



Microhabitat requirements of the uncomphgre fritillary butterfly (*Boloria improba acrocne*) and climate change implications

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Received: 24 January 2023 / Accepted: 22 August 2023
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Abstract

The Uncomphgre fritillary butterfly (*Boloria improba acrocne* Gall LF, Sperling FAH (1980) A new high altitude species of *Boloria* from southwestern Colorado (Nymphalidae), with a discussion of phenetics and hierarchical decisions. J Lepidopterists' Soc 34:230–252 1980) was listed as federally endangered in 1991 and is considered a habitat indicator for alpine ecosystem health. They are found on patches of *Salix nivalis* in isolated habitats of the San Juan Mountains, Colorado, USA. Here, we estimated historical *B. i. acrocne* abundance from annual distance sampling (2003–2020) at seven sub-colonies and sampled current (July 2021) measurements of herbaceous coverage, soil moisture content, and slope, aspect, and elevation at 700 sample sites. We used regression models to test the effects of these microhabitat characteristics on historical abundance. Our results show that increases in slope from 11° to 31°, individual coverage of five alpine plant species (*S. nivalis*, *Geum rossii*, *Phacelia sericea*, *Noccaea fendleri*, and *Lewisia pygmaea*), and soil moisture content between 0.09 m³/m³ and 0.38 m³/m³ positively influence butterfly abundance. However, increases in elevation, bare ground coverage, and presence of *Salix planifolia*, *Aster alpinus*, *Antennaria media*, and *Androsace chamaejasme* were correlated with lower abundance estimates.

Implications for insect conservation Effects of climate change which decrease coverage of these alpine plant species, allow encroachment of lower elevation species, or reduce soil moisture will decrease *B. i. acrocne* abundance. These results emphasize the extinction risk of *B. i. acrocne* due to range limitations and prolonged drought conditions in the Western U.S. By defining additional resource requirements of *B. i. acrocne*, we can model climate effects on survivorship and consider nearby microhabitats that may be habitable by this endangered species.

Keywords Lepidoptera · Climate · Pollinator · Endangered species · Microhabitat · Tundra

Introduction

Background

Climate change is projected to influence overall species abundance and distributions at global, regional, and local scales, which can lead to further alterations in ecosystem structure and function (Weiskopf et al. 2020). Range shifts are favored by milder winters, reduced snowpack, and

altered growing seasons, which have already been observed in alpine ecosystems (Nydick et al. 2012).

The alpine tundra of the southern Rocky Mountains, USA is a distinctive geosystem where the geomorphic processes and climatic conditions are dominant influences on ecosystem development (Grant and French 1990). The San Juan Mountains, a discontinuous range within the southern Rocky Mountains, vary in elevation from 1524 m at their lowest, to 4358 m at the top of Uncomphgre Peak (Rottman and Hartman 1985). These mountains encompass the known range of the Uncomphgre fritillary butterfly *Boloria improba acrocne* Gall and Sperling 1980 (Lepidoptera: Nymphalidae), which is recognized as a possible indicator species of the health of the alpine tundra habitat in the San Juan Mountains (Alexander and Keck 2007).

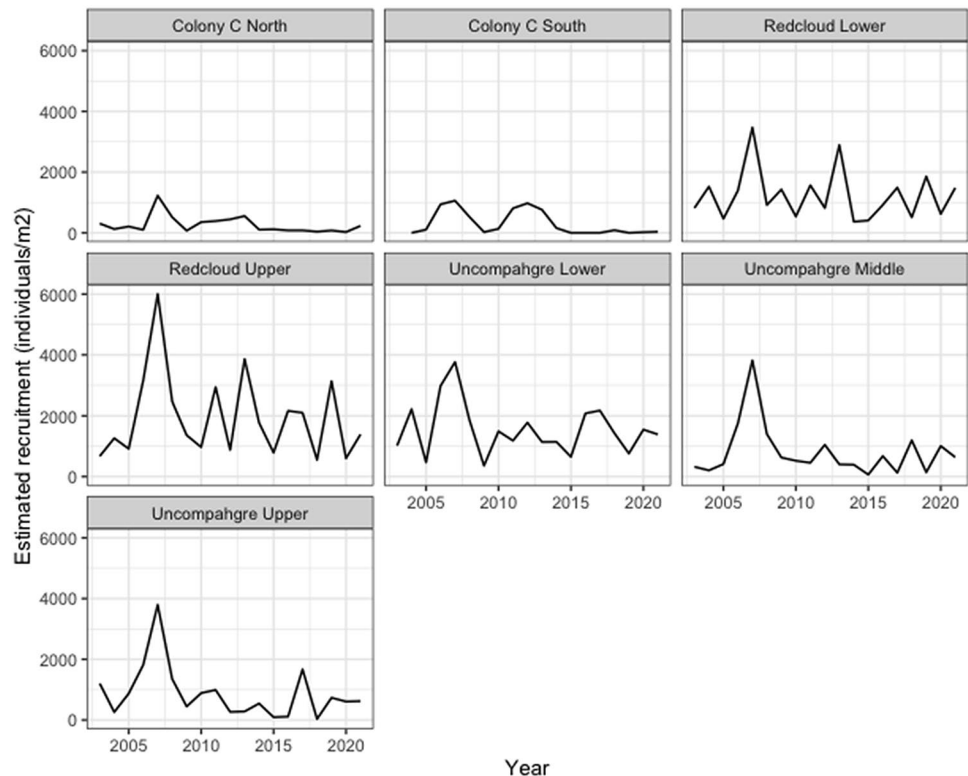
Boloria i. acrocne was discovered below Uncomphgre Peak in 1978 near Lake City, Colorado, USA.

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Fig. 1 Annual (2003–2021) *Boloria improba acrocne*ma recruitment estimated from Distance software 6.0 models (Thomas et al. 2010) at seven sub-colonies within sampling areas at Uncompahgre Peak (Upper, Middle, and Lower), Redcloud Peak (Upper and Lower), and Confidential Colony C (North and South) in Colorado, USA



Phenotypic analyses by Gall and Sperling (1980) described it as a distinct species from its closest relative, the Northern Dainty fritillary (*Boloria improba*). A second colony was discovered near Redcloud Peak, 16 km south of Uncompahgre Peak, in 1982 (Britten and Riley 1994) and additional colonies have since been found at nine additional colonies within this region. Although *B. i. acrocne*ma population size can vary each year due to their biannual life cycle, population estimates appear to remain low in sub-colonies (Fig. 1) due to threats of illegal collection, recreational traffic, livestock and wildlife grazing, and climate change.

Continued concern for the status of this species led to their listing as Federally Endangered (56 F.R. 28,712) in 1991 and implementation of the Uncompahgre fritillary butterfly recovery plan, (U.S. Fish and Wildlife Service 1990; 1994), which is now the subject of one of the longest invertebrate monitoring studies in North America. Distance sampling has been consistently applied as part of their recovery plan since 2003 and uses a counting protocol along permanently marked transects based off recommendations from Buckland et al. (2001). Distance sampling is a method used to estimate population density that accounts for imperfect detection of individuals (Buckland et al. 2001; Williams et al. 2020) and is minimally invasive in that it does not require marking or handling the butterflies (U.S. Fish and Wildlife Service 1994). Distance sampling is performed annually at three of the eleven known *B. i. acrocne*ma colonies located in the San Juan Mountains; the other eight are

visited annually for observations of persistence. Additional unpublished studies have documented *B. i. acrocne*ma host plant preference, ideal habitat and flight parameters, and habitat soil water content sources.

Habitat preferences

Butterflies are considered model species when exploring the effects of climate change because they are often constrained by the limited range of their host plants (Filazzola et al. 2020). *Boloria i. acrocne*ma have a very limited distribution in alpine habitats where patches of snow willow, *Salix nivalis* Hook. (Salicaceae), are present (Monroe et al. 2016). *Salix nivalis* is the exclusive larval food source and the preferred ovipositional substrate for adult females (Scott 1986). Both males and females are considered generalist pollinators during their short, 2–5 day adult period (Gall and Sperling 1980) and will nectar from various floral species. Adults are present for an approximately four weekperiod (late-June to late-July) following snowmelt in their habitats and early studies by Gall and Sperling (1980) describe *B. i. acrocne*ma adults as mostly philopatric due to their weak flight pattern, with low average daily movement not exceeding 50 m within suitable habitat.

Efforts by Britten and Riley (1994) to define suitable habitat of *B. i. acrocne*ma relied on three criteria: (1) the presence of snow willow, (2) northeastern aspects, and (3) elevations greater than 3500 m. These conditions are

necessary but not sufficient to define *B. i. acrocne* occupied habitat. Adult flight behavior observed by Leroux, Keck and Alexander (Unpublished) was also defined by three criteria for optimal flight conditions: (1) light intensity greater than 64,583 lx, (2) wind speeds under 5.6 kph, and (3) temperatures between 8.8 and 16.9 °C. Leroux, Keck, and Alexander (Unpublished) also discerned from field observations that greater inflorescence height led to fewer visitations by *B. i. acrocne* and that they spend a majority of their ideal flight time (approximately 74%) grounded.

Nydick et al. (2012) determined 24% of alpine obligates – especially species endemic to a small geographic area – are at risk of local and regional extinction given future warming and dry scenarios. More specialist species within fragmented habitats have a greater risk of facing extinction due to climate change effects and this risk is especially high if the species are weak dispersers, which is the case for many butterflies (Filazzola et al. 2020; Gilman et al. 2010; Schweiger et al. 2008). Current variations in shrub abundance in alpine and arctic tundra ecosystems are primarily driven by climate change (Wheeler et al. 2016). Lesser snowpack and earlier snowmelt timing may represent two of the most important mechanisms leading to the declines in dwarf shrub communities (Elmendorf et al. 2012) in tundra ecosystems. Climate-driven factors influencing the phenology of *S. nivalis* could also produce challenges for the life cycle stages of *B. i. acrocne* (Britten 1991).

Here, we examine how previous (2003–2020) population estimates of adult *B. i. acrocne* vary with current (July 2021) measurements of herbaceous coverage, soil moisture, and topographic characteristics (slope, aspect, and elevation) along three colonies. We utilized multi-year population monitoring data to define our sampling areas and produce abundance estimates along 127 transect segments covering seven sub-colonies. We then modeled relationships between these fine-scaled habitat characteristics measured during the 2021 field season and previous (2003–2020) *B. i. acrocne* abundance. We predicted: (1) Variation in historical population abundance at transect segments within seven sub-colonies; (2) A positive relationship between increased *S. nivalis* coverage and soil moisture content with *B. i. acrocne* abundance; and (3) A negative influence between increased slope and bare ground coverage on *B. i. acrocne* abundance. Surveying the host plant coverage and herbaceous diversity could reveal areas that are optimal nutrient sources and ovipositional sites within these habitats. In addition, modeling topographic variability in consistently sampled habitats could expose any previously underestimated habitat limitations for this species. With this approach, we aimed to improve understanding of specific habitat preferences of

this federally endangered butterfly, enhance management efforts to include annual monitoring of the microclimate and microhabitat requirements of *B. i. acrocne*, and explain predicted impacts of climate change.

Methodology

Study sites

The study area is within the San Juan Mountains in southwestern Colorado, USA (Fig. 2a). *Boloria i. acrocne* occupy alpine habitats at 11 known colonies within this region, including sub-colonies at three of the largest colonies, Uncompahgre Peak (3 sub-colonies: Upper, Middle, and Lower), Redcloud Peak (2 sub-colonies: Upper and Lower), and a confidential site, Colony C (2 sub-colonies: North and South) (Monroe et al. 2016) (Fig. 2a–c).

Occupied habitats were defined by cumulative observations over more than 20 field seasons and are all located on north to east facing mesic slopes in alpine environments ranging from 3800 and 4100 m above sea level and varying slope grades up to 45° (Williams et al. 2020). Systematic random sampling was implemented in 2003 and transects were established in 30-m increments to extend slightly past the population boundaries (Williams et al. 2020). Transects are marked to ensure location each year and are visited each year for distance sampling, in which population data is gathered by walking transects and marking observations of butterflies in flight and their perpendicular distances from the transect line.

Transect abundance

All analyses for this project were performed using R Statistical Software (v4.1.2; R Core Team 2020).

Distance sampling (Buckland et al. 2001) data from 2003 to 2020 was imported into RStudio (RStudio Team 2020) including variables of sampling date, transect segment, distance from butterfly location to the transect line, and observer. Transect segments are labeled by a letter and number (e.g., A1, A2, A3) which were designated in 2003. Every other transect segment is surveyed every 3–5 days during the flight season to count *B. i. acrocne* individuals.

We used the observation data to derive the annual count of *B. i. acrocne* observations per transect segment. To estimate transect line abundance, we used annual detection probabilities (Table 1) derived from Distance 6.0 software (Thomas et al. 2010) globally pooled model results, which assumed that annual detection probabilities are constant across the entire study area (Thompson 2002).

Fig. 2 **a** Map of study area including two *Boloria improba acroc-* *nema* colonies: Uncompahgre Peak and Redcloud Peak, CO, USA. **b** Uncompahgre Peak Study Area showing location of sampled sub-colonies: Upper, Middle, and Lower in Colorado, USA. **c** Redcloud Peak Study Area showing location of sampled sub-colonies: Upper and Lower in Colorado, USA

We divided annual transect counts by the annual detection probability (Table 1) and summed annual estimates together to produce total *B. i. acroc-* *nema* abundance estimates for each transect segment (See Tables S1–S7, Online Resource 1). Values were calculated for all 127 transects from 2003 to 2020; except for Colony C South where distance sampling began in 2004.

We used these previous estimates to develop regression models of the relationship between *B. i. acroc-* *nema* abundance and transect line in the seven sub-colonies to establish which transect segments to sample for additional habitat characteristics, including transect segments with typically high and low estimates. To do this, we first created constant generalized linear models (GLM) from the glm-mTMB package (Brooks et al. 2017) where abundance ~ 1 . We used different “family=” (Poisson, negative binomial, gamma, binomial, and Quasi-Poisson) options to see which regression type best fit the data based on the lowest Akaike Information Criterion (AIC). A negative binomial generalized linear model (GLM NB) from the MASS package (Venables and Ripley 2002) was created for each sub-colony with abundance as the dependent variable and interactions of transect segment and year as the independent variables (Tables S1–S8, Online Resource 1).

Power analysis

To determine the adequate sample sizes to obtain sufficient statistical power in our field data, we computed two power calculations for balanced one-way analysis of variance tests from the pwr package by Champely (2020). We performed two analyses for each sub-colony because they all vary in size and number of transect segments in place for distance sampling. The first analysis estimated the number of transect segments and the second estimated the number of samples per transect to reach the same power and significance values. We input variables k (number of groups), n (number of observations per group), f (effect size), sig.level (significant level with Type I error probability), and power (power of test with 1-Type II error probability) to reach a power of test (80%) and significance level (5%). Here, k represents the number of transects measured for distance sampling along *B. i. acroc-* *nema* sub-colonies. The effect size (f) was input as NULL, and this parameter was determined by the other variables in the test (Champely 2020).

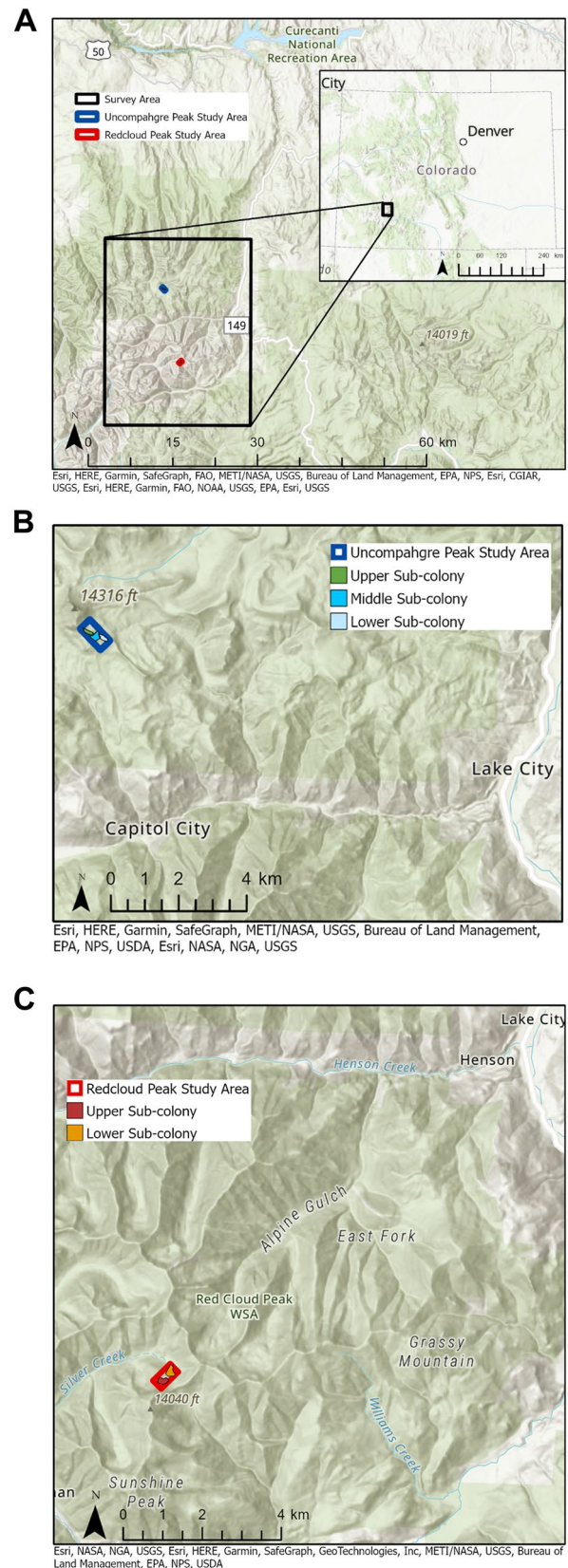


Table 1 Annual (2003–2020) *Boloria improba acrocne*ma detection probabilities using distance sampling global pooled models from the three largest colonies at Uncompahgre Peak, Redcloud Peak, and Colony C in the San Juan Mountains, Colorado, USA

Year	Detection probability
2003	0.32926
2004	0.33091
2005	0.38909
2006	0.30736
2007	0.31844
2008	0.40394
2009	0.31453
2010	0.51000
2011	0.44760
2012	0.40478
2013	0.46115
2014	0.50344
2015	0.35634
2016	0.44600
2017	0.31000
2018	0.50000
2019	0.41000
2020	0.54076

Table 2 Daubenmire (1959) cover class system assigned to each species in a 20 cm by 50 cm quadrat frame at 700 sample sites

Cover class	Range of ce %	Midpoint of range %
1	0 – 5	2.5
2	5 – 25	15.0
3	25 – 50	37.5
4	50 – 75	62.5
5	75 – 95	85.0
6	95 – 100	97.5

Habitat data collection

Stratified random sampling of habitat characteristics along 53 transect abundance and power analysis predetermined transect segments began during the first week of July 2021 following *B. i. acrocne*ma emergence (June 24, 2021). Data collection took place between 09:30 and 14:00, following completion of distance sampling along the sub-colonies to avoid interfering with *B. i. acrocne*ma count observations. Six distance intervals were established from 0.5 m to 5 meters perpendicular to the 30-m transect line using a marked avalanche probe as a lightweight measuring device. Intervals (1–6) and the choice of left or right of the transect line were run through a random number generator to define how far from the transect line each sample was established.

We used the Daubenmire method (Daubenmire 1959) to sample herbaceous coverage at 700 sites. We placed a 20 cm × 50 cm quadrat frame at the randomized locations along the transect segments and assigned each species a cover class (Table 2) based on the proportion of species in the quadrat frame.

Portions of the quadrat frame that were covered by rocks or bare soil were referred to as “Bare ground”. Portions of the quadrat frame covered in grasses, sedges, or rushes were included in a “Graminoids” category. Herbaceous species were identified in the field using the Flora of Colorado (Ackerfield 2015) dichotomous key, and accepted scientific names were confirmed using the Integrated Taxonomic Integration System (itis.gov). Calculations of percent coverage in the quadrat frame were used to characterize species and bare ground proportions within the transect segments (Online Resource 2). Following Daubenmire guidelines (1959), we took images of all 700 quadrats from an observer view and a close-up view for visual evidence of all sample plots.

Additionally, we measured slope (degrees), elevation (meters above sea level), and aspect (degrees from North) at all sample sites (Online Resource 2). Slope was measured using the iPhone Clinometer application and aspect was measured using the iPhone Compass application. Sample site elevation was measured with a sub-meter accuracy GNSS unit (Juniper Geode) and recorded in feet, then converted to meters (Online Resource 3). Additionally, we used Onset HOBO Smart Sensor S-SMx-M005 soil moisture monitoring probes to take two measurements of soil water content at each study site. Two 10-cm probes (Soil moisture 1 and Soil moisture 2) were placed into the surface soil at the sample sites and left in for 30-s intervals. A HOBO USB Micro Station Data Logger recorded the measurements ranging from 0 to 0.550 m³/m³ (volumetric water content), which were read out into the HOBOWare software.

Resource selection model

To examine the variability of previously determined *B. i. acrocne*ma abundance along the study areas in relation to current (July 2021) herbaceous cover and topographic structure, we tested resource selection models. Assuming that some habitat characteristics are selected for by adult *B. i. acrocne*ma over others, this method quantifies that selection for, or avoidance of each measured variable and provides a coefficient explaining the effect of that variable on abundance. Again, we calculated GLMs (Brooks et al. 2017) of different constant models with different “family =” options (Poisson, negative binomial, gamma, binomial, and Quasi-Poisson) and evaluated each model using AIC.

The average of all field measurements (slope, aspect, elevation, soil volumetric water content, and percent vegetation

coverage) was calculated for each transect segment (Online Resource 3). We ran covariate correlation functions for all 42 covariates to observe the closeness of relation in points of the covariates to minimize the number of covariates in our models and avoid overfitting the data. Two covariates with a negative or positive correlation coefficient of 70% or greater resulted in consideration of only one of those variables entering the model.

We constructed a GLM NB which included 13 selected habitat variables and their effect on *B. i. acrocneuma* abundance. We ran the dredge function from the MuMIn package (Bartón 2020) on this model to generate all possible combinations of model properties and performed an automated model selection of subsets, ranking them by lowest AIC (Online Resource 4). Any covariates left out of the dredge function were then added to the best-fit dredge model to test for any changes in model fitness.

A predictor effects function from the “effects” package (Fox 2003) was then used to observe and compare each of the covariate’s predicted effect on abundance (Fig. 3A–M) with 95% confidence intervals. Lastly, we ran an analysis of variance (ANOVA) from the car package (Fox and Weisberg 2019) on our resource selection model to analyze the extent to which historical *B. i. acrocneuma* abundance is affected by each habitat characteristic.

Results

Previous abundance

Previous abundance estimates calculated from annual distance sampling (2003–2020) at the seven sub-colonies totaled 14,041 *B. i. acrocneuma* along 127 transect segments. Annual detection probabilities ranged from 0.30736 to 0.54076 based on the global pooled model results from analyses run through Distance 6.0 software. The abundance data reported here is not an account of the entire population at each sub-colony but is a representative of the previous distribution of *B. i. acrocneuma* based on field observations. Distance sampling data collection at Colony C South began in 2004 so there are no estimates for 2003. Annual transect segment abundance ranges at each sub-colony were as follows: Uncompahgre: Upper (0–65 individuals), Middle (0–44 individuals), Lower (0–148 individuals); Redcloud: Upper (0–84 individuals), Lower (0–78 individuals), Colony C North (0–24 individuals), Colony C South (0–29 individuals). Eight transect segments showed zero estimated abundance, six of which were due to the transect segments only being sampled in the first year (2003) of the monitoring project. These six transect segments were removed from the analysis.

The GLM NB with previous abundance as a function of the factor variables: transect segment and year showed significant positive and negative interactions. Individual transect segments that had significant (p -value < 0.05; two-tailed, logistic regression) high and low log-transformed estimates in our regression model were determined (Tables S1–S7; Online Resource 1). Transect segments with significant high or low previous estimates were considered as sample sites for additional habitat data collection. Transect segments on the edge of *B. i. acrocneuma* habitat we excluded due to many of them being shorter than 30 m.

The effect of year (Online Resource 1; Table S8) in our model represents the change in abundance as sequential years increase from 2003 to 2020 (2004–2020 for Colony C South). Results showed the most consistent negative change on transect abundance at Uncompahgre Peak Upper sub-colony, with significant (p -value ≤ 0.05 ; two-tailed, logistic regression) negative coefficients ranging from -1.35 (SE: 0.35) to -2.97 (SE: 0.49) for five consecutive years (2012–2016; Online Resource 1; Table S8). Uncompahgre Peak Middle and Lower sub-colonies had two years of significant negative coefficients (Middle: 2015 and 2017; Lower: 2005 and 2009) (Online Resource 1; Fig. S2; Fig. S3; Table S8). Model results for both sub-colonies at Redcloud Peak showed only one year with negative significance in 2018 at the Upper sub-colony, and in 2014 at Lower sub-colony (Online Resource 1; Table S8). Colony C South sub-colony had no significant years however, results for Colony C North sub-colony showed a significant negative trend in abundance from 2016 to 2020 represented by negative coefficients (Online Resource 1; Table S8).

Power analysis

Outcomes from power analyses (Cohen 1988; Champely 2020) for all *B. i. acrocneuma* sub-colonies were used to determine sample size for field measurements (Table 3).

The first power analysis estimated the number of transect segments needed for a power of 80% and a significance of 5% with the number of groups represented by the total number of transects (k) within each sub-colony as follows: Uncompahgre: Upper ($k = 21$), Middle ($k = 27$), Lower ($k = 23$), Redcloud: Upper ($k = 16$) and Lower ($k = 16$), and Colony C: North ($k = 16$) and South ($k = 5$). With these sample sizes substituted for k , the number of sample sites within each transect line was calculated by a second power analysis to reach the same power and significance values. All values were rounded to the nearest whole number. The product of the number of transects required per sub-colony (n_1) and the number of samples per transect (n_2) gave the total sample size per sub-colony (n_3) (Table 3). Results showed that adequate sample size for each sub-colony were Uncompahgre: Upper ($n = 104$), Middle ($n = 98$), Lower ($n = 98$), Redcloud:

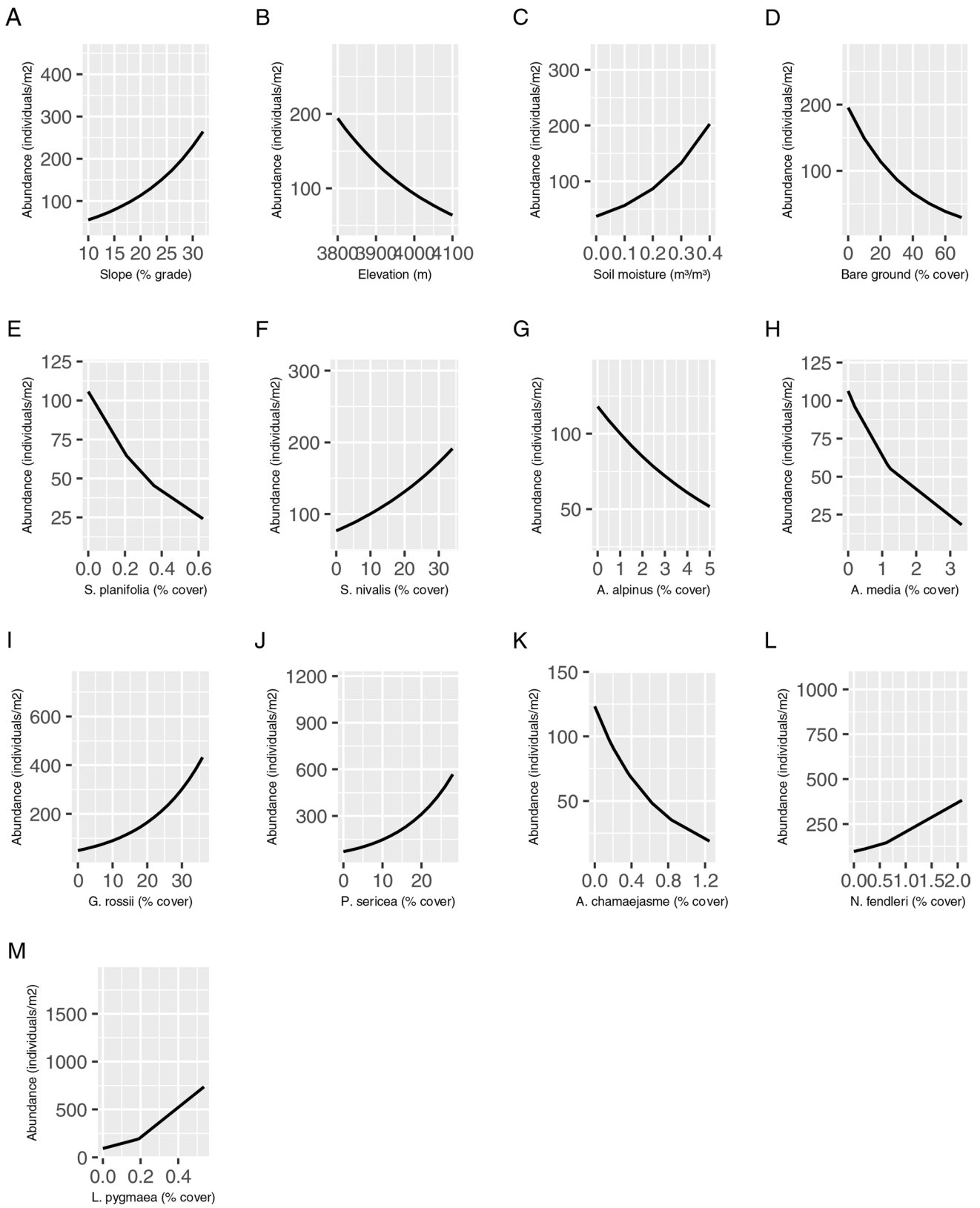


Fig. 3 A–M Single-variable model results showing effects of slope, elevation, soil moisture, bare ground percent coverage, and herbaceous species (*Salix planifolia*, *Salix nivalis*, *Aster alpinus*, *Anten-*

naria media, *Geum rossii*, *Phacelia sericea*, *Androsace chamaejasme*, *Noccaea fendleri*, and *Lewisia pygmaea* percent coverage on *Boloria improba acrocema* historical abundance estimates

Table 3 Power analysis results from number of transects measured annually for distance sampling at seven *Boloria improba acrocneuma* sub-colonies (k), number of transects required (n1), number of samples per transect segment (n2)

Sub-colony	k	n1	n2	n3
Upper Uncompahgre	21	8	13	104
Middle Uncompahgre	27	7	14	98
Lower Uncompahgre	23	7	14	98
Upper Redcloud	19	8	13	104
Lower Redcloud	16	9	12	108
Colony C North	16	9	12	108
Colony C South	5	5	16	80

All values were rounded up to the nearest whole number and the product of n1 and n2 is the total number of sample sites per sub-colony (n3). Power of test (80%), effect size (NULL), and significance level (5%) were kept constant for power analyses of each sub-colony

Table 4 Results of covariate correlation function (cor) representing *Boloria improba acrocneuma* habitat characteristic measurements with high (>0.70) correlation within 700 sample sites at the seven sub-colonies, Colorado, USA

Species or habitat characteristic	Correlation coefficient
Soil moisture 1 and Soil moisture 2	0.95506230
Aspect and Elevation	-0.7110592
<i>C. strictum</i> and <i>M. lanceolata</i> % coverage	0.8701344
<i>H. grandiflora</i> and <i>E. umbellatum</i> % coverage	0.82983285

Upper (n = 104) and Lower (n = 108), and Colony C: North (n = 108) and South (n = 80) (Table 3).

Resource selection model

A covariate correlation function only found high correlation among eight variables. Covariates with a strong downhill (< -0.70) or uphill (> 0.70) linear relationship between each other were the two measures of soil moisture (Soil1 and Soil2), aspect and elevation, *Cerastium arvense* ssp. *strictum* (L.) Ugbor. (Caryophyllaceae) and *Mertensia lanceolata* (Pursh) DC. (Boraginaceae), *Hymenoxys grandiflora* (Torr. & A. Gray ex A. Gray) K.F. Parker (Asteraceae) and *Eriogonum umbellatum* var. *majus* Hook. (Polygonaceae) (Table 4).

The model selection function (mod.sel) (Bartoń 2020) showed the “family = negative binomial” as the optimal family type for the data based on lowest AIC. We created a GLM NB with abundance as the dependent variable and 13 selected habitat covariates as the independent variables. The dredge function (Bartoń 2020) fitted 8,192 different model combinations of 13 habitat covariates and ranked them by lowest AIC (Online Resource 4). After analyzing the models that included the variables omitted from the dredge model, our best fit model resulted in *B. i. acrocneuma* abundance as a function of 15 habitat covariates including interactions of slope, elevation, soil moisture, *S. nivalis*, *Salix reticulata* L. (Salicaceae), *Salix planifolia* Pursh (Salicaceae), *Aster alpinus* L. (Asteraceae), *Minuartia obtusiloba* (Rydb.) House (Caryophyllaceae), *Antennaria media* Greene (Asteraceae), *Geum rossii* (R. Br.) Ser. (Rosaceae), *Phacelia sericea* Graham A. Gray (Boraginaceae), *Androsace chamaejasme*

Fig. 4 Negative binomial generalized linear model coefficient plot including slope, elevation, soil moisture content, percent cover of *Salix nivalis*, *Salix reticulata*, *Salix planifolia*, *Aster alpinus*, *Minuartia obtusiloba*, *Antennaria media*, *Geum rossii*, *Phacelia sericea*, *Androsace chamaejasme*, *Noccaea fendleri*, *Lewisia pygmaea* and bare ground measures from July 2021 on *Boloria improba acrocneuma* historical (2003–2020) abundance estimates

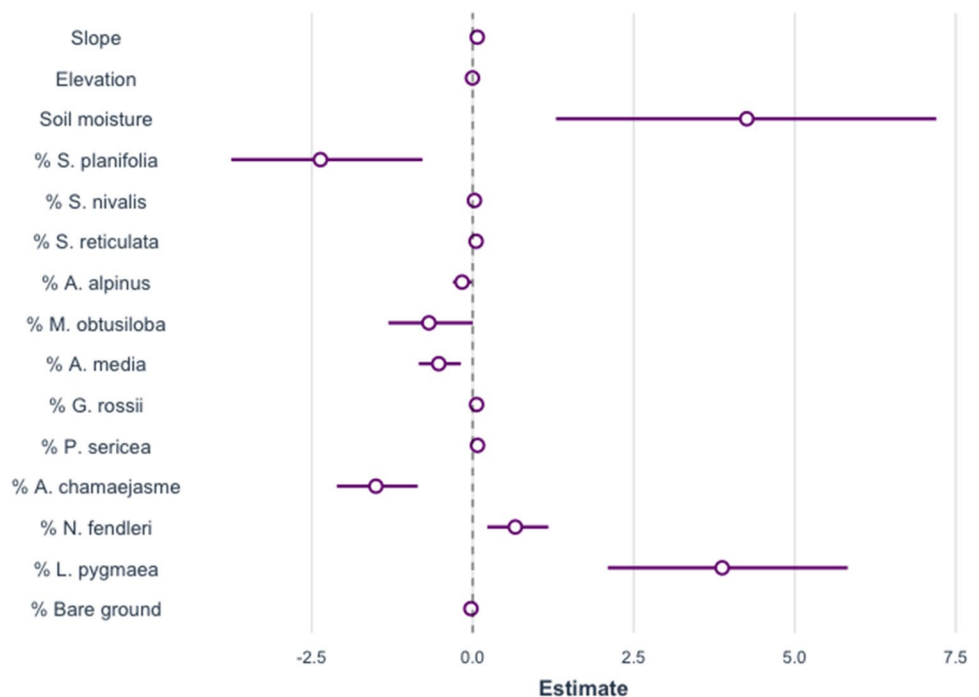


Table 5 Negative binomial generalized linear model results testing the effect of slope (%), elevation (feet), soil moisture content (m³/m³), rock and soil cover (% coverage), and 11 herbaceous species cover (% coverage) on historical *Boloria improba acrocne* abundance estimates (individuals/m²)

Coefficient	Estimate	Lower CI (2.5%)	Upper CI (97.5%)	Std. Error	p-value
Abundance (Intercept)	16.7513553	8.9863130072	24.6687957574	4.0930595	4.27e-05 ^{***}
Slope	0.0708765	0.031607953	0.1115845041	0.0194023	0.000259 ^{***}
Elevation	-0.0011297	-0.0017425264	-0.0005249423	0.0003101	0.000269 ^{***}
Soil Moisture	4.2554676	1.2926526982	7.1967365676	1.4633169	0.003636 ^{**}
<i>S. planifolia</i>	-2.3641487	-3.7484526908	-0.7807213039	0.8103594	0.003530 ^{**}
<i>S. nivalis</i>	0.0269673	0.0086626712	0.0456793135	0.0094808	0.004450 ^{**}
<i>S. reticulata</i>	0.0519680	-0.0006120113	0.1104532222	0.0288024	0.071186
<i>A. alpinus</i>	-0.1654034	-0.3065377364	-0.0151413389	0.0756631	0.028812 [*]
<i>M. obtusiloba</i>	-0.6796559	-1.3092046459	0.0021519748	0.3358371	0.042994 [*]
<i>A. media</i>	-0.5269502	-0.8367736095	-0.1849252005	0.1517311	0.000515 ^{***}
<i>G. rossii</i>	0.0600546	0.0358643173	0.0846799775	0.0113795	1.31e-07 ^{***}
<i>P. sericea</i>	0.0748593	0.0452726101	0.1057985600	0.0158722	2.40e-06 ^{***}
<i>A. chamaejasme</i>	-1.5028406	-2.1100370133	-0.8541111544	0.3260649	4.05e-06 ^{***}
<i>N. fendleri</i>	0.6614735	0.2261394964	1.1753891877	0.2540751	0.009229 ^{**}
<i>L. pygmaea</i>	3.8732150	2.0966605440	5.8219712680	0.9324687	3.27e-05 ^{***}
Bare ground	-0.0270648	-0.0408838436	-0.0132375032	0.0069144	9.07e-05 ^{***}

Significance codes represent if variables are statistically significant: '***'(0, 0.001), '**'(0.001, 0.01), '*'(0.01, 0.05), '.' (0.05, 0.1)

Wulfen ex Host (Primulaceae), *Noccaea fendleri* (A. Gray) Holub (Brassicaceae), *Lewisia pygmaea* (A. Gray) B.L. Rob. (Montiaceae), and bare ground cover (Fig. 4, Table 5).

Plant species identified in study areas but omitted from our final resource selection model due to high correlation with another variable, increased AIC when added to our model, or a non-significant (p-value > 0.050) effect on abundance (Table 6).

Other measured variables excluded from the model were Soil moisture 2, percent coverage of graminoids (various grasses, sedges, and rushes), *Selaginella rupestris* (L.) Spring (Selaginellaceae), and one species of spike moss identified across transect segments.

Our optimal model results (Table 5) confirmed the prediction that *B. i. acrocne* are selecting for sites with greater soil moisture content based on positive coefficient estimates and statistically significant p-values based on two-tailed, logistic regression (Estimate = 4.255, p-value = 0.004; Fig. 3C). They also select for increased percent coverage of their host plant, *S. nivalis* (Estimate = 0.027, p-value = 0.004; Fig. 3F), *G. rossii* (Estimate = 0.060, p-value = 1.310e-07; Fig. 3I), *P. sericea* (Estimate = 0.075, p-value = 2.400e-06; Fig. 3J), *L. pygmaea* (Estimate = 3.873, p-value = 3.270e-05; Fig. 3M), and *N. fendleri* (Estimate = 0.661, p-value = 0.009; Fig. 3L). The results also matched our prediction that bare ground coverage would show a significant negative relationship with *B. i. acrocne* abundance (Estimate = -0.027, p-value = 9.070e-05; Fig. 3D). Average slope grade showed a positive influence on abundance (Estimate = 0.071; p-value = 3.000e-04; Fig. 3A), which did not support our predictions. However, increased elevation

along the transect segments showed a significant negative impact on abundance (Estimate = -0.001, p-value = 3.000e-4; Fig. 3B). Average percent coverage of *A. chamaejasme* (Estimate = -1.502, p-value = 4.050e-06; Fig. 3K), *S. planifolia* (Estimate = -2.364, p-value = 0.004; Fig. 3E), and *A. media* (Estimate = -0.503, p = 0.0005; Fig. 3H) also represent a negative relationship with *B. i. acrocne* abundance. *A. alpinus* (Estimate = -0.165, p-value = 0.035) and *M. obtusiloba* (Estimate = -0.680, p-value = 0.050) additionally showed minor negative effects on abundance and we did not find statistically significant effect in average percent coverage of *S. reticulata* (Estimate = 0.052, p-value = 0.079).

Type II ANOVA results concur with our resource selection model results, except that percent coverage of *M. obtusiloba* and *S. reticulata* are not significant (p-value > 0.050; Wald Chi-square test), meaning not much variation in *B. i. acrocne* abundance can be explained by coverage of these species (Table 7).

Discussion

Previous abundance

We found that total adult *B. i. acrocne* abundance along sampled transects fluctuated at seven sub-colonies from 2003 to 2020, which is also presented in annual recruitment estimates provided by distance sampling analysis (Table 1). Our preliminary analysis of population trends allowed for selection of sample sites along transect segments with both high and low abundance estimates to account for habitat

Table 6 Alpine plant species found within *Boloria improba acroc-nema* habitat at Uncompahgre Peak, Redcloud Peak, and Colony C sub-colonies

Alpine plant species	Nectar host (Leroux et al. 2016)	Present along transects (July 2021)	Included in GLM NB
<i>Androsace chamaejasme</i>	No	Yes	Yes
<i>Antennaria media</i>	No	Yes	Yes
<i>Arctostaphylos uva-ursi</i>	No	Yes	No
<i>Aster alpinus</i>	Yes	Yes	Yes
<i>Bistorta bistortoides</i>	Yes	Yes	No
<i>Caltha leptosepala</i>	Yes	Yes	No
<i>Castilleja occidentalis</i>	No	Yes	No
<i>Castilleja rhexifolia</i>	No	Yes	No
<i>Cerastium arvense</i> ssp. <i>strictum</i> (L.) Ugbor	Yes	Yes	No
<i>Cymopterus montanus</i>	No	Yes	No
<i>Draba crassifolia</i>	No	Yes	No
<i>Draba fladnizensis</i>	No	Yes	No
<i>Eriogonum umbellatum</i>	No	Yes	No
<i>Gentiana prostrata</i>	Yes	No	No
<i>Geum rossii</i>	Yes	Yes	Yes
<i>Hymenoxys grandiflora</i>	Yes	Yes	No
<i>Lewisia pygmaea</i>	No	Yes	Yes
<i>Mertensia lanceolata</i>	No	Yes	No
<i>Micranthes rhomboidea</i>	No	Yes	No
<i>Minuartia obtusiloba</i>	Yes	Yes	Yes
<i>Noccaea fendleri</i>	No	Yes	Yes
<i>Oreoxis bakeri</i>	Yes	No	No
<i>Packera crocata</i>	Yes	No	No
<i>Pedicularis groenlandica</i>	No	Yes	No
<i>Phacelia sericea</i>	Yes	Yes	Yes
<i>Phlox condensata</i>	No	Yes	No
<i>Polemonium confertum</i>	No	Yes	No
<i>Potentilla gracilis</i>	No	Yes	No
<i>Salix arctica</i>	Yes	Yes	No
<i>Salix planifolia</i>	No	Yes	Yes
<i>Salix nivalis</i>	Yes	Yes	Yes
<i>Salix reticulata</i>	No	Yes	Yes
<i>Silene acaulis</i>	Yes	Yes	No
<i>Stellaria longifolia</i>	No	Yes	No

Table 6 (continued)

Alpine plant species	Nectar host (Leroux et al. 2016)	Present along transects (July 2021)	Included in GLM NB
<i>Trifolium dasyphyllum</i>	No	Yes	No
<i>Trifolium nanum</i>	Yes	Yes	No
<i>Wyethia amplexicaulis</i>	No	Yes	No

“Yes” or “No” for each column indicates whether *Boloria improba acroc-nema* have been identified nectaring on plant in Leroux et al. 2016 study, if they were identified along sampled transect segments in our study, and if they were included or not included in our best-fit negative binomial generalized linear model (GLM NB)

Table 7 Type II Analysis of Variance (ANOVA) results of the original resource selection model with abundance as the response variable

Variables	Likelihood ratio	Pr(> Chisq)
Slope	12.7858	0.0003***
Elevation	13.4828	0.0002***
<i>G. rossii</i>	24.0318	9.476e-07***
<i>P. sericea</i>	25.7510	3.884e-07***
Soil moisture	7.8878	0.0050**
<i>S. planifolia</i>	7.9060	0.0050**
<i>S. nivalis</i>	8.3949	0.0037**
<i>S. reticulata</i>	3.7481	0.0529
<i>A. alpinus</i>	4.6232	0.0315*
<i>M. obtusiloba</i>	3.8187	0.0506
<i>A. media</i>	8.4592	0.0036**
<i>A. chamaejasme</i>	18.5684	1.639e-05***
<i>N. fendleri</i>	9.4595	0.0021**
<i>L. pygmaea</i>	19.1439	1.212e-05***
Bare ground	14.5972	0.0001***

Significance codes represent if variables are statistically significant: ‘***’(0, 0.001), ‘**’(0.001, 0.01), ‘*’(0.01, 0.05), ‘.’(0.05, 0.1)

preferences of adult butterflies. Transect segments showing low estimates might be on the edge of ideal habitat or lack the microhabitat requirements for *B. i. acroc-nema*.

Changes in abundance estimates through sequential years also showed variable effects on each sub-colony, with Colony C North and Uncompahgre Peak Upper (highest elevation) sub-colonies showing negative annual trends for the last 13 years. This suggests that fewer *B. i. acroc-nema* were observed along transects than the year prior (Online Resource 1; Table S8). However, other sub-colonies showed increasing annual trends in transect abundance. For instance, Redcloud Lower sub-colony showed sequential increases in abundance from 2015 to 2020. Apart from Colony C South sub-colony, the other six sub-colonies showed significant increases in transect segment abundance in 2007, which is

also confirmed in the recruitment estimates (Fig. 1) produced by distance sampling analysis (Williams, Cohen, and Alexander 2020). We have not seen population estimates similar to those estimated in 2007 and there could be specific climate variables from that year or years prior that led to this boom in population that are unknown.

It should be noted that our confidential sites sampled annually for distance sampling are both smaller in size, Colony C North (2.44 ha) and South (1.74 ha) sub-colonies, compared to Uncompahgre Peak (3.00 ha Upper sub-colony; 3.72 ha Middle sub-colony; 2.46 ha Lower sub-colony) and Redcloud Peak (2.95 ha Upper sub-colony; 2.31 ha Lower sub-colony). Colony C North and South also produce consistently smaller abundance (Fig. 1) than other study sub-colonies. For instance, distance sampling observations counted a total of three *B. i. acrocne* in 2020 and ten in 2021 between the two sub-colonies. These sub-colonies are not near any popular recreation sites and their confidentiality is maintained to prevent illegal collection. However, based on empirical evidence during two field seasons and multiple visits to these sites, these small *B. i. acrocne* habitats are commonly grazed by elk (*Cervus canadensis* Erxleben, 1777) where the other colonies have human recreation impacts that minimize elk presence.

Overall, abundance patterns of *B. i. acrocne* recorded by the Uncompahgre Fritillary Butterfly Recovery Plan reflect low trends of insect biomass in the order Lepidoptera, one of the most widespread orders of insects (Hallmann et al. 2017; 2020). If 2007 recruitment data is omitted, *Boloria i. acrocne* estimates seem to fluctuate at the sub-colony population and transect level (Fig. 1). This could relate to their biannual life cycle, which can result in discrete even and odd-year broods during some years that experience genetic leakage, allowing them to occasionally function as independent populations and persist through their low population sizes (Britten et al. 1994; Monroe et al. 2016).

Habitat requirements and climate change

Larval host plant

For ectothermic organisms, every life stage, even ones difficult to observe, could be key determinants in the species' overall response to warming climates, as Radchuk et al. (2013) found with *Boloria eunomia* larvae. Our resource selection models showed that there could be microhabitat characteristics within these habitats that are selected for or avoided by *B. i. acrocne* during their adult life period. The positive relationship between *B. i. acrocne* abundance and *S. nivalis* percent coverage fits well with previous findings that their host plant is required for the survival of this species (Leroux, Keck, and Alexander Unpublished; Britten and Riley 1994; Scott 1986). However, our results

showed that adults might have preference for other herbaceous species than larvae, which are known to feed on *S. nivalis* (Scott 1986; Britten and Riley 1994).

Wheeler et al. (2016) found that earlier spring snowmelt reduces the performance (longer phenological development periods, lower stem density, smaller leaves, increased likelihood of herbivory and fungal damage) in the widespread, alpine dwarf willow, *Salix herbacea* (Salicaceae). The *B. i. acrocne* host plant, *S. nivalis*, which is an important habitat requirement for the survival of this species could be experiencing similar impacts. Shrub encroachment, a predicted response to climate change, will be mainly driven by taller shrubs, while dwarf shrubs (e.g., all the Salicaceae species found within *B. i. acrocne* habitats) show widespread reductions from warming in other study locations (Elmendorf et al. 2012). Any changes to alpine plant communities causing decreasing phenological timing or fitness of *S. nivalis* could be detrimental to the survival of *B. i. acrocne* and other alpine obligates that rely on these dwarf shrubs for critical life stages.

Nectar source

92% of the alpine plant species identified along *B. i. acrocne* habitat during this study are perennial plants living for more than two years. Two species, *Draba crassifolia* Graham and *Draba fladnizensis* Wulfen (Brassicaceae), are considered annuals or short-lived perennials and *E. umbellatum* was considered a variable perennial. We identified one species of perennial moss, *S. rupestris*, and 15 species of grasses, sedges, and rushes.

Our model showed that, in addition to their host plant, previous abundance estimates of *B. i. acrocne* increased as the percent coverage of *G. rossii*, *P. sericea*, *L. pygmaea*, and *N. fendleri* increased along transects. Leroux Keck, and Alexander (Unpublished) followed 72 *B. i. acrocne* adults for short (5–10 min) periods during the 2016 flight season at Uncompahgre Peak Lower and Redcloud Peak Upper and Lower sub-colonies. They observed adults nectaring on *S. nivalis*, *Salix arctica* Pall. (Salicaceae), *Silene acaulis* (L.) Jacq. (Caryophyllaceae), *G. rossii*, *Caltha leptosepala* DC. (Ranunculaceae), *C. arvensis* spp. *strictum*, *M. obstusiloba*, *A. alpinus*, *H. grandiflora*, *T. nanum* Torr. (Fabaceae), and *Bistorta bistortoides* (Pursh) Small (Polygonaceae), with twice as many visits to *S. acaulis* as any other nectar source. All these perennials were observed along transect segments throughout our study area yet measures of herbaceous coverage of only five of these species were included as independent variables in our best-fit resource selection model (Table 6).

Other herbaceous species where *B. i. acrocne* were observed nectaring by Leroux, Keck, and Alexander (Unpublished) included *Oreoxis bakeri* J.M. Coult. & Rose

(Apiaceae), *Packera crocata* (Rydb.) W.A. Weber & Á. Löve (Asteraceae), and *Gentiana prostrata* Haenke (Gentianaceae), which were not identified along the transect segments in our study (Table 6). Interestingly, *S. acaulis* was not included in our best fit resource selection model but should be included in future studies due to their high visitation by *B. i. acrocneuma* in 2016. Our results for *G. rossii* and *S. nivalis* percent coverage in comparison to *B. i. acrocneuma* nectaring habits in 2016 indicate that these two species are important nectar sources within *B. i. acrocneuma* habitat. *N. fendleri* and *L. pygmaea*, two floral species positively affecting historical abundance in our study, are not represented in the nectaring observations of Leroux, Keck, and Alexander (Unpublished). Both *N. fendleri* and *L. pygmaea* were only identified in small percentages along four transect segments each, yet all but two of these transects had high previous abundance estimates of adult *B. i. acrocneuma*, ranging from an estimated 107 to 459 butterflies. These plant species could act as supplemental nectar sources when butterfly populations are high, or the more abundant nectar sources are low.

In contrast to Leroux, Keck, and Alexander's (Unpublished) observations, our results showed avoidance of habitats with greater percent coverage of *M. obtusiloba* and *A. alpinus*, but *B. i. acrocneuma* have been observed nectaring on these species in 2016. There was no evidence of high correlation between *M. obtusiloba* or *A. alpinus* and lower soil moisture measurements, higher elevations, or greater percentage of bare ground coverage, so further observations of these species in *B. i. acrocneuma* habitats could clarify why our model showed avoidance. *S. planifolia* was also not mentioned in these surveys of *B. i. acrocneuma* and this species was only identified along three transect segments in July 2021, however its presence correlated with lower *B. i. acrocneuma* abundance. As mentioned, the Salicaceae family, especially *S. nivalis*, is an essential characteristic of *B. i. acrocneuma* habitat, yet encroachment of other Salicaceae species could have consequences for this butterfly. Overall, our surveys of host plant coverage and herbaceous diversity combined with previous studies indicate that there could be optimal areas for nutrient sources and ovipositional sites within these habitats.

Habitat limitations

Our results indicate that additional topographic characteristics influence *B. i. acrocneuma* abundance across our study sites. Prior indicators of *B. i. acrocneuma* habitat included northeast facing, mesic slopes between 3800 and 4100 m above sea level and varying slope grades up to 45° (Williams, Cohen, and Alexander 2020). Contrary to our predictions, our model results showed that increasing slope along transect segments positively affected previous abundance

estimates. Slope ranged from 11° to 31° across the habitats which narrows the previously considered slope parameters for this species. This also suggests that even major increases in slope are manageable to *B. i. acrocneuma* adults flying close to the ground and mostly philopatric (Britten et al. 1994). Additionally, these steeper slopes could produce different microclimates such as soil water drainage patterns across *B. i. acrocneuma* habitats.

Results also showed downward trends in *B. i. acrocneuma* abundance as site elevation and percent bare ground cover increased along transect segments. Average site elevation ranged from the lowest, 3801 m measured at Redcloud Peak Lower sub-colony, to the highest at 4099 m measured at Uncompahgre Peak Upper sub-colony. Additionally, transects with less herbaceous resources identified by rock or bare soil had negative effects on historical *B. i. acrocneuma* observations. These results agreed with our predictions, indicating that overall changes to alpine plant community which deteriorate or remove herbaceous coverage and nectar sources are of concern for the conservation of this species. This information also highlights the concern that *B. i. acrocneuma* are at risk of extirpation or extinction due to an upper elevation limit in their already limited geographic range, making them more susceptible to increased competition of species moving up in elevation in their alpine habitat. The upper elevation may be limited based on snow cornice availability above the colonies. Decreases in snow deposition may reduce availability of consistent summer water flow to support habitat and vegetation parameters in *B. i. acrocneuma* habitat.

Lastly, our model results corresponded with our prediction that greater soil moisture volumetric water content, which ranged from 0.09 m³/m³ to 0.38 m³/m³ among our study sites, showed higher historical *B. i. acrocneuma* abundance. Increases in bare ground coverage, whether they are caused by grazing or increased recreation, increased plant and pollinator competition or altered climate could alter the amount of moisture retained on these slopes throughout the growing season. Soil moisture is a key variable influencing the microclimate, soil, plant distribution, nutrient availability, and topography in alpine regions (Zhang and Li 2017) and is of high concern, especially due to prolonged drought conditions in the western United States. A Snow Telemetry and National Weather Service data analysis by Rangwala and Miller (2010) showed that the San Juan Mountain range had one of the highest rates of warming in the United States from 1995 to 2005, which could heavily influence the amount of snowmelt. The effects of climate change could be exacerbated by the fragmented habitats and lack of movement options for *B. i. acrocneuma*. The *B. i. acrocneuma* sub-colonies at Uncompahgre Peak and Redcloud Peak study areas are divided by snow cornices, which develop on mountain ridges and deliver snow to the sub-colonies downslope.

Cornice melt during spring and early summer in the alpine is a key source of erosion, soil moisture, and soil nutrients (Munroe 2018) and are an important supplier of soil moisture to these habitats.

Even slight environmental changes, such as earlier snow melts, lower snowpack, and heightened summer temperatures could have a large effect on this species and other alpine pollinators – hence why butterflies are commonly used as indicators of ecosystem health. We must better understand the microclimate and macroclimate factors that may be influencing this butterflies' requirements during important developmental periods in these surveyed habitats.

Management implications

The conservation efforts of the Uncompahgre Fritillary Butterfly Recovery Plan (U.S. Fish and Wildlife Service 1994) include annual distance sampling at Uncompahgre Peak, Redcloud Peak, and Colony C colonies and field observations at the eight other known colonies in the region. This study used these annual field observations to display patterns in historical adult *B. i. acrocneuma* abundance and highlighted another use for long-term population estimates in understanding habitat preference. Modeling transect abundance shows which parts of these habitats have experienced many or few adults over 18 years of data. Because adult *B. i. acrocneuma* are weak flyers with low daily movement, we can assume that this study was at an adequate scale to observe species-habitat interactions and can, therefore, incorporate these results into future monitoring efforts for this species.

Our results indicate that there are additional microhabitat factors to include in the *B. i. acrocneuma* recovery plan. First, annual population surveys can include observations of adult nectaring activity on alpine plants from our surveys and Leroux and others (2016) including, but not limited to, *G. rossii*, *S. nivalis*, *P. sericea*, *N. fendleri*, *L. pygmaea*, and *S. acaulis*. While current monitoring efforts focus on the three to four-week flight period of *B. i. acrocneuma*, further habitat assessments of these nectar sources should incorporate observations of phenological timing, number of inflorescences, leaf size, and nectar availability. Because alpine plant communities consist of mostly long-lived perennials, as in our study, we can assume longer term vegetation data isn't critical. However, these perennials could face increased pressure from wildlife grazing, which could explain the consistent low counts and population estimates at Colony C North and South and should be considered in management. Additionally, there are pressures of invasive species or lower altitude species moving up in elevation as the alpine climate warms (Inouye 2020) and management efforts should monitor for any changes in species composition within *B. i. acrocneuma* habitat.

A study on the habitat preferences of *Hamearis lucina* found that both larvae and adults of the species held a narrow ecological niche in which slope, aspect, and vegetation type played a role in the microhabitat suitability for the butterfly (Hayes et al. 2018). Our study did not observe larval behavior on *S. nivalis* or their overall presence throughout our study sites. Additional surveys of larval activity could confirm microhabitat requirements and limitations between *B. i. acrocneuma* larvae and adults and model for how these might be impacted by climate change.

To understand the effects of climate on this alpine pollinator, the Uncompahgre Fritillary Butterfly Recovery Plan can incorporate research at macroclimate and microclimate scale to observe characteristics influencing butterfly-habitat interactions. Since our study only took one measure of soil moisture during the short flight season, continuous field measures of soil moisture content, ground temperature, and seasonal precipitation could be performed annually at the three main colonies to provide microclimate data. Light-weight devices could be used to take measurements at back-country habitats for one-time measures to compare to the sites at the main populations at Uncompahgre Peak, Redcloud Peak, and Colony C. In addition, macroclimate data is readily available on multiple online platforms and can be modeled to observe for warming at a regional scale that encompasses the entire range of *B. i. acrocneuma*.

Defining metapopulation structure and requirements can inform management of best efforts for site-specific and population level conservation. Additionally, changes in the parameters can be used to model extirpation or extinction risk for this species, model metapopulation dynamics (Monroe et al 2016) for habitat management decisions or locate potential suitable habitat. Habitat suitability maps have been used by the recovery plan to identify suitable *B. i. acrocneuma* habitats, yet the results of this study could be included in those maps to narrow the scopes of slope and elevation based on our findings.

Taking actions to reduce the occurrence of bare ground or reduce the increase in snow melt are also important management considerations. Recreational trail management in trails that go around or through *B. i. acrocneuma* habitat is critical. Erosion from trails or off trail travel could increase bare ground and immediately decrease *B. i. acrocneuma* abundance. Permit management to eliminate domestic ungulate grazing and the potential for trampling causing bare ground, the introduction of plants to the *B. i. acrocneuma* habitat or the consumption of herbaceous plants needed for *B. i. acrocneuma* persistence is critical.

Conclusion

The results of this study demonstrate the effect of topography, soil moisture, and herbaceous resources on previously estimated abundance of a federally endangered butterfly. Across all study areas, *B. i. acrocneuma* abundance decreased as elevation increased and increased as slope and soil moisture water content increased. Although, the *B. i. acrocneuma* adults are considered generalist pollinators, our model results in conjunction with other studies show they are selecting for certain areas with specific nectar sources in their habitat in addition to the presence of their host plant. Our findings highlight the importance of multi-year surveys in understand the survivorship of *B. i. acrocneuma* and provide evidence for ecological factors not previously considered to be selected for or avoided by this species.

Under future warming climate circumstances, the *B. i. acrocneuma* and other alpine obligates face the added stress of having to adjust physiologically to temperature changes, which are important for ectotherms, or developmentally to altered summer and winter precipitation patterns (Inouye 2020) and the phenological timing of their nectar sources. The effects of climate change which decrease coverage of alpine plant species, especially *S. nivalis*, allow encroachment of lower elevation species, or reduce soil moisture content will threaten the persistence of *B. i. acrocneuma*. Future monitoring efforts should evaluate the abiotic factors of alpine ecosystems and how species might respond under continued warming scenarios. Monroe et al. (2016) indicated that these colonies might persist through low-level migration and “temporal leakage” at these study sites, suggesting this data could also be used to manage suitable habitat for metapopulations of *B. i. acrocneuma*. With formulas of predicted changes in the phenological timing of alpine communities and micro- or macroclimate data, we can further model climate related extirpation or extinction risk of *B. i. acrocneuma* to adequately manage for in the short term and prioritize for the long-term conservation of alpine ecosystems. Protecting current habitat from increasing bare ground due to human recreation or livestock grazing are critical management actions to preventing immediate declines in *B. i. acrocneuma* abundance.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-023-00513-8>.

Acknowledgements This research was conducted in conjunction with the population monitoring surveys under the Uncompahgre Fritillary Butterfly Recovery Plan. We thank the Uncompahgre National Forest, Gunnison National Forest, Rio Grande National Forest, San Juan National Forest, the U.S. Fish and Wildlife, the Bureau of Land Management Gunnison Field Office, the USDA Forest Service Gunnison Ranger District, and Western Colorado University for their support. We thank the professors at Western Colorado University, Robin Bingham,

Ph. D. and Madelon Van de Kirk, Ph. D., for help in their fields of expertise, the 2021 summer field staff (Kjerstine Jones, Sam Finnie, and Alyssa Tatum) and all previous summer field crews, and family and friends for their continued support throughout this project.

Author contributions Andrea Williams conducted microhabitat data collection, wrote the main manuscript text and prepared the figures. Kevin Alexander obtained population data, supervised the research and developed the research concept. Both authors reviewed the manuscript.

Funding Open access funding provided by SCELCS, Statewide California Electronic Library Consortium. This research was partially funded by the U.S. Forest Service, U.S. Bureau of Land Management, U.S. Fish and Wildlife Service.

Data availability All transect abundance data was derived from annual distance sampling counts under the Uncompahgre Fritillary Butterfly Recovery Plan (U.S. Fish and Wildlife 1994) and are reported in annual reports (Williams, Cohen, Alexander 2020; 2021). Population data for Uncompahgre Peak, Redcloud Peak, and Colony C colonies are available upon request.

Declarations

Conflict of interest The authors confirm that they have no conflict of interest with this project.

Research involving human/animals participants No butterflies were intentionally harmed during this project. All research was done under the consent of the Uncompahgre Fritillary Butterfly Recovery Plan (56 F.R. 28712). Butterfly identification was done by recognizing key characteristics of *Boloria improba acrocneuma* taught to surveyors prior to data collection.

Informed consent No data were collected from human participants during this project.

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