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Criteria for determining native distributions of biota: the case of the northern plains killifish in the Cheyenne River drainage, North America[†]

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ABSTRACT

1. Criteria exist to help determine native distributions of species, but they are seldom explicitly used.
2. As an example of their utility, nine revised and expanded criteria are applied to assess the status of northern plains killifish in the Cheyenne River drainage. Use of each criterion is demonstrated. The criteria are: (1) history, (2) detectibility, (3) biogeography, (4) life-history, (5) human affinity, (6) invasion path, (7) invasiveness, (8) phylogenetics, and (9) pre-history.
3. Upon review, only one criterion weakly supports non-native status, whereas five strongly support native status, one weakly supports native status, and two are equivocal.
4. Criteria to determine native distributions provide a rigorous method to assess available information, reveal knowledge gaps, and produce testable hypotheses. As demonstrated here, their consistent use as a cohesive set would greatly improve understanding of species distributions, benefiting conservation efforts and related meta-analyses.

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INTRODUCTION

Determining native distributions is typically the purview of researchers who compose checklists of regional biotas (Bailey and Allum, 1962; Baxter and Simon, 1970). Criteria used to determine species distributions differ among researchers depending on their emphasis and training, and among species studied depending on available information. Webb (1985) and Smith (1986) promoted the use of a set of criteria to increase the rigour and consistency of distributional studies, but this approach has not been widely used (Pyšek *et al.*, 2004). This is a problem because inaccurate distributions confound meta-analyses of distributional patterns (Pyšek *et al.*, 2004) and species falsely identified as non-native may be unprotected or even falsely treated as a threat to biodiversity. Thus, we support the use of the criteria proposed by Webb (1985) and present an example of how the criteria are used to illustrate their utility.

The northern plains killifish (*Fundulus kansae*) is a sensitive species that has declined from portions of its range (Brown, 1986; Cross and Collins, 1995; Peters and Schainost, 2005). Miller (1955) interpreted northern plains killifish of the Cheyenne River drainage (Figure 1) as non-native. He wrote: ‘It *seems probable* that the two recent records for South Dakota represent bait introductions, *possibly* from Angostura Reservoir, a relatively new impoundment on the upper Cheyenne River, into which the species *may* have been carried from the Platte or Niobrara river [emphasis added].’ Subsequent researchers have upheld Miller’s hedged statement without scrutiny (Poss and Miller, 1983; Kreiser *et al.*, 2001). However, as the species declines elsewhere, the conservation significance of populations in the Cheyenne River drainage increases, if they are native. This presents a need to evaluate the statement made by Miller (1955) that is the sole basis for the non-native designation. In doing so, Webb’s (1985)

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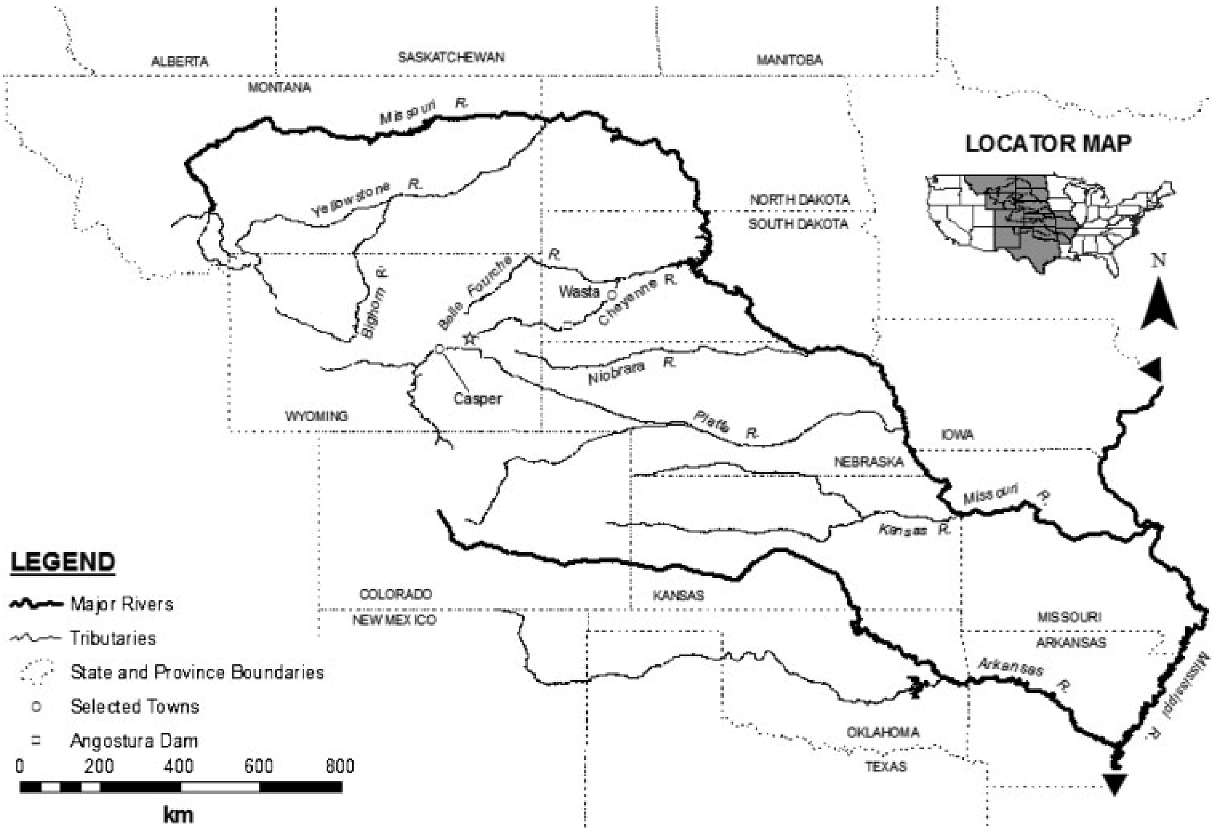

Figure 1. Map of the north-western Mississippi River basin in central North America showing major river drainages and tributary drainages occupied by northern plains killifish (*Fundulus kansae*). The northern plains killifish has historically been considered native to the Arkansas, Kansas, Platte, and Niobrara drainages, but non-native to the Cheyenne and Yellowstone drainages. Features referred to in the text are shown (selected towns, Angostura Dam) and the star indicates the location of the Highland Flats and Sundquist Flats, a region of potential faunal exchange between the Cheyenne and Platte river drainages.

original criteria are revised and expanded and their rigorous use is illustrated to promote their application in distribution studies.

STUDY AREA

The northern plains killifish is native to the Arkansas and Missouri river drainages of North America (Poss and Miller, 1983; Kreiser *et al*., 2001). To the east and west it is largely confined to the Great Plains and Osage Plains physiographic regions (sensu Holliday *et al*., 2002). To the south, it is replaced by the plains killifish (*Fundulus zebrinus*; Kreiser *et al*., 2001). There are no distinct northern boundaries, but the species is presumed native only as far north as the Platte and Niobrara rivers (Poss and Miller, 1983). The Cheyenne River, where it is presumed non-native, is 430 km farther upstream and its headwaters abut those of the Platte and Niobrara rivers (Figure 1).

CRITERIA

Webb's (1985) criteria for presuming native status were specific to plants. To broaden their applicability, his list has been revised and expanded. Criteria used are: (1) history, (2) detectibility, (3) biogeography, (4) life-history, (5) human affinity, (6) invasion path, (7) invasiveness, (8) phylogenetics, and (9) pre-history. The ideology of each criterion and the potential methodology to evaluate them are illustrated below.

History

Historical evidence formed the basis of Miller's (1955) presumption that the northern plains killifish was non-native in the Cheyenne River drainage. He reasoned that absence from a historical collection from the Cheyenne River near Wasta, South Dakota (Figure 1) prior to its detection elsewhere in the drainage was evidence of non-native status. Records of historical surveys from that location were tabulated to evaluate his interpretation, and the index of persistence (PR) was calculated to quantify faunal stability among samples (Meffe and Minckley, 1987). The index of persistence ranges from zero to one: zero indicates no persistence, one indicates total persistence.

The northern plains killifish was present only once in historical collections from the Cheyenne River near Wasta (Table 1). Misidentification with other fish is unlikely given its distinctive appearance (Bailey and Allum, 1962; Baxter and Stone, 1995). The entire fauna had low persistence (PR = 0.39). No species was present in all historical collections. Although 22 species were documented, the most

Table 1. Presence of different fish species in historical samples from the Cheyenne River near Wasta, South Dakota, USA

Species	1939[a]	1950[b]	1951[b]	1994[c]	1996[d]	1997[d]
Goldeye *Hiodon alosoides*[e]						x
Red shiner *Cyprinella lutrensis lutrensis*[e]					x	x
Common carp *Cyprinus carpio*[g]						x
Western silvery minnow *Hybognathus argyritis*[e]					x	
Plains minnow *Hybognathus placitus*[e]	x	x		x	x	x
Sturgeon chub *Macrhybopsis gelida*[e]		x	x	x		x
Plains sand shiner *Notropis stramineus missuriensis*[e]		x	x		x	x
Fathead minnow *Pimephales promelas*[e]				x		x
Flathead chub *Platygobio gracilis*[e]	x	x		x	x	x
Longnose dace *Rhinichthys cataractae cataractae*[e]	x	x		x	x	
Northern river carpsucker *Carpiodes carpio carpio*[e]	x	x			x	
White sucker *Catostomus commersonii*[e]		x				
Shorthead redhorse *Moxostoma macrolepidotum*[e]		x		x		x
Black bullhead *Ameiurus melas*[e]	x	x				x
Channel catfish *Ictalurus punctatus*[e]		x	x	x	x	x
Stonecat *Noturus flavus*[e]		x				x
Northern plains killifish *Fundulus kansae*[f]			x			
White bass *Morone chrysops*[g]					x	
Green sunfish *Lepomis cyanellus*[f]		x				
Orangespotted sunfish *Lepomis humilis*[f]		x				
Sauger *Sander canadensis*[e]					x	
Freshwater drum *Aplodinotus grunniens*[e]					x	

[a]California Academy of Sciences Ichthyology Collection Database.
[b]Bailey and Allum (1962).
[c]Cunningham *et al.* (1995).
[d]Hampton (1998).
[e]Native species.
[f]Native status uncertain.
[g]Non-native species.

in a single collection was 13. Hampton (1998) conducted the two most recent collections (1996 and 1997) using the same sampling methodology. He collected 18 species total, but only five in both years. If the logic of Miller (1955) is applied equally to all fish, meaning that any species not present in initial collections must be non-native, 12 species widely considered as native would be classified as non-native (Table 1). His logic does not account for temporal and spatial variability in fish distributions. Historical fish faunal flux is characteristic of the Cheyenne River and may reflect climatic variability, human impacts, non-native fish impacts, or sampling inconsistencies (Hoagstrom *et al.*, 2007).

Collections from throughout the Cheyenne River drainage suggest northern plains killifish populations are centred in smaller streams. Initial collections from the upper Cheyenne River found the species to be widespread (Baxter and Simon, 1970; Greene *et al.*, 1990; Duehr, 2004). Isolated populations were also present in initial surveys of tributary streams (Newman *et al.*, 1999; USGS, 2001; 2002; 2004; Duehr, 2004). Infrequent collections of northern plains killifish from larger rivers may represent displaced or dispersing individuals or ephemeral populations (Cross, 1967; Pflieger, 1997). For instance, the species was absent from the Belle Fourche River, Elm Springs, South Dakota in high-flow years (Doorenbos, 1998), but persistent in a low-flow year (Hoagstrom *et al.*, 2006). This population probably originated from nearby Elm or Alkali creek. Specimens found in the Cheyenne River near Wasta in 1951 could have been transients from Elk or Sage creeks. Hence, absence of northern plains killifish in some collections from the Cheyenne River near Wasta is attributable to low persistence of the fish assemblage and low habitat suitability.

Detectibility

Detection probabilities estimate the likelihood of detecting at least one individual of a species that is present and can be effectively captured (Bayley and Peterson, 2001). They range from 0 to 1. One indicates a species is present in every collection from a given area. Detection probabilities are based on presence data gathered over small temporal scales (Hayer *et al.*, 2008). Seven stream reaches within the Cheyenne River drainage, South Dakota were sampled in 2005 to determine detection probabilities. Seines and electrofishing over stream reaches greater than 150 m in length were used at all locations to ensure adequate sampling effort (sensu Patton *et al.*, 2000).

Detection probability of northern plains killifish was 0.01, whereas mean detection probability was 0.20 ± 0.27 SD for 37 species (range = 0.00 to 0.66). When present, northern plains killifish are readily captured (Minckley and Klaassen, 1969; Brown, 1986; Schmeidler and Brown, 1990). However, the species commonly has a patchy and transient distribution (Summerfelt, 1967; Fausch and Bestgen, 1997), which accounts for low detection. Low detection probability within the Cheyenne River drainage indicates that sampling effort should have been geographically and temporally extensive prior to designating the northern plains killifish as non-native.

Biogeography

No obvious boundary limits the native range of the northern plains killifish to the north. Potential limiting factors include: (1) isolation, (2) climatic seasonality, (3) habitat uniformity, and (4) increasing cold (Hoagstrom and Berry, 2006). The western distributional limit is associated with increasing cold (mean July air temperature; Quist *et al*., 2004; Brunger Lipsey *et al*., 2005), but presumed native populations occur near Casper, Wyoming, whereas presumed non-native populations reside near the South Dakota–Wyoming border (Baxter and Simon, 1970; Patton, 1997). Mean annual temperature is higher near the South Dakota-Wyoming border than near Casper (Grimm, 2001). Hence, cold cannot account for the presumed northern boundary.

Geographical isolation (430 river km) between the Niobrara and Cheyenne rivers could preclude northward immigration if intervening habitat is inhospitable. However, at least 10 other fish with a variety of life-history traits have reached the Cheyenne River drainage from the south (Hoagstrom and Berry, 2006). Given the lack of geographical barriers, there is no reason to believe northern plains killifish could not have colonized the Cheyenne River drainage. Molecular evidence suggests it colonized the Platte River drainage in the mid-Pleistocene (Kreiser *et al*., 2001), presumably dispersing northward when conditions were relatively warm. Hence, the warmer climate 8000 to 4000 years ago (Strong and Hills, 2005) may have allowed the species to disperse farther north than at present. If so, relict populations most likely would persist in larger tributary drainages, such as the Cheyenne River, which have higher habitat diversity and sustain larger populations (Hoagstrom and Berry, 2006). Smaller, drainages that lie between the Niobrara and Cheyenne have relatively minor tributary habitat (Harland, 2003), presumably providing less suitable habitat for the species. Large hot springs present in the Cheyenne River drainage, but not intervening drainages, may have provided refugia during cold periods that sustained relict populations of northern plains killifish.

Intervening rivers also have high silt loads because they drain the South Dakota Badlands (Galat *et al*., 2005). Northern plains killifish are generally absent from silty streams (Johnson 1942; Gido *et al*., 2002). The hornyhead chub (*Nocomis biguttatus*) also avoids turbid streams (Cross, 1967; Cross and Moss, 1987) and similarly inhabits the Platte and Cheyenne river drainages, but not intervening drainages (Lachner and Jenkins, 1971). Avoidance of silt-laden streams could account for these disjunct distributions.

Faunal exchanges may have occurred between the Platte and Cheyenne river drainages via flooded inter-drainage connections or stream captures (sensu Bailey and Allum, 1962; Cross *et al*., 1986; Mayden 1987). East of Casper, Wyoming, only a low watershed divide (i.e. the Highland Flats and Sundquist Flats) separates the two drainages (Figure 1). Potential faunal exchange in this vicinity provides a direct route between the Platte and Cheyenne river drainages that may have been used by hornyhead chub, northern plains killifish and other species. Northern plains killifish presumably used a similar route to disperse among Platte River tributaries (Johnson, 1942).

Life history

The life history of an invasive fish must be compatible with the local flow regime (Olden *et al*., 2006). Northern plains killifish have an opportunistic life history, evidenced by small size at maturation (<5 cm), small maximum body size (<10 cm), short lifespan (<3 years), protracted spawning season, and limited parental care (Koster, 1957; Minckley and Klaassen, 1969; Brown, 1971; Schmeidler and Brown, 1990). Further, spawning may occur in response to rain (Pflieger, 1997), populations exhibit high resilience under favourable conditions (Summerfelt, 1967; Fausch and Bestgen, 1997), and population structure is responsive to environmental fluctuations (Schmeidler and Brown, 1990). An opportunistic life history is associated with unstable or unpredictable environments (Winemiller, 2005), consistent with the flow regime of the Cheyenne River drainage (Ruelle *et al*., 1993). In addition, northern plains killifish associate with flashier flow regimes within the drainage (Hoagstrom *et al*., 2006). However, an opportunistic life-history is prerequisite for any fish, native or non-native, to persist in the plains and prairies of North America (Dodds *et al*., 2004; Gido *et al*., 2004), so it neither supports nor refutes native status of the northern plains killifish in the Cheyenne River drainage.

Human affinity

The northern plains killifish may withstand increased salinity (Cross and Collins, 1995) or flow regime modifications (Cross and Moss, 1987) caused by humans and may occupy reservoirs (Baxter and Stone, 1995; Lionberger and Hubert, 2007). However, it is not generally associated with reservoirs (Falke and Gido, 2006) and is sensitive to habitat fragmentation, dewatering, and siltation (Brown, 1986; Cross and Collins, 1995; Peters and Schainost, 2005). In the Cheyenne River drainage, it associates with less-disturbed habitats dominated by natives, not disturbed habitats dominated by non-natives (Patton, 1997; Hoagstrom *et al*., 2006). For example, it is absent from the Belle Fourche Irrigation Project (Bailey and Allum, 1962; Newman *et al*., 1999; Duehr, 2004), has disappeared from the Angostura Irrigation Project (Hoagstrom *et al*., 2007), is not associated with polluted waters or high salinities (Patton, 1997; Duehr, 2004), and is absent from tributaries affected by mine tailings, major dams, or urbanization, such as Whitewood Creek, Rapid Creek, and the Fall River (Bailey and Allum, 1962; Newman *et al*., 1999; Duehr, 2004; Hoagstrom *et al*., 2006). The northern plains killifish is not found in reservoirs of the Cheyenne River drainage (South Dakota Department of Game, Fish and Parks, unpublished data). Thus, there appears to be no affinity between northern plains killifish and human disturbance in the Cheyenne River drainage.

Invasion path

Miller (1955) proposed that northern plains killifish were introduced to the Cheyenne River drainage via live-bait release into Angostura Reservoir from the North Platte or Niobrara river drainages, but likelihood of such a transfer seems low. Anglers would have to travel out of state, where they must purchase additional fishing licences and, although some authors note northern plains killifish are used as bait (Koster, 1957; Morris *et al*., 1974; Baxter and Stone, 1995), others consider it poor bait and of low economic importance (Simon, 1951; Cross, 1967; Baxter and Simon, 1970; Beckman, 1970; Woodling, 1985). No authors list it as preferred for use as bait. Remoteness of tributaries that support major populations and absence from Angostura Reservoir (South Dakota Department of Game, Fish and Parks, unpublished data) also argue against this hypothesis.

Incidental release of northern plains killifish with stocked, hatchery fish is another potential means of introduction, but no potential source has been identified. Based on molecular evidence, Kreiser *et al.* (2000) concluded that non-native northern plains killifish in the Colorado River basin originated from the Arkansas River drainage. They did not discuss the likelihood of transfer to the Cheyenne River drainage. Research of hatchery records would better determine the likelihood of this scenario.

Release of aquarium-pet fish is yet another potential means of introduction. Several authors tout northern plains killifish as suitable for aquaria (Simon, 1951; Baxter and Simon, 1970; Beckman, 1970). However, as with live-bait releases, such a transfer would involve several fish being brought into captivity in Wyoming or Nebraska, transported alive across state lines, and subsequently released alive into suitable waters of the Cheyenne River drainage. Given the presumed low number of persons that maintain native fish in aquaria and low human population of the region, this seems unlikely.

Invasiveness

Invasive northern plains killifish are known from the upper Colorado River drainage (Hughes, 1981; Kreiser *et al.*, 2000). There is little doubt they are introduced because the native fauna of the Colorado River drainage is unique, lacking fundulids altogether (Minckley *et al.*, 1986). There are no suitable dispersal routes between the Colorado River drainage and the Missouri or Arkansas river drainages because the Atlantic–Pacific continental divide separates both the river mouths and headwaters. The northern plains killifish is restricted to warm water habitats of relatively low elevations (Quist *et al.*, 2004; Brunger Lipsey *et al.*, 2005), distant from this divide.

The northern plains killifish is presumed non-native in the Yellowstone River drainage, another tributary to the Missouri River (Figure 1). This presumption is speculative (Baxter and Simon, 1970; Lionberger and Hubert, 2007), but there are differences in the history of the species between the Cheyenne and Yellowstone river drainages. In the Yellowstone River drainage, it was first detected in a drainage ditch (Brown, 1971). Populations in Wyoming (Baxter and Simon, 1970) were also in areas developed for irrigated agriculture (Zelt *et al.*, 1999) and several of these locations were previously sampled (Simon, 1951; Baxter and Simon, 1970). The species has become increasingly widespread and abundant (Elser *et al.*, 1980; Holton and Johnson, 2003) and has recently been reported from adjacent drainages, including the Little Missouri River (Holton and Johnson, 2003) and Dry Creek (Melissa Wuellner, personal communication). In contrast, northern plains killifish populations in the Cheyenne River drainage were present in initial collections from all tributary localities, are not associated with human disturbances, have not extended their historical range, and have not invaded adjacent waters.

Phylogenetics

Poss and Miller (1983) documented clinal increases in lateral scale rows and vertebrae of northern plains killifish from south to north. Specimens from the Cheyenne River fit the cline, with the highest average number of lateral scale rows (63 ± 2.2 SD) and vertebrae (35 ± 0.5 SD). Presumed native plains minnow (*Hybognathus placitus*) and plains sand shiner (*Notropis stramineus missuriensis*) exhibit analogous clines (Al-Rawi and Cross, 1964; Tanyolaç, 1973). Geomorphic evidence suggests these fish colonized the Missouri River drainage in the early to mid-Pleistocene (Hoagstrom and Berry, 2006), consistent with molecular-based estimates of northward dispersal by northern plains killifish (Kreiser *et al.*, 2001). These three taxa co-occur across much of their native ranges (Cross, 1967; Baxter and Stone, 1995). Thus, northern plains killifish may have colonized the Cheyenne River drainage during a pre-historic warm period in association with other fish.

Pre-history

Fossil evidence of northern plains killifish in the Cheyenne River drainage is unavailable, but available fossils indicate that post-glacial fish distributions varied over time. For example, the western banded killifish (*Fundulus diaphanous menona*) ascended the Missouri River in early post-glacial time, but was extirpated via subsequent climatic warming (Cvancara *et al.*, 1971; Newbrey and Ashworth, 2004). Conditions that caused the retreat of western banded killifish perhaps facilitated the advance of northern plains killifish.

DISCUSSION

There is substantial support for the native status of northern plains killifish in the Cheyenne River drainage. Of nine criteria, five (history, detectibility, biogeography, human affinity, phylogenetics) provide relatively strong support, one (pre-history) provides weak support, two (life-history, invasion path) are equivocal, and one (invasiveness) supports non-native status. The criterion 'invasiveness' is not convincing as sole evidence for non-native status because it could be used as evidence that northern plains killifish of any river drainage (e.g. the Arkansas) are non-native. Support from other criteria is necessary to make the hypothesis of non-native status defensible.

Hedged statements (sensu Horn, 2001) may influence the designation of native distributions. Accurate designations are important because they influence distributional studies (Pyšek *et al.*, 2004). For example, Hoagstrom and Berry (2006) studied island biogeography of native fish faunas among tributary drainages of the western Missouri River drainage. They found strong relations of drainage area and isolation with native species richness. Designation of the northern plains killifish as native in the Cheyenne River drainage would have strengthened this trend further, because the Cheyenne River drainage is larger and less isolated than many others where the species is absent.

Regional experts who compile species lists are seemingly most qualified to determine native distributions because they have inherent familiarity with the region of interest and consider all species distributions simultaneously. It is riskier for remote researchers to designate species distributions, particularly if they do not consider the whole fauna. For instance, Miller (1955) postulated the non-native status of the northern plains killifish in the Cheyenne River drainage within a taxonomic study of the genus *Fundulus*. Although an ichthyologist of high repute, Miller was not a student of Missouri River biogeography and did not review fish distribution patterns when making his designation. As noted above, use of his logic for all fish would have contradicted convention and led to the conclusion that very few fish were native to the Cheyenne River drainage. Perhaps Miller would have concluded differently if he had adopted the same criteria used for other species, or had applied the criteria presented here.

The criteria presented are used in one form or another within all distributional studies, but are rarely, if ever, used explicitly, consistently, and collectively. Detailed analyses occur most frequently in controversial situations (Kaczynski and Alvarado, 2006; Adams *et al*., 2007). In such cases, use of criteria is often haphazard, presumably based on available information within the experience of the authors. Rigorous use of a pre-determined set of criteria has the benefit of encouraging authors to consider types of information that perhaps they normally would not. Criteria for which little or no relevant information is found reveal knowledge gaps, such as the lack of information on potential hatchery sources of northern plains killifish. Cumulative consideration of all criteria can also help generate testable hypotheses, such as the hypothesis that northern plains killifish populations in tributaries are the source of transient, riverine populations that wax and wane depending on habitat conditions. Ultimately, we contend that consistent use of a universal set of criteria is necessary for more accurate, consistent, and better-documented species distributions and for advancing the science of biological distributions.

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