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Assessing Ecological Function in the Context of Species Recovery

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Abstract

Species interactions matter to conservation. Setting an ambitious recovery target for a species requires considering the size, density and demographic structure of its populations such that they fulfill the interactions, roles and functions of the species in the ecosystems in which they are embedded. A recently proposed framework for an IUCN Green List of Species formalizes this requirement by defining a fully recovered species in terms of representation, viability and functionality. Defining and quantifying ecological function from the viewpoint of species recovery is challenging, both in concept and application, but also an opportunity to insert ecological theory into conservation practice. We propose two complementary approaches to assessing a species' ecological functions: a confirmation approach that starts with a list of the interactions of the species, identifying the ecological processes and the other species that are involved in these interactions, and quantifying the extent to which the species contributes to the identified ecological process; and an elimination approach that infers functionality by ruling out symptoms of reduced functionality, analogous to the Red List approach that focuses on symptoms of reduced viability. Despite the challenges, we believe that incorporation of functionality into species recovery planning is possible in most cases. It is also an essential element of an aspirational conservation vision that goes beyond preventing extinctions, aiming to restore a species to levels beyond what is required only for its own viability. This vision focuses on conservation and recovery at the species level, but also sees species as embedded in ecosystems, influencing and being influenced by the processes in those ecosystems. Thus, it connects and integrates conservation at the species and ecosystem levels.

Introduction

Conservation biologists have long considered a species' place in the complex web of its interactions when setting species-focused conservation goals and targets (e.g., Janzen 1974; Redford 1992; Soulé et al. 2003; Sanderson 2006). This aspect of conservation was recently formalized within a framework proposed for an IUCN Green List of Species, which aims to quantify species recovery to

levels beyond those necessary to avoid extinction, and to provide metrics for measuring the success of conservation measures in terms of progress towards full recovery (Akçakaya et al. 2018). The proposed Green List of Species framework defines a fully recovered species as one that is viable, and ecologically functional, in each part of its indigenous and projected range, and defines functionality of a species as "the degree to which it performs its role as an integral part of the ecosystem in which it is embedded." Different aspects of this role include the species' "influence on or contribution to ecosystem-level processes (e.g., primary production), interactions with other species (e.g., trophic relationships), structural effects (e.g., ecosystem engineering), and intra-specific processes (e.g., migration)." In many cases, ecological functionality of a population will depend on its abundance, density, and demographic structure, which determine the behaviors and interactions of the organisms.

In this essay, we explore the application of the concept of ecological functionality to species conservation. We first review the justification for considering ecological function in the context of species recovery, and explore why this idea, despite a long history of discussion in the conservation literature, has not been explicitly or systematically implemented as a criterion of species recovery. To address this shortcoming, we discuss conceptual and practical challenges of defining and assessing functionality, recommend practical approaches that are based on ecological theory for defining a species' function and determining whether a population is functional, and suggest directions of future research. Although our essay is motivated by the proposed Green List of Species, our ideas apply to all aspects and systems of species recovery planning.

Why consider function in species recovery?

The irreversibility of extinction, and the rapid decline of many species towards extinction, have largely, and appropriately, focused past conservation efforts on ensuring first and foremost that species retain viable populations that ensure their continued existence into the future. However, conservationists have long recognized the need to go beyond this minimal requirement, and to conserve species with "ecologically functional populations" (Conner 1988), or at "ecologically effective densities" (Soulé et al. 2003).

Ecological interactions between species are at the core of the complex web of life on Earth. Conserving species interactions, beyond the conservation of the species themselves, is thus a major conservation goal (Redford and Feinsinger 2001; Soulé et al. 2005). Species interactions, like viability of individual species, are sensitive to human impact (Tylianakis et al. 2008), and may cease to occur in any ecologically meaningful way, even if the species are still present and viable in the ecosystem (Janzen 1974), a process captured by the terms "ecological extinction" or "functional extinction" (Redford 1992; Janzen 2001).

Species are embedded in ecosystems, so they influence and are influenced by ecosystem processes. A major focus of the literature on ecosystem processes and functions has been the relationship between biodiversity and ecosystem functionality (e.g., Cardinale et al. 2012). Although research on this relationship has often focused on aggregated measures of ecosystem function, notably productivity, that are not directly relevant to biodiversity conservation (Srivastava & Vellend 2005), it is generally recognized that conserving processes in an ecosystem requires conserving its components, including species.

A separate but related goal is to conserve species in their natural or wild state. Sanderson (2006) expressed this concept as "having animals acting like animals, not just persisting", and stated that demographic sustainability (i.e., long-term viability) "should be seen only as a threshold requirement, a necessary but not sufficient level" and that conservation targets should consider "interactions, including ecological functions and social dynamics, along with demographic requirements". Related to this are considerations of "wildness". Redford et al (2011) recognized a range of states of species conservation, ranging from captive to self-sustaining; Sanderson (2006) proposed "ecological integrity" of animal populations to synthesize function, behavior, and demography in setting conservation targets; and Caro and Sherman (2012) defined and reviewed disappearance of behaviors (ethodiversity loss). These considerations imply that, in addition to interactions of species with other species, there are certain patterns of intra-specific behavior and social dynamics (such as migration, aggregations, patterns of social hierarchy, etc.) that are characteristic of a species that may disappear as a species declines, even if these smaller populations are not at risk of extinction. Such characteristics may not appear to comfortably fit into a general definition of ecological function of a species (see below), but are nonetheless important indicators of the successful conservation of a species that go beyond the criterion of low risk of extinction.

An important aspect of the concept of functionality is its contribution to a comprehensive approach to conservation across levels of biological organization. Indeed, considering interactions of a species in a community and its contributions to ecosystem processes forms a bridge between conservation at the species level and conservation at the ecosystem level. Another key concept of the proposed Green List of Species framework—the representation of the species across the range of ecological settings to which it is native, as quantified by viability and functionality across areas comprising the native range—forms a bridge between conservation at the species level and conservation at the population level. Hence the proposed framework is designed to integrate conservation at population, species, and ecosystem levels.

Challenges

In this section, we identify several challenges related to assessing species-level ecological functions in the context of species recovery.

Defining function from a species recovery viewpoint

The terminology of ecological function can become confusing, especially when functions of both species and ecosystems are considered. From the perspective of species recovery in general, and the proposed Green List of Species framework specifically, we define *ecological function* as specific to a species, and *ecosystem process* as specific to an ecosystem (see Table 1 for definitions). So, for instance, the contribution of a species to nutrient cycling in a particular ecosystem is an *ecological function* of that species, whereas nutrient cycling itself is an *ecosystem process*, which, if it benefits humans, leads to an ecosystem service.

From a species conservation point of view, we are concerned with several general types of ecological functions, all of which arise from interactions among organisms (see Table 2 for examples). Some functions arise from inter-specific interactions, others from intra-specific interactions (discussed later). Some inter-specific interactions are direct interactions of the focal species with one or few other species; others involve indirect or diffuse interactions of the focal species with many species, and thus are better considered to be at the ecosystem level (Table 1). For example, dispersal of the seeds of a particular tree species by a bat species is an ecological function of the bat species at the level of direct interaction with another species (i.e., the tree species). The contribution of the same bat species to productivity and forest regeneration (for example, through dispersal of seeds of multiple plant species it interacts directly with) is an ecological function of the bat species at the ecosystem level.

These types of inter-specific ecological function are closely related to the concept of *specific effect function* (SEF), which is the "per-unit capacity of a species to influence an ecosystem property or service," measuring the "difference made to a particular process at the ecosystem level by a standard 'amount' of a species" (Díaz et al. 2013). For the purposes of the Green List of Species, SEF multiplied by population size is more relevant than SEF itself, because a species Green List assessment is based on the total contribution of the species' population to the ecosystem process in question.

Another general type of ecological function arises from intra-specific interactions and processes, and involves patterns of behavior and social dynamics that are characteristic of a species, and which may disappear as a result of human impact (Table 2). These include long-distance migration, large-scale

aggregations of individuals, and patterns of social hierarchy. Although this type of ecological function often affects, and is affected by, larger scale ecological processes (such as nutrient cycling; Doughty et al. 2016; see also discussion on "mobile links" below), it involves species-specific behaviors that are considered worthy of conservation effort (Caro and Sherman 2012), even in cases where they do not affect ecosystem processes, and even if (like the other types of functions considered here) they may not be required for a low risk of extinction.

In summary, a working definition of function for the purposes of species recovery may be summarized as totality of the species' interactions, determining its influence on, or contribution to, ecosystem processes, and the patterns of intra-specific interactions, behavior and social dynamics that are characteristic of that species. Note that "function" is a property of the species, while "functionality" (the degree to which the function is performed) is a property of a particular population of the species at a particular time, as it depends on the size, density and demographic structure of the species' population at that place and time.

Although "functionality" is continuous, for practical purposes, it can be assessed in terms of few (or even just two) categories; for instance, Akçakaya et al (2018) proposed to use it as a binary variable (functional or not functional) in the context of the Green List of Species, and Sanderson et al. (2008) suggested breaking the continuum of ecological interactions by bison populations into five categories, from "no contribution" to "exceptional contribution" to local interactions. A binary concept of ecological functionality is also implicit in the concept of "ecological extinction" or "functional extinction"; a population is considered to be functionally extinct (or not functional) if its abundance is too low, or its demographic structure is not suitable, for it to fulfill its ecological roles in the community or ecosystem. Dividing a continuous variable into categories for ease of assessment and communication is common in many fields, including conservation, where the probability that a species is extinct is divided to list species as extinct, possibly extinct and extant (Akçakaya et al. 2017); and the probability that a species will go extinct in the future is divided to sort species into threat categories (Collen et al. 2016).

Some uses of the term "functional extinction" and "ecological extinction" refer to termination of basic demographic processes such as reproduction (e.g., Fan et al. 2014; Roberts et al. 2017). We do not consider these processes as ecological functions in the context of the proposed Green List of Species framework, because populations that do not perform such basic demographic functions would not be viable, and viability is a separate, indispensable component of recovery in the proposed framework and a stated pre-requisite of functionality (Akçakaya et al. 2018).

Our approach to interpreting ecological function differs from other efforts by focusing on the species, not the function. For example, Brodie et al. (2018) propose a method for conserving

functions by focusing on strong interactions, arguing that "critical ecological functions should be another facet of biodiversity that we try to conserve ... in tandem with protecting the taxa ... and the habitats in which they occur." We agree that conservation of functions (Brodie et al. 2018) and ecosystems (Keith et al. 2013) are complementary to conservation of species. Our focus here is incorporating ecological functionality into the assessment of species recovery, which was first formalized by the Green List of Species protocol.

Function as contribution to ecosystem resilience

The ecological function of a species, in terms of its contribution to, or influence on, an ecosystem process, can be described in different ways. In some cases, the more important influence may be on the stability of the ecosystem process (e.g., its resistance or resilience to perturbations), rather than the magnitude of the contribution. A simplistic way of explaining this is in terms of mean vs. variance: some species may contribute in quantity (make a large difference in mean), others may influence the quality, e.g., by helping reduce variability, thus increasing stability or consistency of an ecosystem process. For example, perennial plants may be critical to maintaining soil stability and forage for herbivores during drought, but may contribute only a small portion of these functions in wetter times when short-lived palatable plants are more abundant (Westoby et al. 1989). So, the ecological function of a species may be in terms of its contribution to the stability of ecosystems, e.g., their capacity to resist regime shifts between alternative states, or to recover following a disturbance (Nimmo et al. 2015).

However, the above dichotomy is complicated by the fact that many ecosystem processes are not "stable" in the simple sense of being constant or having a small variability. They are often naturally variable in space and time, especially in small spatial and temporal scales (Oliver et al. 2016), or have natural regime shifts between alternative states. So, the contribution of a species to an ecosystem process may not necessarily stabilize the process when considered at the scale of the species' population(s) in a particular area (a "spatial unit", in the proposed Green List of Species terminology). The functional contribution of some species may even promote variability, as appears to be the case in fire-promoting plants (Bond & Midgley 1995). Nevertheless, a species may contribute to the resilience and recovery of ecosystems at broader spatial and temporal scales, through its contributions to ecological processes at critical times and places as, for example, certain fire regimes maintain diversity at landscape scales (Keith 2012). Thus, contributions of a species to an ecosystem process may appear disruptive at one scale but promote resilience at another. Understanding the scale-dependence of the relationship between measures of resilience of ecosystem processes (such as variability) and the properties of the populations of species (such as

size, density and demographic structure) contributing to those processes remains a challenge. Using resilience as a predictor of functionality would require a deeper understanding this relationship.

Functional and non-functional species in the same ecosystem

Because function is often thought of at the ecosystem level, and because a general goal of conservation is preserving well-functioning ecosystems, it may appear that if one species in an ecosystem is not fully functional, then the ecosystem is not fully functional; and, therefore, no species in the ecosystem can be considered functional. However, this would not be a useful conclusion from a species conservation perspective, because it would not let us know which species need further recovery to make them fully functional. In the context of species Green List assessments, ecological function is species-specific; therefore, assessment of functionality should focus on the species being assessed.

For instance, a prey species could be deemed functional even if its predator populations are not functional or even present. Indeed, what is relevant to assessing functionality at the level of the prey species is whether there are conservation or management actions focused on it that are necessary to its recovery. If the only recovery necessary in this case is that of the predator, regarding the prey species as non-functional would not be useful. However, if the lack of predators (or the fact that the predators are below their functional densities) causes populations of a prey species to become overabundant, and thereby cause disruption of ecological processes or threaten native species, then management actions at the level of the prey may be appropriate and the prey population should be considered non-functional (e.g., seagrass-turtle-shark system; Heithaus et al. 2014). Thus, relationships between functionality and population density or size can be non-linear; a population's density may be too low or too high for the species to be functional. In other words, some species (in this example, predators) being absent or non-functional may cause other species (in this case, prey species) to become non-functional. But, the non-functionality of the prey species in such a case would be based on *their* influence on ecosystem processes, not on their lack of interaction with the predators.

Functional redundancy

Functional redundancy occurs when there is overlap between the functions performed by a number of species, such that changes in one species' contribution to ecosystem processes can be compensated for by contributions from other species (Lawton and Brown 1993). Functional redundancy is an active topic of research and is documented in many ecosystems. It is important to note that redundancy is not a property of the species, but a property of the particular function of a particular species (or set of species). According to ecological niche theory, there are no redundant

species, because each species has a unique niche. However, *some* functions of a species may be redundant, if those functions are also performed by other species in the ecosystem.

Even those functions that appear to be redundant may be performed by different species in different contexts, for example in different times (of day or year) or in different places (microhabitats, strata, ecoregions), making each species' influence or contribution unique and therefore not redundant. In other words, redundancy, like function, is dynamic and spatially heterogeneous, and varies depending on the functions considered.

From the point of view of species recovery assessments, the challenge functional redundancy brings is mostly practical, involving the need to identify contributions of a species and the conditions that allow those contributions. We further discuss these needs in the context of approaches to determining whether a population is functional (see *Assessing Functionality* below). In addition, functional redundancy may appear to reduce the importance of a species' functionality, and hence the priority for its recovery. However, as we discuss in the next section, the point of considering function in species recovery is not to assign importance to species, but to establish a higher threshold for their recovery compared to what is required for their viability. Thus, functional redundancy does not invalidate the need to consider a species ecological function in setting targets for its recovery.

Species "importance" and ecosystem services

A discussion of species functionality in the context of species conservation may be misinterpreted as justifying the conservation of a species based on its functional importance. It is critical to emphasize that neither the proposed Green List of Species framework, nor the IUCN Red List (into which the Green List metrics will likely be integrated) assume any judgment about how "worthwhile" it is to conserve a species. The point of including functionality in species recovery assessments is about setting more ambitious conservation goals than extinction avoidance, and aiming to restore a species to levels beyond what is required only for its own viability, reflecting its overall role in the ecosystem(s) it inhabits. Thus, assessing functionality is a way of expecting more from our conservation efforts, not from the species. Although some species do make larger contributions to ecosystem processes (e.g., keystone species), our purpose is not to use functionality to compare species to each other. Rather, it is to evaluate, for each species, contributions of populations in different parts of its range, relative to the reference level of full functionality across the species range. Hence, being unable to identify "important" functions, or a lack of "strong interactions" (as defined by Brodie et al. 2018), does not preclude the establishment of ambitious recovery targets: they can be based on proxies of functionality, to determine population levels at which to consider a

species "fully recovered" (as defined by Akçakaya et al. 2018) in a particular area (see *Assessing Functionality* below).

Some ecological functions of a species considered in recovery planning may also provide ecosystem services. In other words, the species may contribute to ecological processes that produce benefits for people (Gascon et al. 2015). These may include, for example, supporting services (such as nutrient recycling and soil formation), regulating services (such as decomposition and detoxification) and cultural services (such as recreation and artistic inspiration). In some cases, the most visible (or the only quantified) function of a species may be related to an ecosystem service. For example, there may be a lot more known about the contribution of an insect to pollination of crops than to pollination of rare native plants, even if the latter risk going extinct if the population of the insect species in question is no longer functional.

Even in these cases, we argue that the assessors should consider function from the perspective of the native non-human species that the focal species interacts with, and the natural ecosystems the focal species is native to, rather than benefits to humans. This focus on natural interactions reflects our emphasis on conservation of species for their own sake, rather than an anthropocentric perspective. However, the considerations of functionality (especially during a formal Green List of Species assessment) may also be a good opportunity to catalogue the benefits of biodiversity for human well-being in a more systematic way.

Spatial and temporal variability in functionality

A species may occur in multiple ecosystems, and perform different roles in each, for instance by contributing to different ecological processes, or by interacting with a different assemblage of species. Therefore, its functions can vary across its range, changing in type or magnitude. In order to incorporate this spatial variability, functionality must be assessed separately for each ecosystem or unique ecological setting the species exists in, i.e., within each of the "spatial units" considered in a Green List assessment.

In addition, a species may perform its ecological function across several ecosystems and transfer resources, biota and matter, providing 'mobile links' between them (Lundberg and Moberg 2003; Doughty et al. 2016). In order to incorporate these types of spatial structure and dynamics, functionality for such species needs to be assessed not only in terms of population size and structure, but also in terms of movement dynamics, at the relevant spatial scale.

A species' function can vary across time, as its environment and cohabiting biota changes. Even when the function remains the same, functionality of populations may change, e.g., because of fluctuations in abundance. Some of this can be due to natural cycles or fluctuations in the

environment. In these cases, the species' function, and the functionality of its populations, should be assessed over whole natural cycles, at the temporal scales relevant to the ecosystem processes and their resilience (see discussion above on scale and resilience).

Temporal changes in a species' function can also be a result of human impacts, either locally and regionally (e.g., because of habitat alteration) or globally (e.g., because of climate change). In some cases, human impacts may cause functional species to become deleterious and thus nonfunctional (Carey et al. 2012). These types of temporal shifts or trends in species function can be incorporated into successive Green List assessments, similar to how the Red List status of a species is periodically updated.

Assessing Functionality

Despite the challenges reviewed, we believe that incorporation of functionality into species recovery planning is possible in most cases; it is also an essential element of an aspirational conservation vision. In this section, we present ideas and preliminary guidance for identifying the ecological functions of a species, and determining if a population is ecologically functional.

We propose two approaches, a confirmation approach and an elimination approach. The former aims to identify specific functions of a species, and based on these, determine the functionality of a particular population in a specific time and place. The latter approach infers functionality by ruling out each of a set of symptoms of reduced functionality. For a given species either or both approaches may be applicable, depending on the type of information and expert knowledge available.

The confirmation approach is based on the fact that all species interact with other species, and uses a list of the interactions of the focal species with others as a starting point for identifying its ecological functions. Then, we envision a process of identifying the ecological processes (such as predation, dispersal, facilitation, etc.) that are involved in these interactions (see Table 2 for examples). This information, together with a knowledge of the functional traits that are often associated with such interactions, would allow assessors to identify the ecological conditions that determine the extent to which a particular population of the species (at a specific time and place) contributes to these identified ecological process (i.e., the determinants of functionality; Table 2).

The next step is identifying the variable to assess functionality. As the examples in Table 2 imply, the variable to be measured depends on the function; it could be the total number of seeds dispersed by a mammal, the number of plant species pollinated by an insect, or the contribution (in units of mass or volume per unit time) to distribution of a particular nutrient.

Finally, the relationship between this response variable and population density (or other characteristic, such as demographic structure) of the focal species is established. In some cases, this relationship is non-linear (e.g., a step function, or sharp peak, and even hysteresis), naturally leading to a categorical assessment of functionality (e.g., as functional vs. not functional), based on threshold values of population size, density and structure. Many of the studies cited in Table 2 have identified such threshold values in specific times and places. For example, Estes et al. (2010) estimated a threshold density of 6.3 Sea Otters (*Enhydra lutris*) per km surveyed, below which kelp forests are not maintained along the coast of California. McConkey and Drake (2006) estimated a Flying Fox (*Pteropus tonganus*) abundance index of about 0.8 required for effective long-distance seed dispersal in Tonga. Outcalt et al. (1999) recommend that a minimum Wiregrass (*Aristida stricta*) density of 1 m^{-2} to maintain cover and allow fires to spread in the Atlantic coastal plain. Age structure for pine trees (*Pinus* spp.) must include ≥ 80 years old individuals to allow Red-Cockaded Woodpeckers (*Leuconotopicus borealis*) to excavate nest cavities in southeast US (U.S. Fish and Wildlife Service 2003).

If the function-density relationship is gradual (i.e., close to linear), functionality can be assessed either as a continuous rather than binary variable, or with a subjective threshold (e.g., >50%) that is consistent with the level of ambition of the species recovery objectives. Note that species recovery can be quantified as a percentage of fully recovered even with a binary definition of functionality (see Fig 1 in Akçakaya et al 2018). If more than one function can be identified for a species, functionality can be assessed based on the function that is better studied, the function that is unique among the species in the same ecosystem, the function that allows a better approximation of the species' role and population characteristics prior to major human impacts, the function that requires the highest density, or the function that represents a strong interaction (Brodie et al. 2018).

The elimination approach considers the same types of information discussed above for the confirmation approach, but focuses on the end-result rather than the mechanism. It looks for symptoms of reduced functionality, analogous to the Red List approach of identifying symptoms of reduced viability. We propose a list of questions and considerations to guide the assessors in this process (Table 3), aimed at allowing a systematic consideration of the criteria and evidence for determining whether the size, density and the demographic structure of the species' populations are appropriate for its ecological function(s).

These proposed approaches for determining functionality may not be applicable in some cases, or they may give results that are too uncertain for practical application. In these cases, the Green List framework (Akçakaya et al. 2018) recommends a number of proxies, such as population density in

areas not impacted by human activities (Table 3), which can be used even if no function can be identified.

Future Directions

There is a need for further refinement of concepts and methods to identify and quantify ecological functions of species. Research on functional traits, functional rarity, and the relationships of these concepts to the goals of species recovery may contribute to addressing this need. Functional traits are characteristics of an organism that are relevant to its response to the environment or its effects on ecosystem processes or properties (Violle et al. 2007). Traits that determine a species' response to the environment (called 'Response traits'; Lavorel and Garnier 2002) are more relevant to its viability than to its functionality, whereas traits that determine a species' effects on ecosystem processes or properties (called 'Effect traits') are more relevant to its functionality than to its viability. The same traits can be important both for a species' response to the environment and for its effect on ecosystem processes. But the reverse is also possible: characteristics or traits of a species that determine its response to the environment (thus its viability) may differ from those that determine its effect on ecosystem processes (thus its functionality). Thus, a trait may have no or minor effect on individual fitness but a strong effect on ecosystem properties (Shipley et al. 2016).

Different species may contribute to the same ecosystem process through different combinations of traits and their values. Thus, a unique mapping between traits and functions may not exist. Nevertheless, across species in a particular taxonomic group, there may be a pattern of dependence between traits and functions. Such patterns may be uncovered by appropriate statistical methods. For example, Díaz et al. (2013) used a phylogenetic comparative method (Freckleton et al. 2002) to model how species functionality depends on species trait values.

Although the relationship between traits and functions (e.g., the predictability of ecosystem-level processes from traits) may not be directly relevant to the practical aspects of recovery planning and Green List assessments, its improved understanding may help to identify ecological function(s) of a species through its traits. This would require an analysis involving a group of species whose traits and functions are already known. If such an analysis uncovers strong patterns of dependence between traits and functions, the results may help identify functions of species that share traits with those analyzed and thereby help in situations where the functions of a particular, related, species are not well known.

A related concept is functional rarity of a species, which combines the rarity of the species with the rarity of its traits (Violle et al., 2017). Species rarity is often considered in terms of combinations of geographic range (restricted vs. widespread) and local abundance (scarce vs. abundant). These two

forms of species rarity are combined with two parallel forms of trait rarity, measuring the extent to which species traits are "more or less distinct or redundant within local communities or larger-scale species assemblages" (Violle et al. 2017). The functional rarity framework suggests that the types of rarity relevant to viability (range restriction and local scarcity) may be different from those relevant to functionality (trait distinctiveness and uniqueness), and that many combinations of species rarity and trait rarity are possible. The most distinct combinations of functional traits seem to be supported predominantly by rare species (Mouillot et al. 2013). Thus, even in diverse ecosystems where functional redundancy is expected, rare species disproportionately increase the diversity of ecosystem processes, and they may potentially insure against future uncertainty arising from climate change and other human impacts. More importantly, methods developed to quantify functional rarity could bring insights into the challenging questions of identifying the function of a species, and determining if its populations are functional.

Conclusion

A basic tenet of ecology is that species are not isolated entities. The interactions of a species with other species and other components of biota are an important aspect of its essence, its intrinsic value, and its fundamental connection to Earth's evolutionary heritage. Thus, "conserving nature" requires conserving the interactions among species, as well as the species themselves. This can be achieved in different ways, for example by conserving particular types of functions and interactions (Brodie et al. 2018) or by conservation at the ecosystem level (Keith et al. 2013). The proposed Green List of Species (Akçakaya et al. 2018) is a third approach, which identifies species' current functionality across its range relative to its potential functionality, and so incentivizes the conservation of this functionality. This framework focuses on conservation and recovery at the species level, but also sees species as embedded in ecosystems, and influencing and being influenced by the processes in those ecosystems. Thus, it connects and integrates conservation at the species and ecosystem levels. We recognize, and are working to address, the many challenges to our goal of developing this framework into a practical tool for species assessments and recovery planning that goes beyond the minimal requirement of maintained presence through extinction avoidance.

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TABLE 1: Definitions related to ecological function in the context of species recovery

<p>Ecological function of a species: The totality of the species' interactions, determining its influence on, or contribution to, ecosystem processes, and the patterns of intra-specific interactions, behavior and social dynamics that are characteristic of that species.</p>
<p>Ecological functionality of a population: The extent to which the population fulfils the ecological function(s) of the species in a particular place and time, as determined by its size, density and demographic structure. Ecological functionality can be assessed either as continuous (e.g., a percentage) or as categorical (e.g., as functional vs. not functional).</p>
<p>Direct interactions: A category of the ecological function of a species as determined by its interactions with one or few other species, including pollination, seed dispersal, herbivory and predation (i.e., effects of the species on "ecological processes" as defined by Martinez 1996 and Pettorelli et al. 2017).</p>
<p>Indirect interactions (structural functions): A category of the ecological function of a species as determined by its effects on other species through creation of habitat structures, features and conditions that affect the dynamics of those species.</p>
<p>Diffuse interactions: A category of the ecological function of a species as determined by its effects on other species through contributions to ecosystem processes, such as decomposition, nutrient cycling and redistribution, and maintenance of fire regimes (i.e., effects of the species on "ecosystem processes" as defined by Lovett et al. 2006 and Pettorelli et al. 2017).</p>
<p>Intra-specific interactions: A category of the ecological function of a species as determined by within-species processes and patterns of behavior that are characteristic of the species, such as colony formation and other aggregations, and spatial patterns of movement and dispersion.</p>

TABLE 2: Categories and examples of ecological functions of species, traits often associated with the functions, and the characteristics of a population that determine whether it fulfills the function

General category	Subcategory	Examples of ecological function	Examples of associated traits	Determinants of functionality	References
Direct interactions (incl. trophic functions and cascades)	Pollination	Bumblebees maintaining plant diversity by pollination	Dispersal distance; flight period; voltinism; larval food preference	Sufficient abundance of specialist pollinators; or density of generalists high enough for competition to push individuals to rarer plant species	Heinrich 1979; Aguirre-Gutiérrez et al. 2016
	Seed dispersal	Flying foxes dispersing large seeds	Large home range; ability to fly with seed; long gut-retention time	Population density high enough for antagonistic interactions to cause long-distance dispersal	McConkey and Drake 2006; Oleksy et al. 2017
	Herbivory	Herbivory by parrotfish and others preventing coral-to-macroalgal phase shift in reefs	Diet; body size and age composition (to escape predation)	Population density (which is often a function of fishing mortality)	Mumby et al. 2006
Indirect interactions (structural functions)	Predation	Sea otter predation on urchins maintaining kelp forests; wolf predation on elk maintaining willow ecosystems	Keystone apex predator; large home range; prey preferences; functional response attributes (e.g., handling time)	Population density of the predator high enough to result in the trophic cascade effects	Estes et al. 2010; Ripple and Beschta 2012;
	Habitat creation	Creation of landscape heterogeneity by American Bison	Grazing and wallowing behavior	Population density, spatial distribution, seasonal movement patterns	Sanderson et al. 2008
	Ecosystem engineering	Sediment accretion and modification by seagrasses	Structure of leaves, rhizomes, and roots	Density (shoots/m ²)	Orth et al. 2006; Bos et al. 2007
	Nest supply	Pine trees	Tree	Age structure that	Jackson &

	provision	providing cavities for nesting birds	diameter; heartwood fungal decay	includes older trees	Jackson 2004; USFWS 2003
Diffuse interactions (ecosystem-level functions)	Nutrient cycling or redistribution	Nutrient input to terrestrial systems by breeding salmon populations and their predators	Anadromous life history; large spatial distribution; chemical composition of the body	Population size (biomass); migration distance; presence of detritivores, decomposers, and predators.	Gende et al. 2002
	Maintenance of fire regime	Wiregrass maintaining longleaf pine savannas in the Atlantic Coastal Plain of US	Flammability, fast growth in biomass	Density high enough to maintain fire; spatial distribution large enough for spreading fires	Outcalt et al. 1999
Intra-specific interactions (within-species processes)	Movement	Green-wave surfing and other seasonal movements by ungulates	Learning and cultural transmission of migratory behavior	Population continuity; age structure that facilitates transmission of knowledge; landscape connectivity	Jesmer et al. 2018
	Reproductive aggregations	Forming colonies, leks, spawning aggregations	Mating system, colonial behavior	Sufficient density to overcome sperm limitations (in spawning aggregations) or predation (in colonial species)	Levitan & Young 1995; Schippers et al. 2011

TABLE 3: Types of information to consider in inferring functionality of populations

1. Based on available information on the interactions of the species being assessed with other species, and its ecology in general, consider whether a reduction in population size or density of the species being assessed, or a change in its demographic (e.g., age) structure has the potential to cause non-trivial changes of any of the following types.
 - a. a reduction in the abundance of another native species;
 - b. an increase in the abundance of a non-native species or over-abundance of another species;
 - c. a reduction in a demographic rate in any life stage of another native species (e.g., germination, seed production, nest success, natal dispersal, etc.) that has the potential to decrease its abundance or otherwise reduce its viability;
 - d. a change in any ecosystem process or structural feature (see examples in Table 2);

- e. a change in the typical patterns of behavior (e.g., social interactions, patterns of aggregation, movement) among individuals of the species being assessed or other species.
 2. Comparing areas or subpopulations with different densities or abundances of the species, consider any evidence which suggests that the reduced population size or density of the species, or a change in its demographic (e.g., age) structure has caused or may cause any of the outcomes a-e listed above. It is important to consider that ecological function of a species and its natural density or carrying capacity may be different in different ecological settings. So, this comparison is more relevant between areas or subpopulations with similar ecological characteristics.
 3. Comparing time periods when the species was at different densities or abundances, consider any evidence which suggests that the reduced population size or density of the species, or a change in its demographic (e.g., age) structure has caused or may cause any of the outcomes a-e listed above.
 4. Based on information on the functional traits of the species, and an analysis of relationships between trait and function in similar species, consider the potential that reduced population size or density of the species, or a change in its demographic (e.g., age) structure may cause any of the outcomes a-e listed above.
 5. If no function can be identified for a species, consider the following proxies.
 - a. Pre-impact: Use the natural or pre-disturbance population size or carrying capacity of a species as a proxy for functional density, assuming that at pre-impact densities the species did fulfill its ecological roles and functions. It is important to consider that carrying capacities vary naturally across the range and over time for many species.
 - b. Non-impact: If impacts change over the range of the species, use the population size, density or carrying capacity in apparently non-impacted (or least impacted) areas as a proxy. It is important to consider that carrying capacities vary naturally across the range and over time for many species.
 - c. Similar species: Information from similar species can be useful in determining either the principal ecological functions of the species, and densities that allow these functions; or the non-impact densities that can be used as proxy for functional density. If data allow, information from a number of similar species can be integrated to find relationships between functionality and density.
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