Target Resistance to Tyrosine Kinase Inhibitors in Lung Cancer***, Ibiayi Dagogo-Jack, Jeffrey A. Engelman, Alice T. Shaw
- ***Apoptosis and Cancer***, Anthony Letai
- ***Chemical Carcinogenesis Models of Cancer: Back to the Future***, Melissa Q. McCreery, Allan Balmain
- ***Extracellular Matrix Remodeling and Stiffening Modulate Tumor Phenotype and Treatment Response***, Jennifer L. Leight, Allison P. Drain, Valerie M. Weaver
- ***Aneuploidy in Cancer: Seq-ing Answers to Old Questions***, Kristin A. Knouse, Teresa Davoli, Stephen J. Elledge, Angelika Amon
- ***The Role of Chromatin-Associated Proteins in Cancer***, Kristian Helin, Saverio Minucci
- ***Targeted Differentiation Therapy with Mutant IDH Inhibitors: Early Experiences and Parallels with Other Differentiation Agents***, Eytan Stein, Katharine Yen
- ***Determinants of Organotropic Metastasis***, Heath A. Smith, Yibin Kang
- ***Multiple Roles for the MLL/COMPASS Family in the Epigenetic Regulation of Gene Expression and in Cancer***, Joshua J. Meeks, Ali Shilatifard
- ***Chimeric Antigen Receptors: A Paradigm Shift in Immunotherapy***, Michel Sadelain

ANNUAL REVIEWS | CONNECT WITH OUR EXPERTS
650.493.4400/800.523.8635 (US/CAN)
www.annualreviews.org | service@annualreviews.org

Annual Review of Ecology, Evolution, and Systematics

Volume 47, 2016

Contents

Indexes

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at http://www.annualreviews.org/errata/ecolsys