

Modulation of ecosystem services by animal personalities

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Conservationists rarely consider the roles individuals, with their own unique behavior, physiology, and genome, play in shaping ecosystem processes and consequently ecosystem services, but this is changing. An ongoing surge in research on animal personalities (that is, behavioral differences among individuals that are consistent over time and across contexts) is exposing the ecological roles of individuals to scientific scrutiny. Here, we present four broad examples of ecosystem services that are likely to be shaped by personalities: (1) pollination and seed dispersal, (2) regulation of pest species, (3) ecotourism, and (4) maintenance of soil quality. Although researchers have suggested diverse links between animal personality and ecosystem function, very few have examined this association. We outline a four-step process for quantifying and validating these linkages, leading to application for conservation practitioners, and conclude by recommending that accounting for behavioral variation should be incorporated into the management of ecosystem services.

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"When we try to pick out anything by itself, we find it hitched to everything else in the universe" – John Muir (1911)

The web of ecological connections has many long strands, but conservationists rarely consider the roles of individual organisms – each with its own unique behavior, physiology, and genome – in shaping ecosystem processes and ecosystem services. We routinely evaluate the ecological function for populations of a particular species, especially for keystone or dominant species, but *within* populations there exist only black boxes. An ongoing spate of research on individual behavioral variation among animals – often termed personalities or behavioral types – is opening these black boxes to scrutiny.

Personality has been extensively studied in the fields of animal behavior and evolutionary ecology (Réale *et al.* 2010; Wolf and Weissing 2012) but we are only beginning to learn about the ramifications for entire ecosystems (Brehm *et al.* 2019).

In a nutshell:

- Individual organisms have different personalities that shape their ecological roles and therefore their contributions to ecosystem services
- Understanding how personalities affect processes like pollination and seed dispersal or the regulation of pest species is a promising area for future research
- We propose a road map for ecologists to investigate the role of personalities in modulating ecosystem services and offer management advice based on their results

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While the study of ecosystem services has grown substantially in recent years (Thom and Seidl 2016), ultimately the services provided by animals and plants are considered from the perspective of population averages (ie lumping services provided by each individual and ignoring variation among individuals). But what if individuals were to differ in the amount of service they provide, and what if these differences depended on their personality? To illustrate the role personalities may play in shaping ecosystem services we selected four examples that cover a wide range of services and taxa (Figure 1).

■ Pollination and seed dispersal

Isaac Watts famously penned "How doth the little busy bee/ Improve each shining hour/And gather honey all the day/ From every opening flower!" (Watts 1777). Despite Watt's careful observations, it is unlikely he understood the complexity of these important relationships between bees and flowers. Pollination and seed dispersal are two key ecological processes in which the mobility of animals allows them to provide a crucial service for plants. An estimated 78–94% of global plant species rely on pollination by animals, particularly insects, bats, and birds (Ollerton *et al.* 2011). Bees, and especially honey bees (*Apis mellifera*), are quintessential pollinators that are often used to increase agricultural production. Multiple studies have demonstrated that bee personalities can influence colony survival, as well as facilitate effective pollination in varying habitats. Wray *et al.* (2011) examined differences in collective colony personality and found that more defensive colonies usually exhibited higher foraging activity and better fitness. Walton and Toth (2016) determined that the personality of individual bees can contribute to the division of labor in a hive, whereas Burns



Figure 1. Personality traits may shape four important ecosystem services. (a) In pollination systems “fast and inaccurate” or “slow and precise” foragers may succeed in different foraging situations. (b) Personality traits impact the effect of control methods on pest species, for example, by influencing an individual’s trappability. (c) Much ecotourism, such as the whale-watching industry, is dependent on “friendly”, “curious”, or “playful” individual cetaceans. (d) Prairie dogs (*Cynomys* spp) can transform grasslands with their extensive burrow systems, and individual differences in activity patterns likely mean that some individuals have a disproportionate influence on soil processes. All illustrations are original artwork provided by K Currier.

(2005) found that buff-tailed bumblebees (*Bombus terrestris*) can either be fast and inaccurate or slow and precise foragers, and that these different personalities help individuals succeed in different foraging situations. Accounting for the influence of pollinator personalities may therefore help determine management actions that will maintain effective pollination as an ecosystem service. For example, additional research may reveal if potential relationships between colony- or individual-level personalities could predict the likelihood of colony survival and foraging success in specific types of habitat. Furthermore, manipulating habitat to best suit the personalities of resident bees may increase the odds of hive survival and foster more effective pollination of crops.

Similarly, personality has been shown to influence various stages of seed dispersal by some taxa, most notably species of small mammals (Zwolak and Sih 2020). This includes stages of dispersal from the beginning (ie whether to ignore, immediately consume, or to cache a seed) to the end (eg cache site selection,

dispersal distance, whether an animal returns for the seed, and so forth). For example, Brehm *et al.* (2019) found that active deer mice (*Peromyscus maniculatus*) were more likely to consume a seed than to cache it; likewise, docile red-backed voles (*Myodes gapperi*) often cached seeds in optimal germination sites, while bold voles dispersed seeds farther afield than timid ones. Similarly, Boone *et al.* (2021) established that more docile mice consumed more preferred seeds and cached less preferred seeds, and increasing boldness affected the number of seeds potentially cached. As personality types vary in dispersal effectiveness at different stages, the composition of personality types can influence tree regeneration. Individuals who are fairly effective during all stages of dispersal (for example by dispersing seeds farther, caching them intact, and choosing cache sites that are optimal for germination) are likely better for plant dispersal than individuals who are effective dispersers at some stages, but negatively impact dispersal success in other stages (Zwolak and Sih 2020).

Furthermore, land use can influence the composition of personality types within a stand, suggesting that the way land is managed could negatively impact seed recruitment if certain practices favor specific personality types over others. For example, Brehm *et al.* (2019) reported that managing forest stands using even-aged silvicultural practices may negatively affect seed recruitment because even-aged stands favored mice with more active personality types that were more likely to consume than to cache seeds. This can be

particularly important for plant species that are highly preferred by seed dispersers; some small mammals have the potential to harvest up to 95% of their favored tree seeds, resulting in a substantial reduction of seed recruitment (Lobo 2014). Considering personalities of seed dispersers may therefore provide useful insights for land managers.

■ Regulation of pest species

The regulation of pest species constitutes a key ecosystem service because these species (including both overabundant natives and invasive exotics) cause billions of dollars of damage worldwide each year (Pimentel *et al.* 2005) and pose major threats to human health. For example, more than 23,000 cases of human plague, an often-fatal infectious disease caused by the bacterium *Yersinia pestis* (which is spread by fleas that hitch a ride on one of the world most invasive species, the black rat [*Rattus rattus*]), were reported in the period 1998–2008 (Capizzi *et al.* 2014). While cartoon

characters like Mickey Mouse, Ratbert, and Ratatouille testify to the acknowledgement of personality in rodents, scientists are lagging behind as the effects of animal personality on the regulation of pest species have yet to be tested directly. Nevertheless, we hypothesize that a relationship between personality and the provisioning of this ecosystem service is likely to be present (see also Garvey *et al.* 2020). We found three lines of empirical evidence in support of our hypothesis, which include effects both on pests and on their regulators (ie predators).

First, personality affects ecological parameters of pest species, such as individual survival (Brodin *et al.* 2019) and dispersal (Chapple *et al.* 2012; Michelangeli *et al.* 2017). Second, personality has been shown to affect the response of pests to control methods like insecticides (Morales *et al.* 2013) and trapping (Boon *et al.* 2008; but see Brehm and Mortelliti 2018). Trapping is one of the most common methods for controlling pests (such as rodents) (Capizzi *et al.* 2014) and indeed intraspecific variation in trappability has been found to reduce the effectiveness of pest control methods (Tuytens *et al.* 1999). Third, personality can influence the effectiveness of predators, which are important contributors to biological control methods, or can constitute pests themselves (Moseby *et al.* 2015). For example, empirical studies have found that predator personalities can control the composition of prey communities (Start and Gilbert 2017), which implies a possible effect of personality on biocontrol methods. Conversely, there is also evidence that prey personality influences predation risk (Santos *et al.* 2015). More generally, research has shown that personality may affect foraging, such as food intake (Biro and Stamps 2008), which could potentially impact the effectiveness of biocontrol species. Finally, Royauté *et al.* (2015) found that exposure to pesticides influenced personality expression in the bronze jumping spider (*Eris militaris*), a native predator that controls pest species, which could in turn influence the effectiveness of pesticides. This example demonstrates the effect that artificial control methods (ie pesticides) may have on biocontrol agents (ie spiders) via mediation of personality.

In their recent paper building on signal detection theory, Garvey *et al.* (2020) proposed a framework to incorporate personality research into pest management. Identifying and exploiting individual variation in behaviors related to “feeding, fleeing, fighting, and fornication” – the four core motivators of animal behavior – may maximize the effectiveness of management strategies, and could prove particularly effective in managing rogue (causing disproportionate levels of damage) and recalcitrant (avoiding standard control measures) individuals. Indeed, predator profiling at the individual level has been suggested as a means of controlling invasive predators (Moseby *et al.* 2015) and invasive species in general (Chapple *et al.* 2012).

■ Cetaceans and ecotourism

Moby Dick, one of the world’s most famous – albeit fictional – individual wild animals, is emblematic of a

well-known phenomenon, the variability of cetacean behavior. An armada of whale-watching boats operating from the Azores to Zanzibar has introduced millions of people to individual whales and dolphins that are routinely more “friendly”, “curious”, or “playful” than others. Some cetaceans are recognizable individually and repeatedly approach boats for close encounters that are far more exciting than viewing from a legally mandated distance (Cunningham-Smith *et al.* 2006). Consider “Fungie”, a wild bottlenose dolphin (*Tursiops truncatus*) that attracted millions of tourists to Dingle, Ireland, from 1983 to 2021; he had his own Facebook and Twitter accounts. It is reasonable to surmise that much of the popularity of whale watching is based on interactive individuals, rather than those that keep their distance. Although precise quantification of the economic impact of these individuals is not possible, with annual direct revenues from global whale watching estimated at over US\$2 billion (Cisneros-Montemayor *et al.* 2010), even if only 10% of the industry were dependent on “friendly” individuals, this would be fiscally noteworthy. Unfortunately, quantification of cetacean personalities is quite limited, although multiple papers have qualitatively described personality traits of captive bottlenoses, especially with respect to sociality (eg Highfill and Kuczaj 2010). Individual variation in the behavioral interactions of wild bottlenoses with humans has been studied, but not in a framework that would allow identification of stable personalities (Powell and Wells 2011).

In summary, personalities have been documented in some cetacean species and by extrapolation it seems highly likely that these traits strongly influence their role in whale watching, an economically important cultural ecosystem service. More broadly, nature tourism is a vast enterprise reaching far beyond cetaceans and involving myriad species and ecosystems. Maintaining a safe distance is a recurring theme for viewing wild animals, but there are many cases, especially among primates and other mammals, in which the personality of individual animals has the potential to reach across the divide and affect a person’s experience profoundly. That said, there is also the potential for negative consequences tied to animals becoming habituated to humans, for instance by increasing the likelihood of human–wildlife conflicts (Wilson *et al.* 2020).

■ Soil

Is it farfetched to think that earthworms may have personalities that could shape one of the most critical resources on earth – its soil? Not at all. Charles Darwin devoted over 30 years to experiments on earthworms in his own garden, basing his final book on the topic and noting that some earthworms appeared “timid” whereas others were “brave”, and that some were “neat and tidy” but others were “slovenly” (Darwin 1881). Within the soil’s diverse fauna, earthworms have been widely recognized as key agents in maintaining the quality of agricultural

soils (Briones and Schmidt 2017). In fact, one hectare of agricultural land can contain upward of 7 million earthworms, the activities of which can transfer 20–25 tons of topsoil to the surface each year (Sinha *et al.* 2010). In addition to Darwin's garden experiments, Nakashima *et al.* (2018) demonstrated that individual earthworms differ in their ability to learn and solve problems. These results suggest that individuals may vary in their ability to perform tasks effectively, such as creating burrows and burying organic material. As such, the daily activity patterns of earthworms, and whether they are “tidy” or “slovenly”, likely impact soil characteristics.

If even lowly worms have personalities, what about the thousands of arthropod species that inhabit soils, shredding litter and breaking down material while consuming its surficial bacteria and fungi? Indeed, diverse studies have shown that arthropods exhibit numerous personality traits, including timidity/boldness, activity level, aggression, and even sociality (Kralj-Fišer and Schuett 2014). Modlmeier *et al.* (2015) discussed the potential for nest-building arthropods to impact tropical ecosystems and highlighted case studies where arthropod personalities can impact rates of consumption and diet breadth, and potentially mediate the composition of the arthropod community.

Larger burrowing species, including many small mammals and amphibians, also alter the physical and chemical properties of soil (Platt *et al.* 2016; Mallen-Cooper *et al.* 2019). Prairie dogs (*Cynomys* spp), a burrowing mammal known to alter soil structure and quality, have been termed “ecosystem engineers” due to the extensive burrow systems they construct (Platt *et al.* 2016) and their ability to transform entire grasslands. Several burrowing species have been shown to exhibit consistent individual differences in behaviors that impact activity patterns, space use, and feeding rates. Individual burrowers may affect soil structure and quality to different extents by occupying different spatial niches, dispersing over longer distances, or displaying greater overall activity (Gharnit *et al.* 2020). For example, in the case of prairie dogs, individuals with different personality types may play slightly different roles in the family group (ie exhibiting social niche specialization) (Bergmüller and Taborsky 2010). Highly active individuals may spend more time maintaining and excavating the burrow system, whereas less active individuals may spend relatively more time monitoring for predators. The personality composition of a family group would therefore drive the effects of these ecosystem engineers on soil properties in a grassland ecosystem.

■ Discussion

Busy as a bee or timid as a mouse?

Humans routinely use animals in metaphors to describe human behavior, yet we rarely consider the real-world implications of personality in animals, as illustrated in the

four examples presented above. These examples demonstrate that there is vast potential to explore ways in which the personality composition of a population may affect the ecosystem services that the population provides (Figure 1). In particular, it seems clear that using metrics averaged across populations may be misleading if some individuals have a disproportionate impact (ie acting as keystone individuals). For example, individuals that move seeds or pollen far beyond the population average are likely to play an outsized role in the dispersal of plants (Modlmeier *et al.* 2014), and predators that are more effective at removing invasive prey than average may play a disproportionate role in pest regulation. Similarly, population averages may provide an inadequate understanding of the provisioning of ecosystem services if different segments of the population, representing different personality types, perform quite differently – especially given that the prevalence of those types can change over time for a variety of reasons, including land-use change (Miranda *et al.* 2013; Brehm *et al.* 2019). Consequently, by modifying the proportion of different personality types in a population, we may also be possibly affecting the provision of ecosystem services.

We propose a four-step process for ecologists who wish to investigate the role of personalities in modulating ecosystem services and offer management advice based on their research (Figure 2).

Step 1: foundational work

This step starts with generating hypotheses and gathering evidence of measurable personality traits in a target species (eg is there repeatable variation in boldness in a species known to play an important ecological role? Dingemanse and Wright 2020). Foundational work should also include an assessment of alternative relevant traits that may affect ecosystem services (eg will boldness or aggressiveness have a greater effect on the modulation of services?) and developing accurate methods to measure these traits in the field or lab.

Step 2: assessment

Assessment should be focused on carefully quantifying the relationship between personality and the behavior that produces a service. For example, Brehm *et al.* (2019) found that four personality traits affected the ecosystem service of seed dispersal by detecting significant relationships between these personality traits and seed choice, dispersal distance, seed fate, and cache location. Similarly, Burns (2005) noted that fast, “impulsive” bees likely forage on flowers of simple design whereas slower, “reflective” bees likely forage on complex flowers.

Step 3: validation

Validation requires confirmation of the relevance of personality by estimating the extent to which the actual personality composition of a population affects the provision of a service. This is a necessary step because even in the presence of a

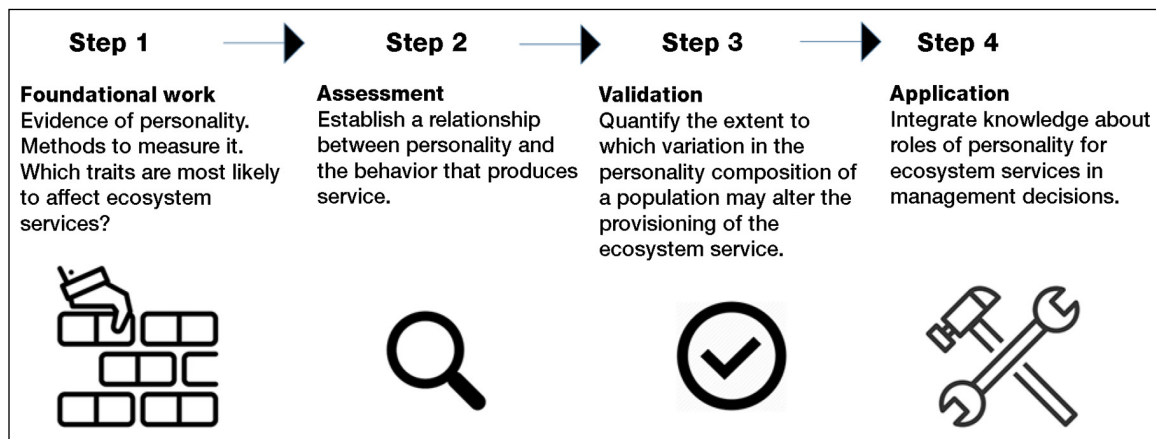


Figure 2. Four-step road map for ecologists planning to investigate the role of personalities in modulating ecosystem services and develop management strategies based on their results.

strong relationship between personality and an ecosystem service, the presence of individuals with varying personality types may possibly compensate for one another. In other words, in some cases population averages may tell the story sufficiently (at least in one place and one time).

Step 4: application

This is the final stage, in which scientists use their knowledge about the roles of personality to inform management decisions. Managing for animal personality is not a futuristic fantasy; humans have indeed been doing it for millennia, primarily through the process of domestication, which involves selecting for certain behavioral types (such as aggressive or docile dogs, rabbits, horses, or cats). Likewise, we routinely remove aggressive individuals from wild populations wherever people concentrate (eg dangerous bears [*Ursus* spp] in parks) and inevitably the most curious individuals are removed when bait is used for hunting. Conservation biologists have long argued that large, diverse populations should be a priority for conservation, but behavioral variation has rarely been explicitly considered. Indeed, given the genetic basis of personality (Dochtermann *et al.* 2015; Bengtson *et al.* 2018), it is possible that when supporting the genetic richness of populations we are also indirectly maintaining a diversity of personalities, but only through future work will we confirm for which species and populations this is true. The direct and indirect empirical evidence we have compiled here strongly suggest that the time is ripe to begin accounting for behavioral variation among individuals in the management of ecosystem services.

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