A habitat suitability model for testing and refining the range of Zuni fleabane, a threatened plant species

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ABSTRACT

Land managers and conservation practitioners need practical tools to protect rare species in light of rapidly changing climate and land use patterns. Habitat suitability models are tools that can inform multiple-use land management decisions and target conservation actions. The narrow endemic Zuni fleabane, *Erigeron rhizomatus*, occurs on lands managed for multiple uses and was listed as threatened under the Endangered Species Act in 1985 due to the main threat of surface mining. Despite intermittent surveys in recent decades, managers still do not have a comprehensive understanding of suitable habitat characteristics or the geographic extent of suitable habitat across its range. We developed and field-validated a habitat suitability model for Zuni fleabane using an iterative, ensemble approach. We tested the null hypothesis that the model would not identify major new populations outside the known range but rather assist in refining the boundaries of known suitable habitat. We also set out to improve our understanding of biotic and abiotic characteristics that define suitable habitat across geographically distant metapopulations. Our model identified areas with *low*, *medium*, *high*, and *very high* probability of containing suitable habitat. We identified a new metapopulation beyond the three known (disproving our null hypothesis) as well as additional suitable habitat within the previously known regions. This model predicts where Zuni fleabane habitat likely occurs and may help land managers and conservation practitioners identify new populations, survey habitat at fine scales, avoid impacts from multiple-use management activities, and recover this threatened species.

KEYWORDS: Zuni fleabane, *Erigeron rhizomatus,* U.S. Forest Service, Bureau of Land Management, U.S. Fish and Wildlife Service, New Mexico, Navajo Nation, ensemble modeling, rare plant, species distribution model, Endangered Species Act, threatened species, species recovery planning, species recovery criteria

INTRODUCTION

In light of rapidly changing climate and land use patterns, land managers and conservation practitioners require all the methods, tools, and resources available to better understand how biological resources are being impacted by human activities and naturally occurring events (Dawson et al. 2011; Urban et al. 2016). Rare plants are no exception to this need. Researchers have successfully applied methods such as habitat suitability modelling, which uses known occurrences and a suite of environmental predictors to identify areas of potentially suitable habitat for a species to inform conservation and management decisions for these species (Crall et al. 2013; Wu and Smeins 2000).

The United States (U.S.) Department of Agriculture Forest Service (USFS) and the Bureau of Land Management (BLM) steward public lands with the mission of maintaining the health, diversity, and productivity of the nation's public lands for the needs of present and future generations. To accomplish this, they manage lands under a principle of multiple-use to accommodate diverse resources, uses, and values (Multiple-Use Sustained-Yield Act of 1960, [16 USC § 528], Federal Land Policy and Management Act of 1976 [43 USC §1701], National Forest Management Act of 1976 [16 USC 1600]). These public lands provide vital habitat for many rare species (Eichenwald et al. 2020), including rare and endemic plants (Stein et al. 2008). However, rare species conservation may compete with other activities conducted on multiple-use public lands including recreation, timber harvesting, surface mining, and energy development. To support effective decision-making for species conservation, land managers need accurate and current spatial information on rare plant habitats.

One rare and endemic plant species of concern in the American Southwest is Zuni fleabane *Erigeron rhizomatus* (Figure 1). Zuni fleabane was listed as threatened under the Endangered Species Act in 1985 (50 FR 16680; ESA) and is listed as endangered by both the state of New Mexico (19.21.2.9 New Mexico Administrative Code) and the Navajo Nation Division of Natural Resources (Navajo Nation Division of Natural Resources Department of Fish and Wildlife 2020). The three known populations of Zuni fleabane exist almost entirely on lands managed by the USFS, the BLM, and the Navajo Nation (Figure 2). Zuni fleabane occurs in discrete but often dispersed habitat patches within a matrix of more broadly occurring vegetative and edaphic communities. Although it has been monitored intermittently over the past 30 years within the three known metapopulations (U.S. Fish and Wildlife Service 2020), the species lacks a comprehensive spatial description of suitable habitat across its range. Despite Zuni fleabane's limited distribution within the western portion of New Mexico and adjacent Navajo Nation, land managers and researchers have struggled to survey all potential habitat. Developing a monitoring [surveying] plan of known populations has also been challenging due in part to the difficulty of navigating the associated rugged terrain and accessing remote habitat in places with few or no roads and trails.

The Zuni Fleabane Recovery Plan (U.S. Fish & Wildlife Service 1988, Amended 2019) contains the following recovery criteria: 1) quantitative population abundance goals to ensure viability of the three known metapopulations (Datil, Chuska, and Zuni Mountain Ranges); 2) permanent withdrawal from mineral entry of occupied habitat or the development and implementation of a habitat management plan, on USFS lands; 3) a post-delisting monitoring plan; and 4) establishment of a robust seed banking program (U.S. Fish and Wildlife Service 2019). A clear understanding of the location and extent of suitable habitat for the species is critical to meeting these recovery criteria. Furthermore, a habitat suitability model could aid in the identification of new areas containing suitable habitat and novel Zuni fleabane occurrences.

Habitat suitability models can help land managers 1) guide search efforts to find new individuals and populations by identifying suitable habitat, 2) identify candidate locations for species [re]introduction or augmentation, 3) better inform and target conservation actions, 4) assess and mitigate the potential impacts of proposed land management actions to rare plant populations and habitats, and 5) enhance the scientific basis of public land decisions (Reese et al. 2019; Sofaer et al. 2019). Developing habitat suitability models together with land managers and other species experts that are suitable for use at local scales (e.g., on USFS and BLM lands) can help address known challenges that managers often face in using habitat models that relate to issues of model access, accuracy, scale, trust, and understanding (Samuel et al. 2024).

Our goal here was to develop a habitat suitability model for Zuni fleabane with land managers and other species experts, using a coproduced, iterative approach, to help inform future habitat conservation and species recovery efforts. Partners included the USFS, BLM, U.S. Geological Survey (USGS), U.S. Fish and Wildlife Service (USFWS), State of New Mexico Energy Minerals and Natural Resources Department (NM EMNRD), and the Navajo Nation. Prior to this study, the known information about Zuni fleabane suggested that this endemic species had relatively narrow habitat requirements that were thought to be reasonably well known following nearly 40 years of listing under the ESA, yet the species has not been comprehensively inventoried even within its previously known range. Therefore, our null hypothesis predicted that the model would not identify novel populations but rather assist in refining the boundaries of the known range. We conducted field validation of the draft model that included new areas of potentially suitable habitat that were identified by the draft model to test this hypothesis. We also set out to improve our understanding of biotic and abiotic characteristics that define suitable habitat for this species across geographically distant populations. Our findings suggest this model can not only help land managers and conservation practitioners plan more informed recovery efforts for Zuni fleabane but also demonstrate the utility of modeling tools such as this for other rare species conservation and recovery efforts.

METHODS

Study area and species description

Zuni fleabane was first collected by H.D. Ripley and R.C. Barneby on May 16, 1943, on a bank of red detrital clay in the Zuni Mountains just south of Fort Wingate in McKinley County, New Mexico (Ripley and Barneby 1943). The species was confirmed by Dr. Arthur Cronquist of the New York Botanical Garden who identified it as a new species and subsequently described the species as *Erigeron rhizomatu*s (Cronquist 1947).

The extent of the study area was defined by species experts based on where Zuni fleabane could possibly occur and included all known occurrences of the species. Species experts conceptualized the extent of possible occurrence as the extent of associated geological formations, including the Chinle Formation, the Baca Formation, and other adjacent formations containing clastic sediments (i.e., Paleogene sedimentary units and Middle Tertiary volcanoclastic sedimentary units). The final extent consisted of a rectangular polygon encompassing high-elevation, forested areas of the selected geological units, and an extension to include a buffer around the west escarpments of Defiance Plateau on the Navajo Nation (Figure 2). From within this study extent, we removed (masked out) all areas identified as urban or agricultural based on the 2016 National Land Cover Database (Dewitz 2019) [NLCD classes 21, 22, 23, 24, and 82]. The remaining area encompassed 160,587 km^2.

Zuni fleabane is distributed among three widely scattered metapopulations: two in western New Mexico and one from the Navajo Nation (Figure 2). We considered these metapopulations using a modified definition from Hanski and Simberloff (1997) adapted to the life history of Zuni fleabane, and we considered a metapopulation to be a general geographic location composed of one to several occupied sites between which it is reasonable to assume that gene flow may occur. Each metapopulation is separated by unsuitable habitat and reasonable distance traveled by pollinators (Roth and Sivinski 2014). The largest and southernmost metapopulation occurs within and adjacent to the Sawtooth and Datil mountains on lands managed by the USFS Cibola National Forest and Grasslands (CNFNG) and BLM in Catron County. The second metapopulation in New Mexico occurs in the Zuni Mountains on lands managed by the CNFNG in McKinley County. This metapopulation contains the type locality for the species and the mountain range from which it takes its common name. The third metapopulation occurs in the Chuska Mountains on Navajo Nation lands in Apache County, Arizona and San Juan County, New Mexico.

Nearly all populations of Zuni fleabane are associated with barren, detrital sandy clay and clay soils derived from the Chinle or Baca Formations (Roth and Sivinski 2014). In the Datil and Sawtooth mountains, it is associated with the Baca Formation which consists of red mudstones, sandstones, and lesser amounts of grey colored claystone and conglomerate soil (Prothero et al. 2004). This formation is thought to represent a braided fluvial-alluvial fan system to the west, and a lacustrine system to the east (e.g., Cather 1982). Occupied substrates typically include fine-textured, weathered soft sandstone or clay strata that are reddish pink to almost white on slopes or cliff benches (Figures 3). An odor of selenium is sometimes detectable on these outcrops – especially when damp (Roth and Sivinski, 2014). Zuni fleabane occurs at elevations between

2,225 m (7,300 ft) and 2,560 m (8,400 ft) on moderate to steep slopes (ca. 20-40 degrees) with north- to east-facing aspects (U.S. Fish and Wildlife Service 2020). Occupied sites are typically open mixed conifer or pinyon-juniper woodlands, although where plants occur on steep slopes, there is often little other vegetation growing. Cibola milkvetch (*Astragalus albulus*) occurs at almost all sites occupied by Zuni fleabane in the Datil and Sawtooth Mountains, which is a secondary indicator of selenium-laden soils (Cannon 1962). Yellow milkvetch (*Astragalus flavus*) is also occasionally present, which is a primary indicator of selenium-laden soils (Cannon 1962).

Other common associates of Zuni fleabane in the Datil and Sawtooth Mountains population include two-needle pinyon (*Pinus edulis*), mountain-mahogany (*Cercocarpus montanus*), oneseed juniper (*Juniperus monosperma*), rubber rabbitbrush (*Ericameria nauseosa*),Navajo yucca (*Yucca baileyi*), broom snakeweed (*Gutierrezia sarothrae*), Indian ricegrass (*Achnatherum hymenoides*), needle and thread (*Hesperostipa comata*), James' buckwheat (*Eriogonum jamesii*), fineleaf hymenopappus (*Hymenopappus filifolius*), goldenweed (*Xanthisma grindelioides*), perkysue (*Tetraneuris argentea*), and purple locoweed (*Oxytropis lambertii*). Some associates occurring in more mesic conditions in shaded habitats at the heads of small canyons and bases of cliffs include Douglas fir (*Pseudotsuga menziesii*), stretchberry (*Forestiera pubescens*) and goldenrod (*Solidago* sp.) (Roth and Sivinski 2014).

In the Chuska Mountains of Arizona and New Mexico and the Zuni Mountains of west-central New Mexico, Zuni fleabane is associated with soils derived from the Chinle Formation. Although similar in texture to the Baca Formation, soils range from reddish-purple, brown, or greenish-grey mudstone and siltstone intermixed with lighter colored sandstone (O'Sullivan 1974)). The Chinle Formation is of Late Triassic age and consists of several members that range from shale to sandstone stretching across a wide geographic range from the Jemez Mountains in central New Mexico to northeastern Arizona (O'Sullivan 1974). Occupied areas in the Chuska Mountains are often on sandy clay soils that are a deep maroon to purplish red hue, which is often more characteristic of soils derived from the Chinle Formation. Occupied substrates in the Zuni Mountains are typically of a gray to brown hue and consist of shale to sandy clay that have eroded into very small indurate pieces, imparting a sandy texture to the soil surface (Roth and Sivinski 2014). Plants occur in both areas on gentle to steep slopes on all aspects at elevations of 2,225 m (7,300 ft) to 2,250 m (7,380 ft) in open, exposed areas or in mixed conifer or pinyon-juniper woodlands; however, occurrences on steep slopes typically have little other ground vegetation present. Dominant associates in the Zuni Mountains include two-needle pinyon, mountain-mahogany, oneseed juniper, Gambel's oak (*Quercus gambelii*), fragrant ash (*Fraxinus cuspidata*), rubber rabbitbrush, Navajo yucca, broom snakeweed, Indian ricegrass, and James' galleta (*Hilaria jamesii*) (Roth and Sivinski 2014). Common associates in the Chuska Mountains include two-needle pinyon, ponderosa pine (*Pinus ponderosa*), Utah juniper (*Juniperus osteosperma*), Rocky Mountain juniper (*Juniperus scopulorum*), Douglas fir, mountain-mahogany, Gambel's oak, Stansbury cliffrose (*Purshia mexicana var. stansburyana*), antelope bitterbrush (*Purshia tridentata*), fragrant sumac (*Rhus aromatica*), Woods' rose (*Rosa woodsii*), rubber rabbitbrush, narrowleaf yucca (*Yucca angustissima*), banana yucca (*Yucca baccata*), broom snakeweed, rose heath (*Chaetopappa ericoides*), Colorado penstemon (*Penstemon* *linarioides* ssp. *coloradoensis*), Indian ricegrass, bottlebrush squirreltail (*Elymus elymoides*), and James' galleta. Indicator plant species for selenium-laden soils are not present in the Zuni Mountains or Chuska Mountains.

Species' threats and recovery criteria

The decline of Zuni fleabane was primarily due to surface mining and uranium exploration activities and possibly off-road vehicle use and livestock trampling on public lands (USFS, n.d.); additional threats may include long-term drought and climate change (U.S. Fish & Wildlife Service 1988). In particular, surface mining for uranium, where allowed, could create surface disturbances that result in permanent loss of habitat and subpopulations (U.S. Fish and Wildlife Service 2019). Uranium mining was ended in 2005 on Navajo Nation Land, and mineral entry has been withdrawn on the BLM's Sawtooth Area of Critical Environmental Concern where the species is known to occur.

Model objectives

The USFS and BLM initiated modelling efforts for Zuni fleabane in 2020, recognizing the need for a comprehensive understanding of its habitat characteristics and the extent of the species distribution. This information is vitally important to support progress toward Zuni fleabane conservation and recovery goals, which include: 1) surveying potentially suitable habitat (to delineate occupied and suitable habitat), 2) withdrawing mineral entry in occupied and suitable habitat to conserve existing populations and provide for connectivity and gene flow between populations, and 3) avoiding disturbance of occupied and suitable habitat to protect existing populations (U.S. Fish & Wildlife Service 1988; U.S. Fish and Wildlife Service 2019). As our modelling objectives became more refined, we developed a working team consisting of representatives from agencies with a vested interest in the conservation of Zuni fleabane, which included the USFS, BLM, USGS, USFWS, NM EMNRD, and the Navajo Nation. Together, we established the objectives for this project, which include 1) estimating and mapping potential suitable habitat for the species across its range and 2) establishing criteria by which to evaluate habitat suitability. The resulting product is expected to play a crucial role in achieving recovery goals such as those listed above.

Coproduction framework

We applied the coproduction framework developed by Jarnevich et al. (2024b) for modeling suitable habitat for rare plant species. The project team included USGS staff with expertise in modeling and coproduction, along with staff from BLM, USFWS, USFS, NM EMNRD, and Navajo Nation with species and multiple-use land management expertise. This framework included regular team meetings to collaboratively explore and decide on model inputs, modeling approach, and model outputs. Staff primarily included wildlife biologists, botanists, and geospatial modelling professionals.

Model inputs

We had two phases of modeling. The first phase involved utilizing occurrence data obtained from the BLM's database (Bureau of Land Management 2023), which included data from New

Mexico Natural Heritage among other sources. These data represented two different geographic areas, the Zuni Mountains and Datil/Sawtooth mountains. We filtered these occurrences using criteria related to observation date and accuracy, as described in Table S1, and to a single occurrence per 100 m to reduce issues of pseudo-replication. This occurrence data processing resulted in 82 species occurrences distributed between the two areas. We developed multiple iterations of the model by altering modeling inputs and incorporating species expert evaluation of outputs. The team agreed upon a model for field validation. The final model was developed using the original set of occurrences, additional occurrences shared with modelers by the Navajo Nation (n=61 after thinning), and new occurrences collected during our field validation effort in 2023 (n=22 after thinning).

Absence data were not available, so we generated 10,000 background points from within a polygon fit around the occurrences excluding private lands, agricultural lands, and urban areas. Private lands have not been surveyed, and agricultural and urban areas were excluded from the analysis.

We started with a suite of environmental predictors developed for modeling five other rare plant species in the region (Jarnevich et al. 2024b), with our species experts determining which were applicable for this species. We then worked with species experts to identify additional predictors that might be essential for characterizing the habitat of Zuni fleabane. We retained 20 predictors from the original set and developed three new predictors. The final suite of predictors represented habitat features related to soils, topography, vegetation cover, and geology (Table S2).

Model fitting

We followed the same model fitting process as Jarnevich et al. (2024b), using five different algorithms (boosted regression tree (Elith et al., 2008), generalized linear model (Hosmer & Lemeshow, 2000), multivariate adaptive regression spline (Leathwick et al., 2006), Maxent version 3.4.1 (Phillips et al., 2017), and random forests (Breiman, 2001)) within the Software for Assisted Habitat Modeling (Morisette et al. 2013) using algorithm default settings and 10-fold cross-validation. We developed multiple iterations of the model, reviewing each with our larger project team to determine appropriate modifications to occurrence data and predictors.

We created an ensemble of the models to meet intended management uses (Figure S1), using those determined by Jarnevich et al. (2024b) but expanded considerations to include application of determining compliance with the ESA and implementation of conservation actions for this federally threatened species. We selected four different threshold rules (calculated based on the omission rate because we only had presence data) to classify the continuous relative suitability predictions into four different model output rasters, each with binary values representing suitable or unsuitable habitat, for each model algorithm. These rules included minimum predicted presence (MPP; all occurrences), 1st percentile (1% of occurrences fell in unsuitable habitat), 10th percentile (10% of occurrences fell in unsuitable habitat), and 25th percentile (25% of occurrences fell in unsuitable habitat; Table S3). The latter three rules were the same as described in Jarnevich et al. (2024b). We added the MPP threshold to capture any suitable habitat to meet USFWS needs for estimation and mapping of ESA-listed species habitat. We then added each algorithms' binary raster for each threshold rule together across algorithms, resulting in four ensemble rasters, with their values representing the number of algorithms predicting a location as suitable under the particular threshold rule. For each of these threshold rule ensemble rasters, we selected a minimum number of models agreeing on suitability to create a subsequent binary raster of suitable and unsuitable habitat at the given threshold. For the MPP threshold rule, we required at least two of the algorithms to agree on suitability. For the remaining three threshold rules, we required at least three of the algorithms to agree on suitability (after Jarnevich et al. 2024b). We constructed the final ensemble raster, representing discrete relative suitability values, by adding these binary (threshold rule model agreement ensemble) rasters together. Values in the final raster range from 0 (no suitability) to four (highest relative suitability derived from the 25th percentile).

Model validation

We generated 75 base validation points for field surveys with an additional 30 extra substitution points using spsurvey::grts in R v4.3.2 (Dumelle et al. 2023). The validation was conducted before deciding to expand the threshold rules to include MPP, so field validation points were distributed across four model suitability classes (unsuitable, medium, high, and very high) both within (n=50) and outside (n=25) the known geographic areas of occurrence. The known geographic area was defined by a 25.75 km (16 mi) buffer around each known occurrence (e.g., the un-thinned set) from the three different geographic regions (i.e., included Navajo Nation occurrences once obtained), and included 13,404.4 km^2 (8.3%) of the study area. Field validation plots were restricted to areas included in the analysis (e.g., no urban, agricultural, or private lands (due to access)) and were required to be within 3 km of a road and more than 500 m from any known occurrence. The number of points was based on anticipated availability and capacity of staff conducting the field work.

Field crews developed field protocols together and calibrated them at a site known to be occupied by Zuni fleabane before visiting field validation plots and collecting data. During calibration, field crews came to a consensus on qualitative habitat characteristic assessment. They then identified, refined, and adjusted metrics to be collected at each plot to best describe the habitat consistently in qualitative and quantitative measures, such as slope, tree cover, plant associates, and how to best describe soil types and amount of rock present (e.g., loose rock, boulders, outcrop). A standard "move" criteria was also established during the calibration phase for survey plots determined to be unsafe for surveyors to sample or inaccessible given the 3 km maximum off-road distance rule. Field crews then visited each field validation plot between 23-May-2023 and 1-Aug-2023, recording species occurrence, a qualitative habitat assessment (unsuitable, marginal, suitable), and abiotic and biotic characteristics within the plot. Characteristics evaluated include: aspect, slope, slope shape, dominant associated species, soil texture and color, woody canopy cover, and ground cover. Photographs were also taken at each plot for later habitat suitability reference (e.g., Figure 3).

Additionally, field crews recorded Zuni fleabane occurrences encountered during travel to field validation plots, which we refer to as "opportunistic" occurrences. These data, as well as occurrence data from the Navajo Nation and from field validation plots, including the qualitative habitat assessments, were not available during the initial model fitting step. We used these data to evaluate performance of our validation model by comparing them to our validation model's predicted habitat suitability. We also compared our validation model's predicted habitat suitability against all known occurrence points that were included in the validation model. Note that all occurrence data (including from the Navajo Nation, field validation plots, and opportunistic sightings) were included in fitting the final model.

To evaluate our null hypothesis that the model would not identify new geographic areas of Zuni fleabane populations but would assist in refining the boundaries of known habitat, we evaluated the distance from newly identified occurrences to the nearest previously known occurrence. For this last evaluation, we combined previously recorded Navajo Nation occurrences (e.g., any *not* from the model validation effort) with the un-thinned occurrences from the other two regions used to fit the validation model to define what was known prior to our modeling effort.

The final model generated during this study is available as a USGS data release (Jarnevich et al. 2024a).

RESULTS

Initial model for field validation

We iterated the model three times, modifying model inputs each time to refine the model. The iterations included developing four alternate model versions, using different sets of predictors with various combinations of elevation and distance to geological formations, before the team agreed on a model acceptable for validation. The species experts determined modifications each time along with which combination of predictors to retain based on review of model outputs, including response curves (e.g., Figure S2), variable importance metrics (e.g., Figure S3), and mapped predictions (e.g., Figure 4), using their species and geographic knowledge to select the model that seemed most ecologically plausible. We confirmed that assessment metrics were acceptable for the model used for field validation (Table S4).

Field validation

Field crews visited 80 field validation plots. All surveyed plots that were qualitatively observed to be suitable had predicted suitability categories of low, medium, or high (Figure 5). However, 16 of the plots that were observed in the field to be 'unsuitable' were predicted to be highly suitable, indicating that the model effectively captured, but potentially overpredicted, suitable habitat for the species.

Zuni fleabane was observed on six of the 80 field validation plots. Of these six plots, one was found outside the known extent (i.e., >16 mi from a known occurrence). There were also 244 occurrences that were opportunistically discovered during travel to field validation plots. Many of these opportunistically discovered occurrences were highly clustered, coinciding with only 72 unique validation model cells (30 m cells). Comparing these 72 new unique opportunistic occurrences with the Navajo Nation occurrences located within 77 unique validation model cells, the validation model accurately predicted suitable habitat at opportunistic occurrences that were all found within the geographic range used to fit the validation model (n = 72 opportunistic occurrences, with 62 located in very high suitability, six in high suitability, and four in medium suitability). The model did not predict suitability as well beyond the geographic range used to fit the validation model (n = 77 within the Navajo Nation, with 16 unsuitable or low suitability, 26 in medium suitability, 25 in high suitability, and 10 in very high suitability) (Figure S4).

There were noticeable differences in predictor values for the Navajo Nation occurrences compared to occurrences from the other geographic areas. Navajo Nation occurrences were at lower elevations with steeper slopes, greater rock index, and greater iron oxide (Figure S5). The general importance of these predictors in the validation model could explain why the Navajo Nation occurrences were more poorly predicted.

Characterization of suitable habitat was improved upon throughout the field validation process by field staff via exposure and experience gained traversing various habitats to access the random points generated by the validation process. This increased understanding of habitat suitability led to field personnel utilizing satellite imagery (USFS-produced LiDAR products) and observed field conditions to incorporate exploratory surveys en route to validation points, which occasionally resulted in documentation of novel occurrences for the species. These novel occurrences included some locations that were outside the parameters that had been previously used to define habitat for the species, including two occurrences found below 2,000 m elevation, where the previously recognized minimum elevation was 2,225 m for the species. These opportunistic points were used accordingly to further strengthen the model output.

Final habitat suitability model

The final model was fit using 165 Zuni fleabane occurrences, including 83 occurrences not used in the validation model, after spatially thinning the survey plot, opportunistic, and Navajo Nation occurrences to one per 100 m. Based on improved characterization of suitable habitat gained during field surveys, the project team considered moving to a 10 m resolution for the models. The team compared a 10 m and a 30 m model based on their expert knowledge and selected the 10 m model to capture the fine-scale topographic heterogeneity in Zuni fleabane habitat. The MARS model was not included in the final ensemble because it was identified as having overly complex response curves and overly specific predictions (indicating overfitting) during model review.

Predictions from the final model were driven by elevation, distance to formations, and soil information from predictors derived from Landsat imagery (Figures S2 and S3). This model indicated preference for higher elevations, areas closer to the Baca and Chinle Formations, and soils with more iron oxide (Figure S2).

The final model predicted a similar amount of the study area as suitable compared to the validation model, but with shifts toward the higher suitability classes (Table 1). The final model performed better than the validation model at appropriately not classifying field-observed marginal and unsuitable habitat as high or very high suitability habitat. Twenty-seven field validation plots that were observed to be unsuitable were predicted as either high or very high suitability by the validation model, whereas only 18 were predicted as such by the final model

(Figure 6). The final model still correctly predicted field validation plots observed to be suitable, with the suitable class having plots predicted as medium to very high.

DISCUSSION

Implications of a coproduced habitat suitability model

We coproduced a habitat suitability model for a federally threatened plant, Zuni fleabane, using a team of modelers, biologists and public land managers from multiple land and species management agencies. We considered three different iterations of the model, with the version for field validation collaboratively determined by the project team. The statistical validation of models is crucial to their predictive success (Fielding and Bell 1997; Franklin 2010), but most often validation relies on examining how well a model predicts a withheld set of the original dataset. Here, we selected a random set of field sites to visit to assess model performance with an independent set of data. Habitat suitability does not equate to occupancy. Therefore, field crews qualitatively assessed suitability using a coproduced field survey protocol developed for this study in addition to searching for Zuni fleabane plants at a randomized set of plots. We used newly collected data from the field validation effort to subsequently improve the model, a method that can help overcome common problems associated with trying to model rare species (Guisan et al. 2006). The models relied heavily on remotely sensed imagery derived predictors, which others have identified as important for indirect detection of rare plants (Cerrejón et al. 2021).

We followed the coproduction process developed by Jarnevich et al. (2024b) to increase understanding, trust, and buy-in of model outputs (Arnott et al. 2020; Beier et al. 2017; Seidl 2015). This process involved close collaboration to determine model inputs, evaluate model iterations for ecological plausibility as well as statistical assessment, and design the format of outputs to meet practitioner needs. Despite following the same methods, the outputs for Zuni fleabane were designed to encompass all possible suitable habitat due to the threatened status of the species under the ESA and the critical need to identify as much suitable habitat as possible. The outputs deviated slightly from methods in Jarnevich et al. (2024b) and estimated a fourth category of suitability (the lowest) to accommodate this need. Coproduction in the development of the survey protocol for the field validation ensured consistency in data being collected, both in terms of the specific types of data collected and calibration of qualitative assessments at plots.

Zuni fleabane is an endemic species with relatively narrow habitat requirements, has been found in only three metapopulations across its geographic range, and has been listed for nearly 40 years; we therefore predicted that the model would not identify major new populations but rather assist in refining the boundaries of known habitat. This hypothesis was disproved. Our study area encompassed a large extent relative to the known geographic range of the species (8.3% of the study area). During field validation efforts, a novel occurrence of Zuni fleabane was found well outside the three previously known metapopulations in an area predicted as suitable. Further search efforts in the region of this new occurrence resulted in the detection of several more Zuni fleabane occurrences in June 2024, all of which largely fell in areas adjacent to or predicted as suitable by the final model.

The model also enhanced our knowledge of the distribution of Zuni fleabane within the known geographic range. We discovered new occurrences within the known range, and our model-predicted habitat suitability matched ground-based qualitative assessments of habitat suitability. These successes of identifying new populations within the broader area of known habitat match those of others using habitat suitability models combined with survey efforts to detect new populations (e.g., Behroozian et al. 2022; Jarnevich et al. 2024b). However, often rare plant modeling studies do not assess habitat beyond known ranges, though others have hypothesized a species may be found farther afield based on study results (Behroozian et al. 2022).

Documentation of new populations is important not only for awareness of managers to apply measures appropriate to long-term conservation, but also for understanding the adaptive capacity of the species in light of changing climate and potential resulting habitat shifts. Our newly discovered occurrences included areas that expanded the known range of Zuni fleabane on its lower latitudinal (southern) extent, and below the elevational range previously used to describe the species. These populations at range-edges living in peripheral or marginal environments may have evolved novel capabilities that may help them persist in more extreme future conditions (Nicotra et al. 2015; Sexton et al. 2009; Teitelbaum et al. 2021). Identification of a new range-edge presents an opportunity to explore questions related to ecological barriers of this rare species and its capacity to adapt to changing climatic and ecological conditions. Retention of individuals and traits from these populations at the warm or “trailing” edge of a species’ distribution can be disproportionally important for species responses to contemporary and future climate change (de Lafontaine et al. 2018; Hampe and Petit 2005; Sexton et al. 2011), where the adaptive responses of individuals have been pushed to species’ limits (Pennington et al. 2021).

Practical applications for Zuni fleabane recovery efforts

This model allows us to predict with relative certainty where suitable habitat for Zuni fleabane occurs and therefore where the species is likely to be found. Land management agencies often struggle in their capacity to hire or procure technical staff to survey vast and remote areas of land for wildlife and plants. This species occurs in remote areas with few roads and trails and with topographically challenging terrain to traverse on foot or by vehicle. Tools such as this model can make planning surveys substantially faster and easier and allow managers to maximize crew field time by more accurately targeting survey areas. The model is intuitive for agency staff to learn and use and can be easily referenced to pinpoint potentially suitable habitat of a given site and evaluate the need for on-the-ground field surveys. Using the model in combination with local biologist and botanist expertise, field visits could more efficiently determine the degree to which a project area may need to be analyzed for potential impacts to Zuni fleabane. This tool is, in many ways, is capable of substantially improving and increasing the pace and scale of conservation efforts and can assist land managers in their efforts to meet recovery criteria listed in the Zuni Fleabane Recovery Plan (U.S. Fish & Wildlife Service 1988, Amended 2019) , each of which is discussed below.

Three of the recovery criteria are focused on measuring the population trend and viability across the known metapopulations (Datil, Chuska, and Zuni Mountain Ranges). Use of this model and information learned through this study can help identify the likely maximum extent of each of the 3 known metapopulations and aid in establishing a sampling design and methods for trend studies through time such that results can be inclusive of, and extrapolated to, the larger population. This utility can also be applied to the recovery criterion that addresses post-delisting monitoring.

The recovery criteria specifically includes the permanent withdrawal of occupied habitat on USFS lands from mineral entry OR the development and implementation of a habitat management plan for lands under USFS jurisdiction (U.S. Fish & Wildlife Service 1988; U.S. Fish and Wildlife Service 2019). This model can help managers determine with more certainty the area of suitable habitat across these lands and target survey efforts to find occupied habitat, identify zones of connectivity, and prioritize areas for withdrawal from mineral entry. Although the species is considered a narrow endemic, it is estimated that up to a third of its habitat in the Datil/Sawtooth area alone has not been surveyed (Roth and Sivinski 2014); access to areas of potential habitat during model testing required navigating steep, erosive, and occasionally inaccessible terrain. A model that can more effectively predict potentially suitable habitat or new populations of Zuni fleabane could allow for a more efficient, focused inventory of the species' range across USFS lands, which in turn would facilitate the mineral withdrawal of occupied lands without the unnecessary mineral withdrawal of unoccupied, unsuitable habitat.

Recovery criteria include a robust seed banking program. Adaptive capacity is an important consideration for both protecting species in the wild and safeguarding them in ex-situ collections. A robust seed banking program involves collection of genetically diverse and representative germplasm samples for long-term storage at ex-situ facilities. Genetically diverse and representative sampling ensures that seed banks contain the plant materials that would be needed to support the resiliency and long-term adaptive capacity of augmented, reintroduced, or introduced populations. Simultaneously conserving peripheral plants—in addition to plants in core populations—is a conservation strategy for ensuring a species' resiliency and adaptive capacity amongst evolving ecological conditions. To representatively sample a species, collectors need accurate information about the extent of the species' range, the extents of its populations, the distribution and abundance of the species within and among its populations, and the ecological diversity of occupied habitats within and among populations (Center for Plant Conservation 2019; Smith et al. 2018). Habitat models empower representative sampling by highlighting areas and delineating extents within which to distribute sampling efforts as well as by suggesting gradations in habitat suitability to stratify sampling across the range. These strategies and resources for conserving adaptive capacity are also applicable for resource managers' efforts to conserve species in the wild.

Limitations of the model

While the model meets the criteria to be considered acceptable in all categories (Table S1, (Reese et al. 2019; Sofaer et al. 2019)), there are potential limitations of model application that users should consider. The model describes relative habitat suitability as it is based on presence-background data, and thus does not reflect occupancy or temporal dynamics that can be important for species. While there were 80 field validation plots, only 25 of them were located in areas outside the known range. This is a small number of plots relative to the ~1,600 km^2 of predicted suitable habitat outside of the known geographic range (Table 1). Observers identified validation plots in the northeastern region of suitable habitat as being suitable, though Zuni fleabane was not discovered at these plots. Field validation of suitable habitat in this area warrants further search for the species. Additionally, the validation model did not perform as well in the Navajo Nation as it did elsewhere, but data from this area were included in fitting the final model. Further validation in this region is also warranted.

Conclusion

Despite some limitations of the model, we were able to estimate habitat suitability across a large study area and identify additional occurrences of Zuni fleabane within the previously known range of the species. Through this process, we discovered multiple novel occurrences. We have outlined many of the potential uses for this model to advance recovery of this federally threatened species. The collaborative nature of our work, with participation from various entities invested in the conservation of this species, along with our iterative and coproduced modeling process, lends support for habitat suitability model use to better inform land management decisions and actions.

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Table 1. Amount (km^2) of the overall study area and of the previously known range predicted as low suitably, medium suitability, high suitability, and very high suitability for both the validation model and the final habitat suitability model for Zuni fleabane.

	Low	Medium	High	Very High	Total suitable
Validation model – study area	2726.6	103.8	33.7	20.7	2884.8
Validation model – known range	1302.9	69.5	26.4	19.1	1418.0
Final model – study area	2680.3	164.6	35.6	48.8	2929.4
Final model - known range	1243.1	100.6	24.2	34.6	1402.5

Figure 1. The focal species, Zuni fleabane, a perennial forb species endemic to the Chinle and Baca Formations of western New Mexico and Navajo Nation, observed in red soils. Photograph credit Erika Rowe.

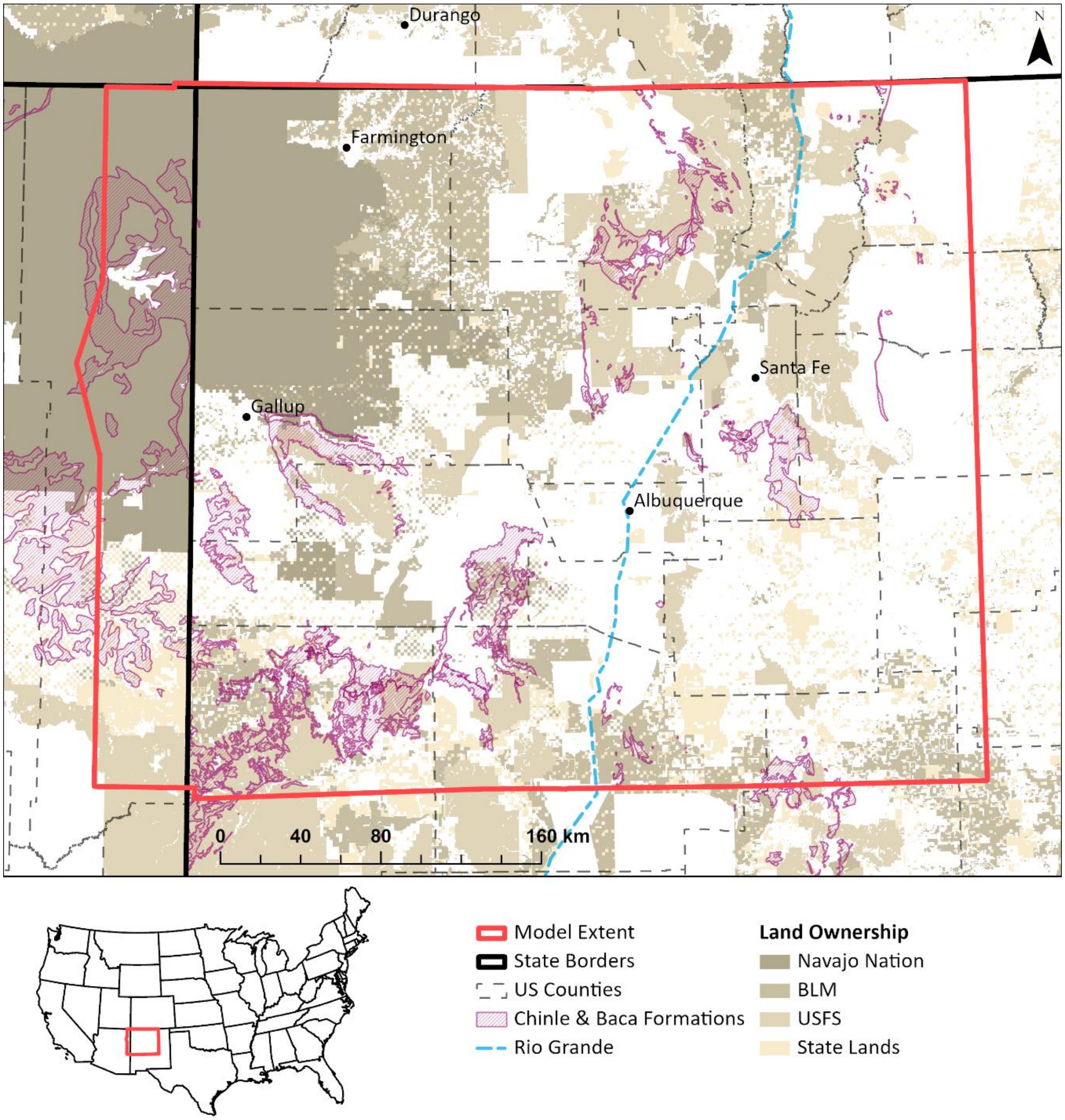

Figure 2. Study area including regions of previously known Zuni fleabane populations and the modeling extent. (Bureau of Land Management [BLM], U.S. Forest Service [USFS])

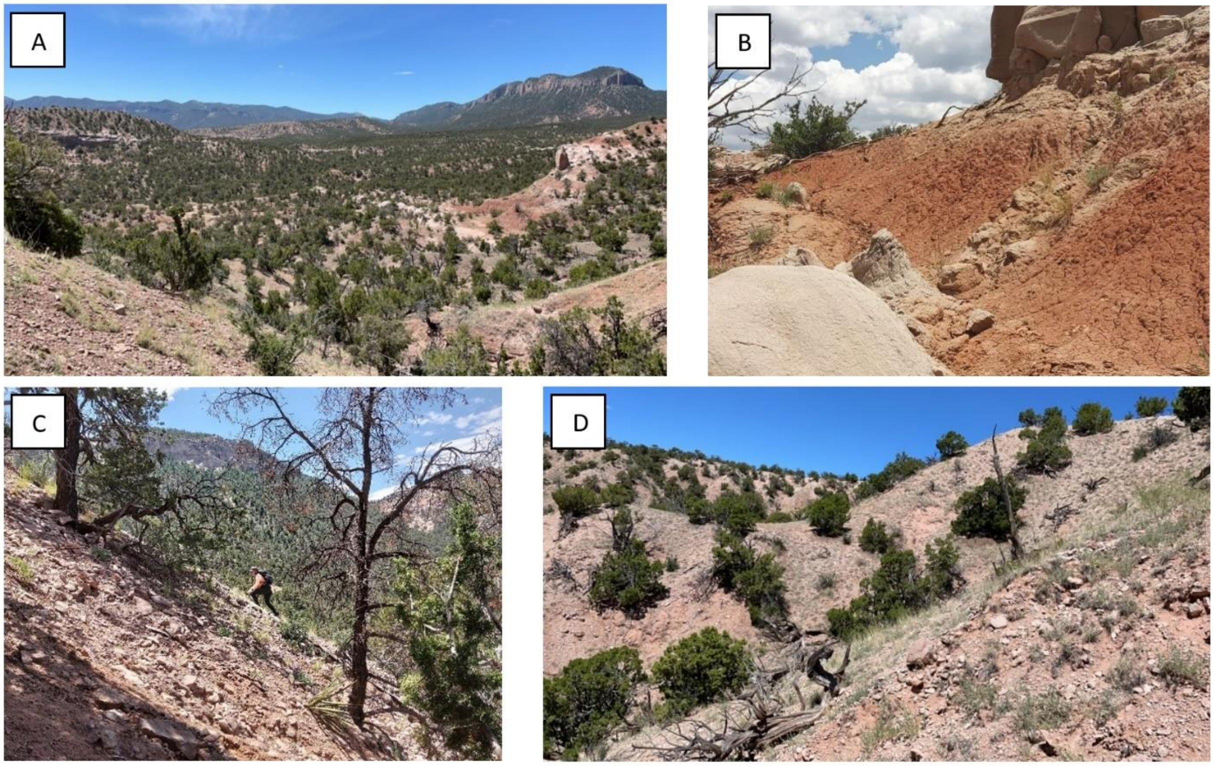

Figure 3. Photographs taken from field validation sites demonstrating the rugged topography and barren outcroppings common in the Chinle and Baca Formations upon which Zuni fleabane may occur(A), closeup of soils and erosion often found in Zuni fleabane habitat (B), field work conducted in variably suitable and forested sites field characterized as “unsuitable” for the target species (C) and common vegetative community of the project with sparse shrub grassland components and steep erodible slopes (D) (Photograph credit Andrea Chavez and Paige Handley).

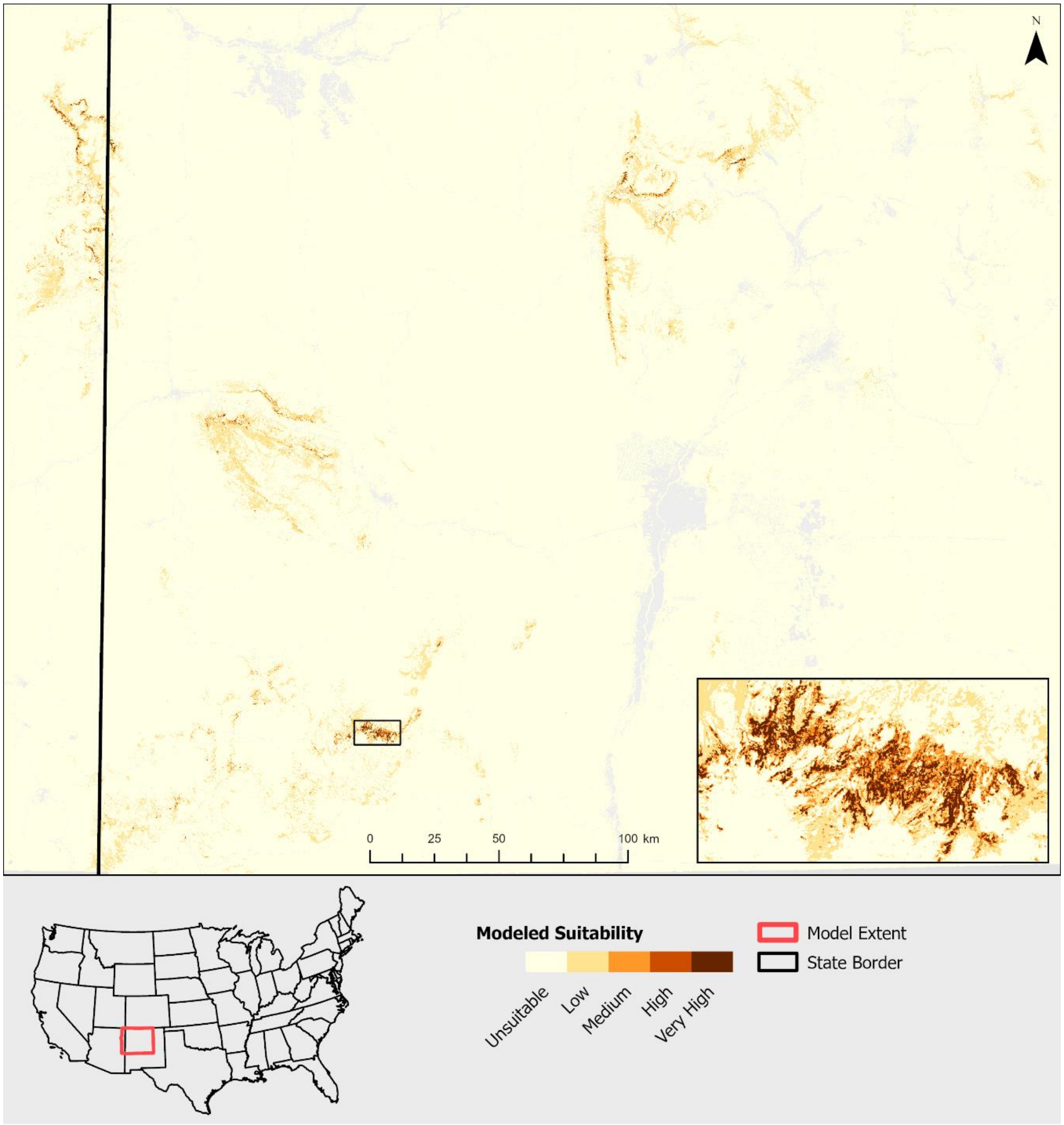

Figure 4. Final habitat suitability model ensemble for Zuni fleabane over the entire study area and zoomed into an area within the southern population, available from Jarnevich et al. (2024a).

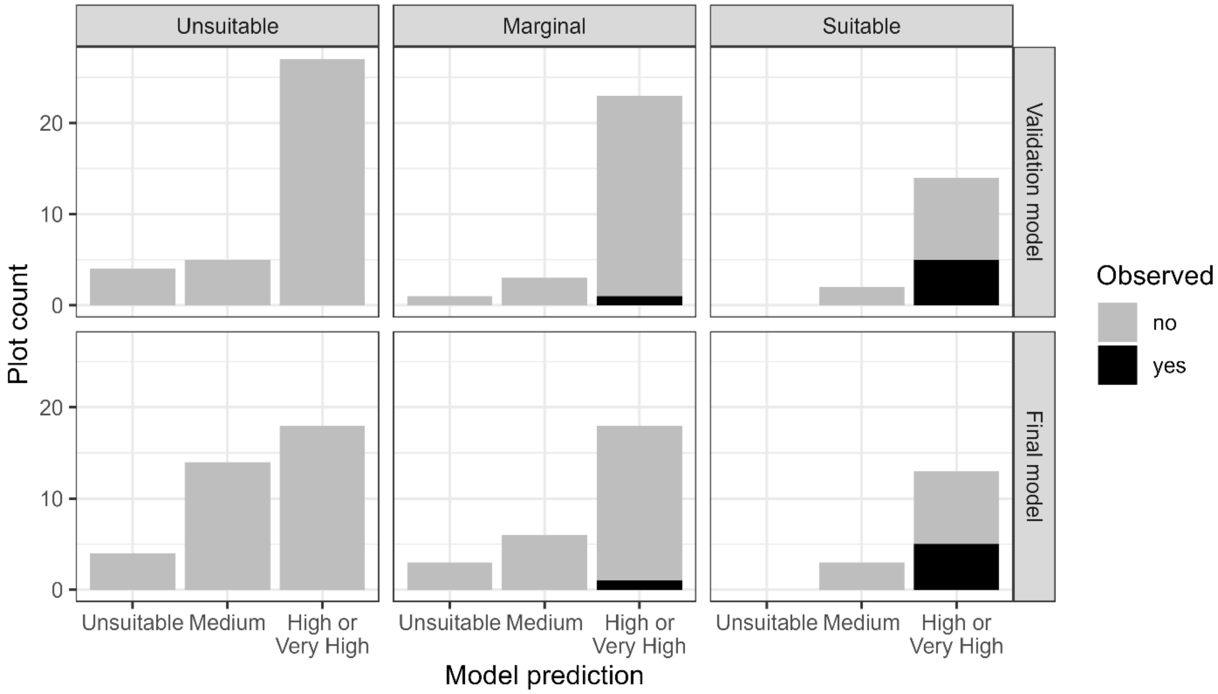

Figure 5. Validation survey results comparing observed habitat suitability to predicted habitat suitability for the validation model and for the final model for Zuni fleabane. The graphs are faceted by the observed qualitative assessment of suitability by the field crew, classifying field validation plots as unsuitable, marginally suitable, or suitable as columns and the model version, validation or final, as rows. The x-axis is predicted suitability from the specified model (unsuitable [includes low], medium, or high [includes high and very high]).

Supplement

Table S1. Assessment rubric for species distribution models based on Sofaer et al. (2019) with the occurrence data category expanded on by Reese et al. (2019). There are four broad categories of assessment with subtopics and rating criteria for acceptable. Color coding in the ‘Zuni fleabane’ column is as follows: Green = Ideal, Yellow = Acceptable, Red = Interpret with caution. More details on each category and topic can be found in the rubric sources. .

Category	Topic	Rating	Zuni fleabane
Species Data	Minimum number of occurrence points	>50 occurrences	Had >50 occurrence points
	Age of occurrences	Majority of occurrence data from 2000 to present	Based on input from species experts, filtered out all data older than 2014, except Navajo Nation data included all shared locations.
	Spatial accuracy of occurrence points	All records have precise location information	The reason given for the age criteria above was that data inside these criteria had reliable location info. Data prior to these dates weren’t collected with GPS
	Status of occurrence data	All record are from a source where data are reviewed, vetted, and quality checked for accuracy	Reviewed occurrence data with species experts to confirm accuracy of points and also look for additional data not represented in our initial points.
	Spatial bias of occurrence data	Records are likely to have been collected opportunistically and/or are clumped, but exhibit (or have been thinned to) an acceptable separation distance	Points are clustered and surveys seem to have been conducted in areas close to previously known populations. We spatially thinned occurrence data to 100m to reduce spatial bias.
	Spatial distribution of occurrences	Records are available across a substantial portion of the species range	Data in final model cover all known populations, but additional populations may exist outside of these areas. Initial model did not include Navajo Nation data due to restricted access.

Category	**Topic**	**Rating**	**Zuni fleabane**
	Background	Sampling of background points mimics sampling biases in data and/or sensitivity analyses have been conducted to evaluate effects of using different background data sets on model predictions.	Background points limited to land ownerships that surveys had been detected on and within the geographic areas that were known to have been surveyed.
	Evaluation data	Based on cross-validation of training data.	Cross-validation of training data.
Environmental Predictors	Ecological and predictive relevance	Selection of predictors justified based on natural history.	Predictors chosen based on expert species knowledge and species-specific predictors were created.
	Spatial and temporal alignment	Predictors encompass the study area and time period. Resolution of predictors is appropriate given uncertainty and for the focal species.	Predictors match sampling period as closely as possible. Used available resolution closest to that desired for mapped products.
Modeling Process	Algorithm choice	Selection of algorithm aligned with objectives, including need for actual versus potential distribution.	Used a range of algorithms (regression based, tree based, machine learning) that were evaluated separately based on *a priori* criteria for inclusion in final model.
	Sensitivity	Assessment of sensitivity to choice of algorithm(s) and selected settings and input data.	Evaluated five different algorithms. Analyzed each algorithm's settings separately based on *a priori* criteria.
	Statistical rigor	Assumptions recognized and considered.	Examined collinearity issues and visually evaluated residual map for spatial patterns.
	Performance	Multiple metrics evaluated and evaluation scores are close to generally accepted levels; ecological plausibility evaluated.	Evaluated multiple evaluation metrics to ensure they met *a priori* criteria. Visually examined mapped products to evaluate ecological plausibility. Field validation of validation model.

Category	**Topic**	**Rating**	**Zuni fleabane**
	Model review	Regional and taxonomic expert review conducted and considered in model revision (when relevant) or use recommendations.	Reviewed by team of species experts. Field validation effort.
Model Products	Mapped products	Continuous map with clear description to interpret range of values. Thresholds based on test data (e.g., sensitivity equals specificity) though not necessarily linked to intended use.	Ensemble of binary maps created for various thresholds that correspond to different intended uses identified by model end users.
	Interpretation support products	Enough information to evaluate every row in this table. Where explanation is a goal, description of included variables and their importance. Opportunity for users to inquire about methods.	Model attributes described. Management community partnered in development of models and the format of delivery.
	Reproducibility	Inputs saved and made available (excepting locations of rare species), scripts, settings, and model results archived.	Because of sensitivity of occurrence data these are not available, but predictors are freely available and model software is freely available. Model outputs are published.
	Iterative	Updated based on expert review and other performance assessments. Not updated based on new field observations.	Model was iterated to develop validation model, field validation results were used to inform final model development.

Table S2. Predictors considered in developing a habitat suitability model for Zuni fleabane. The suite of predictors, began with selecting ones relevant to Zuni fleabane from those developed for modeling habitat suitability of five other rare plant species in northwest/ north central New Mexico (Jarnevich et al. 2024b). The team developed additional predictors specific to this species, too, based on group discussions among species experts.

Predictor name	Description	Source
Elevation	Mosaiced 1/3 arc-second National Elevation Dataset Digital Elevation Model with rgdal in R.	(U.S. Geological Survey 2019)
Slope	Derived from elevation with raster::terrain function in R (Hijmans 2020)	
Topographic Position Index (mTPI)	No modification.	(Theobald et al. 2015)
Continuous Heat-Load Index (CHILI)	No modification.	(Theobald et al. 2015)
Clay simple ratio	Enhance rocks rich in Al-OH, such as clay and sulfate minerals.	Jarnevich et al. (2024a)
Iron Oxide simple ratio	Enhance rocks rich in ferric iron oxide.	Jarnevich et al. (2024a)
Ferrous minerals simple ratio	Ferrous iron highlighted.	Jarnevich et al. (2024a)
Rock index	Highlights mineral deposits, clay, water, and vegetation	Jarnevich et al. (2024a)
Percent clay at 0cm	No modification to download from Soil Landscapes of the United States (SOLUS).	SOLUS (100m) (Nauman et al. 2024)
Percent sand at 0cm	No modification.	SOLUS (100m) (Nauman et al. 2024)
Soil depth	No modification.	SOLUS (100m) (Nauman et al. 2024)
Percent bare ground	1. No modification.; 2. Mosaicked downloaded tiles using ArcGIS.	Global 2010 bare ground (GLAD) (Hansen et al. 2013)
Percent tree cover	No modification.	LANDFIRE's 2020 Forest Canopy Cover (LANDFIRE 2020)
Percent tree cover - LC20	Calculated the maximum tree cover in a 150m circle around each pixel using focal statistics in ArcMap 10.6 Subtracted the local (pixel) value from the focal	LANDFIRE's 2020 Forest Canopy

focal minus local	raster to capture areas near tree cover but without tree cover themselves.	Cover (LANDFIRE 2020)
Percent tree cover - LC20 focal ratio to local	Calculated the maximum tree cover in a 150m circle around each pixel using focal statistics in ArcMap 10.6 Calculated the ratio of the local (pixel) value to the focal raster to capture variation.	LANDFIRE's 2020 Forest Canopy Cover (LANDFIRE 2020)
Uranium	Interpolated raster using inverse distance weighting from uranium content at sites in ArcMap 10.6.	Derived from Smith et al. (2013)
Tasseled cap brightness (TCB) (30m)	Represents variation in soil background reflectance, potentially capturing soil color/ bare ground.	Jarnevich et al. (2024a)
Distance to Chinle and Baca formations	Extracted Baca and Chinle polygons from the State Geologic Map Compilation (SGMC). Derived Euclidean (straight line) distance using the Euclidian Distance tool in ArcMap 10.6.	Derived from Horton et al. (2017)

Table S3. Calculated threshold values for each of four algorithms (boosted regression tree [BRT], generalized linear model [GLM], Maxent, random forest [RF]) for each of four threshold rules (minimum predicted presence, 1st percentile, 10th percentile, and 25th percentile) for the final habitat suitability model for Zuni fleabane.

Algorithm	MPP	1st	10th	25th
BRT	94	95.64	99	100
GLM	26	51.88	95	99
Maxent	1	1.64	6	8
RF	79	81.64	93	96

Table S4. Assessment metrics for the four retained algorithms (boosted regression tree [BRT], generalized linear model [GLM], Maxent, and random forests [RF]), including continuous Boyce index (CBI), area under the curve (AUC), and correlation coefficient for the final habitat suitability model for Zuni fleabane. The latter two have average values across the 10 cross-validation splits included in parentheses. CBI values range from -1 to 1 with values near 0 no different from a chance model (Hirzel et al. 2006), while AUC values range from 0.5 to 1, with values >0.7 generally being considered good (Swets 1988).

Algorithm	CBI	AUC	Correlation coefficient
BRT	1	0.999 (0.998)	0.69 (0.67)
GLM	0.84	0.997 (0.997)	0.7 (0.69)
Maxent	0.7	0.999 (0.998)	0.88 (0.87)
RF	0.99	0.999 (0.999)	0.63 (0.62)

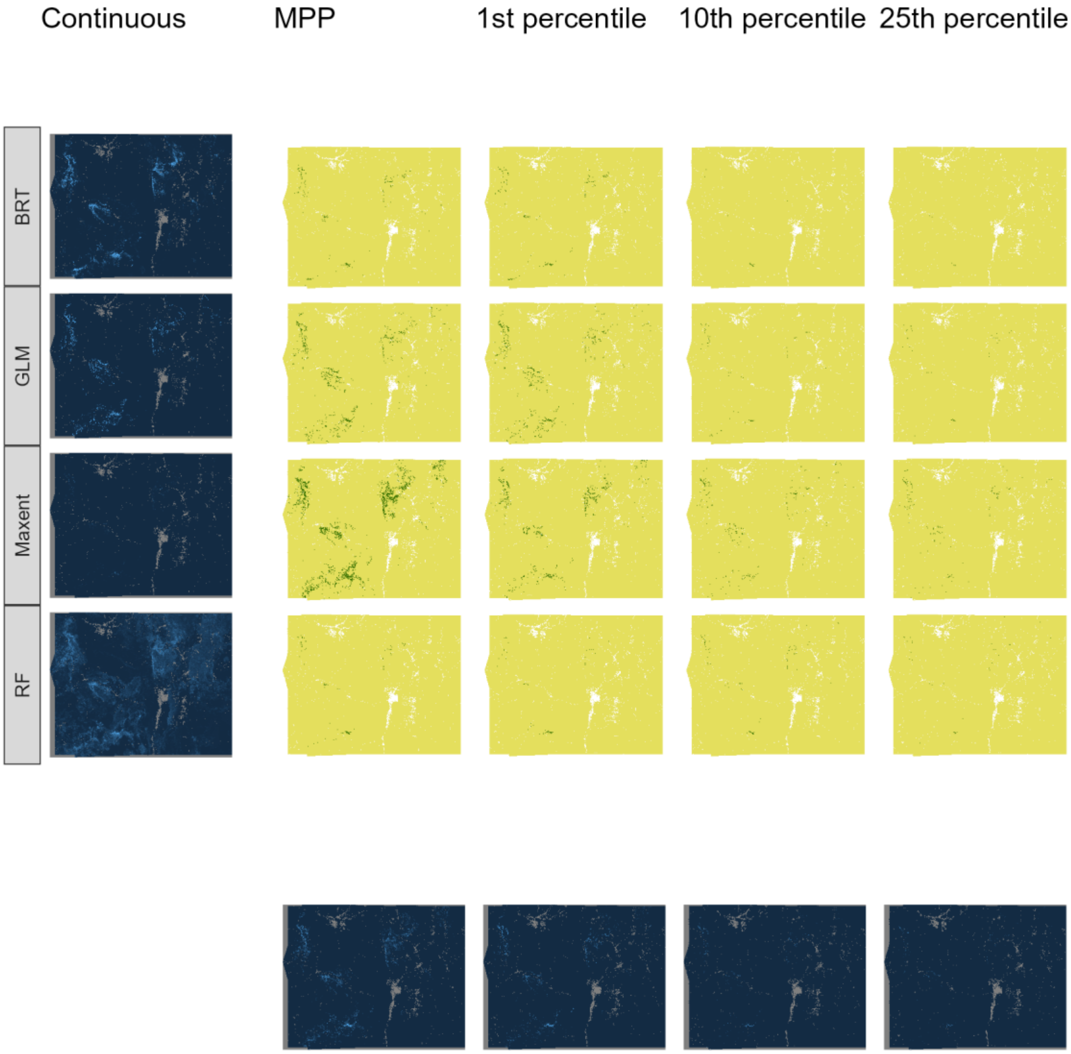

Figure S1. Workflow to produce final habitat suitability model for Zuni fleabane, where the left column shows the continuous prediction from each of the algorithms (boosted regression tree [BRT], generalized linear model [GLM], Maxent, and random forests [RF]). The right columns show the binary maps from the four different threshold rules (Minimum predicted presence [MPP], 1st percentile, 10th percentile, 25th percentile) with yellow indicating unsuitable and dark green indicating suitable. The bottom row is the sum of the binary rasters from each algorithm for each threshold.

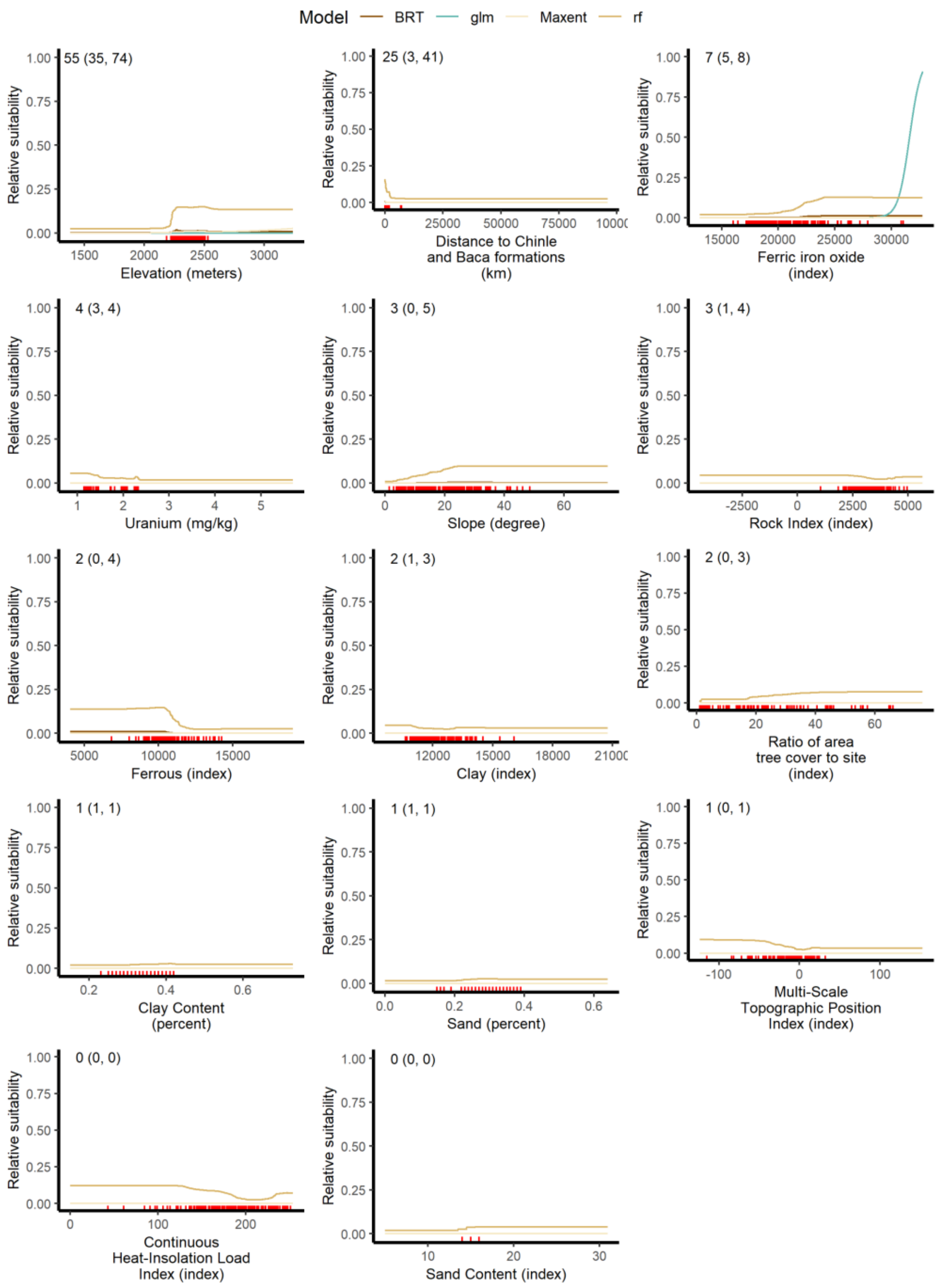

Figure S2. These graphs plot the relative habitat suitability (y-axis) for Zuni fleabane across the range of values for the specified predictor (x-axis). Each line represents one model algorithm (of the retained four: boosted regression tree [brt], generalized linear model [glm], Maxent, and random forests [rf]). Missing lines for an algorithm indicate the predictor was dropped by that algorithm. The red lines along the x-axis represent the values of the presence points used to fit the model. The graphs are arranged by relative importance (Figure S3), with the top left contributing most to models on average. Numbers in the top left of each graphic indicate the mean relative importance with the range (minimum, maximum). Details on species-specific predictors are found in Table S2.

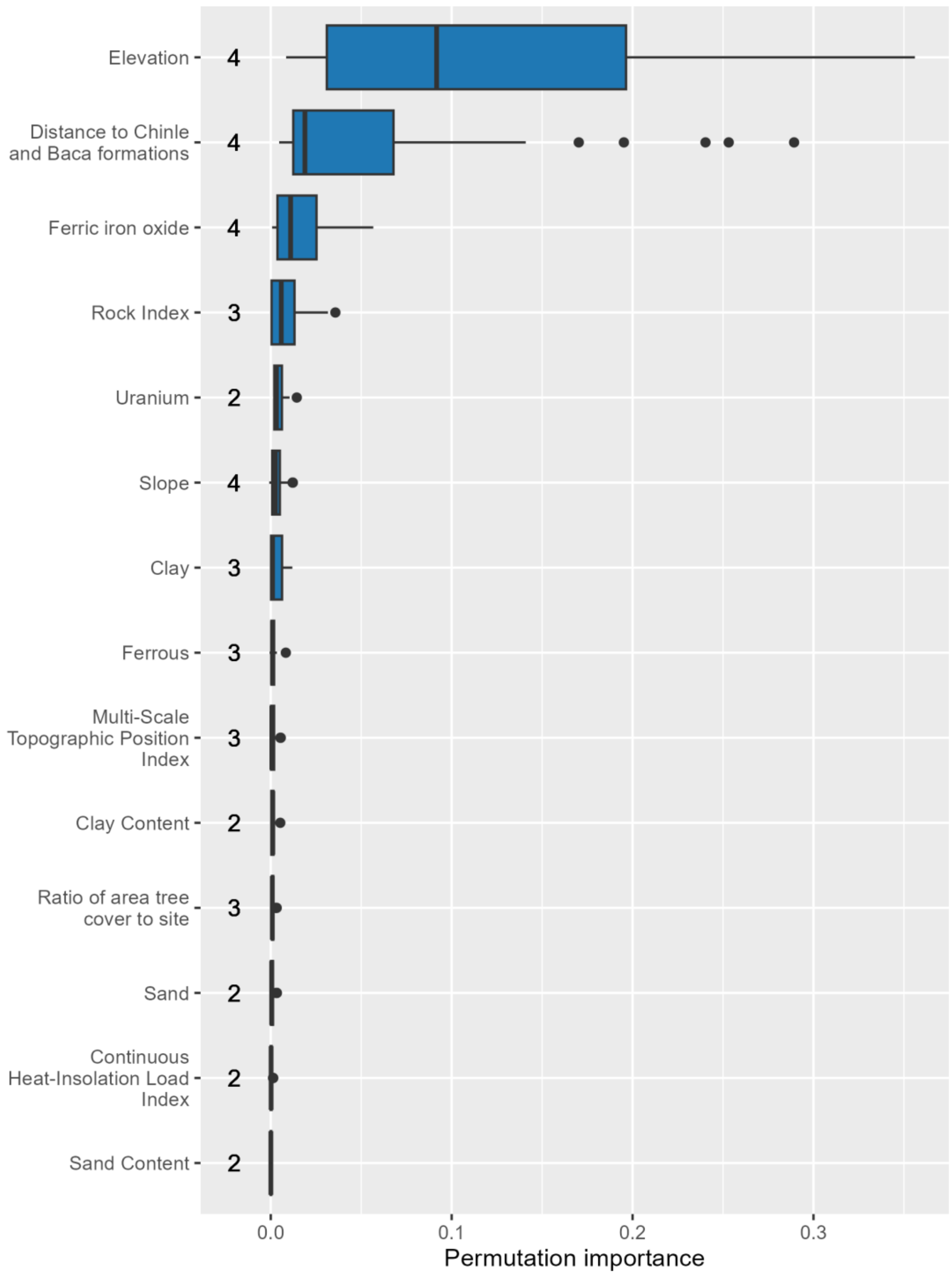

Figure S3. Variable importance of predictors included in the habitat suitability model for Zuni fleabane, assessed using permutation importance. Values for bar plots are the difference in the area under the curve (AUC) with and without permutation between presence and background points from each of the 10 cross-validation splits for each of four model algorithms. The number to the left indicates the number of the four model algorithms (boosted regression tree, generalized linear model, Maxent, and random forests) that retained that predictor as generalize linear model and boosted regression tree have internal variable selection processes.

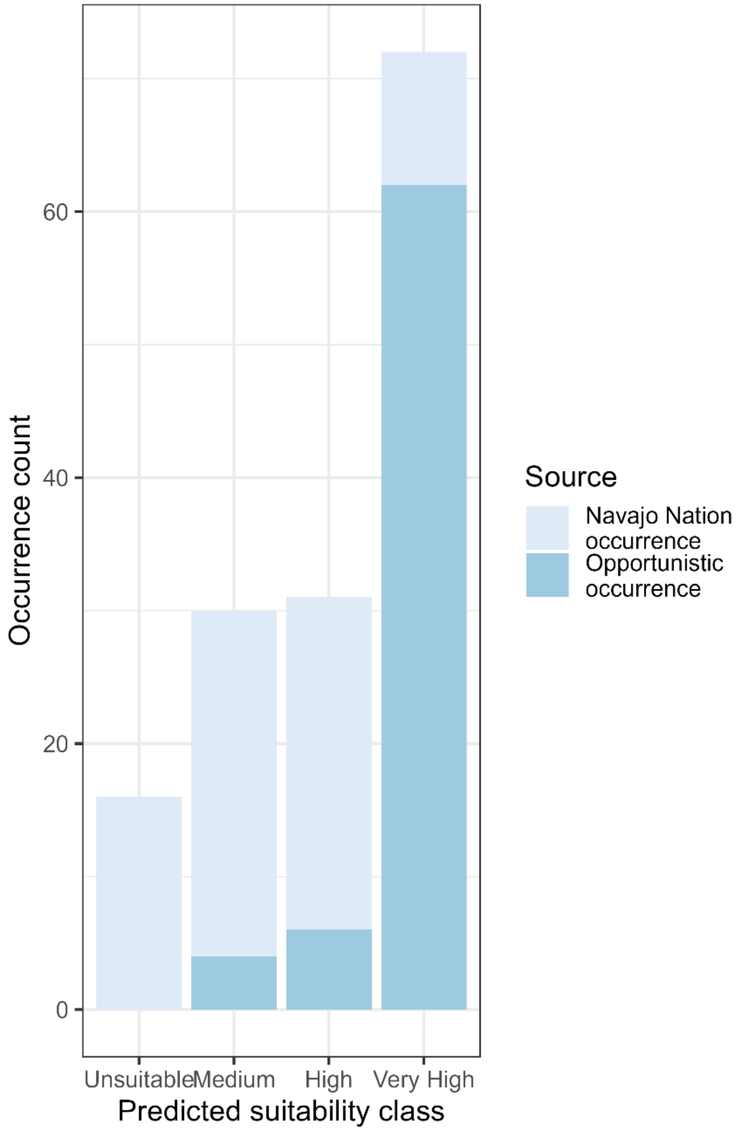

Figure S4. Validation model predicted habitat suitability for the opportunistically collected occurrences of Zuni fleabane during summer 2023 field validation survey efforts and the Navajo Nation occurrences that were not available for validation model fitting.

Figure S5. Histograms of predictor values associated with occurrences used to fit the validation model (n=82) and the additional occurrences from Navajo Nation and field surveys available to train the final habitat suitability model for Zuni fleabane. Yellow bars indicate locations used to train the validation model, while red bars reflect the new occurrences added to fit the final model with the orange indicating the values of overlap between the two sets of occurrences.

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