

30 years of satellite data show imperiled species are most vulnerable to habitat loss on private lands

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ABSTRACT

To stem the ongoing loss of biodiversity, there is an urgent need to distinguish effective and ineffective approaches to protecting species and their habitats. Conservation laws may be strong on paper but ineffective in practice, or vary in effectiveness across different contexts, such as different land ownership and management settings. Using Google Earth Engine and 30 years of Landsat satellite images, we quantify annual habitat change for 24 species on the U.S. Endangered Species List and IUCN Red List across different categories of land ownership, such as federal, state, and private. We show that imperiled species lost very little habitat on federal lands (3.6%), while losses on non-protected private lands (8.1%) were twice as great. Patterns of loss suggest that listing species under the Endangered Species Act was one mechanism limiting habitat loss, and that the law was most effective on federal lands. These results emphasize the importance of federal lands for protecting habitat for imperiled species, but also highlight the need to improve habitat protection on private lands for long-term conservation.

SIGNIFICANCE STATEMENT

We provide the first large-scale, long-term analysis of imperiled species habitat loss under the U.S. Endangered Species Act. Scientists have historically lacked the tools to evaluate patterns of habitat loss at large spatial and temporal scales, and instead focused on small-scale case studies that are insufficient for informing national policy debates. Our results substantiate the importance of federal protections in the United States, indicating that the ESA has successfully reduced habitat loss for imperiled species. They also identify gaps in protection that compromise wildlife conservation. Given the ongoing biodiversity crises, this information is urgently required to objectively assess the effectiveness of national conservation laws and formulate data-driven biodiversity conservation policies and approaches.

INTRODUCTION

Habitat destruction is the primary driver of global biodiversity loss^{1,2}, and minimizing habitat loss is one of the most important goals of conservation^{3,4}. This is particularly important for the conservation of imperiled species, because habitat loss negatively affects population size and biodiversity⁵, lowers animal breeding success⁶, reduces trophic chain length⁷, depresses species dispersal abilities⁸, and minimizes species richness⁹. Given the current global biodiversity crisis¹⁰, it is critical to identify drivers and effective mechanisms preventing future loss. Because of the restrictions that conservation laws can place on development, such policies can be politically contentious. Therefore, rigorous analyses that evaluate the effectiveness of conservation laws are needed to identify successes and shortcomings to maximize biodiversity protection and inform policy decisions.

In the United States (U.S.), the most important law protecting imperiled species is the Endangered Species Act (hereafter, ‘the Act’). However, there have been few broad studies

evaluating how effectively this law protects imperiled species' habitat^{11 12}. This fundamental question is complicated by the possibility of variation in the Act's effectiveness. In principle, the Act prohibits the take (i.e., harming, harassing, killing) of animals on the federal Endangered Species List (hereafter 'listed species'). However, that prohibition is implemented through different mechanisms in different contexts, particularly between federal and non-federal lands. Section 7 of the Act provides a means to authorize the incidental take of listed species from actions authorized, taken, or funded by federal agencies, provided the agency first consults with the U.S. Fish and Wildlife Service (FWS) to ensure the take will not jeopardize the species or adversely modify critical habitat. Section 10, on the other hand, allows for incidental take of listed animals by non-federal entities in return for development of a habitat conservation plan. While both processes are initiated by the regulated party, Section 7 consultation is standard practice for federal agencies, and federal decisions that trigger consultation are publicly visible; by contrast, it is unknown how often private entities eschew the Section 10 process. While either section may apply in any context, Section 7 is likely more frequently evoked on federal lands. Furthermore, federal land management agencies have specific legal and regulatory conservation mandates (e.g., Federal Land Planning and Management Act, the National Forest Management Act) that protect imperiled species. Thus, protections for listed species may be stronger on federally owned lands.

A large-scale, long-term analysis of context-specific habitat loss is urgently required to objectively assess the Act's effectiveness in conserving species. Scientists have historically lacked the data and tools to evaluate patterns of habitat loss at large spatial and temporal scales, and instead focused on small-scale case studies^{13,14}. Because of this, little concrete evidence has existed to explore the impacts of land ownership on species conservation. These limited examples are insufficient to use for informing national policy debates, and the Act has been both credited with preventing extinctions¹⁵ and criticized as burdensome and ineffective^{16,17}. However, recent advances in remote sensing and cloud computing now enable the rapid analysis of long-term global satellite imagery datasets to provide answers to these questions^{18,19}. Here we report on 30 years of total and net habitat loss within the ranges of imperiled species in the U.S. We applied the LandTrendr algorithm²⁰ to Landsat 5, 7, and 8 satellite images in Google Earth Engine to track loss across the contiguous U.S. Our goal was to provide an estimate of the rates of habitat loss experienced by species protected under the Act, and to see if these protections differ based on land ownership.

We quantify habitat loss within the ranges of 24 vertebrate species occurring across the lower 48 states and all U.S. ecoregions, whose distributions encompass both federal and non-federal lands (Table S1). We consider two separate representations of species ranges: The US Geological Survey Gap Analysis Program (GAP) species distribution models and the boundaries used by the Service. The GAP models show the spatial arrangement of environments suitable for occupation by a species, while the Service's boundaries mark the extent of a species range in the

eyes of the Service. Importantly, the Service uses these boundaries rather than where the species could exist when implementing the Act. Thus, we consider GAP models to represent species' potential ecological ranges, while the Service's boundaries represent species' administratively-defined ranges. In addition to listed species, we also evaluate species on the IUCN Red List (hereafter 'Red List species') to provide a reference point for rates of habitat loss for imperiled but legally unprotected species. We categorize land ownership within species ranges into five broad types – Federal, State, Non-Governmental Organization, Protected Private, and Non-Protected – and quantify the percent loss within species ranges in each type. We tally these losses for listed and Red List species for all years between 1987 and 2017.

RESULTS

The net percent habitat loss varied among land ownership types, by listing status (listed vs. Red List) (Fig. 1), across years (Fig. 2) and, for listed species, the species range type (ecological vs. administrative) (Fig. 1). These patterns were indicated by unequivocal support for models containing a three-way interaction between ownership type, year, and either listing status or range ($\Delta WAIC > 13.9$; Table S2). Imperiled species lost the least habitat on Federal lands ($u = 3.6\%$, $sd = 3.8$), which was significantly less than all other types ($\Delta \geq 6.2\%$, $MPE \geq 0.97$). Species lost the greatest amount of habitat on Non-Protected lands ($u = 8.6\%$, $sd = 6.3$). Loss on both Non-protected and Protected Private lands was significantly greater than all other ownership types ($\Delta \geq 15.0\%$, $MPE = 1.00$). There was no difference ($\Delta \leq 1.5\%$, $MPE = 0.69$) between net loss on NGO ($u = 4.5\%$, $sd = 3.8$) and State ($u = 4.6\%$, $sd = 3.6$) lands. Additionally, percent loss was higher within ecological ranges than the administrative ranges used by the Service ($\Delta \geq 14.4\%$, $MPE = 1.00$).

Trends in losses over time also differed among land ownership types (Fig. 2). We consider four possible relationships between annual rates of loss and time: linear, logarithmic, exponential, and quadratic. A linear decline was the best supported model of change in habitat loss over time on NGO lands for both listed and Red List species, indicating consistently decreasing loss rates within this land ownership type (Table 2). Similarly, annual habitat loss increased logarithmically on both Protected and Non-Protected private lands for both listed and Red List species, indicating increasing loss rates that have stabilized over time (Fig. 2). Among Red List species, there was no change in rates of loss over time on State or Protected Private lands (Table 2). Annual loss of habitat for listed species on State lands increased exponentially (Table 2). On Federal lands, quadratic trends indicate decreasing annual loss rates from 1986 to 2005 for listed species, and 1986 to 2008 for Red List species, after which loss rates have been increasing (Fig. 2).

DISCUSSION

Three lines of evidence suggest the Act may be a key mechanism responsible for habitat protection on Federal lands. First, listed species experienced significantly less habitat loss after

they were listed, compared to before they were listed ($\Delta = 25.0\%$, $MPE = 1.00$) although pre-listing data was limited (8 species, with a median of 5 years). Second, habitat loss was relatively consistent among the six agencies managing federal lands in this study. Pairwise differences in percent loss between agencies were not different from zero ($MPE < 0.95$), except that losses on National Oceanic and Atmospheric Administration lands were significantly lower than those on Bureau of Reclamation and Department of Defense lands ($\Delta \geq 6.5\%$, $MPE \geq 0.96$). This consistency among agencies is an indication that agency-specific laws and regulations like the Federal Land Policy and Management Act or the National Forest Management Act were not primarily responsible for reduced habitat loss on Federal land. Third, listed species losing less habitat than Red List species would also signal the Act as a driving mechanism of protection. While this difference was marginal overall ($\Delta = -2.62\%$, $MPE = 0.67$), it was most pronounced on federal lands ($\Delta = -4.57$, $MPE = 0.75$).

Our results indicate that habitat loss for listed species is reduced on Federal lands, and we found some evidence attributing these protections to the Act. However, inefficient protections outside of Federal lands will undermine present and past conservation work. As the ranges of 90% of listed species include some private land¹⁷ and over half of listed species ranges include > 80% private land²¹, high and increasing rates of habitat loss on Non-protected private lands must be a focus for future conservation work. High (Fig.1) and increasing (Fig. 2) losses on State lands also highlight that current state protections are insufficient to protect imperiled species. Losses outside protected areas can create isolated islands of habitat surrounded by destruction^{22,23}, impairing connectivity and creating extinction debts (delayed extinction following habitat loss) for species that may not be immediately noticed²⁴. In addition, habitats naturally change over time²⁵ and ecosystems will transform dramatically with global climate change²⁶. Vertebrates are predicted to shift or shrink their ranges in response to changing environmental conditions²⁷, with protected areas conservatively predicted to lose 20% of their mammal species²⁸. Many imperiled species' ranges will need to shift out of the areas with strong protections into areas with weaker protection²⁸. These findings corroborate a persistent and dire warning about over-reliance on protected and federal lands to conserve biodiversity^{22,29}.

Our findings also highlight challenges to recovering listed species under the Act as it is currently implemented, and the need to consider holistic landscape perspectives that promote conservation on private lands. Listed species recover at relatively low rates³⁰, particularly when funding for recovery is inadequate^{31,32}. While many species have not had enough time to recover after listing¹¹, inadequate protection of habitat outside of Federal lands and current species distributions may also contribute to slow rates of recovery. Greater habitat loss within ecological ranges compared to the administrative ranges used to implement the Act (Fig. 1) are not surprising given ESA interventions are usually limited to these administrative areas and may reflect an inability to protect unoccupied suitable habitat. While unoccupied habitat can be designated as critical habitat, critical habitat is only protected from "adverse modification" by

federal agencies under Section 7; it has no legal protection against private activities with no federal involvement. Protecting species within administrative ranges potentially constrains species to current distributions, limiting both their recovery and their ability to shift ranges with changing environmental conditions³³. Our results highlight that without extending protections to unoccupied habitat recovery may be hampered, especially for wide-ranging species.

Our analyses support the conclusion that federal protections in the United States, including the Endangered Species Act, have successfully reduced habitat loss for imperiled species. However, they also identify gaps in protection that compromise wildlife conservation. To successfully conserve and recover imperiled species, legal protections must be applied equally on federal and private lands through increased enforcement, greater conservation incentives, or compliance assistance. All listed species experienced a net loss of habitat, even on Federal lands, which may be symptomatic of more systemic conservation challenges³⁴. Additionally, imperiled species without legal protection remain at risk, as demonstrated by greater habitat loss among Red List species. As species may become functionally extinct before losing even 30% of their population³⁵, legally protecting species only once they face grave, immediate threats may push species beyond recovery¹⁶. Finally, these results may be different for endangered plants (which were not included in our analyses), as they receive fewer protections under the Act. Species' functional traits extend far beyond their local ecosystem, such as by enhancing carbon sequestration³⁶ or improving human health³⁷. A failure to protect the Earth's biodiversity may thus have consequences beyond species extinctions that ultimately impact human health and welfare.

METHODS AND MATERIALS

Study Species and Area

We measured habitat loss for 24 imperiled species in the contiguous United States (US). Species were selected by consulting lists of vertebrate species documented both by the U.S. Endangered Species Act and the International Union for Conservation of Nature Red List of threatened species³⁸. As of August 2018, the ESA lists 1661 species as endangered or threatened, with 1163 active recovery plans. We selected 24 vertebrate species occurring across most of the lower 48 states, and within all the U.S. ecoregions (*Table S1*), that had ranges containing both federal and non-federally owned land. Our choice of species was also dictated by which had freely available species distribution models from the U.S. Geological Survey Gap Analysis Project (GAP).

We used GAP species distributions to approximate the extent of habitat for each species and restricted our analyses to these areas. While these models can be imperfect and may include areas that are unsuitable for a species, we consider them to represent the best available range approximation created using consistent methodology for many species. For ESA listed species, we also considered the species ranges provided on the U.S. Fish and Wildlife Service (FWS)

endangered species data portal (available at <https://ecos.fws.gov>). These ranges represent the extent of species currently occupied range as determined by FWS, and are the administrative boundaries used by FWS in administering the ESA. To delineate land ownership classes, we used the Protected Areas Database of the U.S. (available at <http://gapanalysis.usgs.gov/padus>) uploaded as an asset in Google Earth Engine. We classified lands as Federal, State, NGO, Protected Private or Non-Protected following the ownership attribute.

Remote Sensing Analysis

LandTrendr is a set of spectral-temporal segmentation algorithms that can be used for change detection in a time series of satellite imagery²⁰. In 2018 the LandTrendr algorithm was ported to Google Earth Engine making large-scale analyses possible³⁹. We used Earth Engine LandTrendr code for change mapping to identify per pixel changes in Landsat imagery between 1986 and 2018. LandTrendr identifies breakpoints in the trajectories of a single spectral index in each image pixel over time. We used breakpoints in NDVI to determine when vegetated habitat was disturbed. To standardize breakpoint thresholds between habitats with variable baseline NDVI values (such as scrubland and forested land), we calculated the mean and standard deviation of NDVI within the range of each species in *Table 2* and set the pre-disturbance spectral value parameter for each species to one standard deviation below the mean. This standardization allowed us to apply a consistent, conservative threshold that detected extreme decreases in NDVI relative to the observed level of variation within an area⁴⁰.

We discarded disturbances less than 450m² and all disturbances that recovered within a single year to reduce oversensitivity. Agricultural areas can confound change detection targeting habitat loss due to the LandTrendr algorithm interpreting inter-annual crop rotations, tiling, and fallow fields as land cover changes. As most crops are on private land, agricultural false-positives become a confounding variable when comparing land change among ownership types. Therefore, we masked LandTrendr output using the U.S. Department of Agriculture 30m resolution Cropland Data Layer from 2017⁴¹, eliminating all areas classified as ‘cropland.’ This created a conservative bias to loss estimates by excluding agriculture conversions prior to 2017. LandTrendr is also likely to identify habitat loss from fire. In most cases, burned areas represent stochastic natural destruction of habitat not directly subject to legal or administrative regulation. In some cases, fire can be a conservation measure itself, as some endangered species actively require large burns for their survival. Considering this, including burned lands would confound results focused on assessing patterns of intentional habitat destruction. Therefore, as a conservative approach, we eliminated burned areas using GIS data from the USDA Forest Service Monitoring Trends in Burn Severity Project⁴², covering all years from 1986 to 2018. We uploaded this data into Google Earth Engine as an asset and used the raster of burned areas as a mask to exclude all areas burned by fire.

Habitat Loss Analysis

LandTrendr produced rasters with the year of greatest disturbance at each pixel, if any was detected that exceeded magnitude, duration, and size thresholds. We calculated habitat loss as the proportion of pixels in each species range and land ownership category that were disturbed. We refer to this measure as the total percent loss. We also calculated these percentages for each year, which we refer to as annual percent loss. For all analyses using annual percent loss, we adjusted estimates to account for ‘global’ variation in rates of development over time. We subtracted the mean annual percent loss across all species and land ownership types in a given year from species specific annual percent loss estimates and refer to this measure as the adjusted annual loss. We use unadjusted percentages in analyses of total loss over the study. Additionally, we excluded years corresponding to the beginning of our data collection (1986) and transitions between Landsat satellites (2001), because these years exhibited extreme peaks in detected loss. Unless otherwise specified, we consider losses for listed species within the FWS range that occurred while the species was listed.

We estimated the effects of land ownership (Zone), time (Year), listing status (Status), and whether the GAP or FWS range is considered (Range) on adjusted annual loss, using linear mixed models. All models included a random intercept per species to account for correlation in repeated measures within the same geographic area (i.e., species range). Models were estimated in a Bayesian framework, using the *rstanarm* package⁴³ for R ⁴⁴. We used default priors and sampled 1,000 iterations of four Markov chains following a 1,000 iteration burn-in period. Chain convergence for all parameters was assessed using the *Rhat* statistic, with $Rhat < 1.1$ used to indicate convergence⁴⁵.

We first fit a candidate set of linear mixed models that included an intercept-only (null) model, and all combinations of the effects of Year, Zone, and Status. This candidate set was fit to adjusted annual loss data from ESA listed and IUCN species within FWS and GAP ranges, respectively. We fit an identical model set to adjusted annual loss data for ESA listed species from within GAP distribution ranges inside and outside of the FWS range, substituting Range for Status. Because Red List species do not have administrative ranges, the candidate sets were fit to different data, and thus were evaluated separately. We used the Watanabe-Akaike Information Criterion (*WAIC*) to measure support among competing models⁴⁶. We used the sum of *WAIC* weights (ω_i) among models including a given variable to measure variable importance, and use $\sum \omega_i > 0.90$ to signify important variation in loss as a function of a given variable. Additionally, we tested for differences in percent loss among land ownership types, between listing status (listed vs. Red List), and between ranges using the maximum probability of effects (*MPE*) and 95% credible interval (CI) around pairwise contrasts. To infer significant differences in rates of loss, we required the coefficient have an $MPE > 95\%$ and a 95% CI that did not include zero.

We considered four trends in habitat loss over time representing four simple, potential patterns of change: linear, logarithmic, exponential and quadratic. To identify the appropriate

trend form, we fit a set of four mixed models to adjusted annual loss data within each zone as a function of year. We identified the most supported relationship as the model receiving the lowest *WAIC* score⁴⁷. To infer meaningful changes over time, we required estimated slope coefficients to have an *MPE* > 95%, and a 95% CI that did not include zero. We compared trends among land ownership types in terms of the form of the trend that was most supported, and whether slopes were positive, negative, or effectively zero. This analysis was conducted for ESA listed and IUCN Red List species separately.

To evaluate whether the ESA was the mechanism responsible for any observed differences in rates of habitat loss, we conducted a series of analyses testing three different expectations. First, we expect ESA listed species to have lower rates of habitat loss than species that are only found on the IUCN Red List (which carries no legal or regulatory authority). We tested this hypothesis using the effect of listing status on total habitat loss within GAP ranges for IUCN species and within FWS ranges for ESA listed species. For listed species, we only considered losses occurring while these species were listed.

Second, we expected lower rates of habitat loss within ESA listed species ranges while they were listed relative to when these species were not listed. We used a linear mixed model with a random intercept per species, and fixed effects on the interaction between listing status and Zone to estimate the effect of ESA listing adjusted annual rates of habitat loss. To infer a significant effect, we required the coefficient have an *MPE* > 95% and a 95% CI that did not include zero.

Finally, we expected to find no differences in rates of habitat loss among federal agencies. Significant differences among agencies would indicate agency-specific regulations (e.g. National Forest Management Act or Federal Land Policy and Management Act) as the mechanism driving reduction of habitat loss. We tested this hypothesis using a linear mixed model predicting total loss on Federal lands within the FWS range of listed species as a function of the federal agency. Agency management was identified by the Protected Areas Dataset of the United States and included the Bureau of Land Management, Bureau of Reclamation, Department of Defense, National Oceanic and Atmospheric Administration, National Park Service, and U.S. Forest Service. We considered contrasts between agencies that had an *MPE* > 95% and a 95% CI around estimated effect sizes that did not include zero to indicate different rates.

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TABLES

Table 1. Model selection results and trend estimates for changes in imperiled species habitat loss over time within different land ownership types. Support for linear, logarithmic (Log), exponential (Exp), and quadratic (Quad) trends are provided in terms of Bayesian *WAIC* scores. Posterior median estimates, 95% credible intervals, and maximum probability of effects (*MPE*) are shown for slope parameters estimated by the most supported (lowest *WAIC*) linear mixed model, indicated in bold.

	Land Ownership	<i>WAIC Score</i>				<i>B Estimate [95% CI]</i>			
		Linear	Log	Exp	Quad	Year, log(Year)	<i>MPE</i>	Year ²	<i>MPE</i>
ESA Listed Species	Federal	-162.2	-164.5	-164.6	-165.6	-0.014 [-0.023, -0.0045]	99.0	3.8e-4 [1.0e-4, 6.0e-4]	98.8
	NGO	279.8	283.0	280.6	283.2	-0.005 [-8e-3, -8e-4]	97.9	NA*	NA*
	State	-558.8	-554.8	-560.2	-559.3	NA*	100.0	8.6e-5 [0.0, 1.2e-4]	100.0
	Protected Private	574.3	568.9	576.8	564.6	0.050 [0.027, 0.074]	100.0	-1.3e-3 [-2.0e-3, -7.0e-4]	100.0
	Non-Protected	-174.8	-185.6	-167.9	-185.3	0.071 [0.048, 0.095]	100.0	NA*	NA*
IUCN Red List Species	Federal	-216.2	-216.8	-213.6	-219.4	-0.013 [-0.021, -0.0054]	99.6	2.9e-4 [0.0, 5.2e-4]	98.2
	NGO	-228.1	-228.4	-227.7	-228.2	-0.003 [-0.0046, -0.0012]	99.7	NA*	NA*
	State	-155.6	-157.6	-157.3	-156.1	-0.007 [-0.029, 0.019]	69.0	NA*	NA*
	Protected Private	112.0	117.7	121.0	122.9	0.008 [-0.039, 0.050]	60.7	NA*	NA*
	Non-Protected	-38.3	-39.0	-36.7	-38.6	0.036 [0.0038, 0.070]	96.6	NA*	NA*

*Linear and logarithmic models did not include a squared term, and exponential models did not include a linear term.

FIGURES

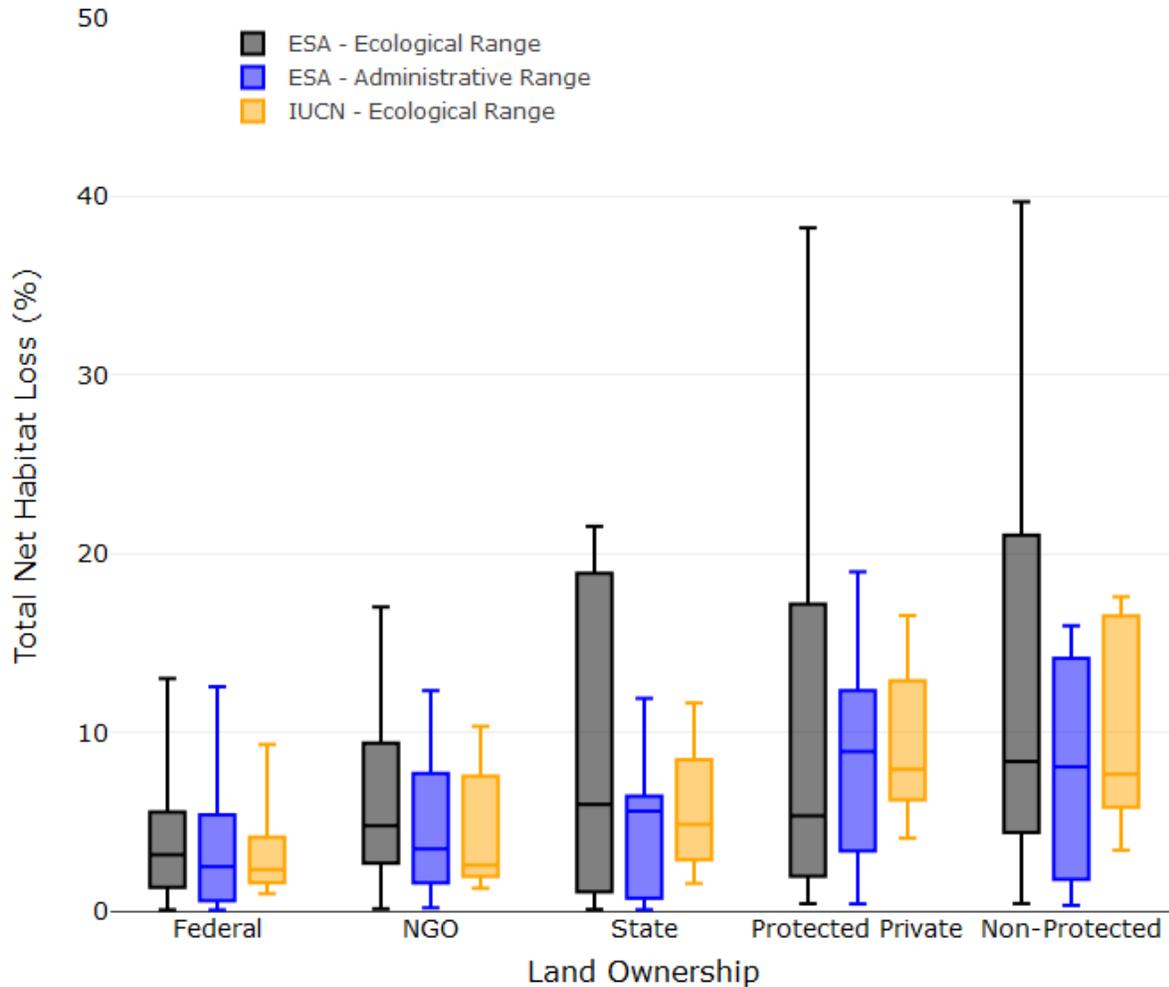


Fig. 1. Rates of habitat loss within imperiled species ranges were lowest on Federal lands, and highest on Non-Protected private lands. Box plots show the distribution of net habitat loss among imperiled species from 1986 to 2017. Percentages differed for ESA listed species (ESA) depending on whether the potential/ecological range (black) or administrative range (blue) was considered. Losses within IUCN species ranges (orange) were not significantly greater than those for ESA listed species.

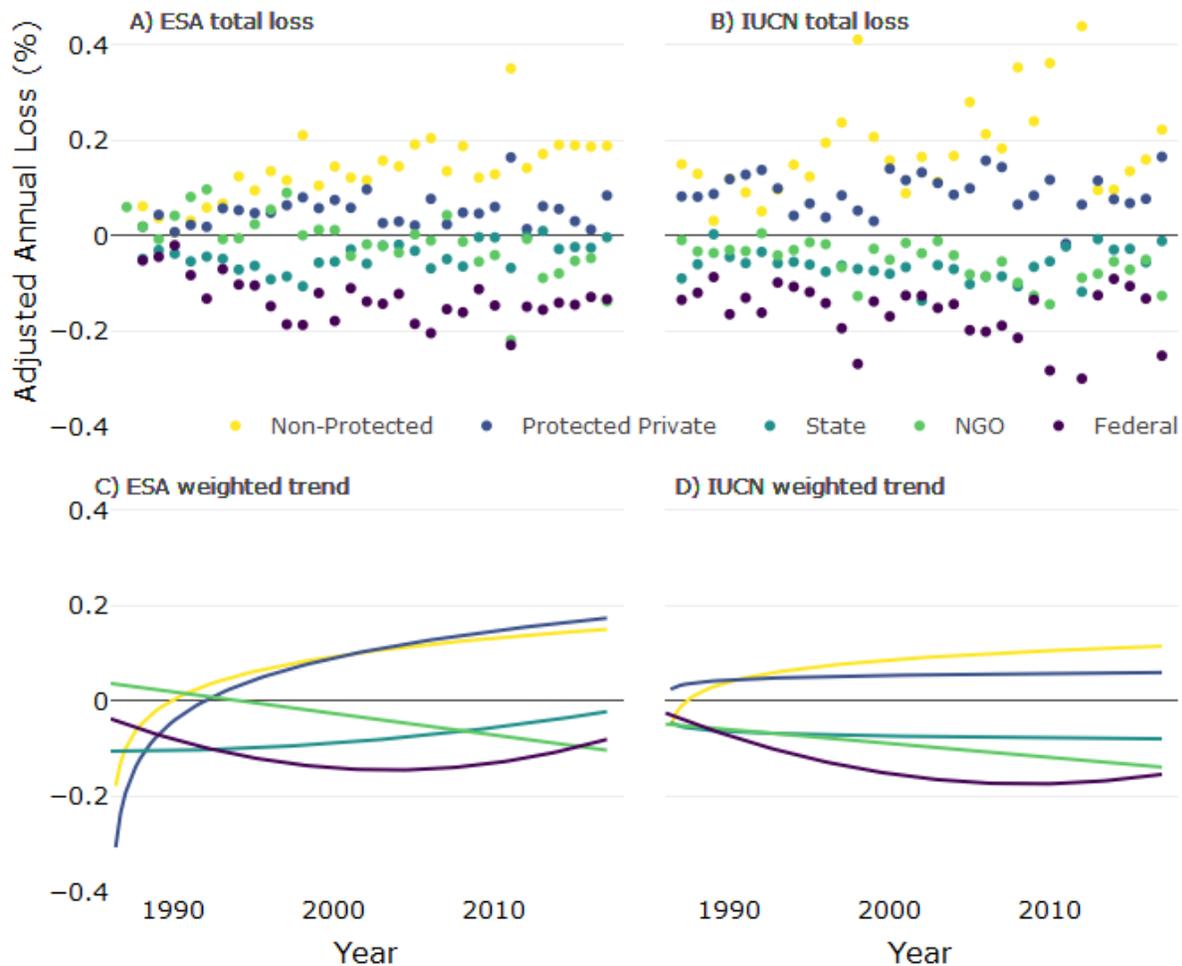


Figure 2. Federal and non-federal lands exhibited different trends in annual rates of habitat loss within imperiled species ranges. Data points (A, B) show the unweighted annual total percent habitat loss across species within each land management zone, adjusted by the mean loss in a given year. Trends over time were similar between (C) ESA listed species and (D) IUCN Red List species. Trend lines were estimated from the marginal relationship between year and adjusted annual loss accounting for random intercepts per species.

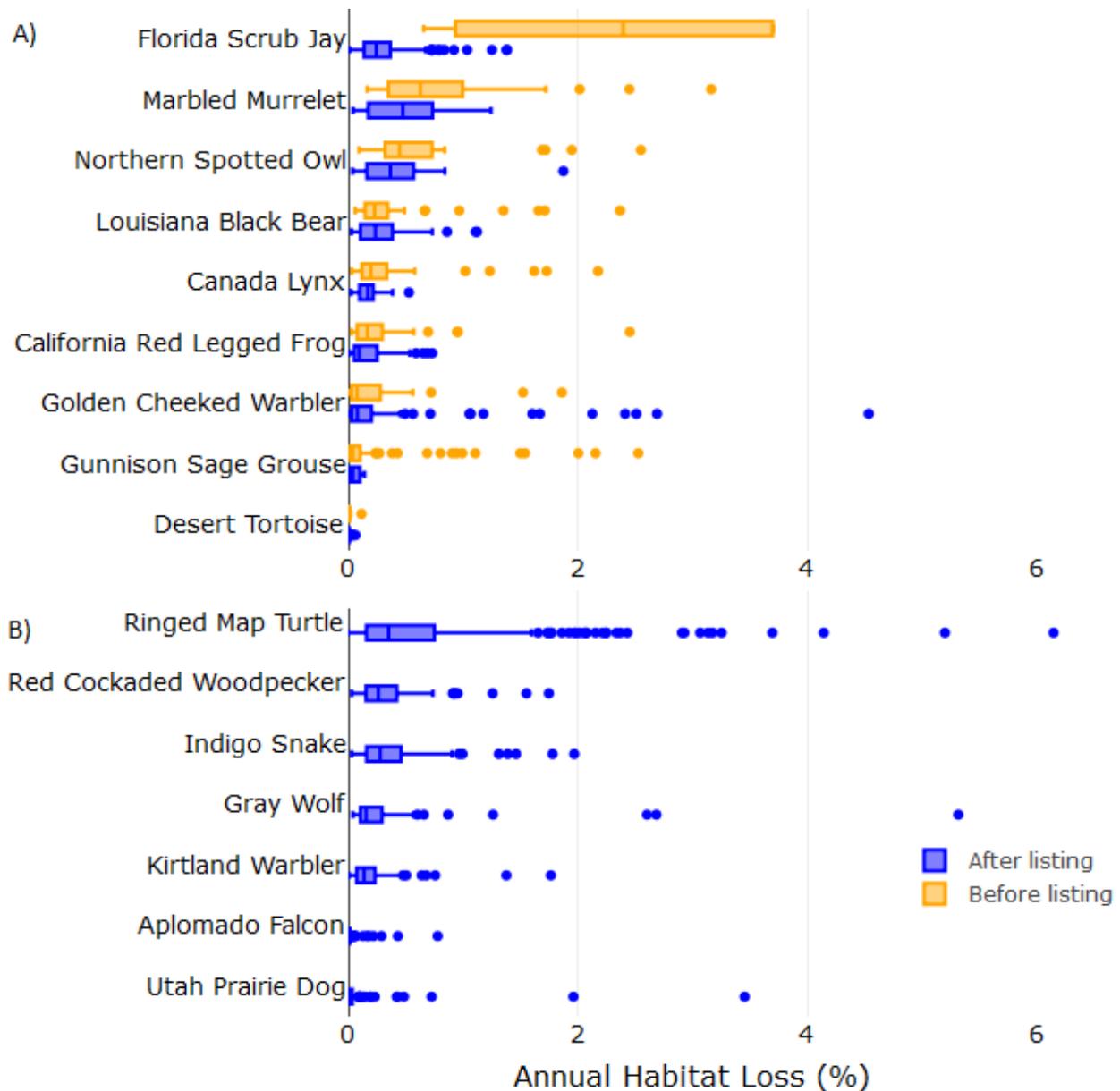


Figure 3. Species lost less habitat within their ranges while they were listed on the Endangered Species List. Box plots show the distribution of annual habitat loss for each ESA listed species as the percentage of species habitat within administrative ranges lost in each year before and after listing (A). Species listed prior to 1986 (B) did not have loss data before listing.

REFERENCES

- ¹ T. M. Brooks *et al.*, Habitat Loss and Extinction in the Hotspots of Biodiversity. *Conserv. Biol.* **16**, 909-923 (2002).
- ² I. Hanski, Landscape fragmentation, biodiversity loss and the societal response. *EMBO. Rep.* **6**, 388-392 (2005).
- ³ L. Fahrig, Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487-515 (2003).
- ⁴ J. M. Hoekstra, T. M. Boucher, T. H. Ricketts, C. Roberts, Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol. Lett.* **8**, 23-29 (2005).
- ⁵ T. M. Donovan, C. H. Flather, Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecol. Appl.* **12**, 364-374 (2002).
- ⁶ S. Kurki, A. Nikula, P. Helle, H. Lindén, Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology* **81**, 1985-1997 (2000).
- ⁷ A. Komonen, R. Penttilä, M. Lindgren, I. Hanski, Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos* **90**, 119-126 (2000).
- ⁸ M. Bélisle, A. Desrochers, M.-J. Fortin, Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* **82**, 1893-1904 (2001).
- ⁹ C. S. Findlay, J. Houlahan, Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conserv. Biol.* **11**, 1000-1009 (1997).
- ¹⁰ D. Western, The biodiversity crisis: a challenge for biology. *Oikos*, 29-38 (1992).
- ¹¹ M. Taylor, K. Suckling, J. Rachlinski, The effectiveness of the Endangered Species Act: A quantitative analysis. *Bioscience* **55(4)**, 360-367 (2005)
- ¹² M. Schwartz, The performance of the Endangered Species Act. *Annu. Rev. Ecol. Evol. Syst.* **39**, 279-299 (2008)
- ¹³ A. Brook, M. Zint, R. De Young, Landowners' responses to an endangered species act listing and implications for encouraging conservation. *Conserv. Biol.* **17**, 1638-1649 (2003).
- ¹⁴ A. Trainor, J. Walters, D. urban, A. Moody, Evaluating the effectiveness of a Safe Harbor Program for connecting wildlife populations. *Anim. Conserv.* **16(6)**, 610-620 (2013)
- ¹⁵ T. Male, M. Bean, Measuring progress in US endangered species conservation. *Ecol. Lett.* **8(9)**, 986-992 (2005)
- ¹⁶ D. J. Rohlf, 6 Biological reasons why the Endangered Species Act doesn't work – and what to do about it. *Conserv. Biol.* **5**, 273-282 (1991).
- ¹⁷ G. M. Brown, J. F. Shogren, Economics of the Endangered Species Act. *J. Econ. Perspect.* **12**, 3-20 (1998).
- ¹⁸ N. Gorelick *et al.*, Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* **202**, 18-27 (2017).
- ¹⁹ X.-P. Song *et al.*, Global land change from 1982 to 2016. *Nature* **560**, 639 (2018).

- ²⁰R. E. Kennedy, Z. Yang, W. B. Cohen, Detecting trends in forest disturbance and recovery using yearly Landsat time series: 1. LandTrendr — Temporal segmentation algorithms. *Remote Sens. Environ.* **114**, 2897-2910 (2010).
- ²¹US Fish and Wildlife Service, “Our endangered species program and how it works with landowners”. <https://www.fws.gov/endangered/esa-library/pdf/landowners.pdf> (2009).
- ²²V. C. Radeloff *et al.*, Housing growth in and near United States protected areas limits their conservation value. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 940-945 (2010).
- ²³R. DeFries, A. Hansen, A. C. Newton, M. C. Hansen, Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecol. Appl.* **15**, 19-26 (2005).
- ²⁴D. Tilman, R. M. May, C. L. Lehman, M. A. Nowak, Habitat destruction and the extinction debt. *Nature* **371**, 65-66 (1994).
- ²⁵F. H. Bormann, G. E. Likens, Catastrophic disturbance and the steady state in northern hardwood forests: A new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. *Am. Sci.* **67**, 660-669 (1979).
- ²⁶D. Bachelet, R. P. Neilson, J. M. Lenihan, R. J. Drapek, Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems* **4**, 164-185 (2001).
- ²⁷G. E. Austin, C. J. Thomas, D. C. Houston, D. B. A. Thompson, Predicting the spatial distribution of buzzard *Buteo buteo* nesting areas using a geographical information system and remote sensing. *J. Appl. Ecol.* **33**, 1541-1550 (1996).
- ²⁸C. E. Burns, K. M. Johnston, O. J. Schmitz, Global climate change and mammalian species diversity in US national parks. *Proc. Natl. Acad. Sci. U.S.A* **100**, 11474-11477 (2003).
- ²⁹C. N. Jenkins, K. S. Van Houtan, S. L. Pimm, J. O. Sexton, US protected lands mismatch biodiversity priorities. *Proc. Natl. Acad. Sci. U.S.A* **112**, 5081-5086 (2015).
- ³⁰M. C. Neel, A. K. Leidner, A. Haines, D. D. Goble, J. M. Scott, By the numbers: How is recovery defined by the US Endangered Species Act? *BioScience* **62**, 646-657 (2012).
- ³¹P. J. Ferraro, C. McIntosh, M. Ospina, The effectiveness of the US endangered species act: An econometric analysis using matching methods. *J. Environ. Econ. Manage.* **54**, 245-261 (2007).
- ³²J. W. Malcom, Y.-W. Li, Missing, delayed, and old: The status of ESA recovery plans. *Conserv. Lett.* **0**, e12601.
- ³³C. Carroll, J.A. Vucetich, M.P. Nelson, D.J. Rohlf, M.K. Phillips, Geography and recovery under the U.S. Endangered Species Act. *Conserv. Biol.* **24(2)**, 395-403
- ³⁴W. Laurance, “Habitat destruction: Death by a thousand cuts” in *Conservation Biology for All* (Oxford University Press, 2010), pp. 73-87.
- ³⁵T. Saterberg, S. Sellman, B. Ebenman, High frequency of functional extinctions in ecological networks. *Nature* **499**, 468-470 (2013).
- ³⁶O. J. Schmitz *et al.*, Animating the carbon cycle. *Ecosystems* **17**, 344-359 (2014).
- ³⁷A. Markandya *et al.*, Counting the cost of vulture decline - An appraisal of the human health and other benefits of vultures in India. *Ecol. Econ.* **67**, 194-204 (2008).

- ³⁸International Union for Conservation of Nature, “The IUCN Red List of threatened Species” version 2018-2 <http://www.iucnredlist.org> (2018).
- ³⁹R. E. Kennedy *et al.*, Implementation of the LandTrendr Algorithm on Google Earth Engine. *Remote Sens.* **10**, 691 (2018).
- ⁴⁰Yang Y *et al.* (2018) Detecting the dynamics of vegetation disturbance and recovery in surface mining area via Landsat imagery and LandTrendr algorithm. *J. Clean. Prod.* 114:2897-2910.
- ⁴¹Boryan C, Yang Z, Mueller R, Craig M (2011) Monitoring US agriculture: the US Department of Agriculture, National Agricultural Statistics Service, Cropland Data Layer Program. *Geocarto Int.* 26:341-358.
- ⁴²MTBS Project: Fire Level Geospatial Data. (USDA Forest Service, U.S. Geological Survey, [2018, July 12]), <http://mtbs.gov/direct-download> .
- ⁴³Goodrich B, Gabry J, Ali I, Brilleman S (2018) rstanarm: Bayesian applied regression modeling via Stan. R package version 2.17.4, <http://mc-stan.org/>.
- ⁴⁴R Development Core Team, R: A language and environment for statistical computing. *R Foundation for Statistical Computing* (2018).
- ⁴⁵Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. *Stat. Sci.* 7:457-472.
- ⁴⁶Watanabe S (2013) A widely applicable Bayesian information criterion. *J. Mach. Learn. Res.* **14**, 867-897 (2013).
- ⁴⁷Watanabe S (2010) Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *J. Mach. Learn. Res.* 11:3571-3594.

SUPPORTING INFORMATION

Table S1. List of imperiled species considered in habitat loss analyses.

Species	Status	Habitat Type
Northern Aplomado Falcon	Endangered (ESA)	Open terrain, scattered trees and shrubs
Appalachian Cottontail	Near Threatened (IUCN)	High elevations, coniferous forests and dense understories
Black Pinesnake	Threatened (ESA)	Upland, longleaf pine forests with herbaceous groundcover
California Red Legged Frog	Threatened (ESA), Vulnerable (IUCN)	Riparian areas
Canada Lynx	Threatened (ESA)	Dense boreal forests
Cerulean Warbler	Vulnerable (IUCN)	Older deciduous forests
Mojave Desert Tortoise	Threatened (ESA), Vulnerable (IUCN)	Valleys with brush scrub
Eastern Spotted Skunk	Vulnerable (IUCN)	Forest habitats, dense understories
Florida Scrub-jay	Threatened (ESA), Vulnerable (IUCN)	Low growing oak and scrubby flatwoods
Golden-cheeked Warbler	Endangered (ESA), Endangered (IUCN)	Juniper and streamside trees
Golden-winged Warbler	Under Review (ESA), Near Threatened (IUCN)	Clearcuts, wet thickets, aspen or willow stands, and tamarack bogs
Mexican Gray Wolf	Endangered (ESA)	Forests, mountains, deserts, brush
Greater Prairie Chicken	Vulnerable (IUCN)	Grassland
Gunnison Sage Grouse	Threatened (ESA), Vulnerable (IUCN)	Sagebrush
Eastern Indigo Snake	Threatened (ESA)	Riparian thickets, cane fields
Kirtland Warbler	Endangered (ESA), Near Threatened (IUCN)	Dense jack pine, clearcuts
Louisiana Black Bear	Delisted Due to Recovery (ESA)	Bottomland hardwood forests

Marbled Murrelet	Threatened (ESA), Endangered (IUCN)	Coniferous forests near coasts
Northern Spotted Owl	Threatened (ESA), Near Threatened (IUCN)	Old growth forests
Pinyon Jay	Vulnerable (IUCN)	Dry mountain slopes near pinyon-juniper forests, sagebrush, chaparral, scrub oak
Red-cockaded Woodpecker	Endangered (ESA), Near Threatened (IUCN)	Old growth pine forests, particularly longleaf pine
Ringed Map Turtle	Threatened (ESA), Vulnerable (IUCN)	Rivers with nearby brush and debris
Rusty Blackbird	Vulnerable (IUCN)	Flooded woods, swamps, marshes
Utah Prairie Dog	Threatened (ESA), Endangered (IUCN)	Low land with abundance herbaceous plants

Table S2. Model selection results from linear mixed models predicting annual percent habitat loss as a function of land ownership (Zone), time (Year), whether species were listed under the ESA or appeared only on the Red List (Status), or whether ecological or administrative ranges were considered (Range). Number of model parameters (K), $WAIC$ scores, differences, and weights (ω_i) are reported. Separate candidate sets were fit for models including Status and those including Range.

	Model	K	$WAIC$	$\Delta WAIC$	ω_i
Status set	Zone by Year by Status	22	3177.0	0	0.99
	Zone by Year	12	3191.0	13.9	<0.01
	Zone by Status	12	3240.2	63.2	0.00
	Zone	7	3245.1	68.0	0.00
	Year by Status	6	3454.9	277.8	0.00
	Year	4	3460.7	283.7	0.00
	Null	3	3465.4	288.3	0.00
	Status	4	3466.0	289.0	0.00
Range set	Zone by Year by Range	22	4095.2	0	1.00
	Zone by Range	12	4161.1	65.9	0.00
	Zone by Year	12	4240.5	145.3	0.00
	Zone	7	4283.1	187.9	0.00
	Year by Range	6	4370.7	275.5	0.00
	Range	4	4385.7	290.5	0.00
	Year	4	4465.6	370.4	0.00
	Null	3	4470.8	375.6	0.00