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Review

# When Do Ecosystem Services Depend on Rare Species?

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**Conservation aims to preserve species and ecosystem services. If rare species contribute little to ecosystem services, yet are those most in need of preservation, tradeoffs may exist for these contrasting objectives. However, little attention has focused on identifying how, when, and where rare species contribute to ecosystem services and at what scales. Here, we review distinct ways that ecosystem services can positively depend on the presence, abundance, disproportionate contribution or, counterintuitively, the scarcity of rare species. By contrast, ecosystem services are less likely to depend on rare species that do not have a unique role in any service or become abundant enough to contribute substantially. We propose a research agenda to identify when rare species may contribute significantly to services.**

## Highlights

Most species in all ecosystems are rare in some form.

Rare species are often assumed to contribute little to ecosystem functioning and services, but evidence has accumulated that rare species can substantially contribute to some ecosystem services in a variety of ways.

Rare species can have direct and indirect contributions to ecosystem services through species interactions.

Research on functional trait uniqueness could provide new insights into the role of rare species in ecosystem services, yet explicit tests of connections between functional traits and measurable contributions to ecosystem processes and services are still needed.

The knowledge of when and to what extent rare species can affect ecosystem services is important for identifying situations in which multiple conservation objectives (protecting biodiversity and providing other ecosystem services) are more or less aligned.

## Why Consider the Role of Rare Species in Ecosystem Services?

The focus of conservation has broadened from conserving nature to also preserving its contributions to people [1,2], often referred to as **ecosystem services** (see Glossary). This raises the question: what factors strengthen or reduce alignment in the objectives of protecting species and providing ecosystem services to people [3–6]? One important but understudied factor is the contributions of **rare species** to ecosystem services [7]. Most species in all ecosystems are rare in some form [7,8]. Rare species also include the species in greatest need of conservation interventions [9,10] to reduce risks from anthropogenic threats or demographic or environmental stochasticity [11–15]. At the same time, rare species are often assumed to contribute little to ecosystem services other than existence **value** or as specialists, because of their small populations or limited ranges (e.g., [9,16]). If this assumption is correct, then management to enhance most ecosystem services will offer little benefit for conserving rare species [6,9]. However, if many rare species often contribute to ecosystem services significantly more than their low abundance would suggest, managing for services could provide added incentives to protect rare and often threatened species, thereby increasing alignment between multiple conservation objectives.

In response, we examine evidence for the role of rare species in providing ecosystem services, asking: how can rare species contribute to ecosystem services? And, under what conditions does rarity imply an important functional role in ecosystem services? In doing so, we provide insights into when conservation for the sake of biodiversity overlaps with conservation for other ecosystem services. This synthesis complements previous studies assessing alignment between biodiversity conservation and ecosystem service objectives. Previous approaches assessed spatial overlap between conservation priorities and ecosystem services [17–19], the roles of uncertainty over which species provide services [3] and habitat fragmentation [20], and tradeoffs between economic development and conservation [21]. Instead, we focus on the

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roles of rare species in ecosystem services, defining rarity as a species that is geographically restricted (e.g., endemics) and/or has a small local population size [8].

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## Categorizing the Ways Rare Species Contribute to Ecosystem Services

Since rare species are those most likely to be lost from ecosystems, thereby driving biodiversity change, their contributions to services will determine how much changes in biodiversity will alter ecosystem services [22]. Most species in nearly all ecosystems are rare, while relatively few, **dominant species** account for most of the total abundance (e.g., [23]). The **mass ratio hypothesis** states that dominant species and their traits contribute most to ecosystem processes (biomass accumulation and productivity), because energy flows mostly through these few species. If so, then relatively few species would perform high levels of ecosystem functions [13,24–26]; rare species would have a negligible role in service provision; and full biodiversity protection would rarely make sense for managers tasked solely with maximizing ecosystem services [6,9,22,27]. However, some ecosystem services have been demonstrated to depend on rare species, in addition to, or instead of, dominant species [7,28–31]. Similarly, rare species are also more likely to have functionally distinct traits and characteristics, which could lead to **unique functional roles** in ecosystem processes and services [32,33]. The questions are which, and how many, rare species matter [22,24,29].

Our understanding of the roles of rare species in ecosystem services is complicated by five challenges. First, rarity is defined differently across studies, preventing a clear picture of how rare species contribute to ecosystem services and the implications for conservation decisions. Conservation biologists and managers commonly consider rarity over the entire range of a species, in terms of small population sizes or restricted extents [9,10] (Figure 2). By contrast, some ecologists studying relationships between biodiversity and ecosystem functions have instead focused primarily on overall species diversity and, when considered, defined rarity in terms of low relative abundance within a local community of interacting species (e.g., [12,31]). Second, experimental studies of species contributions to ecosystem functions seldom include truly rare or threatened species [7,22,34]. Third, some studies have calculated the contribution of a species to an ecosystem service based on its abundance; thus, rare species by default are assumed to be unimportant service providers [6,24,26,35,36]. Fourth, rare species have low detection probabilities of existence [37] and, thus their associated impacts may be underappreciated. Finally, detecting the effects of rare species in short-term studies is especially difficult; their impacts can be indirect, through species interactions and complicated feedbacks, such as by diluting negative density dependence (e.g., Janzen–Connell effects) for more common species and, therefore, are only evident when considering longer time periods [38,39]. Similarly, many studies quantifying the contributions of species to functions and services may not be long enough to observe whether remaining rare species can eventually compensate for the former contributions of lost and declining species. These collective challenges may bias our view of the role of rare species.

To synthesize the roles of rare species, we categorize their potential contributions into five categories (Figure 1): (1) direct contributions when the value of a service depends on the presence of a species more than its abundance or (2) when the value of a service increases as the abundance of the species decreases; (3) contributions greater than expected based on their low abundance, such as through species interactions (e.g., facilitation) or unique functional roles; (4) contributions to services where or when the species is more abundant, despite currently having a small population size in one location or a restricted range; and (5) no significant contributions to any ecosystem service beyond existence value. These categories include services directly provided by the population of a species (Categories 1 and 2 in

Figure 1), such as food production, appreciation of wildlife, and other **cultural** and **provisioning services** [40], and services that depend on functions provided by a community in aggregate, such as carbon storage and other **regulating services** (Categories 3 and 4). We distinguish between per capita contributions (e.g., the **marginal value** per individual, Figure 1A,B) and total aggregate contributions of a species at different scales (e.g., where the species occurs versus globally) (Figure 2B). We review how each way that rare species can contribute will influence alignment between multiple conservation objectives. We also find knowledge gaps and propose a research agenda to identify when rare species may or may not contribute significantly to services now or in the future.

### The Service Depends on a Species' Presence

Some rare species currently contribute directly to ecosystem services where the service is driven by the presence of a species rather than by its abundance (Figure 1A; Boxes 1 and 2) [35,41–43]. For example, recreation experiences, such as safaris, whale watching, and bird watching, often depend on, or are enhanced by, spotting rare species [44,45]. For instance, people visiting zoos preferred seeing rare species more than common species along multiple dimensions (e.g., time spent or physical effort while viewing the species) [46]. Additionally, cultural services, such as cultural identity and sense of place [47,48], may be derived from endemic or rare species for their iconic or spiritual roles, and **relational value** [49]. While being iconic or having relational value is not restricted to rare species, Box 1 provides examples of rare species with these roles. For services like these, the value depends nonlinearly on abundance (Box 2). These types of value, and associated cultural and social norms, have motivated the conservation of endangered species, one form of rare species, increasing alignment (Box 1 [50]).

### Scarcity Is Valued: The Value of a Service Increases as Abundance Decreases

Other rare species directly provide services with a marginal value that increases as abundance decreases, (i.e., with scarcity value; Figure 1B, Box 1) [41,42]. Examples include rare species harvested for **luxury goods** (e.g., sturgeons for caviar [51]), targeted for trophy hunting [52], used for traditional medicine [53], and collected as ornamental species or exotic pets [41] (Box 1). Unlike Category 1, the high value from rarity here can compromise the persistence of these species rather than promote their conservation, without well-defined, secure property rights [41,42].

### Rare Species Contribute Disproportionately Through Indirect Interactions and Unique Functional Roles

Some ecosystem services are provided by the aggregate effects of many species in an ecological community, such as carbon storage (Figure 1C). Rare species can have important roles in these services when they fill unique functional roles (e.g., unique traits, timing of activity, or physical location within an ecosystem) or influence the success of other species that provide services [15,28,31]. These contributions can be greater than expected based on the low relative abundance of a species (Figure 1C), particularly on a per-capita basis or to the total amount of a service at small spatial scales (Figure 2). However, for any given species, these types of contribution to the total amount of a service regionally or globally are likely small (Figure 2).

For this category, rare species can contribute indirectly to services through species interactions. Some rare species modify local environmental conditions in ways that benefit or **facilitate** service providers [7,54,55]. Through another positive interaction, **mutualisms** (e.g., plant–soil interactions), some numerically rare species can also contribute to services more

## Glossary

**Cultural services:** benefits that people receive from interactions with nature that are non-material (e.g., sense of place or inspiration).

**Dominant species:** species with high relative abundance or biomass.

**Drivers:** stressors, threats, or variables that impact ecosystems, species, and their services. Examples include human impacts (e.g., harvesting or land-use change), management interventions (e.g., invasive species eradication), and aspects of global environmental change (e.g., climate change or nitrogen fertilization).

**Ecosystem service delivery:** how people benefit from, use, or value services.

**Ecosystem services:** contributions of nature to humans and their well-being, which are provided by the populations of species as well as by ecosystem functions and processes.

**Facilitation:** the density of one species benefits another species by mediating abiotic or biotic conditions.

**Functional uniqueness:** species with unique characteristics or dissimilar functional traits, compared with the other species and their trait combinations in the local or regional species pool. Functionally unique species are often rare and referred to as ecological outliers.

**Keystone:** a rare species with a disproportionately large impact on the structure and functioning of an ecological community, through influential species interactions (e.g., rare predators).

**Luxury good:** a type of good, service, or product for which demand increases disproportionately as income increases when people become wealthier (in contrast with a normal good). They are typically associated with social status.

**Marginal value:** the added value from having an additional unit of something; here, it refers to the gains in ecosystem service value or benefits from an additional individual of a rare or abundant species.

**Mass ratio hypothesis:** the hypothesis that dominant species and their traits contribute most to ecosystem processes because species affect productivity and total biomass accumulation in proportion to their relative abundance.

than expected based on abundance. For example, some rare or threatened nitrogen-fixing species [56] and their microbial mutualists (often Rhizobia) enhance soil fertility. Their presence, even at low abundances, supports higher biomass production over time in nitrogen-limited grasslands [39]. This increased biomass production is associated with higher biofuel yields [57]. Similarly, in an Alaskan shrub wetland, rare horsetails *Equisetum spp*. (5% of the total biomass of the plant community) acquire and cycle phosphorus, potassium, and calcium efficiently and enhance nutrient availability for uptake by dominant species [7,58].

Second, species can increase overall service provisioning by reducing competition among **service providers**, at least locally. When intraspecific competition is stronger than interspecific competition, as for coexisting species, rare species can stimulate per capita growth rates of service providers by reducing competition [59–61]. For example, individuals of many tree species exhibit greater growth and/or survival at early life stages when surrounded by individuals of other species [57,58]. This can boost ecosystem services that depend on plant growth, such as timber and forage production. More growth is often beneficial but can also be harmful (e.g., algal blooms). These contributions are not a function of rarity *per se*; these species would contribute more if more abundant. However, because most species in an ecosystem are rare, collectively they may have a major role in the impact of species richness on ecosystem functioning [7].

Third, rare species can be **keystone** species or predatory species with disproportionate roles in structuring communities, thereby indirectly contributing to services [7,27]. For instance, in Aleutian kelp forests, rare sea otters (*Enhydra lutris*) [62] limit the abundance of sea urchins (*Strongylocentrotus* spp.) that can overgraze kelp biomass [63–65], indirectly increasing standing-stock biomass and carbon available for carbon storage [66,67]. Through indirect interactions, declines in rare predators might therefore impact services [15]. Similarly, in salt marshes in New England, USA, removing predators that are harvested and, thus, relatively uncommon in the community, such as striped bass (*Morone saxatilis*) and blue crab (*Callinectes sapidus*), indirectly causes *Spartina alterniflora* die-off [68], with consequences for wave attenuation and shoreline stability [69]. Even if not a keystone species, rare species with unique roles in trophic networks, especially with weak interactions, can stabilize foodwebs [70].

Alignment between multiple conservation objectives is strengthened when considering rare species that contribute to services indirectly through species interactions, though we expect these contributions to be local where the species occurs or relevant at the scale at which species interactions play a strong role in per capita or total service provision.

## Rare Species Contribute When and Where They Are More Abundant

For some services, the value of a service scales with the total abundance or biomass of species in a community; therefore, the relative abundance of a species in a community reflects much of its relative contribution (e.g., carbon storage, [36]) (Figure 1D). Rare species that are geographically restricted but locally abundant where they occur can contribute to services where they occur [8], such as giant sequoia *Sequoiadendron giganteum* (Figure 2). In contrast, rare species that are both geographically restricted and have low local abundance where they occur would contribute little to these services. Yet, this class of currently and locally rare species could contribute more to services in other locations, times, or conditions (e.g., under global change) if they become more abundant, through future population growth or **turnover**. This category includes species that were once abundant but are now rare due to disease, overharvesting, or habitat loss and no longer contribute to services to the extent they previously did (e.g., [71,72]). For instance, species that were once extremely common, such as the American chestnut

**Mutualism:** populations of two species benefit each other (e.g., plant–pollinator relationships).

**Provisioning services:** material goods and products that benefit people, such as fish, fiber, and timber, typically derived from population harvest, with market values.

**Rare species:** rarity can be defined in many ways; here, we define rarity as species with restricted geographic ranges or small population sizes (known as numerically rare). Therefore, rare species include threatened and endangered species but are not always threatened [100]. However, rare species are more likely to be at risk, due to demographic stochasticity and other human impacts. We do not consider habitat specificity, another form of rarity, because it relates more to the vulnerability of a species to extinction than its potential contribution to a service.

**Regulating services:** benefits to people resulting from ecosystem processes and multiple ecosystem functions, such as moderation of natural hazards, climate regulation, water quality, and crop pollination.

**Relational value:** the value derived from interacting with nature by ‘doing what is right’, based on fulfiling moral obligations to nonhumans.

**Service providers:** species that directly provide one or more ecosystem services (e.g., pollinators required for crop production, or fish that are harvested for food).

**Supply of ecosystem services:** the amount, typically in biophysical units, that can be used or appreciated by humans.

**Turnover:** changes in the identities of species in a community over time and space.

**Unique functional role:** species or their traits with a different influence on the ecosystem than other species present.

**Value:** nature provides multiple benefits to humans, who weight these benefits and how they impact their happiness and well-being differently, based on preferences, social norms, and ideals. Values can be described in economic and noneconomic terms.

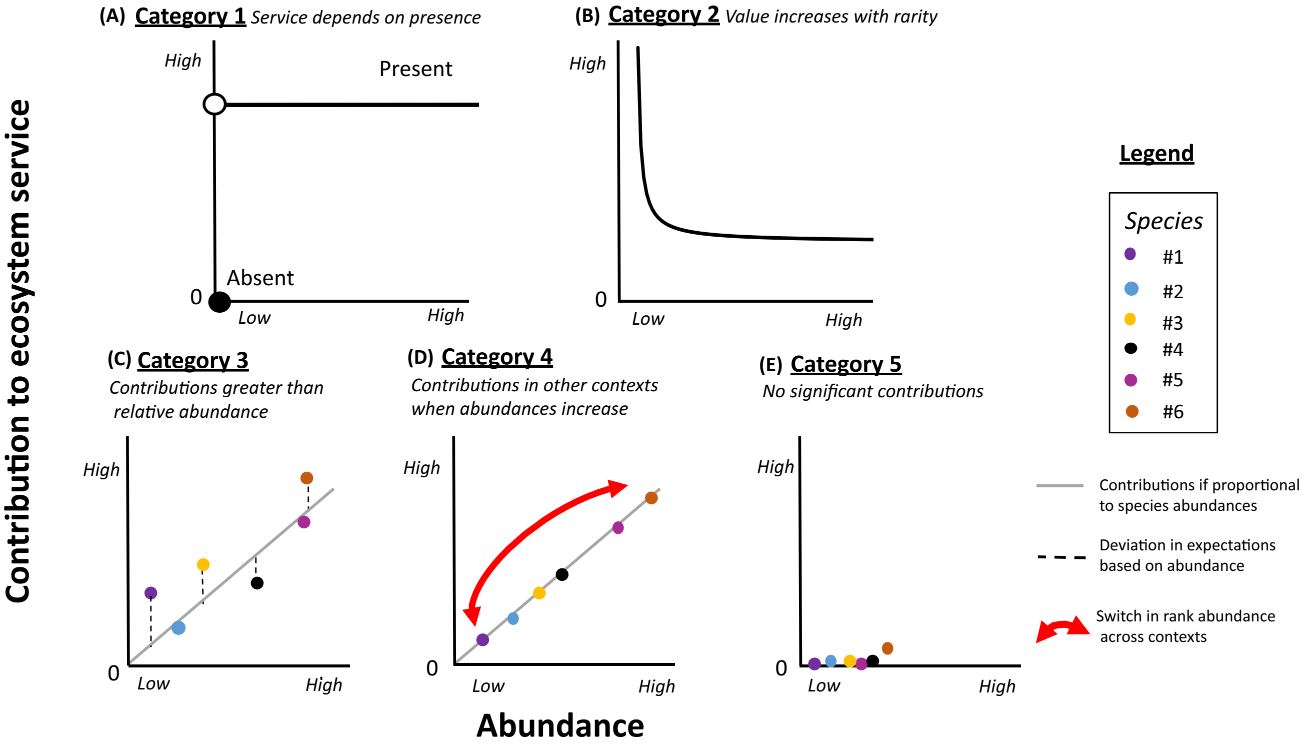

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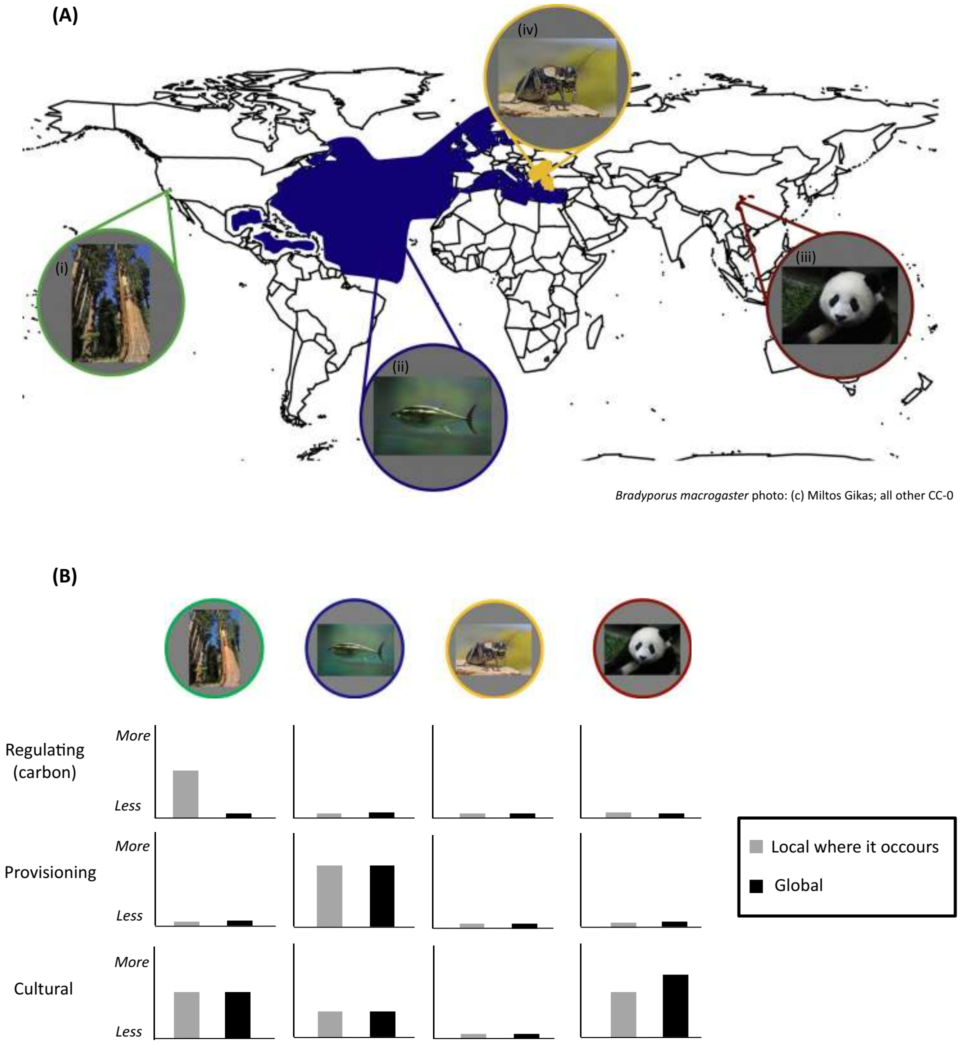
Figure 1. Five Categories for How Rare Species Can Contribute to Ecosystem Services. The contributions of rare species can be assessed on a per capita basis [e.g., the unit change in a service value per individual (A,B)] or as the total contribution of the population of a species per area (C,D) within their range or beyond, regionally or globally (e.g., downstream effects of erosion control or other watershed-type services, carbon storage in a tropical forest contributes to the global carbon cycle, or a harvested population traded and consumed globally; Figure 2 in the main text). (A) Category 1: services that depend on the presence of a rare species more than on its abundance, such as for many cultural services (Box 1 in the main text). (B) Category 2: value increases as abundance decreases, i.e., scarcity value (Box 1 in the main text). (B) shows a nonconstant relationship between marginal value from a service and abundance: the marginal value increases as the population size decreases, as for many luxury goods (Box 1 in the main text; [41,42]). In (C) and (D), the 45° gray line shows what the contributions to the service would be if proportional to the relative abundance of a species in the community (as a 1:1 contribution.) (C) Category 3: the contribution of a rare species to an ecosystem service is greater than its low relative abundance in the community. For instance, contributions of a rare species (i.e., Species #1 and #3) to this service are greater than expected based on abundance, as indicated by deviations from the 1:1 line. This can arise due to species interactions (e.g., facilitation by nitrogen-fixing species can lead to disproportionate contributions relative to their low abundance, and these contributions will increase as their abundance increases). Contributions that are greater than proportional to abundance are not restricted only to rare species (as shown by Species #6). (D) Category 4: for a service that depends on total abundance, locally rare species in one context can become abundant and, thus, contribute more in different times, places, or conditions. For instance, in an extreme case, the rarest and the most dominant species can 'switch', as indicated by the red arrow, such as following changes in grazing management [77,79]. (E) Category 5: currently and locally rare species that will always be rare and never contribute. Box 3 in the main text outlines hypotheses for why different types of rare species could fall into different categories.

*Castanea dentata*, previously sequestered carbon and affected stream hydrology [71]. Indeed, historical reductions in the abundance of common species have resulted in not only extinctions (e.g., the passenger pigeon, *Ectopistes migratorius*), but also large impacts on the functioning and structure of ecosystems and their services (e.g., loss of foundation species in North American forests) [71,72].

Similarly, rare species with small population sizes in one place can be abundant or dominant in other locations or time periods with different abiotic or biotic conditions [22,73]. The temporal [74] and spatial [75] insurance hypotheses state that, in fluctuating and spatially heterogeneous environments, different species are most productive at different times and places, contributing



*Bradyporus macrogaster* photo: (c) Miltos Gikas; all other CC-0

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Figure 2. Relative Contribution of Rare Species Locally versus Globally to Multiple Services. Here, we consider two forms of rarity that relate to how much and whether species contribute to ecosystem services beyond existence value: geographically restricted species and species with small population sizes (numerically rare). Species can be rare in either or both forms, as highlighted by the examples in (A): (i) giant sequoia, *Sequoiadendron giganteum,* is geographically restricted; (ii) Atlantic bluefin tuna, *Thunnus thynnus*, is relatively widespread but has a small population size [62]; (iii) Giant panda, *Ailuropoda melanoleuca*, and (iv) the big-bellied glandular bush-cricket, *Bradyporus macrogaster*, are rare in both forms. (B) We consider total (summed) contributions to regulating (carbon storage), provisioning, and cultural services, and whether we would expect these total contributions to be greater locally versus globally. We hypothesize the total contribution to ecosystem services will depend on: (i) the type of service; and (ii) the scale: local versus global. The total contribution for cultural services is not necessarily scale dependent. For example, pandas are widely appreciated, despite their restricted range and small population size. Similarly, with global trade in fish and the high price per pound of bluefin tuna, its local versus global contributions to this provisioning service can be comparable. In contrast, for geographically restricted species that are abundant within their ranges, contributions to services such as carbon storage can be high locally relative to their total contribution to these services globally (e.g., as for Giant Sequoia). We note that the bar graphs and their level of total contributions to a service locally versus globally are on a relative scale and are conceptual only. The supplemental information online provides the references for the range data of these species.

### Box 1. Examples of Rare Species That Contribute Directly to Ecosystem Services

A population of a species can be a service in its own right. Species can provide cultural services (e.g., spiritual value), rather than through an ecosystem process or function (e.g., water filtration or nutrient cycling) [40]. The value of some provisioning (Figure IA) and cultural (Figure IB) services is derived from the presence, versus absence, of a species, or its value does not increase in a positive linear fashion with abundance (Figure 1 in the main text). Figure IA shows rare species with economic value that increases as abundance decreases, known as scarcity value (Category 2). Rare species in this category include species collected for: ornamental purposes, including fish such as the Banggai cardinal fish (*Pterapogon kauderni*) for aquariums, and plants such as orchids; and species used for traditional medicines, such as rhino horn; luxury goods, such as bluefin tuna (*Thunnus thynnus*); or trophy hunting (not shown). As in these cases, demand for the species typically increases with rarity (and rising incomes) driven, for example, by social status [42]. Positive feedbacks between rarity and value can perpetuate extinction risk [41], decoupling conservation and some ecosystem service goals (including economic and some cultural values). Figure IB shows examples of rare species (from Category 1) that provide cultural services, including from appreciating iconic species such as bald eagles, *Haliaeetus leucocephalus* (in v) and relational values. For example, in Madagascar, social taboos about harvesting threatened species such as the sifaka, *Propithecus edwardsi*,aid conservation efforts [50].

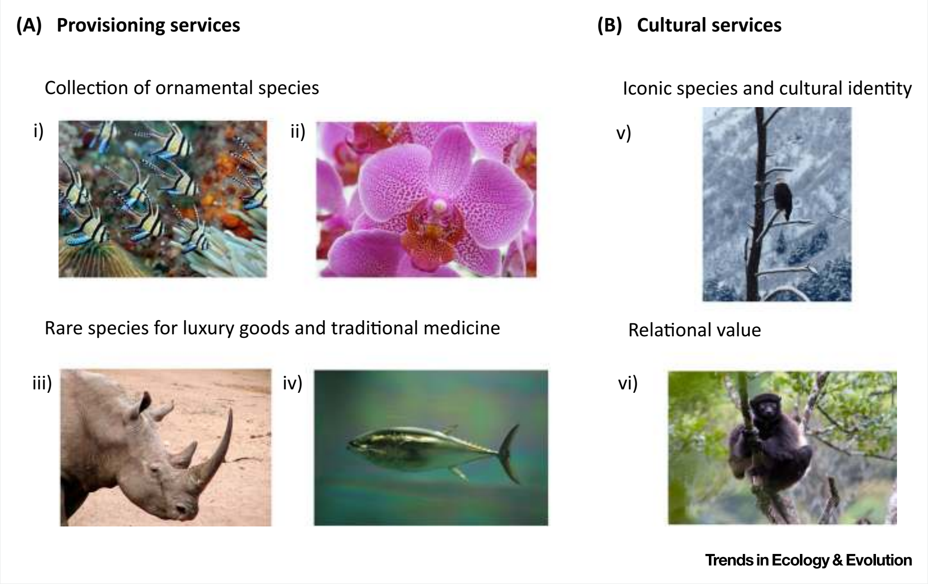

Figure I. Examples of Populations of Rare Species That Contribute Directly to Ecosystem Services. (A) Rare species with economic value where the value increases as abundance decreases, including (i) Banggai cardinal fish (*Pterapogon kauderni*), (ii) orchids (Orchidaceae), (iii) rhino horn, and (iv) bluefin tuna (*Thunnus thynnus*). (B) Rare species that provide cultural services, including (i) bald eagles, *Haliaeetus leucocephalus*, and (ii) sifaka (*Propithecus edwardsi*).

most to ecosystem functioning when and where they dominate. Experiments in grasslands [29,76], grazed and fenced rangelands [73,77], and the rocky intertidal [78] demonstrate this possibility at small scales. For example, fencing can increase otherwise rare legumes in grasslands [77]. Through time, rare species can increase in abundance due to changes in the environment, management (e.g., grazing [79]), human impacts, or declines in their competitors.

Furthermore, rare species that contribute little now or in the past may play key roles in the future through their functionally unique characteristics and/or by increasing in abundance or range. When facing novel conditions, rare species with unique trait combinations may thrive [32,79,80]. For example, as the climate changes, conditions could favor rare tree species so that they become important contributors to aboveground carbon or nitrogen cycling

## Box 2. Moving Beyond Biomass as a Proxy for Ecosystem Services and Contributions to Human Well-Being

Commonly, total biomass or productivity is used as a proxy for other functions and services, yet rare species are more likely to have roles in services that are not directly dependent on biomass production. For some services, such as carbon storage or forage production, total biomass is highly correlated with the service supply**;** however, biomass and productivity are not reliable indicators for many other services. For instance, several hydrological services, including flood attenuation and stormwater retention, are negatively correlated with plant biomass [98].

While services can be measured in terms of biophysical supply, they are ultimately defined as benefits derived from nature by humans. Moving beyond the biophysical supply of ecosystem services to consider **ecosystem service delivery** requires accounting for social and economic determinants of services, including demand and preferences (e.g., Box 1 in the main text). As described in Categories 1 and 2, this can create highly nonlinear, even negative, relationships between the abundance of a species and human well-being, as for luxury goods and cultural services derived from plants and animals. For these services, spiritual motivations, prices, social status, and social networks all influence preferences for particular services from species, including rare ones. As a result, focusing on a subset of services that depend on productivity or biomass, or only on biophysical supply, will underestimate contributions of rare species to services.

[32,36,81]; at high latitudes, symbiotic nitrogen-fixing trees currently have very small population sizes but are predicted to become abundant as temperatures rise [81]. Despite these examples, we know little about which conditions will result in which rare species emerging as significant contributors to ecosystem services. While we note that rare species are often the most likely to be lost from systems [10], we highlight factors that determine whether a rare species is likely to expand in range size or abundance under global change (Box 3).

This logic of potential future contributions from rare species is also reflected in studies on the bioprospecting or option value of biodiversity, which advocate for protecting biodiversity to safeguard the option to discover new uses of species in the future, including for medicine [82,83]. In the future, new diseases or biotechnological breakthroughs could create novel situations in which rare species provide benefits to people (e.g., through pharmaceuticals, bioremediation, bio-engineering, or for agriculture). Rare species that are evolutionarily and genetically unique could contribute disproportionately to bioprospecting value. For instance, past discoveries found that the rare Madagascar rosy periwinkle, *Catharanthus roseus*, contains compounds useful as medicine for childhood leukemia [45]. However, potential value from bioprospecting alone does not always economically justify biodiversity protection, given competing land uses and associated opportunity costs [84].

Managing for some ecosystem services could provide an added incentive to increase the abundances of locally rare species that could contribute substantially to services if more abundant. Targeted management actions can increase species' abundances (e.g., restoration and reintroduction), restoring or enhancing services that these populations support [85]. For instance, overfishing has driven many fish populations to low local abundances; recovering these populations through improved management can enhance not only conservation, but also food production, income, and employment [86].

### Rare Species That Never Contribute Greatly to Ecosystem Services

Although rarity does not preclude important functional roles [7], as the examples above illustrate, there may also be rare species that have had and always will have limited roles in all ecosystem services. Falling into this category would require that a species never increases in abundance enough to contribute substantially, never has a functionally unique role in any service, is not iconic, and does not have scarcity value. A focus solely on ecosystem services beyond existence value would be indifferent to their losses from ecosystems. Alignment may be

### Box 3. A Research Frontier: Future Contributions of Rare Species

Under which conditions and when will the contributions of rare species to services increase in the future? A research frontier is understanding and predicting how the abundances and roles of species in services will change with changing environments, human impacts, and management interventions (Figure 1 in the main text). For rare species, this task presents particular challenges, given the vast number of rare species, their low detection probabilities, and the many possible future scenarios. Uncertainty is also magnified when considering global change, novel environments, and that the contributions of many rare species might be indirect through species interactions. Yet, we generate some hypotheses drawing on knowledge about factors and species traits that promote or perpetuate rarity.

First, some currently rare species could become more abundant or more widespread under global change (Figure 1D in the main text). For example, rare species that are geographically restricted can expand their presence over a larger area if their climatic envelope widens. In contrast, climate change will not necessarily lead to changes in rarity for the species with attributes that perpetuate rarity; their ranges could instead be restricted by topography, dispersal limitation, and/or biotic controls (e.g., inter- or intraspecific competition for resources, predator–prey interactions, parasitism, or mutualisms) that may not change with climate change [99]. Second, in addition to expanding their ranges, rare species may become more abundant where they occur because of extinctions or extirpation of negatively interacting species (competitor, predator, or pathogen release) that respond differently to global change. Third, rare species can also become more abundant with increases in limiting resources (e.g., nitrogen or carbon dioxide fertilization), supporting more individuals overall. As opposed to external drivers, life-history traits of species may also confer rarity, such as low fecundity, poor dispersal, slow growth, and long lifespans. It is less clear if or how these traits, and a the population size of a species associated with these traits, may change with environmental change. A key question, also relevant for rare species, is whether responses of species to global change will be inherently idiosyncratic across types of species and drivers, or if some general rules might exist. If so, anticipating future changes could provide an incentive to facilitate the expansions of certain rare species to climate change (e.g., via adaptive restoration or assisted migration).

weakened if many rare species provide no services beyond existence value. An important question is how many rare species fall into this category (see Outstanding Questions), yet we lack details about the functional contributions of the vast majority of rare species [7,22] and how future environmental change may alter these functional contributions. We hypothesize that species in this category will likely fit the definition of rare in multiple ways, namely a small geographic range and small population sizes where it occurs [8] (Box 3), such as the big-bellied glandular bush-cricket, *Bradyporus macrogaster,* and reveal snake range buckwheat *Eriogonum holmgrenii*, excluding those species that directly contribute to services (Box 1).

## Future Directions

We synthesized ways rare species can contribute to services, directly or indirectly through species interactions, providing some testable predictions (Figure 1; Box 3). A knowledge gap is which rare species could emerge as significant contributors to ecosystem services, directly or indirectly, and under which conditions, given global change. We highlight several opportunities for future research (Boxes 2–3, and Outstanding Questions).

### Selecting and Experimentally Varying Abundances of Rare Species

One way to detect the potential effects of rare species is to experimentally increase or decrease their densities and measure the consequences for the **supply of ecosystem services** (e.g., [13]). However, natural ecosystems contain many more species than experiments can feasibly manipulate. Prioritizing which rare species to include or remove in experiments is therefore necessary (e.g., [30]), but the key question is how. We suggest that this prioritization could be done by adapting existing frameworks for bioprospecting and optimal search used in economics and pharmaceutical research for genetic characteristics (e.g., [83,84]). These approaches can guide selection of rare species to include in experiments when such 'sampling' incurs costs, but the benefits to ecosystem services are uncertain. Considering functional traits, when they predict responses to global changes and/or contributions to ecosystem processes and services, could aid in this prioritization process [87–90].

### Insight into the Roles of Rare Species Under Changing Conditions and Novel Environments

Research on **functional uniqueness** could offer new insights into the roles of rare species in ecosystem services under changing or novel conditions; however, evaluating this promise awaits more explicit tests. Functionally unique species are often rare [32,33]. Recent studies propose that functionally unique, rare species have the greatest potential to take advantage of unique niche spaces, unused resources, or novel conditions (e.g., novel climates) and thereby to increase their contributions to ecosystem processes [12,32,90]. For example, some microbial communities have recovered from environmental stress in part because initially rare taxa became dominant [91]. However, to date, studies measuring functional trait uniqueness have not quantified the consequences of changes in the presence or abundance of species with unique functional traits for functions or services under changing conditions (e.g., [12,32,90]). Quantifying these relationships is a promising direction for understanding connections between rare traits and contributions to services. However, disentangling these relationships will require simultaneously considering: (i) whether a rare species will benefit from, or better tolerate, novel environmental conditions (Box 3); (ii) whether the species or traits also have important roles in ecosystem services; and (iii) how these relationships depend on the socioenvironmental conditions experienced.

Global change experiments or retrospective quasiexperiments can provide insights into the conditions under which species flip from rare to abundant or dominant, including how changes in rare species depend on both species traits and changes in different **drivers** (e.g., land-use change or temperature variability). For example, experiments that simulate future conditions (e.g., eutrophication, warming, or drought) can provide insights into when rare species could become abundant or play different roles in ecosystems under global change (e.g., [92,93]). Analyzing quasiexperiments, provided by global change [94] or past management interventions (e.g., disease outbreaks, establishment of protected areas, or invasions), also provide a way to quantify causal relationships at scales at which randomized experiments are not possible (see [95,96]). With these approaches, we propose that future research could quantify whether trait or phylogenetic information predict changes in functions and services *a priori* (e.g., [89]) and how these effects depend on the abiotic and biotic context (e.g., species and functional trait composition in a community; see Outstanding Questions).

## Concluding Remarks

There is considerable uncertainty over which species, especially rare ones, will emerge as key ecosystem service providers in the future (e.g., due to new discoveries, global change, or changes in management), or which species' contributions will diminish or never increase. This uncertainty enhances the value of biodiversity protection as a hedge for future service benefits (option value) [82,97] and can provide an incentive to protect more species than are presumed critical [3]. Yet, it also highlights important unknowns in expected outcomes for many rare species from a broadened management focus on ecosystem services. We suggest routes for future research to advance knowledge about how much and when rare species contribute to ecosystem services (see Outstanding Questions). Two key research needs are: quantifying contributions of rare species with unique functional roles, particularly under global change, and the potential for rare species to contribute more to services when increasing in abundance (or compensating) following reductions in other species. This knowledge can inform whether managing for ecosystem services has the potential to leave at-risk species vulnerable to losses [9] and, therefore, where to focus limited resources dedicated to biodiversity conservation *per se.*

### Outstanding Questions

Beyond existence value, how many rare species have a significant role in an ecosystem service either today, in the past, or moving into the future?

How many species are rare in one habitat or set of conditions but are common, or even dominant, in another or in the absence of a better competitor? Would many rare species become far more abundant if species that are currently abundant declined in response to an environmental change? Which ones would be impacted?

What is the relative magnitude of the direct versus indirect roles of species in services? Are rare species more likely than the average species to make indirect contributions (e.g., by acting as keystone predators or facilitators)? How many or how much do rare species have important roles in ecosystem services indirectly, through species interactions? Are these indirect effects large or small relative to other drivers of ecosystem services?

What can we learn from quasiexperiments and global change experiments about conditions under which species shift from rare to abundant or dominant? Are these conditions controllable by management? Are responses of certain rare species predictable based on functional uniqueness, traits, or phylogeny *a priori* (e.g., [89])? How much do the consequences from changes in rare species for ecosystem services depend on the traits of those species, abiotic conditions, and the community context (i.e., the species and/or functional composition of the community and interactions within it)?

Are there general rules about how different forms of rare species will respond to global change? Will these responses affect their impact on services or will they be idiosyncratic, differing with the driver of change and species?

How can we better connect studies on functional uniqueness to measurable contributions to services and functions under different conditions? How often are the rarest species in the community also the most functionally unique?

How does that pattern depend on the types of trait considered? How do those traits map onto contributions to different types of services?

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## Supplemental Information

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