

INVITED REVIEW

# Adaptive evolutionary conservation: towards a unified concept for defining conservation units

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## Abstract

Recent years have seen a debate over various methods that could objectively prioritize conservation value below the species level. Most prominent among these has been the *evolutionarily significant unit* (ESU). We reviewed ESU concepts with the aim of proposing a more unified concept that would reconcile opposing views. Like species concepts, conflicting ESU concepts are all essentially aiming to define the same thing: segments of species whose divergence can be measured or evaluated by putting differential emphasis on the role of evolutionary forces at varied temporal scales. Thus, differences between ESU concepts lie more in the criteria used to define the ESUs themselves rather than in their fundamental essence. We provide a context-based framework for delineating ESUs which circumvents much of this situation. Rather than embroil in a befuddled debate over an optimal criterion, the key to a solution is accepting that differing criteria will work more dynamically than others and can be used alone or in combination depending on the situation. These assertions constitute the impetus behind *adaptive evolutionary conservation*.

**Keywords:** adaptive divergence, conservation, conservation units, evolutionarily significant units, evolutionary processes, species concepts

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The exact definition of an “evolutionary novelty” faces the same insuperable difficulty as the definition of the species’ (Mayr 1960).

## Introduction

Faced with the growing challenge in recent years of deriving strategies for salvaging diminishing flora and fauna, conservation biologists and ecologists continue to search for methods that can distinguish unambiguous ‘units’ for conservation purposes. One prominent idea has been the concept of the evolutionarily significant unit (ESU). The ESU was developed to provide an objective approach to prioritizing units for protection below taxonomic levels (Ryder 1986), given that existing taxonomy may not amply reflect underlying genetic diversity and that resources are limited (Avice 1989). Since that time, the concept has been frequently moulded and shaped and various definitions have been formulated (Table 1). ESUs now have both important legal and biological ramifications under the USA Endangered Species

Act (ESA) (Waples 1991, 1995), the Australian Endangered Species Protection Act (Moritz 1994a), and parallel legislation in other countries. Yet, how the ESU should be defined is still heatedly debated (e.g. Moritz 1994b; reviews in Nielsen & Powers 1995; Legge *et al.* 1996; Pennock & Dimmick 1997; Bowen 1998; Duvernell & Turner 1998; Waples 1998; Bowen 1999; Dimmick *et al.* 1999; Karl & Bowen 1999; Moritz 1999; Paetkau 1999; Crandall *et al.* 2000; Goldstein *et al.* 2000). In particular, there is growing dispute with respect to the relative role that ‘neutral’ genetic markers should play compared to other criteria in exercising decisions. Disagreement also centres upon where to focus conservation efforts along the evolutionary continuum of population segments to species (e.g. Moritz *et al.* 1995; Waples 1998). Even the need for such specific terminology in diagnosing conservation units has been questioned (e.g. Crandall *et al.* 2000).

In this review, we first revisit the strengths and weaknesses of various approaches to discerning ESUs around two central themes: their conceptual and operational appeal. We use the overall similarity between approaches to propose *adaptive evolutionary conservation*. This is an integrative framework for imputing conservation units based on the notion that situational circumstances will demand differing

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**Table 1** Evolutionarily significant unit (ESU) criteria since Ryder (1986) and species concepts (modified from Roe & Lydeard 1998)

Author(s)	Criteria
<b>Evolutionarily significant units</b>	
Ryder (1986)	Subsets of the more inclusive entity species, which possess genetic attributes significant for the present and future generations of the species in question
Waples (1991)	A population or group of populations that: (i) is substantially reproductively isolated from other conspecific population units; and (ii) represents an important component of the evolutionary legacy of the species
Dizon <i>et al.</i> (1992)	Populations or groups of populations demonstrating significant divergence in allele frequencies
Avise (1994)	Sets of populations derived from consistently congruent gene phylogenies
Moritz (1994a)	Populations that: (i) are reciprocal monophyletic for mtDNA alleles; and (ii) demonstrate significant divergence of allele frequencies at nuclear loci
Vogler & DeSalle (1994)	Groups that are diagnosed by characters which cluster individuals or populations to the exclusion of other such clusters
Crandall <i>et al.</i> (2000)	Abandon term ESU for more holistic concept of species, consisting of populations with varying levels of gene flow evolving through drift and selection
This review	A lineage demonstrating highly restricted gene flow from other such lineages within the higher organizational level (lineage) of the species
<b>Species concepts</b>	
Biological Species Concept (Mayr & Ashlock 1991)	A species is a group of interbreeding natural populations that is reproductively isolated from other such groups
Evolutionary Species Concept (Simpson 1961; Wiley 1978)	An entity composed of organisms that maintains its identity from other such lineages and has its own independent evolutionary tendencies and historical fate
Cohesion Species Concept (Templeton 1989)	A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms
Phylogenetic Species Concept (Cracraft 1983)	The smallest diagnosable cluster of individual organisms with which there is a parental pattern of ancestry and descent
General Lineage Concept of Species (de Queiroz 1998)	Species are segments of population-level lineages

integrative approaches that may encompass a wide array of justifiable biological criteria in general, but that involves applying them rigorously on a case-by-case basis. We emphasize that the strengths and weaknesses of various operational criteria should not encumber conservation efforts but rather aid managers in conducting sound conservation plans specific to the situation at hand. Elements of this framework are discussed with the hope of ameliorating the challenges of maximizing the probability of preserving genetic diversity and evolutionary potential.

### Historical examination of ESU concepts: conceptual and operational appeal

#### *The dilemma of subspecies in species conservation (Ryder 1986)*

Frustrated with the imprecision of contemporary mammalian taxonomy, Ryder (1986) coined the term ESU as 'a subset of the more inclusive entity species, which possess genetic attributes significant for the present and future generations

of the species in question'. Although it started the ball rolling, Ryder (1986) did not offer many guidelines for operational applications. Moreover, searching for concordance among different information types (e.g. ecological, genetic, physiological), as Ryder (1986) suggested, however appealing, is problematic and potentially limiting for conservation purposes. This is because neutral genetic markers and phenotypic traits will yield different types of information as they may be influenced by different gauges of varying evolutionary forces, making concordance unlikely in many circumstances (Bernatchez 1995; Balmford *et al.* 1998; Smith *et al.* 2000).

#### *The conservation of biological diversity-implications from Pacific salmon (Oncorhynchus spp.) (Waples 1991, 1995)*

Applied presently in legal and management contexts of the USA ESA and National Marine Fisheries Service (NMFS), respectively, Waples' (1991) definition of an ESU possesses the adaptive theme put forth by Ryder (1986) and includes two major criteria that originate from work carried out on

West Coast Pacific salmon. An ESU is defined as a population segment or group of populations that 'is substantially reproductively isolated from other conspecific populations', and 'represents an important component in the evolutionary legacy of the species' (Waples 1991). Waples (1995) clarifies that the second component 'is a product of past evolutionary events and that represents the reservoir upon which future evolutionary potential depends'. The approach is conceptually appealing for two reasons. First, it is integrative, accommodating the use of diverse biological and even environmental information (e.g. life history patterns, genetic population structure, habitat landscape) to discriminate units for protection. Second, it is the only ESU concept that provides a working framework for preserving component parts of already designated ESUs to prevent their extinction (McElhany *et al.* 2000; though see Mundy *et al.* 1995). Moreover, the basic framework of the NMFS ESU concept is flexible enough to be applied broadly to conservation problems such that reproductive isolation does not have to be absolute (e.g. Snake River Sockeye salmon, *Oncorhynchus nerka*) (Waples 1995).

On the other hand, some authors have challenged its applicability at a broadened taxonomic spectrum (e.g. Pennock & Dimmick 1997). Others have questioned the objectivity of the approach, stating that it is less stringent than other methods proposed with respect to diagnosing ESUs (e.g. Moritz *et al.* 1995). These authors point to the definition itself which contains subjective wording such as 'substantially' and 'important' that maybe difficult to implement. While collecting a number of genetic, ecological, behavioural or life history data sets for ESU designations is ideal, it may also be beyond the capabilities of some management jurisdictions. Furthermore, although the first component of the definition (substantial reproductive isolation) can arguably be identified with phenotypic and/or molecular genetic methods, the latter component (important component of evolutionary legacy) is much more difficult to delineate because this implies an understanding of how new species arise (Bowen 1998). On a positive note, considerable theoretical and empirical progress has been achieved in this respect in recent years (reviewed in Schluter 2000), although the issue is still far from being resolved (Bowen 1999). Finally, as Waples (1995) points out, it is not the intent of the NMFS's ESU concept to determine which populations will play an important future role in the evolution of the species. Instead, the goal is to conserve as many of the important genetic building blocks of the species as possible so the course of evolution is unconstrained (Waples 1995).

*Phylogeographical approaches to discerning ESUs*  
(Dizon *et al.* 1992; Avise 1994; Moritz 1994a,b, 1999;  
Moritz *et al.* 1995)

Originating mainly from fisheries management terminology, specifically the re-evaluation of the term 'stock' (e.g. Ricker

1972), Dizon *et al.* (1992) favoured the evaluation of ESUs based on adaptive genetic uniqueness, using various proxies such as behaviour, morphology and geographical localization to infer reproductive isolation and differential selection. Ultimately however, levels of genetic similarity at molecular genetic markers dictate evolutionary distinctiveness of populations under this approach. Similarly, under the phylogeography paradigm (Avise *et al.* 1987), Avise (1994) argued that ESUs be classified on the basis of congruent gene phylogenies which consistently separate populations into their own groups at a biogeographical level.

Moritz (1994a,b) essentially combined the ideas of Dizon *et al.* (1992) and in particular Avise (1994) with his conceptual emphasis of phylogeographical patterning for ESU diagnosis. An ESU is defined as a population (or set of populations) that is 'reciprocally monophyletic for mtDNA alleles' and 'shows significant divergence of allele frequencies at nuclear loci' (Moritz 1994a). From the time that two populations separate, simulation studies indicate that it takes approximately  $4N_e$  generations for there to be a high probability of their having reciprocally monophyletic alleles (Neigel & Avise 1986). This provides a qualitative criterion for defining ESUs based on the distribution of alleles in relation to their phylogeny (Moritz 1994a). Therefore, historical isolation is emphasized because it can produce unique and irreplaceable combinations of genotypes. Conversely, phenotypic divergence is not stressed because it is potentially replaceable if one considers that it can happen rapidly and even recurrently through selection in natural populations (e.g. Taylor & Bentzen 1993; Pigeon *et al.* 1997; Losos *et al.* 1998). Significant divergence in nuclear allele frequencies is required to avoid misidentifying populations that are linked by nuclear, but not organellar gene flow (Moritz 1994a). Operationally, the definition has an advantage of being more stringent than that of Waples (1991) or Dizon *et al.* (1992). It enables conservation biologists to apply molecular genetics while at the same time being able to avoid the dilemma of determining how much genetic variation is enough for warranting protection to a given population(s) of a species.

This approach, however, has some problems. First, while reciprocal monophyly may be feasible, Waples (1995) pointed out that there is no one best method for phylogeny reconstruction, which yields the most-likely phylogeny in all situations. Second, reciprocally monophyletic relationships may not always infer historical isolation (see Crandall *et al.* 2000). Third, the very stringency that reciprocal monophyly affords can be problematic because a single individual in a new sample, if an anomaly, can overturn a population's or group of populations' reciprocally monophyletic status. Fourth, critics (e.g. Crandall *et al.* 2000) argue that the concept does not place enough emphasis on the potential of species to maximize evolutionary success through the maintenance of adaptive diversity (Lande & Shannon 1996; Lynch

*et al.* 1999). This point is exemplified from a multitude of research on recently (e.g. postglacially) founded populations or quickly radiated species assemblages, which do not demonstrate reciprocal monophyly, but which merit formal protection based on heritable phenotypic or ecological diversity (Taylor 1999). Finally, the dependency on reciprocal monophyletic mitochondrial DNA (mtDNA) groupings may make the concept of limited use for phylogeographical studies in plants (Coates 2000). This is because mtDNA evolves 40–100 times slower in plants than in animal mtDNA (Palmer 1992).

Moritz (1994a) does consider that genetic applications in practice reveal a varying amount of phylogenetic separation and sometimes less separation than reciprocal monophyly. To circumvent this problem, Moritz (1994a) proposed the management unit (MU), closely resembling the 'stock' definition of Dizon *et al.* (1992). The MU was intended to be a level of conservation unit below that of the larger ESU that had statistically significant divergence in allele frequencies (nuclear or mitochondrial) no matter the phylogenetic differentiation of the alleles. The focus of the MU is on contemporary population structuring and short-term monitoring rather than historical factors.

More recently, Moritz (1999) proposed a two step approach for defining conservation units. The first step involved identifying and protecting historically isolated sets of populations within a species (ESUs, *sensu* Moritz). Second, within each of these designated ESUs, the potential for adaptive evolution was then maximized, through maintaining population and metapopulation stability, although no guidelines were provided as to how this second step can be applied precisely.

#### *Advocates of the Phylogenetic Species Concept (PSC)*

A number of authors (e.g. Vogler & DeSalle 1994; Barrowclough & Flesness 1996; Amato *et al.* 1998; Cracraft *et al.* 1998; Goldstein *et al.* 2000) use the Phylogenetic Species Concept (PSC) (Cracraft 1983) to propose conservation units by finding characters that cluster groups to the exclusion of other similar ones. The PSC states that the smallest discernible and distinct clusters where one finds a parental pattern of descent and ancestry is considered to be its own entity (Cracraft 1989). Operationally, for the characters assessed, population aggregation analysis (PAA) (Davis & Nixon 1992) can be used to identify hierarchically related groups that are the most inclusive groups of organisms united by fixed or diagnostic character states. The method is therefore conceptually appealing because it avoids the problematic notions of universally applying criteria such as reproductive isolation or phenetic similarity. It is also stringent, making it testable, an important consideration in highly controversial cases (Vogler & DeSalle 1994). Ultimately, proponents of the PSC argue that their approach elevates all diagnos-

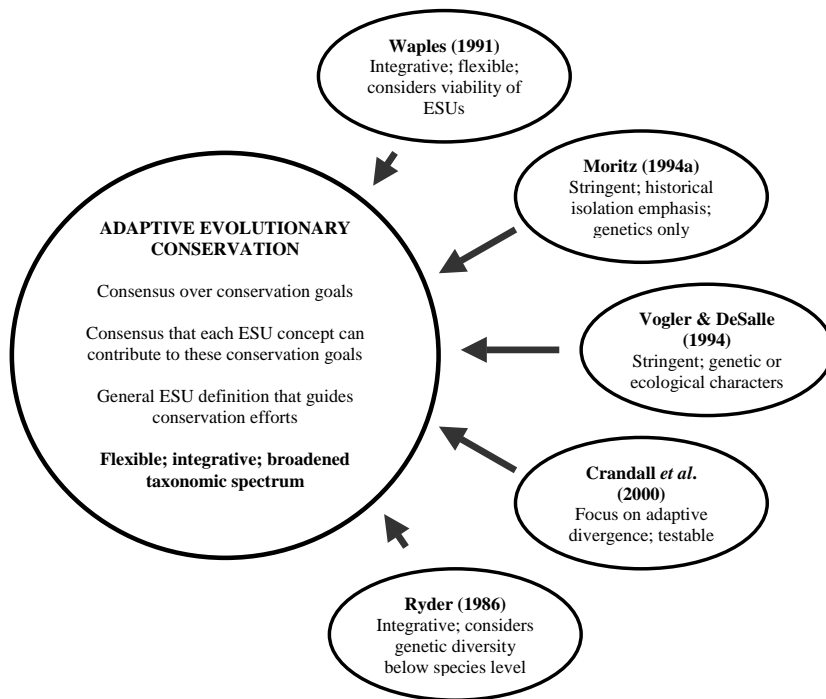
able evolutionary lineages to species. It consequently removes the need to establish ESUs that are not a part of the formal nomenclature (though see Vogler & DeSalle 1994).

With respect to ESUs, opinions regarding application of the PSC are mixed in the literature. Moritz (1994b) argued that the PSC over-splits taxa and thus would promote overprotection. Conversely, Waples (1995) suggested instead that the PSC may underestimate the number of populations in need of protection and that it focuses too closely on the species level. However, clear examples of such complications are scarce in the literature. The characters used to discriminate between groups can be problematic themselves, since they may be difficult to score unambiguously, especially if ecological or behavioural. Indeed, the framework presented to help siphon through 'bad' characters and use only what are deemed 'good ones' needs some improvement and probably has discouraged some researchers from adopting the method (see Vogler & DeSalle 1994; Goldstein *et al.* 2000; for clarification). The PSC approach also lacks flexibility, for like Moritz's reciprocal monophyly, the stringency benefits provided by using diagnostic characters are countered abruptly if a single individual in a new sample is an anomaly for the character being scored. This has implications in situations where only small sample sizes can be obtained (e.g. endangered species), because characters may appear to be diagnostic in small samples by chance, which could lead to potentially erroneous management decisions.

#### *Genetic and ecological exchangeability* (Crandall *et al.* 2000)

Crandall *et al.* (2000) report that the use of the ESU concept outside of the NMFS has evolved towards defining units on the basis of molecular genetic markers alone. Dismayed by the dichotomous 'ESU or not' nature of the concept in general, they suggest a system of discerning important population units based on eight categories of population distinctiveness. Distinctiveness depends on the failure to reject (–) or rejection (+) of the null hypotheses of both historical and recent genetic and ecological *exchangeability* (*sensu* Templeton 1989). Depending on the magnitude of distinctiveness identified within the population (or group of populations) at hand, each is assigned to a particular category that has a specific management recommendation (in general, those entities showing less ecological exchangeability receive greater individual protection). Consequently, Crandall *et al.* (2000) propose that ESU concepts be abandoned altogether and replaced with a more holistic concept of species, consisting of populations with varying levels of gene flow evolving through drift and selection.

The approach of Crandall *et al.* (2000) is both conceptually and operationally appealing because overall it: (i) recognizes the importance of adaptive distinctiveness in populations; (ii) combines genetic and ecological principles; and



**Fig. 1** Adaptive evolutionary conservation conceptual overview, encompassing varying proposed criteria from other evolutionarily significant unit (ESU) concepts and definitions. See main text for explanations.

(iii) is testable, in the form of null hypotheses. Moreover, the approach tries to prioritize objectively conservation value across a broad taxonomic spectrum, including invertebrates and plants. However, the authors criticise the ESU designation because it forces the continuous distribution of genetic diversity into just two categories (ESU or not). Yet, the very basis of their proposed concept does not escape a similar dichotomy, that of *recent* or *historical* exchangeability with an arbitrary 'cut-off'. However, the authors acknowledge that the recent-historical division must be made specific to the situation at hand. In short, if this method is to be adopted by conservation decision-makers, we see three ways in which their recommended management actions should be improved. First, while groups of individuals identified as both genetically and ecologically nonexchangeable in all aspects (recent and historical axes) should be treated as separate species (Fig. 1; Crandall *et al.* 2000), this category is most likely to identify species that are already recognized, making it of limited usefulness to conservation practices. Second, many of the situations in which the management action is to treat the organisms as a single population are also the most difficult to assess. We agree that recent ecological nonexchangeability may be indicative of adaptive divergence necessary for population persistence. However, Crandall *et al.* (2000) do not give evidence of recent genetic nonexchangeability the same weighting even though this could signify an important step toward speciation. Genetic distinctiveness may not mean adaptation, but in some cases nor will ecological nonexchangeability, since there are challenges to demon-

strating heritability of ecological characteristics in practice. Third, Crandall *et al.* (2000) recommend treating groups that demonstrate recent and historical ecological nonexchangeability as distinct entities yet treat groups that have been genetically nonexchangeable (recently and historically) as a single population. Few if any conservation geneticists would doubt that the latter should receive the same treatment as the former.

### Trends observed from an examination of various ESU concepts

Several general trends emerge from reviewing the main approaches to delineating ESUs. First, as noted by Roe & Lydeard (1998) (see also Mayden & Wood 1995), much of the debate over ESU concepts stems from a conflation over the species concepts used to define them (Table 1). In this respect, we concur with the view of de Queiroz (1998) that overall, despite innumerable conceptual perspectives over the years, species concepts are fundamentally not very different from each other. Globally, they are all explicitly or implicitly attempting to define population-level evolutionary lineages, coined by de Queiroz (1998) as the 'general lineage concept of species' (GLC). They are just doing so at differing temporal gauges and/or putting differential emphasis on the role of evolutionary forces, and consequently, on criteria, to identify distinct species. One wonders then why the debate over species concepts should have to be much of an issue at all with respect to the delineation of ESUs. That being said, we do acknowledge that any discussion

of a unified ESU concept inevitably will be formulated relative to a notion of a species. Therefore, in many ways, a unifying ESU concept should ideally operate under a unified species concept.

A second controversy involves the ESU concepts/definitions themselves (Table 1). For example, both the first criterion of Moritz (1994a) and the PSC depend on monophyly for designating ESUs. Moritz's (1994a) definition of a subhierarchical, 'shallower' MU (under the ESU level) resembles the original stock concept applied in fisheries science for almost three decades (Ricker 1972). Likewise, the genetic and ecological exchangeability criteria proposed by Crandall *et al.* (2000), which are based on the effects of character divergence on potential interbreeding (Templeton 1989), are strikingly similar to the first criterion of Waples' (1991) ESU definition (reproductive isolation) and the use of life history and phenotypic character suites for ESU evaluations. In essence, reciprocally monophyletic groups (*sensu* Moritz) suggest an important component in the evolutionary legacy of the species which is in part the product of historical isolation (*sensu* Waples).

A third controversy concerns the time scales involved under the various ESU concepts. Moritz's (1994a) ESU is derived mainly from deep mtDNA sequence divergences typically requiring several hundred thousand to millions of years of historical separation (e.g. Moritz *et al.* 1993; Joseph & Moritz 1994; Schneider *et al.* 1998; Moritz 1999). In contrast, the phylogenetic division in time for ESU designation of Waples (1991) has its origins from work on salmonid populations (e.g. Waples *et al.* 1991; Matthews & Waples 1991) that in some (but not all) cases have only been diverging since the last Pleistocene glaciations in North America (23 000–8000 years ago) (Dyke & Prest 1987). This temporal difference is also highlighted in Crandall *et al.* (2000) where recent and historical time references are incorporated into the criteria for conservation units. Timescale receives less consideration in PSC circles, in that their criterion based on the divergence of characters is devised without the consideration of their potential effects on ecology or reproductive isolation (temporal gradients in the speciation process) (Cracraft 1983). Yet, one may reasonably argue that the timeframe required to evolve alternate diagnostic traits is likely to be important (unless effective population sizes are very small) and comparable to that inferred from the ESU criterion of Moritz (1994a).

Fourth, ESUs are being delineated by emphasizing different ways in which gene flow has been highly reduced. For instance, Waples (1991) discusses reproductive isolation in the biological species sense that considers both genetic and ecological constraints to gene exchanges. Moritz (1994a) accentuates the termination of gene flow through long-term physical isolation. Crandall *et al.* (2000) and other reports on phenotypic differentiation, emphasize a reduction of gene flow at quantitative trait loci through ecological incom-

patibility. To some extent, the PSC approach (e.g. Vogler & DeSalle 1994) also stresses highly reduced gene flow which is necessary to reach alternate fixation of characters from either strong selection at quantitative traits or from physical isolation through landscape barriers or reproductive isolation in sympatry. Dizon *et al.* (1992) also emphasizes reduced gene flow as a means of allowing adaptive divergence.

Finally, it is clear from the above review that the various ESU concepts all possess strengths that are counterbalanced to some extent by inherent uncertainties. From a practical standpoint, we argue that differing approaches may work in varying circumstances more efficiently than others. This implies that designating ESUs should be done flexibly on a case-by-case basis. In particular, there seems to be an objectivity trade-off between using more stringent and 'straight-forward' concepts [e.g. reciprocal monophyly of Moritz (1994a), fixation of characters in PSC approaches (Vogler & DeSalle 1994)], and more integrative approaches such as the NMFS's (Waples 1991). In most cases, the former approaches retain greater objectivity at the expense of using less demanding data analyses in the decision-making process. Conversely, the latter incorporate a multitude of data that may not always be achievable. In the end, this can make a strictly objective decision more difficult to reach.

### Adaptive evolutionary conservation: unifying framework for defining ESUs that reconciles different views

#### Conceptual overview

Our review of ESU concepts guides and supports the unifying conceptual framework of adaptive evolutionary conservation (AEC) proposed here (Fig. 1). First, the ESU concepts themselves share similar conservation goals, and some commonalities lie between them, suggesting that reconciliation is possible. Second, no single ESU concept fulfils all of these conservation goals across all species boundaries but situational circumstances will warrant the use of some over others. This is because various ESU concepts were conceived in situations that necessitated differing working approaches to tackle particular conservation problems along the evolutionary continuum (*evolutionary conservation*). As such, a rigid, universal definition of an ESU across all species may not be possible. However, a general one would help to guide conservation efforts and would allow us to focus on the more important fundamental goals of preserving adaptive genetic variance within species. Therefore, a system that could use the strengths of various ESU concepts, either alone or in combination, while at the same time acknowledging the inherent weaknesses of each, would be useful. Such a system would be able to more readily identify biologically meaningful ESUs, incorporate exceptions as they arise, and have practical

utility in responding to the frequent situation of having limited resources when exercising management judgement. In this manner, AEC emphasizes flexibility in the same way proponents of the *adaptive management* paradigm in ecological circles feel management should function as new information comes in (e.g. Holling 1978; Walters & Holling 1990), hence, the name *adaptive* evolutionary conservation.

Mostly everyone agrees that the main conservation goal should be to preserve both evolutionary processes and the ecological viability of populations (Moritz 1999) by maintaining as many of the important genetic building blocks within the species as possible so that the process of evolution is not excessively constrained (Waples 1995). This implies the importance of salvaging intraspecific ecological and genetic variation in the short, as well as the long-term. Moreover, as mentioned before, there is an emerging consensus that both adaptive divergence and historical isolation should be considered. Each is functionally important and represents an extreme along the continuum of how the accumulation of genetic differences arise by the differential effects of evolutionary forces. For instance, historical isolation, at the very least, most certainly represents an accumulation of novel mutations between populations even though these may not be readily distinguishable by obvious external 'adaptive' differences. Clearly, the origin of novel, favourable mutations in specific populations may in itself be a powerful cause of divergence that can be particularly effective in large populations (Turelli *et al.* 2001). In contrast, adaptive divergence may represent a rapid accumulation of differential genetic differences through directional selection (Lande & Barrowclough 1987; Lynch 1996). A tool such as reciprocally monophyletic mtDNA in gene genealogies has its strengths for applications in populations of animals that have had enough evolutionary time to divide naturally into groups over the species range (Moritz *et al.* 1995). It, therefore, can be viewed as stressing the first extreme, the accumulation of novel and potentially favourable mutations. Conversely, in lineages experiencing rapid adaptive radiations, accumulations of genetic divergence are mainly arising through the opposite extreme, the effect of strong directional selection. Here, tests of ecological exchangeability (Crandall *et al.* 2000) or ecological characters (PSC) may be more appropriate. Therefore, mostly everyone in conservation biology and molecular ecology agrees that the accumulation of 'genetic differences' through reproductive isolating mechanisms are critical factors in defining evolutionary lineages for conservation. This isolation may refer to the strict criterion of genetic incompatibility, but also other factors such as physical isolation or ecological driven divergence that can be inferred from life history characteristics, demonstrably heritable morphological traits or quantitative trait loci, etc.

To be more encompassing for conservation purposes then, we purposely define an ESU under AEC in a general

manner as a lineage demonstrating highly restricted gene flow from other such lineages within the higher organizational level (or lineage) of the species. Here, lineages represent single lines of direct ancestry and descent relative to members of other lineages (de Queiroz 1998; see also Simpson 1961; Hull 1980). This infers that such lineages have followed independent evolutionary trajectories for variable periods of time. Thus, in being sufficiently isolated through highly reduced (or absent) gene flow, each lineage will have limited or no impact on the evolution, genetic variance and demography of other such lineages. In certain circumstances, ESUs will be equated with species (species composed of one evolutionary lineage), whereas in others, a species can include multiple ESUs. ESU lineages in turn can be made up of one or multiple populations or population groupings marked by more pronounced gene flow (e.g. metapopulations), with this being dependent on specific life histories.

In general then, any criteria, *if rigorously applied* as a means for providing evidence of lineage sorting through highly reduced gene flow, are potentially useful for conservation initiatives under the proposed conceptual overview and ESU definition of AEC. It is important to point out that ESU judgement should ideally be based on a combination of ecological and genetic data, although under AEC, ESUs could be designated with molecular genetic markers alone, for example. However, we suggest that in a situation where highly restricted gene flow between lineages is supported (or rejected) in the absence of either evaluations of adaptive divergence or historical isolation, common sense should prevail and potential data limitations should be acknowledged. For example, if there is substantial concern that the species is in jeopardy, and all scientific evidence (even if limited) points to extinction, only one data set could be used to achieve official ESU status for formal protection. Crucial to this exception, as in all ESU designations, is that techniques which consider the statistical power of alternative hypotheses should be used to minimize the probability of protecting 'apparently isolated' units which could ultimately compromise the viability of the species in future contexts (Dizon *et al.* 1995). We can only suggest that the best available biological information be used in exercising such decisions on a case-by-case basis. Keeping these points in mind, and the framework of AEC, examples are discussed below to highlight how AEC might be implemented in practice.

*Ecology matters — Cryan's buckmoth* (*Hemileuca species complex*). Buckmoths are a group of moths with varying life histories and host plants in North America. One particular small group of populations (Cryan's buckmoth) near the eastern Canada/USA border is geographically separated from other eastern *Hemileuca* populations. Molecular genetic analyses (both allozymes and mtDNA sequences) failed

to find any fixed or significant differences in allele or haplotype frequency between Cryan's populations and those from other *Hemileuca* populations (Legge *et al.* 1996). Therefore, Moritz's genetic criteria of reciprocal monophyly and significant nuclear divergence did not suggest the AEC's ESU criterion of highly restricted gene flow, nor did reproductive isolation in the strict sense of genetic incompatibility of Waples, or the PSC. However, a host-plant performance experiment revealed evidence that Cryan's buckmoth larvae consume and grow on a unique plant host, an ecologically significant trait that is presumably based on heritable attributes, for which larvae of other *Hemileuca* populations showed no capability (Legge *et al.* 1996). Given this information, under AEC, the ability of Cryan's buckmoth to use a unique plant host provides evidence that the insect demonstrates unique adaptive genetic differences at QTLs from other such populations within the *Hemileuca* complex. Whether available molecular marker technologies can detect it or not, such ecologically driven adaptive differences could ultimately lead to accumulations of rapid genetic divergence through directional selection (Schluter 2001). Cryan's buckmoth therefore possesses biologically justifiable evidence for being an isolated lineage, making it a strong ESU candidate (as Legge *et al.* 1996 and Crandall *et al.* 2000 suggest) under AEC.

*Evidence of highly restricted gene flow in the absence of adaptive data — robust redhorse (Moxostoma robustum).* The robust redhorse is a rare, riverine, catostomid fish native to a small region of the southeastern USA. Originally described in 1869, representatives of the species were not seen again for more than 100 years until the 1980s (Wirgin *et al.* 2001). Recent attempts to locate extant populations in many rivers from the historical range failed. As part of a conservation initiative for the species, mtDNA analyses were conducted on remaining populations (Oconee and Ocmulgee rivers within the Altamaha drainage, and the Savannah river drainage) to determine genetic relatedness and to assist restoration efforts (Wirgin *et al.* 2001).

Despite the geographical proximity of the two drainages, fixed differences in mtDNA haplotypes were found between them. Unpublished microsatellite data also corroborated the mtDNA data with highly significant allele frequencies detected between drainages (Wirgin *et al.* 2001). Together, these genetic analyses provided evidence of two lineages that were separated by highly restricted gene flow through historical isolation and the accumulation of genetic differences by novel mutations (*sensu* Moritz or first criterion of Waples 1991). Although limited, life history data suggested that one drainage's broodstock was approaching senescence and that habitat degradation was implicated in reducing overall larval recruitment in the robust redhorse (Wirgin *et al.* 2001). Moreover, the two

drainages represent the only remaining gene pools of the fish presently known. All current evidence suggests that the species is flirting with extinction.

Under AEC, the available information from neutral molecular markers provides proxy evidence that long historical isolation has led to the differential accumulation of novel mutations that could be of significance to the viability of the species within each specific drainage. Despite the fact that no rigorous adaptive divergence testing was conducted, each drainage should therefore be granted ESU status to acquire formal protection. In this case, analysing ecologically relevant traits to test adaptive divergence (e.g. Crandall *et al.* 2000) would depend on too many resources and time than are available.

*Species-wide scales, flexibility and practicality: whitefish (Coregonus clupeaformis/lavaretus complex).* Throughout their Northern Hemisphere circumpolar distribution, the whitefish is frequently characterized by the sympatric divergence of forms differing in morphology, diets, and life history traits. A large-scale mtDNA phylogeographical analysis showed that the species complex is composed of five historically isolated lineages that correspond to Pleistocene glaciations in distinct refugia (Bernatchez & Dobson 1994). Rigorous genetic studies of a contact zone between populations originating from different lineages have demonstrated highly reduced gene flow through various reproductive isolating mechanisms, including ecological nonexchangeability (Lu *et al.* 2001), and hybrid breakdown through genetic incompatibility (Lu & Bernatchez 1998). In North America, diversification of two distinct ecotypes along a trophic partitioning of benthic ('normal' ecotype) and limnetic ('dwarf' ecotype) zones within lakes has also arisen. Detailed analyses of mtDNA and nuclear DNA (allozymes or microsatellites) have provided evidence for parallel evolution of these ecotypes (Pigeon *et al.* 1997), suggesting that resource-based natural selection has been responsible in driving population divergence in whitefish (Lu & Bernatchez 1999).

This species complex provides relevant lessons to the formulation of ESUs under AEC. For example, in many cases such as this one, systematics and phylogeographical analyses by means of molecular genetic markers will probably remain an appropriate first step to designating ESUs. This is because they are effective at defining major cohesive groups of populations that are reproductively isolated in the broad sense and consequently, have little or no gene flow between them (e.g. Avise 1994; Bernatchez 1995). With improving technologies, genetic assays are becoming more cost effective as well. Furthermore, there is increasing evidence that parallel phenotypic evolution driven by divergent natural selection has occurred in many species groups in addition to whitefish (reviewed in Schluter 2000). This suggests that phenotypic traits may be more useful



in determining population divisions within ESUs in such species. It, therefore, reiterates that maximizing the probability of conserving evolutionary potential within some species may lie in the differential use of genetic and ecological criteria at different steps, instead of expecting that each will provide equally useful information at any given step (Bernatchez 1995).

With respect to designating ESUs through AEC, whitefish present a special case of extremes. On one hand, there is strong historical evidence to designate ESUs on the basis of accumulated genetic differences (highly restricted gene flow) within each isolated glacial lineage. On the other hand, within each of these lineages, there is also ample biological evidence to suggest that selection is driving rapid phenotypic divergence in some populations. As in the case of Cryan's buckmoth, this ecologically driven divergence could provide evidence of reproductively isolating mechanisms involved in lineage sorting (and a significant reduction in gene flow). AEC argues that in such a case, as in all cases, it is important to come back to the overarching conservation goals. If it is our aim to maximize the probability of protecting the genetic variance within a species, then in many species, including whitefish, this requires considering both the historical and the ecological evolutionary forces that give rise to isolated lineages. Therefore, under AEC, whitefish possess subhierarchical ESUs within other ESUs. Here, the term subhierarchical does not infer subordination but rather a frame of reference on a phylogenetic continuum.

### Benefits of AEC

These diverse examples highlight the need for a more flexible approach, such as AEC, when designating ESUs. On a positive note, they demonstrate that the differences between ESU criteria can help to affirm ESU designations or contribute collectively to the more important conservation goals. Furthermore, these examples exemplify the problems of universally applying criteria of one concept. This should not be viewed as a detriment to the cause. Rather, depending on situational circumstances, in particular, the evolutionary forces being evaluated and the temporal scale being considered, some ESU criteria will work better than others. For example, Moritz's criteria failed in Cryan's buckmoth where the exchangeability of Crandall *et al.* (2000) shined. Yet, conversely, Moritz's criteria enabled ESU status in the robust redhorse where Crandall *et al.*'s could not because of the specification of adaptive divergence tests. In whitefish, both historical and ecological criteria that emphasize the roles of differing evolutionary forces in the formation of evolutionary entities were useful in designating ESUs.

It therefore seems that an integrative system that unifies the strengths of various proposed criteria for the nature of the situation will be able to designate more biologically

meaningful conservation units. Under AEC then, instead of being an impediment to the conservation goals, anomalies within an operational criterion become constructive. For instance, to suggest that the ESU concept be abandoned primarily because in some instances reciprocal monophyly of mtDNA does not make accurate inferences of evolutionary relationships (e.g. Crandall *et al.* 2000) is unproductive. This only suggests that another operational criterion is probably more appropriate in that situation.

### ESU viability

Although not in the scope of this review, it is important to mention that once ESUs have been designated, the challenge becomes avoiding the extinction of the component parts within each to ensure its viability in the long term. From this standpoint, we feel that much can be learned from work done by NMFS (McElhany *et al.* 2000). Briefly, by focusing on the level of the viability of individual populations with corresponding relations to the viability of the ESU as a whole (under the ESA), McElhany *et al.* (2000) provide guidelines to evaluate population viability status of Pacific salmonids based on four population parameters: abundance, demographic growth rate, spatial structure, and genetic diversity. All are justifiably adequate indicators of viability (or conversely, extinction risk). For example, small populations are at a higher risk of extinction than larger ones, all else being equal and population growth rate may suggest the ability of populations to replace themselves (McElhany *et al.* 2000). Spatial structuring can infer habitat quality and thus viability over time periods, and genetic diversity provides the raw material for surviving long-term environmental change (McElhany *et al.* 2000). All of these considerations will of course be weighted against the amount of resources available to a given management jurisdiction.

### Conclusions

Conservation biology is a science where 'time is biotic diversity'. As such, 'it is better to take the time to contemplate probable answers to questions of uncertainty than to seek precise answers to irrelevant questions' (Behnke 1995). A review of the major approaches to discerning ESUs suggests that no single approach will work best in all situations, but that each has its strengths and weaknesses under different circumstances. Yet, they all aim towards preserving the adaptive genetic variance within species. Therefore, maintaining evolutionary potential in the face of uncertainty may be better served by using a more malleable system to delineating conservation units, like AEC, which is able to incorporate the positive attributes of each approach. Just as there is wide consensus that different evolutionary processes give rise to similar entities that we call species (Barton 2001; Hey 2001), there is consensus that entities

which we define as ESUs may arise by the accumulation of genetic differences through the various roles of evolutionary forces (e.g. novel mutations vs. directional selection) through time. The point to consider on the evolutionary continuum will vary with the organism at hand and so too will the criteria used. Differing ESU approaches are only tools in the AEC tool box; they need not conflict with one another, but can operate in a complementary and adaptive fashion. The ESU simply must be flexible.

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This review was stimulated by the authors' common research interests in molecular ecology and conservation biology of aquatic organisms and passion for reconciling differing views. D.J.F is a MSc student assessing the genetic population structure of lacustrine brook charr (*Salvelinus fontinalis*) with applications to conservation and fisheries management. L.B.'s research programme focuses on the understanding of pattern and processes of molecular and organismal evolution, as well as their significance to conservation.

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