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Methods, Tools, and Technologies

Using resiliency, redundancy, and representation in a Bayesian belief network to assess imperilment of riverine fishes

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Abstract

Conservation prioritization frameworks are used worldwide to identify species at greatest risk of extinction and to allocate limited resources across regions, species, and populations. Conservation prioritization can be impeded by ecological knowledge gaps and data deficiency, especially in freshwater species inhabiting highly complex aquatic ecosystems. Therefore, we developed a flexible approach that calculates a species' imperilment risk based on the conservation principles of resiliency, redundancy, and representation (i.e., the "three R's"). Our approach organizes data on species traits, distributions, population connectivity, and threats within a Bayesian belief network capable of predicting resiliency and redundancy within representative ecological settings. Empirical data and expert judgment inform the model to provide robust and repeatable risk assessments for rare and data-deficient species. The model calculates resiliency at hierarchical spatial scales from distributional trends and population strength. Redundancy is estimated from the connectivity and quantities of extant populations. Resiliency, redundancy, and species' inherent vulnerability based on species traits collectively estimate extirpation risk within each unique ecological setting. Extirpation risks across ecological settings characterize representation and are aggregated to estimate global imperilment risk. We demonstrate the model's utility with Piebald Madtom (*Noturus gladiator*), a species petitioned for listing under the U.S. Endangered Species Act. Our results revealed that resiliency, redundancy, and extirpation risks can vary spatially across the species' range while identifying populations where additional sampling could disproportionally reduce uncertainty in estimated global imperilment risk. Our approach could standardize and expedite conservation status assessments, identify opportunities for early management intervention

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of at-risk species and populations, and strategically reduce uncertainty by focusing monitoring and research on priority information gaps.

INTRODUCTION

Modern extinction events greatly exceed background rates for all organisms (Ceballos et al., 2015; Pimm et al., 2014), and aquatic taxa have proven particularly susceptible worldwide to biodiversity threats (Burkhead, 2012; Ricciardi & Rasmussen, 1999). Hundreds of freshwater fish, mollusk, gastropod, and crayfish extinctions occurred in the last century, and many other freshwater taxa are considered imperiled (Burkhead, 2012; Haag & Williams, 2014; Johnson et al., 2013; Pimm et al., 2014). Accelerated extinction rates among aquatic taxa necessitate directed conservation actions to maintain representative diversity and preserve aesthetic, societal, and economic values of aquatic ecosystems (Freitag & Van Jaarsveld, 1997; Taylor et al., 2011). However, financial resources for conservation are often limited, requiring careful prioritization of geographic areas, species, and populations for management actions (Gerber et al., 2018; Joseph et al., 2009; Steen & Barrett, 2015). Legislation, such as the U.S. Endangered Species Act (ESA), is meant to prevent extinction by allocating resources to species with eminent risk of extinction (Wolf et al., 2015). However, protected species designations extend to relatively few species and generally exclude poorly known and understudied species of potential conservation significance.

Insufficient resources for broad monitoring means conservation practitioners often use tools to identify and prioritize limited resources for species with the highest risks of imperilment. Many of these conservation prioritization tools are available to help assess imperilment risk among species by synthesizing similar biological criteria and information on known threats (e.g., Baigún et al., 2012; Gauthier et al., 2010; Gerber et al., 2018; Zhang et al., 2015). These tools can be used for early identification of imperiled species (e.g., International Union for Conservation of Nature Red List) and to inform decisions about official policy designations (i.e., Species Status Assessments under ESA). Qualitative descriptions, point-scoring procedures, and rule sets are typically used to assign conservation priority to the most vulnerable species (Brooks et al., 2006; Game et al., 2013; Mehlman et al., 2004; Taylor et al., 2011). Although there are many

variations of conservation prioritization tools, generally, species that are narrowly distributed and numerically rare are most sensitive to demographic or environmental stochasticity and are high-priority candidates for conservation actions and status designations. Normative factors, unrelated to extinction risk, such as ecological, economic, and social values are also commonly considered by policymakers when prioritizing species (Vucetich et al., 2006).

No conservation prioritization approach has been universally adopted that efficiently integrates dissimilar data sources often used for conservation decision-making within a collective framework (Smith et al., 2018; Waples et al., 2013; Wolf et al., 2015). Although population viability analysis can be a useful tool for projecting extinction risk (Himes Boor, 2014), shortcomings such as reliance on standardized abundance data and unknown population vital rates have limited this method's broad utility (Freitag & Van Jaarsveld, 1997; Game et al., 2013; Wolf et al., 2015). Conservation tools that solely rely on abundance data to support complex computations can propagate hidden biases (Smith et al., 2018), conceal important specific biological criteria (Coates & Atkins, 2001; Given & Norton, 1993), be resource or labor intensive (Brehm et al., 2010; Dulvy et al., 2014), and fail to promote efficient and defensible conservation assessments (Smith et al., 2018). Conservation efforts would benefit from a transparent, consistent, and streamlined approach to identify species, assemblages, and regions for management intervention, especially given the potential workload of assessing hundreds of taxa in species-rich areas, such as the southeastern United States (Elkins et al., 2019).

Conservation efforts to address aquatic stressors have been impeded historically by the high complexity of freshwater ecosystems, data deficiency, and uncertainty associated with conservation status assessments and management strategies (Gregory & Long, 2009; Smith et al., 2018). Available risk assessments are constrained by their inability to account for uncertainty and failed applications to aquatic species, for which necessary distributional, habitat, and natural history knowledge is often unavailable (Brooks et al., 2006; Dulvy et al., 2014; Zhang et al., 2015). More broadly, aquatic taxa are understudied relative to terrestrial taxa (Baigún et al., 2012), and

without a method to represent uncertainty explicitly, these understudied taxa have been excluded historically from conservation status assessments (Given & Norton, 1993; Martín-López et al., 2011). For example, approximately 46% of Chondrichthyes (sharks, sawfish, rays, etc.), 44% of upper Yangtze River species, and 21% of crayfish species were recently described as "data-deficient" using IUCN criteria (Dulvy et al., 2014; Richman et al., 2015; Zhang et al., 2015). However, conservation risk assessments can proceed if model uncertainty and sensitivity of model outputs to data deficiency are communicated effectively to decision-makers (Lawson et al., 2021; Smith et al., 2018).

We describe a probabilistic analysis that evaluates imperilment risk and is grounded in the conservation principles of redundancy, resiliency, and representation (Shaffer & Stein, 2000; Wolf et al., 2015). Our modeling approach (i.e., Bayesian belief network) is flexible and can include expert judgment while quantifying uncertainty in the absence of quantitative data to provide defensible risk assessments for data-deficient aquatic species (Smith et al., 2018). We overview our model by evaluating current imperilment risk of Piebald Madtom (*Noturus gladiator*), an information-limited riverine species petitioned for federal listing under the ESA. This model is broadly applicable to other aquatic taxa worldwide and could be used to calculate imperilment rates among poorly understood taxa in species-rich regions.

METHODS

Ecological theory and the "three R's" framework

Our risk-assessment approach is grounded in the conservation biology principles of resiliency, redundancy, and representation ("the three R's"), which collectively predict a species' long-term viability (Shaffer & Stein, 2000; Smith et al., 2018; Wolf et al., 2015). Resiliency is a species' ability to withstand stochastic disturbances. Redundancy is a species' ability to withstand catastrophic events by spreading risk among multiple populations or across a large area. Representation is a species' ability to adapt to changing environmental conditions over time as characterized by the breadth of genetic, ecological, and environmental diversity within and among populations. Representation is delineated into unique ecological settings, which are often distinguished geographically by distributional gaps and/or physiographic settings (Figure 1). Risks of extirpation within each ecological
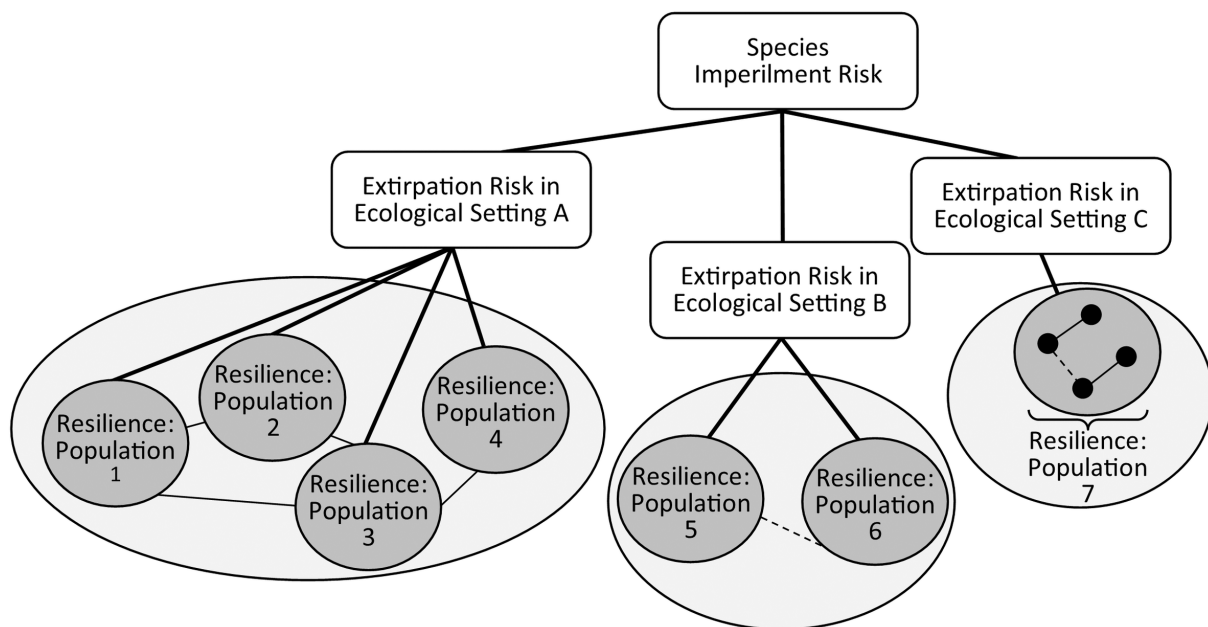
FIGURE 1 Conceptual model depicting the hierarchical relationships among population resiliency, redundancy, and representation that are used to predict imperilment risk. Resiliency of individual populations delineated by management units (dark gray circles) is estimated for each ecological setting (light gray circles). Multiple resilient populations that are connected (connected, thin solid lines; interrupted, thin dashed line) result in high redundancy. Often there are multiple occupied stream segments (black circles) within a population. Representation is high when each unique ecological setting has multiple resilient and connected populations.

setting combine to influence a species' global imperilment risk.

Bayesian belief network

The three R's framework is a useful conceptual model for identifying factors influencing imperilment risk, but the framework has limited application without being converted into a predictive model. Therefore, we developed an initial influence diagram based on the three R's framework that characterized relationships among resiliency, redundancy, taxon vulnerability, and extirpation risk for a species within its representative ecological settings (representation; Figure 2). Then we converted the influence diagram into a quantitative Bayesian belief network model (Figure 3). Bayesian belief networks provide holistic representations of relationships among interacting variables (hereafter, "nodes") in which inferences are drawn collectively from empirical data, expert knowledge, and simulation modeling. Bayesian belief networks have aided conservation decision-making by predicting probabilistic relationships between ecological conditions and future responses (Marcot et al., 2006; Peterson et al., 2013; Stewart-Koster et al., 2010). We followed model-building practices outlined in Marcot et al. (2006) and Marcot (2012) when developing the Bayesian belief network. Our initial model was developed to evaluate imperilment of riverine fishes in the southeastern U.S. biodiversity hotspot, but the model could be
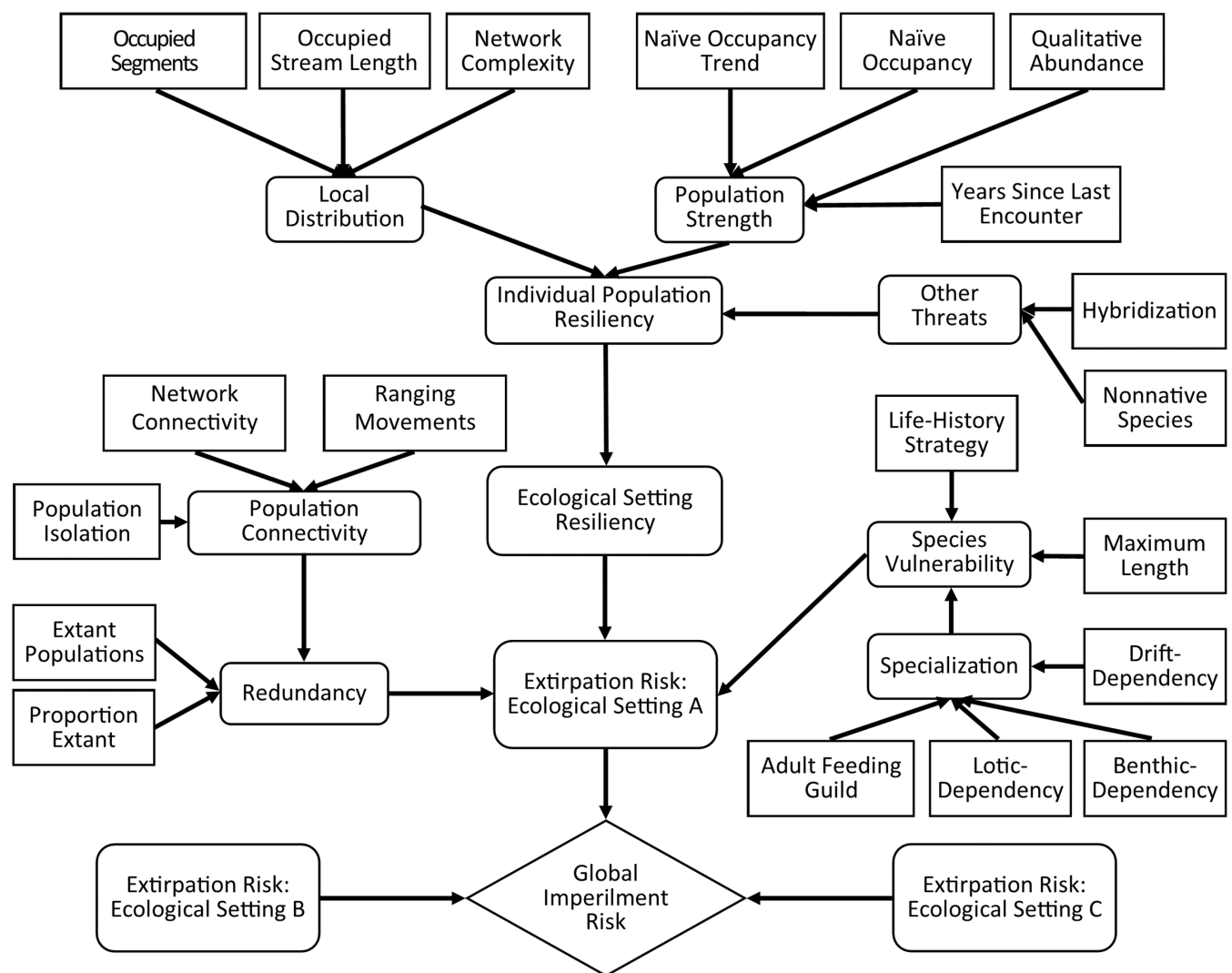
FIGURE 2 Influence diagram used to develop a Bayesian belief network that predicts a species' probability of being at risk of global imperilment (diamond) using population resiliency and redundancy in ecological settings (i.e., representation). The number of ecological settings is equal to the number of significantly different genetic, life history, or geographic population groups across the species range. Only contributing nodes for Ecological Setting A are shown. An Individual Population Resiliency sub-model (group of nodes) is included for each management unit in each area of representation (i.e., ecological setting).
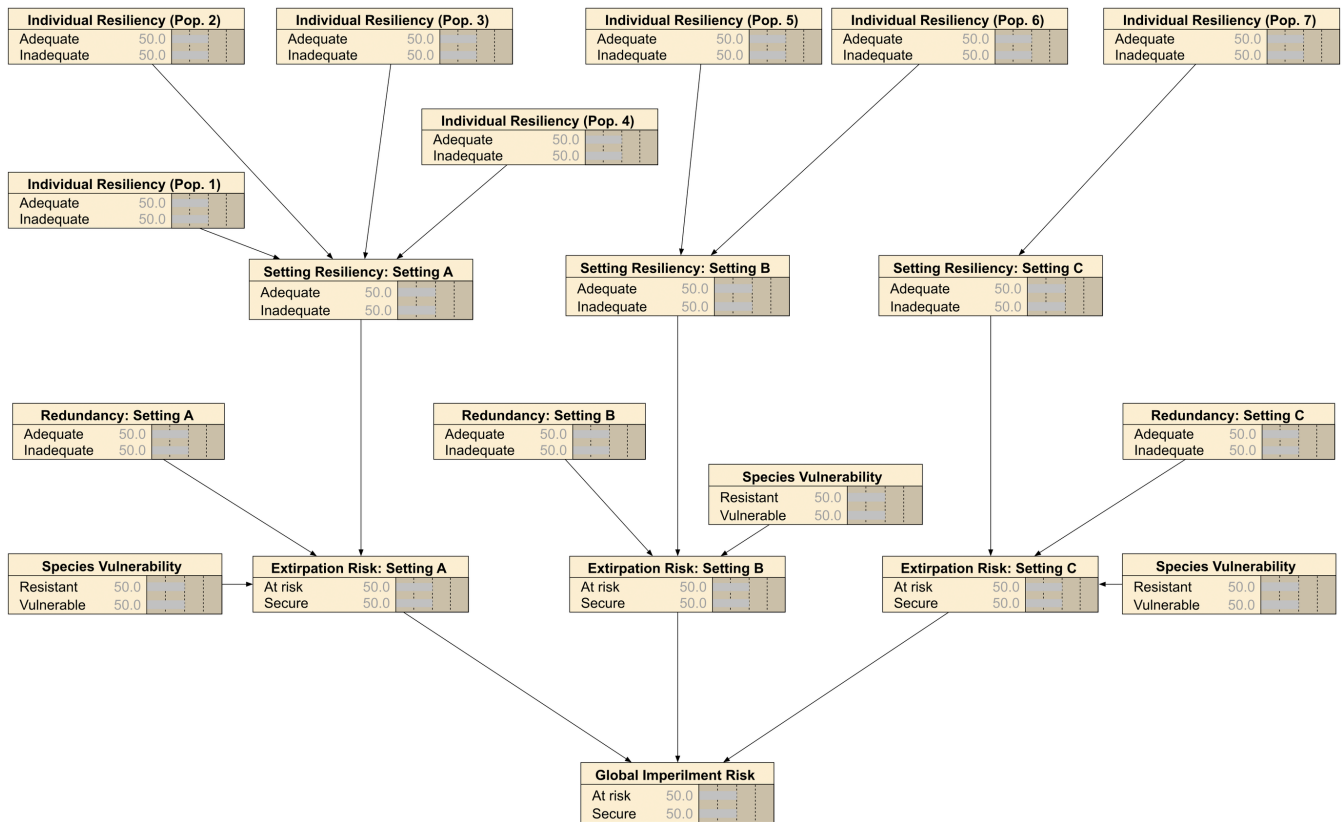
FIGURE 3 Bayesian belief network formatted in Netica that illustrates linkages among population resiliency, redundancy, and species vulnerability and predicts the probability of a species being in an "at-risk" state of extirpation in each ecological setting (i.e., representation). Probabilities within each ecological setting's Extirpation Risk node influence the probability of a species being at risk of global imperilment. This example corresponds to Figure 1 and has seven known populations (Pop1–Pop7) across three unique ecological settings (A, B, and C).

adapted to other taxa and regions because the model is grounded in the three R's framework.

Each node within the Bayesian belief network houses mutually exclusive categorical states. For example, the model's terminal output is a node representing *Global Imperilment Risk* with two discrete states, "at risk" and "secure" (nodes are italicized at first mention and capitalized thereafter; Figure 3). Because states are nonoverlapping and exhaustive, the model estimates complementary probabilities that sum to 1.0 (e.g., "at risk" = 0.35 and "secure" = 0.65). Parent nodes are located peripherally within the network and influence the likelihoods of states within more centrally located child nodes. States within parent nodes are given a likelihood distribution that defines prior probabilities of a species being in each state within a node. For example, geographical rarity is often correlated with higher imperilment risks (Pritt & Frimpong, 2010). Intensive watershed-wide monitoring could convey with high certainty (e.g., Pr = 0.95) that a fish species' distribution within a watershed is restricted to 15 stream km (e.g., *Occupied Stream Length* node's state of "10–25 km"). Alternatively, if a watershed has not been

sampled recently, prior probabilities could be set as uniform across plausible states characterizing categories within the node, Occupied Stream Length, to reflect complete uncertainty in the species' distribution (i.e., equal probabilities among states, Pr, "<10 km" = 0.33; Pr, "10–25 km" = 0.33; Pr ">25 km" = 0.33; Table 1).

Causal linkages among parent and child nodes are represented empirically a priori by conditional probability tables within child nodes (Marcot et al., 2006). Values within conditional probability tables reflect probabilities of a species existing in each state within a child node conditional on probabilities of states within parent nodes. Conditional probability tables can be constructed solely from empirical models for well-informed species, but we used a mixture of expert judgment, literature, and empirical data to parameterize our initial conditional probability tables for data-deficient riverine fishes. Numbers of states within parent nodes determine dimensions of conditional probability tables of child nodes, so we intentionally limited numbers of most parent nodes and node states to ≤4 to minimize complexity of conditional probability tables with two exceptions; dimensions of conditional probability tables for *Individual Population*

Resiliency and Global Imperilment Risk are determined by numbers of contributing management units and ecological settings, respectively, which are specific to the spatial context of an individual species being assessed (described below). We developed our model in Program Netica (Figure 3; version 6.04, Norsys Software Corp., Vancouver, British Columbia) and provide a reproducible example in Program R Version 4.2.1 (see *Data availability statement*).

Spatial context of analysis

The Bayesian belief network is organized hierarchically into multiple nested spatial scales (Figure 1). The coarsest scale encompasses the historically occupied range of a focal species (i.e., Global Imperilment Risk). The species' range is subdivided into mutually exclusive geographical areas (ecological settings) that represent unique underlying genetic, ecological, or physiographic diversity across the species' range (Smith et al., 2018; Wolf et al., 2015). Ecological settings can be further subdivided into management units. Management units can be delineated genetically (i.e., distinct populations), physically (e.g., distinct watersheds or hydrologic units), or practically (agency-defined common management areas). Each management unit generally encompasses a "population," and nodes for each management unit (population resiliency-related nodes described below) represent underlying population characteristics (e.g., demographics, distributional trends through time). Nodes characterizing relationships among management units (redundancy-related nodes described below) within each ecological setting generally represent processes associated with meta-population dynamics (e.g., numbers of source populations and among-population connectivity).

For simplicity within our initial riverine fishes model, we defined management units as historically occupied unique 10-digit Hydrological Unit Codes (hereafter "HUC10"). Within each management unit, distributional sampling records for a focal fish species are joined to the nearest stream segment within the National Hydrography Dataset stream network (USGS & USEPA, 2012). Consequently, unique stream segments delineated by tributary junctions are the spatial grain of occurrences. Multiple occurrences of a focal species within the same segment and on the same date are treated as a single sampling event, and therefore, their abundances are summed. The spatial midpoint of each sampled stream segment serves as the geospatial coordinates to estimate redundancy by calculating the connectivity and isolation of management units within each ecological setting.

Representing the three R's with a Bayesian belief network

Node and state definitions

The Bayesian belief network includes several nodes that collectively predict probabilities of being "at risk" and "secure" within the Global Imperilment Risk node (i.e., terminal node; Figure 2). Model architecture and node-state definitions are based on conservation literature of riverine fishes in the southeastern United States and feedback from conservation practitioners. Most nodes are associated with Individual Population Resiliency (nine parent nodes and four child nodes). Additional nodes predict *Redundancy* (five parent nodes and two child nodes) and *Species Vulnerability* (six parent nodes and two child nodes). Each node that informs population resiliency and redundancy reflects a distinct aspect of the species' threat profile. Ideally, each node in the model represents causal influences of environmental or population attributes on global imperilment risk (Marcot et al., 2006). However, surrogate variables can be used for situations when data are unavailable. We provide further explanation and detailed justification of states within all nodes in Tables 1–3.

Resiliency

Populations that are resilient to environmental stochasticity are likely large, stable or increasing, and within geographical areas with sufficient habitat for individuals to survive and reproduce (Shaffer & Stein, 2000; Smith et al., 2018; Wolf et al., 2015). Several nodes estimate resiliency of the population in each management unit (i.e., Individual Population Resiliency; Table 1; Figure 2). Individual Population Resiliency is influenced by *Local Distribution*, which is a function of the complexity of stream sizes and locations (mainstem and tributaries) where the species occurs (i.e., *Network Complexity*; Fagan, 2002), the number of occupied segments (i.e., *Occupied Segments*), and the species' recent distributional size measured as the maximum stream distance between recent (since year 2000) occurrences (i.e., Occupied Stream Length). We characterize "recent" as since year 2000, but the definition of recent could also be a moving window (e.g., 20 years before assessment, Freeman et al., 2005) or shift with periodic reassessments (i.e., five-year reviews under ESA). Individual

TABLE 1 Parent nodes and discrete states influencing Individual Population Resiliency used to convert the initial influence diagram into a Bayesian belief network.

State name	Definition	Justification
Network Complexity, nominal discrete states		
Mainstem	Only found in mainstem reaches	Distribution within management units of a species among mainstem reaches and tributaries. A population with a complex, dendritic distribution is more resilient (Fagan, 2002).
Single tributary	Found in a single tributary	
Multiple tributaries	Found in multiple tributaries	
Complex	Both mainstem and tributaries	
Occupied Stream Length (km), continuous with discrete states		
Restricted	Stream length <10 km	Recent (since January 1, 2000) occupied stream length, measured as the distance between the farthest upstream and downstream occupied segments.
Moderate	Stream length: 10–25 km	
Widespread	Stream length: >25 km	
Naïve Occupancy (Ψ), continuous with discrete states		
Potentially extirpated	Ψ: ≤0.05	Proportion of unique segments sampled (since January 1, 2000) where the focal species was detected.
Rare	Ψ: 0.06–0.25	
Uncommon	Ψ: 0.26–0.50	
Common	Ψ: >0.50	
Naïve Occupancy Trend (%), continuous with discrete states		
Relatively stable	Trend: Growth or <5% decline	Percentage change in naïve occupancy (occupied segments/total segments sampled) within a management unit between historical (before January 1, 2000) and recent (since January 1, 2000) time periods. Calculation: ([recent Ψ − historical Ψ]/historical Ψ) × 100.
Moderate decline	Trend: 5%–30% decline	
Strong decline	Trend: >30% decline	
Occupied Segments (count), continuous with discrete states		
One	Occupied segments: 1	Number of occupied stream segments within a management unit regardless of time period.
Rare	Occupied segments: 2–5	
Many	Occupied segments: >5	
Qualitative Abundance (count), continuous with discrete states		
Rare	Abundance: <10 individuals	Maximum number of individuals captured in a segment within a management unit on a single date.
Uncommon	Abundance: 10–75 individuals	
Abundant	Abundance: >75 individuals	
Years Since Last Encounter (years), continuous with discrete states		
Recent	Last encounter: <10 years	Number of years since a focal species was last captured within a management unit.
Moderate	Last encounter: 10–30 years	
Historical	Last encounter: >30 years	
Hybridization, nominal discrete states		
Yes	Evidence of hybridization	Presence or absence of hybridization involving a species within a management unit.
No	No evidence of hybridization	
Nonnative Species (count), continuous with discrete states		
Absent	No known nonnative species	Richness of nonnative fishes in a management unit.
Few	Nonnative richness: 1–5 species	
Many	Nonnative richness: >5 species	

Population Resiliency is also influenced by *Population Strength*, which is informed using recent *Naïve Occupancy* (proportion of sampled segments where the species was detected), number of years since last encountered within a management unit (i.e., *Years Since Last Encounter*), and percentage change in naïve occupancy among segments before and since January 1, 2000 (i.e., *Naïve Occupancy Trend*). We also included the maximum abundance reported during any unique sampling event (i.e., same segment on the same date) reported within a management unit as a qualitative index of abundance (i.e., *Qualitative Abundance*).

Individual Population Resiliency could be influenced by threats not immediately reflected in distributional and demographic changes such as realized or potential influences of nonnative species. In the *Other Threats* node, we included the combined deleterious effects of *Hybridization* (i.e., documented presence of hybrids involving the species) and *Nonnative Species* (i.e., nonnative fish richness) detected within a management unit (Table 1). These threats were factors imperiling multiple southeastern U.S. species listed recently as Endangered under the ESA (e.g., Barrens Topminnow, *Fundulus julisia*, Ennen et al., 2021; Candy Darter, *Etheostoma osburni*, Dunn &

Angermeier, 2019). The Other Threats node could be adapted to reflect alternative species-specific threats or habitat conditions (e.g., stream warming, land-use change, and water quality; Noss et al., 2021) or to explicitly accommodate threats outlined by policy (e.g., Five Factors under ESA; Shirey et al., 2022).

After combining Local Distribution, Population Strength, and Other Threats, each management unit will have an Individual Population Resiliency with predicted probabilities of having "adequate" or "inadequate" resiliency. Individual Population Resiliency nodes are averaged to scale risks of individual management units to an overall estimate of *Ecological Setting Resiliency* within each ecological setting.

Redundancy

Redundancy within each ecological setting is estimated using the number and distribution of populations (i.e., HUC10 management units) and metrics for potential meta-population connectivity among management units (Table 2). Redundancy can be considered high when the risk of irreplaceable loss is spread among

T A B L E 2 Parent nodes and discrete states influencing Redundancy nodes used to convert the initial influence diagram into a Bayesian belief network.

State	Definition	Justification
Network Connectivity (%), continuous with discrete states		
Low	Connected populations <25%	Percentage of shortest path connections among populations (management units) uninterrupted by barriers. Population (N) pairwise connections $= N!/(2\,(N{-}2)!)$.
Moderate	Connected populations: 25%–75%	
High	Connected populations: >75%	
Population Isolation (km), continuous with discrete states		
Near	Separated by <15 km	Mean shortest-path distance (km) to the nearest management unit for each management unit in an ecological setting.
Moderate	Separated by 15–50 km	
Far	Separated by >50 km	
Ranging Movements, continuous with discrete states		
Short	Local movements: <5.0 km	Home-range size of adults or observed movement data of adults from empirical research on focal or surrogate species and/or expert elicitation.
Moderate	Ranging movements: >5.0 km	
Long	Migration across discrete habitats	
Proportion Extant, continuous with discrete states		
Low	<0.34	Proportion of known historically occupied management units with naïve occupancy >0.05 since January 1, 2000.
Moderate	0.34–0.67	
High	>0.67	
Extant Populations (count), continuous with discrete states		
Few	0–1 management units	Number of management units with naive occupancy >0.05 since January 1, 2000.
Moderate	2–5 management units	
Many	>5 management units	

multiple resilient populations within each ecological setting (Redford et al., 2011; Wolf et al., 2015). The model characterizes population replication with *Extant Populations* and *Proportion Extant* nodes, which are the sum and proportion of management units with naïve occupancy >0.05 since year 2000, respectively. Hence, this version of the model assumes populations in management units are potentially extirpated where recent naive occupancy is very low or zero, and therefore, these management units do not contribute to redundancy. However, this threshold for recent naïve occupancy could be modified if (1) practitioners have recent evidence demonstrating a population is extant or (2) populations within management units still contribute to redundancy within ecological settings despite having very low naïve occupancy.

High connectivity among populations will facilitate recolonization of extirpated populations, whereas isolated populations have higher risk of permanent extirpation (Perkin et al., 2015; Steen & Barrett, 2015). We represented *Population Connectivity* with three parent nodes: *Ranging Movements*, *Population Isolation*, and *Network Connectivity* (Table 2). Species with broad home ranges are likely better dispersers capable of maintaining population connectivity under natural settings. Therefore, we incorporated the Ranging Movements node based on the literature-reported home-range size of a focal or surrogate species. The model characterizes Population Isolation among populations within ecological settings as the mean fluvial distance of each management unit to the closest occupied segment in a different management unit within the same ecological setting. Stream fragmentation may further isolate populations that were formerly connected, rendering populations more vulnerable to future decline and extirpation (Gido et al., 2016; Perkin et al., 2015); therefore, we characterized potential for population connectivity as the proportion of river network watercourse connections among management units that are uninterrupted by barriers within an ecological setting (i.e., Network Connectivity). We considered pairwise watercourse connections between two management units to be interrupted if the intervening flow path encountered an on-network barrier georeferenced by the Southeastern Aquatic Habitat Partnership (SARP, 2020).

Species vulnerability

The Species Vulnerability node estimates the predisposition of a species to extirpation (Table 3). Parent nodes of Species Vulnerability were informed by reported correlates of imperilment from studies set mainly in the southeastern United States (e.g., Angermeier, 1995; Burkhead

et al., 1997; Kominoski et al., 2018; Pritt & Frimpong, 2010). We qualitatively classified a species into one *Life-History Strategy* among three possible *life-history strategies* ("equilibrium," "opportunistic," and "periodic") based on its or a surrogate's literature-reported generation time, juvenile survival, and fecundity (Winemiller, 2005). Anthropogenic influences generally simplify freshwater ecosystems, thereby favoring species that thrive in stable environments by investing heavily in juvenile survival (i.e., equilibrium strategy; Mims & Olden, 2012). In contrast, riverine species exhibiting periodic and opportunistic strategies are often affected by anthropogenically reduced ecosystem variability. Imperilment vulnerability is also related to the *Maximum Length* of adults; large-bodied species (total length >500 mm) with slower intrinsic population growth (Parent & Schriml, 1995; Zhang et al., 2015) often require connected, wide-ranging habitats to complete their life cycles and are slow to recover from overexploitation making them more prone to imperilment (Winemiller, 2005). At the other extreme, small-bodied species (total length <250 mm) with limited dispersal potential are also at higher risk of imperilment (Angermeier, 1995; Burkhead et al., 1997; Kopf et al., 2017), rendering medium-bodied species least susceptible to imperilment (250–500 mm; Olden et al., 2008; Reynolds et al., 2005).

The interior *Resource Specialization* node integrates elevated imperilment risks associated with specialized resource needs for foraging and reproduction (Pritt & Frimpong, 2010). Species that feed at higher and narrower trophic levels (obligate invertivores and piscivores) are sensitive to food-web disruptions at lower trophic levels (*Adult Feeding Guild*; Olden et al., 2008; Scott & Helfman, 2001). Further, specialized species that feed and/or spawn among stream substrate (*Benthic-Dependency*; Angermeier, 1995; Midway et al., 2015) and fluvial-dependent species that are extirpated by river impounding (*Lotic Dependency*) are prone to imperilment, especially in regions with few natural lentic waterbodies (Kominoski et al., 2018; Reynolds et al., 2005). Finally, fishes with prolonged drift-dependent early life stages that are vulnerable to river fragmentation and drying are at increased risk of extirpation compared to species with non-drifting early life stages (i.e., *Drift-Dependency*; Perkin et al., 2015).

Representation

The broad distribution of resilient populations protects unique genetic diversity, thereby maintaining future adaptive potential (Carroll et al., 2010; Redford et al., 2011; Wolf et al., 2015). Within the three R's framework,

TABLE 3 Parent nodes and discrete states influencing Species Vulnerability used to convert the initial influence diagram into a Bayesian belief network.

State	Definition	Justification
Drift-Dependency, nominal discrete states		
Drift-dependent	Spawning is dependent upon unfragmented river due to drift-dependent early life stages.	Pelagic spawning fishes are more susceptible to local extirpation in areas with low stream connectivity (Perkin et al., 2015).
Other	Other spawning modes that do not require extensive drift distances.	
Adult Feeding Guild, nominal discrete states		
Piscivore	Diet: primarily fish prey	The trophic level at which adults predominately feed may influence imperilment risk; species that feed at higher and narrower trophic levels are more prone to imperilment (Olden et al., 2008; Zhang et al., 2015).
Invertivore	Diet: primarily invertebrate prey	
Other	Diet: primarily feeds at lower trophic levels (e.g., algae, vegetation, and detritus)	
Maximum Length (mm), continuous with discrete states		
Small	Total length: <250 mm	Medium-sized species are less vulnerable to extirpation (Angermeier, 1995; Freeman et al., 2005; Olden et al., 2007; Zhang et al., 2015)
Medium	Total length: 250–500 mm	
Large	Total length: >500 mm	
Benthic-Dependency, nominal discrete states		
Non-benthic	No obligate benthic foraging or spawning	Species with benthic-dependent life stages are more vulnerable to extirpation (Angermeier, 1995; Burkhead et al., 1997; Midway et al., 2015).
Partially benthic	Obligate benthic spawning or foraging	
Fully benthic	Obligate benthic spawning and foraging	
Lotic Dependency, nominal discrete states		
Lotic	Obligate or prefers lotic streams and rivers	Lotic species are extirpated due to impounding and large-scale water infrastructure (Freeman et al., 2005; Kominoski et al., 2018).
Lentic	Prefers lentic waterbodies	
Life-History Strategy, nominal discrete states		
Opportunistic	Species has short life span, small clutch sizes, short generation times, and low investment per offspring. Adapted to variable environmental conditions.	Life-history strategies characterize relationships among juvenile survival, generation time, and fecundity, which provide a general means to predict whether a species has high or low demographic resilience (Winemiller, 2005). Equilibrium life-history strategies generally have lower imperilment risk by benefitting from anthropogenic environmental alterations that reduce ecosystem variability (Mims & Olden, 2012).
Periodic	Species has long life span, large clutch sizes, long generation times, and low investment per offspring. Adapted to moderately dynamic and seasonal changes to environmental conditions.	
Equilibrium	Species has variable life span, small clutch sizes, moderate to long generation times, and high investment per offspring. Adapted to stable environmental conditions.	

ecological settings delineate unique genetic, ecological, behavioral, and environmental diversity. Each ecological setting has nodes for Ecological Setting Resiliency, Redundancy, and Species Vulnerability, which combine to influence the probability of a species being in an "at-risk" state of extirpation within the node *Extirpation Risk* (Figure 2). Thus, the configuration of peripheral nodes within the Bayesian belief network will vary depending on numbers of ecological settings and management units, but core relationships among resiliency,

redundancy, and vulnerability are universal. A taxon with low risks of extirpation across ecological settings has high representation. Finally, Extirpation Risk nodes for each ecological setting combine to collectively predict the probability of being in an "at-risk" state within the Global Imperilment Risk node. Below, we highlight procedures needed to apply a version of the risk-assessment model to a data-deficient species petitioned to be listed as Threatened or Endangered under the ESA.

Case study of Piebald Madtom

Piebald Madtom is a small-bodied catfish endemic to the southeastern United States. This species' data deficiency, rarity, and vulnerable traits make it an instructive case study. Moreover, our familiarity with this species provided real-time feedback on model behavior during model development. Both our risk-assessment model and Species Status Assessments under the ESA are grounded in the three R's framework. However, we caution that this case study uses preliminary data and information available before Piebald Madtom's Species Status Assessment. Therefore, presented results may vary from eventual findings of the Species Status Assessment of Piebald Madtom.

Implementing this imperilment risk model within a Bayesian belief network requires 15 steps organized into four general phases: (1) data solicitation, (2) model development, (3) compiling and informing nodes, and (4) implementation and revision. We overview each phase within the context of Piebald Madtom's case study, but we provide expanded discussion of each step within Appendix S1. We consulted an expert panel of state agency, university, and U.S. Fish and Wildlife Service personnel to implement the model for Piebald Madtom.

Distribution and population strength

Piebald Madtom is restricted to eastern tributaries of the Mississippi River in western Tennessee and Mississippi. Records exist in six river systems: Obion, Big Black, Hatchie, Loosahatchie, Yazoo, and Wolf (Thomas & Burr, 2004). A single specimen was collected in the Mississippi River in 1976; however, this individual likely originated from the nearby Hatchie River (Thomas & Burr, 2004). Only populations in the Obion, Hatchie, and Wolf river systems are considered stable (Johansen et al., 2017). Twenty-one known populations exist worldwide, geographically defined here as unique HUC10 management units, and despite dedicated sampling for more than four decades, many populations are known from only a single stream segment (Appendix S2: Table S1). Individuals have been collected by a variety of sampling methods (i.e., backpack electrofishing, seining, and dip-netting), but little historical data exist on catch per unit effort by gear (Wagner et al., 2019). The most individuals collected during a single sampling event was nine, which was in the Hatchie-Wolf ecological setting. The species has a relatively small and disjunct distribution, exists in naturally low numbers, and is susceptible to habitat degradation that is occurring throughout its range (Thomas & Burr, 2004).

Justification and primary threats

Piebald Madtom is rare throughout its narrow geographical range, and recent sampling efforts suggest that the species has declined since its description (Johansen et al., 2017; Thomas & Burr, 2004; Wagner et al., 2019). Piebald Madtom is particularly sensitive to stream channelization that reduces stream complexity, and to agricultural and forestry practices that degrade riparian areas, reduce woody cover habitats, and increase fine sediment (Johansen et al., 2017). Only the upper Hatchie River system remains relatively undisturbed and has intact riparian bottomland forests that provide woody and organic inputs along a meandering channel. Piebald Madtom populations are presumably being maintained in other highly eroded lower river reaches by recruitment in the upstream reaches (Thomas & Burr, 2004).

Phase 1: Data solicitation

Data were obtained from state agencies (Mississippi Department of Wildlife, Fisheries, and Parks; Tennessee Wildlife Resources Agency) and institutional researchers at Austin Peay State University, University of Southern Mississippi, and University of Mississippi. All sampling data were taken from targeted Piebald Madtom monitoring efforts and include samples where Piebald Madtom were not detected. The collective database represents all targeted sampling efforts in areas with historical Piebald Madtom records before 2021 (100 occurrences spanning 49 unique stream segments; Figure 4). Additional fish sampling data from management units historically occupied by Piebald Madtom were used to enumerate nonnative fish species' richness within each management unit to inform the Other Threats node. Nonnative fish richness within management units was generally low (0–4 species), and there was no evidence of hybridization with other madtom catfishes.

Phase 2: Develop the imperilment-risk assessment model structure

Due to an absence of range-wide genetic data on Piebald Madtom to delineate representative ecological settings, we characterized representative settings by soliciting input from five experts with extensive experience with Piebald Madtom sampling and natural history from state agencies (TN, KY, and MS; Figure 4). We sent a confidential Google Form document to each expert independently to identify the number and distribution of unique ecological settings where Piebald Madtom occurred historically.
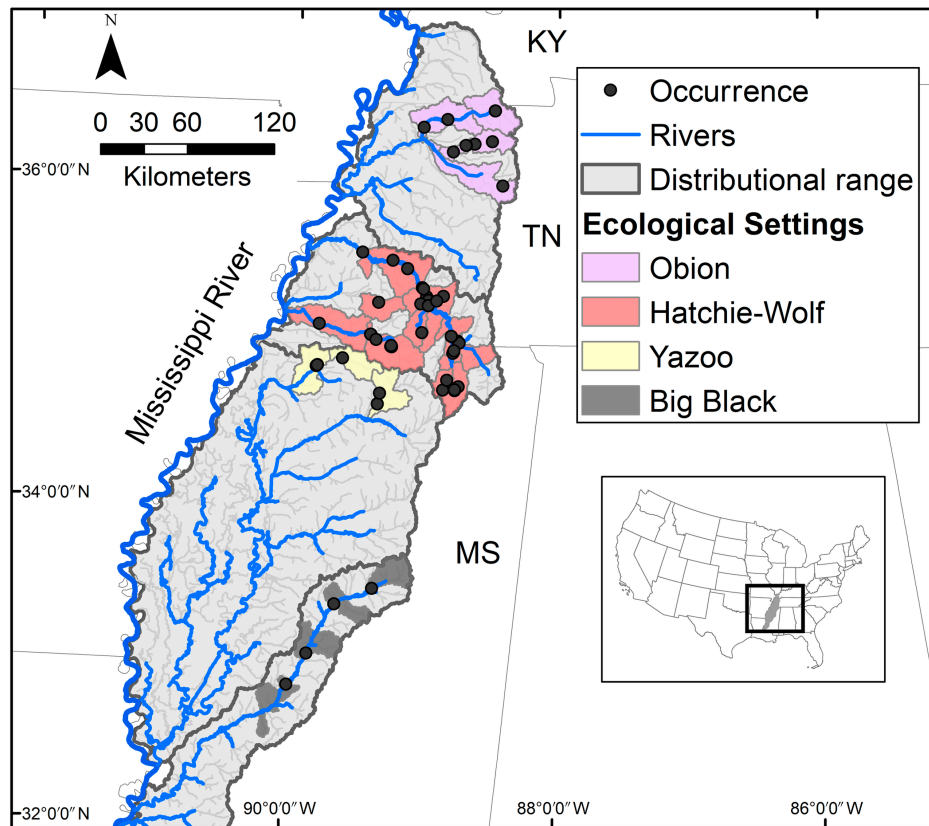
FIGURE 4 Documented occurrences of Piebald Madtom (*Noturus gladiator*) in western TN and MS (USA; $N = 100$ occurrences between 1954 and 2020 spanning 49 unique stream segments). Piebald Madtom subject-matter experts identified four ecological settings representing unique geographical variation among population groups. Shapefile data sources: stream networks (National Hydrography Dataset version 2), state boundaries (U.S. Census Bureau), and watershed boundaries (U.S. Geological Survey Watershed Boundary Dataset).

We presented four plausible options for delineating ecological settings to experts to consider and included an "other" option if none of the presented options were agreeable. Four of the five experts participated by selecting and providing a short justification for the distribution most representative of Piebald Madtom ecological settings. We addressed disagreements using short follow-up discussions. Experts deemed that the six river systems that historically supported Piebald Madtom consisted of four unique ecological settings (Big Black, Hatchie-Wolf, Obion, and Yazoo; Figure 4). However, ongoing genetic research may alter our perception of Piebald Madtom representative ecological settings.

Predicted probability of being at risk of imperilment within the Global Imperilment Risk node is conditional on extirpation risks within individual ecological settings. The conditional probability table that governs probabilities of the states "at risk" and "secure" within the Global Imperilment Risk node was parametrized a priori to give equal weight to each ecological setting's extirpation risk. For example, the Extirpation Risk node for each ecological setting also has two states: "at risk" or "secure."

Given there are four ecological settings (N) contributing to the Global Imperilment Risk node, there are 16 combinations of ecological setting states (2^N) to parameterize within the conditional probability table of the Global Imperilment Risk node. When assuming each ecological setting contributes equally to Global Imperilment Risk and if only one of four ecological settings exists in the "at-risk" state of extirpation, then the a priori parameterized conditional probabilities of being in states of "at risk" and "secure" within Global Imperilment Risk would be 0.25 and 0.75, respectively. Next, we included model nodes for Redundancy, Ecological Setting Resiliency, and Species Vulnerability for each ecological setting.

We included an Individual Population Resiliency node with constituent parent nodes for each of the 21 currently or historically occupied management units (Appendix S2: Table S2). Conditional probability tables for all Ecological Setting Resiliency nodes were parameterized so that the population within each management unit contributes equally to Ecological Setting Resiliency within each ecological setting. All ecological settings had

multiple management units (Figure 4): 4 (Big Black), 10 (Hatchie-Wolf), 4 (Obion), and 3 (Yazoo).

Phase 3: Compile the Bayesian belief network and inform nodes

Recent and historical sampling data were used to inform parent nodes that contribute to Individual Population Resiliency nodes for each management unit (Appendix S2: Tables S2 and S3). Piebald Madtom has been detected in all four ecological settings since 2000 but in only 14 of 18 (78%) sampled management units, and the average naive occupancy within sampled management units declined slightly between management units sampled before and since 2000 (−11.5%).

No sampling has occurred within three management units since 2000, creating uncertainty in the true states for the parent nodes Occupied Stream Length, Naïve Occupancy, Naïve Occupancy Trend, Extant Populations, and Proportion of Extant populations. Therefore, we propagated this uncertainty throughout the Bayesian belief network by apportioning equal prior probabilities among plausible states within these nodes. For example, in the Big Black ecological setting, only two of four management units had been sampled since 2000, confirming at least one population is extant. Sampling effort was low in the other sampled management unit, and two management units had not been sampled at all, rendering uncertainty about the number of management units with persistent populations. Accordingly, we assigned even prior probabilities (Pr = 0.50) to the states "few" (= 0–1 extant populations) and "moderate" (= 2–5 extant populations) within the Extant Populations node because either state was equally likely while specifying there was no probability (Pr = 0.0) of the Big Black setting having "many" (>5) extant populations.

Redundancy nodes were mainly informed using species' distributional data across 49 occupied unique stream segments. There were 569 on-network barriers within management units; however, most barriers occurred within smaller, peripheral streams rather than mainstem corridors connecting management units. For example, the Big Black and Obion ecological settings had 100% barrier-free connections among management units. In contrast, only 64.4% and 33.3% of management units had intervening barrier-free connections in the Hatchie-Wolf and Yazoo ecological settings, respectively (Appendix S2: Table S3).

Parent nodes of the Species Vulnerability node were informed using available literature for Piebald Madtom, open-source web resources (FishTraits, Frimpong & Angermeier, 2009; Fishbase.org, Froese & Pauly, 2021),

and inferred from its sister species, Northern Madtom (*N. stigmosus*). Piebald Madtom has some vulnerable traits that predispose it to imperilment risk including small body size (vs. medium), benthic foraging and spawning dependencies, and reliance on lotic systems (Ross, 2001). However, Piebald Madtom exhibits an equilibrium life-history strategy that is generally more resistant to imperilment and does not have a prolonged drift-dependent early life stage. Altogether, Piebald Madtom is slightly more "vulnerable" (Pr = 0.59) than "resistant" (Pr = 0.41). Conditional probability tables for interior child nodes within the Bayesian belief network for Piebald Madtom are in Appendix S3: Tables S1–S11.

Phase 4: Implement and revise the model

Globally, the probability of Piebald Madtom being in an "at-risk" state of imperilment has been predicted to be 0.51, revealing considerable uncertainty in estimates due partly to distributional data gaps from insufficient sampling. The probability that Piebald Madtom occurs in the "at-risk" state of extirpation varies considerably among the four ecological settings (Figure 5). Populations within southernmost ecological settings had higher probabilities of being at risk of extirpation (Big Black, Pr = 0.71, Yazoo, Pr = 0.51) than populations in more northern ecological settings (Hatchie-Wolf, Pr = 0.40; Obion, Pr = 0.41; Table 4; Figure 5). Altogether, 11 of 21 management units were predicted to have "adequate" Individual Population Resiliency (Pr >0.50). Only the Obion ecological setting had all management units with "adequate" Individual Population Resiliency, while the Big Black was the only ecological setting without any management units with "adequate" Individual Population Resiliency.

The particularly high probability of being at risk of extirpation in the Big Black ecological setting was driven by both low probabilities of "adequate" Ecological Setting Resiliency (Pr = 0.35) and Redundancy (Pr = 0.25; Table 4). However, the lack of recent sampling within two management units within the Big Black ecological setting created considerable uncertainty in Redundancy because the number of extant populations could range from one (no redundancy) to three (2 redundant populations). Using targeted sensitivity analysis, we can reveal that if sampling confirmed Piebald Madtom persists within these two unsampled management units, estimated Redundancy would increase (Pr, "adequate" = 0.67 from 0.25), thereby lowering estimated Big Black Extirpation Risk (Pr, "at risk" = 0.41 from 0.71) and Global Imperilment Risk (Pr, "at risk" = 0.46 from 0.51).

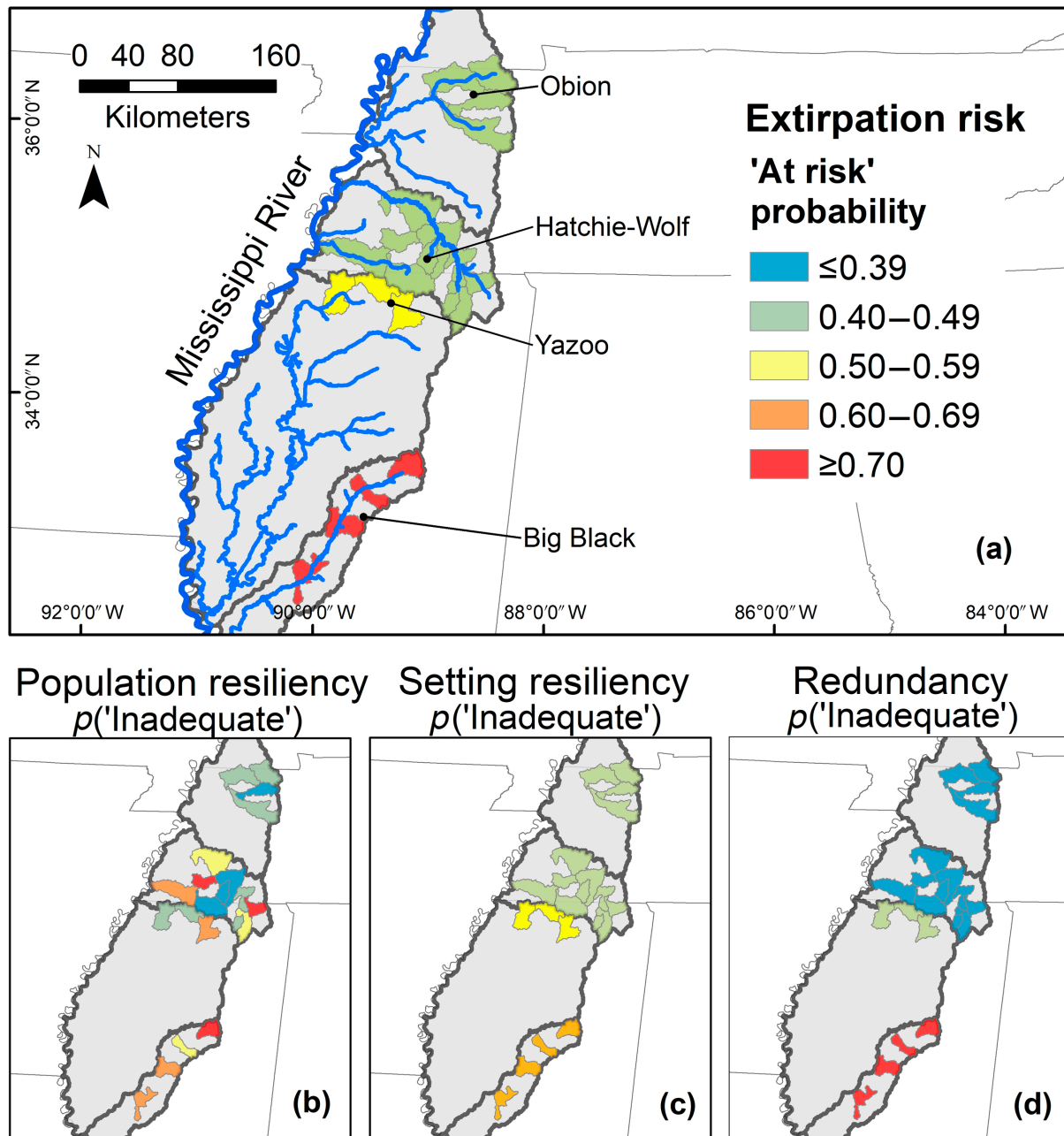Overall, Piebald Madtom is likely at risk of extirpation in portions of its range based on modeled data, but

FIGURE 5 (a) Probability of Piebald Madtom (*Noturus gladiator*) populations within each ecological setting being in an "at-risk" state of extirpation. (b) Probability of the population within each management unit (*N* = 21 units) having "inadequate" Population Resiliency. (c) Probability of an ecological setting having "inadequate" Ecological Setting Resiliency. (d) Probability of ecological settings having "inadequate" Redundancy. Shapefile data sources: stream networks (National Hydrography Dataset version 2), state boundaries (U.S. Census Bureau), and watershed boundaries (U.S. Geological Survey Watershed Boundary Dataset).

TABLE 4 Predicted probabilities of Piebald Madtom (*Noturus gladiator*) in eastern tributaries of the lower Mississippi River in western Mississippi and Tennessee, USA, having "adequate" Ecological Setting Resiliency and Redundancy, and being "at risk" of extirpation by ecological setting.

Ecological setting	Setting resiliency *p*(adequate)	Redundancy *p*(adequate)	Extirpation risk *p*(at risk)
Obion	0.60	0.67	0.41
Hatchie-Wolf	0.52	0.78	0.40
Yazoo	0.50	0.56	0.51
Big Black	0.35	0.25	0.71

there is high uncertainty regarding whether this species exists in an at-risk state of Global Imperilment based on available data. A lack of recent targeted sampling in specific management units contributes to this uncertainty. Further, sensitivity analyses within the model could help prioritize future conservation efforts. Although Yazoo and Hatchie-Wolf ecological settings have lower probabilities of being at risk of extirpation, probabilities of "adequate" population resiliency of individual management units range widely (Hatchie-Wolf, Pr = 0.29–0.78; Yazoo, Pr = 0.39–0.57), indicating local management actions aimed at specific management units could be necessary even in ecological settings with lower risks of extirpation.

DISCUSSION

Management agencies require robust and transparent approaches for prioritizing limited conservation resources for geographic areas, species, and populations in greatest need of conservation (Joseph et al., 2009; Steen & Barrett, 2015; Taylor et al., 2011). Although interest in rigorous quantitative conservation prioritization frameworks has grown in recent years (Brehm et al., 2010; Game et al., 2013; Gauthier et al., 2010), many conservation status assessments still rely heavily on standardized abundance data that are rarely available for data-deficient species, and unstructured input from subject-matter experts (Allendorf et al., 1997). To help minimize biodiversity loss, we provide a quantitative approach that integrates disparate information sources amenable to evaluating imperilment of data-deficient species within the three R's framework.

This risk-assessment tool enables interpretation of various biological indicators of imperilment risk to inform conservation status decisions defensibly, transparently, and repeatably. This model is flexible enough to include a suite of possible information sources including expert judgment in the absence of quantitative data. By clearly stating steps used to assess imperilment risk, this model facilitates the explicit examination of conservation principles, reveals knowledge gaps and uncertainty, and increases the potential for engagement and participation, which can further improve the decision-making process (Joseph et al., 2009). Moreover, the Bayesian belief network provides a platform for quickly evaluating sensitivities of each component within the three R's framework to alternative potential decisions such as conducting research (e.g., determining unknown life-history information), monitoring in under-surveyed areas, and implementing management actions (e.g., barrier removals and reintroductions).

Insufficiently detailed biological and distributional information often restricts utility of prioritization and assessment tools (Coates & Atkins, 2001; Dulvy et al., 2014; Zhang et al., 2015). Without explicit methods to represent uncertainty, understudied species have been historically excluded from conservation status assessments (Bland et al., 2015; Coates & Atkins, 2001; Martín-López et al., 2011). By integrating many different potential measures of distribution and population strength with life-history data while accounting for uncertainty, this tool provides a method to evaluate rare and poorly understood species in need of conservation.

The Species Vulnerability node enables the risk-assessment model to draw from a rich literature base on traits that predispose species to imperilment. This node complements spatially informed nodes of Resiliency and Redundancy by allowing traits to further mediate imperilment risk. This traits-based approach is likely especially valuable in species-rich regions with high levels of endemism where little might be known about an individual species but where there might be several studies on ecologically similar or taxonomically related species within the region. For example, specific natural history information for Piebald Madtom is limited to descriptive accounts (e.g., Ross, 2001) and small-scale studies (Thomas & Burr, 2004; Wagner & Roberts, 2020), but we drew additional information from closely related madtom catfishes (*Noturus* spp.) and broader patterns of imperilment across the biologically rich southeastern United States where imperilment is often correlated with small body size (Angermeier, 1995; Freeman et al., 2005), benthic specialization (Angermeier, 1995; Burkhead et al., 1997; Midway et al., 2015), and lotic dependency (Freeman et al., 2005; Kominoski et al., 2018). This ability to harness knowledge from strength in numbers also diversifies information sources beyond non-standardized distributional collections, which typically have high uncertainty given that dedicated survey effort is often low for non-game freshwater taxa (Fitzgerald, Henderson, et al., 2021).

The hierarchal structuring of the model enables predicting resiliency and redundancy for each ecological setting separately before combining predictions from ecological settings to inform the Global Imperilment Risk terminal node. This capability provides high resolution for practitioners who wish to identify and prioritize specific spatial units that have particularly high risk of imperilment or that disproportionally contribute to uncertainty. For example, within the Piebald Madtom case study, the Hatchie-Wolf ecological setting had relatively high resiliency on average, but several management units within the Hatchie-Wolf setting had low resiliency. Thus, this model could potentially serve as a prescriptive tool for allocating limited management resources. This capability could be especially relevant

for informing conservation decisions in which protected status designations can be given to individual populations and ecological settings (e.g., ESA, Funk et al., 2019). Further, this hierarchy allows predictions to be reaggregated rapidly to align with revised taxonomic classifications as new molecular methods provide greater insight into cryptic species diversity (e.g., Johnson et al., 2018).

An important area of further model development is how to aggregate predictions from fine to coarse spatial units. Here, we aggregated predictions from finer (management units) to coarser spatial units (ecological settings, range-wide) by arithmetically averaging individual risks of finer-grain units. However, practitioners may consider alternative rules such as weighted averaging by population size or area, geometric averaging if trends among management units and settings are correlated, or using predicted extirpation risks of management units as parameters within separate simulation modeling of the extirpation process (McGowan et al., 2020).

This risk-assessment model provides an objective method for informing the likelihood that species are at risk of extirpation within ecological settings and range-wide imperilment. Accordingly, this model could be used as a tool for initial rapid screening of species inventories to identify potentially at-risk species based on available distributional data or as a standardized tool for assigning a formal conservation status. Both applications would require users to adopt explicit risk-tolerance levels, which may vary by the conservation decision context. For example, if the model is used for early detection of at-risk species (e.g., Bland et al., 2015; Pritt & Frimpong, 2010), model users might consider a moderate risk-tolerance threshold for predicted Global Imperilment Risk (e.g., at-risk threshold of Pr >0.50), especially if exceeding this at-risk threshold leads to further data acquisition and investigation to reduce model uncertainty. In contrast, conservation practitioners might be more risk-tolerant if conservation status designations are reserved for species at greatest risk for the purpose of prioritizing limited resources (e.g., at-risk threshold of Pr >0.75). We caution against strictly using predicted risks from this model for conservation status designations that incorporate additional factors unrelated to imperilment risk. For example, predicted risks from this model iteration may not align with designations under the ESA (i.e., *Endangered* and *Threatened*), which are policy decisions that additionally consider socioeconomic impacts of status designations, future threat regimes, and momentum from ongoing conservation actions (Smith et al., 2018). However, pairing standardized modeling approaches with explicit risk-tolerance levels (Cummings et al., 2018) could increase the defensibility of the biological component of ESA and other status designations.

Piebald Madtom is considered here for a case study representative of many data-deficient species in the southeastern United States. However, we caution that our preliminary results should not foreshadow findings within the forthcoming Species Status Assessment of Piebald Madtom under the ESA. We believe after further customization, our model could eventually be used to calculate current imperilment risks—one component of Species Status Assessments—because the model provides a structured quantitative approach for organizing disparate information sources and data types within the three R's framework. Importantly, a Species Status Assessment operates within a broader framework that synthesizes ecological information and considers future threats to species viability in addition to current imperilment risks. Accordingly, calculated risks could change if Piebald Madtom's Species Status Assessment uncovers additional data or ecological knowledge, which could affect the model's inputs, network configuration, and conditional probability tables. For example, additional genetic information on population boundaries may redefine ecological settings, or species experts might identify additional threats that influence species' imperilment risk. Nonetheless, the model is capable of rapidly incorporating these additional sources of information. This ability to incrementally customize the model blends the need for standardization across assessments while providing some flexibility for tailoring assessments to different species and imperilment contexts. Moreover, this flexibility is amenable to subsequent reevaluations of a focal species and allows for incorporating additional information and knowledge through time.

Conservation practitioners who could eventually use the model will continue to be integral to the co-development of this approach. For example, population extirpations are difficult to confirm, creating high uncertainty in the persistence of species within specific management units (Baumsteiger & Moyle, 2017). Therefore, conservation practitioners recommended modifying the Naïve Occupancy node in future model iterations to distinguish between states of extirpation (naïve occupancy = 0.00) and states of extreme landscape rarity ($0.00 <$ naïve occupancy ≤ 0.05). This change would enable incorporating the uncertainty between these two states into the risk assessment by assigning nonzero prior probabilities to each of these two states (e.g., extirpation, Pr = 0.50; extreme rarity, Pr = 0.50). If recent monitoring were to confirm persistence of a population within a management unit, then prior probabilities within the model could be updated to reflect this reduction in uncertainty (e.g., extirpation, Pr = 0.00; extreme rarity, Pr = 1.00).

There are other potential pathways for refining the model depending on model application. For example, if

this model were used to support Species Status Assessments, it would be instructive to ground-truth the model with data from species with existing Species Status Assessments while working with conservation practitioners to refine the model's network architecture and conditional probability tables to better align with ESA requirements. Moreover, the current model does not project imperilment risk under future conditions, so the model would need to be adapted to incorporate risks posed by the numerous threats expected to further jeopardize freshwater species over timescales relevant to the life cycle of a focal species. In future iterations and applications of the model, practitioners might consider using alternative forms of information that could reduce uncertainty among prior probabilities within parent nodes such as employing species distribution models (e.g., Ramirez-Reyes et al., 2021) or expert judgments from formal methods of elicitation (Fitzgerald, Smith, et al., 2021).

While acknowledging the need for further model development and revision, we view this initial model as an important step toward more comprehensively evaluating imperilment risk of aquatic species. We anticipate our model could assist conservation practitioners (1) identify at-risk species as candidates for proactive conservation actions before official government-listing decisions, (2) identify important drivers of imperilment risk and tailor conservation actions in specific settings and watersheds, (3) facilitate greater technical participation among experts, and (4) efficiently identify areas supporting at-risk species (Williams & Johnson, 2015). Both data deficiency and imperilment rates are high among many aquatic groups (Haag & Williams, 2014; Jelks et al., 2008; Johnson et al., 2013; Richman et al., 2015). Tools such as this, which explicitly account for uncertainty and draw from diverse information sources, can help integrate these data-deficient species into priority setting, thereby extending conservation actions to many of the most vulnerable species.

AUTHOR CONTRIBUTIONS
David A. Schumann, Michael E. Colvin, and Kristine Evans secured funding. All authors contributed to conceptual development of project and edited the manuscript. Corey G. Dunn, David A. Schumann, and Michael E. Colvin drafted the manuscript and performed the analyses. Matthew Wagner, David A. Schumann, and Corey G. Dunn curated collection records.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
All model inputs and outputs are disclosed as supplemental material. Specific geolocations of collections for Piebald Madtom are withheld for this sensitive species' protection. Investigators can submit requests for distributional records of Piebald Madtom to database managers at respective U.S. state agencies: Mississippi Department of Wildlife, Fisheries, and Parks (mnhp@mmns.ms.gov) and Tennessee Wildlife Resources Agency (dillon.blankenship@tn.gov, david.withers@tn.gov). All analyses were performed in the software program Netica. Netica is a proprietary software that may be inaccessible to readership, so authors developed a supplemental R script replicating the Netica analysis. Program R code, data, and metadata underwent official reviews and releases per U.S. Geological Survey's Fundamental Science Practices. See data release (Dunn & Colvin, 2023) for model inputs (prior and conditional probabilities), metadata, R code, model outputs, and Netica model: https://doi.org/10.5281/zenodo.10034468.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.