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Opinion

Managing wildlife tolerance to humans for ecosystem goods and services

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Many animals can vary their behaviors to better utilize anthropogenic environments. Wildlife living in highly disturbed environments often show an increased tolerance towards humans. While animal behavior can play a vital role in producing and delivering ecosystem services, we know less about how variation in wildlife tolerance to humans can influence ecosystem services. Increased tolerance to humans changes a variety of animal behaviors, and these behavioral modifications, such as changes to foraging, habitat selection, and movement, can alter the supply and flow of both ecosystem services and disservices. We highlight the need to understand the links between increased tolerance to humans and ecosystem services to develop an effective tool to enhance services while minimizing the risk of creating disservices.

Highlights

Ecosystem services make substantial contributions to the economy and human well-being, but there can also be costly disservices.

Animal behavior is a key process that may modulate a variety of ecosystem services and disservices.

In the Anthropocene, as human–wildlife interactions increase from urbanization and development, many wild animals decrease their fearfulness and become more tolerant to humans.

Incorporating an understanding of increased tolerance-modulated ecosystem service/disservices into ecosystem management may help in the development of management strategies that improve services while reducing disservices.

Human well-being depends on ecosystem services

Human health and well-being largely depend on ecosystems that provide a range of livelihoods and benefits, known as **ecosystem services** (see Glossary). However, recent anthropogenic activities such as urbanization have led to significant biodiversity loss, resulting in widespread reductions of ecosystem services. For example, the decline in pollinator populations, especially wild bees, is having substantial economic impacts on agricultural production [1]. Similarly, the local extinction of apex and keystone predators [e.g., wolves (*Canis lupus*), sea otters (*Enhydra lutris*)] can increase herbivore populations and lead to overgrazing, which increases soil nitrogen concentrations [2].

Anthropogenic activities impact not only the abundance and diversity of wild animals but also their behaviors [3,4]. However, the effect of human-mediated behavioral changes on ecosystem services has received relatively limited attention and is rarely tested empirically compared with population- and species-level impacts. This deficiency is concerning, especially considering the documented behavioral modifications among a diverse array of species in response to increasing human disturbance [5]. Moreover, these behavioral changes can entail economic and social benefits as well as costs [6,7].

Human-induced behavioral modifications affect ecosystem services

Animal behavior plays a crucial role in ecosystem services across various spatial scales [7]. This connection is unsurprising, considering that the behavior of animals, such as foraging and dispersal, is intertwined with ecosystem processes and organismal abundance – core determinants of ecosystem services and disservices [7]. Current studies of **animal personality** also suggest that particular individuals have more distinctive functions in the ecosystem and species interaction than others [8]. Importantly, the forms of individual behaviors and species interactions vary with the environment and are affected by anthropogenic disturbance. It has been widely seen that animals modify foraging and antipredator behaviors in response to human disturbance [5]

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Box 1. Mechanisms of increased tolerance to humans

Although how animals respond to anthropogenic disturbance is species specific, many species show weaker antipredator responses towards harmless humans such as seen in urban and outdoor recreational areas compared with conspecifics in areas with less human visitation (Figure I). Such behavioral modification is known as increased tolerance towards humans and is often measured by antipredator behaviors such as alert distance (AD) (the distance at which animals respond behaviorally to an approaching human), FID (the distance at which animals flee approaching humans), and distance fled (DF) (the distance moved while escaping) [61]. Since it is relatively easy to measure these in the field, these measurements are used across a variety of taxa [9,62].

Increased tolerance can emerge from several different processes. First, animals vary in their tolerance to human disturbance and this could lead to differential sorting, whereby tolerant animals settle near humans and less tolerant ones settle elsewhere. Second, there could be natural selection, whereby less tolerant animals do not survive in human-disturbed areas. Third, there could be habituation, a process by which repeated interactions with non-threatening humans change their assessment of risk associated with humans and this leads to a decline in responsiveness. Fourth, there could be reduced predation risk in human-dominated areas and this reduction of extrinsic mortality risk could be associated with reduced tolerance to humans. Since large predators tend to avoid the areas that are actively visited by humans, individuals released from predation risk could decrease their vigilance to a wide range of dangers including humans, real predators, and novel threats. The degree to which there is fear generalization (i.e., fear of specific danger could be correlated with other dangers) is a topic of considerable importance [63].

Since antipredator behaviors are traded off with foraging and reproductive behaviors, the reduction of antipredator behaviors enables individuals to allocate more time and energy to fitness-enhancing behaviors. Increased tolerance could also have outcomes for humans. When humans can approach tolerant wildlife, this may enhance and promote positive human–wildlife interactions, which could raise people's motivation for biodiversity conservation. However, such behavioral change driven by increased tolerance could also have negative outcomes. It has been suggested that decreased fearfulness towards humans may increase the mortality risk if habituation to humans is transferred to real predators [13]. Additionally, tolerant individuals may increase the risk of pathogen transmission and property damage. Therefore, although feeding animals has been widely used as a form of environmental education and wildlife tourism, it is not recommended in many places [64].

Figure I. Increased tolerance towards humans has been found in a variety of species from terrestrial and aquatic ecosystems, including: (A) large mammals, such as elk (*Cervus canadensis*) in North American national parks; (B) squirrels, such as Eurasian red squirrels (*Sciurus vulgaris*), in urban parks across Eurasian countries; (C) avian species, such as carrion crows (*Corvus corone*) in urban parks in Japan; and (D) shark-diving tourism, such as bullhead sharks (*Heterodontus* spp.), in Japan. Images in (C,D) are from iStock.

Glossary

Animal personality: significant and detectable individual behavioral variation, which is consistent across different times and contexts. Boldness, aggressiveness, exploration, activity, and sociability are common personality traits.

Behavioral syndrome: correlation among behaviors across time and situations.

Cultural services: the nonmaterial benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and esthetic experiences.

Ecosystem disservices: the properties or functions of ecosystems that cause, or are perceived as responsible for, negative effects on human well-being.

Ecosystem services: the contributions that ecosystems make to human well-being.

Habituation-like process: a process by which individuals decrease their antipredator responses as they are repeatedly exposed to harmless or neutral humans. Positive interactions, such as artificial feeding, can strongly reduce antipredator responses towards humans.

Human shield: one of the factors that create predator-free areas; occurs when the presence of humans acts as a shield for prey species because predators tend to avoid areas that are actively visited by humans. This may increase tolerance towards humans in human-dominated environments.

Human–wildlife conflict: human–wildlife interactions that result in negative consequences to human society (e.g., property damage caused by wildlife, disease transmission). Spatial–temporal overlap and decreased distance between humans and wildlife may lead to increased conflicts.

Nature-based health intervention: any program or activity that aims to engage people in nature-based experiences with the specific goal of achieving improved health and well-being.

Provisioning services: the products people obtain from ecosystems, such as food, fuel, fiber, fresh water, and genetic resources.

Regulating services: the benefits obtained from the regulation of ecosystem processes such as climate regulation, natural hazard regulation, water purification and waste management, pollination, and pest control.

humans is one of the commonly observed behavioral changes in animals that live in human-dominated environments (e.g., cities) ([9]; Box 1). It is well known that benign human–wildlife interactions cause **habituation-like processes** in wildlife, and these have been observed in many wildlife species and ecosystems that are heavily used by humans [10–13]. Similarly, for some species, low predation pressure in human-dominated environments can decrease vigilance and increase boldness to humans (i.e., **human shield**) [14], and hence increase tolerance to humans [15]. Given that direct human–wildlife interactions will increase as the human population increases [16], understanding how increased tolerance to humans alters ecosystem services is essential for biodiversity conservation, ecosystem management, and ensuring human health and well-being.

Supporting services: the services necessary for the production of other types of ecosystem services.
Tolerance: a reduction in behavioral and physiological responses to certain threats. Increased tolerance to humans can be seen by an attenuated antipredator response to approaching humans. Increased tolerance is a key behavioral modification for wildlife to better utilize human-dominated environments.

We discuss the impact of increased wildlife tolerance to humans on ecosystem services and suggest a roadmap for its application to ecosystem management. First, we illustrate known and predictable linkages between tolerance modification and ecosystem services and disservices (Figure 1). Next, we develop a decision support tool and suggest guidelines to apply empirical and theoretical knowledge to ecosystem management and outline several key future research areas for this topic.

Consequences for ecosystem services and disservices

The modification of species' tolerance, commonly measured through antipredator boldness, can have downstream effects on other behaviors such as foraging, habitat use, and movement. For instance, bolder individuals spend more time foraging and tend to disperse farther than shyer conspecifics. Likewise, individuals with bolder antipredator responses are more likely to use areas highly disturbed by humans than others [17]. Consequently, increased tolerance to humans can significantly influence services in either positive or negative ways by modifying direct human–wildlife interactions, foraging behavior, and habitat use. Increased tolerance towards humans has known and predictable effects on the four major ecosystem services (**provisioning**, **regulating**, **supporting**, and **cultural services**; Ecosystem Millennium Assessment 2005 [67]) and disservices.

Provisioning services

Some individuals are more likely to be attracted to traps than others. Bighorn sheep (*Ovis canadensis*) have consistent interindividual variation in the likelihood of trappability [18] and such variation is associated with individual boldness. Namibian rock agamas (*Agama planiceps*) that have shorter flight initiation distances (FIDs) (the distance when animals initiate escaping from approaching humans, where shorter FID indicates higher tolerance to humans) were more likely to be trapped than individuals with longer FIDs [19]. A positive association between boldness and trappability has implications for the harvesting of wildlife and fisheries resources. Trout domestication involves artificial selection for highly tolerant phenotypes, increases antipredator boldness, and enhances fishing success in the wild [20].

Regulating services

Many seed-bearing plants and fruits rely on seed dispersal and pollination by animals [21,22]. Zwolak and Sih [23] suggested that proactive individuals (individuals who have higher boldness, aggression, and activity) are likely to disperse and harvest more seeds further from parent trees than reactive conspecifics (individuals who have lower boldness, aggression, and activity). For example, bolder deer mice (*Peromyscus maniculatus*) tend to select larger seeds than shyer conspecifics, and bolder southern red-backed voles (*Myodes gapperi*) transport seeds farther [24]. Increased boldness thus might enhance forest regeneration in anthropogenically disturbed environments. Additionally, relatively bold and exploratory individuals traveled further distances and visited more flowers than shyer individuals [25]; such behavioral tendencies can facilitate cross-fertilization and thus enhance pollination. Hummingbirds are important pollinators in urban environments and since hummingbirds are actively fed by people [26], individuals habituated to humans may be more efficient pollinators than unhabituated individuals.

A release from natural enemies in human-dominated environments may drive overabundance of pest species and this may negatively affect human health and well-being. However, it has also been suggested that a lack of large-sized predators permits middle-sized predators such as hawks [e.g., Cooper's hawk (*Accipiter cooperii*), foxes (*Vulpes* spp.)] to colonize urbanized areas (so-called mesopredator release [27]). Mesopredators that become tolerant to humans could suppress the population growth of less desired species. Insectivores that are highly tolerant to humans may control insects around humans and tolerant scavengers may play an essential role in eliminating carrion and reducing disease risk [28]. For example, obligatory scavengers such as black kites (*Milvus migrans*) are widely distributed in Eurasian agricultural and residential areas [29]. Given a long history of interdependence between humans and scavengers, the current increased tolerance in scavengers may enhance decomposition benefits.

Supporting services

Nutrient cycling is a crucial process in both terrestrial and aquatic ecosystems. Seabirds, in particular, play an important role in transporting nutrients from marine to terrestrial ecosystems by depositing guano at their breeding sites [30]. By modifying tolerance, seabirds may change habitat selection and foraging. For example, tolerant individuals might nest in highly disturbed areas more often than sensitive conspecifics and therefore could transport more nutrients and modify nutrient deposition, which would lead to enhanced nutrient richness in highly disturbed landscapes. Bolder black-browed albatrosses (*Thalassarche melanophris*) foraged closer to breeding colonies than shyer individuals [31], which might permit bolder individuals to return to their colonies more often with nutrients than others. Thus, highly tolerant individuals could become keystones for nutrient cycling.

Additionally, increased tolerance in predators could have cascading effects on plant species by suppressing herbivore populations and reducing overgrazing [32]. This could benefit the conservation of habitats for threatened plants and small animals.

Cultural services

Habituation is often used as a tool to increase contact with wild animals in nature-based tourism and recreation. Great ape tourism, as seen with eastern gorillas (*Gorilla beringei*) and Bornean orangutans (*Pongo pygmaeus*), depends on habituated animals [33,34]. Similarly, marine mammal tourism, such as bottlenose dolphin (*Tursiops aduncus*) tourism at Monkey Mia in Shark Bay, Western Australia [35], which generates millions of dollars annually, is enhanced by specific tolerant individuals.

Direct interactions with nature are increasingly recognized as providing a wide range of health and well-being benefits [16]. In more urbanized and wealthier societies, extensive efforts have been made to develop strategies and programs that enhance people's experiences of nature to improve their health and well-being. These are known as **nature-based health interventions** [36,37]. Increased tolerance towards humans can amplify these benefits. For instance, seeing birds and listening to birdsong are activities that are associated with improved psychological health, such as reduced symptoms of depression and anxiety [38,39]. Thus, if birds become bolder and more likely to approach humans, and this increases their visitation to urban domestic gardens, people can potentially obtain even greater benefits from birds.

Disservices

The reduction of fear in tolerant animals is not universally beneficial to humans. Bolder individuals that settle near humans may create novel challenges. Below we explore these challenges from three distinct viewpoints: economy, health and safety, and esthetics and culture.

Economy

Increased tolerance of animals to humans can often lead to various detrimental economic consequences. For instance, animals that exhibit high levels of tolerance towards humans may frequently cause damage to crops [40]. Likewise, avian excrement can result in chemical damage to houses, cars, and outdoor sculptures [41]. If highly tolerant individuals tend to settle in residential areas, they could be responsible for expensive damage to infrastructures. Of course, the economic costs of increased tolerance derive from other two types of impacts (see later).

Health and safety

Increased direct human–wildlife interactions may enhance the risks of zoonotic disease transmission. Enhancing this risk is the observation that individuals that are bolder and more aggressive than others tend to have higher abundance of parasites and are more likely to be sick ([42–44]). If a **behavioral syndrome** exists (i.e., bolder individuals are more aggressive than shyer individuals), increased boldness may be associated with increased aggression towards humans. Highly habituated Australian magpies (*Gymnorhina tibicen*) and black kites exhibit aggressive behaviors towards humans [45,46]. More seriously, habituated crab-eating macaques (*Macaca fascicularis*) in Bali were highly aggressive towards tourists [47]. This could increase the risk of disease transmission because nonhuman primates carry a variety of zoonoses.

Esthetics and culture

A number of urban birds and mammals have been observed breaking into homes and scattering human rubbish because they readily consume anthropogenic foods [48], and this is likely to be enhanced in areas hosting tolerant individuals. Other esthetic disservices might include unpleasant odors from rotting organic matter that is scattered by individuals that are highly tolerant to humans. Tolerant animals may create noise when inhabiting residential areas. Such

Box 2. How increased tolerance of keystone species modifies ecosystem services

To predict the impact of tolerance modification on ecosystem services, focusing on keystone species may be useful. For example, sea otters (*Enhydra lutris*)*, which are* distributed in the northern Pacific from California, USA to Hokkaido, Japan are the top predators that can restructure the local community in coastal areas. Sea otters are known to regulate the abundance of sea urchins (Echinoidea spp.), which sometimes overgraze kelp (*Strongylocentrotus* spp.), thereby increasing carbon storage and indirectly providing habitats for many species. If sea otters could be habituated to humans and anchored to specific areas, they could play an important role in increasing local biodiversity in areas highly visited by humans (but note there may be novel problems associated with habituated otters that attack humans on surfboards: https://www.youtube.com/watch?v=qFSpNwgc6o8).

In terrestrial ecosystems, some raptors, such as hawks and owls, serve as models of keystone species that function as pest control agents. For example, Ural owls (*Strix uralensis*) in Japan are biological control agents that reduce rodent density. Murano *et al.* [65] showed that the owls were successfully attracted to apple orchards using nest boxes and reduced vole populations by 63% compared with areas without owls. This indicates that owls' increased tolerance to humans can enhance the function of rodent pest control in agricultural areas.

By contrast, large herbivores in terrestrial systems, such as ungulates, can adversely affect ecosystems by browsing vegetation. This could increase soil erosion and drive the decline in bird and insect species diversity, which can impact regulating and supporting services. Additionally, bolder ungulates are more likely to venture onto highways or railways, leading to increased wildlife–vehicle collisions. To minimize these **ecosystem disservices**, it is important to prevent such species from becoming tolerant to human disturbances or to sensitize them (e.g., by aversive conditioning, hazing, or simulated hunting) [59,60,66].

behaviors can drive negative beliefs and attitudes towards these species [49]. Although the risk of increased tolerance-induced disservices has been discussed, there are relatively few empirical studies of them.

Complexities

Since animals often contribute to multiple ecosystem services, increased tolerance may be associated with multiple services simultaneously. For instance, tolerant animals may enhance human well-being while also being able to allocate more time to foraging and food-caching and thus increase seed dispersal. Wildlife tourism may benefit from tolerant animals, but these individuals may also create novel **human–wildlife conflicts** by foraging on crops and damaging property. For those species that provide multiple services, the impact of

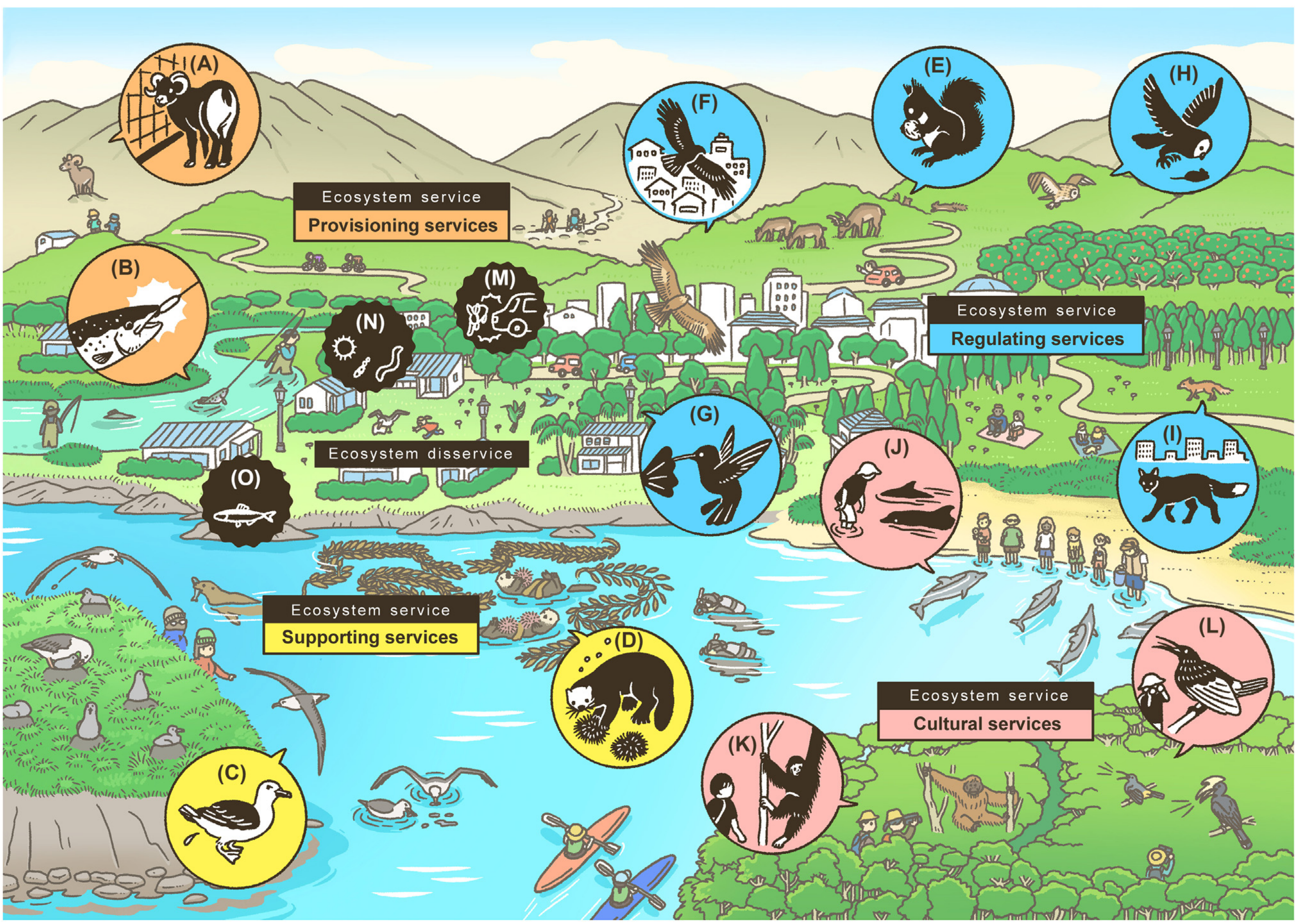

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Figure 1. The predictable impacts of increased tolerance on terrestrial and aquatic ecosystem services. Provisioning services: (A) enhancement of trappability in highly tolerant species that are harvested. (B) Increased vulnerability to fishing as fish become bold. Supporting services: (C) increased nutrient transportation from the ocean to terrestrial ecosystems by tolerant seabirds. (D) Contribution to kelp forest conservation by highly tolerant sea otters. Regulating services: (E) enhancement of seed dispersal by bold squirrels. (F) Increased decomposition benefits by scavengers in urbanized areas. (G) Increased pollination by habituated avian pollinators. (H) Facilitated rodent control by owls, which are attracted to agricultural areas. (I) Enhancement of rodent pest control by mesopredators in urbanized areas. Cultural services: (J) marine ecotourism could be enhanced by interactions with habituated individuals. (K) Increased benefits to humans interacting with tolerant great apes. (L) Amplified human well-being by contact with highly tolerant wildlife. Disservices: (M) increase in the probability of traffic accidents as animals become bold to humans. (N) Increased human–wildlife interactions with bolder or more tolerant individuals could increase the risk of zoonotic disease transmission. (O) Bolder individuals that settle near humans may create conflicts between wildlife and fishermen in aquatic ecosystems.

behavioral changes might influence a variety of ecosystem services in either or both positive and negative ways. To manage systems, we must understand the relationship between increased tolerance and ecosystem services and disservices.

Conservation and management applications

Recent studies have suggested that exposure to humans may domesticate wild animals [50], and this has a suite of expected consequences. Managing an individual's behavior is likely to be easier and less costly than population- or community-scale management. For example, we might be able to modify a species' ecosystem services by managing human–wildlife interactions and habitat characteristics that are likely to influence tolerance [51]. We developed a road map to manage tolerance (Figure 2).

i. Measure tolerance and behavior

Understanding behavioral responses to human disturbance is first step.

- Quantify antipredator behaviors towards human (e.g. FID, AD, DF)
- Differentiate reduction of vigilance and habituation-like process
- Quantify ecosystem functioning-related behaviors (e.g. foraging, spatial use, seed dispersal)
- Develop species specific measurement

ii. Long-term assessment

Tolerance is changeable. Identification of increased tolerance requires temporal or spatial assessment.

- Monitor long-term behavioral modification towards human disturbance
- Monitor tolerance either at the individual or population level
- Measure behavioral variation among habitats that have different human impact (e.g. urban vs rural, urbanization gradient)

iii. Verification

Confirmation of relationship between increased tolerance and ecosystem service modification is essential. Actual impact of increased tolerance on service alteration should be carefully identified.

- Verify links between tolerance and functioning-related behavior
- Verify links between tolerance and human-wildlife interaction and human perception
- Assess if tolerance modification modulates actual service (i.e. provisioning-, regulating-, supporting-, cultural-services, disservice)

iv. Application

Applying ecological evidence and knowledge to management decisions.

- Regulate human-wildlife interaction (e.g. zoning, restrict feeding)
- Make animals sensitized by aversive stimulus (e.g. hunting, hazing)
- Make animals habituated by encouraging harmless interactions (e.g. regulate noise)
- Design local habitat environmental features (e.g. openness)
- Monitor the efficiency of management action

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Figure 2. A roadmap to apply scientific knowledge to ecosystem management. This can be used by field biologists who study the ecological processes of ecosystem services and by wildlife managers to manage services. We focus on four key steps: (i) measuring tolerance and behavior; (ii) long-term assessment; (iii) verification of the actual relationship between increased tolerance and ecosystem service modifications; and (iv) management application. First, one must quantify target species' tolerance towards humans. Flight initiation distance (FID) (the distance when a target animal initiates escape from an approaching human), alert distance (AD) (the distance when a target animal initiates alert to an approaching human), and distance fled (DF) (the distance that a target individual moves while escaping) are common behavioral metrics to quantify tolerance. It is also essential to measure other behavioral modifications that are associated with species' ecosystem functions, such as foraging, habitat use, and movement. Second, long-term behavioral monitoring enables us to detect temporal shifts of tolerance at the individual or population level. Measuring behavioral variation among habitats that have different degrees of human disturbance could be an alternative way to predict changes in tolerance. Third, one must validate the impact of increased tolerance on changes in a species' ecosystem function behaviors. Finally, knowledge of how behaviors affect ecosystem services can be applied. If a service would be positively enhanced, habituation may be encouraged, while increased tolerance should be prevented or animals should be sensitized if increased tolerance drives negative consequences. Any manipulations should be designed in the context of adaptive management, to evaluate their efficacy.

Management of tolerance first requires its quantification (Figure 2i). Quantifying FID is straightforward and these observations can be supplemented by quantifying vigilance and foraging behavior because these activities are directly related to resource use. Studying FID and vigilance simultaneously could separate the confounding mechanisms of increased tolerance (reduction in vigilance versus habituation-like response to humans). Determining whether tolerance and habitat use covary also provides key insights into putative impacts on ecosystem services. Depending on the species, there may be alternative measures of tolerance that could be quantified (e.g., alarm calling).

The degree of tolerance may change over time as animals are exposed to more human disturbance. Arroyo *et al.* [52] reported an increase, over four or five generations, in boldness towards humans in Montagu's harrier (*Circus pygargus*) that experienced repeated exposure to humans over 19 years. This highlights the importance of long-term monitoring to detect mechanisms of changes in tolerance (i.e., plasticity versus evolutionary change), because these changes could influence population persistence and thereby services (Figure 2ii). Given the difficulties of longitudinal studies, mechanistic insights may be gained by studying behavioral variation among habitats that have different degrees of human disturbance (e.g., along urban–rural gradients). The behavioral states found in rural populations could be a benchmark for behavioral modification as a function of human disturbance [53–55].

It is essential to identify links between tolerance and ecosystem services (Figure 2iii). Merz *et al.* [56] showed that personality-mediated foraging behavior affected seed dispersal in voles. While we expect this to be common, few studies have done the necessary work to document these relationships. A good place to start would be to focus on keystone species or ecosystem engineers where we expect the strongest effects [57] (Box 2).

Finally, it may be necessary to create innovative tolerance management plans to manage ecosystem services (Figure 2iv). Current articles suggest that manipulating animals' behaviors can be an effective tool for wildlife and ecosystem management [58]. For instance, aversive conditioning, hunting, or hazing could increase animals' sensitivity [59,60], while exposure to benign and neutral human activities may make animals more tolerant towards human presence. Moreover, since individuals' fearfulness is also associated with local environmental features that influence risk assessment [51], environmental manipulations are additional tools to modulate species' tolerance. For example, if human–wildlife interactions in urban parks create disservices, reducing cover in parks could be used to sustain fearfulness and reduce the emergence of tolerance. Evaluation of management outcomes is essential. For example, intensive harvesting of tolerant individuals may select against increased tolerance, which could either increase or decrease other ecosystem services. Adaptive management is required.

Concluding remarks

In the Anthropocene, we expect humans to modify animals' tolerance to humans. We have outlined the ways that modified wildlife tolerance to humans may affect ecosystem services and suggested a roadmap for their management. We suggested that initial attempts to manage tolerance focus on keystone species or ecosystem engineers because they are likely to have the largest effects. More empirical studies are required (see Outstanding questions), particularly in aquatic ecosystems. Importantly, decreased fear of humans by wildlife can be a double-edged sword: it is often encouraged in some situations because it could buffer the impact of anthropogenic disturbance on wildlife and improve ecosystem services, but it may also create disservices. Increased tolerance towards wildlife may have synergistic impacts on services in conjunction with changes in wildlife abundance and diversity. Our challenge, therefore, is to apply our scientific

Outstanding questions

What are the long-term consequences of increased tolerance on ecosystem services and how do they vary by ecosystem type?

What are the relative strengths of the direct and indirect effects of tolerance on ecosystem services?

Can increased tolerance at the individual scale modulate ecosystem services at the population level?

Does the mechanism of tolerance affect the ability to manage ecosystem services?

What are the most effective methods to measure wildlife's tolerance towards humans?

To what extent does increased tolerance towards humans influence human health and well-being?

Do increase tolerance towards humans and biodiversity loss have synergistic effects on ecosystem services?

What kind of management actions are most effective and sustainable in controlling tolerance?

How does increased tolerance influence ecosystem services differently between terrestrial and aquatic settings?

Which ecosystem service modifications will dominate initially and which management action should be prioritized?

knowledge to practical management actions to maximize the benefits and minimize the costs provided by ecosystems modulated by wildlife that are highly tolerant to humans.

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Declaration of interests

No interests are declared.

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