Anthropogenic Disturbances*
Impacts on Ecological Functions of Animals

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Humans have caused immense disturbances to the Earth’s wild ecosystems. Here, I explain how these disturbances are impacting and altering the essential roles or functions of animals in these ecosystems. Population declines, as well as behavioural and morphological changes in animals as a response to disturbance, alters how organisms interact with each other. Since these interactions define an animal’s role in its habitat, such changes can have devastating impacts on the future of these ecosystems.

Introduction

Humans have wrought devastating changes to the world’s ecosystems. Demand for food and other resources for the Earth’s 7.6 billion people places unprecedented pressure on the Earth’s terrestrial and aquatic environments. We have been the direct or indirect cause of a loss of nearly 60% (on average) of surveyed animal populations. Forest loss and fragmentation are visually obvious, as are some of the immediate consequences of these disturbances. In comparison, losses of animal communities that inhabit these forests are often more insidious, because the visual consequences of animal loss or decline are often delayed. More than two decades ago, Kent Redford [1] drew attention to the vast areas of tropical forest in the neotropics that falsely appeared intact, because of the “presence of soaring, buttressed tropical trees”, but which were largely devoid of the animal life required to sustain those ecosystems. Ecosystems are composed of multiple populations of plants, animals, and other organisms that are

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highly interconnected. The relationships that link any two types of organisms may be trophic (such as predation, herbivory, frugivory) or non-trophic (such as competition or facilitation), and may be mutualistic (benefiting both organisms) or antagonistic (benefiting only one of the organisms). These relationships or ‘interactions’ that provide services are essential to maintaining the ecosystem. These services provided by animals can be termed their ‘ecological function’. For example, seed dispersal is a critical process resulting from a trophic interaction (usually) that is mutually beneficial to the fruit-bearing plant species and animal involved in the interaction. Seed dispersal is also essential for determining where seeds are deposited and whether seeds are likely to survive and germinate. Hence, fruit-eating animals have an important function as seed dispersers because they determine the future plant populations that will occur within ecosystems. Other important functions that animals play in ecosystems include predation (controlling prey populations), pollination (promoting genetic diversity in plant populations and fruit formation), and as detritivores (breaking down organic matter).

Losing animals from seemingly intact forested ecosystems can have important immediate and future ecological consequences. This is due to the disruption these losses cause to the critical interactions that maintain these ecosystems. With the much longer generation times of trees, changes to the structure of tree populations will take a longer time to manifest and future changes are referred to as an ‘extinction debt’. The loss of keystone species (Box 1) is particularly critical. Kent Redford termed forests without (many) animals as ‘Empty forests’ [1] (Box 2) and cautioned the need to identify and address the direct and indirect causes of empty forests (e.g., hunting, extraction of essential resources for animals). However, local extinction of animal populations is preceded by a period of population decline. While these ‘half-empty forests’ are not devoid of wildlife, many essential interactions may still be disrupted due to the reduced number of animals involved in the interactions. Further, even before populations begin to decline, individuals might adapt to the disturbance by chang-
ing their behaviour, and behaviour is a critical determinant of the likelihood of an interaction occurring and the result of that interaction. Populations might even adapt at a morphological or genetic level to the disturbance. All of these potential changes could alter important interactions that the organism is involved in, thereby, altering their functions and threatening the long-term persistence of the ecosystem it inhabits [2].

The aim of this article is to describe the ways in which important interactions between animals and other organisms can be altered by disturbances to their populations, behaviour, and morphology. I consider interactions that directly impact the ecological function of the animal and provide examples from a diversity of habitats—both forested and non-forested.

**Box 1. Keystone Species**

Organisms play essential roles in maintaining the ecosystems they inhabit, but these roles differ in their importance. Keystone species are defined as a species that has a disproportionately large effect on its natural environment. They play unique and essential roles that maintain the integrity of the ecosystem. The decline or disappearance of keystone species will have cascading effects within the ecosystem which will trigger declines in other species. For example, wolves are considered keystone species in North America [3]. The local extinction of wolves (Figure A) from Yellowstone National Park in the mid-1920s resulted in over-grazing of the habitat by the herbivores whose populations and movements were controlled by the wolves. A myriad of other animal species was impacted by these changes, including beaver populations when water flow in streams and rivers was altered by increased herbivory.

![Canis lupus](Source: Jeremy Weber, Flickr, entitled ‘Yellowstone Wolf in Woods’).
Changes to Populations: Loss in Abundance

Population abundance is an important influence on an animal’s ecological function. Reductions in abundance, or even over-abundance, will alter interactions among individuals within a population and also interactions among individuals of different species, due to the altered competition. Populations may also be reduced to such an extreme extent that there simply is no longer enough animals to adequately fulfil an ecological role that was performed in the past (an ‘almost empty’ forest). Called ‘functional extinction’, such a population is one “that has become too low to maintain interactions with other species”, and this is likely the current state of many highly threatened animal populations.

An excellent example of functional extinction is that of the seabird

**Box 2. An Empty Forest**

Lambir Hill National Park, Malaysia is one of the most diverse forests known and supported a complete fauna in the 1980s. The surfacing of a road through the park in 1987 allowed increased access for people and triggered a dramatic increase in hunting pressure. Two decades later, Lambir had lost almost all its large (>1 kg) frugivores that played important roles in seed dispersal (*Figure B*). This has caused pervasive changes in the spatial structure and dynamics of plant populations. A majority of plant species were dependent on the lost animal dispersers, and without them, the seeds fall close to the parent plant where they are vulnerable to seed predators and pathogens [4].

*Figure B*. Hunted wreathed hornbills (Source: Wikimedia commons).
populations in the Aleutian Islands, Alaska. Twenty-nine species of seabirds breed on the islands, and they number more than 10 million individuals. By feeding in the oceans and depositing guano on land, these birds are major transporters of nutrients from the ocean to land, and this role maintains the grassland ecosystems (i.e., they are a keystone species). Arctic foxes were introduced to some of the islands in the late 19th and early 20th centuries to support a declining fur trade. These foxes feasted on the readily available seabirds, decimating their numbers by 97%. Comparisons were made of islands with and without foxes to determine the impact of foxes (and seabird loss) on plant communities [5]. Nutrient deposition on the islands with foxes declined by a similar magnitude as that of the birds, and this transformed these islands from grassland to nutrient-impoverished tundra. Evidently, seabird populations in the Aleutian Islands have become too low to adequately maintain their key ecological function of nutrient deposition.

Such severe declines in animal abundance are not always necessary for the loss of an ecological function (half-empty forests). If an interaction is influenced by density-dependent behaviour, a species may be functionally-extinct or have an ecological function significantly altered even in the absence of a very large population decline. Flying foxes are large fruit bats that play key-stone roles in pollination and seed dispersal on many islands in the tropical Pacific. Because they can only swallow very small seeds, large-seeded fruits are dispersed when they are transported away from the fruiting tree in the mouth of the animal. However, the bats only remove a fruit from the tree when there are sufficient numbers of bats foraging within the plant to induce territorial disputes. The impact of this behaviour on seed dispersal patterns was investigated in the Tongan archipelago of the South Pacific Ocean [6]. The study found that a threshold abundance of bats was required on an island for seeds to be moved beyond the parent tree crown by flying foxes. Below this threshold, bats foraged quietly within the plant crowns and dropped all the seeds beneath the tree (where seed mortality is high), and hence they no longer
fulfilled their keystone ecological function as seed dispersers.

Changes to Populations: Demographic Structure of Populations

Ecological functions performed by animals may exhibit important within-population differences. When this occurs, individuals within a population perform different roles according to their sex, age, size, or individual personality traits. Under these conditions, a change in the demographic structure of a population could cause significant changes to the ecological function performed by the population as a whole. Such a change is probably most likely to be triggered by population decline when a subset of a population is the primary target; for example, selective harvesting of large

Box 3. The Importance of Abundance

Many animal populations—from wildebeest and dabbling ducks to the extinct passenger pigeon—perform (or performed) important roles through their sheer abundance, whereas, the role of individuals is comparatively insignificant (Figure C). Yet, we frequently ignore the requirements of common, abundant species to focus on the endangered species. For example, crop pollination by bees is driven by the abundance of dominant species with rare species contributing little to this ecological function [7]. Hence, abundance is a key feature determining an animal’s ecological function, and it is crucial we place value in not just conserving endangered species, but maintaining, or regaining, its abundance as well [8].

Figure C. Wildebeest migration in Serengeti National Park, Tanzania (Source: Wikimedia Commons).
fish by fishing industries or shooting of male deers with the largest antlers. However, other forms of disturbance (Box 4) might also trigger differential responses by animals due to differing physiological and social requirements, and variation among individuals in their personalities (i.e., shy vs. bold).

Fishing industries and even recreational fishermen, frequently target the largest individuals within a population. The impact of this selection on diet was studied for the California sheephead, which is an important generalist predator in kelp forests off California, USA. Sheephead populations were exploited commercially during the 1990s but after the collapse of the industry due to overfishing, the population was left to recover and had regained its size structure by the year 2000. The larger fish (which were absent in the years of commercial fishing) consumed more sea urchins and other invertebrate grazers which are major herbivores of kelp. Hence, it is the larger fish within the sheephead populations that are essential for fulfilling the ecological function of controlling grazers of kelp [9], and a shift in the demographic structure of the population caused by over-fishing hindered this function.

Individuals may also show personality differences that can impact the interactions in which they are involved. Personality studies have generally been focused quite narrowly on bold vs. shy individuals, and almost no studies have addressed how personality differences might impact ecological function at an individual level. Rafal Zwolak provides examples of how personality might alter seed dispersal by animals [10]: For example, bolder individuals might deposit seeds in riskier areas or individuals with high activity might disperse more seeds and disperse them further. Under some scenarios of disturbance, individuals that are bolder and more active might be more vulnerable (for example, to hunting or persecution), and selective loss of these animals could alter the overall population function as seed dispersers.
 Behavioural Changes Within Populations

Ecological functions performed by animals are a consequence of daily activities such as searching for and consuming food, avoiding being eaten, seeking shelter, and pursuing mates. Hence, it is the ecological and behavioural attributes of animals, as well as their physiological requirements that determine what interactions they become involved in, ultimately determining the functions they perform within an ecosystem. Since animals can re-

Box 4. Anthropogenic Disturbances

The Earth’s wild habitats have undergone immense change due to disturbances caused by humans. Animal populations have been targeted directly due to hunting for bushmeat, trophies, and for the pet and medicine trade. They have also been persecuted as agricultural pests. For example, the South-east Asian apes—orangutans and gibbons—are popular as pets or for use in animal shows. But these pets are taken directly from the forest after the mother ape is killed. Pangolins are considered to be the world’s most trafficked animal, caught largely for use in traditional Chinese medicine. Over 40,000 Mauritian flying foxes were killed by the Mauritian government in 2015 and 2016 because it was believed that they were causing large losses to domesticated fruit crops. All these animals are involved in important interactions, fulfilling important ecological functions that are lost with these massive declines.

Animal populations are also targeted indirectly when their habitats or essential resources are modified by fragmentation, degradation, or more insidiously, by pollution, climate change, and invasive species (Figure D). These indirect impacts can result in population declines of the animal if they are unable to adapt to the change in habitat or resources. Alternatively, they may impact the animal’s behaviour as the animal is forced to alter their ranging, diet or social behaviour as a response to the disturbance.

Figure D. A rainforest fragment surrounded by oil palm plantations on Borneo (Source: Wikimedia Commons).
Animals might alter their behaviour following the decline or disappearance of species in the community that competed with them, preyed upon them, or assisted them in finding food. For example, some bird species form mixed flocks composed of different species hunting for insects. Flock formation is dependent on a core species, and enhance the foraging rates of individuals in the flock. Loss of these core species would impact the efficiency with which non-core species can forage for insects, and thereby, influence their function of controlling the insect populations. Conversely, resource competition between two taxa of bees is seen to positively impact their functional role as pollinators [11]; the loss of one bee taxon, therefore, would negatively impact the pollination services provided by the other. The impacts of predation on behaviour have been relatively well-studied in a range of organisms, and these studies show how the behaviour of prey is altered when predators are lost or removed from an ecosystem. For example, animals as diverse as dugongs and grasshoppers alter their foraging patterns and, therefore, their impact on plant communities when predators are absent [12], [13].

Animals also adapt their behaviour to changes in habitats or resource availability and distribution. Such habitat changes are pervasive across the globe and are, potentially, a major trigger for changes in the ecological functions of animals. Structural habitat changes may occur due to habitat degradation and fragmentation, including structures such as fences. For example, perimeter fences used in the African game reserves have altered the hunting behaviour of African wild dogs; they can hunt larger and stronger prey when a fence is present as they have learnt to drive the prey towards the fence, which impedes their escape. This could have a significant impact on predator-prey dynamics [14]. Not all habitat changes are structural; pollution caused by noise and light have been demonstrated to impact the seed dispersal function of bats and the role of animals in the regeneration of a pine tree species.
Finally, changes in the spatial and temporal availability of resources is a frequent consequence of anthropogenic disturbance and can impact the function of animals. For example, black bears in the US are important seed dispersers of wild fruits but preferentially feed on cultivated fruits in people’s gardens [17], and probably no longer disperse the wild species when this occurs.

Climate change has the potential to alter interactions among organisms in radical new ways since it impacts resources, habitats, as well as the physiology of animals. Studies on diverse animal species have shown the importance of water availability to movement patterns and have demonstrated alterations in behaviour and diet according to temperature and extreme weather conditions. For example, ants are widely known for their mutualism with aphids, which are a major plant pest. Ants defend aphids from ladybirds because they value and extract the ‘honeydew’ produced by the aphids. Yet at increased temperatures, a studied ant species became less aggressive and no longer defended the aphids from the ladybirds [18].

Morphological Adaptation

While morphological changes in animals have been noted in response to fragmentation, resource changes, and climate change, no studies have yet evaluated the impacts these changes might have on the functions for which these animals are important. Animals might also adapt to disturbances in their habitats by eventually adapting morphologically to ensure that they can continue to survive in the altered habitat. Such morphological changes might improve their survival chances while altering the functions they are involved in. While morphological changes in animals have been noted in response to fragmentation, resource changes, and climate change [19] [20], no studies have yet evaluated the impacts these changes might have on the functions for which these animals are important.

Conclusion

Animals have essential functions in maintaining diverse ecosystems across the globe. These functions involve maintaining inter-
actions among species. But these interactions are being increasingly altered due to anthropogenic activities. Population decline (due to demographic change in the population, or when there are simply too few animals left to maintain their interactions) can change an animal’s function within an ecosystem when important behaviours are density-dependent (Figure 1). Since interactions involving animals are often based on their behaviour, behavioural changes in animals, as they attempt to adapt to ecological disturbances, can also affect their function within the ecosystem. These behavioural changes could be triggered by structural (e.g., fragmentation) or non-structural (e.g., pollution) changes, changes in essential resources of the animals, or climate change. Finally, animals might adapt morphologically to a disturbance, and this could influence their capacity to maintain an important function. These losses in key functions performed by animals can have devastating consequences on the future of the ecosystems they inhabit, as the impacts cascade to affect interactions among other animals within the ecosystem.

Figure 1. Summary of the paths by which anthropogenic disturbance can influence an animal’s ecological function by way of population decline or behavioural and morphological changes.
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Suggested Reading


