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Species Rarity: Definition, Causes, and Classification

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In virtually all ecological communities around the world, most *species* are represented by few individuals, and most *individuals* come from only a few of the most common species. Why this distribution of species abundances is so regularly observed among different taxonomic sets in geographically diverse systems is a question that has received considerable theoretical and empirical investigation (Preston 1948, 1962; Harte et al. 1999; Hubbell 2001). Understanding the mechanisms leading to the pattern of few common and many rare species extends beyond basic interest in how natural communities are assembled. It is also of great practical importance to conservation science since human uses of ecosystems can greatly affect the pattern of commonness and rarity in the biota inhabiting those same ecosystems (Lubchenco et al. 1991).

Because budgets for biodiversity conservation are limited, a common strategy for allocating scarce conservation resources has been to focus on species that are thought to have the highest extinction risk (Sisk et al. 1994; Flather et al. 1998). What is the ecological justification for a conservation paradigm focused on rare species? How does one go about distinguishing rare from nonrare species? And what factors contribute to species rarity? We address these questions so as to provide a foundation for why resource managers need to be concerned about rare species and how they can identify them. We also discuss the implications that various causes of rarity have on the choice, and likely success, of management actions to protect and enhance populations of rare species.

Why Do We Care about Rarity?

Among a set of ecologically similar species, those that are rare will have a greater extinction risk than those that are common (Johnson 1998; Matthies et al. 2004). Small populations are more likely to be impacted by chance demographic and environmental events, such as failure to find a mate or reproduce, diseases, floods, and fires (Boyce 1992). Furthermore, the genetic simplification that often accompanies severe population declines can reduce a species' ability to adapt to changing environmental conditions, lead to higher rates of inbreeding and the expression of deleterious genes, or, conversely, lead to outbreeding depression (Ellstrand and Elam 1993; Lande 1995). For these reasons, conservation science has become preoccupied with identifying at-risk species and focusing conservation efforts on those most likely to be lost from the species pool.

The conservation focus on rare species has been further justified by the potential role that rare species may play in maintaining overall ecosystem functionality. How rare species affect ecosystem processes is actually a variant of a much broader and important ecological question: What is the relationship between biodiversity and ecosystem functioning (Loreau et al. 2001)? Our understanding of the relationship between species richness and ecosystem function is incomplete, and this uncertainty is fueling an ongoing debate among ecologists (Kaiser 2000). One contention, call it the "complementarity hypothesis," is that niche differentiation results in unique resource use such that the loss of any species would reduce ecosystem functions (e.g., productivity, nutrient cycling, or resilience) or stability (e.g., cascading extinctions, ecosystem invasibility) (Chapin et al. 1998; Borrvall et al. 2000; Cottingham et al. 2001; Loreau et al. 2001; van Ruijven et al. 2003). An alternative view, call it the "redundancy hypothesis," is that species functions are substitutable. Therefore, a tenable conservation goal under this view would be to judiciously target an appropriate subset of species that provide for key ecosystem functions (see reviews by Schwartz et al. [2000] and Hector et al. [2001]). Yet a third perspective, call it the "facilitative hypothesis," is that the relationship between species diversity and function is an accelerating curve owing to the increased probability of positive species interactions that manifest as increasing marginal gains in functional response as richness increases (Cardinale et al. 2002).

The essence of the biodiversity–functionality debate can be captured with a simple conceptual graphic of three hypothetical curves (fig. 3.1). If

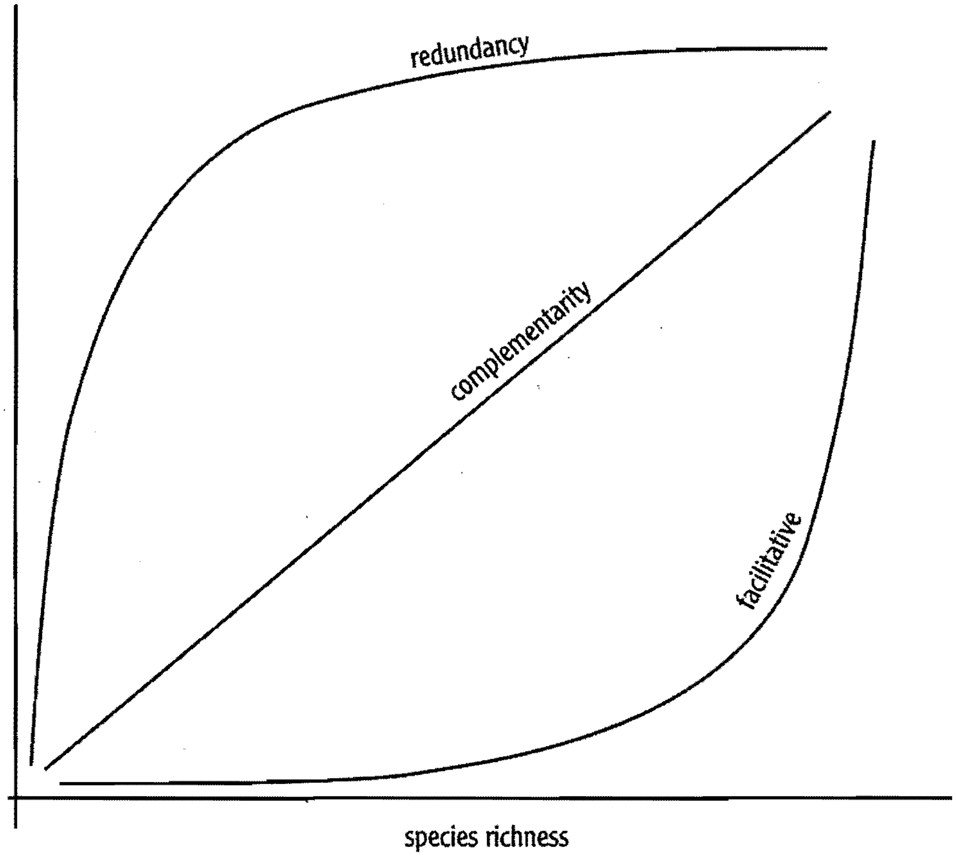

Figure 3.1. Three alternative perspectives on the relationship between biodiversity (species richness) and ecosystem functionality.

ecosystem function (however measured) has a positive linear relationship with species number then there is support for the complementarity hypothesis. If ecosystem function is approached asymptotically with increasing species number, reaching saturation at diversity levels below the full complement of species, then there is support for the redundancy hypothesis. Finally, if functionality is gained at an increasing rate as we move from species-poor to species-rich assemblages, then there is support for the facilitative hypothesis.

Although there appears to be an emerging consensus that ecosystem function is positively related to biodiversity in both terrestrial and aquatic systems (Covich et al. 2004; Balvanera et al. 2006), this qualitative pattern does not distinguish among the functional forms in figure 3.1. Schwartz et al.'s (2000) literature review found that, among observational studies, there was only weak evidence for complementarity, whereas experimental studies more commonly supported redundancy. Evidence in support of facilitative relationships is less common (Cardinale et al. 2002; but see Duarte 2000). Consequently, research results to date have not identified a generally accepted biodiversity–ecosystem relationship. For this reason, attempts to derive practical conservation implications from this research have been controversial and at times contentious, leaving the question unresolved as to what role rare species play in ecosystems.

A number of factors contribute to the ambiguous conservation implications stemming from diversity-function research. First, much of the research is short term and small scale, has focused on a limited set of ecosystem processes, has focused on the diversity–function relationship within a single trophic level, and has not adequately addressed whether diverse regional pools are critical to maintaining local species numbers (Hector et al. 2001; Duffy 2003; Thompson et al. 2005). Second, much of the experimental research has tested these relationships using ecologically unrealistic collections of individuals among species rather than attempting to mimic species-abundance distribution patterns typically observed in natural assemblages (Schwartz et al. 2000). Consequently, the applicability of these experimental findings to nonexperimental systems has been questioned (Symstad et al. 2003). Third, conclusions appear to vary depending upon the kind of ecosystem studied (e.g., forest, grassland, soil, freshwater) and the ecosystem property selected (e.g., primary productivity, nutrient cycling, invasibility) as the functional response variable (Rosenfeld 2002; Balvanera et al. 2006). Evidence in support of each of the three functional forms (fig. 3.1) has been observed within and among studies as the function metric is varied (Duarte 2000). Fourth, scale dependencies (i.e., local versus regional effects) appear to preclude unequivocal expectations for how ecosystem function may behave as species are gained or lost (Chase and Ryberg 2004). Finally, the effect of species on ecosystem function appears to vary depending on their commonness and rarity. For example, Smith and Knapp (2003) found that a threefold reduction in the diversity of rare species had no detectable effect on total above-ground net primary productivity, yet reductions in the abundance of dominant species resulted in immediate and negative impacts on productivity over both years of the study. Conversely, Lyons and Schwartz (2001) found that species assemblages where rare species were removed, reducing overall richness, were more prone to exotic species establishment than were plots where an equivalent biomass of common species was removed.

Given these contrasting results from these pioneering research efforts, a precautionary approach suggests that conserving the full complement of species would be wise until the relationships between biotic structure and ecosystem function are more clearly understood (Rosenfeld 2002; Lyons et al. 2005). Furthermore, ecosystem function is but one argument for the conservation of rare species. There are other, equally legitimate, arguments that derive from legal, ethical, aesthetic, and utilitarian values (see chaps. 9 and 10) that are independent of the functional importance of species (Chapin et al. 1998; Hector et al. 2001; Rosenfeld 2002). Because species abundances are distributed inequitably, and because those that are less abundant are more likely to be lost from regional or local assemblages than common species, a conservation focus on rare species to maintain biodiversity remains justified.

Definitions of Rare Species—How Do We Identify Them?

The concept of rarity has several definitions in common usage, but in the lexicon of conservation biology a species' rarity is most simply based on its distribution and abundance (Gaston 1994). According to Reveal (1981, 42) "rarity is merely the current status of an extant organism which . . . is restricted either in numbers or area to a level that is demonstrably less than the majority of other organisms of comparable taxonomic entities."

An important aspect of this definition is that rarity is a relative, rather than an absolute, concept. Species that are restricted in numbers or spatial occurrence are considered to be rare *relative* to the distribution and abundance of other species making up the pool of interest. Thus it is quite common to see rare species delineated based on some quantile of the frequency distribution of geographic range size, abundance, or both (Gaston 1994). For example, one may choose to define as rare that 10% of species with the lowest abundance estimates. The actual rarity cutpoint selected is a subjective decision, although Gaston (1994, 19) recommends using the 25th quantile because it is practical (for sampling reasons), and it is commonly used in the conservation literature. Such use of quantiles to delineate rare species is restricted to species that are taxonomically (e.g., plants, mammals, passerine birds) or ecologically (e.g., forest interior obligate, serpentine annuals) similar. It is difficult to conceive of how a general threshold of rarity could be applied to a group of species with dissimilar life histories.

One of the weaknesses of the quantile definition of rarity is that a species' status is defined based only on its rank abundance or distribution. Shifts in the species abundance distribution caused by natural or anthropogenic disturbance (e.g., Flather 1996) will not register as an increase or decrease in the number of rare species by the quantile definition. The quantile is a fixed proportion of the species pool, so while the identity of species constituting the "rare" set may change, the number of rare species remains unchanged (assuming a stable species pool size). One way to address this limitation is to define rarity using absolute criteria that focus on the occurrence (e.g., insect species recorded from ≤ 15 10 km survey quadrats from a possible 2862 [Hopkins et al. 2002]) or abundance (e.g., woody tropical plant density < 1 individual/ha [Hubbel and Foster 1986]) of species across some geographic area of interest (Schoener 1987).

Both the relative and the absolute definitions of rarity have been criticized for the lack of an objective ecological justification, and the decision of "where to draw the line" remains a difficult challenge (Magurran 2004, 70). One approach to reduce the arbitrariness of rarity definitions comes from the bioassessment and monitoring literature where reference sites or reference conditions are used to specify the species abundance (or occupancy) distribution expected for pristine or minimally disturbed systems (Reynoldson et al. 1997). Although the definition of rarity among reference sites is still characterized by an arbitrary cutoff, a rarity threshold so defined sets a standard against which to judge whether the degree of rarity is trending toward or away from that expected under the reference conditions.

Three additional issues related to the definition and identification of rare species warrant remark. First, rarity is conditioned on the geographic scale of interest. Certainly a species could be regarded as rare on a local scale (e.g., a management unit within a nature reserve or park), yet common at a regional or global scale. The effects of scale are not trivial since they can greatly affect the number of species that would qualify as rare (e.g., Butchart 2003). There is some evidence that commonness and rarity may be assessed more appropriately if focused on a core set of species within some geographic area of interest (Magurran and Henderson 2003)—removing from consideration those that can be recognized by some criteria as vagrants or other nontarget species.

Second, it should be recognized that the two criteria to judge rarity—geographic range and abundance—are not necessarily independent. One of the more notable macroecological patterns is a positive relationship between a species' range and its local abundance (Brown 1995). Consequently, species with broad geographic ranges tend also to be relatively abundant locally, whereas rare species face a kind of "double jeopardy" (Lawton 1993) whereby their narrow distributions also tend to be characterized by low local abundance. So, although it may be tempting to use distribution and abundance as independent axes to define categories of rarity, perhaps what their interrelationship suggests is that the sets of species identified as rare using a distribution or abundance criterion are likely to be very similar. This has important practical implications since the collection of presence–absence data to quantify species distributions may suffice (He and Gaston 2000) in defining the rare species set, saving the considerable expense associated with estimating species abundance.

Third, sampling artifacts are prevalent among rare species, making their identification as rare problematic (Gaston 1994, 26; McGill 2003). Rare species are often cryptic or furtive or have special life history strategies that can reduce detectability, leading ultimately to substantial underestimates of distribution or abundance if sampling is not done at the appropriate time or place as discussed further in chapters 4 and 5. These detectability issues can cause two kinds of error. Most obviously, underestimates of abundance or range can inflate the number of species considered to be rare. The literature has many examples of a species considered to be rare turning out to be much more abundant or widespread than originally thought (e.g., Espadaler and López-Soria 1991; NavarreteHeredia 1996). A less obvious error can occur when a rare species is not detected at all and is therefore omitted from the rarity list within an area of interest (Green and Young 1993; Venette et al. 2002).

Causes of Rarity

As we reviewed earlier, relatively uncommon species dominate most species assemblages—whether one samples pristine or perturbed systems (McGill 2003). For this reason, there is no ecological justification for treating rarity only as an acquired characteristic of species whose numbers or distributions have been eroded by anthropogenic activities. Rather, the number of rare species varies from place to place because of natural variation in species abundance distributions, or variation in levels of anthropogenic stress. Therefore, the causes of rarity can be lumped into two broad categories: (1) *natural* or *intrinsic* causes defined by a species' inherent biological or ecological characteristics; and (2) *anthropogenic* or *extrinsic* causes defined by harmful human activities that have resulted in limited distribution and abundance, independent of their biology (Pärtel et al. 2005). Although there is a tendency to discuss intrinsic causes of rarity as factors predisposing species to elevated extinction risk that is ultimately governed by human impacts (McKinney 1997), Pärtel et al. (2005) found little overlap between the group of vascular plant species considered intrinsically rare and the group thought to be extrinsically rare. Therefore, a separate discussion of intrinsic and extrinsic causes of rarity seems warranted.

Rarity as an Intrinsic Attribute of Species Assemblages

There is a long and well-known list of inherent biological and ecological attributes that are associated with rare species, and these attributes are often used to classify species into categories of rarity for regulatory or conservation planning purposes (see section on "Classifications of Rare Species and Conservation Priority"). Any assemblage of species is expected to have a relatively high number of species with limited abundances or restricted geographic ranges for no other reason than that the number of individuals and their pattern of occurrence follow a statistical distribution with greater frequencies toward the rare end of the scale. It is important that resource managers acknowledge rarity as an intrinsic property of a suite of species inhabiting any given locale.

Other natural factors that are associated with limited distribution or abundance can be further classified into species traits and ecosystem traits. *Species traits* include those factors affecting basic population vital rates such that species with "slow" life histories (e.g., low growth rates, small litter size, long generation time, few reproductive episodes in a lifetime) may be predisposed to extinction risk (McKinney 1997) and may also be disproportionately represented among species considered to be rare (Pilgrim et al. 2004). Related species traits that may also be associated with rarity include large area requirements, occupying higher trophic levels, complex social structure, high specialization (or low ecological amplitude), low vagility, and large body size (McKinney 1997; Purvis et al.

2000b). *Ecosystem traits* are characteristics of the environments inhabited by species. Some habitats have inherently low carrying capacities (Harper 1977), or suitable habitat may occur only rarely across the landscape (Pärtel et al. 2005), both of which will constrain the observed abundance or occurrence levels of species. Still other environments may be characterized by natural disturbance regimes that act to depress the abundance levels of some species (Boughton and Malvadkar 2002), increasing the likelihood that those species would fall below some defined rarity threshold. Certainly, species traits can interact with ecosystem traits to affect the expression of species rarity. Habitat specificity (species trait), availability of suitable habitat (ecosystem trait), and dispersal capability (species trait) will jointly affect the potential rarity of a species. For example, regional endemics typically have high specificity and are restricted to one or a few sites where their appropriate habitat occurs (Kruckeberg and Rabinowitz 1985).

A final intrinsic factor that may explain some of the variation in observed rarity rates is actually an emergent property of species that share a common taxonomy. Taxon size, or the number of species within a particular taxonomic level (e.g., family, genus), is thought to be a potentially important trait that presages the prevalence of rarity among a set of species. However, conclusions to date are equivocal, with plants and insects showing evidence that diverse taxa have more rare species than expected if rarity occurred randomly among a collection of species (Schwartz and Simberloff 2001; Ulrich 2005), whereas species-poor taxa have disproportionately high rarity among birds and mammals (Russell et al. 1998; Purvis et al. 2000a). An explanation for the observed divergence in the taxon-size effect is being debated, but it may be related to what Kelly (1996) termed the "cost of mutualism." Species whose life histories are linked inextricably, such that the fate of one is conditioned on the fate of the other, may constrain the mutualists to a rarer existence than those not linked in this way. It is noteworthy that such interspecific interactions are prominent among plants and insects. For example, plant species with specialized pollinators or seed dispersers that are declining, or butterflies dependent on endangered larval host plants, are especially vulnerable to these cascading effects (Pilgrim et al. 2004). Indeed, Koh et al. (2004) estimated that there may be as many as 6300 species that are "coendangered" through such symbiotic relationships.

Extrinsic Factors Resulting in Increased Rarity

Human alteration of the environment has become so pervasive that no ecosystem is free of the impacts that Vitousek et al. (1997) attributed to the "growing scale of the human enterprise." Caughley (1994) also observed that human factors are implicated in most post-Pleistocene extinctions. The principal human factors that reduce species abundance have been categorized in various ways—often with metaphorical reference to the "evil quartet" (Diamond 1989, 39) or the "mindless horseman of the environmental apocalypse" (Wilson 1992). Although the factors constituting these lists vary, the common denominators are human land transformations leading to habitat loss and degradation; biotic mixing stemming from the introduction of nonindigenous (exotic) species; direct human exploitation for control, subsistence, or collecting; and pollution through the alteration of biochemical cycles or the introduction of synthetic organic compounds.

Habitat loss and habitat degradation may rank as the most important factors leading to increased rarity—they are certainly the most cited factors contributing to the listing of species as threatened or endangered under the Endangered Species Act (ESA), and imperiled under NatureServe's classification (table 3.1). In the United States, agricultural conversion and its associated land management practices, land conversion for urban and commercial development, and water developments are the top three types of habitat alterations threatening species (Wilcove et al. 2000).

Table 3.1. *The percentage of species listed as threatened or endangered in the United States under the Endangered Species Act or ranked as imperiled under NatureServe's classification whose increased rarity was judged to be affected by five major factors (from Wilcove et al. 2000, 243)*

	Number of Species	Habitat Loss/ Degradation	Exotic Species	Pollution	Exploitation	Disease
		Percent of Species				
All species	1880	85	49	24	17	3
Vertebrates	494	92	47	46	27	11
Invertebrates	331	87	27	45	23	0
Plants	1055	81	57	7	10	1

Habitat loss and degradation also rank as the leading causes of mammal extinctions in Mexico (Ceballos and Navarro 1991), are implicated in 70% of the vertebrates considered to be imperiled in China (Li and Wilcove 2005), and in 84% of 488 endangered species in Canada (Venter et al. 2006).

After habitat loss and degradation, interactions with exotic species are considered the next most important cause of species imperilment in the United States (Flather et al. 1994; Wilcove et al. 2000). Exotic species affect nearly 50% of imperiled or federally listed species (see table 3.1), and are particularly harmful to the native biota inhabiting island systems (Simberloff 1995). Exotic organisms can contribute to the rarity of species through a number of mechanisms, including predation, pathogenesis, competition, hybridization, and alteration of disturbance regimes (Crooks 2002). For many rare species, the spread of exotic species can further reduce the odds of recovery. Such is the case with four species of endangered fish in the greatly altered lower Colorado River ecosystem, where predation by nonnative fish precludes their recruitment (Minckley et al. 2003). Declines in some mammal species in Mexico have been linked with the introduction of cats, pigs, goats, and rats (Ceballos and Navarro 1991). The accidental or intentional introduction of nonnative species is increasingly being recognized as contributing to the decline of species worldwide (Pimentel et al. 2000). However, the prevalence of exotic species introductions as a factor contributing to species rarity does vary greatly among studies. In an analysis of the global Red List of Threatened Species maintained by the International Union for the Conservation of Nature and Natural Resources (IUCN), Gurevitch and Padilla (2004) found that only 6% of imperiled taxa listed exotic species as either a direct or an indirect factor contributing to their decline, and Li and Wilcove (2005) found that the threat of alien species was cited in only 3% of imperiled Chinese vertebrates.

Pollution and human exploitation are the next most important factors listed as contributing factors to imperiled species in the United States. Some pesticides, such as DDT, were considered the primary cause of increased rarity among a number of bird species, but have now been banned in the United States. Unfortunately, some pesticides prohibited in the United States are still widely used in other countries, such as Mexico, and may be responsible in declines of insectivorous bats (Ceballos and Navarro 1991). Other forms of pollution, including siltation and agricultural amendments, continue to be an important cause of rarity, especially among aquatic species in the United States (Wilcove et al. 2000). The rapidity with which pollution agents can decimate species is well illustrated by recent population collapses among several Old World vultures across the Indian subcontinent—collapses that were ultimately traced to birds feeding on livestock carcasses treated with a common antiinflammatory drug (Green et al. 2004). Direct exploitation by humans is often highlighted as an important factor contributing to rarity. However, overexploitation is blamed for the listing of only 17% of threatened and endangered or imperiled species in the United States (see table 3.1). Even fewer species (7.6%) are on the global IUCN Red List because exploitation is considered an important factor in their population decline (Gurevitch and Padilla 2004). However, as is the case with most of these factors, the relative importance of exploitation does vary among taxa and locale. In Canada, overexploitation contributed to declines of 32% of endangered species (Venter et al. 2006); in Estonia, an estimated 31% of plants are threatened by collection (Pärtel et al. 2005); and overexploitation is cited as a contributing factor to increased rarity of 78% of imperiled Chinese vertebrates (Li and Wilcove 2005).

Management Implications

Understanding the causes of rarity is fundamental to developing strategies to reduce extinction threats associated with species rarity. Indeed, the particular causes of rarity may dictate the suite of management approaches that will be most successful in species recovery efforts (see chap. 8). Moreover, if the likelihood of success is a criterion used to set conservation priorities (see Mace and Lande 1991), then an understanding of rarity could also help identify which species are most likely to respond to management efforts.

For instance, species that are naturally rare, and those that have been so over evolutionarily significant periods of time, may have life history characteristics adapted to their rarity. Species that are intrinsically rare may not warrant management directed at intensive "population recovery" efforts, for there may be very little practical opportunity for accomplishing such a conservation objective. For these species, extensive efforts to protect their habitat (see "Locations of Target Species at Risk" in chap. 6)

Table 3.2. *Conservation priorities based on population trajectories and causes of species rarity*

Population Trajectory	Cause of Rarity: Intrinsic (natural)	Cause of Rarity: Extrinsic (anthropogenic)
Increasing	No immediate conservation concern	Population recovering, conservation priority conditioned on deviation from historical occupancy or abundance
Stable	No immediate conservation concern	Population maintaining, conservation priority conditioned on deviation from historical occupancy or abundance
Decreasing	High conservation priority but prospects for recovery may be limited	High conservation priority but prospects for recovery may be great

may be sufficient to ensure their persistence. Certainly the "double jeopardy" (Lawton 1993) associated with small populations and restricted distributions makes extinction risk a concern for naturally rare species, but it may be that conservation priorities can only be set after considering extrinsic factors that may be further eroding the population or distribution of intrinsically rare species (table 3.2).

Conversely, species that have become rare rather recently due to human land transformation activities or direct exploitation may not have life history characteristics that are adapted to low numbers and may actually be more threatened with extinction than intrinsically rare species. However, extrinsically rare species may, paradoxically, be more responsive to management actions designed to ameliorating the anthropogenic threats (see table 3.2; see also Barrett and Kohn 1991; Gaston and Kunin 1997). Among the rare flora of Estonia, Pärtel et al. (2005) estimated that nearly 50% (of 301 species) would benefit if land management on grassland, agriculture, and forestry lands shifted from intensive to more traditional extensive land management (see "Maintaining Disturbance Regimes" in chap. 7). An additional 18% of species threatened by collecting would benefit from upgrading legal regulations and public education. Such examples provide hope that rare species with declining population trajectories driven largely by extrinsic factors have high prospects for recovery if shifts in public values are sufficiently strong to alter our resource management behavior and the way we derive goods and services from ecosystems (see chaps. 9 and 10).

Rarity and Threat

Species considered threatened with extinction will more than likely also be considered rare. The converse is not necessarily true. A species may qualify as rare but may not be considered at risk of extinction (Gaston 1994). This may seem to contradict an earlier statement that rare species are more likely to become extinct than common species. However, we are not comparing rare with common species here. Rather, if we restrict our comparison to those species determined to be rare, not all will share the same probability of persistence—which is to say that the risk of extinction will vary. Consequently, one element considered in establishing conservation priorities is to focus on the subset of rare species that are under the greatest threat or most vulnerable to extinction (Mace and Lande 1991).

One of the early reviews of the concept of threat was completed by Munton (1987) and many of the criteria for evaluating threat are the same criteria that have been used to define rarity—a confounding of terminology that is common in the literature. However, Munton's (1987) review highlights the role of population dynamics in evaluating threat. Rare species that have been, in the recent past, declining in abundance or occupancy are more threatened than rare species with stable or increasing trends. Furthermore, the degree of threat assigned to a species can also be affected by the predicted trends in distribution or abundance in response to various human impacts. These early, sometimes characterized as subjective, efforts to evaluate threat based on population dynamics actually foreshadowed the emergence of population viability analysis as a standard approach to persistence probability estimation (Boyce 1992). Unfortunately, the substantial data requirements for formal viability assessments will limit the number of species for which a viability-based threat assessment can be completed (see "Conservation of Individual Species Based on the Concepts of Population Viability" in chap. 6). However, there is emerging evidence that categorizations of threat can be predicted using a combination of intrinsic life history traits and estimated population variances from temporal monitoring programs—a much more limited and feasible set of data requirements when compared to a typical population viability analysis. Fagan et al. (2001) were able to rate the vulnerability of more than 750 species into three broad extinction threat categories. They were also able to show for mammals that body size, age at first reproduction, and average number of offspring correctly predicted the extinction threat category for 83% (60 of 72) of species.

Until further research can verify whether the "shortcut" approach examined by Fagan et al. (2001) has broad applicability, uncertainty (i.e., data-poor species) will continue to plague efforts to evaluate threats to rare species. Obviously, uncertainty affects which species can be evaluated, but it can also affect how we assign species into certain threat categories. Under the precautionary principle, conservationists often pursue a risk-averse strategy such that species may be placed in a higher threat category, or at least placed in a category that acknowledges the uncertainty (e.g., suspected threatened), to guard against treating a species as relatively secure when it is in fact at risk. Given the lack of knowledge about the status of species in most taxonomic groups, this strategy has the potential to designate a large number of species as threatened with extinction due to their "little known" status (Mace 1994; and see chap. 4). The risk-averse strategy for judging extinction threat is a double-edged sword. On the one hand it guards against an undesirable and irreversible outcome—species extinction (Prato 2005). On the other hand, inaccuracies in judging threats may erode public support for biodiversity conservation (Roberts and Kitchener 2006).

Classifications of Rare Species and Conservation Priority

A number of strategies have been proposed to classify the members of an assemblage into rarity categories. Perhaps the best known classification strategy for rare species is Rabinowitz's (1981; Rabinowitz et al. 1986). Her classification is based on three attributes: geographic range (wide, narrow), local abundance (somewhere large, everywhere small), and habitat specificity (broad, restricted). This leads to eight classes: one abundant class, where a species has a wide geographic range, is abundant in some places, and has broad habitat requirements; and seven different forms of rarity.

A number of classification strategies have been proposed to assign conservation priorities to rare species. We reviewed a subset of strategies used by nongovernmental organizations and various countries in an attempt to identify factors used in assigning conservation priorities (table 3.3). Our intent in selecting the strategies we reviewed was not to be comprehensive,

Table 3.3. *Examples of strategies and ecological attributes used in assigning species to rarity and conservation priority classes*

Ecological Attribute Strategy	Range/ Distribution	Distribution Trend	Occupancy (area or pattern of occurrence)	Abundance	Abundance Trend	Ecological Specialization	Reproductive Potential	Taxonomic Distinctiveness	Fragility	Habitat Condition/ Protection	Threat	Population Viability
Rabinowitz (1981)	X		X	X		X						
Millsap et al. (1990)	X	X	X	X	X	X	X	X			X	
Burke and Humphrey (1987)	X		X	X		X						
Ceballos and Navarro (1991)	X		X				X				X	
Partners in Flight (Hunter et al. 1993; Dunn et al. 1999)	X		X	X	X						X	
Cofré and Marquet (1999)	X		X	X		X	X	X	X		X	
Pärtel et al. (2005)	X		X	X		X				X	X	
Master et al. (2000) NatureServe (2006)	X	X	X	X	X			X	X	X	X	
IUCN (2001, 2005)	X	X	X	X	X					X	X	X
Canada's Species at Risk Act (Irvine et al. 2005)	X			X	X						X	X
Australia's EPBC Regulations 2000 (OLD 2004)	X	X		X	X							
Mexico's SEMARNAP (2002)	X			X	X					X	X	
U.S.'s ESA (Fish and Wildlife Service) *	X			X				X		X	X	

*Criteria associated with determination of threatened and endangered species under the Endanagered Species Act (PL-205, 87 Stat, 884, as amanded).

but rather to demonstrate how different factors contributing to rarity are incorporated in various classification schemes for assigning conservation priorities to rare species. The majority of the classification strategies we reviewed used measures of distribution and abundance to identify rare species, then assigned them into conservation priority classes. This pattern was expected given that distribution and abundance are fundamental to discussions of rarity. Trend information in either abundance or distribution was used in many classification strategies to help identify species that may not currently qualify as rare but may be on a trajectory toward rarity in the future. The pattern of spatial occurrence was used in over half of the classifications reviewed as a means of capturing the fine-scaled pattern of landscape occupancy. The spatial occurrence pattern differs from species distribution in that it considers whether a population occurs somewhat ubiquitously or patchily throughout its geographic range, and can reflect whether a species is a habitat specialist.

In addition to geographic range, abundance, and habitat specialization, other ecological attributes may be considered in assigning conservation priorities to rare species. Intrinsic, or natural, attributes that can place species at higher risk include a low reproductive potential (Millsap et al. 1990; Ceballos and Navarro 1991), taxonomic distinctiveness (Millsap et al. 1990; Cofré and Marquet 1999), and fragility, or a species' sensitivity to perturbations or intrusions of its biological or physical environment (Master et al. 2000). Extrinsic factors, including habitat condition and amount of habitat occurring in protected areas (Pärtel et al. 2005), as well as other anthropogenic threats to the species are considered in nearly all of the strategies we reviewed to assign conservation priorities to rare species. Only two strategies use an assessment of population viability, which incorporates both intrinsic and extrinsic factors in an attempt to estimate extinction probability. Population viability is a function of population size, number, and condition of occurrences and trends in these factors, as well as threats and landscape connectivity (Master et al. 2000).

The strategies we reviewed differ in the classes (or rankings) of rare species. NatureServe (2006) assigns global (G), national (N), and state (S) level ranks that define the spatial scale over which relative imperilment is assessed. This geographic identifier is followed by a whole number between 1 and 5 to indicate the conservation status of plants, animals, and communities (Master et al. 2000; NatureServe 2006). The numbers are defined as 1, critically imperiled; 2, imperiled; 3, vulnerable to extirpation or extinction; 4, apparently secure; and 5, demonstrably widespread, abundant, and secure. A species that is critically imperiled on a rangewide basis would be ranked as G1, whereas a species ranked as S1 would be critically imperiled in a particular state, regardless of its status elsewhere. Criteria used in ranking species include (1) total number and condition of occurrences, (2) population size, (3) range extent and area of occupancy, (4) short- and long-term trends in the foregoing factors, (5) threats, (6) fragility, and (7) number of adequately protected populations (Master et al. 2000).

The IUCN Red List of Threatened Species is based on risk of extinction criteria (IUCN 2001, 2005). The main criteria used in assessing extinction risk include (1) population size, (2) geographic range (both extent of occurrence and area of occupancy), and (3) population size trajectory. However, concepts of threat are also recognized within these criteria, including degraded habitat quality, levels of exploitation, and the effects of introduced taxa, hybridization, pathogens, pollutants, competitors, or parasites (IUCN 2001). Further, the Red List criteria have procedures for recognizing and dealing with three types of uncertainty: natural variability, semantic uncertainty, and measurement error (Akçakaya and Ferson 2001). The recommended approach is precautionary as opposed to evidentiary and provides plausible ranges of parameters used to evaluate the criteria (IUCN 2001).

Canada, Australia, and Mexico use IUCN criteria as a basis for their national strategies for assigning conservation priorities to rare species. Canada's recently passed Species at Risk Act recognizes "endangered species" as "wildlife species facing imminent extirpation or extinction" and "threatened species" as "a wildlife species that is likely to become an endangered species if nothing is done to reverse the factors leading to its extirpation or extinction" (Irvine et al. 2005). Criteria for designating a species as endangered include (1) a declining population size; (2) a small distribution with declining or fluctuating abundance; (3) a small, declining population size; (4) a very small population size; or (5) a probability of extinction in the wild > 20% in 20 years or five generations, whichever is longer (Irvine et al. 2005).

Australia recognizes "critically endangered," "endangered," and "vulnerable" species based on the total number of mature individuals, the degree to which populations of a species have become reduced, the estimated rate at which the number of individuals will continue to decline, the degree to which its geographic distribution is precarious for its survival and how restricted the distribution is, and the probability of the species' extinction in the wild (Office of Legislative Drafting 2004).

Mexico recognizes species that are in danger of becoming extinct, threatened species, and species subject to special protection (SEMARNAP 2002). Species classified as in danger of becoming extinct are characterized by drastic recent reductions in their distribution or population sizes, which have reduced their viability due to factors such as destruction or modification of their habitat, overuse, or diseases. Threatened species are in danger of becoming extinct if factors that negatively affect their population viability by diminishing their population size or destroying their habitat are not addressed. Species subject to special protection are in danger of becoming threatened by factors affecting their population viability and for which special recovery actions are needed to restore their populations, habitat, or associated species necessary for their recovery.

In contrast to strategies based on the IUCN criteria, the U.S. Fish and Wildlife Service identifies "endangered" or "threatened" species for protection under the ESA. "Endangered" refers to a species "in danger of extinction throughout all or a significant portion of its range," and a "threatened" species is "likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range" (Endangered Species Act, 16 U.S.C. §§ 1531-36, 1538-40, Sec. 3(6) and Sec. 3(20)). Criteria used to classify species into these rarity categories include (1) present or threatened destruction, modification, or curtailment of its habitat or range; (2) overutilization for commercial, recreational, scientific, or education purposes; (3) disease or predation; (4) inadequacy of existing regulatory mechanisms; or (5) other natural or human-made factors affecting its continued existence.

Our intent in reviewing these classification strategies was to provide an overview of the kinds of ecological attributes that are considered in assigning species to rarity categories. We have resisted evaluating which of these strategies, by some standard, is "the best" for conserving rare species for a number of reasons. First, the selection of an existing classification strategy, or the decision to develop a new strategy, will depend on the resource manager's conservation objectives (see chap. 2). Moreover, the conservation strategies we review in table 3.3 vary in their data requirements, with some focusing primarily on current distributional characteristics (e.g., Ceballos and Navarro 1991), and others requiring distributional and abundance trend data, or data on demographic rates (e.g., Millsap et al. 1990).

The kinds of data available will certainly affect resource managers' decisions about which classification strategy to implement.

Such considerations notwithstanding, others have evaluated the relative strengths and weaknesses of rarity classification systems. De Grammont and Cuarón (2006) reviewed 25 systems used in North America to categorize threatened species. Based on 15 characteristics that relate to risk categories, criteria, and other system characteristics, they ranked the IUCN (2001) system as having the highest number of desirable characteristics. In particular, the IUCN (2001) system was superior in that it clearly defines categories and criteria, was the only system that considers uncertainty in the assessment, and was applicable at both national and regional levels (de Grammont and Cuarón 2006). Their recommendations for improving the IUCN (2001) assessment approach focused on defining locations quantitatively and removing subjective words such as "typically." Rodrigues et al. (2006) also found the IUCN (2001) assessment protocols to be useful and noted the need for compiling point locality data that will be useful in both identifying priority sites for conservation and rapidly updating species conservation assessments in the future. Other authors (e.g., Eaton et al. 2005) have concurred on the need to remove subjectivity in IUCN (2001) protocols, especially in regard to the persistence potential of species whose status is secure in other regions. Although varying objectives and data availability will affect the choice of which rarity classification schemes can be used, perhaps what these evaluation efforts offer is a rigorously defined goal that resource managers can strive to meet with incremental inventory improvements over time (see chap. 5).

Conclusion

Rarity in natural systems is common. In any given species assemblage, most species will be relatively rare, whereas only a few will be common. Rarity is most often defined by two attributes: a species' distribution and its abundance. Species are considered rare if their area of occupancy or their numbers are small when compared to the other species that are taxonomically or ecologically comparable. Conservation science is concerned with how natural or human-caused changes to ecosystems affect both the number of species considered to be rare, and the population trends of species that are rare. Because species abundances are distributed inequitably, and because those that are less abundant are more likely to be lost from regional or local assemblages than common species, a conservation focus on rare species in order to maintain biodiversity appears justified.

However, given that species might be naturally rare and not considered at risk of extinction, conservation science must also consider the immediacy of the threats to species in order to identify those rare species that have the greatest likelihood of being lost. A number of strategies for classifying rare species have been proposed, with most using information on the current status or trends in the distribution and abundance of a species either to determine if a species qualifies as rare or to categorize the species into a rarity type. Conserving rare species should focus on factors that have resulted in increased rarity: habitat loss and degradation, introduction or invasion of exotic species, pollution, and direct human exploitation. Species that have become rare recently due to extrinsic human activities may not have life history characteristics that are adapted to low numbers and may actually be more threatened with extinction than intrinsically rare species but may also be more responsive to management actions that address the anthropogenic threats.

Although rarity is common among taxonomic groups that are well studied, our current understanding of rarity may in fact be biased. Much of the world's biodiversity remains poorly studied and our ignorance about the full complement of species inhabiting a given locale limits our ability to quantify "who is" and "who is not" rare and this impedes our ability to assess potential impacts of resource management activities on RLK species. This leads to what Molina and Marcot call the "conundrum" of little-known species, the implications of which are the subject of the next chapter.

Acknowledgments

We would like to thank Tom Sisk (Northern Arizona University) for providing some very constructive and insightful comments that improved our presentation of species rarity issues. Suzy Stephens (Rocky Mountain Research Station) is also acknowledged for her electronic graphics support.

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