Beyond PVA: Why Recovery under the Endangered Species Act Is More than Population Viability

SHAYE WOLF, BRETT HARTL, CARLOS CARROLL, MAILE C. NEEL, AND D. NOAH GREENWALD

Recovery criteria under the Endangered Species Act are the objective, measurable targets for determining whether the recovery of listed species has been achieved. Existing criteria have been criticized as inconsistent and poorly supported. Recent proposals for improving those criteria have recommended framing them around population viability analysis (PVA) and setting criteria on the basis of extinction risk thresholds. Used in isolation, however, a PVA-centered approach is prone to limiting the scope of recovery, is too data intensive to be useful for most species, and risks misrepresenting normative recovery thresholds as objective. We recommend a framework based on the three Rs—the ecological principles of representation, resiliency, and redundancy—which makes use of multiple analytical approaches for setting recovery targets, including PVA when appropriate. We argue that the three Rs framework better fulfills the ESA's comprehensive recovery mandates for achieving geographic representation, ecosystem conservation, and threats abatement while overcoming data and budget limitations pervasive in recovery planning today.

Keywords: recovery plan, recovery criteria, Endangered Species Act, endangered species, population viability analysis

The fundamental purpose of the US Endangered Species Act (ESA) is not only to prevent extinction but also to recover species to the point that they are no longer threatened or endangered. To achieve these purposes, the act requires development of recovery plans "for the conservation and survival" of listed species (16 U.S.C. § 1533(f)(1)). These plans must specify the "objective, measurable criteria" by which it is determined that recovery has been achieved (16 U.S.C. § 1533(f)(1)(B)). Over the past 20 years, numerous reviews have identified shortcomings in recovery criteria, showing that they often lack a clear biological rationale; are inconsistently applied across species in ways that do not appear to be based in biology; are not sufficiently objective and measurable; and are set below the levels necessary for long-term persistence, ecological viability, and evolutionary capacity (Tear et al. 1995, Foin et al. 1998, Clark et al. 2002, Gerber et al. 2002, Neel et al. 2012, Himes Boor 2014).

To overcome these shortcomings, recent publications have recommended a more central use of population viability analysis (PVA) in recovery planning to provide objective, measurable recovery criteria (Doak et al. 2014, Himes Boor 2014). PVA is a quantitative model-based approach that uses demographic and abundance data to estimate the probability of extinction or a related measure of population viability such as quasiextinction (Beissinger and Westphal 1998, Morris and Doak 2002). Himes Boor (2014) recommended that PVA be used to provide the organizing framework for recovery plans. In this approach, PVA modeling results are used to develop recovery criteria that define a species with a chosen level of extinction risk. Moreover, the author suggests that PVA offers the only means to develop objective, measurable recovery criteria (Himes Boor 2014).

We agree that the failure to define and consistently employ a clear, transparent, science-based protocol for implementing recovery contributes to many of the problems with recovery criteria. We disagree, however, that PVA alone provides an adequate or practical overarching framework to overcome current shortcomings in recovery planning. First, a recurrent problem is the failure of criteria to fulfill the ESA's statutory mandates for recovery, which is not easily cured by a PVA-centered framework. Second, because of pervasive data limitations, PVA is too data-intensive to be possible or reliable for many listed species. Finally, PVA-derived recovery criteria are based on normative thresholds of extinction risk and do not inherently provide more scientifically robust or transparent criteria than do other methods.

Instead, we recommend a recovery-planning framework based on the conservation biology principles of representation, resiliency, and redundancy—the *three Rs*—for reducing extinction risk and maintaining self-sustaining

BioScience 65: 200–207.
doi:10.1093/biosci/biu218 Advance Access publication 21 January 2015

populations (Shaffer and Stein 2000). The three Rs framework is comprehensive enough to fulfill the ESA's recovery requirements for geographic representation, ecosystem conservation, and threats abatement. The framework can make use of PVA for determining recovery criteria but can also use other analytical approaches when PVA is not appropriate, given the resource-limited, data-poor environment typical of recovery planning. Although the existing recovery planning guidance document (NMFS 2010), written by the US Fish and Wildlife Service (USFWS) and the National Marine Fisheries Service (hereafter, *the services*) generally recommends the use of the three Rs, it provides no instruction on how these principles should be implemented. To realize the benefits of a three Rs approach, additional guidance to effect this approach is urgently needed.

Below, we discuss the recurrent failure of recovery criteria to fulfill the ESA's statutory requirements for recovery. We first review legal and policy considerations that are often ignored or discounted in discussions of recovery planning, because they set the stage for comparing a PVA-centered with a three Rs framework. We then discuss the limitations of a PVA-centered framework for providing an overarching framework for recovery. Finally, we present specific recommendations for developing objective, measureable criteria from the three Rs framework that meet the ESA's recovery mandates.

The ESA's recovery mandates

Any framework for recovery planning must fulfill the ESA's statutory recovery requirements, be based on the best available science, and be legally defensible as interpreted by the courts. The act requires the services to "conserve" threatened and endangered species and the ecosystems on which they depend (16 U.S.C. § 1531(b)), where "conserve" is defined as bringing to the point where the protections of the act are no longer needed (16 U.S.C. § 1532(3)). A recovered species is one that is no longer endangered or threatened, meaning that it is not currently "in danger of extinction… throughout all or a significant portion of its range" nor is it "likely to become" so "in the foreseeable future" (16 U.S.C. § 1532(6) and (20)). The act also requires that threats be eliminated or managed for a species to be considered recovered (16 U.S.C. § 1533(a)(1)). Finally, recovery plans must contain the "objective, measurable criteria which, when met, would result in a determination… that the species be removed from the list"; site-specific management actions; and time and cost estimates (16 U.S.C. § 1533(f)(1)(B)). In summary, recovery under the ESA requires a sufficiently low extinction risk (e.g., the species is not likely to become in danger of extinction in the foreseeable future) over an appropriate geographic extent (i.e., all significant portions of range), coupled with ecosystem conservation and threats abatement. The ESA does not define quantitative thresholds for achieving these goals, but both the statute and courts provide some guidance on what these components must encompass.

Geographic representation

The third in a series of federal laws designed to protect imperiled species, the Endangered Species Act of 1973 was the first to include a geographic component to endangerment by allowing a species to be protected if it was threatened or endangered in a "significant portion of its range," even if it was secure elsewhere. The 1966 and 1969 predecessors protected only species at risk of worldwide extinction (i.e., the Endangered Species Preservation Act of 1966, Pub. L. 89-669, and the Endangered Species Conservation Act of 1969, Pub. L. 91-135). Congress noted that this was "a significant shift" in how the services should evaluate species for listing, because it allowed the protection of species that were secure in some portions of their range but severely imperiled or extirpated elsewhere (H.R. Rep. No. 412, 93rd Cong., 1 Sess. (1973)). Consideration of a significant portion of a species' range is therefore important for determining recovery. If an *endangered* species is at risk throughout all or a significant portion of its range, it follows logically that a *recovered* species must be secure throughout all significant portions of its range (Vucetich et al. 2006, Carroll et al. 2010). Although "significant portion" and "range" are not explicitly defined under the ESA, the act's provisions for habitat acquisition, reintroduction, translocation, and the designation of critical habitat in areas unoccupied at the time of listing, as well as relevant case law (*Defenders of Wildlife v. Norton*, 258 F.3d 1136 (9th Cir. 2001)), indicate that Congress intended for recovery to be geographically broad in scope and to include the species' historic range in its consideration (Carroll et al. 2010).

The services have resisted definitions of "significant portion of its range" that would require them to uniformly consider the historic range in listing and recovery decisions (USFWS and NMFS 2014). However, failure to set recovery criteria for geographic representation in a consistent and biologically justified way can lead to significant disparities. For example, the USFWS recently proposed to delist the gray wolf (*Canis lupus*) in the lower 48 United States, even though it occupies only 5% of its historic range (Neel et al. 2012), but did not propose to delist the bald eagle (*Haliaeetus leucocephalus*) until populations were recovered in all five recovery regions that encompassed virtually all of its historic range (USFWS 2007). Given that both of these species were biologically viable at the global level when they were listed in the 1970s, there are no scientific reasons why the geographic scope of recovery varied so greatly.

Ecosystem conservation

Congress made clear that ecosystem conservation for listed species is fundamental: "The purposes of this Act are to provide a means whereby the ecosystems on which endangered species and threatened species depend may be conserved" (16 U.S.C. § 1531(b)). Ecosystem-focused criteria are important not only for ensuring sufficient habitat quantity, quality, and connectivity, but also for restoring the ecological function of species by maintaining abundance at a level that provides a particular ecosystem function (Soulé et al. 2005, Estes et al. 2010). If ecological function is not considered, a species could be declared *recovered* even while remaining functionally extinct. Restoring a species' ecological role is particularly important for strongly interactive species that are key to ecosystem structure and function such as keystone species, foundation species, ecosystem engineers, and top predators (Soulé et al. 2005, Carroll et al. 2006). A recent example is the ecosystem delisting criterion for the northern sea otter (*Enhydra lutris kenyoni*) in southwestern Alaska, which requires otter abundance to reach population levels that bring about a shift of more than half of otter habitat to a kelp-dominated state (USFWS 2010).

Threats abatement

A species can only be considered *recovered* when the five threat factors set forth by the ESA, including the loss of habitat or range, exploitation, disease, inadequacy of protective regulations, and other factors (16 U.S.C. § 1533(a)(1)) are eliminated or managed so that the species can persist without ESA protection. Recovery criteria that fail to address the threat factors and "measure whether threats… have been ameliorated" have been found unlawful (*Fund for Animals v. Babbitt*, 903 F. Supp. 96 (D.D.C. 1995) and *Defenders of Wildlife v. Babbitt*, 130 F. Supp. 2d 121 (D.D.C. 2001)). As was noted in the recovery planning guidance document (NMFS 2010), demographic recovery alone does not indicate that a species is secure from underlying threats. Listed species can meet population-based recovery criteria because of intensive management interventions even though major threats remain. For example, the California least tern (*Sterna antillarum browni*) has exceeded its numeric recovery goals by a factor of six, in large part because of predator control at nest sites and fencing to reduce human disturbance, but the root threats remain, and populations are highly dependent on intensive management (USFWS 2006). Likewise, Kirtland's warbler (*Setophaga kirtlandii*) has achieved population recovery criteria through brown-headed cowbird (*Molothrus ater*) control and prescribed burns to maintain jack pine habitat, whereas most underlying threats remain (USFWS 2012a). The USFWS has recommended downlisting for both species rather than delisting, because threat abatement has not been realized. In contrast, the Aleutian Canada goose (*Branta canadensis leucopareia*) was delisted in 2001 following the removal of nonnative foxes from its nesting islands, protection of its wintering habitat, and hunting closures, which removed the main threats to the species (USFWS 2001). These examples illustrate that recovery requires that threats be abated through improved extrinsic conditions (e.g. invasive species removed) or through the adoption of adequate regulatory mechanisms to address human behavior.

The services' recovery planning guidance

The recovery planning guidance document (NMFS 2010) affirms the act's broad mandate for recovery, defining it as "the process by which listed species and their ecosystems are restored and their future is safeguarded to the point that protections under the ESA are no longer needed." The guidance document (NMFS 2010) specifically directs recovery plans to take a "comprehensive approach" to recovery that includes threat abatement and ecosystem recovery and in which the species' historic and current range are considered. It states that recovery plans must "ensure the health of its habitat and ecosystem functions rather than the narrower view of looking at the species only." However, the guidance document (NMFS 2010) only requires that recovery criteria meet two standards: They must address the threats facing the species, although the document provides no specific direction on how to do so, and they must be measurable and objective, although the document provides little clarity as to what these terms mean. Therefore, there is clearly a need for the services to provide more-specific guidance on how recovery criteria should fulfill the ESA's recovery mandates.

PVA as a framework for recovery

Himes Boor (2014) recommended that recovery criteria be based on "population viability modeling methods that incorporate demographics, limiting factors, threats, future management actions, and uncertainty." Without this, she argued that recovery criteria "will continue to fall short of the ESA's objective, measurable mandate." When PVA is not possible because of data limitations, the structure and data requirements of PVA should be used as the organizing framework of the recovery plan, and recovery criteria should be expressed in the interim as an extinction risk threshold, whereby recovery occurs when a PVA model yields a probability of extinction less than X% over Y years (Himes Boor 2014).

We agree with Himes Boor (2014) that objective, measurable criteria should be quantitatively, temporally, spatially, and statistically specific, with explicit scientific justification. However, we see significant limitations with the practical application of a PVA-centered framework for setting recovery criteria that meet the ESA's mandates. First, a PVA-centered framework is prone to limiting the scope of recovery, because PVA does not address key components of recovery required under the act. PVA modeling methods estimate the likelihood that a population or populations will be above some minimum size at a given future time (Morris and Doak 2002). However, the statutory language of the ESA indicates that recovery is broader than populations meeting minimum abundance thresholds to exceed a chosen extinction risk threshold. Rather, it requires recovered populations to be geographically representative, ecologically functional, and evolutionary viable, for which threats are abated so that species can persist without the provisions of the act. The most commonly implemented count-based and structured PVAs are focused on the abundance and demography of single populations and fail to address species-level recovery. Complex PVA, such as multisite or spatially explicit PVA, have the potential to inform aspects of geographic distribution (e.g., the number and distribution of populations), ecosystem characteristics (e.g., patch size), and threats management (e.g., changes in mortality sources) needed to meet a specified extinction probability. However, these data-intensive models do not address key facets of recovery, such as the conservation and restoration of ecological and evolutionary processes and representation across the historic range. As such, PVA-based criteria run the risk of declaring the species *recovered* when one or a handful of populations meet an extinction-risk threshold but encompass only a small portion of a species' historic range and no longer meaningfully perform their ecosystem function.

Second, data inadequacies for most listed species—including the lack of basic abundance data required by even the simplest count-based PVAs—limit the use and reliability of PVA for setting recovery criteria that meet the ESA's recovery mandates (Beissinger and Westphal 1998, Morris et al. 2002, Crone et al. 2011, Flather et al. 2011, Neel et al. 2012, Zeigler et al. 2013). For example, 67%–98% of 1174 species with recovery plans historically lack data on population size, at listing or at plan writing (Neel et al. 2012). Time series data for abundances and stage- or age-based demographic rates are even scarcer, and when they are available, demographic data typically come from one or a few populations over short time frames (Crone et al. 2011, Ziegler et al. 2013). Because of these data limitations, PVA is not feasible for most listed species. Furthermore, even when PVA is applied, it may not provide sufficiently precise or accurate estimates of the demographic status or the minimum population size needed to stay above a chosen extinction probability for even one population or a few populations (Crone et al. 2011, Zeigler et al. 2013) and would fail to inform range-wide recovery. For example, in a recent review, Zeigler and colleagues (2013) found that of 280 published PVAs for listed and unlisted plant species, most were parameterized with 5 years or less of demographic data and did not address important factors, such as stochasticity, density dependence, seed banks, vegetative reproduction dormancy, threats, or management strategies (Zeigler et al. 2013). Because population growth rates for different populations of the same species or for the same population at different time periods often were significantly different, PVA estimates from limited spatiotemporal data cannot be generalized over a species' range or over long time scales in ways that inform recovery criteria (Johnson et al. 2010, Zeigler et al. 2013).

We are particularly concerned with the recommendation by Himes Boor (2014) to express recovery criteria for species for which PVA is not possible solely in terms of a viability standard, with the instruction that population and threat reduction targets needed to yield that level of risk be specified when sufficient data have been collected. Because of the ubiquity of data limitations, this approach would leave the majority of listed species without concrete recovery targets for the number, size, or distribution of populations, no specific threat reduction targets, and no clear way to gauge progress toward recovery. This strategy is legally and practically problematic, because it would allow the services to avoid substantial recovery planning by deferring decisionmaking and target-setting based on the promise future PVA analyses in plan revisions that may never be undertaken. Indeed, the ESA, itself, does not require revisions to recovery plans. Combined with minimal annual funding allocation for most species (Schwartz 2008), the likelihood that the services will update recovery plans and revise placeholder viability criteria is low. Overall, only 20% of all recovery plans have been updated (see the supplemental material). Recent status reviews of 15 South Florida plants illustrate that "temporary" placeholder viability-based recovery criteria are typically never refined (see the supplemental material).

Finally, we disagree with Himes Boor (2014) that PVA yields recovery criteria that are more scientifically robust and transparent than "any other approaches used to set recovery thresholds." PVA modeling results are highly dependent on data quality (i.e., the use of proxy data, age and stage classes, variance estimates, the inclusion of catastrophes, differences in sampling protocol), data set length, modeling assumptions, model structure, and validation of results and assumptions (Beissinger and McCullough 2002). These important methodological caveats are not always acknowledged or transparent to those without technical expertise, including managers implementing recovery plans, although they can lead to different population forecasts and management recommendations.

Moreover, targets for PVA-centered criteria are based on an "acceptable" extinction risk threshold, and do not escape the normative decisionmaking required of other methods of setting thresholds. As was noted by Shaffer (1981) in his original development of PVA, there is no exact value that connotes viability. Although having a lower extinction risk indicates that a species is more secure, there is no scientific basis for claiming that a 6% probability of extinction over 100 years equates to threatened or endangered status, whereas a 5% probability equates to viability and recovery. Moreover, PVA may fundamentally mislead a decisionmaker regarding the true risks to a species. A use of short time horizons in PVA may falsely inflate the perceived security of the species. For example, a 95% chance of persisting for 100 years may suggest a sufficiently low extinction risk to justify delisting. However, that same PVA—if run over a longer time frame—may also demonstrate that a species only has a 20% chance of persistence for 200 years and only 6% chance of persistence over 300 years (Shaffer and Samson 1985).

When the services have specified extinction risk thresholds in recovery criteria, they have used a wide spectrum of normative thresholds. For example, the viability standard for delisting the dwarf lake iris (*Iris lacustris*; less than a 5%

probability of extinction in 20 years) is less precautionary than that for the Hawaiian crow (*Corvus hawaiiensis*; less than a 5% probability of extinction in 100 years), and both are less precautionary than for the Steller's eider (*Polysticta stelleri*; less than a 1% probability of extinction in 100 years; USFWS 2002, 2009, 2012b). Downlisting criteria for 15 South Florida plants (20%–90% probability of persistence for 100 years) are particularly problematic because of the large range of extinction risk deemed acceptable within each species and the low probability of persistence considered acceptable (see the supplemental material). In contrast, Shaffer (1981) "tentatively and arbitrarily" proposed a definition of a viable population as one having a 99% probability of persisting for 1000 years. If PVA-centered criteria are used, we support application of a more uniform, precautionary, and transparent viability standard across listed taxa, in place of the *ad hoc* and relatively nonprecautionary risk thresholds discussed above.

The three Rs approach to recovery

We recommend a more holistic and comprehensive framework for recovery planning based on the conservation biology principles of representation, resiliency, and redundancy (the *three Rs*) proposed by Shaffer and Stein (2000) for lowering extinction risk and maintaining self-sustaining populations. In essence, the three Rs require a recovered species to be present in multiple large, resilient populations arrayed across a range of ecological contexts. Representation requires the protection of populations across the full range of ecological settings of a species' range, meeting the ESA's geographic representation mandate. Resiliency encompasses population-specific attributes that increase long-term persistence in the face of disturbance. Resiliency can also address related issues regarding threats abatement and recovery of ecologically effective populations. Redundancy requires establishing multiple populations in each ecological setting to spread extinction risk and to increase species' viability. The three Rs are rooted in findings from ecological theory and empirical studies (e.g., Diamond 1975, Ellstrand and Elam 1993, Gaston 1994, Frankham 2005) that, all else being equal, larger range, more populations, larger populations, larger habitat areas, sufficient gene flow, and more intact ecosystems all lower extinction risk.

Any successful recovery planning framework must explicitly require that recovery criteria fulfill the ESA's recovery mandates. In order to meet these mandates, a three Rs framework must require that all plans include a standard checklist of recovery criteria under each of the three Rs that are objective and measurable, meaning quantitative and temporally and spatially specific, and that set targets for geographic representation, ecosystem recovery, and threats abatement; provide a range of analytical tools for determining the recovery targets for each criteria which can accommodate data constraints; include an explicit justification for each criterion that explains the scientific rationale and analytical approach for setting that target; and require future data collection, collection protocols, and analyses to fill important data gaps needed to better inform recovery.

A primary advantage of a three Rs framework is that criteria can be developed using multiple analytical approaches—including PVA—as appropriate, depending on the data constraints for each listed species. By allowing for a range of analytical approaches, recovery planners can set quantitative population and threat reduction criteria based on the best-available information and can require future data collection and analyses when needed. We recognize that setting meaningful recovery targets is challenging in a data-limited environment. However, we argue that provisional quantitative targets, even when they are chosen on the basis of expert opinion (e.g., Martin et al. 2012) or limited historical information on abundance and range, better serve imperiled species in need of immediate conservation action than the placeholder viability standards that would predominate in a PVA-centered approach. Provisional targets can be refined when resources and information are available to update the recovery plan with more data-driven analyses. We also recognize that all recovery targets, regardless of the analytical approach, involve both normative and scientific components. The normative dimension, influenced by societal values and risk tolerance, specifies the "acceptable" extinction risk (i.e., how much is enough to achieve recovery?), whereas the scientific dimension informs the conservation measures that will lower extinction risk and determines whether a species meets that level of risk (Vucetich et al. 2006). We recommend that the rationale for each criterion clearly distinguish between the scientific and normative bases for those targets.

In tables 1 and 2, we recommend recovery criteria under the three Rs framework that should be included in all recovery plans, including examples of quantitative criteria, analytical approaches for setting targets, and the supporting scientific frameworks. Specifically, we recommend that representation criteria include quantitative targets for protecting and restoring populations across the full range of ecoregions or ecological communities of a species' historic range. Representation criteria should specify the percentage of the historic and current range over which recovery will occur and why some portions are considered "significant" and some not. Achieving representation criteria can lower extinction risk by protecting genetic diversity, local adaptations, and ecological interactions across the range (Carroll et al. 2010).

Redundancy criteria should include quantitative targets for establishing multiple populations or habitat areas in each ecological setting. Targets for the number of populations in each ecological setting can be informed by current and historic population distribution and by viability-based approaches such as incidence function models and spatially explicit metapopulation models when data are available. Redundancy criteria can lower extinction risk by buffering populations from environmental variation, reducing the chance of extirpation from catastrophic events and

Table 1. Recommendations for applying the concepts of representation and redundancy to developing objective and measurable recovery criteria.

Principle	Tenet	Recommended measures	Example objective and measurable recovery criteria	Example scientific foundation and analytical tools	References
Representation	Represent historic range	Percentage of historic range over which recovery will occur	Restore species to a range size that represents x% of historic range	Abundance–distribution relationships	Brown (1984), Gaston (1996), Channell and Lomolino (2000)
Representation	Represent full range of ecological settings across historic range	Number or percent of ecological settings across the historic range over which recovery will occur	Protect and restore at least one population in each ecoregion or vegetation type across the historic range; protect and restore x% of the habitat for the species in each ecoregion or vegetation type across the historic range; maintain the elevational range occupied by the species	Risk spreading by reducing covariance among populations in the same habitat; inclusion of genetic diversity in populations locally adapted to different environments	Pressey et al. (1981), Neel and Cummings (2003)
Redundancy	Protect multiple populations	Number of populations, occurrences, or sites in different geographic areas and ecological settings	Maintain x populations in each specified ecological type	Abundance–distribution relationships; metapopulation theory	Brown (1984), Hanski et al. (1995)

Note: The references cited in this table are available in the supplemental material.

Table 2. Recommendations for applying the concept of resiliency to developing objective and measurable recovery criteria.

Principle	Tenet	Recommended measures	Example objective and measurable recovery criteria	Example scientific foundation and analytical tools	References
Resiliency	Population size: Maintain higher abundance	Individual abundance within populations	Maintain a harmonic mean of x individuals in each population for y years	Small population and declining population paradigms	Soulé (1987), Gabriel and Burger (1992), Blackburn and Gaston (2002), Matthies et al. (2004)
Resiliency	Population stability: Maintain stable and increasing populations	Population stability and growth	Maintain populations that are stable or increasing through x years	PVA; occupancy modeling	Shaffer (1981), Noon et al. (2012)
Resiliency	Maintain or restore historic connectivity	Distribution of distances among habitat patches and/or a specified effective connected area or connectivity rate	Ensure the median distance among occupied habitat patches does not increase by more than x%; restore habitat such that the connectivity-corrected habitat amount is increased by x% to reflect historic conditions; restore a connectivity rate of greater than x genetically effective migrants per generation	Effects of fragmentation and reduced gene flow; graph theoretic approaches to quantifying connectivity; incidence function models; PVA	Urban and Keitt (2001), Pascual-Hortal and Saura (2006), Ferrari et al. (2007), Saura and Pascual-Hortal (2007), Saura et al. (2011), Carroll et al. (2013), Neel et al. (2014)
Resiliency	Conserve ecosystems on which listed species depend	Habitats of appropriate type, size, and quality to include necessary ecosystem components to support listed species	Manage x number of habitat patches to maintain or restore canopy size distribution such that y% of tree canopy is in the z size class to provide nest trees	Species-habitat relationships; niche theory	Grinnell (1917), Morrison et al. (2006)
Resiliency	Maintain or restore species' ecological roles	Measures of ecosystem function or species interaction	Ensure listed species is sufficiently abundant to maintain x% of its habitat in a kelp-dominated state	Ecologically effective density	Soulé et al. (2005), Estes et al. (2010)
Resiliency	Eliminate or manage threats	Reduce or eliminate the probability of a threat occurring and/or reduce the magnitude of its effects. Ensure that sufficient management regime is in place to keep threat in abatement for foreseeable future	Reduce probability of conversion of habitat to suburban development by protecting x% of remaining unprotected habitat; reduce magnitude of invasive species effects by removing species x from y acres of habitat annually	Expert knowledge; Bayesian network modeling; multiple competing hypotheses; PVA	Peery et al. (2004), Marcot et al. (2006), Amstrup et al. (2010), Fuentes and Cinner (2010), Martin et al. (2012)

Note: The references cited in this table are available in the supplemental material.

increasing the probability of maintaining natural gene flow and ecological processes.

Resiliency criteria should include targets for population size and population trend. Establishing larger populations helps buffer against genetic, demographic, and environmental stochasticity. Maintaining stable or growing populations over a specified time period is important to understanding whether recovery will continue over the long term. PVA can potentially play a role in guiding the selection of population targets when sufficient data are available. Where data are not sufficient for PVA, historic population sizes can provide guidance for the size of individual populations. Tools for helping assess trends across multiple populations include occupancy modeling based on species presence and absence data (Noon et al. 2012) and multisite PVA. Resiliency criteria should also include criteria for habitat quality (i.e., the extent and distribution) and connectivity (i.e., links to other populations), because larger total amounts and patches of habitat help support larger, genetically diverse populations more able to withstand perturbations. Tools for assessing habitat extent, distribution, and connectivity include graph theoretic models (e.g., Neel et al. 2014), incidence function models, and spatially explicit population models. Ecosystem criteria can also include targets for restoring species' ecological roles by establishing ecologically effective densities (i.e., enough individuals over a sufficiently wide geographic distribution to restore the species' ecological role), particularly for keystone species, foundation species, ecosystem engineers, and top predators (Soulé et al. 2005, Estes et al. 2010).

Criteria for threat abatement derived from a formal threat assessment and prioritization, which is recommended by the recovery planning guidance document (NMFS 2010), can be integrated into a comprehensive three Rs analysis. Such an assessment would require explicit measures of how each threat has been eliminated or will be controlled now and in the foreseeable future and require that a management regime be in place to ensure that the threats do not return. PVA can inform threat reduction targets when sufficient data exist on how threats affect population growth or vital rates, but other methodologies for conducting threat assessment, such as Bayesian network modeling (Marcot et al. 2006) and expert opinion (Martin et al. 2012), can inform targets when demographic data are limited.

The three Rs framework is also well suited to addressing emerging threats to species, such as climate change and ocean acidification, for which scientific data and understanding are rapidly evolving. Many of the conservation actions required by recovery criteria under the three Rs approach—such as increasing a population's size, range, connectivity, and habitat restoration—are important steps for reducing extinction risk and increasing resilience to climate change (Heller and Zavaleta 2009, Pearson et al. 2014). In addition, the flexibility of approaches under the three Rs for setting the threat reduction targets allows planners to set criteria for reducing climate threats, such as actions to reduce greenhouse gas emissions and increase a species' resilience to climate change (Povilitis and Suckling 2010), even when sufficient data are not available to conduct more data-intensive, climate-based PVA (e.g., Brook et al. 2009).

Conclusions

There are many factors that limit the fulfillment of the ESA's mandate for recovery, including insufficient funding, poor enforceability, and challenges to on-the-ground implementation. In addition, a fundamental limitation continues to be recovery criteria that are vague or too lenient to ensure the long-term persistence of species across the landscape (Neel et al. 2012, 2013). Although PVA may be useful as a component of comprehensive recovery planning when adequate data are available, we recommend against its use as an overarching framework for developing recovery criteria. PVA is particularly suited to ranking the importance of threats or management actions, identifying life stages or demographic rates that may be limiting population growth in order to target management of those stages, and identifying gaps in data and monitoring that can be used to improve data collection and analysis (Beissinger and Westphal 1998, Morris et al. 2002). As a way forward, we urge scientists and conservation practitioners to continue to develop rigorous analytical tools, including PVA, to support recovery criteria under a three Rs framework that provides a practical means of addressing the ESA's comprehensive recovery mandates given the significant data limitations and budget constraints inherent in recovery planning today.

Supplemental material

The supplemental material is available online at *http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biu218/-/DC1*.

References cited

Beissinger SR, McCullough DR, eds. 2002. Population Viability Analysis. University of Chicago Press.

Beissinger SR, Westphal MI. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62: 821–841.

Brook BW, Akçakaya HR, Keith DA, Mace GM, Pearson RG, Araújo MB. 2009. Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. Biology Letters 5: 723–725.

Carroll C, Phillips MK, Lopez-Gonzalez CA, Schumaker NH. 2006. Defining recovery goals and strategies for endangered species: the wolf as a case study. BioScience 56: 25–37.

Carroll C, Vucetich JA, Nelson MP, Rohlf DJ, Phillips MK. 2010. Geography and recovery under the US Endangered Species Act. Conservation Biology 24: 395–403.

Clark JA, Hoekstra JM, Boersma PD, Kareiva P. 2002. Improving US Endangered Species Act recovery plans: Key findings and recommendations of the SCB recovery plan project. Conservation Biology 16: 1510–1519.

Crone EE, et al. 2011. How do plant ecologists use matrix population models? Ecology Letters 14: 1–8.

Diamond JM. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7: 129–146.

Doak DF, Himes Boor GK, Bakker VJ, Morris WF, Louthan A, Morrison SA, Stanley A, Crowder LB. 2014. Recommendations for improving recovery criteria under the US Endangered Species Act. BioScience 65: XXX–XXX.

Ellstrand NC, Elam DR. 1993. Population genetic consequences of small population size: implications for plant conservation. Annual Review of Ecology and Systematics 24: 217–242.

Estes JA, Tinker MT, Bodkin JL. 2010. Using ecological function to develop recovery criteria for depleted species: Sea otters and kelp forests in the Aleutian Archipelago. Conservation Biology 24: 852–860.

Flather CH, Hayward GD, Beissinger DR, Stephens PA. 2011. Minimum viable populations: Is there a 'magic number' for conservation practitioners. Trends in Ecology and Evolution 26: 307–316.

Foin TC, Riley SPD, Pawley AL, Ayres DR, Carlsen TM, Hodum PJ, Switzer PV. 1998. Improving recovery planning for threatened and endangered species. BioScience 48: 177–184.

Frankham R. 2005. Genetics and extinction. Biological Conservation 126: 131–140.

Gaston KJ. 1994. Geographic range sizes and trajectories to extinction. Biodiversity Letters 2: 163–170.

Gerber LR, Hatch LT. 2002. Are we recovering? An evaluation of recovery criteria under the US Endangered Species Act. Ecological Applications 12: 668–673.

Heller NE, Zavaleta ES. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142: 14–32.

Himes Boor G. 2014. A framework for developing objective and measurable recovery criteria for threatened and endangered species. Conservation Biology 28: 33–43.

Johnson HE, Mills LS, Stephenson TR, Wehausen JD. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20: 1753–1765.

Marcot BG, Steventon JD, Sutherland GD, McCann RK. 2006. Guidelines for developing and updating Bayesian belief networks applied to ecological modeling and conservation. Canadian Journal of Forest Research 36: 3063–3074.

Martin TG, Burgman MA, Fidler F, Kuhnert PM, Low-Choy S, McBride M, Mengersen K. 2012. Eliciting expert knowledge in conservation science. Conservation Biology 26: 29–38.

Morris WF, Doak DF. 2002. Quantiative Conservation Biology. Sinauer.

Morris WF, Bloch PL, Hudgens BR, Moyle LC, Stinchcombe JR. 2002. Population viability analysis in endangered species recovery plans: Past use and future improvements. Ecological Applications 12: 708–712.

Neel MC, Che-Castaldo JP. 2013. Predicting recovery criteria for threatened and endangered plant species on the basis of past abundances and biological traits. Conservation Biology 27: 385–397.

Neel MC, Leidner AK, Haines A, Goble DD, Scott JM. 2012. By the numbers: How is recovery defined by the US Endangered Species Act? BioScience 62: 646–657.

Neel M[C], Tumas HR, Marsden BW. 2014. Representing connectivity: quantifying effective habitat availability based on area and connetivity for conservation status assessment and recovery. PeerJ (art. e622) doi:10.7717/peerj.622

[NMFS]. National Marine Fisheries Service. 2010. Interim Endangered and Threatened Species Recovery Planning Guidance, version 1.3. NMFS.

Noon BR, Bailey LL, Sisk TD, McKelvey KS. 2012. Efficient species-level monitoring at the landscape scale. Conservation Biology 26: 432–441.

Pearson RG, et al. 2014. Life history and spatial traits predict extinction risk due to climate change. Nature Climate Change 4: 217–221.

Povolitis A, Suckling K. 2010. Addressing climate change threats to endangered species in U.S. recovery plans. Conservation Biology 24: 372–376.

Schwartz MW. 2008. The performance of the Endangered Species Act. Annual Review of Ecology, Evolution, and Systematics 39: 279–99.

Shaffer ML. 1981. Minimum population sizes for species conservation. BioScience 31: 131–134.

Shaffer ML, Samson FB. 1985. Population size and extinction: A note on determining critical population sizes. American Naturalist 125: 144–152.

Shaffer ML, Stein B. 2000. Safeguarding our precious heritage. Pages 301–322 in Stein BA, Kutner LS, Adams JS, eds. Precious Heritage: The Status of Biodiversity in the United States. Oxford University Press.

Soulé ME, Estes JA, Miller B, Honnold DL. 2005. Strongly interacting species: conservation policy, management, and ethics. BioScience 55: 168–176.

Tear TH, Scott JM, Hayward PH, Griffith B. 1995. Recovery plans and the Endangered Species Act: Are criticisms supported by data? Conservation Biology 9: 182–195.

[USFWS] US Fish and Wildlife Service. 2001. Final rule to remove the Aleutian Canada goose from the federal list of endangered and threatened wildlife. Federal Register 66: 15656.

———. 2002. Steller's Eider Recovery Plan. USFWS.

———. 2006. California Least Tern (*Sternula antillarum browni*) 5-Year Review Summary and Evaluation. USFWS.

———. 2007. Endangered and threatened wildlife and plants; removing the bald eagle in the lower 48 from the list of endangered and threatened wildlife, final rule. Federal Register 72: 37346.

———. 2009. Revised Recovery Plan for the ʻAlala (*Corvus hawaiiensis*). USFWS.

———. 2010. Draft Recovery Plan for the Southwest Alaska DPS of the Northern Sea Otter (*Enhydra lutris kenyoni*). USFWS.

———. 2012a. Kirtland's Warbler (*Dendroica kirtlandii*) 5-Year Review Summary and Evaluation. USFWS.

———. 2012b. Dwarf lake iris (*Iris lacustris)* Draft Recovery Plan. USFWS.

[USFWS and NMFS] US Fish and Wildlife Service and National Marine Fisheries Service. 2014. Final policy on interpretation of the phrase "significant portion of its range" in the Endangered Species Act's definitions of "endangered species" and "threatened species." Federal Register 79: 37577.

Vucetich JA, Nelson MP, Phillips MK. 2006. The normative dimension and legal meaning of *endangered* and *recovery* in the US Endangered Species Act. Conservation Biology 20: 1383–1390.

Zeigler SL, Che–Castaldo JP, Neel MC. 2013. Actual and potential use of population viability analyses in recovery of plant species listed under the US Endangered Species Act. Conservation Biology 27: 1265–1278.

Shaye Wolf (swolf@biologicaldiversity.org) is the climate science director, Brett Hartl is the endangered species policy director, and D. Noah Greenwald is endangered species program director at the Center for Biological Diversity, based in Tucson, Arizona. Carlos Carroll is the director of the Klamath Center for Conservation Research, in Orleans, California. Maile C. Neel is an associate professor in the Department of Plant Science and Landscape Architecture and the Department of Entomology at the University of Maryland, in College Park.