Review

Quantitative tools for implementing the new definition of significant portion of the range in the U.S. Endangered Species Act

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Abstract: *In 2014, the Fish and Wildlife Service (FWS) and National Marine Fisheries Service announced a new policy interpretation for the U.S. Endangered Species Act (ESA). According to the act, a species must be listed as threatened or endangered if it is determined to be threatened or endangered in a significant portion of its range (SPR). The 2014 policy seeks to provide consistency by establishing that a portion of the range should be considered significant if the associated individuals' "removal would cause the entire species to become endangered or threatened." We reviewed 20 quantitative techniques used to assess whether a portion of a species' range is significant according to the new guidance. Our assessments are based on the 3R criteria—redundancy (i.e., buffering from catastrophe), resiliency (i.e., ability to withstand stochasticity), and representation (i.e., ability to evolve)—that the FWS uses to determine if a species merits listing. We identified data needs for each quantitative technique and considered which methods could be implemented given the data limitations typical of rare species. We also identified proxies for the 3Rs that may be used with limited data. To assess potential data availability, we evaluated 7 example species by accessing data in their species status assessments, which document all the information used during a listing decision. In all species, an SPR could be evaluated with at least one metric for each of the 3Rs robustly or with substantial assumptions. Resiliency assessments appeared most constrained by limited data, and many species lacked information on connectivity between subpopulations, genetic variation, and spatial variability in vital rates. These data gaps will likely make SPR assessments for species with complex life histories or that cross national boundaries difficult. Although we reviewed techniques for the ESA, other countries require identification of significant areas and could benefit from this research.*

Keywords: adaptive capacity, endangered, extinction risk, population viability, threatened species

Herramientas Cuantitativas para la Implementación de la Nueva Definición de Porción Significativa de la Extensión en el Acta de Especies Amenazadas de los EUA

Resumen: *En 2014 el Servicio de Pesca y Vida Silvestre (FWS, en inglés) y el Servicio Nacional de Pesqueras Marinas anunciaron una nueva interpretación política para el Acta de Especies Amenazadas de los EUA (ESA). De acuerdo al acta, una especie debe estar enlistada como amenazada o en peligro si se ha determinado que está amenazada o en peligro en una porción significativa de su extensión. La política de 2014 busca proporcionar consistencia al establecer que una porción de la extensión debería ser considerada como significativa si "la extracción de los individuos asociados causaría que la especie entera quede como amenazada o en peligro". Revisamos 20 técnicas cuantitativas usadas para evaluar si una porción de la extensión de la especie es significativa de acuerdo con la nueva guía. Nuestras evaluaciones están basadas en los criterios 3R – redundancia (es decir, amortiguamiento de una catástrofe), resiliencia (es decir, habilidad para sobrellevar lo estocástico), y representación (es decir, la habilidad para evolucionar) – que el FWS usa para determinar si una especie amerita estar enlistada. Identificamos necesidades de datos para cada técnica cuantitativa y consideramos cuáles métodos podrían implementarse dadas las limitaciones de datos típicos de las especies raras. También identificamos sustitutos para las 3Rs que podrían usarse con datos limitados. Para evaluar la disponibilidad de datos potenciales, evaluamos siete especies ejemplo valorando datos en sus evaluaciones de estado de especie, los cuales documentan toda la información usada durante una decisión de listado. En todas las especies, un SPR podría evaluarse robustamente con al menos una medida para cada una de las 3Rs o son suposiciones sustanciales. Las evaluaciones de resiliencia aparentaron ser las más restringidas por los datos limitados, y muchas especies carecieron de información sobre la conectividad entre subpoblaciones, variación genética y variabilidad espacial en tasas vitales. Estos vacíos de datos probablemente hagan que las evaluaciones SPR sean complicadas para las especies con historias de vida complejas o que atraviesan fronteras nacionales. Aunque revisamos técnicas para la ESA, otros países requieren la identificación de las áreas significativas y podrían beneficiarse con esta investigación.*

Palabras Clave: capacidad adaptativa, en peligro, especies amenazadas, riesgo de extinción, viabilidad poblacional

Introduction

The Endangered Species Act (ESA) of 1973 is the primary legislation for preventing species extinctions in the United States and provides a process for protecting threatened and endangered species. Under the law, a species is considered endangered if it is "in danger of extinction throughout all or a significant portion of its range" (16 U.S.C. §1532[3.6]) and threatened if it is "likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range" (16 U.S.C §1532[20]). Here, the term species refers to any taxonomic level eligible for protection, including species, subspecies, and distinct population segments (DPSs) of vertebrates. The ESA and subsequent amended versions do not provide guidance on how to interpret significant portion of its range (SPR). This omission has led to concerns that interpretations of significant by federal agencies and the courts could be inconsistent (e.g., Waples et al. 2007; D'Elia et al. 2008).

In response to legal challenges (e.g., *Defenders of Wildlife v. Norton*, 258 F.3d 1136, 9th Cir. 2001; *EPIC v. NMFS*, No. C-02-5401, N.D. Cal. 2004), listing decisions have increasingly relied on biological tests for determining whether a population was significant (e.g., USFWS 1998, 2007). To clarify the SPR matter, in 2014, the U.S. Fish and Wildlife Service (FWS) and National Marine Fisheries Service (NMFS), the agencies charged with implementing the ESA, announced an interpretation of SPR and general guidance on implementation (USFWS & NMFS 2014). Based on the new SPR policy, a portion

of a species' range will only be considered significant if, without the individuals in that portion, the species is at risk of becoming endangered throughout its entire range immediately or within the foreseeable future (USFWS & NMFS 2014). The key point of this definition is that significant means that the portion of the range is biologically important for the viability of the species rather than a large area (Bruskotter & Enzler 2009). The 2014 policy also defines range as the current rather than the historical geographic range (USFWS & NMFS 2014), which puts the new definition of significant into context.

The new policy interpretation of SPR involves predicting what will happen to the entire species if the species is extirpated from a portion of its range. In making these determinations, the FWS or NMFS first determine if a species is endangered or threatened throughout its entire range (Fig. 1a). If the species is not threatened or endangered throughout its entire range, the agencies then assess whether the species should be listed as threatened or endangered based on an SPR by using one of 2 decision pathways that vary the order of 2 determinations (Fig. 1b): is any portion of the species' range considered significant" and is the population in that area threatened or endangered (i.e., threat analysis)? If the portion of the range under consideration is a DPS of a vertebrate species, the DPS would be listed, whereas the entire species would not (USFWS & NMFS 2014).

With the definition of significant clarified, the next challenge is to identify methods to guide the implementation of this new definition. The FWS and NMFS state that "quantitative data and methodologies are not required if
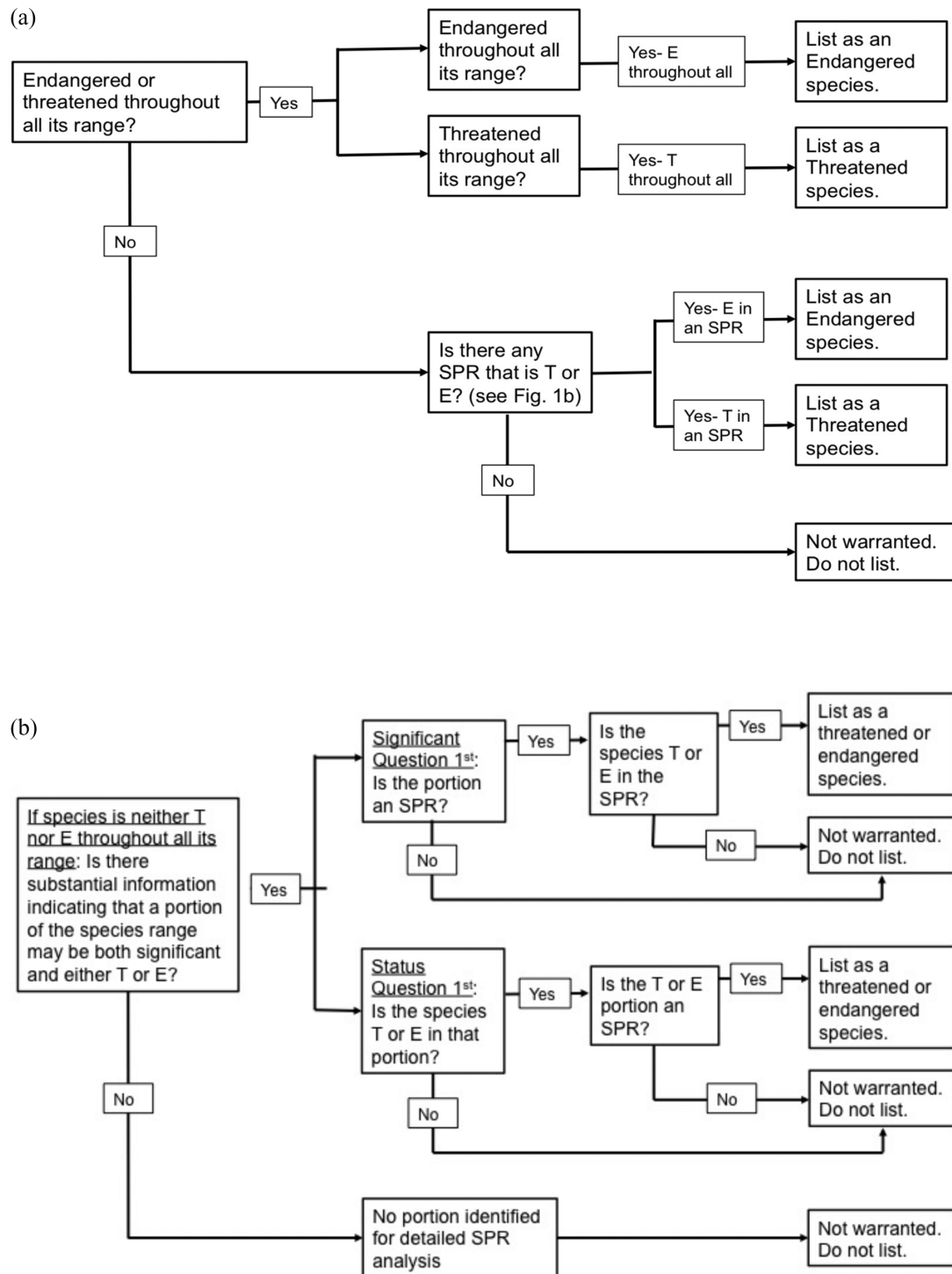
Figure 1. Decision process for (a) listing a species and (b) listing a species under the Significant Portion of Rang (SPR) policy as threatened (T) or endangered (E) under the U.S. Endangered Species Act. The SPR is determined based on redundancy, resilience, and representation. Reproduced from USFWS and NMFS (2014) figs. 1 and 2.

the data available do not allow for quantitative analyses" (USFWS & NMFS 2014:37600). The agencies provide an example of how to determine whether a portion of a species' range is significant without quantitative data. In this example, a species has only two portions of range

and would lose its redundancy (i.e., how well the species is buffered from catastrophic events) if one portion were eliminated. Either portion of the range could therefore be considered an SPR, making the species' listing determination relatively straightforward. However, many species

have multiple, connected populations or occur over continuous ranges. A lack of sufficient quantitative data in these cases makes a listing decision based on an SPR difficult. Species that have many distinct populations or larger continuous ranges may require quantitative modeling to assess whether any subpopulations constitute a significant portion of the range. The agencies admit quantitative analyses would be "ideal" (USFWS & NMFS 2014), so it is worthwhile to assess which analyses are feasible to conduct under this new policy. The purpose of our paper is to provide this assessment to aid agencies in using robust methods and data to inform listing decisions.

Waples et al. (2007) developed a framework for conceptualizing and performing SPR decisions. They considered SPR cases for species distributed continuously or as metapopulations and those incurring loss of genetic diversity through three hypothetical scenarios. They argue that, although other frameworks could be used in SPR decisions, an approach focusing on the viability of the species is consistent with the goal of defining an endangered species, albeit challenging to implement. To deal with these challenges, more work is needed to identify the different quantitative tools that could be used to make SPR decisions.

We reviewed quantitative techniques available for assessing whether species should be listed based on the new SPR policy. We also assessed data needed to implement these techniques and the major challenges to implementing this policy from a quantitative perspective. To better understand whether the information is available to use these techniques, we assessed the data presented in completed species status assessments for seven species and determined whether each metric could be performed for an SPR analysis. Species status assessments document all the information about a species used during a listing decision. The ESA states that listings should be based on the best scientific and commercial data available. As such, we considered the methods that would make the best use of the available data and allow the FWS and NMFS to make evidence-based decisions. The new SPR policy and its underlying framework have been criticized (reviewed in Wilhere [2017]) and are currently under litigation (Center for Biological Diversity and Defenders of Wildlife v. USFWS 2014), but an in-depth discussion of this debate is beyond the scope of this paper. Further, we neither support nor oppose the 2014 SPR policy; rather, we sought to provide scientific guidance to support listing decisions given that this policy is in place and being implemented.

Analyses

The FWS has developed and is beginning to use species status assessments (USFWS 2015) when implementing the ESA to separate the process of information gathering on a species from decision making for listing. Species status assessments have 3 stages: compiling background biological information, evaluating current species condition, and forecasting species responses to future environmental conditions and conservation efforts. The FWS uses the 3Rs approach to determine if a portion of a species' range is significant by asking if the removal of individuals in that portion will affect at least one of the 3Rs: redundancy (Is the species secured against unforeseen catastrophes?); resilience (Can the species sustain itself while facing demographic and environmental stochasticity?); and representation (Does the species have enough diversity to adapt to changing environmental conditions?) (Shaffer & Stein 2000). The NMFS uses similar criteria known as the four viability characteristics: abundance, spatial distribution, productivity, and diversity of the species (McElhany et al. 2000). We focused on the 3Rs, because the majority of listing decisions fall under FWS jurisdiction. The degree to which each of the 3Rs must be affected before the portion of the range is considered significant is a policy decision. However, scientific literature can help quantify potential impacts on the 3Rs as a result of the loss of individuals in a portion of the species' range.

Redundancy

The redundancy criterion is a measure of how well a species is buffered from catastrophes (Mangel & Tier 1993; Wilcox & Elderd 2003). Redundancy is based on the precautionary principle: because uncertain and unforeseen events occur, there should be a sufficient number of populations and connections between them to provide protection from disasters. Redundancy contains at least three aspects: number of populations, connectivity among populations, and the populations' viability (Mangel & Tier 1993). Reducing these could lower the species' ability to recover and recolonize areas after catastrophic events. Catastrophic disturbances (e.g., floods, fires, disease) may eliminate entire populations (Akçakaya & Baur 1996; Hatfield et al. 2004), and having more populations provides a safety net against these events (Quinn & Hastings 1987). Higher connectivity allows more rapid recolonization after a catastrophe and perhaps higher rates of escape during a catastrophic event (Gresswell 1999). Some populations may have high viability in the face of catastrophes (i.e., geographic context makes catastrophes rare) and act as refugia, whereas others may not (Fordham et al. 2013*b*).

Several approaches estimate redundancy, and information on population dynamics, movement, and the frequency, extent, and magnitude of catastrophes on a species will assist in SPR-related decisions. When high levels of information on the species' population dynamics are available, spatially explicit population viability analyses (PVAs) (Beissinger & McCullough 2002) can be used to assess the probability of population or subpopulation

extinction given known or modeled catastrophe regimes (Lande et al. 2003; Perkins et al. 2008). These approaches can be used to model the impact on overall population viability of extirpation of the species from a portion of the range (Peterson et al. 2003; Taylor & Norris 2010).

If data for PVA are not available, simpler, but less robust, measures of redundancy are available. For example, GIS-based approaches combined with knowledge of a species habitat requirements can be used to create representative habitat maps (e.g., Tulloch et al. 2016). These can be overlaid with maps of historical catastrophes (e.g., fire, flood, storm surge) to estimate the extent of catastrophes and what areas might act as refugia versus those frequently affected. The number of populations provides a simple measure of redundancy, but more robust estimates incorporate the viability of these populations and the rates at which catastrophes affect them. It is important to identify and maintain refugia where species can withstand catastrophes so that individuals can recolonize other areas after catastrophes (Spiller et al. 1998; Bateman et al. 2015).

A portion of the range may be significant if extirpation from that area would result in substantial reduction in a population process, such as connectivity, that leads to reduced viability. Spatially explicit PVA approaches can be tailored to show how connectivity changes when part of a species' range is lost and if this change affects population viability (Table 1). A less data-intensive alternative is to estimate graph-theory metrics that measure the degree of connectivity across a network of subpopulations and how these change if habitat is removed (e.g., Urban et al. 2009). Landscape-resistance models can provide similar information (Zeller et al. 2012). When species have continuous but heterogeneous spatial distributions, the effects of habitat loss and fragmentation on connectivity may need to be treated differently than when species occupy discrete habitat patches (Waples et al. 2007). Metrics of landscape fragmentation are available (Hargis et al. 1998), but the relationship between the degree of fragmentation indicated by many metrics and extinction risk is unclear (i.e., How does fragmentation score translate to extinction probability?), which makes them difficult to use to directly inform SPR decisions.

When information on a species is lacking, redundancy analyses could be addressed using the spatial distribution, frequency, and magnitude of catastrophes in combination with general information on a species' spatial ecology, life history, or population dynamics (Table 1). For example, if a species' range becomes smaller than the area affected by historic catastrophes (e.g., area burned, extent of disease spread) and a portion of the range is removed, then the species may be at considerable increased risk regardless of the connectivity of the population (Frank & Wissel 1998). Similarly, if a species has a low reproductive rate and sporadic monitoring data suggest it recovers slowly from catastrophes, then ex-

tirpating a species from the portion of its range subject to few catastrophes may raise the average catastrophe frequency across the population and result in population decline. In this case, an SPR analysis could be used to determine whether the average frequency of catastrophes across subpopulations would increase (i.e., by removal of refugia) if a portion of the range were eliminated.

Resilience

A population is resilient if it can sustain itself under environmental and demographic stochasticity (Holling 1973; USFWS 2015). The impacts of demographic and environmental variation on population viability are modeled using several different techniques depending on available data and specific questions being addressed (Mills 2013). Theory suggests demographic stochasticity has less of an impact on population persistence than catastrophes or environmental stochasticity, but demographic stochasticity can affect viability when population sizes are small (i.e., <100 individuals [Lande 1993]). The impact of stochastic variation on population dynamics is often examined through sensitivity analyses, which are used to assess how changes in demographic model parameters affect population-level measures such as abundance, growth rate, age structure, extinction risk, and harvest levels. Methods for sensitivity analysis include analytical sensitivities and elasticities, life-stage simulation analysis, and manual perturbations (e.g., Taylor & Norris 2010; Taylor et al. 2012).

A portion of a species' range could be an SPR if removing it would substantially reduce the species' ability to withstand demographic and environmental variability. For the SPR analysis, extinction risk for the global population could be estimated with and without the individuals in the proposed SPR under varying levels of demographic and environmental stochasticity (Table 1). However, the impact of extirpating individuals from certain areas on population persistence in combination with stochasticity may require a considerable amount of demographic and spatial information. Assuming the underlying model accurately represents system dynamics, this general analysis type is likely to be robust for the needs of the new SPR policy. In cases where an SPR decision involves a species with spatial structure, such as a migration or metapopulation, the high data demands of some of these methods, including the need for demographic information across multiple locations and connectivity, may make it infeasible (Hostetler et al. 2015).

An alternative approach quantifies the per capita contribution of a subpopulation (i.e., individuals occupying a portion of range) to the species as a whole (Figueira & Crowder 2006; Runge et al. 2006), which provides a proxy for resilience. This approach yields the number of individuals that an average individual in a subpopulation contributes to the population in the next time step and

Table 1. Selected approaches for determining a species' significant portion of range (SPR) based on redundancy, resiliency, and representation and data required for determining whether a species' population or populations constitute an SPR.

Criteria category[a]	Criterion[b]	Approach	Example metric	Data required	Explanation	Citation
Redundancy	number of subpopulations	population viability analysis (PVA); spatially explicit population models	probability of extinction	abundance survey data, vital rate data, connectivity, potentially habitat quality information	greater number of viable subpopulations indicates greater ability to recover after catastrophes	Pettifor et al. 2000
		count number of subpopulations	number of occupied subpopulations	occupancy or occurrence	presences of species in more areas indicates greater ability to recover after catastrophes; presence is a surrogate for a healthy subpopulation	Simberloff & Abele 1982
		representative habitat maps	Gini coefficient	historical and current habitat distribution maps	presences of species in more areas indicates greater ability to recover after catastrophes; habitat maps are a surrogate for healthy subpopulations	Tulloch et al. 2016
	connectivity	graph-theoretic metrics	degree, betweenness, quality-weighted area	in the simplest metrics, requires only subpopulation locations; often uses habitat area and movement. data required varies depending on metric	portions of the range with higher connectivity will allow species to recolonize areas more quickly after catastrophes	Urban et al. 2009
Resilience	capacity to absorb change	sensitivity analysis	sensitivity of population growth rate to removal of subpopulations under stochasticity	abundance survey data, vital rate data, and potentially habitat quality information	simulates the ability for the species to persist after the removal of a portion of the range given demographic and environmental stochasticity	Caswell 2001; Mills 2013; Wiederholt et al. 2013

Table 1. Continued

Criteria category[a]	Criterion[b]	Approach	Example metric	Data required	Explanation	Citation
		per capita contribution of subpopulation to species	per capita contribution	relative abundance survey data, vital rate data, and potentially habitat quality information	can show importance of different habitat patches, and how differently-ranked patches are distributed across the landscape	Figueira & Crowder 2006; Runge et al. 2006
		metapopulation metrics	subpopulation value	spatial configuration of habitat patches, occupancy/ occurrence, connectivity	shows importance of habitat patches to metapopulation capacity, persistence	Ovaskainen & Hanski 2003
	population size	abundance estimation	hierarchical models	abundance survey data, detection probability	larger populations are better able to withstand demographic and environmental stochasticity	Lande 1993; Wilcox & Elderd 2003
	adaptive capacity	evolutionary simulation models	extinction probability, population size after environmental change	ecological, demographic, genetic, genomic, selection, heritability	simulate ability to adapt with and without portions of the range	Gienapp et al. 2013; Hoban 2014
Representation	standing genetic variation	genetic variability within and among subpopulations	population adaptive index (PAI), average heterozygosity, allelic diversity, polymorphism, F_{ST}	genetic; genomic	portions of the range with high variability in adaptive alleles, high genetic variation, or unique genetic variation are most likely to contribute to future evolution	Frankham et al. 2004; Bonin et al. 2007

Continued

Table 1. Continued

Criteria category[a]	Criterion[b]	Approach	Example metric	Data required	Explanation	Citation
	ecological/ phenotypic variability	phenotypic variability within and among subpopulations	phenotypic data	data on morphological, behavioral, physiological traits	portions of the range with distinct phenotypes likely have unique heritable traits that could contribute to future evolution	Shafer & Wolf 2013
	population size	abundance estimation	hierarchical models	abundance survey data, detection probability	larger populations have greater genetic variability and delay time to extinction, prolonging the time available to adapt	Royle & Dorazio 2008; Carlson et al. 2014
	diversity across niches	species distribution models, occupancy modelling	probability of suitable conditions	occupancy/occurrence and environmental factors	portions of the range occupying unique niches or habitats are likely to contain unique adaptive variation that could contribute to future evolution	Elith & Leathwick 2009

[a]Key question related to SPR: redundancy, would loss of a portion of the range significantly decrease the ability of the species to withstand catastrophes across its entire range; resilience, would the loss of a portion of the range significantly decrease the ability of the species to withstand demographic stochasticity across its entire range; representation, would the loss of a portion of the range significantly decrease the ability of the species to adapt to long-term changes in the environment, such as climate change?
[b]Metric that determines whether a portion of the range is significant. A portion of the range may be considered an SPR if its removal causes a large change in the criteria.

the population growth rate (e.g., Puckett & Eggleston 2016). Per capita contributions incorporate emigration, immigration, survival, and reproductive rates of residents and emigrants. The per capita contribution multiplied by the total population size for a subpopulation indicates a subpopulation's total contribution of individuals to the population. The portion of a species' range occupied by a subpopulation or combination of subpopulations could be considered an SPR if its total contribution makes up a large proportion of the annual contribution to the entire population (Table 1). This approach has been applied in a small number of cases (e.g., Griffin & Mills 2009; Newby et al. 2013) and may be quicker and less computationally intensive than some types of sensitivity analyses, but it has similarly intensive data requirements in that it requires capture-recapture, radiotelemetry, or other types of data. Although promising, more work is needed to determine what factors affect the reliability of contribution metrics for resilience.

Where subpopulations are connected by movement and exchange of individuals, an alternative approach is to use metapopulation metrics (Table 1). For example, the value of a subpopulation to the overall network can be estimated by the change in metapopulation capacity (Hanski & Ovaskainen 2000) caused by the removal of that subpopulation (e.g., Bulman et al. 2007). Other metapopulation metrics (Ovaskainen & Hanski 2003) determine the contribution of a subpopulation to population viability, metapopulation size (i.e., number and size of habitats in a metapopulation), colonization events over the long-term, and metapopulation persistence (e.g., Minor & Urban 2007). These metrics generally require data on the location of habitat patches and connectivity between patches, which can be estimated with geographic distance (Hanski 1994). Alternatively, other metrics, such as population size, can be used as proxies for resilience that require fewer data (Table 1), and the portion of a species' range occupied by a subpopulation could be considered an SPR if it constituted a large fraction of the total population.

Representation

The representation criterion requires maintenance of species' evolutionary capacity to adjust to long-term anthropogenic change. Under the SPR policy, analyses must determine whether the removal of individuals in a portion of the range would limit the species' evolutionary capacity. Evolution can be constrained genetically by insufficient additive genetic variation or demographically if the population declines too rapidly for the spread of adaptive genes (Gomulkiewicz & Houle 2009). Evolutionary rescue occurs when adaptation through natural selection increases the population growth rate in a changing environment and prevents extinction (Gonzalez et al. 2013). Theoretical and laboratory studies show that evolution-

ary rescue is more likely if a species has a large (pre-stressor) population size, high potential for movement to affect gene flow, high levels of standing genetic variation, high mutation rate, and is subject to moderate rather than rapid changes in environmental conditions relative to generation time (Osmond & de Mazancourt 2012; Carlson et al. 2014). Further, larger populations tend to have higher levels of genetic variation (Frankham 1996). For determining an SPR, the relationship between standing genetic variation, population size, and likelihood of evolutionary rescue (Carlson et al. 2014) will be critical in assessing whether a portion of the range is significant. Due to these relationships, a portion of the range would be considered significant if its extirpation in that area would substantially decrease the standing genetic variation of the species or the overall population size. An area could also be an SPR either because the individuals have higher genetic variation than in other areas or because those individuals have unique genetic variation (i.e., high genetic differentiation from other areas or subpopulations).

If sufficient data exist, modeling approaches can be used to predict rates of adaptation required to maintain a population under future conditions. For instance, simulation models can be used to assess adaptive capacity (Hoban 2014; Richardson et al. 2016) by synthesizing genetic, ecological, and demographic data (Gienapp et al. 2013). These types of models could be modified to simulate the loss of a subpopulation and its impacts on a species' adaptive capacity to assess whether the portion of the range occupied by a subpopulation is an SPR (Table 1). However, having this much data is unlikely for most species. Another metric for assessing adaptive capacity of subpopulations is the population adaptive index (PAI), which requires robust spatial genetic data (Bonin et al. 2007) that is also not available for most species (Table 1).

For species with moderate amounts of genetic information, standing genetic diversity could be measured using techniques from quantitative or population genetics for all subpopulations of the species (Table 1). Useful measures of genetic variation include average heterozygosity, allelic diversity, and polymorphism (Frankham et al. 2004). Genetic differentiation among subpopulations can be estimated with F_{ST} or related statistics used to estimate the proportion of genetic variation in subpopulations relative to the total amount of variation. At present, most genetic data on wild populations involves presumptively neutral genetic markers. Advances in conservation genomics are likely to provide a broader set of metrics in the future through the identification of adaptive loci and spatial variability in genes at those loci (Shafer et al. 2015).

In the absence of genetic measures, alternative measures that require fewer data may serve as proxies of genetic variability. There is general support for genetic differentiation among subpopulations that have different

environmental conditions or phenotypes (Shafer & Wolf 2013) as long as the homogenizing effect of gene flow is relatively limited (Mills & Allendorf 1996). Species distribution models can be used to measure the range of environmental conditions occupied by a species. This can be modeled using historical occupancy data and environmental predictors to determine habitat conditions (Elith & Leathwick 2009). Parts of the range occupied by a subpopulation or combination of subpopulations may be considered SPRs if they contain unusual features or if species in this part of the range have unusual phenotypes (i.e., behavior, morphology), although data on habitat conditions and phenotypes across the geographic range will be necessary to identify an SPR based on these proxies.

Threat Analysis

Assuming that a portion of the range satisfies one of the 3R significance criteria, a threat analysis is also required to determine whether the species should be listed as threatened or endangered based on an SPR (Figure 1b). A detailed review of threat analysis is beyond the scope of this paper. Briefly, threats can be incorporated in multiple types of models such as population viability, ecological-niche models, or time-series analyses (Oberhauser & Peterson 2003; Wiederholt & Post 2010; Flockhart et al. 2015). These models can accommodate threat information, but the extent of the threats needs to be supplied in order to calculate metrics for the 3Rs. Where information for detailed threat modeling does not exist, expert knowledge is often employed to obtain likely impacts from threats (Kuhnert et al. 2010; Martin et al. 2012), although this is inherently subjective. However, Bayesian approaches, including Bayesian belief networks (Smith et al. 2007), offer a means of incorporating expert knowledge through prior distributions specifying parameter means and levels of uncertainty (Kuhnert et al. 2010).

Data Needs

The availability of data and amount of time necessary to perform analyses are key practical constraints on the quantitative determination of significance under the new SPR policy. An important question likely to arise is what data are available that can be used to determine the significance of a portion of the range under each of the 3Rs? Decisions are typically made based on existing information without expenditures on gathering new data. The time available to make determinations can also influence the complexity of analyses used.

The FWS does not require specific levels of information be available for an SPR determination. According to Waples et al. (2007: 970), a "lack of a specific type(s)

of information should not preclude application of this biologically based framework to SPOIR[SPR] determinations." There are many approaches, requiring various levels of data complexity, available to assess redundancy, resiliency, and representation when determining significance under the 2014 SPR policy (Table 1). For redundancy and resilience, minimum information includes occurrence, habitat use, and distribution maps. At the opposite extreme, complex spatially explicit population models parameterized with demographic and movement data can be used to assess the impacts of losing the individuals in a portion of the range. Geospatial approaches and their calculated metrics are intermediate in this data-complexity and data-needs continuum. A robust analysis of representation requires detailed genetic data that are often not available, whereas estimates of population size, movements of individuals, and the range of environments the species occupies are more often available. However, new molecular analysis tools, particularly noninvasive sampling, are increasing the availability of detailed genetic data (Allendorf et al. 2013).

To assess the availability of data needed to perform SPR analyses, we evaluated the species status assessments available through the data.gov database on 10 May 2016. Six species status assessments encompassed information on seven different species (Table 2). For each species, we determined whether the data were available to inform each metric in Table 1 and rated each metric as follows: 1, metric could be implemented robustly; 2, metric could be implemented with significant assumptions; 3, metric could not be implemented at all (i.e., data are not available or the number of assumptions that would need to be made would make the analysis uninformative). Criteria for rating each metric are given in Supporting Information. At least one of the SPR metrics could be implemented for each of the 3Rs either robustly (i.e., a rating of 1) or with significant assumptions (i.e., a rating of 2) for every species (Table 2, justifications given in Supporting Information). Generally, resiliency appeared harder to evaluate in an SPR context, because fewer resiliency-related data were available than redundancy-related or representation-related data, which both have more proxies available for which fewer data are needed. However, our analyses had a very low samples size. Representation has two metrics for which the data need is so high that they could not be implemented for any of the species evaluated (evolutionary simulation models) or could be implemented for only one species (ecological and phenotypic variation).

We also identified types of data frequently missing that are needed for many metrics to evaluate the presence of an SPR. Most species lacked information on connectivity among populations, which is useful in all 3Rs. Vital-rate information was often available for species but typically for only one area or a very small portion of the species' geographic range. Vital rates frequently vary in space

Table 2. Assessment of metrics' usefulness in determining whether an area is an SPR based on the information presented in each species status assessment for 7 species.[a]

Criterion and metric	Data required	Brazos River shiners[b]	Eastern Massassauga rattlesnake	New Mexico jumping mouse	Page Spring snail	Rio Grande cutthroat trout	Sonoran Desert tortoise
Redundancy							
PVA; spatially explicit population models	abundance survey data, vital rate data, connectivity, potentially habitat quality information	2	2	3	3	2	2
count number of subpopulations	occupancy or occurrence	1	2	1	1	1	1
graph-theoretic metrics	in the simplest metrics, requires only subpopulation locations; often uses habitat area and connectivity	2	2	2/NA	3	2	2
Representative habitat maps	historical and current habitat distribution maps	1	1	1	1	1	1
Resilience							
sensitivity analysis	abundance survey data, vital rate data, and potentially habitat quality information	2	2	3	3	2	2
per capita contribution	abundance survey data, vital rate data, and potentially habitat quality information	2	2	3	3	2	2
metapopulation metrics	spatial configuration of habitat patches, connectivity	2	2	2/NA	3	2	2
population size	abundance survey data, detection probability	2	2	2	2	1	2
Representation							
evolutionary simulation models	ecological, demographic, genetic, genomic, selection, heritability	3	3	3	3	3	3
genetic variability within and among subpopulations	genetic, genomic	3	2	3	3	1	1
ecological and phenotypic variation	trait variability across space	3	2	3	3	3	3
abundance estimation	abundance survey data, detection probability	2	2	2	2	1	2
species distribution models, occupancy modeling	occupancy/occurrence and environmental factors	1	1	2	1	1	2

[a]Key: 1, the metric could be used robustly; 2, metric could be used with substantial assumptions; 3, metric could not be used; NA, unlikely that the metric would be calculated due to no connectivity among populations.
[b]Includes 2 species with identical ratings.

(Hayes et al. 1996; Fordham et al. 2013*a*). Assuming otherwise may dramatically alter the results of SPR analyses. Research on the effects of connectivity and spatial variability in vital rates on SPR analyses (e.g., through sensitivity analyses) may help identify when they will and will not alter the conclusions for listing decisions. Conducting formal expert elicitation could efficiently fill data gaps for SPR analyses when no relevant literature, models, or data sets are available for particular parameters (Kuhnert et al. 2010; Martin et al. 2012). Regardless, we identified a need for research on connectivity and spatial variability in vital rates for rare and declining species that may be evaluated for possible listing under the ESA.

Challenges for Implementation

The main challenges facing an SPR determination are data availability and complex life histories. Decision makers are faced with a trade-off between the level of certainty an approach provides and the amount of data available on the species. Approaches providing the most certitude may require data that are unavailable for all but the most well-studied species. The assumptions of the simplest models in Table 1, which are based on the most basic and readily available data, are generally not applicable in highly dynamic systems. In most cases, more detailed information than is currently available for most species will be necessary to parameterize the sophisticated models most capable of representing population dynamics and informing assessments of population risk as required by the 3Rs analysis. However, these data are not collected routinely for most species. Species with habitat spanning international borders are at a further disadvantage because of inconsistent or incomplete monitoring throughout their range (Culver et al. 2009), making SPR determinations particularly challenging. Using qualitative methods to choose appropriate habitat-quality metrics guided by a decision-theoretic framework (Nicol et al. 2016) may help ensure an efficient SPR determination process while improving anticipated outcomes.

Complex life histories of certain species further limit understanding of their population dynamics and raise challenges for the SPR determination process. Migratory species occupy a diversity of habitats, often over large geographic ranges, and encounter different political and geographic regions over an annual cycle (Sherry & Holmes 2000). Nomadic species also occupy large geographic ranges, tracking resources that vary seasonally and yearly (Jonzén et al. 2011). For these types of species, occupancy is necessarily dynamic, demographically independent subpopulations may not exist, and therefore understanding population risk requires more sophisticated data and models.

Relevance in Other Contexts

Although the SPR determination is specifically a U.S. policy, determining the contribution of individuals in a portion of a species' range to overall species' viability is an issue that wildlife managers and decision makers outside the United States need to consider (Carroll et al. 2010). For example, in Australia, species may be listed under the Environmental Protection and Biodiversity Conservation Act of 1999 based on the area of occupancy where there is a "continuing decline in the area, extent and/or quality of habitat." Although the Australian policy clearly defines area of occupancy as the "smallest area essential at any stage to the survival of existing populations of a taxon" (similar criteria to SPR), the significance of a given occupancy area is defined only in terms of the number or percentage of individuals in one subpopulation. As such, the question of significance is relevant in at least two countries, and our assessment of the U.S. policy can be applied in other countries where similar rules have been or are being implemented.

Conclusion

Overall, we found a wide variety of quantitative approaches for assessing the SPR in the context of redundancy, resiliency, and representation. Choice of a given approach should be based on the available data for a given species. Although there are clear benefits to assessing an SPR with detailed demographic and genetic information across space, there are alternatives that require fewer data. Based on our limited sample of species assessments, typically only lower-level quantitative approaches (i.e., proxies) for assessing SPR can be made, and this is due to limited population and genetic information for many species. Such lower-level quantitative assessments should be treated with caution and the assumptions behind these approaches should be explicitly recognized. Further, for species with dynamic occupancy of habitat patches (e.g., migratory and nomadic species), simpler proxies will likely be inadequate for assessing risk, and more sophisticated data and models will be necessary for determining an SPR. The new SPR rule could lengthen the process and increase the cost of listing decisions due to the amount and types of information required.

These insights speak to the utility of many different metrics and the caveats that must be made when determining whether a species has an SPR relevant for listing under the ESA. Further research will be needed to determine whether these metrics will be easier to implement for different types of organisms and the reliability of different proxies for assessing the loss of the individuals in a portion of a species' range based on redundancy, resiliency, and representation.

Acknowledgments

Supporting Information

Description of criteria used to evaluate data availability present in species status assessments for metrics identifying significant portions of species' ranges (Appendix S1) and justification of ratings of data availability in species status assessments for calculating metrics measuring relative importance of portions of the species' range (Appendix S2) are available online. The authors are solely 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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