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The Importance and Benefits of Species

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Humans depend on biodiversity in myriad ways, yet species are being rapidly lost due to human activities. The ecosystem services approach to conservation tries to establish the value that society derives from the natural world such that the true cost of proposed development actions becomes apparent to decision makers. Species are an integral component of ecosystems, and the value they provide in terms of services should be a standard part of ecosystem assessments. However, assessing the value of species is difficult and will always remain incomplete. Some of the most difficult species' benefits to assess are those that accrue unexpectedly or are wholly unanticipated. In this review, we consider recent examples from a wide variety of species and a diverse set of ecosystem services that illustrate this point and support the application of the precautionary principle to decisions affecting the natural world.

Introduction

The ongoing growth in human population and resource consumption is changing the planet in fundamental ways. One consequence of this growth is the loss of biodiversity, which is typically estimated either by the net movement of species towards higher categories of extinction risk or as the rate at which species are actually going extinct. By either measure, biodiversity loss is on the rise. As species disappear we lose both known and unknown benefits they provide. We begin this review by discussing some well-known examples of the importance of species (Box 1). We then proceed to answer the question: 'what have species done for me lately?' The short answer is: 'plenty!'

The ecosystem services approach, which works towards a more sustainable society, is one prominent means by which threats to species might be reduced while improving human well-being. Ecosystem services are the benefits people derive from ecosystems. Some of these are readily understood, such as the benefit of a forest that is harvested for timber. Timber provision is an ecosystem service and with varying inputs from people it can be sold as a good for human use via markets that set its price. However, most ecosystem services are not bought and sold. The trees used for timber provision depend upon biological and abiotic components of the forest (providing, for example, regulation of regional climate or of tree pests and diseases) that could be assigned value, but are generally taken for granted. Likewise, the same trees that provide timber might also provide other services such as water purification or recreation. Because there is no set price for these services, trees could be valued based on their timber value — the monetized service — simply because this value is known in economic terms. Over the past two decades, various researchers, non-profit organizations, and governments have attempted to assess the value of different ecosystem services in order to demonstrate their significance to society. The assumption has been that by establishing the true value of these services society will stop destroying the biodiversity on which they depend.

Although the ecosystem services approach has been criticized [1], it could benefit species [2]. Nonetheless, the relationship between ecosystem services and species conservation is complex [3]. Species, such as the trees in the example above, are key components of ecosystems and crucial in supporting human well-being [4–7]. However, the attempt to assign value to ecosystem services means that different species will be deemed to have differing degrees of value. This sliding scale of species' value is problematic for at least two reasons: first, to some, it could run counter to the intrinsic value of biodiversity as an established international norm [8]; second, in practice, it is very difficult to assess the value of species because it not only depends on the properties of that species as they are currently understood but on the changes to the environment and society over time. The difficulty of assessing species' value is most apparent when we consider ecosystem services provided by species that are unexpected.

Box 1. Well-known examples of benefits provided by species to humanity.

The best-known benefits are those related to either providing food or facilitating recreation and other cultural activities. Globally, fishers catch >90 million tons of fish each year for human consumption, representing more than 8% of the animal protein consumed. Nearly 40 million people fulltime are employed in fishing directly. Fish exports from the developing world — including aquaculture, which accounts for about half — are worth more than all other agricultural commodities combined [76]. The commercial value of fish is staggering, but fish are often worth a lot even when they are not sold. Consider all of the people who travel to see colorful fish on coral reefs. Consider, too, recreational fishers (33.1 million in the U.S. and about 25 million in Europe [77,78]). Hunting terrestrial mammals or birds for subsistence and sport has similar importance. Millions of people travel to see mammals and birds in far-flung countries.

Classic indirect benefits from species include those derived from the fungus *Penicillium chrysogenum*, from which the antibiotic penicillin was isolated. By the 1960s the tiny fraction of cultivable soil microbes were exhausted and synthetic approaches to drug development began to take over [79]. In the years since, antibiotics have been overused, resulting in an increased prevalence of drug-resistant pathogens, such as MRSA (methicillin-resistant *Staphylococcus aureus*). But just as *Penicillium* species are denizens of soil, so are the microorganisms that appear to have the best chance of beating drug resistance. The discovery of new methods to culture soil microbes *in situ* and the use of specific growth factors have made it possible to grow microbes that were previously ‘uncultivable’ (thought to be about 99% of the total). Already these developments have yielded compounds that could eliminate drug-resistant pathogens [79]. Soil microbes are not the only organisms in nature that have yielded pharmaceuticals. The compound vinblastine, for instance, is derived from Madagascar’s rosy periwinkle (*Catharanthus roseus*). In part as a result of this drug, the five-year odds of surviving acute lymphoblastic leukemia (the most common cancer afflicting children) have increased from less than 10% to over 90% [80]. Likewise, basic research into the venom of a snake, the South American bushmaster (*Lachesis muta*), uncovered a previously unknown pathway to regulate mammalian blood pressure, the angiotensin system. That finding paved the way for angiotensin-converting enzyme (ACE) inhibitors that benefit hundreds of millions of people [81].

Species research for solutions to medical problems is an age-old endeavor. The pursuit of compounds that could lead to breakthrough drugs features prominently in the development of the Nagoya Protocol on Access and Benefit-Sharing in the Convention on Biological Diversity [82]. But drugs are just a small part of the many ways in which the medical field makes use of species and there are certainly other industries that utilize species for profit [49]. A famous example of the unexpected commercial value of a species is *Thermus aquaticus*, a bacterium isolated from hot springs in Yellowstone National Park and described in 1968 [83]. This species is essential to the polymerase chain reaction (PCR), which enables DNA to be multiplied many times over in a short amount of time. The heat-tolerant DNA polymerase used in PCR, known as Taq, comes from *Thermus aquaticus*. It supports an industry that generates tens of billions of dollars.

Efforts to calculate the economic value of species are not new. The importance of ecosystem services has been recognized throughout history, with economists taking note from the mid- to late 18th century onwards [9]. For much of this time, contributions of species to society were at the forefront of the thinking about ecosystem services, and the rationale for this has remained unchanged. For example, a recent article [10] reviewing the ecosystem services birds provide concluded that: “Further research to better understand the economic value of birds will enable better policy and restoration practices, promote and justify bird conservation efforts, and ultimately demonstrate the vital connections among human well-being, intact ecosystems, and the preservation of avian biodiversity” (page 8, [10]). This statement is essentially the same as that of F.J. Wenninger who wrote in 1909: “People must be educated to realize the economic value of the birds. This knowledge, more than anything else, will materially lessen the desire to destroy birds and will preserve one of our nation’s most valuable assets” (page 109, [11]). Today, ecosystem service assessments focusing on species [10,12–15] are complemented by others focusing on habitat types or regions. The species assessments can highlight a diverse set of services [16], even if they will never be able to measure all the unanticipated or hard-to-quantify benefits that species provide.

A flurry of newly published research demonstrates surprising links between individual species or suites of species and ecosystem function that directly benefit people. In most cases, the links between species and function support hypotheses of the nexus of environment, economic development, and human well-being [17,18]. We list a small number of examples that occur outside the traditional provisioning services (e.g., timber, fisheries, medicinal plants; Table 1). These examples underscore the importance of the option value of biodiversity, or the “value of preserving the option to use services in the future” (Box 2) [17]. This also provides evidence that a shift in the burden of proof concerning species’ value is warranted. The precautionary principle with regard to the continued existence of species should guide development and conservation decisions at all scales.

Regulating Ecosystem Services

Regulating ecosystem services are the benefits we derive from ecosystem processes (e.g., carbon storage, water quality, disease regulation). Consider carbon storage by plants: a recent review [19] listed the evidence for biodiversity underpinning this service as equivocal at best. However, two years following that review, new research [20] showed that complementary effects of a diverse set of plant species does indeed lead to greater carbon storage. More surprisingly, it is now clear that the presence of predatory species leads to increased carbon storage. These findings are not limited to well-known examples of apex predators such as wolves, but include species of all sizes in terrestrial,

Table 1. Unexpected benefits species provide to humans.

Service and category		Ecosystem service	Species	Ecological role/function	Description of benefit
Provisioning services	Food	Improved crop yield	Fungi (*Funneliformis mosseae* & *Rhizophagus irregularis*)	Inoculation of chickpea with locally-sourced arbuscular mycorrhizal fungi (AMF) increased yields more than foreign-sourced AMF	Increased crop yield [42]
	Biofuel	Provision of bioenergy feedstock	*Agave* species	Produces abundant fiber	Produces abundant fiber and could produce ethanol without indirect land use change [46]
	Fiber	Potential for improved fiber production	*Panaque* catfishes	*Panaque* catfishes digest wood fibers in a way that could have applications for paper making if the micro-organisms (and enzymes) could be identified	Digestive system of catfish might hold solutions to making paper using less energy [45]
	Biochemicals	Potential for advances in antifouling and adhesion technology	*Mytilus* blue mussels	Use complex chemicals to attach to surfaces under difficult circumstances, and deter other organisms from attaching to it	Possibility of massive fuel savings to marine vessels and adhesives that could have medical applications [47–50]
Regulating services	Biocontrol	Control of herbivorous pests	Insectivorous birds	Predator of pests	Increased coffee yield [43]
	Climate	Carbon storage	*Pisaurina mira* (spider)	Just the presence of spiders (and the fear they induce) reduces grasshopper herbivory; thus increasing carbon storage	Increased carbon capture and climate change mitigation [23]
	Health	Disease reduction	Large herbivores	Compete with rodents for food	Reduction of rodent numbers, and thus of fleas as well as the diseases they carry [37]
	Water	Nutrient cycling	Freshwater mussels & oysters	Filter nutrients from the water column	Improved water quality and nutrient cycling [31,32]
	Erosion	Regulation of grazing by herbivores along streams	Wolves & cougars	Allows recruitment of tree species in riparian areas	Reduced erosion along streams [35]
	Multiple supporting & regulating	Carbon storage, fish nursery, natural hazard regulation	Fiddler crabs	Excavate burrows throughout wetlands	Increased primary production and health of saltmarshes and mangroves [27–30]
Cultural services		Inspiration	Brazilian three-banded armadillo	Not required for this particular ecosystem service	Cultural icon for hundreds of millions who watched the 2014 FIFA World Cup [67,69]
Cultural services		Inspiration	Black robin	Not required for this particular ecosystem service	Symbol of pride for the Chatham Islands, New Zealand [70]
Cultural services		Inspiration	Tiger quoll	Not required for this particular ecosystem service	Helps promote beverage sales and to raise awareness for the conservation of tiger quolls [72]

freshwater, and marine environments [21,22]. For example, fear of the spider *Pisaurina mira* alters feeding habits of grasshoppers, thus reducing herbivory [23]. Reduced herbivory translates into increased carbon storage because the plants have an increased area for photosynthesis and they no longer need to allocate resources to defend against grasshopper attacks (Figure 1). A similar trickle-down effect on carbon storage in forested ecosystems has been observed with woodland salamander predation on invertebrates. The presence of salamanders reduced invertebrate populations leading to increased leaf litter retention, hence increased carbon storage [24].

Saltmarshes and mangroves provide valuable ecosystem services including: carbon storage, fish nursery habitat, and protection from severe weather [17,18,25,26]. In 1985, research showed that burrows created by fiddler crabs (*Uca pugnax*) increased soil drainage, soil oxidation-reduction potential (that

Box 2. Option value of biodiversity

An option value is defined as the value of preserving the option to use services in the future [17]. In the context of biodiversity, an option value usually refers to preserving a value that has yet to be quantified or even identified. A quasi-option value is the value of preventing irreversible decisions until new information is available to indicate whether there is an unexpected value to people. Herein, we speak of the option value as a value to be preserved by and for society as a whole [84]. If the future value is preserved for use by others or an heir, it is termed a 'bequest value' [17]. Although option values typically deal with values that are not yet known, they can also apply to values that might be known but that are subject to changes in importance over time. Thus, people are creating field guides and checklists for groups such as hydroids, millipedes, and land snails [85–87]. The fact that none of these groups enjoys the popularity of bird-watching does not mean they will forever remain obscure. Bird-watching existed in the 19th century, but its popularity today would have been unimaginable at that time.

is, tendency to acquire electrons; a common measure of water quality), and belowground decomposition of plant debris, which in turn led to significant increases to the primary productivity of the saltmarshes (Figure 1) [27]. Recently, fiddler crabs have proven to be so effective at promoting saltmarsh growth that they alone can compensate for herbivory from marsh periwinkles (*Littoraria irrorata*) that would otherwise demolish the habitat [28]. Fiddler crabs are also now known to dramatically increase leaf production, trunk diameter and height of mangrove trees, providing a substantial boost to their ecosystem services [29,30].

Water quality has perhaps been the regulating service most frequently associated with healthy ecosystems. The importance of filter feeding mussels in nutrient cycling and removing harmful substances (both biotic and abiotic) is well known in marine environments. However, for oysters the enormity of this regulating service is only now being reliably estimated as ranging from $5,500–$99,000 per hectare [31]. For freshwater mussels such an assessment is probably a long way off, because the complex nature of this service is just beginning to be uncovered [32]. Where there are no mussels, scientists have discovered that tadpoles provide some of the same nutrient cycling services [33,34]. Erosion prevention is another important regulating service linked to water. In an unlikely species–service connection, recent research has shown that the predation impact of large predators on herbivores yielded better and more structured recruitment of tree species in riparian habitats, thereby securing river banks and limiting erosion [35].

For the past decade, there has been disagreement over the importance of biodiversity in maintaining human health. This debate revolves around the 'dilution effect', whereby the presence of intact ecosystems with multiple species is believed to discourage effective disease transmission. Although there are a number of examples of such dilution, some authors have argued that they are case-specific, and unlikely to be a major factor in human health overall [36]. However, new research suggests that biodiversity loss can release prominent carriers of human disease agents from predation and competition. For example, increased numbers of rodents harboring fleas that carry the bacterial pathogen *Bartonella* resulted from the removal of large herbivore competitors in Kenya, and because rodents are known carriers of numerous zoonotic pathogens the phenomenon may be widespread [37] (Figure 1). Similarly, the loss of native predatory fish along with land-use changes has increased the number of snails carrying *Schistosoma* parasitic flatworms in Lake Malawi [38]. Lastly, the inadvertent poisoning of Indian vultures in the 1990s led to a 99% drop in their abundance within a short period of time. The loss of these scavengers gave rise to an increased population of feral dogs resulting in a surge in rabies cases throughout the subcontinent [39].

Provisioning Ecosystem Services

Provisioning ecosystem services are the ecosystem benefits that result in products that we consume (e.g., food, fibers, biofuels). For instance, numerous species have been identified whose presence increases crop yields. Pollination makes headlines with the recent declines of bees, yet only in the past two years have we begun to understand the extent to which wild insects enhance agriculture [40], and the multitude of services that wild bees provide in terms of crop market value (for example, by prolonging the shelf life of fruit and improving appearance [41]). Lesser known discoveries of species supporting food production, however, are common. Inoculation of chickpeas with native rather than non-native fungi enhances yield [42]. Recent research [43] has clarified how species control pests and, as chemical agents become less effective, researchers are turning again to solutions based on species [44]. In some instances, different kinds of ecosystem services can be linked [3], as, for example, when birds were shown to act as biocontrol agents for herbivorous pests and their presence in mixed landscapes increased crop yields for coffee farmers; thus, birds are simultaneously providing regulating and provisioning services [43].

As we mentioned in the beginning of this review, investigating nature for innovation goes beyond medicine; it also goes beyond agriculture. Catfish in the genus *Panaque*, for example, would seem to be an unlikely candidate for better ways to manufacture paper, yet enzymes produced by bacteria in the catfish's digestive tract could serve that end [45] (Figure 1). Biofuels that are more carbon neutral than fossil fuels may have potential in climate change mitigation. While much current research explores algae as a large-scale biofuel, there is also potential for *Agave* plants to serve as a biofuel through increased fiber production that does not rely on irrigation or result in indirect land use change [46].

Blue mussels (*Mytilus edulis*, *M. galloprovincialis*, and *M. californianus*) are harvested as part of a growing industry, but the full provisioning ecosystem services they provide, or lead to, are only now becoming obvious. Biofouling is the process whereby species settle on marine structures. Many different organisms attach to ship hulls and create drag, clog power plant intakes, or damage gas and oil platforms by growing on their surfaces. Recently scientists have been investigating the surfaces of blue mussels, to which few species attach. They found that both the structural characteristics as well as the chemical composition of the shell surface deter the attachment of many kinds of larva, and there are efforts underway to

Figure 1. Species providing unexpected benefits to humans.
Top left: presence of the nursery web spider (*Pisaurina mira*, inset) induces fear in red-legged grasshoppers (*Melanoplus femurrubrum*), which leads to lower herbivory, thus more standing biomass and increased carbon capture (photo of spider, Eric R. Eaton/bugeric.blogspot.com; photo of grasshopper, Leyo via Wikimedia Commons). Top right: fiddler crabs (*Uca pugnax*) create burrows that lead to stronger mangroves and more productive saltmarshes (photo: Steve Nanz/stevenanz.com). Bottom left: zebras (*Equus quagga*) and other large herbivores regulate rodent populations by competing with them for food, which lowers the prevalence of ticks carrying disease-causing *Bartonella* spp. (photo: ©Anup Shah/naturepl.com). Bottom right: *Panaque schaeferi* is a newly described species of catfish in a genus whose members have unique gut bacteria that can digest wood and may prove beneficial to producing paper using less energy (photo with permission from [88]).

artificially mimic these properties [47]. In another development, blue mussels use adhesive and byssal threads to quickly attach themselves to surfaces [48]. The adhesive has been found to be about twice as strong as an industrial epoxy under ideal conditions, yet mussels accomplish this in saltwater [49]. This last point is significant and has materials scientists trying to understand, and mimic, the metal-polymer complexes involved because adhesives that work in liquid environments have many applications, particularly in surgical medicine [50]. Blue mussels are such common species, yet we are only now beginning to understand the multitude of benefits they yield for people via direct provisioning and indirect inspiration or biomimicry.

What if Certain Species Were Missing from an Ecosystem?

The importance of species to ecosystem function, and ultimately to goods and services, can become apparent through their loss. Consequences of loss can be immediate and easily determined, as is often the case with ecological engineers that modulate the availability of resources to other species [51,52], keystone species that have disproportionate ecological impacts given their abundance [53], and foundation species that create and define entire ecosystems [54]. Certain species guilds, such as frugivores, have been shown to be particularly important in terms of maintaining ecosystem processes [55–57]. However, over time, or when the missing species is part of a complex chain of interactions, the role of the missing species may become obscured. Scientists, for example, routinely detect or formulate hypotheses regarding the absence of prehistoric megafauna, but present day changes in species composition resulting from the loss of megafauna can also be dramatic but are hard to predict. The impact of a species loss on ecosystem services also depends on the degree of redundancy in the system (i.e., are there similar species that are capable of replacing the ones missing?) [58,59]. Thus, redundancy is a key component of resilience, and attempts to replace the ecological functions of missing species have met with varying success [59,60].

Increasingly, there is evidence of the importance of rare species to ecosystem function. This evidence comes from multiple habitats and has been shown both theoretically and experimentally. The largest study of this kind [61] investigated the diversity of unique functional traits represented by rare species in coral reef fishes, alpine plants, and tropical trees. In each system, rare species represented large portions of the functional traits present, leading the authors to emphasize the importance of rare species conservation. Similarly, long-term experimental studies of grasslands show that, while individual species vary in importance, most species (including uncommon ones) boost ecosystem functioning over time, because different species traits are important under differing climatic situations [62]. Functional redundancy in this case might appear prevalent in the short term, but later be shown to represent unique functional traits [63]. The importance of rare species to ecosystem function has also been demonstrated in other habitats. For instance, experimental removal of rare tropical fishes in a mesocosm study altered many ecosystem functions [64], as did the removal of rare sessile species from rocky intertidal marine plots [65].

Cultural Ecosystem Services

Cultural ecosystem services are notoriously hard to measure (but techniques are improving [66]), and novel examples of the ubiquity of species-mediated benefits to humanity become apparent every day. The number of corporate campaigns and logos, sport team mascots, and symbols of national identity is testament to how species are woven into society. Some of this is pure marketing but much of it represents a deeper connection — in short, species resonate with people. Cultural ecosystem services do not remain constant over time and increasingly we see that the benefits provided by species can accrue not only to people, but

Figure 2. Cultural services provided by species.
Top: Brazilian three-banded armadillos (*Tolypeutes tricinctus*) in defensive posture reminiscent of a football — a behavior that led to this animal becoming the official mascot of the FIFA 2014 World Cup in Brazil (mascot version, inset) (photo of mascot, Celso Pupo/Shutterstock.com; photo of armadillo, © Mark Payne-Gill/naturepl.com). Bottom: Black robin (*Petroica traversi*) of the Chatham Islands, New Zealand was reduced to a single breeding pair in 1980. It now numbers 250 individuals [71] and has been a source of pride for islanders, appearing on stamps (inset), coins, and even as the symbol of a local gin distillery (photo of stamp, rook76/depositphotos.com; photo of bird, Robin Bush/Oxford Scientific/Getty Images).

to the species themselves along with the ecosystems upon which they depend. A high profile example was the appropriation by the Fédération Internationale de Football Association (FIFA) of the Brazilian three-banded armadillo (*Tolypeutes tricinctus*) to serve as the mascot *Fuleco*™ (a combination of the Portuguese words for football and ecology) for the 2014 World Cup (Figure 2) [67]. The IUCN Species Survival Commission has engaged FIFA in exploration of mechanisms through which the enormous marketing revenue derived from this cultural ecosystem service can be re-invested in safeguarding the threatened species and its habitat [68,69]. Similar examples at a smaller scale include black robin (*Petroica traversi*), which is endemic to the Chatham Islands of New Zealand and was once regarded as the rarest bird on Earth [70]. At its low point in 1980, only a single breeding pair remained and it is from them that the entire extant population of 250 individuals is derived [71]. In conjunction with this remarkable conservation success, the species was supported in a number of ways (Figure 2). This is not an isolated example. Others include tiger quoll (*Dasyurus maculatus*) from southeastern Australia that now appears on the labels of a local brewery to help market beer and raise awareness [72]. There are even whole conservation strategies devoted to systematically fostering people's innate connection with local species [73], yet the subcategory of cultural ecosystem services called 'inspirational value' to which each of these examples belongs is among the least studied of all ecosystem services [74].

Conclusions

It is impossible to uncover the ecological roles that each of the millions of species plays, let alone all of their benefits to humans. Nonetheless, documentation of these benefits is an important endeavor; current efforts to refine and apply classification schemes for livelihoods, use and trade, and ecosystem services in the IUCN Red List will mark a substantial contribution. As better data become available, it will also become increasingly possible to test the hypothesis that phylogenetic diversity predicts option value [75] — that is, that evolutionary novelty underpins potential but as-yet-unexpected human utility. In the meantime, the demonstrable links between individual species and ecosystem services that are critical to humanity should, at a minimum, eliminate the burden of proving the relevance of species, and give way to an intelligent approach founded on the precautionary principle. The examples in this review highlight a diverse set of species and services, in ways that are direct, complex, and often unexpected. Taken together, they suggest that just because we generally don't know what most species' roles in nature are, they are not unimportant.

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