

RESEARCH NOTE

Documenting at-risk status of terrestrial ecosystems in temperate and tropical North America

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Abstract

The International Union for Conservation of Nature (IUCN) Red List of Ecosystems (RLE) is an emerging global standard for ecosystem risk assessment that integrates data and knowledge to document the relative risk status of ecosystem types. Here, we summarize initial findings from applying four IUCN RLE criteria to 655 terrestrial ecosystems in temperate and tropical North America, or 8.5% of the global land surface. A series of indicators are measured for each criterion to address trends in ecosystem extent (A), the relative restricted nature of its distribution (B), and the extent and relative severity of environmental degradation (C), and the extent and relative severity of disruption of biotic processes (D); all to gauge the probability of range wide “collapse.” Ecosystems are listed as collapsed, critically endangered, endangered, vulnerable, near threatened, least concern, data deficient, or not evaluated. Taking uncertainty into account, 219 (33%) of terrestrial ecosystem types were listed as threatened (i.e., either critically endangered, [7%], endangered [14%], or vulnerable [13%]). Examples include tallgrass prairies, oak savannas, longleaf pine woodlands, floodplain forests, mesic hardwood forests, and dry tropical forests. Historically, these threatened ecosystems occurred across about 45% of the continental study area, and today account for about 30%. The RLE provides one important focus for prioritizing conservation effort.

KEYWORDS

critically endangered, ecosystem degradation, endangered, IUCN Red List, loss in extent, restricted distribution, vulnerable

1 | INTRODUCTION

The crisis in biodiversity loss is best addressed by conservation actions directed at multiple levels of ecological organization, from genetic diversity to species, ecosystems, and landscapes. An ecosystem focus is one critical level that addresses ecosystem processes and patterns, links species to ecosystem functions, and helps characterize the overall

condition of the landscape (Noss, 1987). This need has led scientists to develop methods for assessing ecosystem risk as a complement to species risk assessment (Master et al., 2012; Nicholson et al., 2009; Noss et al., 1995). These efforts have been bolstered globally by the International Union for Conservation of Nature (IUCN), which initiated development of a global standard for ecosystem risk assessment (Keith et al., 2013), as a complement to the Red List of

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Threatened Species (Mace et al., 2008). In 2014, IUCN established a goal of assessing all ecosystems globally by 2025. Within North America, the RLE also complements the NatureServe conservation status assessment process (Master et al., 2012), which is maintained across the NatureServe Network of Natural Heritage Programs, including at subnational levels.

This analysis was undertaken to use the IUCN Red List of Ecosystems (RLE) to document the status of all terrestrial ecosystems across temperate and tropical North America and the Caribbean. This region represents a broad cross section of both terrestrial ecosystem diversity and land use history. While some of the most intensive land uses anywhere in the world occur here, there are also extensive areas of relatively intact ecosystems. This analysis used data developed at continental, national, and regional scales, anticipating that subsequent analysis would build upon this using locally available data. Our approach serves as a demonstration for accelerating progress toward the IUCN 2025 goal with other assessments around the world.

Red List assessments for species estimate the risk of extinction. They are grounded in population theory and measures to assess trends in population viability (Mace et al., 2008). In contrast to species, ecosystems do not go extinct. Instead, they transform in a number of ways from one recognizable state to another (Newton, 2021). The primary ecological unit of interest is not the populations of a given species; but instead, the recurring assemblage of species, their interactions, and their associated geophysical setting. Therefore, ecosystem risk assessment is grounded first on theory of ecological community assembly (Wieher & Keddy, 2001), which explains how recurring species composition reflects biogeographic history, patterns in the physical environment, and dynamic ecological processes. Second, it is grounded in the theory of ecological resilience (Gunderson, 2000), explaining how species assemblages respond to changes in ecological processes that cause an observable departure from or return to expected species composition.

Ecosystem risk assessment therefore aims to document change in expected species composition and ecological processes. For ecosystems, the analog to species *extinction* (i.e., population collapse) is “*ecological collapse*,” or the *transformation* of species composition and ecological processes to an alternate condition from that which was previously supported, along with loss of resilience to recovery (Keith et al., 2013). The “collapse” of a given example of an ecosystem may occur abruptly or gradually, but is expressed where ecological conditions have been transformed beyond recognition, where identifying features have been lost, and the ecosystem has been replaced by a different, often novel, ecosystem, including

replacement by agriculture or urban development (Keith et al., 2013; Newton, 2021).

Building upon prior published results (Comer, 2021) centered on grasslands and savannas, we systematically apply Red List criteria to all, in order to assign each ecosystem type in the region to red list categories of as collapsed (CO), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC), data deficient (DD), or not evaluated (NE).

2 | MATERIALS AND METHODS

We analyzed text, tabular, and spatial data on 655 upland, wetland, and riparian ecosystem types to create a comprehensive view of ecosystem status for the 11.6 million km² area of temperate and tropical North America and the Caribbean. This area encompasses approximately 27% of the Americas and 8.5% of the global land surface (excluding Antarctica). It extends from the northern limits of temperate Canada (54°38'N) to tropical latitudes in southern Panama (7°11'N).

Given the depth of information involved in this assessment, here we provide a high-level treatment of each step of the process. Please see online appendices (Supporting Information) for in-depth background on the ecosystem classification and maps used and an illustration of the assessment process (Appendix S1), for descriptions and conceptual models for the ecosystem types addressed (Appendix S2), and detailed results (Appendix S3).

Bland et al. (2017) recommend steps to apply the IUCN criteria beginning with classification and description of each ecosystem type to be assessed and development of a conceptual model to organize information about factors that cause environmental degradation or disruption of biotic processes. We used a well-developed classification of upland and wetland ecosystems (Comer et al., 2003; Josse et al., 2003), mapped distributions of each (Comer et al., 2020) (Appendix S1). Depending on the characteristics of each ecosystem type (Appendix S2) and available data, appropriate indicators were then selected for measurement under each assessment criterion. The classification of ecosystem types used in these assessments had to be suitable for describing recurrent species composition, be practical for mapping, and adequate to support assessment under IUCN criteria.

2.1 | Criteria and indicators of risk status

Keith et al. (2013) published the IUCN framework for risk assessment, including five primary criteria (A–E)

and sub-criteria that address trends in distribution and in ecological condition. Criterion A and B address patterns in ecosystem type distribution, including trends in range wide extent (A) and current distributions where they are highly restricted (B). Criteria C and D address trends in environmental degradation and disruption of biotic processes, respectively. Criterion E is applied where a probabilistic model is available for assessing a given ecosystem type. Since these models are not currently available for any types addressed here, we did not attempt to apply Criterion E.

Under Criteria A, C and D, component sub-criteria address trends over different time periods. These include long-term trends, such as those taking place since industrial-scale land uses were initiated in the 18th century, trends of the past 50 years up to the present, and trends from the present over the next 50 years. Criterion B addresses only the present time period, but measures distribution of the ecosystem types in two forms (called extent of occurrence [EOO] and area of occupancy) using standardized spatial grids (Appendix S1). A third Criterion B3 is for ecosystem types occurring in very few, small locations, prone to effects of human activities or stochastic events; suitable for treatment with local data.

Under each sub-criterion, the relative severity in each trend indicates the relative risk of range wide ecosystem collapse for listing as CR, EN, or VU. Therefore, each sub-criterion addresses the relative proportion of the range wide distribution of the ecosystem impacted at different levels of relative severity, each corresponding to a level of risk of collapse. For example, under sub-criterion C3 for long-term environmental degradation, a type could surpass the threshold for listing as VU if >70% of its extent occurs with >70% relative severity, OR >90% of its extent occurs with >50% relative severity, OR >50% of its extent occurs with >90% relative severity (Appendix S1). Importantly, while the RLE methodology emphasizes establishment of a “collapse threshold” for each indicator, conceptual and technical challenges to doing so are well acknowledged (Bland et al., 2018) and establishing a bounded range of values for a collapse threshold is allowable. In this study, we established the 90% severity score for each indicator as the upper bound of the range of values for the ecosystem collapse threshold.

We used predicted distributions of the potential/historical extent of each ecosystem type as a foundation for comparison against current distribution and extent (for indicator scores under A3, B1, and B2) (Comer et al., 2020). We also used a series of maps of current condition overlain on current type distributions, to calculate indicator scores under C3 and D3. These included indicators of landscape intactness or condition (C3) (Hak & Comer, 2017), invasive plant species (C3) (Hak & Comer, 2020),

and alteration of natural fire regimes (D3) (Swaty et al., 2011) as appropriate for each type (Appendix S1).

Where data were evaluated but deemed inadequate for measurement, a listing of DD was applied, and if all criteria lacked data, then, no attempt was made to address a specific criterion and the type was listed as NE. Overall status is based on the most severe rating of any of the component sub-criteria, that is, if a type is listed as CR under by any indicator, it receives an overall listing of CR. Given inherent uncertainty in the application of these criteria and indicators to each assessment, we applied expert judgment to express ranges for both individual categories and the overall listing. For example, EN (VU-EN) indicates EN status for the ecosystem, but taking uncertainty in measurement into account, might be listed as either VU or EN (Bland et al., 2017). This option was used where one or more sub-criteria scores of DD introduced uncertainty into the overall RLE result (Appendix S1).

3 | RESULTS

Figure 1 provides a mapped overview of red list assessment results. The individual types are first displayed in terms of their approximate historical location and their overall RLE category. In preindustrial times (e.g., pre-1750) these types encompassed >95% of the land surface of temperate and tropical North America. One can see concentrations of CR ecosystems where historic patterns of land conversion for cropland agriculture have been concentrated in recent centuries. Temperate grasslands and savannas, especially where relatively humid climates supported tallgrass prairies and oak savanna, or the California Central Valley, as well as fertile bottomlands like the lower Mississippi River valley, encompass many of these types. EN ecosystems historically extended over large expanses of converted or degraded forests, wetlands, and grasslands from the Atlantic Coastal Plain and adjacent Appalachian Mountains, the Midwest, Canadian Prairies, Southern California coast, and Central Valley of Mexico. As compared with CR and EN listed types, VU types are much more varied in their distribution, encompassing forests in the Northeast and Midwest, Gulf Coastal Plain, mixed grass prairies and semidesert steppe of the western Great Plains, Rocky Mountains, and Pacific Northwest, as well as dry tropical forests throughout Mexico, Central America, and the Caribbean. The second image indicates current location of assessed ecosystems with all current land uses depicted in white (Figure 1). Land uses include intensive agriculture and urban or industrial forms of land use where natural ecosystems have been entirely converted. The presence of

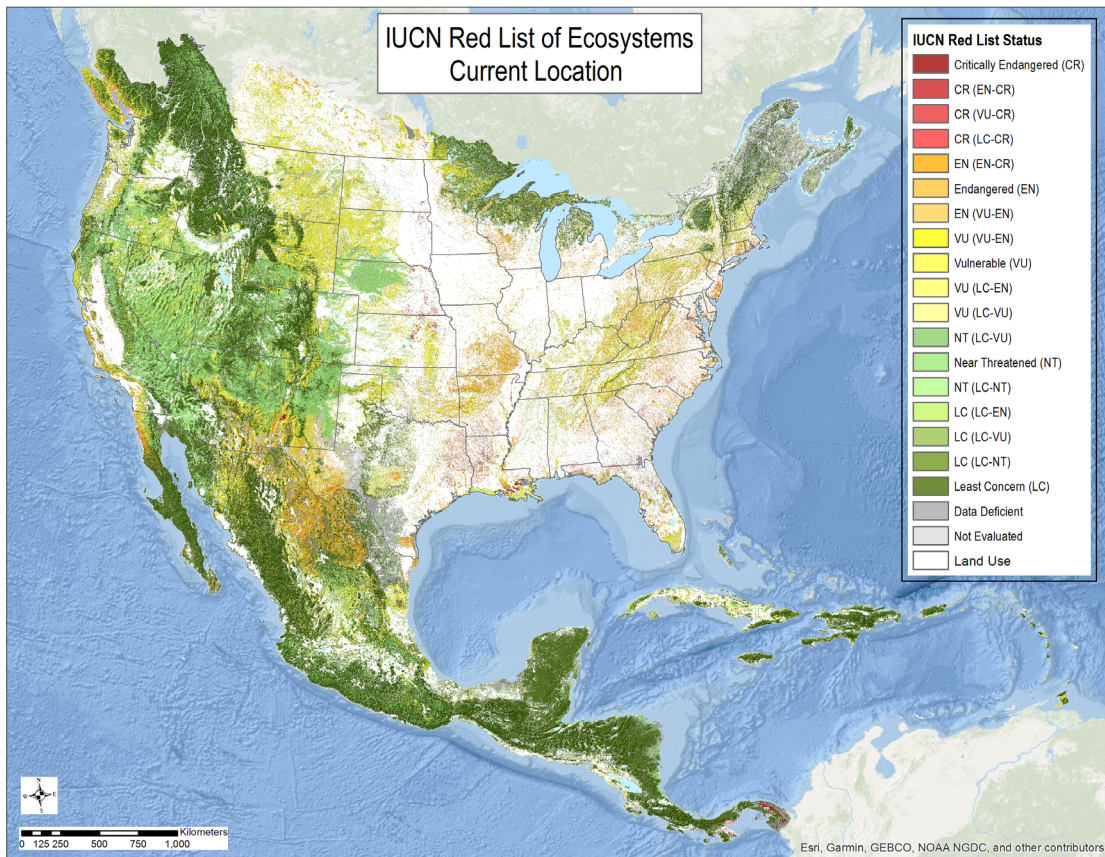
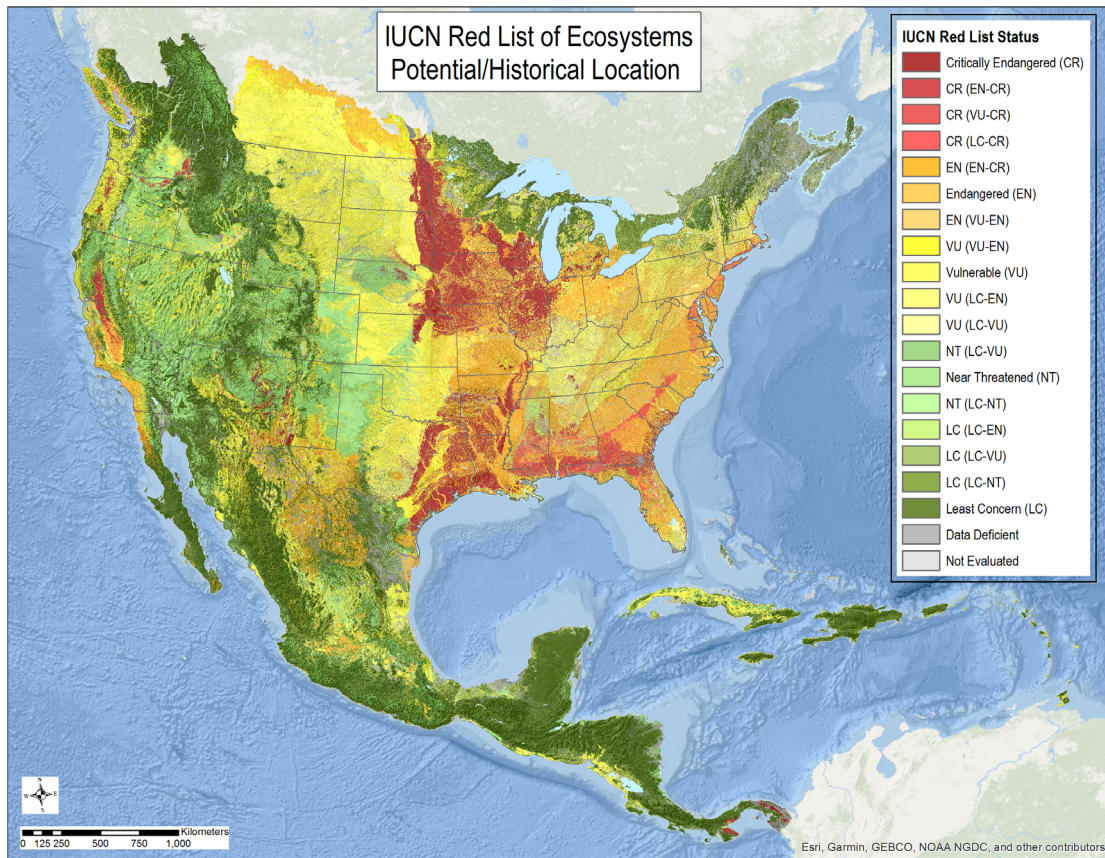


FIGURE 1 Mapped overview of Red List assessment results displayed by potential/historical location (top) versus current location (bottom)

TABLE 1 Count, percent, and extent (both potential/historic and current) of ecosystem types by overall Red List status for temperate and tropical North America. Types can only be listed within one category and range scores (e.g., CR [EN-CR] indicate uncertainty and possible range of scores)

RLE status	No. types	% Types	Total potential extent (km ²)	% Historic land area	Sum of current land area (km ²)	% Total land area
CR	41	6%	775,162	6.75%	78,947	1.05%
CR (EN-CR)	5	1%	76,014	0.66%	9083	0.12%
CR (LC-CR)	1	<1%	243	<0.01%	241	<0.01%
EN (EN-CR)	7	1%	134,846	1.17%	43,958	0.59%
EN	61	9%	1,041,279	9.07%	322,426	4.30%
EN (VU-EN)	23	4%	374,372	3.26%	275,106	3.67%
EN (LC-EN)	1	<1%	4834	0.04%	1995	0.03%
VU (VU-EN)	10	2%	135,895	1.18%	52,050	0.69%
VU	72	11%	2,672,396	23.28%	1,470,144	19.62%
VU (LC-EN)	10	2%	279,344	2.43%	213,990	2.86%
VU (LC-VU)	20	3%	166,242	1.45%	183,892	2.45%
NT (LC-VU)	3	<1%	37,972	0.33%	13,375	0.18%
NT	43	7%	1,438,823	12.53%	1,131,782	15.11%
NT (LC-NT)	3	<1%	122,358	1.07%	148,454	1.98%
LC (LC-EN)	1	<1%	17,056	0.15%	25,402	0.34%
LC (LC-VU)	6	1%	79,059	0.69%	57,818	0.77%
LC (LC-NT)	6	1%	45,002	0.39%	57,818	0.77%
LC	178	27%	3,308,093	28.81%	2,868,761	38.29%
DD	153	23%	732,060	6.38%	439,833	5.87%
NE	11	2%	40,629	0.35%	96,200	1.28%
Total	655		11,481,679	100%	7,491,275	100%

Abbreviations: CR, critically endangered; DD, data deficient; EN, endangered; LC, least concern; NT, near threatened; RLE, Red List of Ecosystems; VU, vulnerable.

these converted lands does not imply ecosystem “collapse,” but as noted above, remnants of natural ecosystems known to occur there historically were assessed and are now CR or EN.

Of the 655 types treated, 251 (38.3%) are listed as CR, EN, or VU (Table 1). Within these 251 are those listed with a range of values, such as VU (LC-EN). If we exclude types whose uncertainty is not a threatened status (i.e., NT, LC) the total drops to 219 (33.4%). Given uncertainty in listing types, 47 (7.2%) were listed as CR, 92 (14.0%) as EN, and 112 (17.0%) as VU. Additionally, 49 types (7.5%) were listed as NT and 191 (29.2%) as LC. There were 153 types (23.4%) that were DD, and 11 types (1.7%) were NE.

Table 1 summarizes aerial extent of ecosystems categorized by Red List status. Ecosystems categorized as CR historically encompassed over 7% of the area, but today occupy 1.2% (approximately 88,000 km²). Ecosystems categorized as EN historically encompassed about 13.6% of the study area, and today occupy 8.6%. Ecosystems

categorized as VU historically encompassed over 28.3% of the study area, and today occupy 25.6%. This pattern reflects the role of land conversion versus degradation as influences on Red List status. North American ecosystems categorized as CR are far more likely to have been converted to intensive land uses over almost all of their historical extent. In contrast, those categorized as VU retain larger proportions of their historical extent, but now occur in degraded condition.

Ecosystems listed as NT and LC are estimated to have historically encompassed 44% (7% for NT, 29% for LC, respectively) of the continental study area. Today these same types occupy fully 57.5% (16% for NT, 38% for LC, respectively) of the study area. While counter-intuitive, this reflects conditions where relatively common types have likely been altered in composition and are subsequently mapped today compositionally similar types. There are also cases where some forms of ecosystem degradation, such as wildfire suppression, have resulted in expansion of some types into the area historically occupied by types in

adjacent areas (Weisberg et al., 2007), resulting in an overall homogenization in vegetation.

Finally, the 23.4% of types listed as DD for this assessment historically encompassed some 6.4% of the area, and today occupy about 5.9%. While we can approximate the total area for these types combined, we cannot rely on the available data for individual estimates, and that is why these were treated as DD. Combining DD with those NE indicates that about 93% of the continental study area was treated in this assessment.

Figure 2 summarizes Red List status for ecosystems organized by vegetation formations as defined by the hierarchical taxonomy of the International Vegetation Classification (IVC) (Faber-Langendoen et al., 2014) (Appendix S1). The IVC formations describe vegetation with dominant and diagnostic growth forms that reflect

global macroclimatic conditions as modified by altitude, seasonality of precipitation, substrates, and hydrologic conditions. These concepts are comparable to the global ecosystem typology that emphasizes ecosystem function (Keith et al., 2020) and these relationships are captured in tabular form in our results detail (Appendix S3).

Figure 2 orders the IVC formations by the proportion of the 655 assessed ecosystem types within each of 24 IVC formations (Appendix S1), with cool temperate forest and woodland encompassing 19.1%, temperate flooded and swamp forest (13.3%), and temperate grassland and shrubland (11.6%), down to tropical thorn woodland with just 0.3%. From Figure 2, one can see relatively high proportions of types assigned to CR, EN, or VU among several of the most diverse formations (i.e., those with many types). Warm temperate forest and woodland types stand out

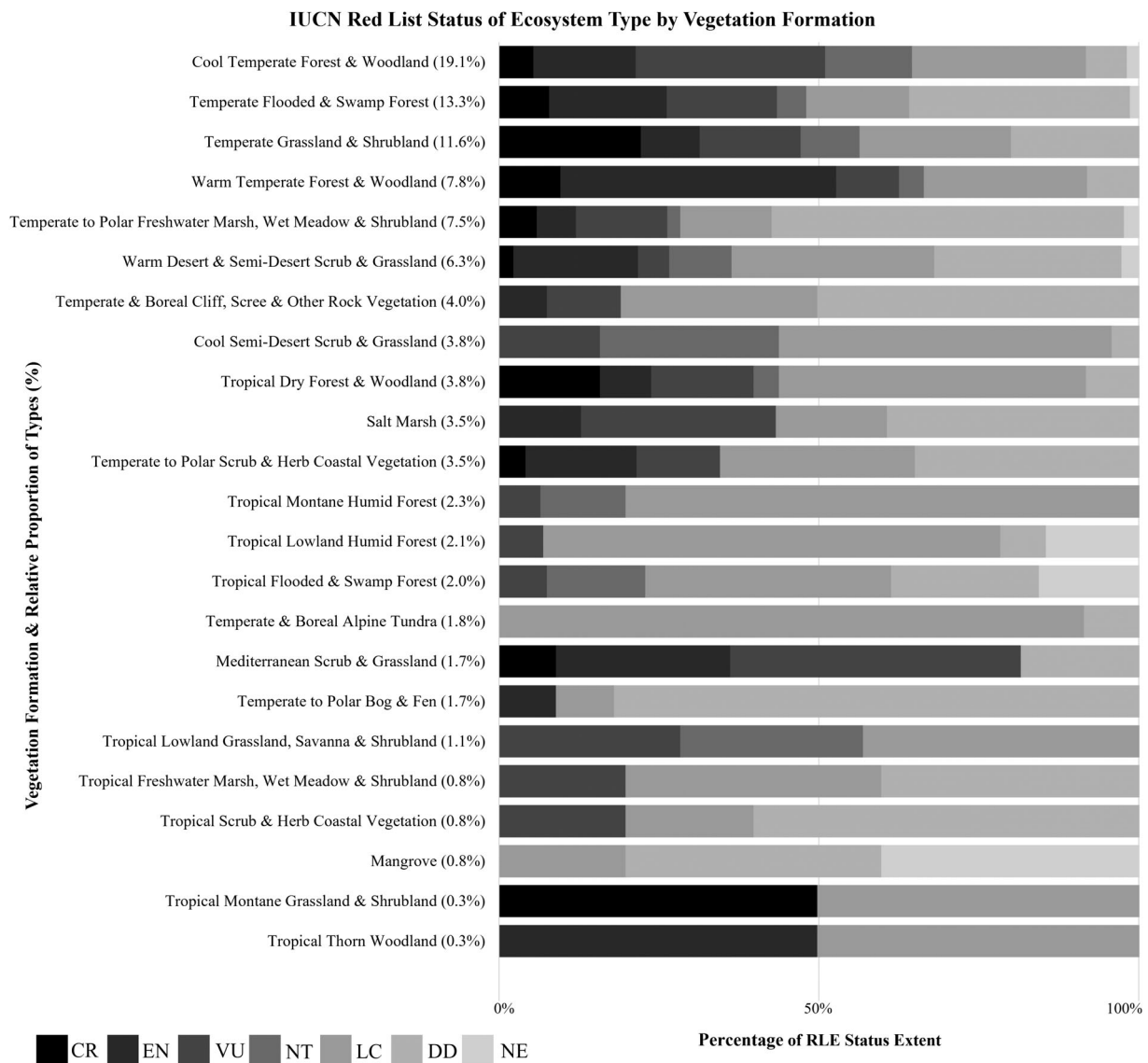


FIGURE 2 Red List status sorted by relative proportion of types classified within vegetation formations

with >50% assigned to CR, EN, or VU. These include ecosystems, such as Atlantic Coastal Plain Upland Longleaf Pine Woodland (EN). Similarly, temperate grassland and shrubland (e.g., Central Tallgrass Prairie), cool temperate forest and woodland (e.g., North-Central Interior Oak Savanna), tropical dry forest (e.g., Darien Deciduous to Xeric Forest), and Mediterranean scrub and grassland (e.g., California Central Valley and Southern Coastal Grassland) all stand out with >40% of types assigned to these Red List categories.

Among the 187 wetland ecosystems—each tied to one of the seven primary wetland formations (Figure 2)—6 (3.2%) are listed as CR (e.g., Great Lakes Wet-Mesic Lakeplain Prairie), 19 (10.2%) are EN (e.g., Lower Mississippi River Flatwoods), and 24 (12.8%) are VU (e.g., Great Plains Prairie Pothole). Overall, 46 types (24.6%) are listed as NT or LC. A total of 80 types (42%) of wetland types were listed as DD (Appendix S3).

3.1 | Factors contributing to at-risk conservation status

Each of the Red List criteria represent a different contribution to risk of collapse for a given ecosystem type. Anywhere from one to four criteria were used to assess ecosystem risk. See Table 2 for summary counts of ecosystem types within each of the Red List categories under each criterion. Reduction in geographic distribution since 1750 (A3), Restricted distribution (B1 and B2), Environmental degradation since 1750 (C3), and Disruption of biotic processes since 1750 (D3) are the five sub-criteria contributing to overall Red List scores. Results from each of the sub-criteria are briefly summarized below.

3.1.1 | A3. Reduction in distribution since 1750

Intensive land conversion was concentrated in the eastern USA and adjacent Canada starting in the 1700s, and even earlier in portions of Mesoamerica and Caribbean. Much upland and wetland conversion for agriculture throughout the North American midsection made this region a “breadbasket” for the world food production (Gauthier et al., 2003). Harvesting of temperate forests for timber generally proceeded over large areas in an east-to-west pattern throughout the 1800s and up through the mid-20th century (Whitney, 1996), with many areas subsequently converted for agricultural use or development. While land use patterns have continued to change in selected areas, such as with ongoing deforestation in Central America and rapidly urbanizing

metropolitan areas (Grau & Aide, 2008), the past 50 years have likely seen slower patterns of land conversion than in some other parts of the world (Brown et al., 2005). Given a lack of adequate data to treat sub-criterion A1 (reduced distribution over the past 50 years) we focused on A3 (Appendix S1).

For the 421 types assessed under A3, 21% (88 types) are threatened in some form, with 26 types (6%) listed as CR (>90% loss), 25 (5.9%) listed as EN (>70% loss), and 37 (8.7%) listed as VU (>50% loss). These types are concentrated in grassland (e.g., Texas Blackland Tallgrass Prairie), savanna (e.g., California Central Valley Mixed Oak Savanna), and forest (e.g., North-Central Interior Maple-Basswood Forest) lands found on highly productive soils that were historically targeted for conversion for agriculture. Other types were primarily affected by timber harvest and other more extensive land uses like forestry and grazing (e.g., Southern Atlantic Coastal Plain Wet Pine Savanna and Flatwoods) or have been converted for urban and industrial land uses (e.g., Southern California Coastal Scrub) (Appendix S3).

3.1.2 | B1. Restricted geographic distribution

Sub-criterion B1 addressed the restricted current distribution of ecosystem types. Ecosystems with a very restricted distributions have an increasing probability of catastrophic or spatially contagious events that could result in range wide ecosystem collapse (Gaston & Fuller, 2007). A standard way to measure sub-criterion B1—the EOO—is to use a minimum convex polygon that encompasses the current range of each type and to evaluate ongoing threat and decline. Thresholds are set for VU at <50,000; EN <20,000; and CR <2000 km² (Appendix S1).

For the 496 types assessed under this sub-criterion, 31 types (6.2%), are among those listed as CR, EN, or VU under this criterion. Most are grassland and forest types found in restricted substrates or climates, including Klamath-Siskiyou Lower Montane Serpentine Mixed Conifer Woodland, South Florida Cypress Dome, or “patch prairies” like Eastern Highland Rim Prairie and Barrens in central Tennessee (Appendix S3).

3.1.3 | B2. Restricted geographic distribution

Sub-criterion B2 is the “area of occurrence”—measures using the number of 100 km² spatial units that encompass the current range wide distribution of each type, followed by an evaluation of ongoing threat and decline. Thresholds are set for VU at <5000 km², EN <2000 km², and CR <200 km² (Appendix S1).

Red List status	Count of types					Overall status
	A3	B1	B2	C3	D3	
CR	44	1		2	24	41
CR (EN-CR)						5
CR (LC-CR)						1
EN (EN-CR)						7
EN	54	14	2	23	74	61
EN (VU-EN)				11	1	23
EN (LC-EN)						1
VU (VU-EN)	1					10
VU	60	16	7	43	58	72
VU (LC-EN)						10
VU (LC-VU)						20
NT (LC-VU)						3
NT	19		3	46	37	43
NT (LC-NT)						3
LC (LC-EN)	1				1	1
LC (LC-VU)				1		6
LC (LC-NT)						6
LC	221	475	493	22	273	178
DD	249	137	136	397	162	153
NE	6	12	14	110	25	11
Total	655	655	655	655	655	655

Abbreviations: CR, critically endangered; DD, data deficient; EN, endangered; LC, least concern; NT, near threatened; RLE, Red List of Ecosystems; VU, vulnerable.

TABLE 2 Count of types and by overall RLE status and RLE subscores for temperate and tropical North America

For the 496 types assessed under this sub-criterion, just 2 types were listed as EN and 7 types as VU, including California Mesic Serpentine Grassland, Caribbean Montane Wet Serpentine Woodland, San Lucan Evergreen Forest and Woodland, and Talamancan Upper Montane Meadow, found in southern Costa Rica and adjacent Panama (Appendix S3).

3.1.4 | C3. Environmental degradation since 1750

For red listing, our indicators of environmental degradation focused on abiotic structures and processes that directly influence biotic composition for the ecosystem type. Indicators include wildfire regimes in fire-dependent ecosystems, and geophysical processes in many specialized ecosystems. The indicators are assessed across the entire distribution of the ecosystem type, so that the proportional extent of environmental degradation can be quantified at several levels of relative “severity.” Relative severity at <30–50% indicates relatively intact natural

conditions and relative severity >90% implies that conditions are rapidly approaching collapse (Bland et al., 2018).

Wildfire regime (frequency, intensity, patch size, etc.) is central to the function of many North American ecosystems, shaping vegetation structure and composition of forests, shrublands, and grasslands, especially throughout temperate and boreal latitudes (Kilgore, 1981; Nowacki & Abrams, 2008). We selected *fire regime departure* as a primary indicator suitable for measuring relative degradation of key ecological process common to 147 upland and wetland ecosystems in temperate North America. Because wildfire suppression and alteration has been pervasive across temperate North America since the early 20th century, modern conditions reflect the cumulative effect of policy and practice over 100 years. Therefore, we applied existing departure measures to C3, expressing environmental degradation since preindustrial times (Appendix S1).

Of the 147 types assessed using this sub-criterion, 78 (53%) were listed as CR, EN, or VU using the fire regime indicator of long-term environmental degradation, with only 2 types (1.3%) listed as CR, 23 (15.6%)

listed as EN, and 53 (36%) listed as VU. Types in these categories tended to be strongly fire-dependent forests and grasslands that have been subjected to extensive landscape fragmentation and fire suppression. These ecosystem types included many forests types of the Atlantic and Gulf Coastal Plain (e.g., Florida Longleaf Pine Sandhill), central Appalachian, Ozark, and Ouachita mountains (e.g., Ozark-Ouachita Dry Oak Woodland), dry forests of the Great Lakes and Northeast regions (e.g., North-Central Interior Dry Oak Forest and Woodland, Northern Atlantic Coastal Plain Pitch Pine Barrens), woodlands of the intermountain West (e.g., Southern Rocky Mountain Ponderosa Pine Woodland) and chaparrals in California (e.g., Northern and Central California Dry-Mesic Chaparral). Wildfire has also been introduced through invasive species into some subtropical desert types (e.g., Chihuahuan Mixed Desert and Thornscrub) (Appendix S3).

3.1.5 | D3. Disruption of biotic processes and interaction since 1750

These measures focus on elements of biotic composition, structure, or processes that directly alter biotic composition for the ecosystem type. We assembled two primary indicators of biotic disruptions and combined them as appropriate for different groups of related ecosystem types. The landscape fragmentation indicator assesses pervasive effects of fragmentation on species dispersal, introduction and spread of invasive species, and other disruptions of biotic processes (Fischer & Lindenmayer, 2007). Second, since many assessed types occurring in western interior cold deserts are known to be affected by invasive annual grass expansion, we aimed to establish an indicator of relative invasion severity. In parallel to environmental degradation measures, the relevant forms of biotic process disruptions that we can measure have been pervasive across this area since the 18th and 19th centuries, so modern conditions reflect the cumulative effect of policy and practice of that 200⁺ year timeframe. Therefore, we applied these two indicators to D3, expressing disruption to biotic processes and interactions that have been ongoing since preindustrial times (Appendix S1).

Of the 465 types assessed the two indicators for this sub-criterion, 155 (33%) were listed as CR, EN, or VU; with using landscape condition and invasive plant models as indicators of long-term disruption of biotic processes. Of these 155, 24 types (15.4%) listed as CR, 72 (46%) listed as EN, and 48 (31%) listed as VU. These types tended to be concentrated among eastern forests, wetlands, and prairies (e.g., Northeastern Interior Dry-Mesic Oak Forest) as well as forests of the Atlantic and

Gulf Coastal Plain (e.g., Northern Atlantic Coastal Plain Hardwood Forest) (Appendix S3).

4 | DISCUSSION

The RLE provides a powerful indicator of ecosystem health for governments and civil society to consider when addressing ecosystem level conservation. For example, places supporting threatened ecosystems (CR, EN, or VU) may be prioritized for investments in ecological restoration and sustainable development. Drawing attention to areas with CR, EN, and VU ecosystems can be a powerful catalyst for wider conservation actions in those places. The Key Biodiversity Areas (KBAs) provide one example of how to integrate global Red List categories (CR-VU) into the process of identifying conservation sites (Smith et al., 2019). Sites that can encompass 5% of the current global extent of CR or EN ecosystems, or 10% of the same for VU ecosystems, trigger identification for inclusion in the global network of Key Biodiversity Areas. Landscapes supporting NT and LC ecosystems should also be well represented in more comprehensive conservation plans in order to minimize future loss of vital ecological processes (Aycrigg et al., 2013; Comer et al., 2018; Comer et al., 2020). The Post-2020 Global Biodiversity Framework to conserve 30% of lands by 2030 should certainly include rigorous analysis of ecosystem representation. Ecosystem distributions used in this analysis directly support those efforts.

Red List criteria, along with maps used to score indicators of these sub-criteria, point to more specific triggers of ecosystem decline (e.g., landscape fragmentation, invasive species impacts, fire regime alteration) and the places where targeted threat abatement may be most appropriate. Given increasing urgency to document ecosystem status and trends and report progress in international agreements like the Convention on Biodiversity, indices such as those measuring relevant change in ecosystem area and health (Nicholson et al., 2020; Rowland et al., 2019) are being proposed that build directly on Red List sub-criteria.

4.1 | Major drivers of risk

Although humans have affected ecosystems in North America throughout the Holocene, a more pronounced human footprint coincided with industrial revolution followed by waves of human population growth and expansion. Criterion A3 effectively addresses the long-term trends in land conversion for agriculture and subsequent urban or industrial land uses, and it is a major contributor to the current Red List status of many ecosystems. However, ecosystem alterations, often radiating out from lands

converted to more intensive land uses, also have a pervasive effect on ecosystem function and health. Patterns emerging from our indicators for Criteria C and D, including landscape condition, alteration to wildfire regimes for fire-dependent temperate ecosystems, suggest that a very large proportion of these ecosystems occur today in an ecologically compromised state.

4.2 | Evaluation of Red List methods

Our continental application of RLE protocols provided a useful test of proposed IUCN methods, including aspects of the process relating to ecosystem classification, mapping, assessment, and reporting.

4.2.1 | Ecosystem classification

A primary challenge to red listing ecosystems is a limited global consensus on ecosystem classification. We benefited from a relatively long history of classification development in the Americas and recent coordinated effort that has led to the classifications used here. There is also expanding coordination among ecologists involved in vegetation-based classification, offering us the opportunity to structure terrestrial ecosystems within a hierarchical taxonomy. Our analysis indicates that the type and scale of typology we used is both feasible for red listing and retains sufficient thematic detail for subsequent conservation action on the ground (Comer et al., 2016; Neely et al., 2001). These units align approximately with the “Group” or “Alliance” scales of the hierarchical taxonomy of International Vegetation Classification (IVC) (Faber-Langendoen et al., 2014). Given that this effort provides a representative continental scale coverage extending over temperate and tropical latitudes, the number of types and proportional area encompassed by this study would suggest that a similar global terrestrial ecosystem classification might include 5–7000 units. Into the future, use of the IVC also provides the ability to apply these assessments at multiple scales, from macrogroup (e.g., Ferrer-Paris et al., 2019) to alliance. In the United States and Canada, applying RLE assessments in conjunction with NatureServe conservation status assessment also provides the ability to conduct assessments at subnational (state, province, territorial) scales (Master et al., 2012).

4.2.2 | Mapped distributions (A3, B1, B2)

Advances in data and methods for ecosystem mapping made this assessment possible, and with additional

ecosystem classification and consolidation of georeferenced ecosystem observations, the distribution information used here is feasible across the globe. Keith et al. (2013) recommended a distribution map scale of approximately 450 m pixel resolution. Our experience suggests that this resolution, or perhaps a finer resolution of 270 m pixel resolution, is both desirable and feasible globally. However, our experience here using data at 30–90 m resolution also illustrates the limitations of treating classification units that naturally occur at relatively fine spatial grain, such as localized wetland types, some riparian communities, or coastal ecosystem types. Over 20% of types lacked adequate distribution data to apply some or all of the A–D criteria. This can result from national or continental mapping efforts that lack sufficient input data locally to adequately map type distributions for some rare and localized types. For more specialized ecosystem types naturally occurring in small patches or in linear configuration, there is no substitute for systematic field documentation.

The IUCN sub-criteria B1 and B2 (1–2), while providing one standardizing mechanism to accommodate variable distribution data, rely on numerical thresholds (rather than percentage thresholds) that can interact with the thematic resolution the classification used in assessment. Although these thresholds have been tested through simulations (Keith et al., 2017; Murray et al., 2017) some 4% of the types assessed here are listed as threatened under B1 or B2. The established IUCN thresholds would benefit from additional comparative analysis of our data with cases where other classification scales were used (e.g., Ferrer-Paris et al., 2019), informing this aspect of RLE assessment.

4.2.3 | Environmental degradation (C) versus disruption of biotic processes and interactions (D)

While treated separately in this study, from our experience these two categories can be hard to distinguish because of interactions between the two. One clear case from our analysis includes invasive plants (biotic disruption) introduced into cold desert shrubland directly affect wildfire regimes (environmental degradation). This challenge is compounded by the need to acquire appropriate data sets to measure each of these, where spatial models developed to address condition must combine factors to be effective.

Related to this is the challenge of defining a clear threshold of ecological collapse, and then identifying where that threshold has been crossed in all locations of the ecosystem across its range (Bland et al., 2018). We

contend that what one is attempting to achieve here is more a categorization of conditions with a plausible range (translated here to an upper bound of 90% severity), rather than determining whether or not any seemingly precise threshold has been crossed.

Climate change: Climate change effects may interact with a number of RLE sub-criteria. Given that some effects are already manifested in some ecosystems, this should be an area of concentrated attention for RLE assessments. We particularly point to two primary sub-criteria, A2 (a and b) for change in extent, or C2 (a and b) for environmental degradation, forecasted to occur over a 50-year time frame including the present. For example, under A2, sea level rise and the predicted loss in extent of coastal ecosystems may be one common case. For C2, our index of climate change vulnerability for ecosystems and habitats (Comer et al., 2019) may be used to estimate the proportional extent of each ecosystem type facing climate change threats at multiple levels of severity. This index combines measures of climate exposure against a series of measures for climate change sensitivity and adaptive capacity to score each type—by 100 km² area of its distribution—in categories from very high, high, moderate, to low relative severity of climate change vulnerability. We have begun to accumulate results from our index for over 50 terrestrial ecosystems addressed in this analysis, but we chose not to include them here until we have more complete results for North America.

4.2.4 | Collapsed (CO) status

In this analysis, we did not identify any ecosystem as “CO” range wide. Perhaps, as we continue to track these ecosystems over time, that may yet occur. It is safe to presume that, in a continent that is as heavily transformed as North America, there were ecosystems that were never documented prior to their elimination (Noss, 2012).

4.2.5 | Criterion E—Quantitative model prediction of range wide collapse

For the terrestrial ecosystem types treated here, it remains unclear if quantitative risk models could be devised to predict range wide collapse within a reasonable bounds of uncertainty. It is very difficult to account for all prevalent risk factors when ecosystem types extend over large areas and are affected by similarly complex patterns of land use and ecosystem stress. This criterion is more likely to apply to narrowly endemic terrestrial ecosystems (Burns et al., 2015)—or aquatic ecosystems like

the case of the Aral Sea in Central Asia (Micklin, 2007)—with naturally restricted distributions where inherent connectivity among its locations could support a model with sufficient predictive power.

4.2.6 | Coping with uncertainty

Given the complexity of ecosystems and our limited knowledge and data, there will always likely be uncertainty involved with the red listing process for ecosystems. With the continental scope of this analysis, and our reliance on remote sensing based spatial data sets, we utilized the option to assign categories to types within a plausible range like EN (VU-EN). This provided a practical indication of our confidence in overall scores. Plausible range was almost all narrow (e.g., CR-EN, EN-VU, VU-NT, or VU-LC) indicating that the ecosystem may truly fall in either of two adjacent RLE risk categories. This was often triggered by DD scores from some key component measures, such as A3 or C3. A3 scores of DD resulted most often from challenges in mapping potential/historic distribution of the type of interest. Type-specific knowledge of the C3 measure of Fire Regime Departure led to expert judgments to limit the effect of that measure relative to other component analysis measures. These were two primary areas pointing to types and indicators that could use additional investments in data and analysis to increase our confidence in their scores.

4.3 | Building on this analysis

Of the 655 types treated here, 24% were designated DD based on limitations in available data. These types often require more specialized mapping, or targeted data on their ecological condition, to move forward with assessment. For example, a number of wetland types only occur in relatively small patches or narrow riparian zones, and some upland types are found in narrow coastal zones or on rare geophysical substrates. Analyses for A1 could be targeted for areas and ecosystem types (e.g., surrounding major urban areas) where urban land conversion has been most concentrated in recent decades. A2 could subsequently be assessed in targeted locations either through land use growth models, or as noted above, integrating climate change effect through models of sea level rise.

We hope to make data and tools used in this assessment widely available to other researchers to catalyze expanded usage and refinement of the RLE in North America.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Patrick J. Comer: Conceptualized effort, gathered data and support, designed methodology and conducted analysis, drafted and finalized manuscript and appendices. John C. Hak: Gathered data, conducted spatial analysis, documented data, reviewed and edited manuscript. Emily Seddon: Supported analysis and graphics for manuscript.

DATA AVAILABILITY STATEMENT

All data products are available either on public web pages (https://transfer.natureserve.org/download/Long-term/Ecosystems_NA_RLE/) or upon request of the corresponding author (pat_comer@natureserve.org; pcomer0318@gmail.com).

ETHICS STATEMENT

All data used are publicly accessible and institutional ethics review was not required.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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