A practical framework for identifying genetic subpopulations and ESUs: insights for IUCN assessments and broader management

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Abstract

Species conservation assessments, such as the International Union for Conservation of Nature (IUCN) Red List and Green Status of Species, guide global conservation priorities by evaluating species' extinction risk and recovery status. Although such frameworks provide scope to include genetic information, this aspect of biodiversity, which is critical for species' fitness and adaptive potential, remains underrepresented. The Kunming–Montreal Global Biodiversity Framework now explicitly highlights genetic diversity, offering an opportunity to strengthen its integration into these assessments. While the IUCN can account for subpopulations, these units are rarely applied, and Evolutionarily Significant Units (ESUs) remain formally unacknowledged. Incorporating these genetic units could enhance representation of adaptive genetic diversity and better inform conservation planning and decision-making, though defining them can be difficult when data are limited. We propose a flexible framework that integrates molecular and non-molecular evidence to identify subpopulations and ESUs across taxa and contexts.

Keywords

Conservation policy

Evolutionarily Significant Unit

Genetic diversity

IUCN species assessments

Subpopulations

176 ***Main Text***

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Box 1: Key terms

CBD the United Nations Convention on Biological Diversity is the foremost authority and key international treaty on biodiversity, which includes explicit commitments and agreements to conserve and monitor biodiversity (https://www.cbd.int/). The Kunming-Montreal Global Biodiversity Framework (KMGBF) is a recent agreement adopted in December 2022 with commitments from 196 signatory nations. The agreement provides a pathway for halting and reversing global biodiversity loss. Importantly, genetic diversity is explicitly recognized in this agreement as a core component of biodiversity that must be conserved, monitored, and reported.

Evolutionarily Significant Units "ESUs" are lineages demonstrating highly restricted gene flow from other such lineages within the higher organizational level of species (Fraser and Bernatchez 2001). Due to limited gene flow, these subpopulation networks follow their own evolutionary trajectories and thus are likely to house unique adaptive genetic diversity (Funk et al. 2012; Figure 1c).

A population within the IUCN Red List framework is defined as the total number of individuals of the taxon (i.e, species or subspecies) (IUCN 2001; Figure 1a), which differs from its common biological usage (IUCN 2003). Due to the multiple definitions of this term, we have avoided it in the remainder of this manuscript.

Subpopulations in the IUCN Red List framework are geographically or otherwise distinct groups in a population between which there is little demographic or genetic exchange (typically one successful migrant individual or gamete per year or less; (IUCN 2001; Figure 1b).

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179 **Why list Subpopulations and Evolutionarily Significant Units in IUCN assessments?**

180 Genetic diversity is the foundational level of biodiversity but remains rarely considered in
181 global conservation programs (e.g., neglected in protected area design, Paz-Vinas et al. 2025;
182 species recovery plans, Pierson et al. 2016; in IUCN assessments, Schmidt et al. 2023; and in

recent policy like the European Union Nature Restoration Law, O'Brien et al. 2024). Though the recently adopted United Nations Convention on Biological Diversity (CBD; Box 1) Kunming-Montreal Global Biodiversity Framework includes explicit commitments to conserve and monitor genetic diversity (Target 4; CBD 2022, da Silva et al. 2026), a greater integration into other conservation initiatives is urgently needed to help address the decline of global genetic diversity.

Irreversible allelic diversity and heterozygosity loss have been documented across hundreds of species (Leigh et al. 2019, Shaw et al. 2025). Human activities are frequently leading to the extirpation of entire subpopulation networks (Ceballos et al. 2017, Mastretta-Yanes et al. 2024), which likely harboured distinct alleles and possibly local adaptations, representing a loss of unique evolutionary trajectories. Genetic diversity underpins fitness, resilience, and adaptive potential (Reed and Frankham 2003, Swindell and Bouzat 2005, Hughes et al. 2008, Harrisson et al. 2014, Frankham 2015, Ørsted et al. 2019, DeWoody et al. 2021, Kardos et al. 2021, Meek et al. 2023, van Oosterhout et al. 2025), and its erosion is closely linked with species extinction risk through reduced capacity to respond to environmental change or disease threats (Frankham 2005, Evans and Sheldon 2008, Polishchuk et al. 2015). Importantly, demographic recovery of a population does not imply genetic recovery, lost genetic variation may remain depleted for many generations, highlighting the need to maintain distinct subpopulations and ESUs (Nei et al. 1975, Frankham 2005). Thus, losses in genetic diversity represent a threat to all levels of biodiversity.

The International Union for Conservation of Nature (IUCN) and its Red List of Threatened Species (a catalogue of over 163,000 species) is the international standard in assessing the extinction risk of species based on the best available information. Extinction risk is calculated on the occupation of the focal species' historical range, census size and trends, habitat quality and fragmentation level (IUCN 2001), but genetic diversity is not formally included in assessment criteria (Schmidt et al. 2023, van Oosterhout 2024). As a result, Red List conservation status is not directly correlated with remaining levels of genetic diversity or magnitude of loss (Leigh et al. 2019, Mastretta-Yanes et al. 2024, Shaw et al. 2025). In the more recently established IUCN Green Status of Species (IUCN 2021), recovery of pre-impact

census size is assessed as a measure of conservation success. Although genetic diversity is not explicitly assessed, it is sometimes discussed in Green Status assessments. In some cases, species with substantial, irreversible genetic diversity loss have received high Green Status recovery scores, despite persistent risk of inbreeding and limited adaptive capacity (e.g., Alpine ibex; Brambilla et al. 2020). Though IUCN conservation status (i.e., extinction risk and recovery status) does not directly prescribe protection or species management, greater consideration of genetic diversity is necessary to identify important groups in need of protection.

The recently adopted genetic diversity indicators in the CBD Kunming-Montreal Global Monitoring Framework (KMGBF) provide inclusive access to genetic diversity assessment without necessarily requiring molecularly-derived information (Mastretta-Yanes et al. 2024, Hoban et al. 2025). These indicators track the maintenance of genetic diversity by assessing and monitoring key evolutionary processes, such as the persistence of subpopulations, connectivity between them, and the retention of adaptive variation across species. In practice, this means that even in the absence of genome-wide data, information from ecological surveys, demographic records, and well-documented populations can be used to infer whether genetic variation is being preserved and whether evolutionary processes are likely to continue. Adopting a similar approach within IUCN assessment criteria is a potential way to include genetic concerns without the need for scarce molecular data (less than 1.5% IUCN Red List assessed species have accessible molecular data, Paz-Vinas et al. 2025). Building on the KMGBF approach, the framework presented here offers a method to identify within-species units at scales relevant for evolutionary processes, which could inform assessments, within the IUCN and more broadly, to highlight units that contribute to overall genetic diversity.

Conservation-relevant evolutionary processes can be categorized into two spatiotemporal scales (Figure 1). Short-term processes, such as gene flow and genetic drift, shape the genetic structure of species over relatively few generations across “subpopulations”. Subpopulations, as defined under the IUCN, are akin to the common biological usage of “populations” (see key terms in Box 1) and correspond to the units used for genetic indicators in the Global Biodiversity Framework (Figure 1b). Longer-term processes, including environmental

adaptation (i.e., response to natural selection) and the accumulation of alleles through mutation, shape the evolutionary trajectory of a species across networks of several subpopulations. These distinct networks are known as “Evolutionarily Significant Units” (hereafter ESUs) (Allendorf et al. 2022; Figure 1c). ESUs can follow their own evolutionary trajectory and may occupy unique or different ecological niches to other units within their species. Identifying and considering ESUs can help maintain evolutionary processes beyond individual units, supporting broader ecosystem function. We note that the distinction between short and long timescales may not always be time dependent, as some evolution can occur rapidly. However, we note that we explicitly do not consider human-mediated (e.g., selection for desirable phenotypes) or drift driven change (e.g., due to human isolation) as valid evolutionary trajectories for ESUs.

The IUCN currently assesses species at three levels: species (Figure 1a), subspecies, and subpopulations (Figure 1b). While ESUs (Figure 1c) are not formally recognized as a separate unit of assessment, they represent biologically meaningful within-species groups that may not be captured by subspecies or subpopulation delineations (e.g., Cape parrot, Coetzer et al. 2015; Leopard skink, Prates et al. 2023). Subpopulations are a recognized unit, but fewer than 5% of species have them delineated on the Red List (Janet Scott, Programme Officer at IUCN, written communication, April 2024), reflecting the lack of standardized usage. Considering subpopulations and ESUs in species assessments could provide additional insight into the structure and evolutionary potential of species, supporting more nuanced conservation prioritization and decision-making.

Conservation Units, including ESUs, have a longstanding history in scientific conservation assessments. The term ESU was first conceptualized by Ryder (1986), and subsequent studies have proposed varying criteria to define them as conservation-relevant units (overview in Fraser and Bernatchez 2001). However, challenges arise in standardizing ESU delineation due to the multidisciplinary nature of conservation science and differing approaches to genetic and ecological data (e.g., Moritz 1994, Crandall et al. 2000, Funk et al. 2012). For example, ecological factors such as habitat specialization or behavioral differences play a role in the divergence of ESUs and might be overlooked if genomic data alone are used to determine them.

In turn, similar phenotypes that are underpinned by different genomic adaptations can also be overlooked if phenotypic data alone are used (Fenster and Dudash 1994). A holistic approach that integrates genetic and non-genetic metrics, including adaptive and ecological variation, has been recommended to improve comparability and relevance (Fraser and Bernatchez 2001, Robertson et al. 2014).

To support the consideration of ESUs and subpopulations in IUCN and other conservation assessments, we present a comprehensive and flexible framework for standardized ESU identification and improved subpopulation delineation. Our aim is that by identifying unique genetic units their passive loss could be mitigated by the identification of units at risk of extinction (i.e., extinction of unique variation or disrupted evolutionary processes). Though we have developed our framework specifically to support IUCN assessments, we acknowledge dividing species into subpopulations or ESUs could unintentionally impact downstream conservation management decisions. A recent meta-analysis found a strong historical tendency in conservation management to define units as genetically distinct through data misinterpretation and/or weak or no evidence (Liddell et al. 2021). These divisions have previously led to erroneously isolated units that unnecessarily increased extinction risk (e.g., *Perameles gunni*; Weeks and Rypalski 2021). We strongly stress that division of species into subpopulations or ESUs through any framework does not indicate a need to manage units in isolation (e.g., Senn et al. 2014) but rather could be used to help highlight unique units at risk of extinction and in need of protective actions (e.g., translocations; habitat restoration) to prevent irreversible genetic diversity loss or disruption of evolutionary processes. We also draw attention to the risk assessments included throughout this paper.

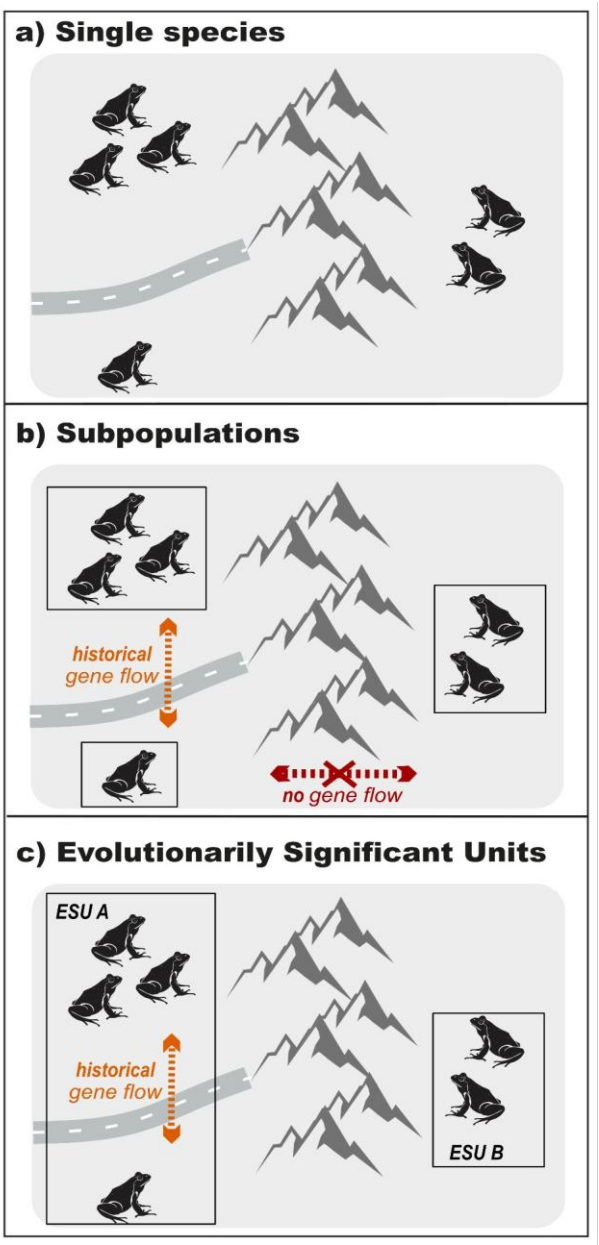

Figure 1 - Within the IUCN assessment guidelines, listing of distinct groups can occur at species (a), subspecies- (not shown), or subpopulation (b) levels. We suggest the inclusion of Evolutionarily Significant Units "ESUs" (c). Note that one or several subpopulations together can form an ESU and their grouping is determined by gene flow. In this cartoon example, gene flow is depicted as being restricted between the ESUs by geographical barriers (mountains). The two subpopulations on the left side of the panel were historically linked by gene flow, while this was interrupted by a road, we do not consider them ESUs because the interruption of their gene flow is anthropogenic and they have the same historical evolutionary trajectory thus they are one ESU.

Subpopulation and ESU standardized framework

The framework we outline here for standardized identification of subpopulations and ESUs has two steps: first, identifying genetically meaningful subpopulations and, second, grouping these into ESUs. Though we recognize the existence of several ESU frameworks (e.g., Fraser and Bernatchez 2001, Funk et al. 2012), a framework using multiple lines of evidence is necessary for objective and standardized identification of IUCN-relevant groups.

Three types of data are used in this delineation framework: genetic, recorded biological and inferred evidence (Figure 2a). Genetic evidence derives from genetic or genomic markers (e.g., single nucleotide polymorphisms [SNPs], microsatellites, mitochondrial haplotypes) and is leveraged to assess differentiation and/or evolutionary distinctiveness, including adaptive divergences, of groups within a species. Recorded biological evidence does not require genetic data (e.g., observed biogeographic patterns, variation in transmitted traits) and comes directly from individuals in the assessed focal species. Inferred evidence also does not require genetic data and is not directly observed in the focal units, e.g., is deduced from biogeographic patterns based on modelling techniques. To guide assessors, we have comprehensively listed categories, specific analyses within each evidence-type and data that can be used (Table 1).

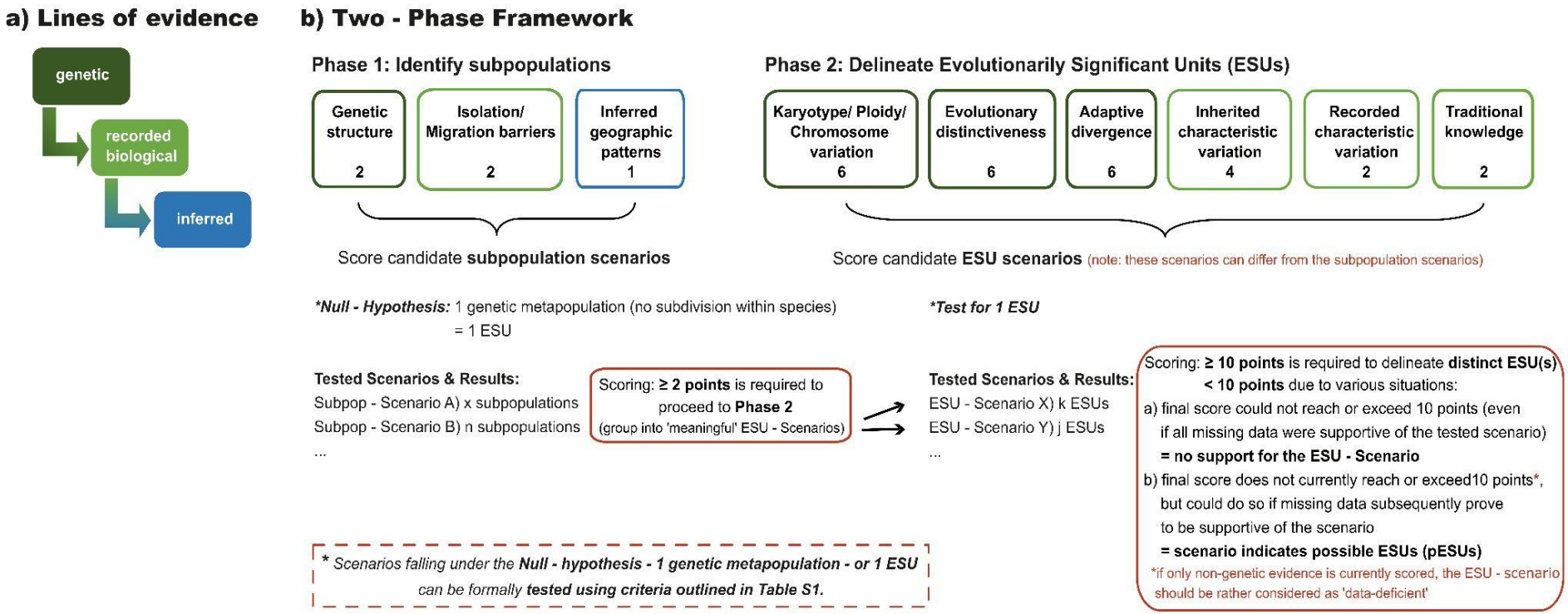

Figure 2 - a) Lines of evidence and b) the Two-phase framework to assess the strength of evidence for subpopulations and Evolutionarily Significant Units (ESUs). Different lines of evidence are highlighted in dark green, green or blue. Scores for each evidence category are indicated within the boxes. Higher scores indicate increased support. The scores quantify how informative each category of evidence is in assessing the likelihood that a subpopulation or ESU is distinct. The framework is followed using different 'candidate scenarios' for various supported groupings of the species. In the case of conflicting evidence, assessors should divide the species into all different 'scenarios' and score each scenario separately. If no data or unclear data are available a score of 0 should be awarded and the evidence category is marked as 'missing'.

Table 1 Three categories of evidence used in the two-step framework to delineate subpopulations and ESUs, each containing multiple lines of evidence. For each line of evidence, a description of the methods and metrics used to assess it, examples of supporting studies, and the main risks of over- or under-splitting units are provided. Scores assigned to each line of evidence are also shown. Additional details on the risks of over- and under-splitting for each line of evidence and references are provided in Supplementary material, Section C.

Types of evidence	Description	How to assess?	Example studies using evidence categories	Main Risks of over- and under-splitting	Score
Genetic evidence					
Genetic structure *(Phase 1)*	Substantial genetic structure and fragmentation mostly determined by limited gene flow between subpopulations.	a) structure-like analyses such as Structure, Admixture plots, PCA, DAPC, D-stats b) high pairwise Fst values (relative to the species wide pairwise levels), c) abundance of private alleles, that indicate long term limited gene flow between subpopulations	e.g., Abbott and Double 2003	Over-splitting: cluster detection bias, over-estimation of genetic differentiation by visual inspection, over-interpreting private alleles Under-splitting: generally low risk	2
Karyotype, ploidy, and chromosome structure variation *(Phase 2)*	Documented heritable differences in chromosome number, ploidy, or chromosome structure between candidate ESUs.	Using conventional cytogenetic methods (e.g., chromosome counting, karyotyping), flow-cytometry and/or molecular cytogenetics (with structural variant detection softwares) to detect: a) karyotype variation b) differences in ploidy levels between units c) Structural variation of chromosomes between units d) evidence of no/rare/unfit hybrids between proposed units.	e.g., Ferreira et al. 2017, Ahrens et al. 2020, Hollenbeck et al. 2022	Over-splitting: misinterpreting neutral karyotype variation as evidence for ESUs Under-splitting: missing important karyotypic differences due to insufficient sampling or low technical resolution	6

Types of evidence	Description	How to assess?	Example studies using evidence categories	Main Risks of over- and under-splitting	Score
Evolutionary distinctiveness *(Phase 2)*	Genetic evidence of reproductive isolation, due to highly restricted or no gene flow between focal ESUs that may have fuelled evolutionary distinctiveness.	a) reciprocal monophyly b) molecular estimates of divergence time. In complex cases, follow clades supported by ≥75% bootstrap or posterior probability values, derived from a statistically valid evolutionary model and tree-building method.	e.g., Moritz 1994, Moritz and Faith 1998, Walsh et al. 2024	Over-splitting: over-interpretation of reciprocal monophyly or long divergence times (dependent on methodology used and species context/history), assuming no current gene flow means no historical gene flow Under-splitting: over-interpretation of lack of reciprocal monophyly, overlooking variation across the genome	6
Adaptive divergence *(Phase 2)*	Robust genetic evidence of candidate ESUs harbouring unique local adaptation(s) driven by selection (e.g., environmental, sexual selection) that are not shared with other ESUs.	a) robust genomic signals of local adaptations supported by multiple selection detection methods and ideally in combination of non-genomic information (e.g., Gene-environment associations using Bayenv, RDA, RandomForest) b) evidence of stable hybrid zones	e.g., Bonin et al. 2007, Rodríguez-Quilón et al. 2016	Over-splitting: false positives in outlier tests, environment-based detection confounded by neutral structure, hybrid zones misinterpreted as ESU boundaries Under-splitting: no outlier detection due to low statistical power, ignoring hybrid zone context	6

Types of evidence	Description	How to assess?	Example studies using evidence categories	Main Risks of over- and under-splitting	Score
Recorded biological evidence					
Isolation and barriers to migration *(Phase 1)*	Subpopulations show evidence of isolation (i.e., long-term signs of restricted gene flow due to geographic, environmental, or temporal differences) between them. Alternatively, subpopulations show evidence of recently restricted gene flow due to human mediated change (e.g., habitat fragmentation, extirpation of connecting subpopulations etc).	a) occupation of different biogeographical zones (e.g., habitat maps, maps on environmental patterns) b) occupation of discrete remnants of historical habitats with little to no chance of natural migration between habitat patches.	e.g., Hewitt 2004, Lorenzen et al. 2012	Over- and undersplitting: misinterpretation of observed patterns as natural-long term patterns, misidentification of species or environmental drivers for species	2

Types of evidence	Description	How to assess?	Example studies using evidence categories	Main Risks of over- and under-splitting	Score
Inherited characteristic variation *(Phase 2)*	Candidate ESUs show consistent heritable differences in life history or ecologically/species important traits (e.g., body size, colour, breeding time, use of spawning grounds).	a) heritable differences in focal traits observed in common garden experiments or other robust analytical tests (e.g., cross-fostering, trait measurements controlling for environmental variation)	e.g., Small et al. 1998, Wainwright et al. 2008	Over-splitting: confusing plasticity with adaptation, overinterpretation non-functional traits, neglecting distorted variation in small subpopulations Under-splitting: failing to recognize evolved differences in phenotypic plasticity	4
Recorded characteristic variation *(Phase 2)*	Candidate ESUs show consistent differences in traits that are locally transmitted but not robustly shown to be heritable (acquired behavioural or phenotypic differences; environmentally modified traits)	a) cultural/learnt behavioural differences unique or specific between units b) acquired/transmitted traits (e.g., foraging techniques, alternative migration routes, regional birdsong 'dialects'; methylation differences; body size differences) c) general field-based morphological and functional trait assessments	e.g., Gu et al., 2021; Lundberg et al., 2017; Sanchez-Donoso et al., 2022; Toews et al., 2019	Over-splitting: misinterpretation of acquired behaviours or phenotypic differences as barriers to gene flow Under-splitting: study bias (lack of studies in general = data-deficiency, study selection bias)	2

Types of evidence	Description	How to assess?	Example studies using evidence categories	Main Risks of over- and under-splitting	Score
Traditional knowledge *(Phase 2)*	Distinctiveness between candidate ESUs based on indigenous, local, or traditional knowledge.	a) recorded differences based on traditional and information local knowledge (according to the IUCN ILK framework, IUCN, 2022). This encompasses information that is not yet statistically analysed, information that is analysed should be counted as inherited or recorded characteristics.	e.g., a proposed tool to use ILK species assessments (Montanari and Kanagavel 2017)	Over- and undersplitting: if not all relevant stakeholders are consulted, leading to a biased perspective	2
Inferred evidence					
Inferred geographic patterns *(Phase 1)*	Subpopulation differentiation and fragmentation modelled from the focal species through e.g., species distribution modelling approaches, or measured/ observed from closely related species.	a) subpopulation disjunction from co-occurring species used as a proxy b) phylogeographic and/or biogeographic evidence from co-occurring species c) assumption of biogeographical data/refugia without direct evidence d) dispersal distance and buffer according to the CBD indicators		Over-splitting: overinterpretation of detected patterns when they don't reflect genetic differentiation Under-splitting: patterns in co-occurring species as proxies can obscure detected differences	1

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To enable the application of a pre-defined threshold for delimiting subpopulations or ESUs, each line of evidence is given a score. The value of the score corresponds to the strength of evidence. Scores range from 1 to 6. Values of 6 are for evidence-types that offer the strongest support (i.e., genetic/genomic signals of prolonged reproductive isolation and/or local adaptations). A score of 6 is only possible in Phase 2, as these differences occur between ESUs. Scores of 4 and 2 are given to strongly suggestive evidence categories that reflect genetic divergence or non-molecular signs of local adaptation. A score of 1 is given to data that are entirely inferred, such as information from projections (e.g., maps, species distribution models) or information inferred from closely-related species. This is a common, but high-risk evidence-type, and its low score reflects this associated risk. The relative weighting of evidence-types reflects the IUCN's nature of evidence rule for assessment criteria (see IUCN 2024). A score of 0 is given if there is no data available. The framework does not allow for fractions or partial scores, scores are in even increments to support quick summing. We have strived to keep the scoring system simple, but a degree of complexity is needed to capture all outcomes.

To determine the number of divisions, assessors should leverage the collected evidence from the categories detailed in Table 1 and divide the species into the most likely groups of subpopulations and ESUs, each grouping is called a 'candidate scenario'. Focus should be on the most likely or relevant groupings, particularly those that may exhibit signs of isolation. Detailed step-by-step guidance on applying these criteria is provided in the accompanying guidance document at https://github.com/iucn-CGSG/Subpop-ESU-Webtool. In the case of conflicting evidence, assessors should divide the species into the potential'scenarios' and score each scenario separately then take the highest scoring. Different scenarios can be tested for Phase 1 and 2 and subpopulations can be grouped into a smaller number of ESUs. Comprehensive testing of scenarios based on existing knowledge, covering e.g., 1-7 subpopulations or ESUs is unnecessary, as many will be lacking sufficient data. The results of the scenario with the highest score (note this may be different for ESUs and subpopulations) could be used for listing assessment. When defining subpopulations, note that subpopulations can also be driven by human-mediated fragmentation or disruption of gene flow, whereas ESU divisions are likely to be more anciently derived.

To identify distinct subpopulations a total score of ≥ 2 is required in Phase 1. If multiple scenarios are tested, the scenario with the highest score is used. If scores are tied, we recommend choosing the high-score scenario, based on the most robust data (e.g., higher

resolution genetic marker). If two or more distinct subpopulations are delineated, the assessor then tests for ESUs in Phase 2. The scores from Phase 1 do not carry over to Phase 2, because in Phase 2 new candidate scenarios can be tested as it is unlikely that the number of subpopulations and ESUs are identical. A minimum score of 10 is needed to delineate distinct ESUs. This can only be reached if genetic or genomic evidence is collected for the species (Figure 2b and Table 1). At least one genetic evidence category is needed as a 'yes', coupled with either another genetic evidence category or with significant differences in inherited or acquired characteristics and/or traditional knowledge, to support a scenario with distinct ESUs. If fewer than 10 points are scored, the candidate scenario can either be regarded as (a) 'not supported', because 10 points cannot be reached or exceeded even if all missing data were supportive of the tested scenario; or (b) as a 'possible ESU (pESU)' scenario, because the minimum threshold of 10 points could be reached or exceeded if missing data subsequently prove to be supportive of the tested scenario. However, if a candidate scenario currently only scores in recorded biological evidence-types (so non-genetic), the scenario should be regarded as 'data-deficient' rather than as a pESU scenario. At the end of Phase 2, assessors should select the scenario with the highest score.

If no candidate scenarios can reach the minimum threshold of two points in Phase 1 or reach 10 points in Phase 2 (even if missing data could be acquired) the species may comprise a single genetic metapopulation (a set of spatially discrete or semi-discrete groups of individuals that are connected through sufficient gene flow to maintain shared genetic variation) and therefore a single ESU. Assessors can specifically test a scenario with one metapopulation (Phase 1) and one ESU (Phase 2). However, in order to test for a metapopulation or single ESU, compelling evidence indicating the lack of distinctiveness within the species has to be present and scored (criteria are outlined in Table S1 in the Supplementary material, section A). For consistency in the scoring, the same scoring system as for testing multi-subpopulations or -ESU scenarios is applied.

This framework has been tested thoroughly on a variety of species across different taxonomic groups (Table 2) with two detailed examples shown in Box 2 and Box 3 and the best supported candidate scenarios are visualized in Figure 3 and Figure 4. The thresholds of 2 points in Phase 1 and 10 points in Phase 2 are based on the extensive testing of these species, expressing different data availability and characteristics. We envision that as the framework is applied, more evidence types and exceptions will arise, and the framework could be adjusted

accordingly. In order to test this framework and further improve it, we are currently testing species listed in the IUCN Green Status of Species framework (IUCN 2021).

Table 2 - List of species tested using the proposed framework under different candidate scenarios. Only the highest scoring scenarios for Phase 1 (subpopulations) and Phase 2 (ESUs) are shown, as these best support the number of units tested. Scores are shown as points obtained out of the total points available. Relevant data sources supporting each scenario are provided as well as the IUCN Red List and Green Status.

Species or subspecies	**Phase 1**	**Phase 2**	**Genetic Data and studies considered**	**IUCN Red List status**	**IUCN Green Status**
Common Eland (*Tragelaphus oryx*)	**2 subpopulations** (4/4 points)	**1 ESU** (12/18 points)	Mitochondrial DNA (Gagnon and Chew 2000, Lorenzen et al. 2010, 2012)	Least Concern	*not assessed*
Mountain Zebra (*Equus zebra*)	**2 subpopulations** (4/4 points)	**2 possible ESUs** (8/14 points)	Mitochondrial and microsatellite data (Moodley and Harley 2005, Kotzé et al. 2019)	Vulnerable	*not assessed*
African buffalo (*Syn cerus caffer*)	**2 subpopulations** (4/4 points)	**2 ESUs** (22/22 points)	Nuclear genomes, mitochondrial and microsatellite data (Van Hooft et al. 2002, Smitz et al. 2013, 2014, de Jager et al. 2020, 2021, 2025, Quinn et al. 2023, Colangelo et al. 2024, Talenti et al. 2024)	Near Threatened	*not assessed*
Rodrigues fruit bat (*Pteropus rodricensis*)	**1 subpopulation** (4/4 points)	**1 ESU**	Microsatellite data (O'Brien et al. 2007)	Endangered	*not assessed*
Iberian lynx (*Lynx pardinus*)	**2 subpopulations** (2/4 points)	**1 ESU** (10/16 points = human mediated admixture due to captive breeding and translocations)	Microsatellite and whole-genome sequencing data (Rodríguez and Delibes 2003, Johnson et al. 2004, Pertoldi et al. 2006, Abascal et al. 2016, Casas-Marce et al. 2017, Kleinman-Ruiz et al. 2017)	Vulnerable	Largely Depleted

Species or subspecies	Phase 1	Phase 2	Genetic Data and studies considered	IUCN Red List status	IUCN Green Status
African penguin (*Spheniscus demersus*)	**1 subpopulation** (2/4 points)	**1 ESU**	Microsatellite data (Labuschagne et al. 2016)	Critically Endangered	Largely Depleted
Western leopard toad (*Sclerophrys pantherina*)	**4 subpopulations** (2/4 points)	**2 possible ESUs** (6/12 points)	Mitochondrial and microsatellite data (Measey and Tolley 2011, da Silva et al. 2017, Stephens al. 2022)	Endangered	*not assessed*
Yellow-tufted honeyeater (*Lichenostomus melanops*)	**2 subpopulations** (4/4 points)	**2 possible ESUs** (8/14 points)	Microsatellite data, mitochondrial DNA and nuclear Sequences (Pavlova et al. 2014, Harrisson et al. 2016)	Least Concern	*not assessed*
Sable Antelope (*Hippotragus niger*)	**5 subpopulations** (4/4 points)	**5 possible ESUs** (6/16 points)	Mitochondrial genomes (Rocha et al. 2022)	Least Concern	*not assessed*
Black rhinoceros (*Diceros bicornis*)	**7 subpopulations** (4/4 points)	**7 possible ESUs** (6/16 points)	Mitochondrial DNA, microsatellite data, nuclear genomes (Moodley et al. 2017, Sánchez-Barreiro et al. 2023)	Critically Endangered	Largely Depleted
Rewarewa tree (*Knightia excelsa*)	**2 or 4 subpopulations** (2 scenarios scored 4/4 points = Assessment should be done by species experts)	**2 ESUs** (12/16 points)	Whole-genome sequencing data (McCartney et al. 2024)	Least Concern	*not assessed*
Hawaiian Koa (*Acacia koa*)	**7 subpopulations** (4/4 points)	**4 ESUs** (10/16 points)	Microsatellite data and GBS (genotyping-by-sequencing) data (Shi 2003, Fredua-Agyeman et al. 2008, Baker et al. 2009, Gugger et al. 2018)	Vulnerable	*not assessed*

Species or subspecies	Phase 1	Phase 2	Genetic Data and studies considered	IUCN Red List status	IUCN Green Status
Black Wildebeest (*Connochaetes gnou*)	**1 subpopulation** (4/4 points)	**1 ESU**	Mitochondrial and microsatellite data (Corbet and Robinson 1991, Vrahimis et al. 2016, Grobler et al. 2018)	Least Concern	*not assessed*

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Box2: **Hawaiian Koa (*Acacia koa*)**

In this box we present the results of all the tested candidate scenarios for the Hawaiian koa (*Acacia koa*). Background information and detailed testing output is provided in Supplementary material, Section B and in the guidance document at https://github.com/iucn-CGSG/Subpop-ESU-Webtool. The best supported candidate scenarios are visualized in Figure 3.

Phase 1: Three candidate scenarios are tested:

Subpopulation scenario 1: Genetic clustering and pairwise Fst values based on microsatellite data suggest **two subpopulations**: one on Kauaʻi and one spanning Hawaiʻi, Maui, and Oʻahu (Fredua-Agyeman et al. 2008). No clear migration barriers were detected, and no indirect evidence of fragmentation was available. Thus, only genetic structure supported the subdivision.

Subpopulation scenario 2: Genetic clustering and pairwise Fst values based on single nucleotide polymorphisms (SNP) data suggest **seven subpopulations** (Kauaʻi, Maui, and Oʻahu each with one, plus four on Hawaiʻi), though some overlapping clusters likely reflect human-mediated dispersal and are a side product of restoration programs (Gugger et al. 2018; Figure 3 for visualization). No clear migration barriers were detected, and no indirect evidence of fragmentation was available. Thus, only genetic structure supported the subdivision.

Subpopulation scenario 3: Natural occurrence patterns across the four Hawaiian Islands suggest **four subpopulations** (Kauaʻi, Maui, Oʻahu and Hawaiʻi), aligned with distinct habitats (can be considered different biogeographical zones) and potential migration barriers (Baker et al. 2009). However, genetic/genomic studies did not confirm strong structure, and no indirect fragmentation evidence was available. This scenario is supported mainly by biogeographic isolation.

	Subpopulation-scenarios		
	2 subpop	**7 subpop**	**4 subpop**
Is there evidence of genetic structure? *(2 points)*	Yes	Yes	No
Is there evidence of natural isolation or subpopulation fragmentation (through migration barriers)? *(2 points)*	No	No	Yes
Is there inferred evidence of likely subpopulation fragmentation? *(1 point)*	No data	No data	No data
Final scores	**2 points**	**2 points**	**2 points**

Interpretation of Phase 1: All three candidate scenarios meet the minimum threshold of two points, and therefore qualify as subpopulation scenarios. Thus, all three candidate scenarios in Phase 1 scored are moved onto Phase 2.

When scores are tied as seen in this example (all three candidate scenarios scored two points), we recommend selecting the one based on the most robust data to maximize the conservation efforts of genetic diversity. In this example we would consider scenario 2 (seven subpopulations) as the one scenario based on the most robust data. Distinct subpopulation clusters were identified using high-resolution genomic markers (11,000 SNPs from >300 samples via genotyping-by-sequencing). Although microsatellites remain valuable in population genetics, scenario 1 is unlikely to represent the true subpopulation structure. Instead, it might better reflect higher-level structuring at the ESU level, along with scenario

3 (four islands subpopulations). Therefore, the seven subpopulation scenario better represents subpopulation structure.

Phase 2: The same three candidate scenarios are tested:

ESUs scenario 1: Genetic data support two groups (Kauaʻi vs. Hawaiʻi–Maui–Oʻahu) which are tested as **two distinct ESUs**, but no additional evidence (karyotype, adaptive divergence, or inherited characteristic variation) supports this split. Missing data was identified when scoring for evolutionary distinctiveness, recorded characteristic variation and traditional knowledge. Provenance tests revealed phenotypic differences across all four islands, but these did not align with the two-ESU grouping. Overall, this scenario scored zero points.

ESUs scenario 2: Genomic data identified seven subpopulations, which are tested as **seven distinct ESUs**, but admixture within the island of Hawaiʻi contradicts the ESU definition of restricted gene flow. No evidence supported karyotype variation, evolutionary distinctiveness, or adaptive divergence. Provenance tests revealed phenotypic differences across all four islands, but these did not align with the seven-ESU grouping. Missing data was identified when scoring for recorded characteristic variation and traditional knowledge. Overall, this scenario scored zero points.

ESUs scenario 3: Natural occurrence patterns identified four subpopulations, which are tested as **four ESUs**. Adaptive divergence linked to precipitation supports four ESUs corresponding to the four islands (Gugger et al. 2018). These are reinforced by provenance tests showing inherited phenotypic differences matching the island divisions (Baker et al. 2009). No evidence supported karyotype variation and missing data was identified when scoring for evolutionary distinctiveness, recorded characteristic variation and traditional knowledge. Overall, with genomic and phenotypic evidence, this scenario scored 10/16 points.

	ESUs-scenarios		
	2 ESUs	**7 ESUs**	**4 ESUs**
Is there inherited variation in chromosome numbers, ploidy level or chromosome structure? *(6 points)*	No	No	No
Is there evidence of long-term reproductive isolation? *(6 points)*	No data	No	No data
Is there evidence of local adaptation or adaptive divergence? *(6 points)*	No	No	Yes
Is there evidence of inherited characteristic differences? *(4 points)*	No	No	Yes
Is there evidence supporting transmitted characteristic differences? *(2 points)*	No data	No data	No data
Is there traditional knowledge suggesting distinctiveness between units? *(2 points)*	No data	No data	No data
Final scores	**0 points**	**0 points**	**10 points**

Interpretation of Phase 2: Scenario 3 scored 10/16 points, providing the best-supported ESU scenario and highlighting that each Hawaiian Islands (Kauaʻi, Maui, Oʻahu and Hawaiʻi) can be considered a separate ESU.

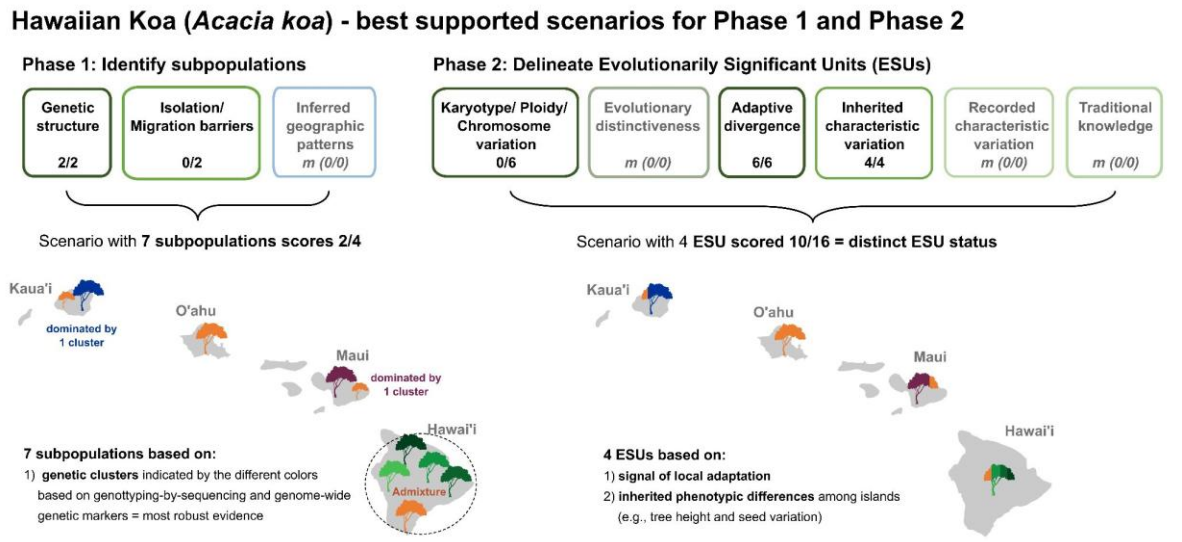

Figure 3 - Visual summary of the best-supported scenarios for Phase 1 and Phase 2 of the Hawaiian Koa tree (Acacia koa) case study. The top panel summarizes the evidence categories and scores (e.g., 2/2). Categories with insufficient data are assigned "m" for missing and are given 0 points. The lower panel presents a schematic illustrating the outcomes for each best-supported scenario. Each tree symbol represents a single genetic unit, with colours representing unique units. Further details are provided in Supplementary material, Section B.

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Box3:* Black Wildebeest (*Connochaetes gnou)

In this box we present the results of all the tested candidate scenarios for the Black wildebeest (*Connochaetes gnou*). Background information and detailed testing output is provided in Supplementary material, Section B. The best supported candidate scenarios are visualized in Figure 4.

Phase 1: one candidate scenario is tested:

Subpopulation scenario 1: Genetic analyses using mitochondrial DNA (Corbet and Robinson 1991) and microsatellites (Grobler et al. 2018) showed no clustering, suggesting one single metapopulation, with ongoing migration and no isolation barriers (Vrahimis et al. 2016). No indirect evidence was available to indicate the absence of fragmentation. Thus, this scenario is supported mainly by a lack of genetic structure and a lack of biogeographic isolation.

	1 Metapopulation scenario
Is there no genetic structure? *(2 points)*	Yes
Are there records of continuous occupation of the range with frequent migration between all regions? *(2 points)*	Yes
Is there inferred evidence of no subpopulation fragmentation? *(1 point)*	No data
Final scores	**4points**

Interpretation of Phase 1: Overall, the one subpopulation scenario scored 4/4, exceeding the threshold and supporting the null hypothesis that the black wildebeest represents a single subpopulation which can be regarded as a genetic metapopulation and therefore a single ESU no progression to Phase 2 was needed.

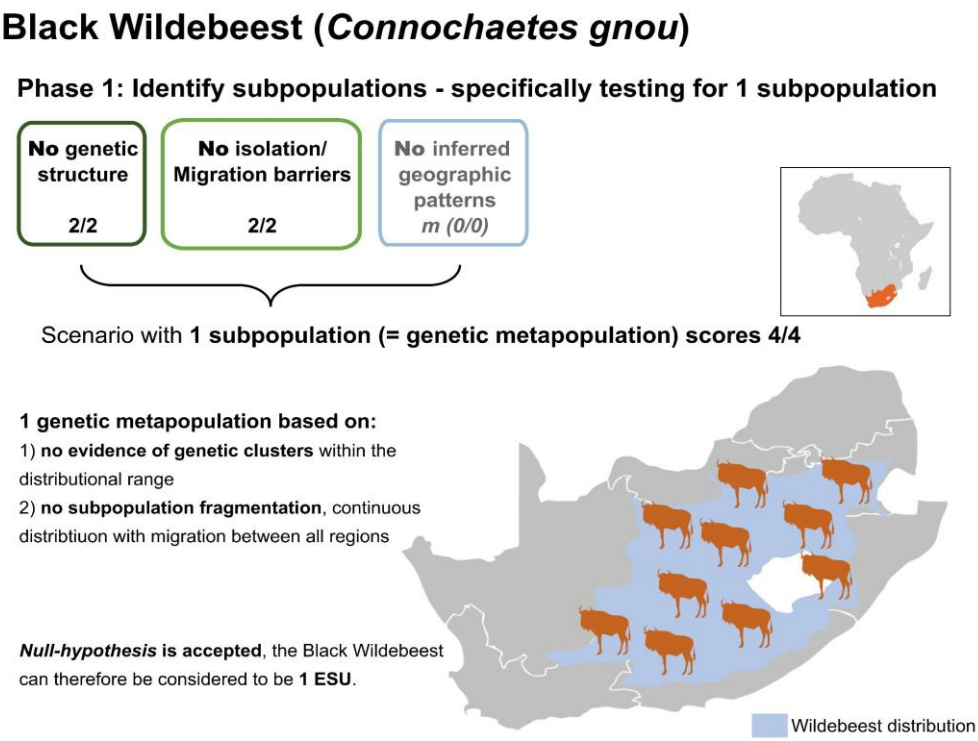

Figure 4 - Visual summary of the best-supported scenarios for Phase 1 and Phase 2 of the Black Wildebeest (Connochaetes gnou) case study. The top panel summarizes the evidence categories and scores. Categories with insufficient data are subdued in colour and assigned m for missing and are given 0 points. The lower panel presents a schematic illustrating the outcomes for each best-supported scenario. The blue polygon represents the metapopulation distribution within South Africa. Further details are provided in Supplementary material, Section B.

ESU and subpopulation division - risks and limitations

Choosing whether or not to split species into smaller units comes with an inherent risk of 'under- or over-splitting' that is amplified when non-molecular data are used because genetic divisions may be cryptic (Frankham et al. 2019). Over-splitting a species into several ESUs could artificially inflate estimated extinction risks. Conversely, under-splitting a species could give a falsely optimistic picture of extinction risk or Green Status or inhibit species management actions, in turn exacerbating extinction risk and fueling genetic diversity loss (Frankham et al. 2019, Liddell et al. 2021). Careful interpretation is therefore critical, as ESU delineation influences threat assessments, management decisions, and recognition of adaptive potential in global conservation policy. An extensive risk assessment has been developed for

the framework to help assessors and experts balance these challenges (Supplementary material section C and Table 1). However, balancing the patterns identified with their uncertainty often requires genetic knowledge. Authors conducting molecular research can support managers and assessors by offering clear lay summaries of their results in publications and depositing data in open access repositories to support reuse (Leigh et al. 2024). In turn assessors can seek advice from trusted sources during evaluations.

In the future, advances in genomics will provide us with deeper biological insights that could be relevant to management. For example, genetic load consists of deleterious alleles whose frequency and presence can vary across isolated genetic units. Undoubtedly, a diversity of genomic data types could become increasingly important for the effective management of ESUs (Dussex et al. 2023). Nevertheless, we have not yet included genetic load as a criterion in this framework, because it remains challenging to identify and is less relevant for ESUs delineation, which focuses on the evolutionary heritage that conservation managers aim to preserve (more details provided in the Supplementary material, Section D and van Oosterhout et al. (2025)). Though we have designed a framework that is not entirely reliant on molecular data, it is an important line of evidence where resolution will also improve in the future and reassessments could be needed. Genetic or genomic data, often best capture long-term processes of adaptation (i.e., natural selection) and the accumulation of mutations that shape evolutionary trajectories (Allendorf et al. 2022). Data quality and resolution—such as uneven sampling, low marker density, or poor study design—can inflate or obscure signals of population genetic structure. The type and density of sequence data (e.g., microsatellites, SNP arrays, or GBS) strongly influence the resolution of ESU (and even subpopulation) delineation, with low-density markers or sparse sampling increasing the likelihood of misclassification. These limitations underscore that ESU boundaries should be treated as working hypotheses, subject to refinement as new evidence emerges.

How Subpopulations and Evolutionarily Significant Units could fit into Conservation Assessment Frameworks

The importance of delineating biologically meaningful units is underscored by recent cases where molecular evidence has reshaped IUCN Red List assessments. In some species, weakly supported subspecies designations were shown to be unfounded, leading to their collapse or consolidation (e.g., *Puma concolor*; Culver et al. 2000, Nielsen et al. 2015; *Panthera tigris*; Goodrich et al. 2015, Wilting et al. 2015). In other cases, genomic data revealed deep

evolutionary divergences that had been obscured under traditional taxonomy, prompting recognition of distinct units with separate conservation assessments (e.g., giraffes, *Giraffa* spp.; Fennessy et al. 2016, Coimbra et al. 2021, Bertola et al. 2024; African elephants, *Loxodonta* spp.; Roca et al. 2001, Gobush et al. 2021). These examples illustrate how outdated or unfounded subspecies classifications may misdirect conservation resources, whereas delineating ESUs and subpopulations provides a more robust, evolutionarily grounded basis for assessments.

The framework proposed here provides a standardized approach for identifying and delineating subpopulations and ESUs, which could potentially inform existing IUCN frameworks and assessments (Red List and Green Status of Species). Within the Red List, for example, delineated subpopulations and ESUs could be documented under the taxonomy section or accompanying metadata to provide context on within-species genetic diversity. In some cases, this approach could serve as a more biologically grounded replacement, or supplement, to traditional subspecific assessments, particularly where subspecies designations are weakly supported or inconsistent across taxa. This information might support more nuanced assessments of extinction risk, particularly for subpopulations that are highly differentiated or potentially at risk due to fragmentation or isolation (Criterion B; IUCN 2024). In the Green Status of Species (IUCN 2021), delineating ESUs could offer additional insight into the retention of historical genetic diversity alongside existing measures of range and population recovery. Once subpopulations or ESUs are delineated, genetic data or proxy measures could inform indicators such as ecosystem functionality (IUCN 2024), providing context on evolutionary processes.

Both phases of this framework can provide complementary information relevant to Red List assessments under Criterion B, which considers species with subpopulations that are severely fragmented (i.e., smaller than necessary to support a viable population; IUCN 2024). Severe fragmentation is currently inferred from habitat fragmentation alone. Information on subpopulations within the same ESU, particularly where high human-mediated genetic differentiation is observed, could provide complementary evidence to inform assessments on fragmentation. Furthermore, identifying ESUs could help distinguish whether observed subpopulation fragmentation is recent and harmful, or an ancient pattern that is unlikely to influence extinction risk.

Delineation of ESUs can also assist with prioritizing site-based protection measures, from local to regional scales. Many conservation initiatives are focused on site-based protection (e.g., 30x30, Protected and Conserved Areas; CBD 2022). Understanding which ESUs are present could help highlight the differential conservation value of sites across a species' range and ensure that unique ESUs are not overlooked. The IUCN tool recently developed to support site prioritization is the 'Global Standard for the Identification of Key Biodiversity Areas' (KBAs; IUCN 2016). While ESUs often span multiple KBAs, standardized ESU delineation could provide additional evidence for identifying KBAs under criteria related to distinct genetic diversity (criteria A1, B1 & B2 for threatened species). This information could also contribute to assessments of relative value of KBAs supporting species that are not currently threatened or range-restricted (criteria D&E), by highlighting the presence of unique within-species genetic units.

Importantly, delineating subpopulations and ESUs can help identify units experiencing different threats across a species' range. Recognizing these differences allows for unit-specific assessments of extinction risk or recovery, highlighting subpopulations that may require targeted conservation actions. This approach enhances the utility of the third level of IUCN assessments, ensuring that management priorities reflect both the evolutionary and ecological realities of within-species variation. Moreover, the units identified through this framework represent a first step toward linking ecological and evolutionary groupings to quantitative genetic indicators, such as the KMGBF's headline indicator - the proportion of populations with an effective population size greater than 500 individuals. By defining biologically meaningful units in Phase 1, these groupings could subsequently serve as the basis for estimating effective population sizes and monitoring genetic diversity at scales relevant for conservation action.

In this paper, we outlined a two-step framework to standardize the delineation of subpopulations and ESUs by integrating genetic and non-genetic evidence. By providing a consistent approach to recognise biologically meaningful within-species units, the framework can complement existing IUCN assessments, offering additional context on species' genetic structure and evolutionary processes. Such information could inform conservation priorities,

support more nuanced interpretation of recovery or extinction risk indicators, and contribute to efforts at maintaining and enhancing global genetic diversity.

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Author contribution statement

This manuscript and project were led by JCG and DML.

The funding for the IUCN workshop was secured by SP-E and GS.

JG, DML, GS, MEH, IMR, SP-E, acted as the project steering committee.

EJ secured funding for a follow up workshop through Newcastle University.

LDB, PB, AB-O, JMdS, JAD, AF, JAG, CEG, MEH, CH, AK, AJM, ELJ, AJP, JCP, IMR, HS, GS, PS, CVO all contributed to the discussions, conceptualization, and writing of the framework and manuscript.

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

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