Conservation Biology

Research Note

Vascular plant extinction in the continental United States and Canada

Wesley M. Knapp,[1] Anne Frances,[2] Reed Noss,[3] Robert F. C. Naczi,[4] Alan Weakley,[5] George D. Gann,[6] Bruce G. Baldwin,[7] James Miller,[8] Patrick McIntyre,[9] Brent D. Mishler,[10] Gerry Moore,[11] Richard G. Olmstead,[12] Anna Strong,[13] Kathryn Kennedy,[14] Bonnie Heidel,[15] and Daniel Gluesenkamp[16]

[1]North Carolina Natural Heritage Program, Asheville, NC, 28805, U.S.A., email Wesley.knapp@ncdcr.gov
[2]NatureServe, 2550 South Clark Street, Suite 930, Arlington, VA, 22202-3926, U.S.A.
[3]Florida Institute for Conservation Science, 112 Half Moon Trail, Melrose, FL, 32666, U.S.A.
[4]Institute of Systematic Botany, New York Botanical Garden, 2900 Southern Blvd., Bronx, NY, 10458-5126, U.S.A.
[5]Biology Department, North Carolina Botanical Garden, University of North Carolina at Chapel Hill, Campus Box 3280, Chapel Hill, NC, 27599-3280, U.S.A.
[6]The Institute for Regional Conservation, 100 E. Linton Blvd. #302B, Delray Beach, FL, 33483, U.S.A.
[7]Jepson Herbarium & Department of Integrative Biology, University of California, 1001 Valley Life Sciences Bldg. #2465, Berkeley, CA, 94720-2465, U.S.A.
[8]Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis, MO, 63110, U.S.A.
[9]NatureServe, 2550 South Clark Street, Suite 930, Arlington, VA, 22202-3926, U.S.A.
[10]University and Jepson Herbaria & Department of Integrative Biology, University of California, 1001 Valley Life Sciences Bldg. #2465, Berkeley, CA, 94720-2465, U.S.A.
[11]National Plant Data Team, United States Department of Agriculture, 2901 East Gate City Blvd., Suite 2100, Greensboro, NC, 27041, U.S.A.
[12]Department of Biology and Burke Museum, University of Washington, Seattle, WA, 98195, U.S.A.
[13]Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, TX, 78744, U.S.A.
[14]United States Forest Service, 333 Broadway Blvd. SE, Albuquerque, NM, 87102, U.S.A.
[15]Wyoming Natural Diversity Database, University of Wyoming1000 E. University Avenue, Laramie, WY, 82071, U.S.A.
[16]California Native Plant Society, 2707 K Street, Suite 1, Sacramento, CA, 95816, U.S.A.

Abstract: Extinction rates are expected to increase during the Anthropocene. Current extinction rates of plants and many animals remain unknown. We quantified extinctions among the vascular flora of the continental United States and Canada since European settlement. We compiled data on apparently extinct species by querying plant conservation databases, searching the literature, and vetting the resulting list with botanical experts. Because taxonomic opinion varies widely, we developed an index of taxonomic uncertainty (ITU). The ITU ranges from A to F, with A indicating unanimous taxonomic recognition and F indicating taxonomic recognition by only a single author. The ITU allowed us to rigorously evaluate extinction rates. Our data suggest that 51 species and 14 infraspecific taxa, representing 33 families and 49 genera of vascular plants, have become extinct in our study area since European settlement. Seven of these taxa exist in cultivation but are extinct in the wild. Most extinctions occurred in the west, but this outcome may reflect the timing of botanical exploration relative to settlement. Sixty-four percent of extinct plants were single-site endemics, and many occurred outside recognized biodiversity hotspots. Given the paucity of plant surveys in many areas, particularly prior to European settlement, the actual extinction rate of vascular plants is undoubtedly much higher than indicated here.

Keywords: conservation, extinction rate, rarity, single-site endemics, taxonomy

Article impact statement: *The number of presumed extinct plants from the continental United States and Canada is much greater than previously recognized.*

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Extinción de las Plantas Vasculares en Canadá y los Estados Unidos Continentales

Resumen: Se espera que las tasas de extinción aumenten durante el Antropoceno. Todavía desconocemos las tasas de extinción actuales de las plantas y muchos animales. Cuantificamos las tasas de extinción de la flora vascular de los Estados Unidos Continentales y Canadá a partir del asentamiento de los europeos. Recopilamos datos sobre especies aparentemente extintas mediante la consulta de bases de datos sobre conservación, búsquedas en la literatura y el escrutinio de la lista resultante con botánicos expertos. Ya que la opinión taxonómica varía ampliamente, desarrollamos un índice de incertidumbre taxonómica (ITU). La ITU abarca desde la A hasta la F, en donde la A indica un reconocimiento taxonómico unánime y la F indica el reconocimiento taxonómico por un sólo autor. La ITU nos permitió evaluar rigurosamente las tasas de extinción. Nuestros datos sugieren que 51 especies y 14 taxones infraespecíficos, que en conjunto representan a 33 familias y a 49 géneros de plantas vasculares, se han extinguido en nuestra área de estudio desde el asentamiento de los europeos. Siete de estos taxones existen en cultivos, pero se encuentran extintos en vida libre. La mayoría de las extinciones ocurrieron en la parte oeste del área de estudio, aunque este resultado puede reflejar el momento de la exploración botánica en relación con el asentamiento europeo. El 64% de las plantas extintas eran endémicas de un sitio único y muchas tuvieron presencia fuera de los puntos calientes de biodiversidad. Dada la escasez de los censos botánicos en muchas áreas, particularmente previo al asentamiento europeo, la tasa actual de extinción de las plantas vasculares es sin duda mucho más alta de lo que se indica en este estudio.

Palabras Clave: conservación, endemismos de sitio único, rareza, tasa de extinción, taxonomía

Introduction

Much recent attention has been devoted to the rates at which plants and animals are going extinct (e.g., Pimm & Raven 2000; Ceballos et al. 2015; Pelletier et al. 2018; Humphreys et al. 2019). Although we know that current extinction rates far surpass background rates (Pimm et al. 2014; Ladel 2019), quantifying extinctions is still critically important for improving the accuracy of extinction estimates and predictions. Reliable information on extinction, threats, and recovery will help conservation practitioners prevent extinctions more effectively. Some 450,000 species of vascular plants are extant globally, approximately 3.5 times the number of vertebrate species (Pimm & Joppa 2015; Ceballos et al. 2015). Because plants are the foundation for most terrestrial ecosystems, documenting plant extinctions is an urgent need.

Plant extinctions have been analyzed globally (Pelletier et al. 2018; Humphreys et al. 2019) and for California (Rejmánek 2018). However, a detailed analysis of plant extinctions has not been conducted for the continental United States or Canada. We thoroughly analyzed the extinct vascular plants of the continental United States and Canada (i.e., contiguous United States, Alaska, and Canada) based on literature review, herbarium research, and fieldwork. These data on extinct plants provide a baseline for monitoring extinctions during the Anthropocene (Waters et al. 2016) and are intended to improve the assessment of extinction rates over time.

Methods

We created our list of presumably extinct plants from numerous sources, starting with recent literature (e.g., Flora of North America (1993-2019), state and regional floras, and monographs). We vetted these data with conservation databases (e.g., NatureServe Explorer (2020*a*) and Jepson eFlora (2020)). Finally, we consulted regional experts to assess the taxonomic merit and the extinction status of the list.

To evaluate which published names represent meritorious taxa, we developed an index of taxonomic uncertainty (ITU), a new method to determine scientific consensus of a taxon. Publications on species' extinctions typically reference a single taxonomic authority, largely omitting the discussion of taxonomic uncertainty (Ceballos et al. 2015; Pelletier et al. 2018; Humphreys et al. 2019; Le Roux et al. 2019). Yet, taxonomic uncertainty is critically important for putatively extinct taxa. Extinct taxa have higher levels of taxonomic uncertainty than extant taxa because researchers cannot conduct robust genetic research from very small samples, often limited to herbarium specimens rather than live plants.

To calculate the ITU, we vetted each name by reviewing the literature, mostly monographic and floristic treatments, in which each taxon was critically evaluated against other related taxa by an expert. We did not use taxonomic databases to calculate the ITU because these often reflect other published literature rather than novel taxonomic evaluations. If authors of consulted literature universally accepted a taxon as a distinct entity, regardless of taxonomic rank, it received a score of A. If a taxon was placed in synonymy by some authors but the majority recognized it as distinct, it received a score of B. If the name was usually placed in synonymy but numerous treatments still recognized the taxon as valid, a score of C was applied. Scores of D and F were applied if a taxon was rarely recognized (i.e., <85% of the time) or never recognized after initial publication of the name, respectively. If a name did not appear as a recognized taxon in a floristic work and was not listed in synonymy, the source was not used in the ITU calculation. We included extinct taxa with and ITU of A, B, or C. Taxa with scores of D and F were excluded but are listed in Supporting Information.

To determine whether taxa should be assigned a conservation status of extinct, we followed NatureServe methods (Faber-Langendoen et al. 2012), the North American standard, because most plants (species and infraspecies) of the United States and Canada have been assessed at least once. The International Union for Conservation of Nature (IUCN) Red List of Threatened Species (hereafter red list), the international standard, includes assessments for <15% of plant species in the continental United States and Canada. NatureServe assessment categories are presumed extinct (GX for species; TX for infraspecies) and possibly extinct (GH for species; TH for infraspecies), whereas IUCN uses extinct (EX) and critically endangered (possibly extinct) (CR[PE]). For both systems, categories are based on previous survey effort and the likelihood of rediscovery. Due to the high degree of uncertainty surrounding modern extinctions, we use the term *extinct* for simplicity when discussing both categories.

Taxonomically meritorious taxa thought to be extinct were assessed using NatureServe's Conservation Rank Calculator (NatureServe 2020*b*), and taxa categorized as GX, TX, GH, or TH were considered extinct. The red list currently shows only 2 of our 65 extinct taxa as extinct, critically endangered (possibly extinct), or extinct in the wild (IUCN 2019). To further compare our results with the red list, we assessed a subset of 11 extinct plants with the IUCN extinction assessment tool (Akçakaya et al. 2017; Keith et al. 2017; Thompson et al. 2017; IUCN 2020). These 11 were selected because they were well dispersed across the study area, represented a diversity of distributions (i.e., single site endemics vs. broad geographic ranges), and sufficient information was available to support assessment decisions.

Each extinct taxon was searched through the Botanic Gardens International Database (BGCI 2019) to determine whether any institution reported having ex situ collections of extinct species. Positive findings were further vetted with each garden.

Results

We found that 65 taxa (51 species and 14 infraspecific taxa) of vascular plants from the continental United States and Canada have gone extinct or possibly extinct since European settlement (33 GX and 32 GH). Based on 1565 as the date of first European settlement and that the native flora of the study area is about 15,882 taxa (USDA PLANTS Database 2020), the extinction rate was 0.14 taxa/year or 1.4 per decade. The extinct flora represented 0.4% of the total flora and included 5 small trees, 8 shrubs, 37 perennial herbs, and 15 annual herbs (Table 1). These extinctions represented 33 families and 49 genera (Table 1). Asteraceae (8), Fabaceae (7), Rosaceae (7), and Boraginaceae (6) had the most extinctions, whereas Cyperaceae (1), Orchidaceae (1), and Poaceae (2) were poorly represented. The most affected genera were *Crataegus* (4), *Astragalus* (3), *Cryptantha* (3), and *Plagiobothrys* (3). *Cryptantha* and *Plagiobothrys*, both in the Boraginaceae, represented all known extinctions for this family. Supporting Information includes data on geographic locations of the extinct plants, date of last observation, life history, habitat, putative cause of extinction, family, whether the taxon was known only from the type, and general notes. Figure 1 shows locations of extinct plants.

Extinctions were heavily concentrated in the southwestern United States (Fig. 1). The U.S. states with the most extinctions were California (19), Texas (9), and Florida and New Mexico (4 each). Canada had a single extinction. The New England states had 5 extinctions, despite not being a biodiversity hotspot. Of the extinct taxa, 42 (64%) were apparently single-site endemics (having an extremely narrow and clustered distribution with an area of occupancy of ≤ 6, 1-km^2 grid cells). Twenty taxa (31% of the extinct plants) were known only from the type specimens. Since 1995, 4 extinct species from the continental United States were described as new to science from herbarium vouchers (Mosyakin 1995; Brown 2000; Johnston & Ertter 2010; Knapp et al. 2020*b*).

We document 7 plants as extinct in the wild (EW), defined here as a species with no naturally occuring populations, surviving only in cultivation (Table 1). Of the 7 EW plants, 4 were not previously recognized as such before this study. Two extinct plants are reported from ex situ gardens in the Botanic Gardens Conservation International Database (BGCI 2019). These identifications are yet to be confirmed by reporting institutions and are denoted as EW? (Table 1). Three additional species were reported from BGCI as having ex situ collections, but communications with the reporting institutions revealed these to be misidentifications.

Forty-one taxa had ITUs of A, 14 of B, and 9 of C. A single taxon was so recently recognized as distinct that an ITU could not be calculated. An additional 80 taxa were determined to have ITUs of D or F.

Our red list assessments resulted in all 11 taxa categorized as EX or CR(PE). Compared with NatureServe assessments, in most cases, GX aligned with EX and GH aligned with CR(PE); however, in 2 cases, the red-list category was EX and NatureServe's category was GH. In the case of the 2 published red-list assessments, the NatureServe and IUCN Red List assessments aligned (Supporting Information).

Table 1. Extinct plants of the continental United States and Canada with extinction qualifier, taxonomic family, life-history grouping, geographic distribution, and corresponding A, B, or C (ITU) score.

Scientific name (extinction qualifier)[a]	*Family*	*Life history*[b]	*Distribution*[c]	*NatureServe rank*[d]	*ITU*[e]
Agalinis caddoensis Pennell	Orobanchaceae	AH	LA	GH	A
Arctostaphylos franciscana Eastw. (EW)	Ericaceae	S	CA	GHC	A
Astilbe crenatiloba (Britton) Small	Saxifragaceae	PH	TN	GX	B
Astragalus endopterus (Barneby) Barneby	Fabaceae	AH	AZ	GH	A
Astragalus kentrophyta A. Gray var. *douglasii* Barneby	Fabaceae	PH	WA	G5TX	A
Astragalus robbinsii (Oakes) A. Gray var. *robbinsii*	Fabaceae	PH	VT	G5TX	A
Atriplex tularensis Coville	Chenopodiaceae	AH	CA	GX	A
Blephilia hirsuta (Pursh) Benth. var. *glabrata* Fern.	Lamiaceae	PH	VT	G5TH	B
Boechera fructicosa (A. Nelson) Al-Shehbaz	Brassicaceae	PH	WY	GH	B
Brickellia chenopodina (Greene ex Wooton & Standl.) B.L. Rob.	Asteraceae	S	NM	GH	B
Brickellia hinckleyi Standl. var. *terlinguensis* (Flyr) B.L. Turner	Asteraceae	S/SS	TX	G2TH	A
Calochortus indecorus Ownbey & M. Peck	Liliaceae	PH	OR	GX	A
Calochortus monanthus Ownbey	Liliaceae	PH	CA	GX	A
Calystegia sepium (L.) R. Br. ssp. *binghamiae* (Greene) Brummitt	Convolvulaceae	PH	CA	G5TX	C
Castilleja leschkeana J.T. Howell	Orobanchaceae	PH	CA	G5TX	B
Castilleja uliginosa Eastw.	Orobanchaceae	PH	CA	GX	C
Cirsium praeteriens J.F. Macbr.	Asteraceae	PH	CA	GX	B
Corispermum pallidum Mosyakin	Chenopodiaceae	AH	WA	GH	A
Crataegus austromontana Beadle	Rosaceae	T	AL, TN	GH	B
Crataegus delawarensis Sarg. (EW?)	Rosaceae	T	DE	GH	C
Crataegus fecunda Sarg. (EW)	Rosaceae	T	AR, IL, KY, MO	GXC	B
Crataegus lanuginosa Sarg. (EW)	Rosaceae	T	MO	GH	A
Cryptantha aperta (Eastw.) Payson	Boraginaceae	PH	CO	GH	A
Cryptantha hooveri I.M. Johnst.	Boraginaceae	AH	CA	GH	A
Cryptantha insolita (J.F. Macbr.) Payson	Boraginaceae	PH	NV	GH	B
Dalea sabinalis (S. Watson) Shinners	Fabaceae	PH	TX	GH	A
Digitaria filiformis (L.) Koeler var. *laeviglumis* (Fernald) Wipff	Poaceae	PH	NH	G5TH	B

Continued

Table 1. Continued.

Scientific name (extinction qualifier)[a]	*Family*	*Life history*[b]	*Distribution*[c]	*NatureServe rank*[d]	*ITU*[e]
Diplacus traskiae (A.L.Grant) G.L. Nesom	Phrymaceae	AH	CA	GX	A
Eleocharis brachycarpa Svenson	Cyperaceae	AH	TX & MX	GH	A
Elodea schweinitzii Casp.	Hydrocharitaceae	PH	NY, PA	GHQ	C
Erigeron mariposanus Congdon	Asteraceae	PH	CA	GX	B
Eriochloa michauxii (Poir.) Hitchcock var. *simpsonii* (Hitchc.) Hitchc.	Poaceae	PH	FL	G3G4TH	A
Euonymus atropurpureus Jacq. var. *cheatumii* Lundell (EW?)	Celastraceae	S	TX	G5THQ	C
Franklinia alatamaha Marshall (EW)	Theaceae	S	GA	GXC	A
Govenia floridana P.M. Br.	Orchidaceae	PH	FL	GX	A
Hedeoma pilosa R.S. Irving	Lamiaceae	PH	TX	GH	A
Helianthus nuttallii Torr. & A. Gray ssp. *parishii* (A. Gray) Heiser	Asteraceae	PH	CA	G5TX	A
Helianthus praetermissus E. Watson	Asteraceae	AH?	AZ?, NM	GH	C
Isocoma humilis G.L. Nesom	Asteraceae	PH or SS	UT	GH	A
Juncus pervetus Fernald	Juncaceae	PH	MA	GX	B
Lechea lakelae Wilbur	Cistaceae	PH	FL	GX	A
Lycium verrucosum Eastw.	Solanaceae	S	CA	GX	A
Marshallia grandiflora Beadle & F.E. Boynton	Asteraceae	PH	NC	GX	N/A
Micranthemum micranthemoides (Nutt.) Wettst.	Linderniaceae	AH	DC, DE, MD, NJ, NY, PA, VA	GH	A
Monardella leucocephala A. Gray	Lamiaceae	AH	CA	GX	A
Monardella pringlei A. Gray	Lamiaceae	AH	CA	GX	A
Narthecium montanum (Small) Grey	Nartheciaceae	PH	NC	GX	C
Orbexilum macrophyllum (Rowlee ex Small) Rydb.	Fabaceae	PH	NC	GX	A
Orbexilum stipulatum (Torr. & A. Gray) Rydb.	Fabaceae	PH	KY	GX	A
Paronychia maccartii Correll	Caryophyllaceae	PH	TX	GH	A
Plagiobothrys lamprocarpus (Piper) I.M. Johnst.	Boraginaceae	AH	OR	GX	A
Plagiobothrys lithocaryus (Greene ex A. Gray) I.M. Johnst.	Boraginaceae	AH	CA	GX	A
Plagiobothrys mollis (A. Gray) I.M. Johnst. var. *vestitus* (Greene) I.M. Johnst.	Boraginaceae	PH	CA	G4?TX	A
Polygonatum biflorum (Walter) Elliott var. *melleum* (Farw.) R.P. Ownbey	Asparagaceae	PH	MI, ON	G5TH	C

Continued

Table 1. Continued.

Scientific name (extinction qualifier)[a]	Family	Life history[b]	Distribution[c]	NatureServe rank[d]	ITU[e]
Potentilla multijuga Lehm.	Rosaceae	PH	CA	GX	A
Potentilla uliginosa B.C. Johnst. & Ertter	Rosaceae	PH	CA	GX	A
Proboscidea spicata Correll	Martyniaceae	AH	TX & MX	GH	B
Prunus maritima Marshall var. *gravesii* (Small) G.J. Anderson (EW)	Rosaceae	S	CT	G4TXCQ	C
Quercus tardifolia C.H. Mull.	Fagaceae	T	TX & MX	GH	B
Ribes divaricatum Douglas var. *parishii* (A. Heller) Jep.	Grossulariaceae	S	CA	G5TX	A
Rumex tomentellus Rech.f.	Polygonaceae	PH	NM	GH	A
Sesuvium trianthemoides Correll	Aizoaceae	AH	TX	GH	A
Sphaeralcea procera Ced. Porter	Malvaceae	PH	NM	GH	A
Tephrosia angustissima Shuttleworth ex Chap. var. *angustissima*	Fabaceae	PH	FL	G1TX	A
Thismia americana Pfeiff.	Burmaniaceae	PH	IL	GH	A

[a] *Abbreviations: EW, extinct in the wild; EW?, species reported as extant through Botanical Gardens Conservation International but whose identity could not be confirmed.*
[b] *Abbreviations: AH, annual herb; PH, perennial herb; S, shrub; SS, subshrub; T, tree.*
[c] *States or provinces: AL, Alabama; AR, Arkansas; AZ, Arizona; CA, California; CO, Colorado; CT, Connecticut; DC, District of Columbia; DE, Delaware; FL, Florida; GA, Georgia; IL, Illinois; KY, Kentucky; LA, Louisiana; MD, Maryland; MA, Massachusetts; MX, Mexico; MI, Michigan; MO, Missouri; NC, North Carolina; NH, New Hampshire; NJ, New Jersey; NM, New Mexico; NY, New York; NV, Nevada; ON, Ontario; OR, Oregon; PA, Pennsylvania; TN, Tennessee; TX, Texas; UT, Utah; VA, Virginia; VT, Vermont; WA, Washington; WY, Wyoming.*
[d] *Abbreviations: GH, globally historic species; GX, globally extinct species; G1, critically imperiled species; G2, imperiled; G3G4, split rank between G3 (vulnerable) and G4 (apparently secure); G4, apparently secure species; G5, secure species; C-qualifier, known from cultivation; Q-qualifier, taxonomically questionable; TH, infraspecies globally historic; TX, infraspecies globally extinct; ?, uncertainty of rank.*
[e] *Index of taxonomic uncertainty score: A, taxon universally accepted; B, taxon accepted by majority and rarely placed in synonymy; C, taxon usually placed in synonymy but numerous treatments recognize as distinct.*

Discussion

Extinction is difficult to prove, which makes determination of what constitutes an extinct species uncertain (Diamond 1987). Rediscoveries of some taxa may occur. Each taxon reported on here has been sought in the field, but not rediscovered. Our results showed previous analyses of plant extinction vastly underestimated the number of extinctions in the continental United States and Canada.

Recent authors suggest that nearly 600 plants have gone extinct globally, with 38 extinctions in 16 U.S. states (Humphreys et al. 2019). Knapp et al. (2020*a*) disputed this estimate based on the inclusion of 14 taxa that were either extant or too taxonomically dubious. Despite reducing the extinction estimate in Humphreys et al. (2019) by eliminating extant or dubious taxa, our results showed a more dire situation: 65 extinct taxa in 31 U.S. states, the District of Columbia, and Ontario. These results indicate that nearly twice as many taxa have gone extinct, over a much larger geographic area, than previously estimated.

The cause of any extinction is difficult to determine (Le Roux et al. 2019). Unless the species was a single-site endemic whose habitat was destroyed, the cause of an extinction is often hypothetical. Nevertheless, direct anthropogenic disturbances (i.e., habitat alteration or destruction) are the single largest contributor to extinction. Only 2 species in our dataset had broad geographic ranges (defined as found in 4 or more states). The reasons for these extinctions are unknown but were likely multifaceted.

We suspect the actual number of extinct plants is considerably higher than reported, but data limitations abound. Twelve species new to science are discovered each year, on average, in California alone (Ertter 2000), suggesting an untold number of plants went extinct before scientific discovery. Much of the eastern United States was affected by European settlement before botanical exploration began. Florida, with the highest concentration of endemic plants in the North American Coastal Plain biodiversity hotspot (Noss et al. 2015), likely lost many endemic plants before they were described. Our data document 4 extinct plants in Florida, but it is unlikely that this hotspot would lose fewer plants than a

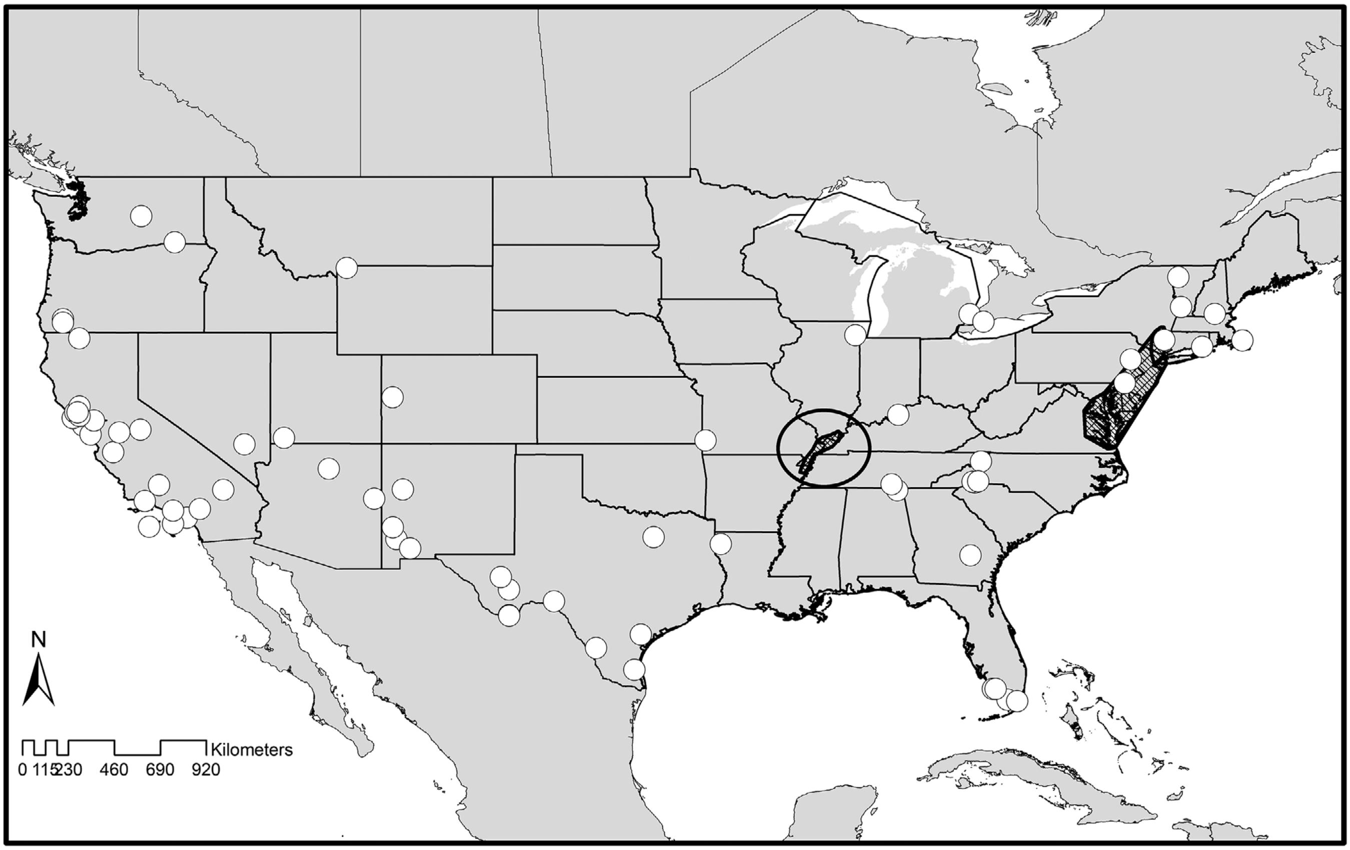

Figure 1. Locations of plant extinctions (dots, georeferenced specimen locations; shaded polygons, broader ranging species).

less diverse area of similar size, such as New England (5 in our data).

The geographic distribution of extinctions is heavily concentrated in the southwestern United States (Fig. 1). Topographic, climatic, and habitat heterogeneity of the drier parts of the U.S. West is associated with a high diversity of narrow endemic species that may be inherently vulnerable to extinction. However, we suspect the disproportionate number of extinctions in the U.S. southwest cannot be explained solely as an artifact of biodiversity patterns. Compared with the eastern states, western states had much more botanical exploration before widescale settlement (McKelvey 1956; Lewis & Clark 2003). Nevertheless, some landscapes, such as large areas of California, underwent such extreme habitat transformation by invasive Eurasian grasses and forbs prior to careful botanical documentation that their pre-European condition is controversial (Minnich 2008).

Much remains to be learned in the developing scientific arena of extinction documentation. Extinct species are still being described from old herbarium specimens, underscoring the importance of continued documentation of the flora and support of museum collections (Bebber et al. 2010). Almost certainly, additional taxa will be described after they have gone extinct. Collection and sampling bias influences the knowledge of the extinct flora. The Cyperaceae, Orchidaceae, and Poaceae are among the most diverse families of plants, yet only 4 members of these families are known to be extinct from our study area. *Govenia floridana*, the only member of the Orchidaceae, was pushed to extinction by overcollecting (Gann et al. 2002). Cyperaceae and Poaceae are notoriously undercollected and underinvestigated. The Boraginaceae had 6 extinction events, and these could have phylogenetic implications because *Crypantha* and *Plagiobothrys* constitute much of the clade corresponding to subtribe Amsinckiinae (Simpson et al. 2017).

The role of seed banks and botanical gardens in maintaining ex situ collections is of growing importance, as recognized by the Center of Plant Conservation and its partners (Miller et al. 2016). However, of the 7 EW taxa we documented, the conservation value of 4 had not been recognized before this study. Without these gardens, these taxa would be extinct. To prevent future extinctions, the rarest plants should be prioritized for both in situ and ex situ conservation.

Preventing extinction is the lowest bar for conservation success, yet species still go extinct. Our results indicated that 64% of extinct plants were historically known from only a single site or collection. Although determining whether an extinct species was a single-site endemic is problematic, because a single historical collection may not represent the total geographic range of a species, we argue that preventing further extinction requires prioritizing single-site endemics. Our preliminary data indicated 92 extant, single-site endemic plants in the continental United States and Canada (NatureServe 2020*a*). Unfortunately, in situ conservation efforts have often moved away from small-site protection, despite recent analyses showing small, isolated patches are disproportionately important for biodiversity (Wintle et al. 2018). A renewed focus on conserving small sites, as a complement to landscape-level conservation, is needed if the goal is to prevent extinctions. Many factors are predicted to increase future extinction rates for rare plants, including climate change and accelerated land-use change resulting from human population growth (Enquist et al. 2019). With greater effort on ex situ and in situ conservation for rare plants, especially single-site endemics, many future extinctions may be prevented.

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Supporting Information

Additional data (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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