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Essay

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 International Union for Conservation of Nature 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 in concept and application, but also an opportunity to insert ecological theory into conservation practice. We propose 2 complementary approaches to assessing a species' ecological functions: confirmation (listing interactions of the species, identifying ecological processes and other species involved in these interactions, and quantifying the extent to which the species contributes to the identified ecological process) and elimination (inferring functionality by ruling out symptoms of reduced functionality, analogous to the red-list approach that focuses on symptoms of reduced viability). Despite the challenges, incorporation of functionality into species recovery planning is possible in most cases and it is essential to a conservation vision that goes beyond preventing extinctions and aims to restore a species to levels beyond what is required for its viability. This vision focuses on conservation and recovery at the species level and 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.

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Evaluación de la Función Ecológica en el Contexto de Recuperación de Especies

Resumen: Las interacciones entre especies son de importancia para la conservación. La definición de una meta ambiciosa de recuperación para una especie requiere considerar el tamaño, la densidad y la estructura demográfica de sus poblaciones de tal manera que lleven a cabo las interacciones, papeles y funciones de las especies en los ecosistemas donde viven. Un marco de referencia propuesto recientemente para una Lista Verde de Especies de la Unión Internacional para la Conservación de la Naturaleza (UICN)formaliza este requerimiento mediante la definición de una especie completamente recuperada en términos de su representación, viabilidad y funcionalidad. La definición y cuantificación de la función ecológica desde la perspectiva de la recuperación de especies es un reto conceptual y de aplicación, pero también es un oportunidad para insertar la teoría ecológica en la práctica de la conservación. Proponemos 2 métodos complementarios para evaluar las funciones ecológicas de una especie: confirmación (listado de interacciones de la especie, identificación de procesos ecológicos y otras especies involucradas en estas interacciones) y eliminación (inferencia de la funcionalidad descartando los síntomas de reducción en la funcionalidad, análogo al método de la lista roja que enfoca los síntomas de reducción en la viabilidad). A pesar de los retos, la incorporación de la funcionalidad en la planificación de la recuperación de especies es posible en la mayoría de los casos y es esencial para una visión de la conservación que vaya más allá de la prevención de extinciones y que tenga como objetivo restaurar a una especie a niveles más allá de lo que se requiere para su viabilidad. Su visión se centra en la conservación y recuperación a nivel de especies y ve a las especies como componentes de los ecosistemas, influyendo y siendo influenciadas por los procesos en esos ecosistemas. Así, conecta e integra la conservación a nivel de especies y ecosistemas.

Palabras Clave: impacto de la conservación, lista verde de especies, optimismo en la conservación, planificación de la conservación, recuperación de especies

摘要: 物种间的相互作用对保护至关重要。设定远大的物种恢复目标需要考虑其种群大小、密度和种群统计结构, 以确保物种能在其所处的生态系统中实现种间互作和物种自身的作用与功能。最近提出的《国际自然保护联盟 (IUCN) 绿色物种名录》框架正式纳入了这项需求, 提出从代表性、生存力和功能性三个方面来定义完全恢复的物种。从物种恢复的角度来定义和量化其生态功能, 在概念和应用上都具有挑战性, 但这也是在保护实践中引入生态学理论的重要机遇。我们提出了两种互补的方法来评估物种的生态功能: 一是直接确认, 即列出物种的互作、确定互作中涉及的生态学过程和其它物种, 并量化物种对该生态过程的贡献;二是消除法, 即通过排除功能性受损后的症状来推断功能, 这与红色名录中关注生存力降低后的症状的方法类似。虽然还存在上述挑战, 但在大多数情况下将功能性纳入物种恢复计划是可行的, 而且这对于不仅旨在防止灭绝、更要将物种恢复到生存所需水平的保护愿景来说至关重要。这一愿景强调物种水平的保护和恢复, 将物种视为生态系统的一部分, 影响着生态系统过程的同时也受其影响。因此, 它也连接和整合了物种及生态系统水平的保护。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 保护成效, 保护规划, 物种绿色名录, 物种恢复, 保护乐观主义

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 International Union for Conservation of Nature (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 conservation success in terms of progress toward full recovery (Akçakaya et al. 2018). The proposed 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 . . . , interactions with other species . . . , structural effects . . . , and intraspecific processes . . . " In many cases, ecological functionality of a population depends on its abundance, density, and demographic structure, which determine the behaviors and interactions of the organisms.

We explored the application of the concept of ecological functionality to species conservation. We reviewed the justification for considering ecological function in the context of species recovery and considered why this idea has not been explicitly or systematically implemented as a criterion of species recovery. To address this shortcoming, we delineated conceptual and practical challenges of defining and assessing functionality; considered practical approaches based on ecological theory for defining a species' function and determining whether a population is functional; and examined directions of future research. Although we were motivated by the Green List of Species, our ideas apply to all aspects and systems of species recovery planning.

The Case for Considering Function in Species Recovery

The irreversibility of extinction and rapid decline of many species have largely, and appropriately, focused past conservation efforts on ensuring foremost that species retain viable populations that ensure their continued existence. 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. Conserving species interactions, beyond the conservation of the species themselves, is thus a major conservation goal (Redford & 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 through "ecological extinction" or "functional extinction" (Redford 1992; Janzen 2001), even if the species are still present and viable in the ecosystem (Janzen 1974).

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 is 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, "animals acting like animals, not just persisting" (Sanderson 2006). Demographic sustainability (i.e., long-term viability) "should be seen only as a threshold requirement, a necessary but not sufficient level" and conservation targets should include interactions (e.g., ecological functions, social dynamics, and demographic requirements) (Sanderson 2006). Wildness is a related consideration. Redford et al. (2011) recognized a range of states of species conservation, 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 patterns of intraspecific behavior and social dynamics (e.g., migration, aggregations, and patterns of social hierarchy) characteristic of a species that may disappear as its populations decline, even if these smaller populations are not at risk of extinction. Such characteristics may not appear to fit in a general definition of *ecological function of a species*, but are nonetheless important indicators of successful species conservation that go beyond the criterion of low extinction risk.

Considering functionality in species recovery contributes to a comprehensive approach to conservation across levels of biological organization. Considering interactions of a species in a community and its contributions to ecosystem processes forms a bridge between species-level and ecosystem-level conservation. Another key concept of the Green List framework—representation of the species across the range of ecological settings, as quantified by viability and functionality across areas comprising the native range—forms a bridge between species-level and population-level conservation. Hence, the framework is designed to integrate conservation at population, species, and ecosystem levels.

Challenges

Defining Function from a Species Recovery Viewpoint

Ecological function terminology can be confusing, especially when functions of both species and ecosystems are considered. Relative to species recovery in general, and the Green List of Species framework specifically, we define *ecological function* as specific to a species and *ecosystem process* as specific to an ecosystem (Table 1). So, for instance, the contribution of a species to nutrient cycling in an 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.

For species conservation, there are several general types of ecological functions to consider, all of which arise from interactions among organisms (Table 2). Some functions arise from interspecific interactions, others from intraspecific interactions. Some interspecific 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 at the ecosystem level (Table 1). For example, dispersal of the seeds of a particular tree species by a bat, an ecological function of the bat species, is a direct interaction between the 2 species. The contribution of the same bat species to productivity and forest regeneration (e.g., through dispersal of seeds

Table 1. Definitions of terms related to ecological function in the context of species recovery.

Term	*Definition*
Ecological function of a species	totality of the species' interactions, determining its influence on, or contribution to, ecosystem processes and the patterns of intraspecific interactions, behavior, and social dynamics characteristic of that species
Ecological functionality of a population	extent to which the population fulfils the ecological function or functions of the species in a particular place and time, as determined by its size, density, and demographic structure; can be assessed as either continuous (e.g., percentage) or categorical (e.g., functional vs. not functional)
Direct interactions	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])
Indirect interactions (structural functions)	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
Diffuse interactions	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])
Intraspecific interactions	category of the ecological function of a species as determined by within-species processes and patterns of behavior characteristic of the species, such as colony formation and other aggregations and spatial patterns of movement and dispersion

of multiple plant species) is an ecological function of the bat species at the ecosystem level.

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

Another general type of ecological function arises from intraspecific interactions and processes. It involves patterns of behavior and social dynamics characteristic of a species that may disappear as a result of human impact (Table 2), including long-distance migration, large-scale aggregations of individuals, and patterns of social hierarchy. Although such ecological functions often affect, and are affected by, large-scale ecological processes (e.g., nutrient cycling [Doughty et al. 2016]), they involve species-specific behaviors considered worthy of conservation (Caro & Sherman 2012), even in cases where they do not affect ecosystem processes and even if they may not be required for a low risk of extinction.

A working definition of *function* for application to species recovery may be summarized as totality of the species' interactions, determining its influence on or contribution to ecosystem processes, and the patterns of intraspecific interactions, behavior, and social dynamics characteristic of that species. Function is a property of the species, whereas functionality (degree to which the function is performed) is a property of a particular population of the species at a particular time because it depends on the size, density, and demographic structure of the species' population at that place and time.

Although functionality is continuous, it can be assessed in terms of few (or even just 2) categories, for instance, as a binary variable (functional or not functional) in the context of the Green List (Akçakaya et al 2018), or as a range of categories from "no contribution" to "exceptional contribution" to local interactions (Sanderson et al. 2008). A binary concept of ecological functionality is implicit in the concept of ecological extinction or functional extinction. A population is considered 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. 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 a species will go extinct is divided to sort species into threat categories (Collen et al. 2016).

Some uses of the terms *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 did not consider these processes ecological functions in the context of the Green List 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 framework (Akçakaya et al. 2018).

Our approach to interpreting ecological function focuses on the species, not the function. In contrast, for

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

General category	*Subcategory*	*Example ecological function*	*Example associated traits*	*Determinants of functionality*	*Reference*
Direct interactions (includes 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 & 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
	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 & Beschta 2012
Indirect interactions (structural functions)	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 provision	pine trees providing cavities for nesting birds	tree diameter; heartwood fungal decay	age structure that includes older trees	Jackson & 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 United States	flammability; fast growth in biomass	density high enough to maintain fire; spatial distribution large enough for spreading fires	Outcalt et al. 1999
Intraspecific 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 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

example, Brodie et al. (2018) propose conserving functions by focusing on strong interactions, arguing that "critical ecological functions should be another facet of biodiversity [conservation] . . . 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) is complementary to conservation of species. Our focus, however, is incorporating ecological functionality into the assessment of species recovery, which was first formalized in the Green List of Species protocol.

Function as Contribution to Ecosystem Resilience

Influence of a species on an ecosystem process can be described in different ways. Sometimes, the more important influence is on the stability of the ecosystem process (e.g., its resistance to perturbations), rather than the magnitude of the contribution to the process. In other words, some species contribute in quantity (make a large difference in mean), whereas others influence the quality (e.g., help 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 its contribution to the stability of ecosystems (e.g., capacity to resist regime shifts or recover following a disturbance) (Nimmo et al. 2015).

However, the dichotomy is complicated because many ecosystem processes are not stable in the sense of constancy or small variability. They often vary naturally in space and time, especially at small spatial and temporal scales (Oliver et al. 2015), or have natural regime shifts between alternative states. So, the contribution of a species to an ecosystem process may not necessarily stabilize the process at the scale of the species' population in a particular area (*spatial unit* in Green List of Species terminology). The functional contribution of some species may even promote variability, as with fire-promoting plants (Outcalt et al. 1999). 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; 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-dependent relationship between measures of resilience of ecosystem processes (such as variability) and properties of the populations of species (e.g., size, density, and demographic structure) contributing to those processes remains a challenge. Using resilience as a predictor of functionality requires deep understanding of this relationship.

Functional and Nonfunctional Species in the Same Ecosystem

Because function is often thought of at the ecosystem level and 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. Therefore, no species in the ecosystem can be considered functional. This is not a useful conclusion for species conservation because it does not elucidate which species need help to be fully functional. With species Green List assessments, ecological function is species specific; therefore, assessment of functionality focuses 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. What is relevant to assessing functionality of the prey species is whether there are conservation actions focused on it that are required for its recovery. If the only recovery necessary is that of the predator, regarding the prey species as nonfunctional is not useful. However, if lack of predators (or predators being below their functional densities) causes overabundance of populations of a prey and thereby causes disruption of ecological processes or threatens native species, then management actions directed at the prey may be appropriate and the prey population should be considered nonfunctional (e.g., seagrass–turtle–shark system [Heithaus et al. 2014]). Thus, relationships between functionality and population density or size can be nonlinear; a population's density may be too low or high for the species to be functional (i.e., some species being absent or nonfunctional may cause other species to become nonfunctional). But, the nonfunctionality of the prey population in such a case would be based on its influence on ecosystem processes, not on its lack of interaction with predators.

Functional Redundancy

Functional redundancy occurs when there is overlap between the functions of species, such that reduction in one species' contribution to ecosystem processes can be compensated for by contributions from other species (Lawton & Brown 1993). Functional redundancy is a property of the function, not a property of the 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 other species in the ecosystem also perform them.

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

With 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. Functional redundancy may appear to reduce the importance of a species' functionality and hence its recovery priority. However, the point of considering function in species recovery is not to assign importance to species, but to establish a higher threshold for species' recovery relative to what is required for viability. Thus, functional redundancy does not invalidate the need to consider a species' ecological function in setting recovery targets.

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. Neither the Green List framework nor the IUCN Red List judges how worthwhile it is to conserve a species. The point of including functionality in species recovery assessments is to set more ambitious conservation goals than extinction avoidance and to aim to restore a species to levels beyond what is required for its own viability, reflecting its overall role in the ecosystem it inhabits. Thus, assessing functionality is a way of expecting more from our conservation efforts, not from the species. Although some species make larger contributions to ecosystem processes, our purpose is not to use functionality to compare species with 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 so-called important functions or a lack of "strong interactions" (Brodie et al. 2018) does not preclude the establishment of ambitious recovery targets. Targets can be based on proxies of functionality to determine population levels at which to consider a species "fully recovered" (Akçakaya et al. 2018) in a particular area.

Some ecological functions of a species considered in recovery planning may also provide ecosystem services (i.e., species may contribute to ecological processes that produce benefits for people) (Gascon et al. 2015). These may include supporting services (e.g., nutrient recycling and soil formation), regulating services (e.g., decomposition and detoxification), and cultural services (e.g., 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, a lot more may be known about the contribution of an insect to pollination of crops than to pollination of rare native plants, even if the latter are at risk of extinction if the population of the insect species is no longer functional.

Even in these cases, assessors should consider function from the perspective of the native nonhuman 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 catalog the benefits of biodiversity for human well-being more systematically.

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. 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 & Moberg 2003; Doughty et al. 1996). 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 because its environment and cohabiting biota changes. Even when the function remains the same, functionality of populations may change, for example, 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.

We propose 2 approaches to determining whether a population is functional: confirmation and elimination. 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 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.) involved in these interactions (see Table 2 for examples). This information, together with 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 nonlinear (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. (2016) estimated a threshold density of 6.3 sea otters (*Enhydra lutris*) per kilometer 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 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 individuals ≥80 years old to allow Red-cockaded Woodpeckers (*Leuconotopicus borealis*) to excavate nest cavities in the southeastern United States (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. 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. Table 3 contains a list of questions and considerations to guide assessors in this process aimed at allowing a systematic consideration of the criteria and evidence for determining whether the size, density, and demographic structure of the species' populations are appropriate for its ecological function or functions.

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 & Garnier 2002]) are more relevant to its viability than its

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 nontrivial changes of any of the following types:
   a. reduction in the abundance of another native species;
   b. increase in the abundance of a non-native species or overabundance of another species;
   c. 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. change in any ecosystem process or structural feature (examples in Table 2);
   e. change in the typical patterns of behavior (e.g., social interactions, patterns of aggregation, and movement) among individuals of the species being assessed or other species.
2. Compare areas or subpopulations with different densities or abundances of the species, considering any evidence that suggests that 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. 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. Compare periods when the species was at different densities or abundances, considering any evidence that suggests that 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 predisturbance population size or carrying capacity of a species as a proxy for functional density, assuming that at pre-impact densities the species fulfilled its ecological roles and functions. Consider that carrying capacities vary naturally across the range and over time for many species.
   b. Nonimpact: If impacts change over the range of the species, use population size, density, or carrying capacity in apparently unaffected (or least affected) areas as a proxy. 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 nonimpact densities that can be used as proxies for functional density. If data allow, information from a number of similar species can be integrated to find relationships between functionality and density.

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 identify ecological functions of a species through its traits. This would require analyzing the patterns of dependence between traits and functions of a group of well-studied species. If such an analysis uncovers strong patterns, 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 2 forms of species rarity are combined with 2 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 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 problems 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. It 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 extinction avoidance.

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