Elemental Conservation Units: Communicating Extinction Risk without Dictating Targets for Protection

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Abstract: *Conservation biologists mostly agree on the need to identify and protect biodiversity below the species level but have not yet resolved the best approach. We addressed 2 issues relevant to this debate. First, we distinguished between the abstract goal of preserving the maximum amount of unique biodiversity and the pragmatic goal of minimizing the loss of ecological goods and services given that further loss of biodiversity seems inevitable. Second, we distinguished between the scientific task of assessing extinction risk and the normative task of choosing targets for protection. We propose that scientific advice on extinction risk be given at the smallest meaningful scale: the elemental conservation unit (ECU). An ECU is a demographically isolated population whose probability of extinction over the time scale of interest (say 100 years) is not substantially affected by natural immigration from other populations. Within this time frame, the loss of an ECU would be irreversible without human intervention. Society's decision to protect an ECU ought to reflect human values that have social, economic, and political dimensions. Scientists can best inform this decision by providing advice about the probability that an ECU will be lost and the ecological and evolutionary consequences of that loss in a form that can be integrated into landscape planning. The ECU approach provides maximum flexibility to decision makers and ensures that the scientific task of assessing extinction risk informs, but remains distinct from, the normative social challenge of setting conservation targets.*

Keywords: conservation policy, designatable unit, distinct population segment, ecological exchangeability, elemental conservation unit, endangered species, evolutionarily significant unit, replaceability

Unidades de Conservación Elementales: Comunicando el Riesgo de Extinción sin Imponer Objetivos para Protección

Resumen: *Los biólogos de la conservación en general están de acuerdo con la necesidad de identificar y proteger la biodiversidad por debajo del nivel de especies pero aun no han resuelto cuál es el mejor método. Abordamos dos temas relevantes de este debate. Primero, distinguimos entre la meta abstracta de preservar la máxima cantidad de biodiversidad única y la meta pragmática de minimizar la pérdida de bienes y servicios ecológicos considerando que la pérdida de biodiversidad parece inevitable. Segundo, distinguimos entre la tarea científica de evaluar el riesgo de extinción y la tarea normativa de seleccionar objetivos para protección. Proponemos que se proporcione asesoría científica sobre el riesgo de extinción en la escala significativa más pequeña: la unidad de conservación elemental (UCE). Una UCE es una población demográficamente aislada cuya probabilidad de extinción en una escala de tiempo de interés (por decir, 100 años) no es afectada sustancialmente por la inmigración natural desde otras poblaciones. Dentro de este marco de tiempo, la pérdida de una UCE pudiera ser irreversible sin la intervención humana. La decisión de la sociedad de proteger una UCE debiera reflejar valores humanos que tienen dimensiones sociales, económicas y políticas. Los científicos pueden informar sobre esta decisión proporcionando consejo sobre la probabilidad de que una UCE se pierda y de las consecuencias ecológicas y evolutivas de esa pérdida de manera que puedan ser*

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integradas a la planificación del paisaje. El método UCE proporciona máxima flexibilidad a los tomadores de decisiones y asegura que la tarea científica de evaluar el riesgo de extinción proporciona información, pero permanece distinta de, al reto social normativo de definir objetivos de conservación.

Palabras Clave: especies en peligro, intercambio ecológico, política de conservación, reemplazamiento, segmento poblacional distinto, unidad de conservación elemental, unidad designable, unidad evolutivamente significativa

Conservation Goals and Human Values

What biodiversity should humanity conserve? If the goal is to protect the maximum amount of unique biodiversity and irreplaceable evolutionary legacy, then choosing targets for protection is primarily a scientific matter. For instance, conservation units have been defined based on evolutionary vicariance with the expectation that more unique adaptations will have arisen through independent evolution in ancient lineages than in recent lineages (e.g., Moritz 2002). Nevertheless, given that expanding human populations continue to erode biodiversity, a more urgent and pragmatic goal for conservation might be to minimize the undesirable consequences of losing biodiversity. Human welfare is most influenced through the direct and indirect goods and services that wildlife provide. For example, Norton (1995) claims that no environmental value is more defensible than the sustainability principle, which asserts that "each generation has an obligation to protect productive ecological and physical processes necessary to support options necessary for future human freedom and welfare." On this view choosing appropriate targets for protection requires scientific advice about the components of biodiversity as well as appropriate consideration of the importance of these components to human society.

Some conservationists also emphasize the intrinsic value of biodiversity (e.g., Callicott 1989) and the importance of long-term evolutionary potential (Frankel 1974; Erwin 1991). We suggest that these considerations warrant less attention in practical decisions about conservation. Ethical arguments for the intrinsic value of populations or species, implying a moral obligation to maintain biodiversity, still lack a convincing rational foundation (Norton 1995). Similarly, uncertain are our obligations to generations of humans in the further future (Parfit 1984, Mulgan 2006). In contrast, rational arguments do provide decisive reasons to act to maintain biological diversity for human utility in the immediate future, at least over the next 100 years (Norton 1991); to consider the welfare of all sentient organisms by giving equal consideration to relevant interests (Singer 1993); and to resolve ethically conflicts that inevitably arise between the legitimate interests of humans and sentient nonhumans (Franklin 2005). Thus, our most decisive (rational) arguments for conservation all pertain to the ecological roles of biodiversity and to the ethical treatment of other organisms, not to evolutionary history or to evolutionary future per se. We acknowledge the need to maintain evolutionary processes (e.g., adaptation) that are essential to maintaining ecological processes, but we place greater emphasis on ecological than evolutionary values in biodiversity conservation.

Conserving Biodiversity below the Species Level

In determining which components of biodiversity are essential for maintaining ecological processes, conservation biologists face challenges related to both the structure and function of biodiversity. The structure of biodiversity is hierarchical, and the taxonomic species category is only one of a number of abstract levels. Species are not real entities like genes, organisms, or populations, but categories or hypotheses about evolutionary groups (Hey 2001). In practice, species nomenclature is often inconsistent across taxa, reflecting uncertainty in the ability or willingness of scientists to differentiate various forms of organisms (splitters vs. lumpers). Species often comprise widely divergent populations with different local ecological roles, adaptations, and evolutionary histories. Targeting protection at only the species level therefore neglects structural and functional components of biodiversity. Population diversity is declining about 10 times faster than species diversity (Hughes et al. 1997; Ceballos & Ehrlich 2004), and this loss of populations poses a more serious threat than is reflected in the loss of species (Meffe & Carroll 1997).

Norton (1998) describes how the focus of protecting biological resources has evolved from protecting single species to sustaining ecosystem health and compares the merits of moving from endangered-species legislation to alternative legislation that protects ecosystems, processes, or populations. He considers it folly to dismantle protection of endangered species until ecosystem-level characteristics can be defined in a scientifically and politically acceptable manner. He also dismisses legislation to protect endangered populations on the grounds that it would be too expensive to protect every population.

We recommend shifting the focus of conservation from species to populations because ecological processes at the level of populations (rather than species) sustain the ecosystem services that benefit humans (Diaz et al. 2006). Nevertheless, we recognize that populations themselves are not objects for conservation and that not all populations can be protected. Instead, we view populations as the building blocks for conservation planning. We propose a framework for assessing the probability and biological consequences of losing populations and, thus, for providing the scientific information that decision makers need to protect the components of biodiversity that are most valuable to humanity (and in principle other sentient creatures).

Conflating Tasks

Scientific assessments of biodiversity tend to be concerned with global evolutionary values instead of locally important ecosystem services (Vermeulen & Koziell 2002). When large conservation units based on evolutionary criteria become the targets for protection, the scientific task of assessing extinction risk is conflated implicitly with the normative task of setting priorities for conservation, and other values might be preempted. For example, an endangered lineage of Pacific salmon that qualifies as an evolutionarily significant unit (ESU) because of its evolutionary distinctiveness (Waples 1991) will be protected under the U.S. Endangered Species Act (ESA) independent of its ecological value, which might be considerably less than that of other endangered populations that do not qualify individually as ESUs. Our concern parallels that of Vucetich et al. (2006), who argue that "specifying the conditions for endangerment (i.e., acceptable and unacceptable levels of extinction risk) is a fundamentally normative determination" and that the requirement within the ESA "to determine endangerment 'solely on the basis of the best scientific and commercial data available' does not mean scientists have exclusive right to determine the normative dimensions of specifying the conditions of extinction." These concerns reflect the view that conservation is not primarily about biology, but about people and the choices they make for themselves (Balmford & Cowling 2006).

The Elemental Conservation Unit Approach

We propose a 6-step approach that delineates science and society's conservation responsibilities and improves the communication of science advice to decision makers as part of adaptive management (Fig. 1): step 1, identify the elemental conservation unit (ECU) for the time frame of concern based on knowledge of population structure and isolation; step 2, assess threat status, a proxy for the probability that the ECU will become extinct within this time frame given existing threats and demography; step 3, evaluate on the basis of ecological and evolutionary criteria the potential for recovery or replacement of the ECU; step 4, evaluate the direct or indirect ecological and evolutionary value of the ECU to humans and thus identify the biological consequences of its loss; step 5, designate the full conservation status for each ECU with terminology (see Table 1) that captures science advice from steps 2 to 4; and step 6, inform (but not lead) the public process

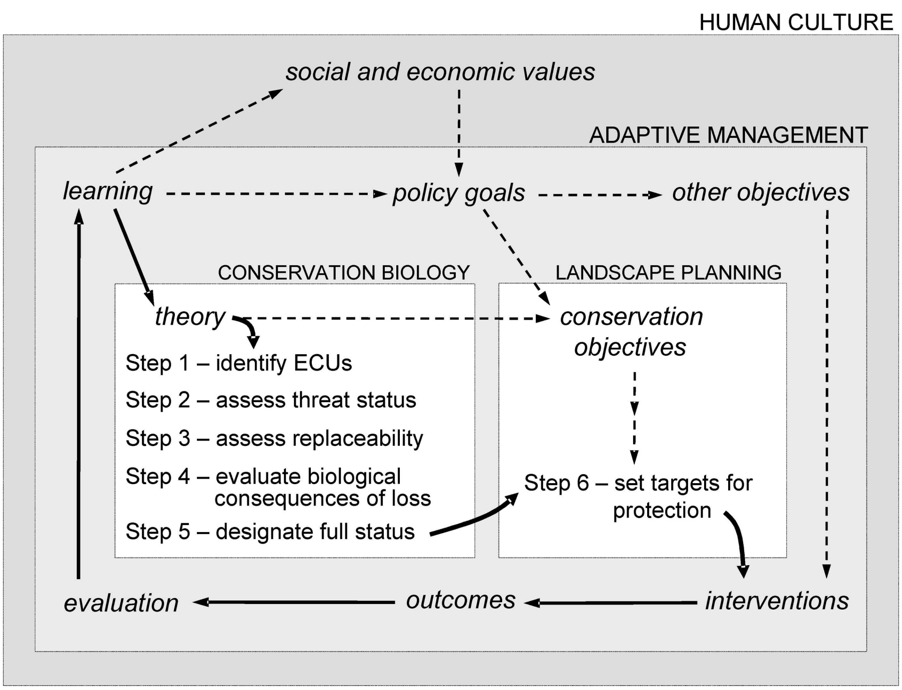

Figure 1. Flow chart of the elemental-conservation-unit approach to designating conservation status (steps 1–6). The chart illustrates how conservation biologists could inform landscape planners within a context of adaptive management to sustain ecosystem benefits.

Table 1. Definitions of key terms.

Entities
- DPS: distinct population segment; entity below the species level that is eligible for protection under the U.S. Endangered Species Act
- DU: designatable unit (sensu Green 2005); entity below the species level that is eligible for protection under the Canadian Species at Risk Act
- ecolog: an ECU (elemental conservation unit) that is ecologically exchangeable with another ECU; exchangeability might exist in both directions (reciprocal ecolog) or be limited to one direction (donor and recipient ecologs) (Fig. 2)
- ecotype: an ECU (elemental conservation unit) that is not ecologically exchangeable with any other ECU (Fig. 2)
- ESU: evolutionarily significant unit (sensu Waples 1991); entity below the species level that is eligible for protection under the U.S. Endangered Species Act as a DPS for Pacific salmon
- ECU: elemental conservation unit; a demographically isolated population whose probability of extinction over the time scale of interest (say 100 years) is not substantially affected by natural immigration from other populations

Modifiers (Fig. 3)
- exchangeable: having genetic and phenotypic adaptations for population viability and ecological function in another ecosystem such that ecological processes are not compromised (see ecolog)
- nonreplaceable: indicates ecological processes could not be restored either because no donor ecolog exists or because no suitable habitat exists
- nonsubstitutable: not ecologically exchangeable (see ecotype)
- recoverable: indicates a transplantable ecolog and suitable habitat exist such that ecological processes could be restored, likely without change in evolutionary potential
- replaceable: indicates a substitutable ecolog and suitable habitat exist such that ecological processes could be restored but with some change in evolutionary potential
- substitutable: ecologically exchangeable but with some change in evolutionary potential given the different evolutionary history
- transplantable: ecologically exchangeable with no expected change in evolutionary potential given the similar evolutionary history

of setting targets for protection at the landscape or bioregional level. Step 6 allows biologists to exercise their legitimate role as educators and providers of information without dictating society's priorities for conservation action.

Step 1: Identify Elemental Conservation Units

The ECU is the smallest population unit for which extinction risk can be assessed independently of other population units. We suggest ECUs are the most appropriate targets for risk assessment for 2 reasons. First, ECUs are self-sufficient gene pools whose fate determines where the species exists on the landscape. Second, knowing the conservation status of ECUs allows decision makers maximum flexibility to identify conservation actions that serve the greater public interest, given that population units targeted for protection may be equal to or higher, but not lower, in the hierarchy of biodiversity than the ECU.

The geographic size of an ECU varies both within and among species due to differences in the extent of migration among populations. Migration rate among populations affects extinction probabilities and the potential for natural rescue and is therefore critical to defining the ECU. The size of an ECU also depends on the time frame of interest; populations that are isolated on one time scale might be components of a metapopulation on a longer time scale. To assess extinction risk for Pacific salmon, the U.S. National Marine Fisheries Service identified independent populations that are "sufficiently isolated that immigration does not substantially affect the population dynamics or extinction risk over a 100-year time frame" (McElhany et al. 2000). We adopted this approach to identify ECUs.

The time frame of 100 years has many other precedents in practical decisions about conservation. For example, the World Conservation Union (IUCN) stipulates 100 years as the maximum period to be considered in the IUCN Red List criteria (IUCN 2006), and the state of Western Australia has drafted a 100-year biodiversity conservation strategy (DEC 2006). The 100-year period lacks justification from the perspective of wildlife given the variation in generation length across species, but it has philosophical and biological justification with respect to ethical obligations within human society. It is roughly the maximum human lifespan and 3–4 human generations into the future, beyond which time personal identities become uncertain and the coefficient of genetic relatedness to descendents approaches zero.

Research is needed to resolve the threshold of isolation that is most appropriate for delineating ECUs relative to the 100-year time frame. Waples and Gaggiotti (2006) suggest that under an ecological paradigm, populations could be defined as units with a threshold immigration fraction $m < 0.1$, meaning that <10% of individuals in the breeding population are immigrants. This threshold value is based on limited evidence that the transition to demographic independence occurs when m falls below about 10% (Hastings 1993). Further study is warranted because a lower threshold for m would result in fewer and larger ECUs.

Demographic isolation can be inferred from estimates of gene flow based on selectively neutral genetic data, observational migration data for individuals, range disjunction, and evidence of dispersal capability. Population delineation might be somewhat arbitrary in the case of clines and metapopulations, but discontinuities in gene flow typically do exist. Data will seldom be sufficient to establish the existence of ECUs in the hypothesis-testing sense, but the goal is to inform decision makers about the most likely population structure. To ensure consistency, simple quantitative criteria based on proxies for gene flow could be used to develop and document the strength of evidence for demographic isolation.

Step 2: Threat Status

The goal in step 2 is to provide a scientific assessment of the probability that the ECU will remain viable for 100 years if current circumstances prevail. The formal enterprise for estimating extinction probability—population viability analysis (PVA)—requires considerable effort to take into account everything that is known and not known (Goodman 2002). This requirement continues to limit the full application of PVA to situations involving the most controversial decisions. Nevertheless, PVA has greatly refined our understanding of the intrinsic and extrinsic factors that determine extinction probability, which in turn, has motivated the development of shortcut quantitative criteria for assigning populations to ranked threat categories (Mace & Lande 1991).

For IUCN Red Book listing, threat status is designated as the highest category triggered under any of 5 quantitative criteria (IUCN 2006). These criteria were designed to be flexible in terms of data required because little is known about most endangered species, and in terms of the population unit to which they apply, requiring only that rescue potential through immigration be negligible (Mace & Lande 1991). Both these attributes make the criteria suited to assessing the threat status of ECUs. The IUCN criteria are also used for national designation in Australia and Canada. In this paper we used the Canadian status categories (extinct, extirpated, endangered, threatened, special concern, not at risk) to denote threat status, without prejudice to the normative dimension of status categories under endangered species legislation (Vucetich et al. 2006).

Step 3: Potential for Recovery or Replacement

We considered whether human interventions might sometimes be sufficient to replace an ECU that has been lost by drawing on biodiversity in other extant populations. Step 3 includes criteria to evaluate, first, genetic and phenotypic resources in other potential donor populations and, second, habitat suitability, the most widespread threat to recovery.

ECOLOGICAL EXCHANGEABILITY

Some ECUs will be ecologically exchangeable in the sense that they can survive and perform the same ecological role at different geographic locations. This sense resembles but is not identical to that proposed by Templeton (1989) and adopted by Crandall et al. (2000). An ECU that lacks adaptations required for survival or ecological function in a new ecosystem will not be ecologically exchangeable. In our terminology (Table 1), exchangeable ECUs are ecologs and nonexchangeable ECUs are ecotypes (Fig. 2a). An ECU might be a reciprocal ecolog because ecological exchangeability exists in both directions. If exchangeability is unidirectional, the donor ecolog must be distinguished from the recipient ecolog (Fig. 2b; e.g., generalist vs. specialist forms, freshwater vs. marine forms). The loss of an ecolog is an "ecological extirpation," whereas the loss of an ecotype is an "ecological extinction" in the sense that human actions, such as transferring individuals from one ECU to another, might rescue an extirpated ecolog, but cannot rescue an extinct ecotype.

Nonexchangeability can be inferred directly from empirical evidence if reasonable efforts to transplant populations have failed, or indirectly from evidence of significant genetic adaptations, such as morphological or physiological divergence. Nonexchangeability can also be presumed given evidence of long isolation in habitats

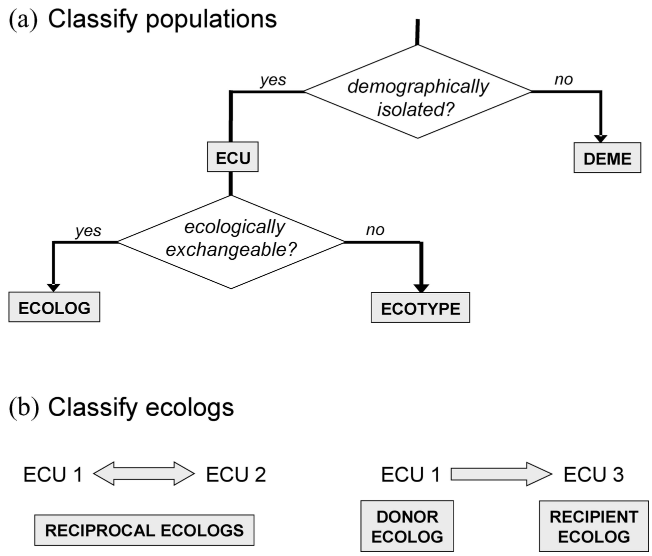

Figure 2. Decision tree for diagnosing elemental conservation units (ECU): (a) populations are classified as demes, ecologs, or ecotypes in pairwise tests for demographic isolation and ecological exchangeability and (b) based on the nature of ecological exchangeability, ecologs can be further classified as reciprocal, donor, or recipient ecologs (see text for discussion of criteria).

with different selective regimes, as, for example, when populations exhibit significant differences at selectively neutral genes and inhabit markedly different habitats or different ecogeographic regions. Simple quantitative criteria based on proxies for adaptive differentiation can be used to make consistent judgments (with appropriate precaution) about the strength of evidence for ecological exchangeability. Some arbitrariness is inevitable, but again, the goal is to inform decisions with the best information available in a context of adaptive management.

EVOLUTIONARY EXCHANGEABILITY

Elemental conservation units with a shared evolutionary lineage are likely to have more similar evolutionary potential than ECUs with dissimilar evolutionary lineages. To capture this distinction, we further defined ECUs as transplantable if demographic isolation from a donor ecolog has been recent (relative to other ECUs within the species), but only substitutable if the isolation is not recent. If no donor ecolog exists, an ECU is *nonsubstitutable* (Fig. 3a). Loss of a transplantable ECU has fewer evolutionary implications than the loss of a substitutable or nonsubstitutable ECU.

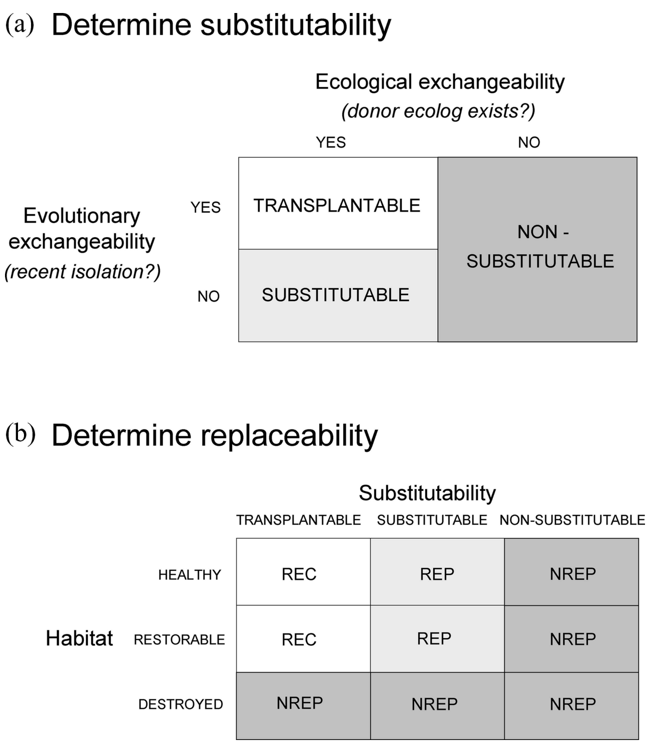

Figure 3. Classification scheme for determining (a) substitutability and (b) replaceability of populations in step 3 of the elemental-conservation-unit approach (REC, recoverable; REP, replaceable; and NREP, nonreplaceable).

HABITAT SUITABILITY

To indicate the adequacy of the habitat or niche to support a transplanted or substituted population, an ECU is designated recoverable only if the habitat is healthy or restorable and another transplantable donor ECU exists. An ECU is replaceable if habitat is healthy or restorable, and the best donor ECU is considered merely substitutable (ecologically exchangeable but with a long history of isolation). In all other cases the ECU is nonreplaceable (Fig. 3b).

Step 4: Biological Consequences of Loss

In step 4 the biological consequences of the loss of an ECU are evaluated by considering both its role in the ecosystem (e.g., Allendorf et al. 1997) and its evolutionary significance to humanity. For instance, loss of an ECU might cause the ecosystem to shift to lower states of productivity, a significant biological consequence (Borer et al. 2006). Apex predators that structure lower trophic levels or producers required by upper trophic levels also have obvious ecological significance (Smith et al. 2007). So too do obligate mutualists; loss of a particular insect pollinator can end the future of a plant community. Conservation biologists already use the concept of keystone species (Libralato et al. 2006), and ecologists are making progress at understanding the ecological roles of individual species (Helfield & Naiman 2006), although more progress is urgently needed.

Biologists also ought to provide information on relevant evolutionary properties of the ECU that would be lost (van der Heide et al. 2004). Absent a reliable procedure for actually ranking option value or evolutionary potential (e.g., Faith 2001), it might be sufficient to report whether the history of ecological isolation (vicariance) is recent or ancient relative to other ECUs within the species. Ancient vicariance will have afforded a greater opportunity for the independent evolution of new characters that would likely affect option value and evolutionary potential. Remnants of already globally diminished lineages may hold larger significance as a function of their rarity (MacAvoy et al. 2007). The development of criteria to measure ecological and evolutionary consequences of loss should be a priority; for our present purposes, we merely describe consequences as low, medium, or high.

Step 5: Full-Status Designation

The fifth step is to summarize the scientific advice about extinction risk for each ECU by grouping the individual terms that summarize threat status, replaceability, and the biological consequences of loss. Thus, an ECU is designated *endangered nonreplaceable low* when it is endangered, could not be replaced once extinct, and the biological consequences of its extinction are low from an ecological perspective. An ECU is *endangered* *recoverable high* if another donor ecolog exists and the ecological impact of loss is high. Some combinations are excluded by definition (e.g., recoverable ECUs are merely at risk of becoming extirpated, whereas irreplaceable ECUs are necessarily at risk of becoming extinct).

Step 6: Setting Targets for Protection

The final step is to move the biological knowledge captured in step 5 into planning at the landscape level so that conservation targets can be set through a rational process of societal decision making. This requires a format and process that makes the information useful for weighing and balancing competing demands. Although all ECUs warrant consideration for protection, they will not have equivalent conservation value to humans. Ultimately, the value of an ECU will be determined from cultural, economic, and political perspectives, generating conflicting priorities that must be resolved during prioritization. Societal objectives for conservation will have to be articulated clearly at this stage if biodiversity is to be protected in a coherent way. Input will be required from stakeholders (e.g., landowners, ranchers, hunters, and fishers, environmentalists, conservationists, regional business owners, and resource-extraction industries) and professionals (biological and social scientists, economists, lawyers, government representatives , and representatives of entitled groups such as aboriginals).

Geographic information systems (GIS) can incorporate multiple layers of information (biological, stakeholder, and professional) into larger-scale landscape assessments without sacrificing information at the local scale. When there are numerous ECUs within a taxonomic species, scientific advice about extinction risk can be presented in detail at the elemental scale or summarized in assessments at larger spatial scales or longer time frames. Input from biologists is therefore required during the planning process on, for example, the best ways to maintain genetic exchange among populations to promote adaptability in the foreseeable future (emphasized by Crandall et al. 2000). Iterative reassessment of risk might be required if decisions at the landscape scale allow the loss of particular donor populations in the near term, thereby affecting the ecological exchangeability of the remaining ECUs. Human interventions (planned or not) produce outcomes that can be evaluated to allow learning as part of adaptive management (Fig. 1). Given the limited state of our understanding about ecological and evolutionary exchangeability, it may be advisable to speed up the learning process through deliberate experimentation where adverse consequences are limited.

Examples

We illustrate the ECU approach with 2 examples involving salmon, which are highly valued by society and exhibit complex population structure. The first concerns efforts to reestablish the Atlantic salmon (*Salmo salar*) in Lake Ontario; the second concerns multiple life history types in the sockeye salmon (*Oncorhynchus nerka*). Both species are primarily migratory and anadromous. In both species some populations remain their entire lives within freshwater (landlocked or resident), typically spawning in tributaries and growing to adulthood in a lake. Their precise homing to spawning sites in discrete water bodies has promoted the evolution of local adaptations in traits such as egg size, body coloration, prey selection, migration timing, and age and size at maturity (e.g., Hendry & Stearns 2004). Both species play a significant ecological role in their transport of nutrients from the ocean or lake to spawning tributaries, through death and deterioration of carcasses, and are typically important predators that shape community structure in freshwater.

Atlantic Salmon in Lake Ontario

Atlantic salmon were once abundant throughout northeastern North America, but their decline has been widespread. The population of Atlantic salmon in Lake Ontario bred in 40 tributaries and probably grew to adulthood in the lake (COSEWIC 2006). The population declined rapidly in the mid-1800s due to loss of spawning habitat and overexploitation, with the last known Atlantic salmon killed by an angler in 1896. To reestablish the population, government agencies in Ontario and New York State released thousands of juvenile Atlantic salmon during the periods 1867–1884, 1905–1912, 1935–1964, and 1987 to present. More than 10 strains have been used as broodstock (from Maine, Vermont, New York, Nova Scotia, New Brunswick, and Quebec) (Dimond & Smitka 2005). About half of these strains were landlocked and half anadromous, and they differed greatly in their genetic and ecological characteristics. As yet, no introductions have succeeded in reestablishing a reproducing population in Lake Ontario, even though the spawning habitat has been improved significantly and fishing is regulated (Greig et al. 2003). In 2006 the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) formally designated the Lake Ontario population as extirpated.

We suggest that Atlantic salmon in Lake Ontario comprised at least one nonreplaceable ECU and should now be considered an extinct ecotype. Moreover, because the Atlantic salmon was 1 of only 3 top predators in Lake Ontario and was caught by the barrel full during spawning migrations into tributaries, its extinction has likely had a high ecological impact on the Lake Ontario ecosystem. This ECU would be designated “extinct high” to reflect the likely ecological consequences of its loss.

Multiple Life-History Types in Sockeye Salmon

The following is a more complex, hypothetical (but plausible) example in which sockeye salmon are

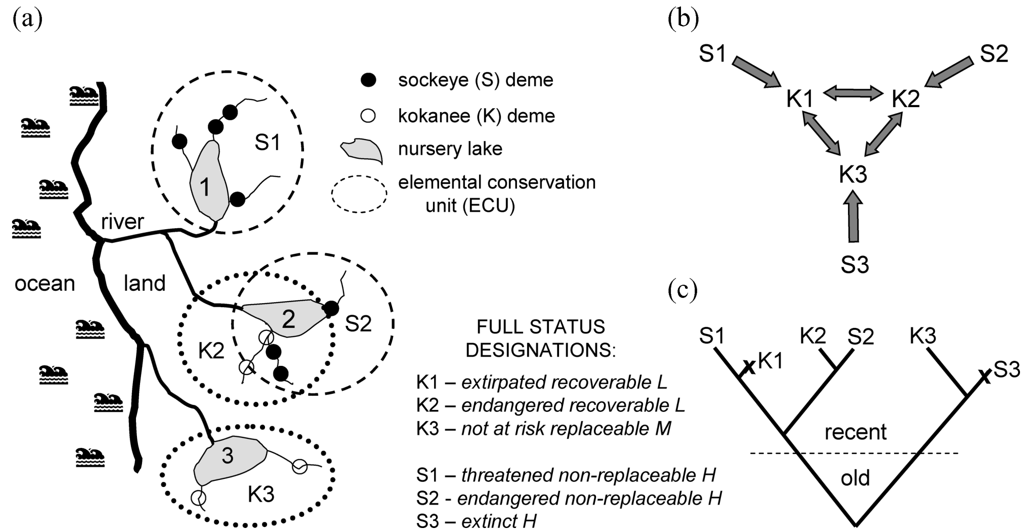

Figure 4. Illustration of the elemental-conservation-unit (ECU) approach for designating conservation status for populations of Pacific salmon with multiple life histories. First, (a) ECUs are delineated by examining demographic isolation of 11 extant demes of sockeye salmon (7 anadromous sockeye, solid circles; 4 nonanadromous kokanee, open circles); 2 other ECUs no longer exist. Second, threat status for extant ECUs is determined (S1, threatened; S2 and K2, endangered; K3, not at risk). Third, (b) inferences about ecological exchangeability, (c) evolutionary vicariance, and habitat status (not pictured, see text) are included to assess replaceability. Fourth, the ecological and evolutionary consequences of loss are evaluated as high (H), medium (M), or low (L) (see text). Fifth, full conservation status is designated to summarize and communicate science advice about overall risk, including threat status, replaceability, and biological consequences of loss.

reproductively isolated in 3 separate rivers, but also exist sympatrically as different life history forms (Fig. 4a). Within each river the resident freshwater form (called kokanee) evolved in sympatry from the migratory marine form (called sockeye), and the 2 forms became genetically and demographically isolated ($m \ll 0.1$) (a process described by Wood & Foote 1996). Multiple spawning demes exist within each river, but these are not demographically isolated within the same form. There are no kokanee in river 1 and no anadromous sockeye in river 3. This implies 6 ECUs, of which only 4 are extant.

The 3 rivers (and associated nursery lakes) are similar ecologically, so we presumed, on the basis of evidence reviewed by Wood (1995), that the kokanee ECUs are all reciprocal ecologs such that kokanee introduced from any of the 3 rivers could fill the ecological role of kokanee lost in any other river (Fig. 4b). In contrast we considered each sockeye ECU an ecotype because attempts to transplant sockeye have almost always failed to establish new sockeye populations because of the specificity of evolved adaptations for marine migration routes (Wood 1995). Despite these failures, sockeye transplants to suitable habitat have frequently given rise to new kokanee populations; thus, we predict that a kokanee ECU can be recreated from a related sockeye ECU if the habitat is suitable. The reverse path of evolution is so rare that we considered it unlikely that a sockeye ECU could be recreated from a kokanee ECU. In this hypothetical example, the genetic evidence indicates early isolation of the ECUs in river 3 from those in rivers 1 and 2 and relatively recent isolation of ECUs in river 1 from those in river 2 (Fig. 4c). Fisheries and other human activities currently endanger both forms in river 2 and threaten the sockeye ECU in river 1, but the habitat in both rivers is considered healthy or restorable. Kokanee in river 3 are not at risk.

We concluded that the sockeye ECUs are all nonreplaceable, that the kokanee ECU in river 3 (K3) is replaceable, and that the other kokanee ECUs are both recoverable despite the fact that K1 no longer exists. Loss of anadromous sockeye would have high ecological significance (largely because of the marine-derived nutrients they provide); loss of kokanee is likely of low ecological significance in lakes where sockeye exist and of medium ecological significance in lakes where sockeye no longer exist. This scientific insight about risk is captured by the following status designations: S1, threatened nonreplaceable high; S2, endangered nonreplaceable high; S3, extinct high; K1, extirpated recoverable low; K2, endangered recoverable low; K3, not at risk replaceable medium.

Practicality of the Approach

Our proposal to focus on ECUs may raise concerns about workload (there will be too many) and feasibility (not enough information is available). The number of genetically distinctive populations per 100,000 km^2 is estimated at 316 in terrestrial molluscs, 50 in amphibians, 10 in freshwater fish, 5.6 in mammals, 0.06 in birds and conifers, 0.01 in reptiles, and 0.003 in marine fish. (Hughes et al. 1997). Additional populations will likely qualify as ECUs without being genetically distinctive, and a multiplicity of ECUs will likely exist within species inhabiting freshwater environments, islands, or mountain tops, where opportunity for dispersal is severely restricted. The greatest opportunities for ecological exchangeability may also exist in such cases, where otherwise similar habitats exist as discontinuous patches. In the face of such complexity, our approach reminds us that nonexchangeable ECUs represent important components of biodiversity and that it may be in society's best interests to protect them.

On the other hand, the challenge of identifying ECUs need not be as complex as the challenge of identifying species in poorly studied taxa. People generally study and gain understanding about the ecology and evolution of organisms that they value. Consequently, it can be more feasible to identify ECUs and assess their conservation status precisely when it is most desirable to do so. Where understanding is limited, more must be assumed, but the perceived consequences of error will be reduced. The ECU approach involves some arbitrariness and perhaps increased workload, but alternative approaches have their own arbitrary elements, compromise flexibility, and forfeit opportunities to protect the sustainability of local ecological benefits.

Problems with Current Approaches

To illustrate these concerns, we contrasted 2 approaches currently used in North America to define the units of biodiversity below the species level that are eligible for protection under the U.S. ESA and the Canadian Species At Risk Act (SARA).

The Evolutionarily Significant Unit and the ESA

For Pacific salmon the National Marine Fisheries Service (NMFS) has adopted the ESU as an operational definition of "distinct population segment" (DPS), the smallest entity eligible for protection under the ESA (Waples 1991). The ESU concept is essentially the evolutionary species concept applied at a finer scale (Mayden & Wood 1996). It diagnoses monophyletic lineages (hence real entities) that are isolated from one another and deemed to have evolutionary significance within the species concept.

A recent federal court case in Oregon (U.S.A.) (*Alsea Valley Alliance v. Evans* 2001) illustrates a practical problem with the focus on monophyly in ESUs (Waples 2007). The NMFS delineated an ESU of coho salmon (*O. kisutch*) to comprise a monophyletic group of populations, including all hatchery populations recently derived from the wild populations (Fig. 5). Knowing that some hatchery populations lack ecological exchangeability with wild populations due to rapid evolution within the artificial hatchery environment, NMFS used the ESA to protect only the wild populations and those hatchery populations deemed essential to recovery of the wild populations. The court ruled that the ESA allows listing of only 3 types of units (species, subspecies, and DPSs) and that

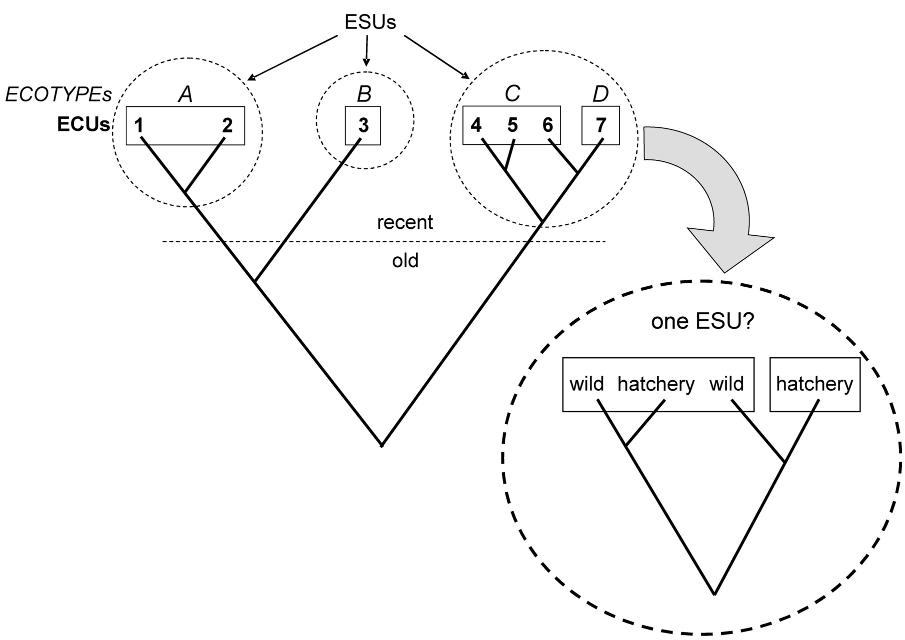

Figure 5. Illustration of evolutionary relationships among 7 elemental conservation units (ECU), 4 ecotypes, and 3 evolutionarily significant units (ESU). The monophyletic nature of the ESU implies that closely related hatchery ECUs (5 and 7) must be included with wild populations as targets for protection under the ESA given that the ESU is defined as the operational definition of "distinct population segment," the smallest unit eligible for listing under the Endangered Species Act.

because NMFS had previously defined the ESU as the operational definition of DPS for Pacific salmon, NMFS could not define smaller units within the ESU for separate treatment under the ESA. In other words, hatchery populations were not legally distinguishable from wild populations, and hatchery fish had to be considered in ascertaining whether the ESU was at risk. In this case the focus on a large monophyletic unit (the ESU) became an obstacle to protecting the entities of primary concern (the wild populations).

To add to the uncertainty, another federal judge recently ruled that hatchery fish can be protected under the ESA, but cannot be counted in determining whether an ESU is at risk (R. McClure, *Seattle Post-Intelligencer*, 12 June 2007). The ECU approach avoids these issues because individual ECUs within the ESU (see Fig. 5) can receive different levels of protection according to their conservation value, which depends largely on the ecological context, including the degree of hatchery supplementation.

Pennock and Dimmick (1997) also argue that the ESU approach unduly limits flexibility and ignores that Congress' original intent in adding the phrase "distinct population segment" to the ESA was to allow protection of species in limited parts of their range and to give different designations to different populations. Waples (1998) defends the ESU approach as consistent with the original intent of Congress citing statements that decisions should be based solely on the basis of the best scientific and commercial data available; he argues that a lack of standards for defining distinct population segments would weaken protection for wildlife because petitions for listing populations are likely to fail without scientifically rigorous arguments in the face of substantial economic and social costs to listing. Crandall et al. (2000) argue that historical (evolutionary) legacy is generally less important for conservation than functional (ecological) diversity and suggest that the ESU terminology "be abandoned and replaced with a more holistic concept of a species, consisting of populations with varying levels of gene flow evolving through drift and natural selection."

The Designatable Unit and SARA

Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has adopted the designatable unit (DU) as an operational definition of *wildlife species*, the smallest entity eligible for protection under SARA. Green (2005) proposed the DU as a pragmatic approach to portray extinction risk within a taxonomic species in an attempt to avoid the epistemological problems inherent in defining species and conservation units. Units below the taxonomic species level are assigned conservation status only when a single species-wide designation fails to portray significant differences in extinction risk across the species' range. Designatable units that have the same conservation status are aggregated because they are not needed to portray extinction risk for the taxonomic species. The aggregation step offers the convenience of fewer designated units, but discards information potentially useful to conservation planning. Green (2005) does not specify the characteristics of a DU, leaving its identification subject to individual interpretation.

Since the act's proclamation in 2003 and our writing in 2007, about one-quarter of the biodiversity designated as endangered or threatened by COSEWIC has not been protected by federal listing in SARA. Several explanations exist for these decisions not to list (Mooers et al. 2007), but we suggest that the inadequacy of the information provided by COSEWIC to the federal government, including the uncertainty with DUs and the limited information on biological consequences, is partly responsible. We think protection of Canadian biodiversity would improve if COSEWIC assessed ECUs and provided their extinction probabilities and biological consequences without defining conservation targets. The federal government could then use COSEWIC's information as one important part of the planning process, as described in step 6. We are therefore suggesting that ECUs replace DUs as the operational definition of *wildlife species* under SARA.

Conclusions

We have outlined a framework for assessing the probability and biological consequences of losing elemental units of biodiversity that provide the ecosystem and aesthetic services that humans value. This scientific advice is provided to societal decision makers and planners in a form that is convenient for weighing competing interests before choosing targets for protection. The approach correctly distinguishes the scientific from the normative aspects of conservation planning. Some readers may regard this approach as unrealistic, or fatal to biodiversity protection, preferring instead that conservation biologists assess the status of wildlife and set the targets for protection. Nevertheless, conservation biologists cannot take the public where they do not wish to go, as is evident in the North American experience, where scientifically assessed biodiversity goes unprotected because of other societal values (and perhaps poor information). Ultimately, society has the right to decide whether the value of conservation exceeds the expense. Scientists are obliged to provide society with the best possible advice about biological risk and to assist decision makers in combining this with other social, economic, and political information. Through this assistance, conservation biologists will help society articulate objectives for biodiversity conservation and to comprehend, and it is hoped reduce, the ecological consequences of its loss.

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