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The taxonomic basis of subspecies listed as threatened and endangered under the endangered species act

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More than 170 subspecies are listed as threatened or endangered under the US Endangered Species Act. Most of these subspecies were described decades ago on the basis of geographical variation in morphology using relatively primitive taxonomic methods. The US Fish and Wildlife Service defaults to subspecies descriptions by taxonomists working with specific groups of organisms, but there is no single definition of subspecies across plants and animals. Valid tests today usually entail molecular analyses of variation within and among populations, although there is no reason that behavioral, ecological or molecular characters could not be used, and include tests for significant differences between samples of the putative endangered subspecies and its nearest geographic relatives. We evaluated data gathered since subspecies listed under the ESA were described finding about one-third are valid (distinct evolutionary taxa), one-third are not, and one-third have not been tested. Therefore, it should not be assumed that because a subspecies occurs in a checklist, it is taxonomically valid. If the US Fish and Wildlife Service intends to continue listing subspecies, we suggest that they convene taxonomic experts representing various groups of organisms to provide a minimal set of criteria for a subspecies to be listed under the ESA.

KEYWORDS

endangered species act, subspecies, taxonomic status, listing criteria, taxonomic methods

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> *Taxonomic assignments inevitably shape perceptions of biological diversity. Therefore, it is disconcerting that many subspecies and species descriptions trace to very limited information, often gathered in the last century, on the distributions of a small number of (usually morphological) traits with unknown genetic basis. Yet once a Latin binomial or trinomial is in the literature, the group of organisms to which it refers almost automatically assumes an aura of reality that may or may not be commensurate with its true evolutionary distinctiveness. Given the overriding importance of taxonomy on biodiversity recognition and management, increased attention should be devoted to taxonomic assessments (from molecular as well as other data)* (Avise 1992).

Introduction to the endangered species act and taxonomic categories

The legislative basis for much of the conservation effort in the United States is the Endangered Species Act (ESA), passed in 1973 and modified in 1978, 1982, and 1988. Given its title, one might expect it to apply only to species, but in fact it also can be used to list subspecies and distinct population segments (vertebrates only) as threatened or endangered. Listing decisions usually come about when either a U.S. citizen or organization, or the Fish and Wildlife Service itself, determines that the population size of one of these taxonomic entities places it in danger of extinction (endangered) or in almost as much peril (threatened). The species or subspecies is placed on a list of candidate species, and the Fish and Wildlife Service is directed to use the best available scientific or commercial data in making a ruling as to whether the taxon merits listing as endangered or threatened. In this paper we examine the taxonomic category or rank of subspecies. In particular, we determine whether modern tests of subspecies limits have confirmed the validity of listed subspecies, most of which were described more than a half-century ago, as described by National Academy Member John C. Avise in the opening quote.

Taxonomic background and the concept of subspecies

Systematists, taxonomists, and evolutionary biologists have struggled to define the term *species* for a century and a half. The biological species concept recognizes a species as a diagnosably distinct population or group of populations that is reproductively isolated from other such populations or groups. Lineage concepts, on the other hand, such as the phylogenetic species concept, recognize diagnosable populations or groups of populations as species irrespective of whether they can hybridize with other such groups (Cracraft, 1983; de Queiroz, 2007). That is, diagnosable subspecies of biological species would more than likely be considered phylogenetic species (Barrowclough et al., 2016). Many other species concepts have been offered, including recent ones that search for congruence among multiple loci or character sets: so-called species-delimitation approaches (Malaney et al., 2017). Below the level of the species, some species concepts recognize subspecies.

What exactly is a subspecies?

A subspecies is a formal taxonomic category that is specified by three Latin names: the genus name, the species name, and the subspecies name. Definitions of subspecies range from whatever a taxonomist says is valid to multi-character genetic and morphological assessments (Zink, 1997). Some favor a rule in which 75% of individuals in a subspecies must be separable from 99% in another subspecies—clearly an arbitrary standard. Taylor et al. (2017) suggest that "a subspecies is a population, or collection of populations, that appears to be a separately evolving lineage with discontinuities resulting from geography, ecological specialization, or other forces that restrict gene flow to the point that the population or collection of populations is diagnosably distinct". We believe that this definition provides sufficient criteria for recognizing a subspecies as valid and potentially qualified to be listed under the ESA should it become threatened or endangered. Although subspecies are listed under the ESA, the US Fish and Wildlife Service (USFWS) has no set definition of subspecies, instead relying on peer-reviewed literature that reflects the views of taxonomists in different groups. The USFWS maintains a website called the Integrated Taxonomic Information System (ITIS) where subspecies are classified as valid or invalid.[1] According to the USFWS, "ITIS taxonomy is based on the latest scientific consensus available and is provided as a general reference source for interested parties" but the evidence for subspecies validity is not given, and the evaluations cannot be verified. It would be beneficial to all involved if the USFWS would at least provide a minimal set of criteria for determining whether a subspecies is listable. For a review of historical views on subspecies, see Supplementary Information.

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[1] ITIS: Integrated Taxonomic Information System (home page), accessed May 31, 2022, https://www.itis.gov/servlet/SingleRpt/SingleRpt.

Subspecies studies: some good and some bad

Rigorous descriptions of subspecies has not historically been the status quo. Consider the Rio Grande subspecies (*Meleagris gallopavo intermedia*) of the North American wild turkey. The subspecific part of the scientific name, *intermedia*, was justified by the author (Sennett, 1879) because it was his opinion that the turkey's appearance was "intermediate" between two other subspecies. Exactly where it starts and stops being intermediate was not noted. To evaluate subspecies, one needs to refer to the specimens on which the original descriptions were based. Although an outlier, the subspecies of white-tailed deer (*Odocoileus virginianus leucurus*) from the Columbia River area was described on the basis of a single specimen, which was later consumed by the hunter who harvested it, and no remains were deposited as a museum voucher specimen (Gavin and May, 1988).

There are examples in which subspecies correspond to genetically or morphologically defined units that have experienced evolutionarily independent histories and therefore qualify for listing under the ESA. For example, the spotted owl (*Strix occidentalis*) has three subspecies: the northern spotted owl (*S. o. caurina*), California spotted owl (*S. o. occidentalis*), and Mexican spotted owl (*S. o. lucida*). Barrowclough et al. (2006, 2011) show that each subspecies is genetically distinct, with a narrow hybrid zone between northern and California spotted owls. Vázquez-Miranda et al. (2017) show that subspecies of the LeConte's thrasher (*Toxostoma lecontei*) found in the Vizcaino Desert of Baja California, and populations to the north, are genetically distinct and qualify as units worthy of conservation status. Catanach et al. (2021) provide a textbook example of how a subspecies should be tested with modern methods. They examined the status of the hawk *Accipter straitus venator* from Puerto Rico using ultra-conserved elements (nuclear DNA), mitochondrial DNA (mtDNA), and morphology. Their study shows that the specimens from the island formed a discrete genetic cluster, and in fact they suggest *A. s. venator* be raised to a full species. These are three examples of subspecies that meet the criteria of Taylor et al. (2017). For a discussion of the views of scientific societies on subspecies see Supplementary Information.

At least two perceived uses of subspecies

Remsen (2005) and Taylor et al. (2017) make it clear that a valid subspecies should be a discrete taxonomic entity with diagnostic boundaries defined by concordant patterns of morphology or genetics. Others (e.g., Haig et al., 2006; Winker, 2010) suggest that subspecies are not discretely differentiated populations but can have "fuzzy" edges owing either to ongoing introgression (gene flow) or to insufficient time having elapsed since the cessation of genetic exchange (the so-called lag effect). Winker (2010) considers subspecies a gold mine of testable hypotheses in evolutionary biology. Indeed, this can be an important function of subspecies, but such subspecies should not be construed as worthy of conservation status under the ESA—only those that are discretely differentiated should be considered worthy of conservation status. The reason is that otherwise, there will be thousands of such arbitrarily defined subspecies that could be accorded taxonomic trinomials and therefore qualify for listing.

What constitutes a strong test of subspecies limits?

Barrowclough (1982) wrote "A named subspecies carries at least the connotation of phenotypic uniformity over an area" and added "a useful subspecies concept will have to have as a goal the same objective as other taxonomic categories-predictiveness". By predictiveness, Barrowclough (1982) noted that a subspecies must be supported by a "concordance of geographically varying characters that do not simply form clines". A strong test of a listed subspecies, as envisioned by Taylor et al. (2017), would include the comparison of statistically adequate samples from throughout listed subspecies with samples of other subspecies, preferably those geographically adjacent. Listed subspecies should have at least two geographically spaced samples (if possible), allowing a researcher to test whether each sample is more closely related to the other than to samples from other subspecies. There should be no sampling gaps that would give the illusion of real genetic or morphological discontinuities (see Rising, 2001) owing simply to geographic distance between sampling localities. Evidence of taxonomic distinctiveness could be gathered from several character systems, including morphological, behavioral, molecular or ecological, with preference perhaps given to modern molecular methods. All data must be publicly available, and the analyses must be clearly described. The data should show concordant geographic splits in multiple character systems (Barrowclough, 1982), which would confirm a hypothesis of evolutionary independence. This sets a high bar for taxonomic descriptions of subspecies (Luo et al., 2018).

Molecular methods have revolutionized tests of subspecies and their evolutionary independence (Avise, 1992). The foundation of the ESA rests on the assumption that listed entities are evolutionarily independent. If one examines morphological characters, which are likely under strong selection, one does not expect a single evolutionary history to emerge. The reason is that characters often respond idiosyncratically to opposing environmental dimensions, and therefore picking one morphological character to draw subspecies boundaries ignores alternative patterns in other characters. Only when a suite of morphological or genetic characters all show the same pattern can one safely infer that the pattern reflects the history of population subdivision. It is also the case that some valid, evolutionarily distinct lineages (e.g., subspecies) have experienced morphological stasis and represent cryptic taxa, and only molecular datasets reveal their existence (Moyle and Campbell, 2022). If this is widespread it raises the question of whether all declining populations need to be studied irrespective of degree of morphological distinctiveness using genomics.

Unlike morphological characters, molecular characters used to date are often considered "selectively neutral"—that is, not influenced unduly by natural selection—and hence the only reason for congruent geographic patterns is that they reflect a common underlying evolutionary history. Patten and Remsen (2017) claimed that neutral genetic characters should not be expected to map to subspecies boundaries. However, subspecies described by morphology often are inconsistent with evolutionarily independent groupings because the one or two characters used to in subspecies description do not reflect the historical pattern of population fragmentation. That is, characters responding to selection gradients might not be concordant with the history of population isolation revealed by selectively neutral characters. It is not surprising that many subspecies lack neutral molecular genetic support. However, it is not the genetics that failed; instead, the conflicting patterns among morphological characters result in their failure to reflect true evolutionary patterns, those upon which subspecies should be based.

Is there such a thing as too much resolving power with modern genetic methods?

New molecular methods, often-called next-gen, have resulted in the possibility of surveying thousands to millions of loci, often in the form of single nucleotide polymorphisms. The El Segundo blue butterfly (*Euphilotes battoides allyni*) is a federally listed subspecies found along the coast of southern California. Dupuis et al. (2020) used a sophisticated molecular analysis of 54,305 SNPs and found that this subspecies is distinct. However, north and south along the coast are six additional, equally distinct genetic clusters. Either there are too few subspecies of *E. battoides* or the newer techniques will find minor differences of statistical importance irrespective of subspecies boundaries—differences of tenuous biological significance.

Saglam et al. (2017) used nuclear genomics to test subspecies limits in two trout, *Oncorhynchus clarkii seleniris* and *O. c. henshawi*, which were ambiguous with mtDNA. Their analyses of 500,000 reads per individual found that both subspecies were highly distinctive. A subspecies of great interest to conservation biologists is the southwestern willow flycatcher (*Empidonax traillii extimus*). In the only authoritative statement on subspecies in North America, the American Ornithologists' Union (1957) Checklist, this subspecies was not accepted, although it had been described nine years earlier (Phillips, 1948). Data sets on mtDNA, amplified fragment length polymorphisms, niche modeling, and song vocalizations supported the AOU's decision to not designate *E. t. extimus* as a valid subspecies (Zink, 2015; Zink, 2016; see Theimer et al., 2016; Mahoney et al., 2020). Ruegg et al. (2021) analyzed variation in 105,000 single nucleotide polymorphisms (SNPs) from 175 individuals and concluded that the subspecies was valid. However, there are sampling gaps between *E. t. extimus* and the subspecies to the north (*E. t. adastus*), there are no samples from the southern extent of the range in Mexico (see below), and there is no assessment of isolation by distance. The samples from California, within the range of *E. t. extimus*, do not group with those in the eastern part of the subspecies' range. Thus, Ruegg et al. (2021) found geographic differentiation in genetic variation throughout the range of the species, but whether the data recover the limits of *E. t. extimus* as described by Phillips (1948), and that which is listed under the ESA, is unclear. Similarly, Vandergast et al. (2022) claimed that the coastal California gnatcatcher (*P. c. californica*) was distinct, in contrast to a similar next-gen study by Vázquez-Miranda et al. (2022). Vandergast et al. (2022) used a phenogram instead of a phylogenetic analysis, and did not emphasize that their genetic measures showed a cline that was not stepped; additionally, they did not clarify that the limits they suggested do not match the listed subspecies. Therefore, they found some genetic variation but it is not supportive of subspecies limits.

Thus, the next-generation sequencing methods need to be interpreted with caution so as not to confuse sampling and genetic gaps (see below) and so as not to cherry-pick SNPs that favor one hypothesis over another. Given examination of enough SNPs, it would be likely to find some in only one or a few populations, making it seem like support for their distinctiveness. That is, one might exclude characters that suggest a different pattern, whereas overall differentiation should be assessed across all characters (e.g., SNPs). That is, conflicting characters should be a part of the analysis so as not to bias the result to a preconceived conclusion. In addition, next-gen methods do not guarantee similar findings from different labs, as in the case of the California gnatcatcher (Vandergast et al., 2022; Vázquez-Miranda et al., 2022).

Economics and subspecies: the cost of invalid subspecies

Costs of preservation vary widely within and among different groups of organisms (Gordon et al., 2020). At the level of full species, the average cost of preserving a bird

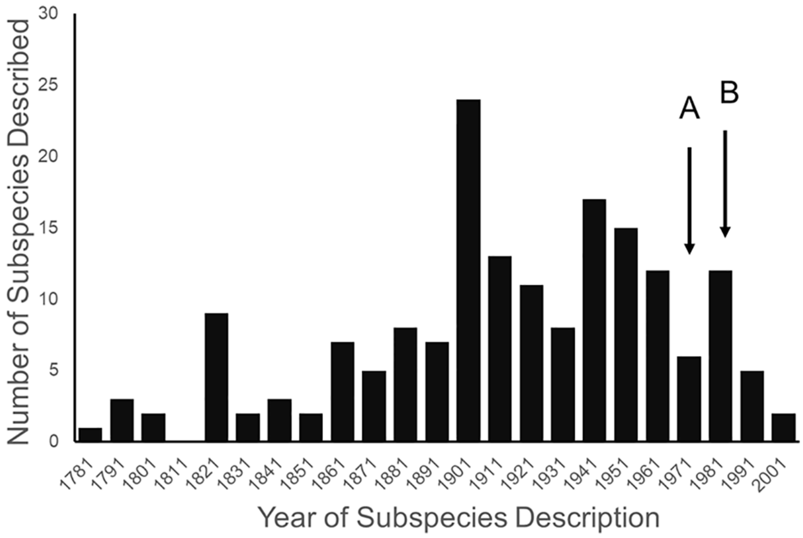

FIGURE 1
Distribution of years in which subspecies listed under the endangered species act were described. Arrow **(A)** marks the beginning of the use of allozymes in studying genetic variation in natural populations, and arrow **(B)** marks the beginning of the use of mitochondrial DNA.

species in the United States is $2,571,017, with a wide range of variation. According to Gordon et al. (2020), mammals cost 8–26 times more on average to conserve than plants, and bird species cost 5–30 times more to conserve than plants and 6–14 times more than aquatic invertebrates.

The coastal California gnatcatcher (*Polioptila californica californica*) is listed as threatened. Its range includes the densely populated area of southern California from Palos Verde Peninsula south to the border with Baja California (and farther south to the end of Baja California Sur, where it becomes relatively common). The validity of the subspecies has been challenged (Zink et al., 2000; Zink et al., 2013; Zink et al., 2016) and defended (McCormack and Maley, 2015), and recent genomics data show that it is not evolutionarily distinct and hence not a valid subspecies (Vázquez-Miranda et al., 2022). The USFWS has suggested that excluding this habitat has come at a cost of at least $1 billion (Gordon, 2018). Fortunately, much of the land occupied by the coastal California gnatcatcher is currently preserved by habitat conservation plans (Winchell and Doherty, 2018), and gnatcatcher populations are apparently genetically connected (Vandergast et al., 2019).

Review of subspecies listed under the ESA

Most ESA-listed subspecies were described before 1950 (137 of 175), and 150 (86%) were described before 1966 (see Figure 1), using methods that involved assessments of morphological variation. We note that in fishes, more emphasis is placed on protecting Evolutionary Significant Units, which are not afforded names in the Linnean System; that is, relatively few subspecies of fish are listed under the ESA. The ESA also allows protection of Distinct Population Segments (US Fish and Wildlife Service, 1996), although we do not discuss this category in this paper. It was not until 1966 that the first molecular methods appeared that could be used to test subspecies limits.

The molecular methods used evolved from relatively crude assessment of distinguishing alleles at protein-coding loci (allozyme electrophoresis) to studies involving thousands of base-pairs at the DNA level. Most molecular examinations (n = 92) of subspecies limits used mtDNA (n = 67), and some were combinations of mtDNA and microsatellites (n = 19) or mtDNA and nuclear DNA (n = 14). Evaluations of listed subspecies vary widely in their sampling size, from a single individual to over 100 samples. Given the variation in the areal extent of listed subspecies' distributions, a diversity in sampling size is not surprising; however, the relative percentage of the distribution covered by sampling also varies widely. In several cases researchers were able to include only a single population represented by one individual, thus making inferences of population distinctiveness difficult.

We examined 165 listed subspecies to determine how many were supported by modern analyses (see Table 1: 11 have been removed the USFWS in ITIS; https://www.itis.gov/). As noted earlier, a valid test would include multiple samples within the subspecies and comparisons with adjacent samples. Seven subspecies have been removed from the list because, according to the ITIS website, they have been elevated to species or there

TABLE 1 Review of Subspecies Listed under the US Endangered Species Act.

Genus	Species	Subspecies	Valid?	Reference
Birds				
Accipiter	*striatus*	*venator*	yes (island)	Catanach et al. (2021)
Acrocephalus	*familiaris*	*kingi*	yes (island)	Fleischer et al. (2007)
Ammodramus	*maritimus*	*mirabilis*	no	Avise and Nelson (1989)
Ammodramus	*savannarum*	*floridanus*	no	Bulgin et al. (2003)
Amphispiza (Artemisiospiza)	*belli*	*clementeae*	no	Karin et al. (2018)
Buteo	*platypterus*	*brunnescens*	no data	
Calidris	*canutus*	*rufa*	no	Buehler et al. (2006)
Charadrius	*nivosus*	*nivosus*	yes	Jackson et al. (2020)
Colinus	*virginianus*	*ridgwayi*	no	Williford et al. (2014)
Columba	*inornata*	*wetmorei*	no (only haplotype frequencies differ)	Young and Allard (1997)
Empidonax	*traillii*	*extimus*	equivocal	Zink (2015); Ruegg et al. (2021)
Eremophila	*alpestris*	*strigata*	yes	Drovetski et al. (2005)
Falco	*femoralis*	*septentrionalis*	not tested	
Gallinula	*galeata*	*sandvicensis*	prob. (endemic to Hawaii, no test of other ssp.)*	
Gallinula	*chloropus*	*guami*	prob. (endemic to Guam, no test of other ssp.)	Miller et al. (2015)
Grus	*canadensis*	*pulla*	not tested	
Halycon	*cinnamomina*	*cinnamomina*	not tested*	
Himantopus	*mexicanus*	*knudseni*	not tested	
Lanius	*ludovicianus*	*mearnsi*	yes, historically	Caballero and Ashley (2011)
Laterallus	*jamaicensis*	*jamaicensis*	no (+/−)—equivocal	Girard et al. (2010)
Myadestes	*lanaiensis*	*rutha*	not tested	
Pipilo (Melozone)	*crissalis*	*eremophilus*	not tested*	
Polioptila	*californica*	*californica*	no	Zink et al. (2013, 2016)
Polyborus/Caracara	*plancus*	*audubonii*	not tested	
Puffinus	*auricularis*	*newelli*	prob. species*	
Rallus	*longirostris*	*obsoletus*	no	Maley and Brumfield (2013)
Rallus	*longirostris*	*levipes*	no	Maley and Brumfield (2013)
Rallus	*obsoletus/ longirostris*	*yumanensis*	no	
Rostrhamus	*sociabilis*	*plumbeus*	no	Haas and Kimball (2009)
Sterna	*dougallii*	*dougallii*	yes (prob. undersplit)	Byerly (2021)
Sterna	*antillarum*	*browni*	no	Draheim et al. (2010)
Strix	*occidentalis*	*lucida*	yes	Barrowclough et al. (2011)
Strix	*occidentalis*	*caurina*	yes	
Tympanuchus	*cupido/americanus*	*attwateri*	no	
Vireo	*belli*	*pusillus*	yes	Klicka et al. (2016)
Zosterops	*conspicillatus*	*conspicillatus*	yes	Slikas et al. (2000)
Fish				
Acipenser	*oxryinchus*	*desotoi*	no (no comparisons)	
Catostomus	*discobolus*	*yarrowi*	yes	Bangs et al. (2020)
Crenichthys	*baileyi*	*grandis*	yes	Campbell and Piller (2017)
Crenichthys	*baileyi*	*baileyi*	yes	Campbell and Piller (2017)
Cyprinodon	*nevadensis*	*mionectes*	no	Martin (2010)
Cyprinodon	*nevadensis*	*pectoralis*	no	Martin (2010)
Gila	*robusta*	*jordani*	not tested	
Gila (Siphateles)	*bicolor*	*mohavensis*	not tested	
Gila (Siphateles)	*bicolor*	*snyderi*	not tested	

(Continued)

TABLE 1 Continued

Genus	Species	Subspecies	Valid?	Reference
Lepidomeda	*mollispinis*	*pratensis*	not tested	
Notropis	*simus*	*pecosensis*	not tested	
Oncorhynchus	*clarkii*	*stomias*	once, not anymore	Metcalf et al. (2012)
Oncorhynchus	*clarkii*	*henshawi*	yes	Metcalf et al. (2012); Saglam et al. (2017)
Oncorhynchus	*aguabonita (mykiss)*	*whitei*	no, prob. introgressed with rainbow trout*	
Oncorhynchus	*clarkii*	*seleniris*	yes	
Rhinichthys	*osculus*	*nevadensis*	not tested	
Rhinichthys	*osculus*	*oligoporus*	not tested	
Rhinichthys	*osculus*	*lethoporus*	not tested	
Rhinichthys	*osculus*	*thermalis*	not tested	
Herptiles				
Ambystoma	*macrodactylum*	*croceum*	not tested	
Ambystoma	*mavortium/ tigrinum*	*stebbinsi*	not tested, prob. introgressed	Storfer et al. (2014)
Crotalus	*willardi*	*obscurus*	no	Holycross and Douglas (2007)
Cryptobranchus	*alleganiensis*	*alleganiensis*	no*	Tonione et al. (2011)
Cryptobranchus	*alleganiensis*	*bishopi*	no*	Tonione et al. (2011)
Eumeces	*egregius*	*lividus*	no	Branch et al. (2003)
Kinosternon	*sonoriense*	*longifemorale*	not tested	
Masticophis	*lateralis*	*euryxanthus*	prob., intergrades*	Richmond et al. (2016)
Nerodia	*clarkii*	*taeniata*	no	
Nerodia	*erythrogaster*	*neglecta*	no*	
Pituophis	*melanoleucus*	*lodingi*	no (genomics)	Nikolakis et al. (2022)
Pseudemys	*rubriventris*	*bangsi*	not tested*	
Inverts				
Anaea	*troglodyta*	*floridalis*	not tested	*Anaea*
Apodemia	*mormo*	*langei*	yes/no—equivocal	Proshek et al. (2015); Dupuis et al. (2018)
Callophrys	*mossii*	*bayensis*	no molecular data	*Callophrys*
Cicindela	*dorsalis*	*dorsalis*	no*	Vogler and De Salle (1994)
Cicindela	*nevadica*	*lincolniana*	not studied*	*Cicindela*
Cyclargus	*thomasi*	*bethunebakeri*	not tested (within ssp. analysis)	
Cyclargus	*thomasi*	*bethunebakeri*	not tested (within ssp. analysis)	
Desmocerus	*californicus*	*dimorphus*	no	Nagarajan et al. (2020)
Epioblasma	*florentina*	*curtisii*	prob. extinct*	Rogers et al. (2001)
Epioblasma	*florentina*	*walkeri*	yes (no bootstrap support)*	Rogers et al. (2001)
Euchloe	*ausonides*	*insulanus*	not tested	
Euphilotes	*battoides*	*allyni*	yes	Dupuis et al. (2020)
Euphilotes	*enoptes*	*smithi*	not tested	*Euphilotes*
Euphrydryas (Euphydryas)	*editha*	*taylori*	not tested	*Euphrydryas* (*Euphydryas*)
Euphydryas	*editha*	*bayensis*	not tested*	*Euphydryas*
Euphydryas	*editha*	*quino*	yes (morph), not tested	not tested
Glaucopsyche	*lygdamus*	*palosverdesensis*	not tested, may be distinct	
Hemiargus	*ceraunus*	*antibubastus*	not tested	
Heraclides (Papilo)	*aristodemus*	*ponceanus*	yes (mtDNA COI sequences)	Shiraiwa et al. (2014)
Hesperia	*leonardus*	*montana*	not tested	
Hypolimnas	*octocula*	*marianensis*	not tested*	
Icaricia	*icarioides*	*missionensis*	not tested	

(*Continued*)

TABLE 1 Continued

Genus	Species	Subspecies	Valid?	Reference
Icaricia	*shasta*	*charlestonensis*	not tested	
Icaricia (*Plebeus*)	*icarioides*	*fenderi*	not tested	
Leptotes	*cassius*	*theonus*	not tested	
Lycaeides (*Plebejus*)	*melissa*	*samuelis*	yes (AFLP)*	Gompert et al. (2006)
Lycaeides (*Plebejus*)	*argyrognomon* (*anna*)	*lotis*	not tested*	
Megalagrion	*nigrohamatum*	*nigrolineatum*	prob., small n—equivocal	Jordan et al. (2003)
Mesodon	*clarki*	*nantahala*	not tested*	
Neonympha	*mitchelli*	*mitchelli*	yes	Hamm et al. (2014)
Neonympha	*mitchelli*	*francisci*	no	Hamm et al. (2014)
Pseudocopaeodes	*eunus*	*obscurus*	not tested	
Pyrgus	*ruralis*	*lagunae*	not tested	
Quadrula	*cylindrica*	*cylindrica*	n = 1, so not tested*	
Quadrula	*cylindrica*	*strigillata*	n = 1, so not tested*	
Rhaphiomidas	*terminatus*	*abdominalis*	not tested	
Speyeria	*zerene*	*behrensii*	not tested	Miller et al. (2016); De Moya et al. (2017)
Speyeria	*callippe*	*callippe*	not tested	De Moya et al. (2017)
Speyeria	*zerene*	*myrtleae*	not tested	De Moya et al. (2017)
Speyeria	*zerene*	*hippolyta*	no	McHugh et al. (2013); Miller et al. (2016)
Strymon	*acis*	*bartrami*	not tested	
Mammals				
Antilocapra	*americana*	*sonoriensis*	yes, network unrooted	Klimova et al. (2014)
Aplodontia	*rufa*	*nigra*	yes()?—equivocal	Piaggio and Jeffers (2013)
Bison	*bison*	*athabascae*	no*	Pertoldi et al. (2010)
Canis	*lupus*	*baileyi*	no	Fredrickson et al. (2015); Cronin et al. (2015)
Corynorhinus	*townsendii*	*ingens*	no	Piaggio and Perkins (2005); Weyandt et al. (2005)
Corynorhinus	*townsendii*	*virginianus*	no (yes if ssp. boundary changed)	Piaggio et al. (2009)
Dipodomys	*nitratoides*	*exillis* (*exilis*)	no	Patton et al. (2019)
Dipodomys	*heermanni*	*morroensis*	no	Benedict et al. (2019)
Dipodomys	*merriami*	*parvus*	no	Hendricks et al. (2020)
Dipodomys	*nitratoides*	*nitratoides*	no	Patton et al. (2019)
Emballonura	*semicaudata*	*semicaudata*	no (island)	Colgan and Soheili (2008)
Enhydra	*lutis* (*lutris*)	*kenyoni*	yes (translocations)	Larson et al. (2021)
Enhydra	*lutris*	*nereis*	yes	Larson et al. (2021)
Glaucomys	*sabrinus*	*coloratus*	yes (RMZ unpubl. analysis of mtDNA sequences in GenBank)	
Herpailurus	*yagouaroundi*	*tolteca*	no	Ruiz-García and Pinedo-Castro (2013)
Herpailurus (*Puma*)	*yagouaroundi*	*cacomitli*	no	Ruiz-García and Pinedo-Castro (2013)
Microtus	*californicus*	*scirpensis*	no, nested in *M. cal.**	Neuwald (2010)
Microtus	*pennsylvanicus*	*dukecambelli*	yes, should be species*	Jackson and Cook (2020)
Neotoma	*floridana*	*smalli*	not tested*	
Neotoma	*fuscipes*	*riparia*	no*	Matocq et al. (2012)
Odocoileus	*virginianus*	*leucurus*	no	
Odocoileus	*virginianus*	*clavium*	yes	Zink et al. (2020)
Oryzomys	*palustris*	*natator*	not tested	Tursi et al. (2013)
Ovis	*canadensis*	*nelsoni*	no	Buchalski et al. (2016)
Ovis	*canadensis*	*sierrae*	yes (1 mismatched haplotype)	Buchalski et al. (2016)

(Continued)

TABLE 1 Continued

Genus	Species	Subspecies	Valid?	Reference
Perognathus	*longimembris*	*pacificus*	no	Swei et al. (2003)
Peromyscus	*polionotus*	*ammobates*	yes* (some overlap)	
Peromyscus	*polionotus*	*phasma*	*	
Peromyscus	*polionotus*	*allophrys*	yes*	
Peromyscus	*gossypinus*	*allapaticola*	not tested*	
Peromyscus	*polionotus*	*trissyllepsis*	yes* (some overlap)	
Peromyscus	*polionotus*	*niveiventris*	yes* (some overlap)	Degner et al. (2007)
Peromyscus	*polionotus*	*peninsularis*	yes* (some overlap)	
Pteropus	*mariannus*	*mariannus*	yes (island)	Brown et al. (2011)
Puma	*concolor*	*coryi*	once, not anymore	
Puma	*concolor*	*concolor*	no	
Puma	*concolor*	*puma*	North American likely diff. from South American	Saremi et al. (2019)
Puma	*concolor*	*couguar*	yes, but includes all NA	
Puma	*concolor*	*costaricensis*	yes	Saremi et al. (2019)
Puma	*concolor*	*anthonyi*	no or not tested	
Puma	*concolor*	*cabrerae*		
Rangifer	*tarandus*	*caribou*	yes	Klütsch et al. (2012)
Sorex	*ornatus*	*relictus*	yes	Maldonado et al. (2001)
Sylvilagus	*bachmani*	*riparius*	no	Rippert (2017)
Sylvilagus	*palustris*	*hefneri*	no	
Tamiasciurus	*hudsonicus*	*grahamensis*	yes	Fitak et al. (2013)
Thamnophis	*eques*	*megalops*	yes	Wood et al. (2018)
Thamnophis	*sirtalis*	*tetrataenia*	no	Janzen et al. (2002)
Thomomys	*mazama*	*pugetensis*	not tested?	
Thomomys	*mazama*	*glacialis*	not tested?	
Thomomys	*mazama*	*tumuli*	not tested?	
Thomomys	*mazama*	*yelmensis*	not tested?	
Urocyon	*littoralis*	*catalinae*	no	Hofman et al. (2015)
Ursus	*arctos*	*horribilis*	no	Miller et al. (2006)
Vulpes	*macrotis*	*mutica*	not tested*	
Vulpes	*vulpes*	*necator*	equivocal	Statham et al. (2012)
Zapus	*hudsonius*	*luteus*	yes	Malaney et al. (2012)
Zapus	*hudsonius*	*preblei*	no	Ramey et al. (2005); Malaney and Cook (2013)

*The Integrated Taxonomic Information System considers the subspecies invalid. (In most cases, the basis for an invalid conclusion is a change in the scientific name of the described subspecies.)

This list does not include other subspecies already considered invalid by the Integrated Taxonomic Information System: Aerodramus vanikorensis bartschi, Bufo hemiophrys baxteri, Drymarchon corais couperi, Epicrates monensis monensis, Epioblasma torulosa gubernaculum, Epioblasma torulosa rangiana, Epioblasma obliquata obliquata, Epioblasma torulosa torulosa, Epioblasma obliquata perobliqua, Epioblasma florentina florentina, Gasterosteus aculeatus williamsoni, Lasiurus cinereus semotus, Oxyloma haydeni kanabensis.

was a data error in the description. We found that the bulk of the remaining subspecies are distributed relatively equally among three categories: supported, not supported, and not tested (Figure 2). This summary suggests that a listed subspecies has a fifty-fifty chance of being consistent with the criteria listed by Taylor et al., 2017).

We found that the ITIS classification departs from our summary. More than 40 of the 51 subspecies (78%) that were not supported by our evaluation were considered valid on the ITIS website.

Summary and future considerations

The molecular methods used to test subspecies have evolved greatly over the past few decades, owing to a large increase in resolving power. With the new potential to describe genomes of individuals, some issues should be recognized. First, if sampling is not evenly spaced, sampling gaps will give the illusion of discrete taxonomic boundaries (Figure S1). Also, if a gap in the range is caused by anthropogenic elimination of intermediate areas, the populations might appear distinct, albeit not from

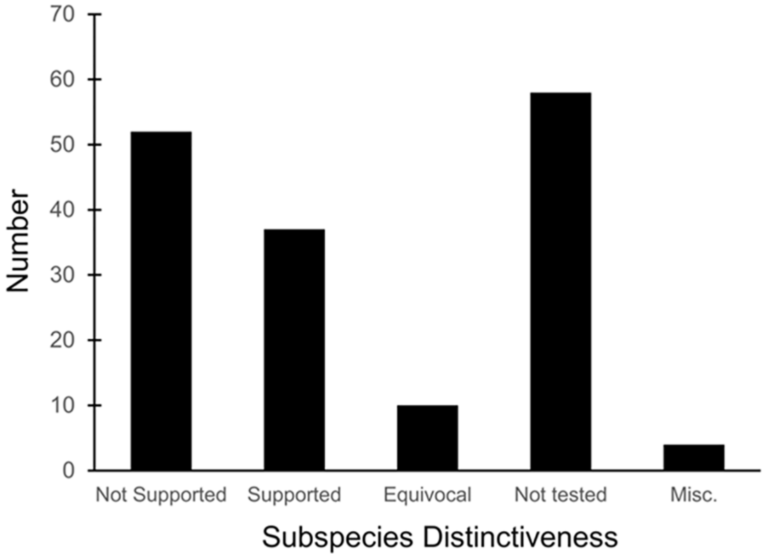

FIGURE 2
Distribution of results of evaluation of listed vertebrate subspecies. “Not tested” means samples from listed subspecies were not compared with samples from adjacent subspecies, there were too few samples, or samples were not examined.

natural evolutionary processes. Subspecies limits cannot be tested without a clear and rigorous sampling protocol.

It is possible for a subspecies that is not evolutionary distinct (a category that includes many subspecies) to be ecologically important—perhaps important enough to merit listing. Examples might include keystone species such as large carnivores: the Florida panther, for instance. However, providing quantitative data of ecological importance might be as large a task as documenting taxonomic distinctiveness. The lack of consistency among subspecies definitions used in ESA listings is a major failing of taxonomists. To further the use of taxonomic work in conservation decisions, this failing ought to be addressed.

The path forward

We understand that some will have the view that all subspecies proposed for listing should be accepted at face value because they might be valid but not protected because of no current tests of their validity, hence, their loss would be lamentable (a Pascal’s Wager argument). We argue here that given the high cost of subspecies preservation and the fact that roughly 50% of subspecies tested are supported by modern methods, it should be unacceptable to list a subspecies under the ESA without modern analyses confirming Taylor et al. (2017) criteria. It should be incumbent upon the USFWS to seek consensus among taxonomists who work on different groups or organisms to agree on a list of minimal criteria for a subspecies to be listed under the ESA so that listing decisions are transparent.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

RZ designed project, conducted analyses, wrote the draft. LK gathered raw data and edited the manuscript. Both authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2022.971280/full#supplementary-material

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