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Temporal analysis of threats causing species endangerment in the United States

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Abstract

Understanding temporal variation of threats that cause species endangerment is a key to understand conservation strategies needed to improve species recovery. We assessed temporal variation in the threats to species listed under the United States Endangered Species Act (ESA) as identified by the United States Fish and Wildlife Service (USFWS) and National Marine Fisheries Service (NMFS). Based on initial review of ESA listing decisions and literature, we identified six overarching threat categories: habitat modification, overutilization, pollution, species–species interaction, demographic stochasticity, and environmental stochasticity. We screened listing decision documents to determine threat occurrence (i.e., presence/absence of a given threat in a listing decision) for each threat category for all species listed between 1975 and 2017. We evaluated how the number of threats and specific threat occurrences changed over the past four decades. We found that the number of threats per listing decision increased more than twofold from an average of 1.5 (95% CI: 1.3–1.7) threats in 1975 to 3.7 (95% CI: 3.4–4.0) threats in 2017. Threat occurrence increased for habitat modification, environmental stochasticity and species–species interaction, while it decreased for overutilization since 1975 and for demographic stochasticity and pollution since the mid-2000s. The documented increase in number of threats at time of listing may be due to a growing human population exerting increased pressure on species persistence, improved scientific advancement in understanding factors influencing species endangerment, or prolonged time taken for more recent species to be listed under the ESA. We believe that key federal and state governmental regulations have resulted in a documented decrease in overutilization, demographic stochasticity, and pollution, and we recommend large-scale strategies combined with local planning efforts to address the growing threats of habitat loss, environmental stochasticity, and species–species interaction.

KEYWORDS
Endangered Species Act, environmental regulations, policy, temporal, threats

Authors after Haines are listed in alphabetical order

1 | INTRODUCTION

A drastic decline of global biodiversity driven by human activity is leading to the sixth mass extinction (Barnosky et al., 2011; Ceballos et al., 2015; Pimm et al., 2014). To slow and reverse species extinction, understanding temporal trends that cause species endangerment is an important first step to identify both effective and ineffective conservation strategies. Species that become threatened with extinction in the United States (U.S.) are listed under the Endangered Species Act (ESA), and their management is turned over to the federal government. This pattern of species protection is similar to other countries, where species extinction prevention requires national governmental intervention (e.g., Canada's Species at Risk Act of 2002, United Kingdom's Wildlife and Countryside Act of 1981, Australia's Endangered Species Protection Act of 1992, and New Zealand's Conservation Act of 1987).

In the United States, the ESA was created to protect and recover imperiled species and the ecosystems upon which they depend (ESA, 1973; Scott, Goble, & Davis, 2006). Any person or agency (governmental or nongovernmental) can petition the U.S. Fish and Wildlife Service (USFWS) or National Marine Fisheries Service (NMFS) to list a species under the ESA (ESA section 4(b)(3)(A)). This initiates a review process, published as a listing decision in the U.S. Federal Register (2017), in which the USFWS or NMFS use a five-factor threat analysis for determining if a species warrants federal protection (ESA sec. 4(a)(1)):

"(a) the present or threatened destruction, modification, or curtailment of its habitat or range;

(b) overutilization for commercial, recreational, scientific, or educational purposes;

(c) disease or predation;

(d) the inadequacy of existing regulatory mechanisms; and.

(e) other natural or manmade factors affecting its continued existence".

If the USFWS or NMFS determine a species to be warranted for protection under the ESA, a species is listed as either endangered, "…in danger of extinction within all or a significant portion of its range…" (ESA sec. 3(6)), or threatened, "…likely to become an endangered species within the foreseeable future…" (ESA sec. 3(20)). Since passage of the ESA and its amendments, the number of U.S. species requiring federal protection (which include distinct population segments "… group of populations that is discrete from other populations of the species and significant in relation to the entire species." [National Oceanic and Atmospheric Administration, 2017]) has grown from 137 between 1967 and 1973 to 1,663 in 2019, with 43 species considered recovered under the ESA (U.S. Fish and Wildlife Service, 2019).

Based on the increasing number of species listed under the ESA and the low rate of recovery, a draft bill is being presented to the U.S. Congress to turn authority of threatened and endangered species management over to the states (Camacho, Robinson-Dorn, Yildiz, & Teegarden, 2017). In the United States, local state agencies are the primary managers of biodiversity. For the last century, however, these state agencies have focused mainly on take regulations for "game" and "sport fish", and have largely ignored the greater biological diversity, that is, nongame species (Evans et al., 2016; Goble & Freyfogle, 2002). In 2005, the Wildlife Conservation and Restoration Program and the State Wildlife Grants Program (SWAPs) was initiated to incentivize states to expand efforts to conserve nongame species, with the purpose of preventing the need to list these species under the ESA (Lerner, Cochran, & Michalak, 2006). However, since passage of these acts, the number of species requiring federal protection continues to increase, albeit not as dramatically as before (Evans et al., 2016), and, in comparison to the ESA, current state laws are inadequate to achieve conservation success and species recovery (Camacho et al., 2017).

It is hard to determine what efforts outside of the ESA are reducing threats to biodiversity, and a lack of basic understanding of the dynamic nature of threats causing species to require federal protection can undermine recovery efforts (Lawler et al., 2002). Past analyses have identified habitat degradation/loss, invasive species, pollution, and transient human disturbances as the biggest threats causing species to become listed under the ESA (Evans et al., 2016; Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998). However, these studies did not quantify the change in these threats over time to identify trends or changes in the nature of pervasive threats. Lessons learned from this type of analysis could help determine which threats are increasingly causing species to become threatened with extinction, and what strategies are needed to address these threats. If managers and policy makers can understand trends in current threats, they can address problems proactively and reduce the need for species listing under the ESA (Gratwicke, Lovejoy, & Wildt, 2012). Also, identification of threats that are declining can help identify successful conservation strategies and polices, which can help inform conservation efforts within and beyond U.S. borders (Langpap, Kerkvliet, & Shogren, 2018).

To understand temporal trends in threats causing species endangerment, we reviewed listing decisions published between 1975 and 2017 by the USFWS and NMFS for species protected under the ESA. The objectives of our study were to (a) quantify the number of threats included in ESA listing decisions between 1975 and 2017 and (b) evaluate variation over time in the probability of a given threat being included in a listing decision. To our knowledge, this is the first evaluation of temporal changes in threat occurrence for U.S. species listed under the ESA as outlined in federal listing documents.

2 | METHODS

2.1 | Threat coding

We searched Final Rule Federal Register listing documents, accessed through the USFWS's Environmental Conservation Online System Database (ECOS; U.S. Fish and Wildlife Service, 2019) and The U.S. Federal Register Database (U.S. Federal Register, 2017), for occurrence of threats to species, which included distinct population segments, at time of listing. We included domestic species in our analyses occurring in the United States and the 16 U.S. territories. Species were systematically divided among authors based on their taxonomic expertise. For each species we coded presence/absence of a given threat category as a binary value (1 = threat category included in listing document; 0 = threat category not included in listing document). From September 2014 through September 2017, authors met weekly via web conferencing and biannually in person to improve standardization of threat coding and evaluate best practices of data collection.

We accessed U.S. Federal Register (2017) documents for 1,732 domestic species from 1967 through 2017 to develop a database of threats. We used the proposed listing documents in cases where final listing documents were unavailable or lacked information on threats to species. We omitted from analyses 132 species listed before 1975 because their listing decisions did not include threat factors. For species listed between 1975 and 2017 (n = 1,600), we did not include 23 species whose listing decisions lacked inclusion of threats, 20 species that were listed but subsequently delisted due to new findings or errors in listing decision, and 8 species that were listed based on their "similarity of appearance" to an already listed species (for list of species see Appendix S1). Overall, we classified threats in listing documents for 1,549 U.S. domestic species.

We defined six overarching threat categories that allowed for standardized comparisons (Appendix S2). These categories were based on our preliminary review of threat factors defined in USFWS and NMFS listing documents, and threats identified by Wilcove et al. (1998) and Evans et al. (2016). Our threat categories included:

1. habitat modification (Factor A in listing decision document, including domesticated animal effects),
2. overutilization (Factor B in listing decision document),
3. pollution (e.g., agriculture and mining runoff, sedimentation, eutrophication),
4. species–species interaction (Factor C in listing decision document; e.g., invasive species, disease, herbivory, predation, hybridization, etc.),
5. demographic stochasticity (Factor E in listing decision document; e.g., Allee effect, geographic and genetic limitations),
6. environmental stochasticity (Factor E in listing decision document; e.g., rising temperatures, intense weather events, climate change, etc.).

We did not include factor D (i.e., "inadequacy of existing regulatory mechanisms") because these regulatory mechanisms did not allow for standardized comparisons.

We identified threats on the basis of key words, of which exemplar key words are listed in Appendix S2. We identified fire as habitat modification if human ignited, otherwise it was specified as a stochastic event. We determined "small" and "isolated populations" to be a demographic stochastic threat only when listed under threat factor "E" in the Federal Register document. Sedimentation, erosion, and dust were determined to be a habitat modification threat when they were associated with human activities such as development, mining and dredging. Sedimentation was considered pollution if it contained herbicides, pesticides, fertilizer, zinc, mercury, sewage, or other chemicals. Sedimentation, erosion, and run-off associated with agricultural activities and roads were also considered pollution. Sedimentation and erosion were both labeled as environmental stochasticity when they were associated with storms, flooding and other random events. When erosion and sedimentation were stated with no association, they were identified as habitat modification. Any negative impacts to listed species caused by dams/reservoirs and dredging were labeled as habitat modification. It is important to note the identification of threats impacting species at time of listing were not always based on robust available biological information, but sometimes on the judgment by an expert (Easter-Pilcher, 1996; Wilcove et al., 1998).

We did not include potential threats in our analysis because these threats had inherent uncertainty that we could not compare or standardize; therefore we focused on actual current threats at time of listing. Threats were considered potential if the listing decision document directly stated them as a potential threat, or if potential language such as "may," "could," "possibly," "perhaps," "would," or "if" preceded the threat. If language such as "planned," "most likely," "probably," "believed," "presumably," and "is" preceded threats, they were included in our database. When a species was classified as "vulnerable," "at risk," or "susceptible" to a given threat, that threat was included in the database.

Threats that historically affected species but were no longer active were not included in our database. If a threat lacked a temporal association, we assumed it was current and therefore included it in the database. If a threat, historic or not, caused a current threat, both were included. If the cause of a threat was not specified (e.g., die offs, turbidity), we did not include the threat in the database.

2.2 | Threat classification agreement

To assess threat classification agreement between observers, we randomly selected 184 species (12% of species) from the total pool of species. Random selection of species was stratified across taxonomic groups (hereafter, taxa) and weighted by total number of species in a given taxa. Threats for randomly selected species were identified by assessment observers who were blind to the initial observer's classifications. Agreement was determined when original and assessment observers concurred that a given threat was either present or absent for a given species. Assessment for each threat category was calculated by dividing the number of species in agreement by the total number of species assigned to a given assessment observer. Observer agreement was calculated by dividing the sum of species in agreement across the six threat categories by the total number of species assessed in all six threat categories. Last, we calculated overall agreement by dividing the sum of species in agreement across the six threat categories and all observers by the total number of threat categories across all selected species (i.e., 184 species multiplied by six threat categories = 1,104; Appendix S3).

2.3 | Statistical analyses

In our statistical analyses, we considered the species pool not as a census but rather as a subset of species from the pool of species that could potentially be listed under the ESA. At the ESA level, we only included 89% of species that were listed due to various reasons outlined above. At the International Union for Conservation of Nature (IUCN) level, Harris et al. (2012) found that for most taxa, approximately 40–80% of species listed by IUCN were not listed under the ESA. Although species were not randomly selected, they represent a subset of species that could be potentially listed under the ESA.

We quantified changes in number of threats impacting a species at time of its listing and occurrence of a given threat in a listing decision between 1975 and 2017. We regressed number of threats, ranging between 0 and 6, impacting a species at time of its listing against year of listing on the basis of count-based models with negative binomial error structure. We chose negative-binomial error structure because mean and variance of number of threats were not equal as required for a Poisson error structure (Zuur, Leno, Walker, Saveliev, & Smith, 2009).

We performed logistic regression analyses to estimate changes in occurrence for a given threat in listing decisions between 1975 and 2017. We estimated the latent variable occurrence for a given threat by relating annual threat presence/absence to year of listing.

In both count and logistic regression models, we modeled lead USFWS geographic region and taxa as random factors on the basis of generalized linear mixed-effect models using the lme4 package (Bates, Machler, Bolker, & Walker, 2015) in R 3.5.0 (R Core Team, 2018). We used mixed-effect models because variation in number of threats and threat occurrence could vary among lead regions, due to geographic and institutional differences (USFWS vs. NMFS), and variation in number of species for each taxa ranging between 2 and 910. We coded the eight USFWS lead regions separately (code = 1–8) and coded NMFS as one region (code = 9). We defined taxa on the basis of the USFWS (ECOS; U.S. Fish and Wildlife Service, 2019) taxa classification: Amphibians (31 species), Arachnids (12 species), Birds (52 species), Clams (69 species), Conifers and Cycads (4 species), Corals (13 species), Crustaceans (28 species), Ferns and Allies (38 species), Fish (139 species), Flowering Plants (910 species), Insects (86 species), Lichens (2 species), Mammals (72 species), Reptiles (40 species), and Snails (53 species). In both models we included a random intercept but no random slopes, as our aim was to make inferences across all, but not individual, taxa. We did not include genera as a random factor because of the high frequency of monotypic genera (62%, 696 genera in total). We also did not include Lichen in the analyses because it contained only two species.

In all models, we centered and scaled differences between year of listing and 1975 (Δ year), and evaluated linear, quadratic ($y = \beta_0 + \beta_1$ [Δ year] + β_2 [Δ year ^{2}]), and log-based pseudo-threshold ($y = \beta_0 + \beta_1 \log_e$ [Δ year +1], Scherer, Muths, & Noon, 2012) associations. We identified the best candidate model on the basis of the information-theoretic approach (Burnham & Anderson, 2002) and graphed models with the lowest Akaike Information Criterion (AIC) values. Unless otherwise stated, we report means and 95% confidence intervals.

3 | RESULTS

For native species listed in the United States under the ESA, we were able to identify threats at listing for 1,547 species. On average, a listed species suffered from 2.93 (95% CI: 2.87–2.99) threats at time of listing. We found that at listing 1,258 species were impacted by habitat loss, 1,026 by demographic stochasticity, 816 by species–species interaction, 722 by environmental stochasticity, 437 by pollution, and 274 by overutilitzation.

3.1 | Threat classification agreement

Overall, threat classification agreement was 88% (Appendix S3). Classification agreement varied among observers ranging between 81 and 100% (average = 89%, *SD* = 7%; Appendix S3). Average agreement across all threat categories was 88% (*SD* = 3%; range 85–93%), with highest agreement for the pollution threat category (93%) and lowest for habitat modification, environmental stochasticity, and demographic stochasticity threat categories (85%). Our threat classification agreement was comparable to other group assessments of U.S. federal documents on listed species (Hoekstra, Clark, Fagan, & Boersma, 2002; >80%).

3.2 | Number of threats

Number of threats per listing decision, ranging between 0 and 6, increased more than twofold from an average of 1.5 (95% CI: 1.3–1.7) threats in 1975 to 3.7 (95% CI: 3.4–4.0) threats in 2017 (Figure 1, Table 1, Appendix S4). The association between threats per listing decision and year was quadratic with number of threats increasing up until 2012 and then slightly decreasing.

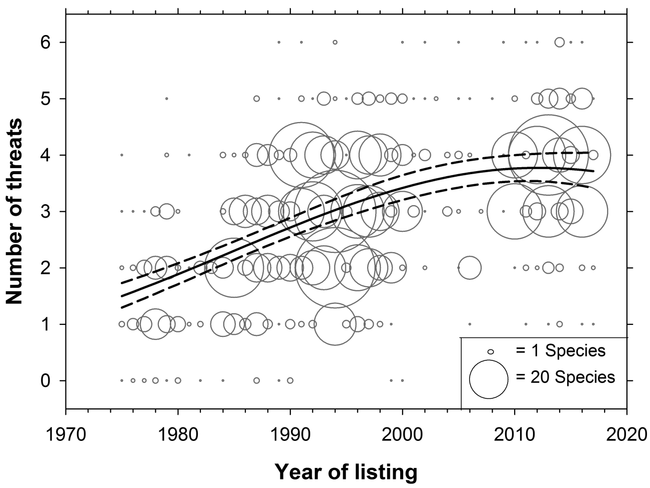

FIGURE 1 Relation (± 95% CI) between numbers of threats documented in a given species' listing decision and year of listing between 1975 and 2017. Association is shown on the basis of scaled and centered year of listing (year of listing—1975), with unscaled years added for illustrative purposes, and back-transformed number of threats. Bubbles represent number of species with the same number of threats at time of listing (range = 1–43 species). For parameter estimates of negative binomial regression analysis see Table 1 and for model selection see Appendix S4

We identified species listed with no current actual threats (i.e., these species were impacted by potential threats, not current threats as defined by our classification, methods are outlined above) between 1975 and 2000 but not thereafter (for list of species see Appendix S5). We also identified species listed with a maximum of six threats post 1989 (for list of species see Appendix S5).

Estimates for the random intercept variance for taxa (*SD* = 0.07) was low, indicating little variation in number of threats attributed to taxa (Table 1). We found sum of squares for lead regions to be 3% of within lead regions sum of squares. Because so little variation was attributable to lead region, all models did not converge when it was included as a random factor. We therefore removed lead region from analyses and only included taxa as a random factor.

3.3 | Changes in threat occurrence

Threat occurrence increased for five of six threats from 1975 to 2017 (Table 1, Figure 2, Appendix S6). The only threat showing a consistent decline in occurrence was overutilization, which decreased linearly, but for the other five threats, change in occurrence differed in effect size and model form (linear vs. nonlinear associations). For two threats, occurrence increased linearly. Occurrence of habitat modification increased gradually, whereas occurrence increased dramatically for environmental stochasticity. For the other three threats, we found a quadratic association between threat occurrence and year of listing. Occurrence peaked for demographic stochasticity in 2003 and for pollution in 2002 but did not reach a peak for species–species interaction (Figure 2).

Ranking of threats differed between 1975 and 2017 (Figure 2). In 1975, we found that the top threat of habitat modification was at least twofold higher in threat occurrence over the next highest threats, overutilization and species–species interaction. The other three threats ranked from highest to lowest included demographic stochasticity, environmental stochasticity, and pollution. In contrast, by 2017 the highest threat occurrence category included habitat modification, environmental stochasticity, and species–species interaction threats, which had threat occurrences at least two to five times higher compared to pollution and overutilization threats, respectively. Threat occurrence for demographic stochasticity was intermediate between the highest and lowest ranking threats.

The estimated variances for the random intercepts in threat occurrence analyses were considerable but not in number of threat analyses (Table 1). Random-intercept variation for taxa differed among threats (range *SD*: 0.26–1.11; Table 1). The *SD* for the pollution threat variation was quadruple that of environmental stochasticity, while

TABLE 1 Variance associated with random factors and parameter estimates for final models relating number of threats and threat occurrence to year of listing for 1,547 species on the basis of negative binomial and logistic mixed-regression models, respectively

		Random factor[a] (*SD*)		β_0			β_1 or β_2		
Analyses	**Variable form**	**Taxa**	**Lead region**	**Estimate**	**LCI**[b]	**UCI**[b]	**Estimate**	**LCI**	**UCI**
Total number of threats[c]	Quadratic	0.07	NA[d]	1.17	1.10	1.23	0.23	0.20	0.27
							−0.08	−0.11	−0.05
Individual threats[e]:									
Habitat modification	Linear	0.70	0.87	2.08	1.32	2.85	0.59	0.42	0.75
Overutilization	Linear	0.73	0.99	−1.27	−2.09	−0.46	−0.20	−0.36	−0.04
Pollution	Quadratic	1.11	0.71	0.21	−0.60	1.03	0.57	0.39	0.75
							−0.59	−0.75	−0.43
Environmental stochasticity	Linear	0.26	0.39	−0.29	−0.66	0.07	1.32	1.16	1.47
Species–species interaction	Quadratic	0.73	0.66	−0.04	−0.70	0.61	0.64	0.51	0.78
							0.14	0.02	0.26
Demographic stochasticity	Quadratic	0.72	0.54	1.10	0.51	1.70	0.63	0.49	0.77
							−0.55	−0.67	−0.42

[a]Random intercept for taxa ($n = 14$) and lead region ($n = 9$).
[b]Lower (LCI) and upper (UCI) confidence interval.
[c]For results of model selection, see Appendix S4.
[d]Model did not converge when lead region was included as random factor, see Results for details.
[e]For results of model selection, see Appendix S6.

overutilization, species–species interaction, and demographic stochasticity had intermediate *SD*s (Table 1). Similarly, random-intercept variation for lead regions also differed among threats (range *SD* 0.39–0.99; Table 1), with overutilization having the highest and environmental stochasticity having the lowest variation.

4 | DISCUSSION

Between 1975 and 2017 the number of threats per ESA listing decision increased more than twofold (Figure 1). The number of native species in the United States impacted by habitat loss at time of listing continues to increase, and in the last 30 years the number of listed species threatened by species–species interaction and environmental stochasticity has exponentially increased (Figure 2). The increasing frequency of these threats over time point to the importance of federal protection for rare species. However, the number of species whose populations are negatively impacted by overutilization has declined steadily over time, and in the last 20 years the number of species threatened by pollution and demographic stochasticity at time of listing has declined (Figure 2), suggesting conservation success outside of the ESA.

We see three potential explanations why recently listed species are facing more threats at time of listing. First, the population size of the United States has increased by nearly 50% from 1975 to 2016 (U.S. Census Bureau, 2017), resulting in increased land use for agriculture, resource extraction, and urban/suburban development (Theobald, 2010) to expand economic development across the United States, adding increased pressure on biodiversity (Czech & Krausman, 1997; Dobson, Bradshaw, & Baker, 1997; Wilcove et al., 1998). Second, our improved understanding of factors influencing species endangerment due to advances in ecological and conservation research can more easily identify threats (Evans et al., 2016). Put in temporal context, the Society for Conservation Biology was established in 1986, more than a decade after the enactment of the ESA. Since then, advances in tracking devices, geographical information systems, computational analyses, molecular techniques, and landscape ecology have all improved understanding of species endangerment (Primack & Sher, 2016). Third, funding for the ESA has not kept pace with species listing (Evans, 2017), and inadequate funding increases time to listing (Puckett, Kesler, & Greenwald, 2016), therefore more recently listed species may have suffered more threats at time of listing due to a more prolonged listing process caused by recent budgetary constraints. We recommend a further detailed analysis looking at 90-day findings, 12-month findings, and proposed listing documents in comparison to final listing decisions to quantify the increase in the number of threats impacting species over time.

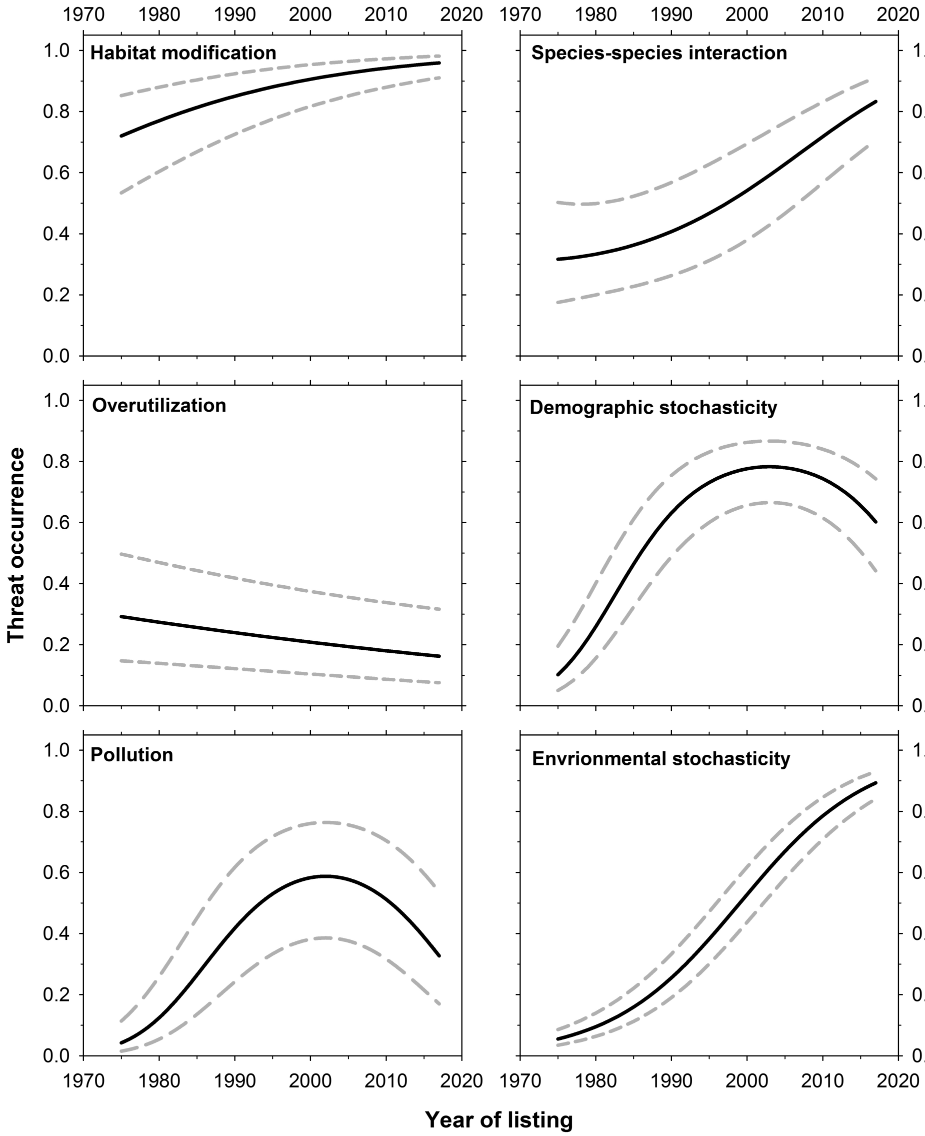

FIGURE 2 Changes (± 95% CI) in threat occurrence for six threats included in listing decisions between 1975 and 2017. Associations are shown on the basis of scaled and centered year of listing (year of listing—1975), with unscaled years added for illustrative purposes, and occurrence (back transformed from logit scale). For parameter estimates of logistic regression analyses see Table 1 and for model selection see Appendix S6

We found that habitat loss continues to be a top threat through time causing species to require federal protection. An extensive body of research also found habitat loss or modification to be a leading threat causing species to require ESA protection (Czech & Krausman, 1997; Dobson et al., 1997; Evans et al., 2016; Wilcove et al., 1998), and several analyses have documented extensive land cover conversion in the United States, as well as globally (Theobald, 2010; Venter et al., 2016). It appears current federal and state regulations are not adequate enough to prevent habitat loss, which may result in species requiring listing under the ESA.

Hatch et al. (2002) found that species found exclusively on federal lands are more likely to be improving than those on mixed or private land. Although nearly 8% of land in the lower 48 states in the United States is protected, based on the IUCN reserve criteria (Categories I–VI; Jenkins, Van Houtan, Pimm, & Sexton, 2015), most protected areas in the western United States overlap with areas of low productivity (Leu, Hanser, & Knick, 2008) and low biodiversity (Scott, Csuti, Jacobi, & Estes, 1987). As a result, most endangered species are found, at least in part, on private lands (Evans et al., 2016; Jenkins et al., 2015). Therefore, more efforts are needed to communicate and work with private landowners to conserve species in the United States to avoid the need for ESA protection. Federal deregulatory incentive programs are provided by the USFWS to help avoid the need for species listing; however, the overall effectiveness of these programs remains uncertain, with many considered time consuming, inaccessible and too complex for private landowners (BenDor, Vitro, & Riggsbee, 2017; Evans et al., 2016). That said, federal deregulatory incentive programs have been effective at preventing species listing for the New England cottontail (*Sylvilagus transitionalis)* (U.S. Fish and Wildlife Service, 2015) and populations of the Greater sage-grouse (*Centrocercus urophasianus*) (Pidot, 2018). These programs require federal officials to work very closely with local agencies, industry, and private landowners in order to be successful (Pidot, 2018). Expanding federal programs to provide tax incentives and relaxed regulations for private landowners that protect and manage for declining species, may help to curb habitat loss to maintain population numbers and avoid listing, especially when coupled with technical advice provided by governmental and nongovernmental agencies such as the Natural Resources Conservation Service or The Nature Conservancy.

While habitat modification was the most common threat included in listing decisions since 1975, we found that environmental stochasticity and species–species interaction joined habitat modification in the tier of most crucial threats to listed species by 2017, with environmental stochasticity emerging as a top threat, mainly in the form of climate change (e.g., rising sea levels, more severe storms, increased drought events etc.). Previous research predicted that species will face increasing threats from global climate change (Evans et al., 2016), and from rising numbers of exotic species (Hellmann, Byers, Bierwagen, & Dukes, 2008; Wilcove et al., 1998). In addition, the impacts from environmental stochasticity and species–species interaction can be synergistic, with species becoming more susceptible to exotic and invasive species in a changing environment (Freed, Cann, Goff, Kuntz, & Bodner, 2005; Garrett, Dendy, Frank, Rouse, & Travers, 2006). Our results suggest that conservation efforts outside of the ESA are currently not able to deal with these threats.

More efficient recovery efforts must take into consideration future climatic conditions caused by climate change as well as species–species interactions. For example, recent research has provided guidelines on how to integrate climate change into conservation plans (Bernazzani, Bradley, & Opperman, 2012; Evans et al., 2016; Nuňez et al., 2013). These include establishing habitat connectivity (e.g., corridors, stepping stones) to accommodate dispersal and range changes for listed species, restoration of habitat that is sustainable into the future instead of being limited to historical vegetation composition, and increased adaptive management and biological monitoring efforts to evaluate conservation success. These strategies require both national and international scale planning.

Large-scale strategies are also needed to address the threats of species-species interaction. For instance, to address the issue of problem plant species, Weber (2017) developed an exemplar reference guide for global invasive plant species that includes strategies on how best to control these species. The Department of Interior's National Invasive Species Council (www.doi.gov/invasivespecies/) provides national leadership to sustain and expand federal efforts to prevent, eradicate, and control invasive species to restore ecosystems. These efforts include developing models that predict where expansions in problem species geographical ranges will occur based on changing climate conditions, as well as provide the required resources to control problem species. The control of invasive or problem species has been important in the recovery of federally listed species (e.g., Black-capped Vireo [*Vireo atricapilla*], Aleutian Canada Goose [*Branta hutchinsii leucopareia*], Tinian Monarch [*Monarcha takatsukasae*], Eggert's sunflower [*Helianthus eggertii*], island night lizard [*Xantusia riversiana*]; U.S. Fish and Wildlife Service., 2019).

Though the main threats to biodiversity are universal, there may be different degrees of prevalence/effect in specific nations. For example, we found three threats (overutilization, pollution, and demographic stochasticity) that have decreased in occurrence in the U.S. Overutilization occurrence decreased linearly between 1975 and 2017, while pollution occurrence increased up to the 2000s but then decreased (Figure 2). We hypothesize that these findings are attributable to federal and state environmental laws having a positive effect on species populations. In comparison to other countries worldwide, the United States has developed a governance that establishes sustainable harvest regimes for "game" animals and enforcement of "take" regulations to avoid overutilization of biodiversity at the state level. Funding for these state efforts comes from federal taxation of hunting and fishing equipment (Federal Aid in Wildlife Restoration Act of 1937 and Federal Aid in Sport Fish Restoration Act 1950; Decker et al., 2015). Overutilization in the United States is also mitigated by the federal Lacey Act of 1900 which regulates interstate trade of biodiversity. Countries that lack these types of policies and funding resources can suffer high rates of biodiversity loss due to poaching and overharvest (Maxwell, Fuller, Brooks, & Watson, 2016). For pollution, we hypothesize that passage of certain environmental regulations, such as the Clean Air Act and Clean Water Act, have improved conditions for biodiversity. For example, native fish populations steadily increased while those for exotic species decreased in Illinois Rivers as a result of the Clean Water Act (Gibson-Reinemer et al., 2017), and the red spruce forest ecosystem of the Central Appalachian Mountains recovered in response to reduced acidic air pollution since passage of the Clean Air Act (Mathias & Thomas, 2018). A perplexing result of our research is the quadratic association between demographic stochasticity occurrence and year of listing (Figure 2). A possible explanation for the recent decline in demographic stochasticity as a reason for listing may be due to most of the range-restricted species (e.g., arthropods found in caves, fish in small pools, amphibians in small underwater caves etc.), which suffer most from demographic stochasticity, being listed before the mid-2000s. We are currently conducting a finer-scale analysis of threats associated with specific taxa to explain changes in threat occurrence over time to validate this hypothesis.

Another potential explanation for the recent reduction of threats from pollution and demographic stochasticity since the 2000s is the passage of the 2005 Wildlife Conservation and Restoration and implementation of SWAPs. Evans et al. (2016) stated that only a few states use funds from these programs to conserve species at risk of extinction, while many still focus their efforts on "game" and "sport fish" and other charismatic species. In spite of this criticism, many states do use funding from this program to support nongame biologists to focus on biodiversity protection. Further funding for state agencies, such as the proposed Recovering America's Wildlife Act (H.R. 4647), coupled with federal oversight on funding, could provide states the ability to reduce threats to declining species so they can avoid listing under the ESA.

Although we focused on imperiled species in the United States, our analysis can provide insight to implementing conservation strategies and regulations internationally. Many nations around the globe have implemented federal policies to protect imperiled species (e.g., Canada's Species At Risk Act of 2002, United Kingdom's Wildlife and Countryside Act of 1981, Australia's Endangered Species Protection Act of 1992, and New Zealand's Conservation Act of 1987). Globally, the ESA is considered one of the most powerful environmental laws to prevent the loss of biodiversity (Gerber et al., 2018; Malcom & Li, 2018). Species that face threats from habitat loss, species–species interaction and environmental stochasticity (especially with regard to climate change) depend on protections from the ESA and require large-scale conservation efforts at both the national and international level. Outside the ESA, effective national polices, such as the Clean Water and Lacey Acts, can address threats from pollution and overutilization. In addition, when national policy is coupled with local conservation efforts, such as support of state agencies through taxation, private landowner deregulatory incentive programs and SWAPs, threats to biodiversity (e.g., habitat loss and overutilization) can be better addressed to prevent species decline and listing under the ESA.

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CONFLICT OF INTEREST

None of the authors will obtain any direct financial benefits from this paper and authors declare no potential conflict of interest.

AUTHOR CONTRIBUTION

The ideas for this paper were developed by all authors. Data collection was conducted by all authors. M.L. and A.M.H performed statistical analyses. Paper was written mainly by M.L., A.M.H., and D.M.C., but all authors contributed to editing sections.

DATA ACCESSIBILITY

Data and R code are available on GitHub (https://github.com/matthiasleu/Leu-et-al_Cons-science-and-practice).

ETHICS STATEMENT

Our study did not involve human participants or live animal subjects.

ARTICLE IMPACT STATEMENT

We identified habitat modification, species interactions and environmental stochasticity as top current threats to species endangerment.

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SUPPORTING INFORMATION

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

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