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The importance of animal behavior for ecosystem services

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Animal behavior plays a critical role in the delivery of ecosystem services, yet the study of animal behavior and ecosystem services rarely intersect. The study of behavior-mediated ecosystem services should be prioritized, focusing on the conditions that allow these critical behaviors to persist and adapt to global change.

The importance of ecosystem services

Ecosystem services are defined as the 'benefits people derive from ecosystems'. Through the Millennium Ecosystem Assessment[i], scientists have identified four broad categories of ecosystem services: (i) provisioning services which include the material benefits people derive from nature, such as food, fuel, and medicinal services; (ii) regulating services which include the benefits obtained from the regulation of ecosystem processes, such as climate regulation, flood control, and disease control; (iii) cultural services which include the nonmaterial benefits people derive from nature, such as recreation and esthetic experiences; (iv) supporting services which facilitate the production of other ecosystem services and include biomass production, oxygen synthesis, nutrient cycling, and soil formation and retention.

Why are ecosystem services so important? Besides the market value, which has been estimated at $125 trillion/year (remarkably higher than the Global Domestic Product, which is estimated at $84.71 trillion) [1], ecosystem services make human life possible and reframe the way people think about and value nature[ii] [2]. Animal behavior (here intended in its broadest sense, including movement and other activities) plays a critical role in the delivery of ecosystem services (Figure 1), yet this is rarely acknowledged. As an example, **imprinting** (see Glossary) behavior in salmonid species is fundamental for the delivery of several provisioning, regulating, and cultural services provided by these species [3]. Young salmon imprint on the stream-specific chemical signature of their natal stream, which allows their homing behavior. Knowledge of imprinting affects restocking strategies, with consequences for the billion-dollar salmon industry[iii]. Similarly in whales, social behaviors such as playing and mating are fundamental for the cultural services provided by these species ($2.5 billion in yearly revenue from tourism and about 19 000 associated jobs around the world [4]; Figure 1). Foraging and social **learning** in bees are pivotal to the regulating service of crop pollination, which has been valued at $387 billion annually [5]. Likewise, foraging behavior of frugivore species is critical for the supporting service of seed dispersal (Figure 1). As an example, the large seeds of *Cryptocarya mandioccana* (a hardwood tree) are primarily dispersed by one bird (the jacutinga *Pipile jacutinga*) and two primate species (the Southern muriqui *Brachyteles arachnoides* and the brown howler *Alouatta guariba*) and their contribution to carbon sequestration has been valued at US$15.42 per hectare/year [6].

Ecosystem services, animal behavior, and global change

Many ecosystem services result from the interaction between species [7], with foraging behavior playing a key role (Figure 1). Examples include nutrient cycling by dung beetles, seed dispersal by granivorous rodents, pollination by bees, and pest control by foraging bats. All these interactions are behavior mediated and triggered by external signals such as the color of flowers, the size and odor of seeds, and the acoustic cue of a flying insect prey. Indeed, these often entail some kind of learning, such as associative learning in bees, which allows them to associate floral traits with rewards in nectar.

Global change will affect these interactions and animal behavior will play a critical role in determining whether or not the interactions persist. The decrease or extinction of species performing key behaviors will lead to a direct loss of ecosystem services. As an example, the loss of overhunted primate and tapir seed dispersers in the Amazon was found to lead to the loss of up to 38% aboveground biomass [8]. In the case of species range shifts caused by global change, the level of **plasticity** and **flexibility** in key behaviors (such as foraging behavior) will play a critical role in affecting interaction rewiring. This is defined as a reassembly of interactions among species [9]; it occurs, for example, if a plant species has lost its insect pollinator, and a new pollinator species learns to

Glossary

Behavioral flexibility: changes in behavior due to conditions of the environment at a given moment.
Behavioral plasticity: production of different behavioral phenotypes from a genotype, depending on the environmental conditions.
Conditioning: learned association between two events, such as the association between an action and a reward (i.e., bees finding nectar in flowers with certain colors) or an action and a negative experience, such as eating a toxic prey.
Imprinting: a type of learning in animals, which happens in the early phases of an individual's life, the effects of which can last a lifetime. Imprinting can affect parent recognition, as well as mate, food, and habitat choice.
Learning: adaptive changes in an individual's behavior as a result of experience.
Rigid behavior: behaviors that are relatively fixed and cannot be changed with learning.

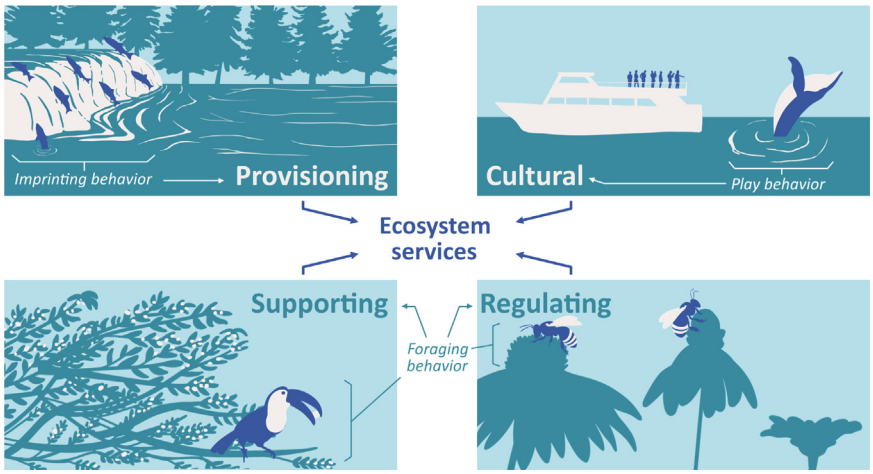

Figure 1. Animal behavior and ecosystem services. Four example behaviors that are critical for the delivery of the four types of ecosystem services: imprinting in salmons, foraging in bees and birds, and playing in whales.

use it as a resource. The likelihood of an interaction rewiring taking place may depend on the positioning of the key behavior on the continuum from **rigid behavior** to learning. Purely rigid behavior may not allow rewiring, unlike behaviors that are more plastic and flexible in nature. As an example, rodents disperse seeds, such as oak acorns, thus contributing to a key supporting service. The choice of seeds and subsequent caching behavior (i.e., hiding the seed) which contribute to this service are thought to be the result of a mix of innate abilities as well as learning [10]. Empirical research has shown that they may readily select, cache, and thus disperse novel seeds (i.e., seeds of species they have never encountered before), demonstrating that their behavior is sufficiently plastic and flexible to allow rewiring [10]. Likewise, hummingbirds have been shown to pollinate alien plant species, providing further evidence for a behavioral-led rewiring [9]. Unfortunately, we also know of rigid behaviors that may lead to the loss of ecosystem services. For instance, sea turtles are threatened by the consumption of solid waste[iv] such as plastic bags. This results from their relatively rigid foraging behavior that leads to turtles' inability to learn to distinguish between prey (such as jellyfish) and plastic bags. As a consequence, the several ecosystem services provided by these species, such as nutrient transportation and tourism [11], are lost because of this rigidity.

How can we incorporate animal behavior into the management of ecosystem services?

The study of animal behavior and that of ecosystem services rarely intersect (but see [12,13]). As researchers, we need to prioritize the study of behaviors clearly linked to ecosystem services. In particular, we need to further our understanding of the conditions needed for those behaviors to be expressed. Is the behavior learned? How flexible or plastic is such a behavior? Does it vary extensively among individuals? Such knowledge is fundamental to managing ecosystem services, such as predicting the likelihood of interaction rewiring taking place, or informing if and to what extent we can teach certain behaviors to animals. Teaching behaviors to wild animals is not science fiction and has, in fact, been an effective strategy in many threatened systems. As an example, an endangered marsupial, the northern quoll *Dasyurus hallucatus*, is threatened by the invasion of the highly toxic cane toad *Bufo marinus,* which they consume. Researchers were able to successfully induce an aversion to the invasive cane toads in juvenile northern quolls, by feeding them a dead toad containing a nausea-inducing chemical [14]. Such interventions are possible only because of a detailed understanding of the predatory behavior of quolls.

In many instances, we are already indirectly teaching wild animals to adapt and thus guarantee the performance of ecosystem services, without explicitly being aware of it. For example, practices such as assisted migration in plants[v] may promote behavioral adaptation in pollinators and dispersers and thus facilitate the likelihood of interaction rewiring, even though this is not explicitly a consideration in these programs.

Conservation biologists and practitioners may argue that we do not have the time to invest in pursuing a systematic understanding of key behaviors and the conditions needed for those behaviors to be expressed in our ever-changing planet. Indeed, conservation biology is a 'mission-oriented crisis discipline' with an explicit focus on predictions rather than mechanistic explanations. I would argue, however, that management of behavior-mediated ecosystem services can only be achieved through a systematic understanding. In the following I list three examples where the systematic understanding of behavior has allowed for the delivery of ecosystem services:

(i) Salmon hatcheries hold fish in water taken from rivers in which the fish will be released to ensure imprinting and thus successful homing[vi] (Figure 1 and Figure 2A)
(ii) Several light control programs have been implemented to reduce the disorientation of sea turtle hatchlings (which orient toward the bright lights) and guarantee they follow the correct path toward the sea, which is also important for imprinting on the natal beach[vii] (Figure 2B)

Figure 2. Examples of behavior-mediated management interventions that may help the delivery of ecosystem services. (A) Imprinting salmon hatchery allowing salmon to imprint to the stream where they will be released; (B) sign from the city of Boca Raton in Florida (USA) where street lights are turned off to allow sea turtle orientation and imprinting. Sea turtles and salmon species play a key role in providing several provisioning, regulating, and cultural ecosystem services, such as food provisioning, nutrient transportation, and recreation. Photo credits: (A) Carkeek Watershed Community Action Project; (B) Wikimedia Commons.

(iii) Vultures, which play a role in several ecosystem services such as disease regulation, organic waste removal, sanitation, and nutrient recycling, are reared with puppets for reintroductions, to avoid imprinting on humans. Likewise antipredator training (largely based on the principles of **conditioning**) has become increasingly common for relocation and reintroduction [15].

A detailed understanding of all behavior-mediated ecosystem services would of course be impossible; nevertheless, a paradigm shift is required and we need a much stronger focus on the conditions that allow these critical behaviors to persist and adapt to global changes. Researchers must prioritize understanding the conditions that allow plasticity (i.e., the expression of different behavioral phenotypes, which are important for ecosystem services [13]) and also the conditions that allow learning to take place. Likewise, practitioners should incorporate the critical role played by animal behavior for the management of ecosystem services (e.g., animal-mediated seed dispersal plays a key role for fostering carbon sequestration, thus is very relevant for the UN-REDD program[viii]).

Viewing nature through the eyes of ecosystem services is sometimes controversial, yet is highly effective: Payments for Ecosystem Services programs exist in more than 60 countries worldwide [2]. Nevertheless, despite the critical importance of animal behavior for the delivery and maintenance of ecosystem services in a changing world, very few studies explicitly link animal behavior, ecology, and the study of ecosystem services. I argue that a 'cross-pollination' (no pun intended!) between these disciplines is absolutely necessary for ensuring that animal behavior is further incorporated into the management of ecosystem services.

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Declaration of interests

No interests are declared.

Resources

[i]www.millenniumassessment.org/en/index.html
[ii]www.fao.org/ecosystem-services-biodiversity/
[iii]www.fao.org/in-action/globefish/market-reports/salmon/en/
[iv]www.iucnredlist.org/species/3897/119333622#assessment-information
[v]www.fs.usda.gov/ccrc/topics/assisted-migration
[vi]www.carkeekwatershed.org/imprinting-salmon/
[vii]https://conserveturtles.org/project-overview-stc-beachfront-lighting-program/
[viii]www.un-redd.org/about/programme

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