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Review

Geography and Recovery under the U.S. Endangered Species Act

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Abstract: *The U.S. Endangered Species Act (ESA) defines an endangered species as one "at risk of extinction throughout all or a significant portion of its range." The prevailing interpretation of this phrase, which focuses exclusively on the overall viability of listed species without regard to their geographic distribution, has led to development of listing and recovery criteria with fundamental conceptual, legal, and practical shortcomings. The ESA's concept of endangerment is broader than the biological concept of extinction risk in that the "esthetic, ecological, educational, historical, recreational, and scientific" values provided by species are not necessarily furthered by a species mere existence, but rather by a species presence across much of its former range. The concept of "significant portion of range" thus implies an additional geographic component to recovery that may enhance viability, but also offers independent benefits that Congress intended the act to achieve. Although the ESA differs from other major endangered-species protection laws because it acknowledges the distinct contribution of geography to recovery, it resembles the "representation, resiliency, and redundancy" conservation-planning framework commonly referenced in recovery plans. To address representation, listing and recovery standards should consider not only what proportion of its former range a species inhabits, but the types of habitats a species occupies and the ecological role it plays there. Recovery planning for formerly widely distributed species (e.g., the gray wolf [Canis lupus]) exemplifies how the geographic component implicit in the ESA's definition of endangerment should be considered in determining recovery goals through identification of ecologically significant types or niche variation within the extent of listed species, subspecies, or "distinct population segments." By linking listing and recovery standards to niche and ecosystem concepts, the concept of ecologically significant type offers a scientific framework that promotes more coherent dialogue concerning the societal decisions surrounding recovery of endangered species.*

Keywords: *Canis lupus*, ecosystem protection, endangered species, geographic distribution, gray wolf, population viability, representation

Geografía y Recuperación Bajo el Acta de Especies en Peligro de E. U. A.

Resumen: *El Acta de Especies en Peligro de E. U. A. (AEP) define una especie en peligro como una "en riesgo de extinción en todo, o una porción significativa de, su rango de distribución." La interpretación prevalente de esta clausula, centrada exclusivamente en la viabilidad de especies enlistadas sin considerar su distribución geográfica, ha llevado al desarrollo de criterios de enlistado y recuperación con deficiencias conceptuales, legales y prácticas. El concepto "en peligro" de AEP es más amplio que el concepto de riesgo de extinción biológica ya que los valores "estéticos, ecológicos, educativos, históricos, recreativos y científicos" conferidos*

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a las especies no son fortalecidos necesariamente por la mera existencia de las especies, sino por la presencia de una especie en la mayor parte de su distribución previa. Por lo tanto, el concepto de "porción significativa de su rango" implica un componente geográfico adicional para la recuperación que puede incrementar la viabilidad. Aunque el AEP difiere de otras leyes para la protección de especies porque reconoce que la geografía contribuye a la recuperación, se parece a la "representación, resiliencia y redundancia" del marco de referencia de la planificación de la conservación referido comúnmente en los planes de recuperación. Para abordar la representación, los estándares para el enlistado y la recuperación no solo deben considerar la proporción del rango previo ocupado por una especie sino también los tipos de hábitat que ocupa una especie y el papel ecológico que desempeña. La planificación de la recuperación de especies de amplia distribución previa (e.g., el lobo gris [Canis lupus]) ejemplifica la manera en que se debe considerar el componente geográfico implícito en la definición de "en peligro" del AEA para la determinación de metas de recuperación mediante la identificación tipos ecológicamente significativos o variación de nicho en la distribución de especies, subespecies o "segmentos distinguibles de la población" enlistados. Al vincular los estándares de enlistado y recuperación con los conceptos de nicho y ecosistema, el concepto de tipo ecológicamente significativo ofrece un marco de referencia científico que promueve un diálogo más coherente en relación con las decisiones concernientes a la recuperación de especies en peligro.

Palabras Clave: *Canis lupus*, distribución geográfica, especies amenazadas, lobo gris, protección de ecosistemas, representación, viabilidad poblacional

Introduction

Two recent decisions to remove species from the U.S. Endangered Species Act's (ESA) list of threatened and endangered species—one celebrated and the other a subject of controversy and litigation—raise important questions about the significance of species geographic distribution in legal efforts to conserve biodiversity. In 2007, the U.S. Fish and Wildlife Service (FWS) removed the Bald Eagle (*Haliaeetus leucocephalus*) in the contiguous United States from ESA's threatened list to wide acclaim, after populations had been restored in five regional recovery areas covering virtually all of the birds' historic range (FWS 2007). In contrast, gray wolves (*Canis lupus*) were declared recovered in 2009 in all or parts of five western states despite the species continued absence from the majority of its former range in these states (FWS 2009). The 2009 rule replaced a previously proposed rule that would have declared the species recovered in three additional states from which it was entirely absent (FWS 2003). This contrast in the geographic scope of recovery efforts for Bald Eagles and wolves highlights legal and biological inconsistencies in management of endangered species that can only be resolved by proper consideration of geography in listing and recovery actions.

The effectiveness of laws aimed at conserving biological diversity depends to a significant extent on creation and implementation of effective standards for deciding when to apply—and when to remove—legal protections for species or other listed entities. Under the ESA, such standards guide both listing decisions and development of recovery criteria used for guiding conservation actions and making delisting determinations. Recent court decisions and scientific publications have criticized what these sources portray as the arbitrary nature of standards that form the basis of both listing and recovery determinations under the statute (Greenwald et al. 2006). In particular, recent interpretations of listing and recovery standards focused only on listed species overall viability without regard to their geographic distribution present fundamental conceptual, legal, and practical shortcomings. The ESA's definition of an endangered species is the source of the act's recognition of the geographic element of listing and recovery. Congress intended the ESA's concept of endangerment to be broader than the biological concept of extinction risk and to encompass human-centered and ecological goals that are furthered by a species presence across much of its former range. In this review, we demonstrate that use of a geographic representation component in listing and recovery standards is not only sound conservation policy, but also implicit in the language of the act, and we clarify how such a standard could be implemented.

Statutory Background

Although the third in a series of laws aimed at protecting and recovering imperiled species, the ESA of 1973 was the first to recognize that endangerment has a geographic component by extending legal protections to species facing conservation problems in only a portion of their range. The ESA provides legal protections only to species—a term legally defined to include species, subspecies, and "distinct population segments" (DPS) of vertebrates—listed as "threatened" or "endangered" under a prescribed legal process. The law, however, is not a model of clarity in how it defines key thresholds, for example, the line separating endangered species from threatened species and the line dividing listed species from those deemed recovered and thus removed from

Table 1. Viability and geographic criteria contained in major national and international endangered-species protection legislation and protocols referenced in this paper.*

Framework	*Date*	*Region*	*Viability component*	*Geographic component*
Endangered Species Act	1973	United States	in danger of extinction	significant portion of range
Environment Protection and Biodiversity Conservation Act	1999	Australia	at risk of extinction in the wild	geographic distribution is precarious for the survival of the species
Species at Risk Act	2000	Canada	facing imminent extirpation or extinction	small extent of occurrence or area of occupancy
"Three R" framework (Shaffer & Stein 2000)	2000	Global	resiliency, redundancy	representation
IUCN Red List criteria (IUCN 2001)	2001	Global	population size and trend	area of occupancy, extent of occurrence
NatureServe vulnerability criteria (Faber-Langendoen et al. 2009)	2009	Global	population size, number of occurrences	area of occupancy, range extent

**Some protocols contain additional criteria not listed in this table.*

the lists of threatened and endangered species. The ESA defines *endangered species* as any species "at risk of extinction throughout all or a significant portion of its range" (16 U.S.C. §1532(3.6)) and *threatened species* as those likely to become endangered in the "foreseeable future" (16 U.S.C. §1532(20)). Clearly, these definitions encompass species facing ongoing threats to their viability. Although the phrase "significant portion of its range" (SPOR) indicates that a species geographic distribution is relevant to whether it is threatened or endangered, the precise role geography plays in ESA listing and recovery determinations is less apparent.

The ESA allows for designating listed "species" (DPS) below the biological species level in order to protect and conserve species before large-scale declines occur that would necessitate listing a species or subspecies throughout its entire range (Fay & Nammach 1996). Canada's Species at Risk Act (SARA) contains similar provisions that allow listing of designable units on the basis of evolutionary significance and discreteness, including unique ecological setting (Hutchings & Festa-Bianchet 2009). Nonetheless, SARA, like the precursors of the ESA of 1973 (the U.S. Endangered Species Preservation Act of 1966 and Endangered Species Conservation Act of 1969), lacks any reference to SPOR and defines a listed "species" as endangered only if it faces "imminent extirpation or extinction'' throughout its entire range (Table 1). Thus, Hutchings and Festa-Bianchet (2009) conclude that "this difference in definitions makes it more likely that a species will be assigned a threatened status in the US than in Canada." The ability to designate listed units below the species level thus is but one facet of the ESA of 1973's requirement that geography be considered in listing and recovery, and this ability does not obviate the need for consideration of the significance of portions of the range of these listed units.

Prior to 2000, the federal agencies responsible for administering the ESA (U.S. Fish and Wildlife Service and National Marine Fisheries Service [Services]) took the position that a "species" (species, subspecies, or DPS) could only be listed as endangered or threatened throughout its entire range or not at all and found SPOR relevant only in assessing whether a species vulnerable status within a significant portion of its geographic range imperiled the species as a whole. After 2000 the Services began applying a different approach, which was formalized in 2007 when the Department of Interior solicitor issued a legal opinion concluding that a species facing extinction within a SPOR could be listed as threatened or endangered within that geographical area alone, meaning that the more secure populations of the species occurring outside the area would not receive protection under the ESA (USDI 2007).

In the same opinion, the solicitor asserted that the term *range* refers to a species current range rather than its historic range, reasoning that the statutory definition of *endangered species* refers to places where a species is in danger of extinction, not where it is already extinct. Finally, the solicitor deemed that a portion of a species current range could be designated significant for reasons other than mere size, such as if the area is biologically important to the species or if "the various values listed in the Act. . .would be impaired or lost if the species were to become extinct in either that portion of the current range or in the current range as a whole" (USDI 2007). The 2007 solicitor's opinion thus recognizes SPOR as a freestanding basis for listing and recovery and recognizes the human-centered values recounted by Congress in the act's first section as criteria for determining significance (USDI 2007).

Although the solicitor's opinion supports increased consideration of geography in listing and recovery actions, it is legally and biologically problematic in at least two aspects: the definition of *range* as including only a species current range and the ability to limit the boundaries of listed species to only the most threatened portions of current range (Enzler & Bruskotter 2009; Greenwald 2009). The latter strategy is inconsistent with the statute's requirement that only species, subspecies, or DPS are listable entities (16 U.S.C. §1532 (16)) and biologically problematic because protection of a larger biologically defined unit (e.g., a metapopulation) may be necessary to sustain threatened subpopulations (Gilpin 1987). This strategy might also be expected to decrease coordination of management strategies between neighboring jurisdictions and thus accentuate risks from inadequate regulatory mechanisms, one of the ESA's five threat factors (16 U.S.C. §1533 (A)(1)(D)).

In contrast to the museum-piece approach to biodiversity policy exemplified by the solicitor's opinion, other authors have drawn on the ESA's language and legislative history to propose that, because a recovered species is one that no longer qualifies as threatened (16 U.S.C. §1533(4)(g)), it must at that point securely occupy all but an insignificant portion of its range (Vucetich et al. 2006). Such a strategy acknowledges the importance of conserving populations and the variation among them (Ceballos & Ehrlich 2002). Vucetich et al. (2006) primarily considered the quantitative dimension of SPOR by showing how the ESA requires a recovered species to occupy some minimum proportion of its former range. This proportion necessarily varies by species because the unique status of a given species must be considered in deciding what constitutes a significant portion of historic range (*Defenders of Wildlife v. Norton*, 258 F.3d 1136, 9th Cir. 2001). Here, we show how the concept of SPOR also has a qualitative dimension that involves the types of habitat a species occupies and the ecological role it plays in those areas. Taking into account both the qualitative and quantitative dimensions of SPOR results in a better understanding of the ESA's mandate to "protect species and ecosystems upon which they depend" and resolves inherent conceptual and practical problems in the current approach, including the solicitor's opinion, by establishing a clear relationship between geographic distribution and the legal notion of endangerment and recovery.

Interpretation and Application of the ESA's Definition of *Range*

Controversy over interpretation of the ESA's phrase *significant portion of its range* first arose in the context of a dispute over whether flat-tailed horned lizards (*Phrynosoma mcallii)* should be listed as threatened or endangered. Although the Ninth Circuit Court of Appeals found the language of the statute "puzzling" and "inherently ambiguous," it rejected FWS' position that it would examine the status of a species in significant portions of its range only as part of an assessment as to whether the entire species was threatened or endangered. The court instead concluded that "a species can be extinct 'throughout . . . a significant portion of its range' if there are major geographical areas in which it is no longer viable but once was" (*Defenders of Wildlife v. Norton*, 258 F.3d 1136, 9th Cir. 2001 [p. 1145]). The court's decision was a key factor in convincing the Department of Interior solicitor to reverse the Services' previous legal interpretation of SPOR and conclude that the agency in fact has the authority to list or delist a species in only a SPOR, as opposed to throughout its entire range. The solicitor's interpretation of the term *range* as referring only to species often much-reduced current range effectively decoupled ESA listing decisions from any meaningful consideration of the species historic geographic distribution. Even more problematically, the Services have applied this definition of range to determine what constitutes recovery, allowing the agencies to declare success in restoring a listed species—and hence to remove it from the ESA's protected rolls—even though the species may inhabit only a relatively small fraction of its historic geographic range.

Several problems arise from defining recovery primarily by reference to species diminished range at the time they were listed as threatened or endangered. This interpretation ignores the biological justifications for consideration of spatial population dynamics in population viability analysis (Gilpin 1987). Because few species can be recovered without significantly increasing population size accompanied by expansion into suitable but unoccupied habitat, the ESA specifies that critical habitat for a threatened or endangered species may include "areas outside the geographical area occupied by the species at the time it is listed"(16 U.S.C. §1532 (3.5)(A)(ii)). The solicitor's interpretation results in inconsistent ad hoc determinations of significance (Enzler & Bruskotter 2009; Greenwald 2009). It provides a perverse incentive for destruction of habitat and individuals to ensure that little current range exists. It is inconsistent with successful recovery programs focused on species that at one time had no current range outside of captivity (e.g., Mexican wolf [*Canis lupus baileyi*], red wolf [*Canis rufus*], California Condor [*Gymnogyps californianus*], black-footed ferret [*Mustela nigripes*]). It fails to recognize that conditions within species current ranges may have so deteriorated as to effectively prevent full recovery there, thus requiring recovery efforts to also focus on conservation opportunities elsewhere within a species historic range or, in light of ongoing or probable habitat shifts due to climate change, in areas beyond a species historic distribution (McLachlan et al. 2007). Lastly, it stands at odds with Section 3(3) of the ESA, which unambiguously recognizes "transplantation" of individuals as a valid conservation tool.

On the other hand, taking *range* to mean simply historic range can itself raise questions such as what period in history, or what if historic range cannot be restored? We therefore propose that *range*, in the context of SPOR's application to defining species listing and recovery, means historic range that would provide suitable habitat if application of what the ESA defines as "conservation" measures removed or mitigated the threat factors that led to the listing of a species as threatened or endangered. This definition provides more-precise biological and legal elements of the definition of range, fulfills the restorative mandate of the ESA, and removes perverse incentives to destroy habitat provided by the interpretation in the solicitor's opinion. This interpretation of range also has a legally sensible relationship to several other aspects of the ESA in that (1) removal and mitigation of threat factors is an important ESA process, (2) threat factors are central aspects of listing and delisting decisions, and (3) this interpretation of range corresponds to objective and measurable recovery criteria. The objective, measurable nature of this meaning of *range* is exemplified by recent models that quantify habitat quality for endangered species in terms of the level of threat factors as they currently exist on the landscape or would exist given mitigation and restoration efforts (Carroll et al. 2006). The comparison of the extent of currently suitable habitat with that of potential habitat given mitigation of threat factors distinguishes this approach from that applied by the Services in recent delisting actions (FWS 2009). These modeling techniques also may be used to identify opportunities for extending a species range if necessary in light of ongoing or likely alterations of habitat conditions caused by climate change.

Representation, Resiliency, and Redundancy

In assessing whether a particular geographic area is a significant portion of a species range for listing and recovery determinations, FWS has frequently invoked the "three R" framework of Shaffer and Stein (2000) (see Supporting Information for 38 listing or recovery rules involving the 3-R framework). In essence, the 3-R framework states that, to be considered recovered, a species should be present in many large populations arrayed across a range of ecological contexts (Shaffer & Stein 2000). The 3-R framework's frequent citation by the Services and other conservation-planning practitioners suggests that it qualifies as an example of the "best scientific…data available," which the ESA mandates should inform listing and delisting decisions (16 U.S.C. §1533(b)(1)(A)). The 3-R framework parallels the ESA in that it links the concepts of geography and viability by combining protection of representative examples of ecosystem types or species populations with two additional factors typically associated with population viability. First, resiliency may be associated with factors such as population size that describe a single subpopulation (Shaffer & Stein 2000). Second, redundancy of such subpopulations in a metapopulation enhances viability through the spreading of risk (Den Boer 1968). Conservation planners have frequently proposed representation as an important complement to viability-related goals because it allows consideration of biological diversity at multiple scales (e.g., populations, ecotypes, and species) (Shaffer & Stein 2000).

The FWS has used the 3-R framework to address SPOR by categorizing areas of a species range as supporting core or peripheral populations (Enzler & Bruskotter 2009). Under this argument, core populations contribute to the redundancy, resiliency, and representation of the overall species, whereas peripheral populations do not. For example, the final-listing rule for Preble's jumping mouse (FWS 2008) provides that a portion of the species current range is judged to be "significant" if it "contributes substantially to the representation, resiliency, or redundancy of the species…at a level such that its loss would result in a decrease in the ability to conserve the species." When in 2003 FWS first used the 3-R framework to help determine SPOR, they took the position that the status of a species in a SPOR was relevant only in determining whether the entire species should be listed or delisted (FWS 2003). Nevertheless, the 2007 solicitor's opinion endorsed the Services' authority to list or delist a species in a SPOR regardless of the conservation status of the species as a whole. Under this interpretation of SPOR, a population's contribution to the status of the entire species would be legally irrelevant to assessing the significance of the area inhabited by the population under consideration. Thus, the manner in which the Services have continued to apply the 3-R framework in determining SPOR is inconsistent with the solicitor's opinion.

The FWS' recent explanation of its use of resilience and redundancy also reveals the fundamental problem inherent in the agency's use of these factors in reference to the entire species to determine whether a portion of a species range is significant. The agency notes that "in considering significance, the Service asks whether the loss of this portion likely would eventually move the species toward extinction, but not to the point where the species should be listed as threatened or endangered throughout all of its range"(FWS 2008). Under an interpretation of the ESA that focuses only on viability, however, the statute does not protect species from any incremental increase in their likelihood of extinction; the law only protects species that are endangered or likely to become endangered in the foreseeable future. Thus, if loss of a species in a portion of its range decreases the species resiliency and redundancy to the point where the entire species is in danger of extinction, then the entire species is eligible for listing as threatened or endangered. If not, the incremental increase in extinction risk, although of conservation concern, is not relevant in terms of the ESA's listing thresholds.

The Services have also applied representation to assess significance in terms of a population's contribution to the viability of the entire species. For example, in its decision to de-list Bald Eagles in the contiguous United States, FWS asserted that "the portion [of the species range at issue in assessing SPOR] should be evaluated to see how it contributes to the genetic diversity of the species" (FWS 2007). Although representation of genetic diversity is one reason to consider geography, it does not by itself encompass the concept of representation described in Shaffer and Stein (2000). Those authors defined *representation* as a species presence across the diversity of ecosystems inhabited by the species and by the species role in ecosystem processes. Representation applies primarily to a population itself (e.g., by examining whether the species absence in a portion of its range would have significant ecological consequences or whether a given portion of a species range includes ecosystem types not found elsewhere in the species range) rather than to a population's contribution to the entire species. Representation should thus be the factor among the 3 Rs of most assistance in evaluating whether a portion of a species current range is significant when the services determine whether to protect or recover a species in a given geographical area.

Because a population's extinction risk is never zero, the viability component of listing and recovery actions involves a normative dimension (i.e., specifying what level of endangerment is acceptable) and a scientific dimension (i.e., determining whether a species meets that level of endangerment) (Vucetich et al. 2006). Although threat-assessment criteria prioritize which species are most at risk of extinction, they typically do not offer justification for why one level of risk is acceptable and another is not (IUCN 2001). Gilpin (1987), one of the few authors to consider the normative aspects of this issue, argued for considering risks of extinction for 200-year time frames simply because he believes humanity's immediate challenge is to eke through the next two centuries while losing as few species as possible.

Evaluating the implications of a species geographic distribution for listing and recovery similarly involves normative and biological determinations. The solicitor's opinion recognizes as much when it concludes that the Services, in determining whether a portion of a species range is significant, "could consider... the portion of the range in terms of the various values listed in the Act that would be impaired or lost if the species were to become extinct in either that portion of the current range or in the current range as a whole." In other words, the Services could decide if a portion of a species range is significant by assessing the "esthetic, ecological, educational, historical, recreational, and scientific" values that would be lost if the species were extirpated from (or never restored to) that portion of their range.

Public debate and litigation concerning recovery standards for formerly widely distributed carnivores, such as the gray wolf (*Canis lupus*) (e.g., *Defenders of Wildlife v. Hall*. CV-08-56-M-DWM, Montana District Court. 2008) have evolved into a complex debate over long-term genetic risks stemming from narrowly distributed or fragmented populations, rather than directly debating normative issues that ultimately determine the geographic extent of recovered populations (VonHoldt et al. 2008). For the vast majority of species of concern, the best available quantitative estimates of extinction risk have limited utility in guiding listing decisions or development of recovery criteria. Although the best available science indicates that many species require an effective population size (N_e) on the order of several thousand to achieve genetic viability (Lande 1995), this general knowledge of genetic viability does not allow one to infer the level of genetic diversity necessary for viability of a specific population. The imprecision of knowledge has been used by some to argue that genetic viability may be important in principle, but cannot be considered in recovery criteria in the absence of specific information. An additional benefit of properly considering SPOR is that situations in which a species is well distributed throughout its historic range (i.e., securely occupies all but an insignificant portion of its range) will generally correspond with the conditions necessary for genetic viability. Ultimately, proper consideration of geographic recovery goals and SPOR serves the ESA's policy goals by promoting more informed public debate on the normative decisions involved in recovery planning than could be an exclusive focus on viability.

Geographic Listing and Recovery Criteria as a Means for Ecosystem Conservation

The language of the ESA indicates Congress was concerned about the role of species within their ecosystems. In addition to including ecological value as one of the benefits species provide (16 U.S.C. §1531[a][3]), the statute includes as one of its three stated purposes conservation of "the ecosystems upon which endangered species and threatened species depend." The loss of a species over much of its historic range—even if the losses are not sufficient to place the entire species at risk of extinction—removes much of the ecological contributions made by the species (Soulé et al. 2005). The Services interpret this section of the ESA as implying that ecosystems should be protected, not for their own sake, but only when they are necessary for a species conservation and conclude that "despite [the ESA's] orientation toward conservation of ecosystems, the Services do not believe that the Act provides authority to recognize a potential [population] as significant on the basis of the importance of its role in the ecosystem in which it occurs" (Fay & Nammach 1996).

In contrast to the Services' interpretation, proper consideration of representation in listing and recovery decisions can address the novel aspects that the concept of SPOR brought to the ESA of 1973's definition of endangered species and create a more-coherent linkage

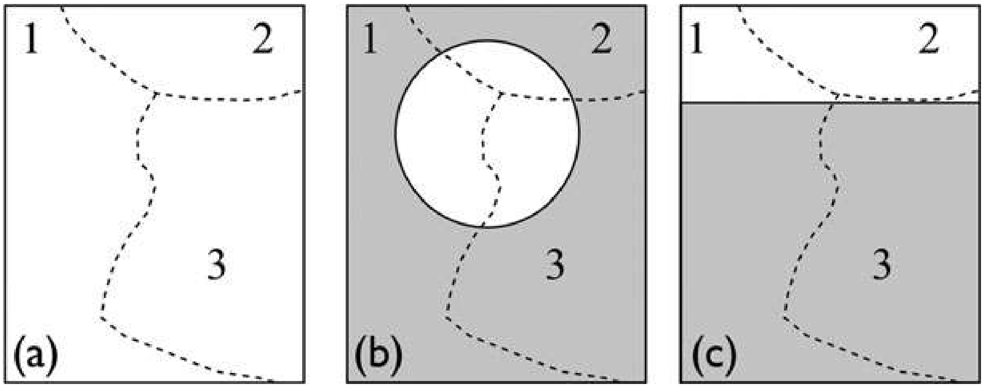

Figure 1. (a) A region that supports three ecologically significant types (numbers and dotted lines). An ecologically significant type represents ecotypic variation occurring within the extent of a listed species, subspecies, or distinct population segment. (b) and (c) The same species range as in (a) under two different scenarios (white, species extirpated from 25% of the area; gray, species securely occupies 75% of the area). The argument could be made that the quantitative dimensions of the concept of significant portion of range (SPOR) are satisfied in both panels (b) and (c). Nevertheless, the qualitative dimension of SPOR (i.e., representation) may only be satisfied for panel (b), where each ecologically significant type of the species securely occupies all but an insignificant portion of its range.

between the act's mandate to protect species and ecosystems. Specifically, the fundamental nature of a population and its ecological niche tightly link the ESA's dual goals of species and ecosystem conservation. Individual organisms that comprise a listed entity (species, subspecies, and distinct DPS) commonly exhibit systematic variation over geographic space with respect to life history or ecology (e.g., variation in diet, habitat use, or influence on the ecosystem they inhabit). Such variation in ecological process or function may be represented as variation in a species niche, defined as the set of ecological relationships that connect a population to the ecosystem it inhabits (Elton 1927; Odum 1959). Although such ecotypic variation may in some cases correlate to genetic population structure (Geffen et al. 2004), it is expected that, especially in highly vagile, wide-ranging species such as the gray wolf, ecotypes or geographic units relevant to consideration of SPOR may not be sufficiently distinct demographically or genetically to warrant DPS status (Rosen 2007).

Delineation of ecologically significant types on the basis of information on habitat types within the extent of a listed entity (e.g., a DPS) can clarify that several significant portions of range may exist within the geographic range of a listed entity (Fig. 1). This approach resembles the solicitor's opinion in that it recognizes ecological and human-centered values as criteria for determining SPOR. Nevertheless, it avoids the legal and biological shortcomings of the solicitor's opinion that the Services may list or delist a species in only a SPOR, as opposed to throughout its entire range.

Ecologically significant types are identified by knowledge of systematic variation in niche among individuals of the listed entity derived from studies of habitat use, diet, or genetics. In the absence of species-specific data, ecologically significant types might be delineated on the basis of ecoregions, which are typically defined on the basis of prevailing climate and vegetation (Olson et al. 2001). In other cases, delineation of ecologically significant types can be linked to consideration of genetics via methods that correlate genetic population structure variation with geographic or ecological factors (Geffen et al. 2004; Carmichael et al. 2007). By considering variation below the scale of listable entities, the concept of ecologically significant types compliments other aspects of the ESA that recognize the value of protecting variation among populations that qualify as subspecies or DPS.

Considering Geography in Recovery: the Case of the Gray Wolf

Because the gray wolf was formerly widely distributed throughout a variety of ecosystems, the species illustrates the practical consequences of differing interpretations of SPOR and provides an example of potential applications of the concept of ecologically significant type. In particular, wolves' well-documented ecological importance (Hebblewhite et al. 2005) helps clarify that many of a species key values stem not from whether they continue to merely exist, but from where they occur and whether they perform their ecological function. Applying a viability-based interpretation of SPOR, the FWS in 2009 determined that gray wolves in Montana, Idaho, northern Utah, and the eastern thirds of Oregon and Washington—collectively designated as the Northern Rocky Mountains DPS—could be delisted because they satisfied recovery criteria concerning population size (a metapopulation of at least 30 breeding pairs of wolves [FWS 2009]). In response to comments critical of its decision, the agency asserted that "[o]ccupancy across large portions of the historical range, unless required to preclude the Northern Rocky Mountains DPS from again becoming threatened or endangered, are beyond the requirements of the Act" (FWS 2009:15143).

In contrast, the geographic component of the ESA's definition of endangerment implies the need to consider the distribution of recovered wolf populations across their former geographic range in respect to ecologically significant types. For example, the current Northern Rocky Mountains DPS is primarily composed of areas within the Northern Rocky Mountain Forests ecoregion, but also contains areas of eastern Montana that are within the ecologically distinct northern Great Plains (FWS 2009). Wolves in the two areas were historically distinguished by their diet, ecosystem role, and morphological characteristics (Young & Goldman 1944). Recovery of a population of wolves in northern Rocky Mountain forests, although a laudable achievement, should not excuse the FWS from attempting restoration of wolves to the northern Great Plains where feasible. Similarly, the Mexican wolf was formerly distributed across the southwestern United States and northern Mexico. The subspecies attained higher densities in mesic mountainous areas characterized by abundant prey populations than in lower-elevation arid ecosystems (Brown 1983). Recovery of arid-lands populations, although potentially more challenging than recovery to mesic habitat, may be necessary to fulfill the ESA's geographic recovery component. In addition to consideration of ecotypic variation, an assessment of ecosystem dynamics both with and in the absence of wolves should be a factor in FWS' determinations of whether these areas constitute a significant portion of wolves' current or historic range.

Conclusion

The value of other species to humans and their role in the ecosystems they historically inhabited lies not merely in their continued existence, but in their existence in a given place or places. Congress recognized this when it afforded the Services authority to list a species in portions of their range and when it directed the Services to consider what constitutes a significant portion of range in listing and recovery actions. Nevertheless, by narrowly interpreting their authority—both in listing decisions and decisions about recovery and delisting—the Services have neglected to implement Congress's mandate regarding the geographic representation of imperiled species.

Although the complementary role of geographic and viability-related standards for threat assessment is widely acknowledged in an international context (IUCN 2001; Gaston & Fuller 2009; Table 1), the ESA is unusual in that it contains geographic criteria that reference ecological and societal goals (the "esthetic, ecological, educational, historical, recreational, and scientific value [of species] to the Nation and its people") that are not encompassed by consideration of the viability or extinction risk of the species. The ESA's multifaceted concept of endangerment could be criticized for lacking legal clarity when compared with the more restricted focus of recent endangered-species statutes in Canada and Australia (Table 1). Although quantitative standards developed to assess species viability may indeed be poorly suited to evaluating other human-centered and ecological goals fulfilled by recovering imperiled species (Possingham et al. 2002), this should not preclude us from fulfilling the ESA's mandate to protect such values. At the same time that the Services have restricted their focus to viability issues in an effort to avoid litigation and other controversies, ecologists have broadened their focus to acknowledge the multifaceted nature of endangerment and the importance of conserving diversity and ecosystem dynamics at multiple scales (Ceballos & Ehrlich 2002; Soulé et al. 2005). Shaffer and Stein (2000: 308) conclude:

> . . .we will be challenged to recognize our conservation targets in a way that captures the full spectrum of such natural variation across the landscape, and on a geographic scale that can truly encompass this ecological diversity and its attendant processes. The principle of representation—saving some of everything—will require identifying conservation targets not simply as species and communities but as the complexes of populations, communities, and environmental settings that are the true weave of biodiversity.

Three decades after enactment of the ESA, society has not yet answered the question of how much of the landscape ought to be shared with the nonhuman world. An inclusive debate of this issue is contingent on understanding the meaning of the ESA's definition of an endangered species. The ecological notions of population, niche, and ecosystem contribution offer the dialogue a coherent, scientific framework that acknowledges the values of imperiled species recognized by Congress and is accessible to most citizen stakeholders. Without considering geography in this dialogue, we risk misapprehending the very concept of what it means to protect and then recover threatened and endangered species.

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Supporting Information

Examples of the use of the concepts of resilience, redundancy, and representation in rules for endangered species developed by the U.S. Fish and Wildlife Service are available as part of the online article (Appendix S1). The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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