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Potential climatic refugia in semi-arid, temperate mountains: Plant and arthropod assemblages associated with rock glaciers, talus slopes, and their forefield wetlands, Sierra Nevada, California, USA

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ABSTRACT

Unique thermal and hydrologic regimes of rock-glacier and periglacial talus environments support little-studied mountain ecosystems. We report the first studies of vascular plant and arthropod diversity for these habitats in the central Sierra Nevada, California, USA. Surfaces of active rock glaciers develop scattered islands of soil that provide habitat for vegetation. Total plant cover relative to the entire surface area of two rock glaciers was 0.2–1.7%. Vascular plant diversity was high relative to reference sites, with 16–28 species observed on 0.1–1 ha total area of soils patches on each rock glacier. Species had upland- and cold-adapted traits, and were primarily perennial herbs and subshrubs. Complex wetland environments in the forefield of two rock glaciers and two talus slopes supported a high diversity of vascular plants, with sedges and graminoid taxa abundant as well as other cold-environment, wetland-adapted, perennial herbaceous species. Talus forefields were small (mean, 0.6 ha) yet supported 65 vascular plant species each; larger rock-glacier forefields (mean, 11 ha) supported 48-84 species each, with diversity greater at the larger site. Relative to reference sites, taxonomic diversity on the wetlands associated with periglacial landforms overlapped that on reference wetlands. Arthropod diversity at the same four rock-glacier and talus wetlands was significantly higher than at reference wetlands, with overall abundance three times greater on the rock-associated wetlands. Forty-seven of the 60 arthropod families collected were more abundant in rock glacier and talus wetlands than in reference meadows. On average, 17 families (26 morphospecies) were observed on the talus wetlands and 45 families (69 morphospecies) on rock-glacier wetlands. Cicadellid leafhoppers and aphids were dominant on the rock-associated wetlands whereas chloropid flies were most abundant on reference sites. Given the known thermal and hydrologic capacity of rock-glacier and talus environments to resist warming, these distinct ecosystems might become increasingly important as mountain refugia for a diversity of biota in the future.

1. Introduction

Blocky landforms such as rock glaciers and talus slopes are common in mountain regions worldwide, especially in ranges that experienced Pleistocene glaciation and occur in cold periglacial environments (Giardino and Vitek, 1988; Barsch, 1996; Curry and Morris, 2004; Sass, 2006). The paucity of fine sediments in these landforms and dominance of large clasts create an open lattice-like internal environment that promotes ground thermal regimes distinct from adjacent upland soils (Humlum, 1997; Harris

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and Pedersen, 1998; Hanson and Hoelzle, 2004; Juliussen and Humlum, 2008). Micro-climatic processes, including cold-air drainage, Balch ventilation, chimney flow circulation, and evaporative cooling, partly decouple internal thermal regimes from ambient climates, and depress matrix temperatures below that of external free-air (Haeberli, 1973; Harris and Pedersen, 1998; Millar et al., 2013). Cumulatively, the cooling processes have been shown to promote development and retention of persistent ice, either glaciogenic or periglacial, in many of these landforms (Clark et al., 1994; Sawada et al., 2003; Haeberli, 2005), and to lower regional permafrost elevations by as much as 1000 m (Delaloye and Lambiel, 2005). Springs and seeps issuing from these landforms often persist throughout the warm, dry season when other springs desiccate, and have colder water than springs from other sources (Krainer and Mostler, 2002; Millar et al., 2013). Forefields of these landforms are cooled as a result of downslope air flow in summer that promotes cold-air venting from the base of the rocky fronts (Sawada et al., 2003; Zacharda et al., 2007; Millar et al., in press).

These factors jointly contribute to development of stable wetlands in the forefields of rock glaciers and talus slopes. In some parts of the world these habitats have been shown to support cool-adapted plant species at elevations below their typical ranges (Sasaki, 1986; Gude et al., 2003; Freppaz et al., 2008). Further, although the blocky surfaces of rock glaciers and taluses are mostly soil free, scattered soil patches can form on the mantles and snouts of these features, and develop plant cover (White, 1976; Burga et al., 2004; Caccianiga et al., 2011). At least one study has shown these soil patches to support cold-adapted flora, with potential capacity as long-term refugia (Fickert et al., 2007). The presence or absence of plants on rock glacier surfaces has been debated as an indicator of whether the landform is active (ice embedded and moving) or relict (ice melted and stagnant; Tomaselli and Agostini, 1990; Cannone and Gerdol, 2003). The internal matrices of blocky landforms provide habitat for microbes (Williams et al., 1997) and other fauna that require persistent cool conditions or escape from extreme heat. For example, the predatory rhagidiid mite, *Rhagidia gelida*, a cryo-indicator of periglacial environments, has been documented to occur in scree habitats at anomalously low elevations in the Czech Republic (Zacharda et al., 2005), and diverse invertebrate groups including mites, spiders, springtails and beetles occurred within talus slopes elsewhere in central and eastern Europe at elevations lower than expected (Růžička and Zacharda, 1994; Molenda, 1996). The widespread North American mammal, American pika (*Ochotona princeps*), a poor thermoregulator and sensitive to high temperatures, is restricted to cool talus and rock glacier habitat and adjacent wetland forefields where it forages (Smith and Weston, 1990). Large alpine mammals that feed on carrion, such as wolverine (*Gulo gulo*), also use the cool interior of taluses to cache carcasses, often locating their dens nearby (Inman et al., 2012). Taken together these blocky landforms and their forefield wetlands create unique environments, and, with their associated microbes, plants, and animals, constitute distinct yet little described mountain ecosystems (Kubat, 2000).

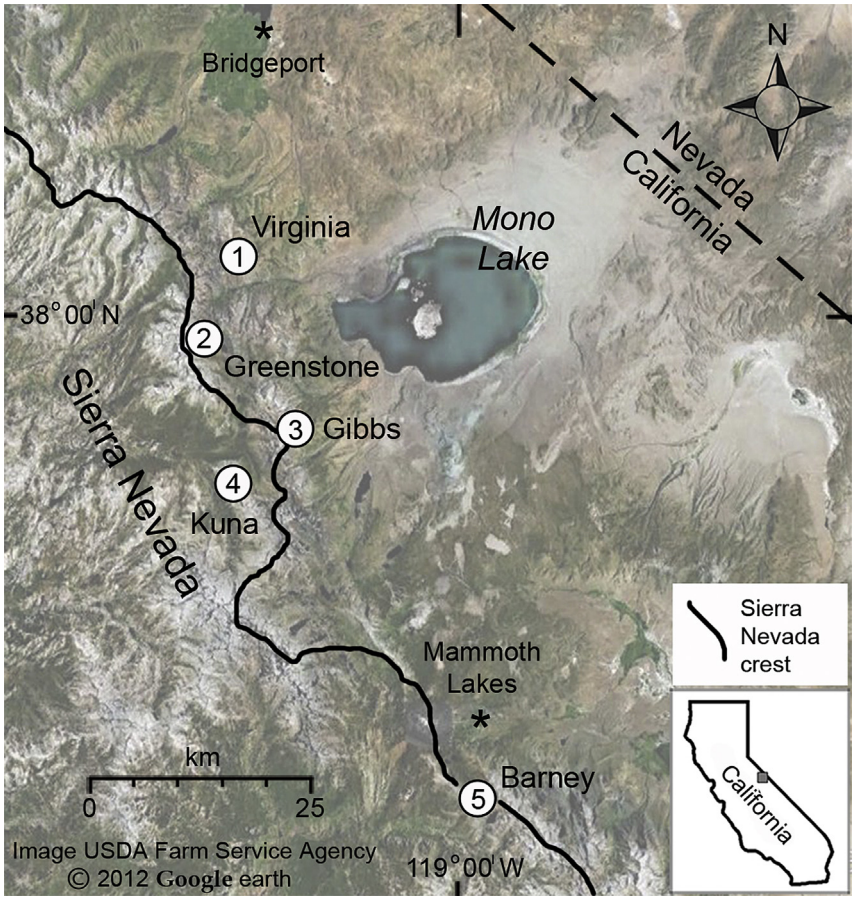

Fig. 1. Locations of sampling sites for rock-glacier plant diversity (sites 3 [Gibbs], 5 [Barney]), rock-glacier/talus wetland plant diversity, and rock-glacier/talus wetland arthropod diversity surveys (talus wetlands, sites 1 [Virginia], 2 [Greenstone]; rock-glacier wetlands, sites 4 [Kuna], 5 [Barney]), central Sierra Nevada, California.

Thermal processes and ecological associations of rock glaciers and taluses have been studied mostly in temperate European and Japanese mountains and in arctic environments. At lower latitudes, and in warmer and semi-arid ranges such as the Sierra Nevada, California, rock glaciers and taluses have been less studied despite their widespread distribution in glaciated canyons of the central and southern Sierra Nevada (Kesseli, 1941; Millar and Westfall, 2008). Early research in this range focused on glaciogenic rock glaciers and the potential for stratified ice to serve as paleoclimatic archives (Clark et al., 1994; Konrad and Clark, 1998). More recently, studies have addressed rock-glacier distribution (Millar and Westfall, 2008), hydrologic and thermal regimes (Millar et al., 2013, in press), and rock-glacier movement (Liu et al., 2013). These studies document unique thermal regimes and hydrologic conditions, and suggest that persistent ice is embedded in many high-elevation Sierran features.

The ecosystem roles of talus and rock glaciers in the Sierra Nevada have been studied primarily for their value as habitat for pikas and other small mammals (Grinnell and Storer, 1924; Smith, 1974; Peacock and Smith, 1997; Millar and Westfall, 2010; Millar et al., 2013). Wetlands are important reservoirs of biodiversity in semi-arid mountain ranges, and, in the Sierra Nevada, meadow classifications and floristic assessments have described biota and assemblages related to rocky environments and wet meadows generally (e.g., Fites-Kaufman et al., 2007; Holmquist et al., 2011; Weixelman et al., 2011). Floristic studies of high elevation habitats, including wetlands, have focused on the southern portions of the Sierra Nevada (Benedict, 1983; Kimball et al., 2004). The only floristics research directly associated with rock glaciers is that of Franklin (2012), including evaluation of *Linanthus pungens* as a model species for herbchronological investigation and documentation of the species' growth response to temperature and snowpack (Franklin, 2013). Beyond these efforts, no focused studies have been conducted on the ecological diversity or potential unique biodiversity of rock glacier and talus ecosystems. In that these landforms are likely to retain their thermal and hydrologic capacities longer than other environments under future warming climates, the ecosystems have potential to serve as long-lasting, cool-environment refugia (Fickert et al., 2007; Leopold et al., 2011).

Our goals in this study are to describe and assess floristic and arthropod biodiversity of rock glacier and talus ecosystems in the central Sierra Nevada, and to establish baseline data for future monitoring. We evaluated vegetative diversity and extent of plant habitat on the rocky surfaces of two rock glaciers, and vegetative and arthropod diversity in the forefield wetlands of two rock glaciers and two talus slopes. While primarily descriptive in nature, we hope to document preliminary ecological characteristics of these ecosystems and encourage future research on their biodiversity and potential as ecological refugia during warming climates.

2. Methods

2.1. Study locations and field methods

Five study sites were included, with overlap among floristic and arthropod studies; all sites except one were located on the eastern slope of the central Sierra Nevada (Fig. 1, Table 1). Sites were selected as 1) representative of typical rock glacier and talus features in that part of the range, both in landform and wetland forefields (Millar and Westfall, 2008); 2) a subset of areas for which information exists on thermal regimes (Millar et al., 2013, in press); 3) likely containing persistent ice (Millar et al., 2013); 4) known occupied habitat of American pikas (Millar and Westfall, 2010), and 5) a subset of rock glacier locations used by Franklin (2013) in herbchronological research.

Table 1
Location and environmental context of study sites, including three rock glaciers and two talus slopes. Coordinates are given for the center base of the blocky landform, at the border of the forefield wetland.

Site	Latitude (deg)	Longitude (deg)	Elevation (m)	Aspect	Substrate	Area (ha)		Studies
						Rock glacier or talus	Forefield wetland	
Rock glaciers								
Gibbs	37.89728	−119.19185	3091	N-NE	Metamorphic	4.7	0.12	a
Kuna	37.84913	−119.25588	3393	NE	Granitic	7.2	0.84	b, c
Barney	37.57030	−118.97295	3095	NE to SE	Metamorphic	14.9	3.14	a, b, c
Talus slopes								
Virginia	38.04381	−119.28177	3190	N	Metamorphic	0.6	0.60	b, c
Greenstone	37.97730	−119.29229	3093	N	Granitic	0.4	0.65	b, c

Studies:
a, rock-glacier vegetation.
b, wetlands vegetation.
c, wetlands arthropods.

The rock glacier surface floristic study was conducted on Gibbs rock glacier south of Lee Vining, California, and Barney rock glacier, west of Mammoth Lakes, California (Fig. 2A, B). Gibbs rock glacier is a small feature below the cliffs of Mt. Gibbs and situated near the escarpment front of Gibbs canyon. Adjacent to Gibbs rock glacier on upland slopes are diverse alpine plant communities and just below the rock glacier are upper subalpine forests comprising whitebark pine (*Pinus albicaulis*), lodgepole pine (*Pinus contorta* ssp. *murrayana*), and mountain hemlock (*Tsuga mertensiana*). The larger Barney rock glacier, situated in upper Mammoth Creek Canyon near Barney Lake, heads in a small alpine cirque along the Mammoth Crest, and extends 0.4 km downslope into a subalpine forest having similar composition to that at Gibbs rock glacier.

At each rock glacier we mapped the location and measured the area of all soil-vegetation patches larger than 3 m^2 on the rock glacier front (snout), top, and sides (Fig. 3). For patches less than 50 m^2 we inventoried all plants, noting species and frequency. For patches $\geq$50 m^2 we inventoried all plants in one to five randomly placed 5 m^2 (5 m × 1 m) and/or 10 m^2 (10 m × 1 m) plots, with the number and size of plots depending on the relative density of plants on each patch and the shape of the patch. Plants not identified in the field were field pressed and carried to the office for later evaluation. The taxonomic authority for plant identifications

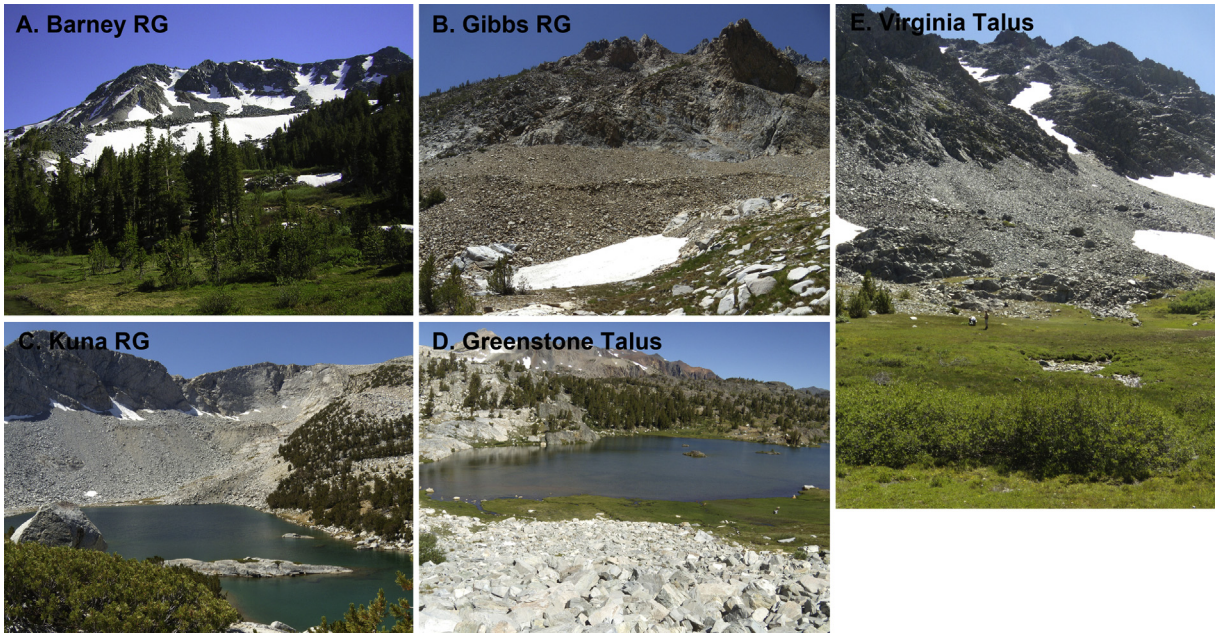

Fig. 2. Overview of study sites. A. Barney rock glacier. B. Gibbs rock glacier. C. Kuna rock glacier. D. Greenstone talus. E. Virginia talus.

in all studies was Baldwin et al. (2012). Field work was conducted in July and August, 2006 and 2007.

We used prior studies at the San Joaquin Roadless Area (SJRA, 4400 ha; Constantine-Shull, 2000) and the Harvey Monroe Hall Research Natural Area (HRNA, 1571 ha; Taylor, 1984) as reference floras. These locations lie within the latitude, longitude, and elevation zone of our sites, although each area encompasses far larger and more heterogeneous environments, and spans far more elevation zones than our single point locations. Nonetheless these were the best sites available for comparison. From the annotated species lists for those sites, we extracted taxa associated with rocky, scree, and talus environments, and those occurring at elevations between 2800 m and 3400 m. These locations include a heterogeneous group of rocky environments excluding rock glaciers. Differences in taxonomic identification and nomenclature – despite our effort to synonymize names – further limit the extent to which these lists serve as ideal references. Finally, the considerable age of the reference collections and the differences in weather contexts of the survey years could confound comparison. For both the HRNA and the SJRA studies, surveys were conducted during multi-year periods of record high precipitation (early 1980s, mid-late 1990s; WRCC, 2013). This period contrasts with the survey years for the present study, which were moderately (2006) and extremely (2007) dry years. In that most of the species observed were perennial, bias in survey-year weather might be negligible. As no abundance information was available for the reference locations, only species presence–absence data could be compared.

The wetland vegetation study was conducted on the forefields of two rock glaciers (Barney and Kuna) and two talus slopes (Virginia and Greenstone; Table 1, Fig. 2A, C, D, E). Kuna rock glacier and both talus slopes are located above treeline and dry, upland vegetation types are adjacent to the rocky landforms and to their forefield wetlands. At each location, we mapped the perimeter of the zone of influence of the rock glacier or talus, defining the latter as wetlands below the rocky snouts with borders distinct from adjacent dry upland soils (Fig. 4). We stratified patches of common vegetation and/or distinct environments (e.g., wet meadow versus riparian-shrub habitat) within the perimeter of the wetlands. For each patch we mapped the boundaries, listed all vascular plant species observed, and noted non-vascular types present from walking systematically through the entire patch; no plots or transects were installed. After each patch was inventoried, we estimated abundance subjectively for each species per patch, using the protocol of the Multi-Summit Target Region, summit-area-section methods, from the international Global Observation Research Initiative in Alpine Environments (GLORIA) program, and sorting abundance into five categories (Pauli et al., 2013). Field work was conducted in July and August, 2011 and 2012.

The arthropod study was conducted on the same forefield wetlands as the vegetation study (Table 1). At each wetland, two representative patches were chosen for assessment, and for these we evaluated coarse vegetation structure, a key component of arthropod habitat. Percent bare ground; percent green (live vegetation) cover; percent standing brown (senescent vegetation) cover, and percent litter cover were estimated using a randomly-oriented point-intercept transect that was centered in each of two subsample locations within each of the two patches at each site. In addition, canopy height, litter depth, habitat complexity (a measure of relative density of micro-habitat elements), and shoot density (total number of stems of all taxa per unit area) were measured at two random locations along each transect (total of eight measurements at each rock glacier and talus site). We measured shoot density with a 0.125 m^2 quadrat, and estimated habitat complexity with the pole-touch method (Bestelmeyer and Wiens, 2001).

Arthropod assemblages were evaluated at each of the talus/rock-glacier locations by a sample that consisted of 50 standard sweep-net sweeps (New, 1998; Southwood and Henderson, 2000), divided as 25 sweeps at each of the two subsample locations within each of the two replicate patches (total of 100 sweeps at each rock feature). The sweep net had a 30.5 cm aperture and 0.5 × 0.75 mm mesh size. To minimize disruption, sweeping was done before collecting vegetation data at the sites (additional sampling details in Holmquist et al., 2010, 2013a). Arthropod sampling was conducted in August, 2012.

Fig. 3. Barney and Gibbs rock glaciers, showing soil patches with vegetation on the rock glacier surfaces. A. Barney rock glacier. B. Gibbs rock glacier.

We compared arthropod diversity of the rock-glacier/talus wetlands with reference wetlands that had been measured using similar methodology by the same researchers although in different years. The reference site database was a subset from a large dataset of a previous study (total 80 sites; Holmquist et al., 2011). From this pool, we selected eight sites with the following characteristics: wetlands not associated with periglacial rocky landforms, sampled during August of the previous Sierra Nevada drought year (2007) to be comparable to 2012, located near 3000 m, having similar spatial extent to the current study, and having similar canopy height (an important predictor of arthropod assemblage structure in Sierra wetlands; Holmquist et al., 2011).

2.2. Analysis

2.2.1. Rock-glacier vegetation

At each of the two rock glacier locations, cover data were calculated for area of soil-patch relative to the entire rock-glacier, area of vegetation (total and by species) relative to total soil extent and to the entire rock-glacier, and area of vegetation (total and by species) by patch. Vegetative cover for each species was estimated by measuring the crown area of 10 randomly selected individuals at each site, and using the mean value as the crown area per individual, multiplying by the number of plants per area of analysis. Differences in species composition, (presence/absence) were analyzed between the two rock glaciers by canonical correspondence analyses (JMP; SAS, 2011). For the cover data, we converted percent cover per patch to the proportional cover for each species relative to the total cover for all species. Compositional differences in cover between sites, converted to plant counts, and plant functional traits were tested by nominal logistic analysis (JMP; SAS, 2011). Plant functional traits were adapted from Körner (2003) and the GLORIA program (Grabherr et al., 2000; Apple, M., pers. comm.). To assess species occurrence on the rock glaciers relative to the altitudinal distribution of the species in the Sierra Nevada, we extracted elevation ranges from the Baldwin et al. online database (http://ucjeps.berkeley.edu/IJM; accessed May, 2013) for the latitude band of the rock glacier locations.

Four ecological diversity/similarity indices were calculated. The Shannon index (H^I) is a measure of abundance and evenness, with higher values indicating greater numbers of species and evenness. Values range from 0, a single species in the sampling unit, to log q, where q is the number of species in the sampling unit and the species are evenly distributed. We used the natural log computation of H^I, summed over plots. H^I by plot was converted to effective numbers (N(1)) by e^{H1}. Simpson's index of diversity (H_2) is the likelihood of individuals belonging to identical species (values range from 0–1), with lower values indicating higher diversity (Colinvaux, 1976; Legendre and Legendre, 1998). Effective numbers per plot (N[2]) from H_2 were computed by $1/H_2$ (Ludwig and Reynolds, 1988). We also computed the probability of interspecific encounter ($1 - H_2$) per plot. Species dominance, the degree to which a species was more numerous (greatest proportion of cover) than others was also calculated per plot. The Sørensen index (values range from 0, no species overlap, to 1, complete overlap; Magurran, 2004) measures similarity between groups and is appropriate when comparing presence-absence data. The probability of interspecific encounter is a diversity index that estimates the probability that two plants of different species would be sampled consecutively. Although primarily used for animals, it was calculated here to compare with values used in the arthropod study (detailed below).

2.2.2. Rock glacier/talus wetland vegetation

Species and plant functional groups were assessed with nominal logistic analysis for differences among patches within wetlands; among the four wetlands; and between the wetland types (rock-glacier or talus slope wetland). To explore plant cover relationships, we rendered the five abundance classes into relative proportions as follows: Each abundance class was assigned a value from 0.1% (rare) to 80% (dominant). For each wetland patch, the abundance percentages for each species were summed and divided into the percent cover of individual species to derive cover values relative to 100% or the total vegetative cover in each patch. In this way, cover ranged from <0.0001% to 30%. Differences in cover among sites were also assessed by contingency and ordinated by canonical correspondence analysis. Elevation relationships and ecological diversity and similarities were analyzed as in the rock glacier floristic data.

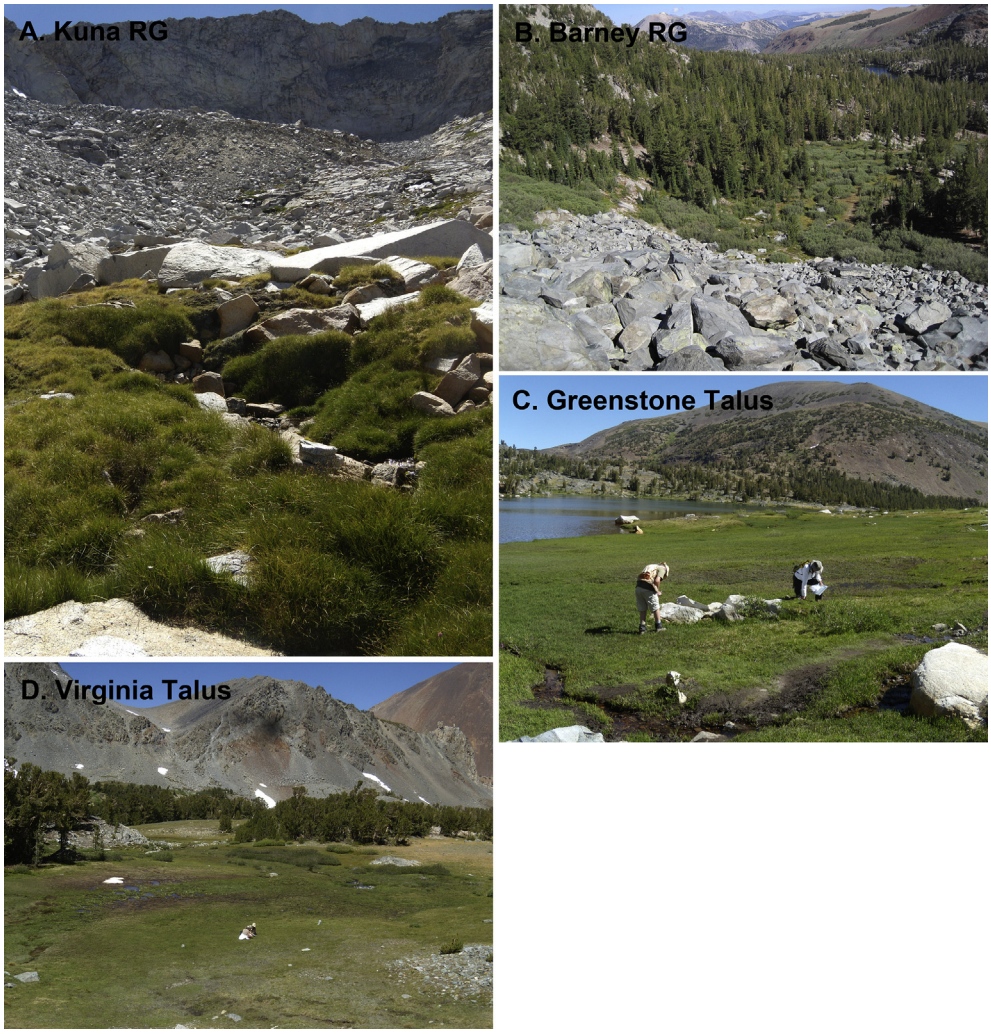

Fig. 4. Rock-glacier and talus wetlands. A. Kuna rock glacier. B. Barney rock glacier. C. Greenstone talus. D. Virginia talus.

Taxa annotated as associated with diverse wetlands habitats and at elevations between 2800 and 3400 m were extracted from species lists compiled for the SJRA (Constantine-Shull, 2000) and the HRNA (Taylor, 1984) and used for comparison to observed data.

2.2.3. Rock glacier/talus arthropods

Samples were identified to family (see also Fahrig and Jonsen, 1998; Koricheva et al., 2000) and morphospecies (grouping of individuals that an experienced taxonomist recognizes as likely to represent separate species on the basis of morphology; Kremen et al., 1993; Oliver and Beattie, 1996; Hoback et al., 1999; Derraik et al., 2002). Our study was unusually broad in that we analyzed responses across all arthropod families; this approach is more likely to detect patterns that structure ecosystems (Fahrig and Jonsen, 1998; Koricheva et al., 2000; Pocock et al., 2012). This work was not intended to be a species inventory, which would have been beyond the scope of this study.

Univariate response variables included abundance, richness, dominance, expected number of morphospecies (i.e., rarefaction, $E(S_3)$; Hurlbert, 1971; Heck et al., 1975; Magurran, 2004), and probability of interspecific encounter (PIE, an evenness measure; Hurlbert, 1971). Expected number of species is similar to a diversity metric and compensates for differing abundances in samples, e.g., a sample of 1000 individuals would be expected to have more species than a sample of 10 individuals, even if the area sampled was equivalent. The approach scales species richness to the abundance of the least-abundant sample to offset the influence of abundance on richness.

We computed $E(S_3)$ and PIE using DIVERSITY 1.4 (Hunt Mountain Software). Variables were log transformed (log $(y + 1)$), with the exception of a single proportional variable, which was square-root transformed $((y)^{0.5} + (y + 1)^{0.5})$. Analyses were primarily via two-tailed, independent *t*-tests, as well as two-tailed sign tests, and Kolmogorov–Smirnov two-sample tests (Magurran, 2004) using SYSTAT 12. Power for the rock glacier versus talus field comparisons was as low as 0.1 (G*Power; Mayr et al., 2007) because of the small number of samples. We used the Sørensen similarity index (Magurran, 2004) for assessing assemblage similarities. We constructed rank abundance plots (Magurran, 2004; Underwood and Fisher, 2006; Savage et al., 2011) and compared the distributions with Kolmogorov–Smirnov two-sample tests (Magurran, 2004).

We also investigated differences in assemblage structure across all taxa using multivariate approaches. We first did a multi-response permutation procedure (MRPP; McCune and Grace, 2002; Peck, 2010) using PC-ORD 6 (MjM Software), followed by a permutational analysis of dispersion using PERMDISP2 software developed by MJ Anderson (see also Anderson, 2001; Ratkowsky, 2008). The response and explanatory matrices contained all sites. The response matrix included families that were collected in at least two samples (34 families; McCune and Grace, 2002; Peck, 2010; Poos and Jackson, 2012), and we relativized the matrix by

maximum abundance for each family. The final matrix had a coefficient of variation of 40%, and 69% of the cells contained zeros. The explanatory matrix included a coding variable for each group of sites. We used the Sørensen distance measure and rank-transformed the distance matrix prior to the MRPP. There were 9999 permutations for the permutational analysis of dispersion.

3. Results

3.1. Rock glacier vegetation

Soil patches were distributed across the surfaces of both rock glaciers, although there was greater abundance on flatter ridge tops and at the bases of furrows than on steep faces. Soil patches supporting vegetation ranged from very small (<3 m^2) to large (>1000 m^2; Table 2). We identified a total of 33 plant taxa at the two rock glaciers, including 16 taxa on 13 soil patches on Gibbs and 28 taxa on 48 soil patches at Barney (Tables 2 and 3). All taxa were perennial, and the majority was herbaceous with deciduous foliage (69%, Gibbs; 54%, Barney); shrubs and subshrubs were next most common (31%, Gibbs; 29%, Barney). Eleven taxa occurred in common at both sites, which represented 69% of the total Gibbs flora and 39% of the Barney flora. The cumulative area of soil patches composed 2.8% of the total rock glacier area at the smaller Gibbs rock glacier and 7.4% of the larger Barney rock glacier.

Plant cover on the patches varied widely by species, with the smaller and rarer taxa (e.g., *Boechera lemmonii* and *Cryptantha flavoculata*) composing <0.001% of the cumulative patch area, and larger shrubs with cover >1% (Table 3). *Linanthus pungens* had the greatest cover on Gibbs rock glacier (1.5% of the cumulative patch area), and *Ribes cereum* had the greatest cover on Barney rock glacier (12.0%). Greater diversity, larger plants, and larger patch areas at Barney likely contributed to the significantly different cover values between the sites, with vegetative cover of 6.3% versus 23.7%, respectively, for Gibbs and Barney rock glaciers relative to total patch area. Total plant cover relative to the entire rocky landform was 0.2% at Gibbs and 1.7% at Barney. High diversity within patches and among patches within sites overwhelmed the overall distinction of the two rock glacier floras, such that species composition and cover-by-species were not significantly different between sites in the nested non-parametric analysis of variance. However, on the basis of mean species cover between sites, the two sites were significantly different on the non-parametric ANOVA (contingency analysis) and correspondence analysis of the data (Fig. 5A, Table 5). Sørensen similarity index between Barney and Gibbs rock glaciers flora was moderate in value (0.5), corroborating the relatively high patch diversity within sites (Table 4C). The median middle-elevation of the species distribution ranges for species growing on the two rock-glaciers was 60 m lower than the elevation of the sites.

Table 2
Vegetation patch information and taxonomic diversity for each location and study.

Study/location	Number of veg patches	Vegetation patch size (m^2)			Total patch area (ha)	Total patch area:rock glacier area (%)	Number of taxa[a]
		Minimum	Maximum	Mean			
Rock glacier vegetation							
Gibbs Valley	13	3	493	108.2	0.1	3	16
Barney Lake	48	6	1075	228.9	1.1	7	28
Forefield wetland vegetation							
Talus forefields							
Virginia Canyon	7	220	1515	857	0.6	96	65
Greenstone Lake	6	314	2395	1081	0.7	148	65
Rock glacier forefields							
Kuna Lake	12	37	3114	702	0.84	12	48
Barney Lake[b]	4	681	21,161	7849	3.14	21	84
Forefield wetland arthropods[c]							
Talus forefields							17, 26
Virginia Canyon	2	800	1200	1000	0.2	32	14, 21
Greenstone Lake	2	800	1200	1000	0.2	45	10, 12
Rock glacier forefields							45, 69
Kuna Lake	2	800	1200	1000	0.2	3	28, 41
Barney Lake	2	800	1200	1000	0.2	1	35, 52

[a] Vascular plant species diversity for vegetation studies; arthropod family and morphospecies diversity for arthropod study.
[b] For the Barney Lake forefield we classified vegetation into zones rather than patches, see text.
[c] Patch size represents pre-determined sample areas; within these two subsample areas were each 200 m^2.

Table 3
Species observed on the Gibbs Canyon and Barney Lake rock glaciers, with elevation ranges for the species from Baldwin et al., (2012) and online, extracted for the latitude of the rock glaciers, plant functional traits, and vegetative percent cover over the cumulative soil patch area.

Genus	Species	Plant functional traits			Elev range (m)		Rock glacier veg		Pct cover:total patch area	
		Life form	Woodiness	Leaf habit	Lower	Upper	Gibbs	Barney	Gibbs	Barney
Antennaria	*rosea*	PH	H	DEC	2400	3700		X		0.02
Aquilegia	*pubescens*	PH	H	DEC	2650	3650		X		0.39
Athyrium	*distentifolium* var. *americanum*	BR	H	DEC	3000	3500		X		<0.01
Boechera	*lemmonii*	PH	H	DEC	2900	4100	X	X	<0.01	<0.01
Calamagrostis	*purpurascens*	GR	H	DEC	2900	3600		X		0.03
Castilleja	*applegatei*	PH	H	DEC	500	3650	X		0.03	
Castilleja	*nana*	PH	H	DEC	2700	4100	X		0.03	
Cirsium	*scariosum*	PH	H	DEC	2000	3500		X		0.04
Crepis	sp.	PH	H	DEC				X		<0.01
Cryptantha	*flavoculata*	PH	H	DEC	2000	3100	X		<0.01	

Table 3 (*continued*)

Genus	Species	Plant functional traits			Elev range (m)		Rock glacier veg		Pct cover:total patch area	
		Life form	Woodiness	Leaf habit	Lower	Upper	Gibbs	Barney	Gibbs	Barney
Elymus	*elymoides*	GR	H	DEC	1000	4300	X	X	1.06	3.11
Eremogone	*kingii* var. *glabrescens*	SS	SFTC	EVG	2100	3800		X		0.30
Ericameria	*discoidea*	SS	SFCS	EVG	2900	3800		X		3.23
Ericameria	*suffruticosa*	SS	SFCS	DEC	2500	3800	X	X	1.82	0.66
Erigeron	*compositus*	PH	H	DEC	3000	4300	X	X	1.18	0.33
Erigeron	*pygmaeus*	PH	H	DEC	2900	4000	X	X	0.07	0.06
Eriogonum	*incanum*	PH	H	DEC	2500	3800	X	X	0.04	0.06
Eriogonum	*lobbii*	PH	H	DEC	2900	3750	X		0.12	
Eriogonum	*ovalifolium* var. *ovalifolium*	PH	H	DEC	1800	4200		X		0.34
Holodiscus	*discolor* var. *microphyllus*	SH	F	DEC	2100	3300		X		0.18
Hulsea	*algida*	PH	H	DEC	3000	4200	X		0.09	
Linanthus	*pungens*	SS	F	DEC	1700	4000	X	X	1.47	5.38
Monardella	*odoratissima*	PH	H	DEC	2000	3500		X		0.75
Pellaea	*breweri*	BR	SFTC	EVG	2500	3700		X		0.01
Penstemon	*heterodoxus*	PH	H	DEC	2400	3900		X		0.01
Phacelia	*hastata*	PH	H	DEC	2300	4000		X		0.02
Phlox	*condensata*	SS	F	EVG	3000	4200	X	X	0.10	0.26
Pinus	*albicaulis*	T	AR	EVG	2600	3700	X	X	0.06	0.02
Poa	*secunda*	GR	H	DEC	200	3800		X		<0.01
Primula	*suffrutescens*	PH	SFTC	DEC	3000	3500		X		0.24
Ribes	*cereum*	SH	F	DEC	2000	3850	X	X	0.15	8.23
Silene	*sargentii*	PH	H	DEC	2900	3800	X	X	0.08	0.02
Solidago	*multiradiata*	PH	H	DEC	2500	4000		X		0.14
Total number of species							16	28		

Plant functional traits:
Life Form: T, tree; SH, shrub; SS, sub-shrub; PH, perennial herb; AH, annual herb; GR, graminoid; BR, bryophyte; FFL, fern & fernlike.
Woodiness: AR, aborescent; F, fruticose; SFCS, suffruiticose; SFTC, suffrutescent; H, herbaceous.
Leaf Form: EVG, evergreen; DEC, deciduous.

Table 4
Means (SE) of vegetation diversity and similarity metrics (based on patch-level data). Shannon and Simpson indices, probability of interspecific encounter, and % species dominance at A. rock glacier surfaces and B. rock-glacier and talus wetlands. Sørensen's similarity index values for C. rock glacier surfaces and D. rock-glacier and talus wetlands and their respective reference sites. Number of species indicated is lower than total count of taxa because some taxa were not identified to species level.

A. Rock glacier surfaces			B. Rock-glacier and talus wetlands			
Indicator	Rock glaciers		Rock glacier wetlands		Talus wetlands	
	Barney	Gibbs	Barney	Kuna	Greenstone	Virginia
Total number of species	27	16	80	42	60	61
Number of species/patch	5.0 (3)	4.8 (2)	42 (16)	15.6 (7)	32.7 (9)	30.7 (6)
N1 (Shannon index)	3.1 (1.3)	2.6 (0.6)	19.2 (6)	6.0 (3)	13.2 (4)	16.0 (4)
N2 (Simpson index)	2.6 (1.1)	2.2 (0.5)	14.8 (6)	5.0 (3)	9.5 (4)	12.0 (4)
Probability of inter-specific encounter	0.54 (0.19)	0.52 (0.12)	0.92 (0.02)	0.74 (0.12)	0.88 (0.05)	0.91 (0.03)
% Species dominance	58.3 (18)	61.3 (12)	16.4 (7)	41.1 (16)	22.2 (9)	71.8 (6)

C. Sørensen indices, rock glacier surfaces and reference sites			D. Sørensen indices, rock-glacier and talus wetlands and reference sites				
	Gibbs rock glacier	Rock glaciers combined		Barney rock glacier	Kuna rock glacier	Greenstone talus	Wetlands combined
Barney RG	0.5		Kuna	0.44			
Reference sites			Greenstone	0.59	0.63		
Hall RNA		0.22	Virginia Talus	0.51	0.53	0.61	
SJRA		0.17	Reference sites				
			Hall RNA				0.59
			SJRA				0.36

Table 5
Species observed at the Virginia Canyon and Greenstone Lake talus wetlands and at the Barney Lake and Kuna rock glacier wetlands, with associated plant functional traits and elevation ranges. Plant functional traits as in Table 3.

Genus	Species	Plant functional traits			Elev range (m)		Wetland forefield taxa			
		Life form	Woodiness	Leaf trait	Lower	Upper	Virginia talus	Green-stone talus	Kuna RG	Barney RG
Agoseris	sp.	PH	H	DEC				X	X	
Agrostis	*humilis*	GR	H	DEC	2500	3300				X
Agrostis	*variabilis*	GR	H	DEC	2000	3800			X	X
Allium	*validum*	PH	H	DEC	2400	3500	X			X
Antennaria	sp.	PH	H	DEC						X

(*continued on next page*)

Table 5 (*continued*)

Genus	Species	Plant functional traits			Elev range (m)		Wetland forefield taxa			
		Life form	Woodiness	Leaf trait	Lower	Upper	Virginia talus	Green-stone talus	Kuna RG	Barney RG
Antennaria	*corymbosa*	PH	H	DEC	2000	3400	X	X	X	X
Aquilegia	*formosa*	PH	H	DEC	200	3200				X
Arnica	*mollis*	PH	H	DEC	2000	3400				X
Botrychium	*simplex*	FFL	H	DEC	2500	3200		X		X
Calamagrostis	*muiriana*	GR	H	DEC	2500	3900	X	X	X	X
Calamagrostis	*stricta* ssp. *inexpansa*	GR	H	DEC	1500	3000			X	
Caltha	*leptosepala*	PH	H	DEC	2700	3000	X			
Calyptridium	*umbellatum*	PH	H	DEC	2100	3150			X	
Carex	sp.	GR	H	DEC						X
Carex	*abrupta*	GR	H	DEC	2000	3500	X			
Carex	*aquatilis*	GR	H	DEC	2000	3200	X	X		
Carex	*athrostachya*	GR	H	DEC	1000	2950	X			
Carex	*aurea*	GR	H	DEC	1500	3200	X			
Carex	*deflexa* var. *bootii*	GR	H	DEC	2500	3800			X	
Carex	*filifolia*	GR	H	DEC	2000	3600	X	X	X	
Carex	*fissuricola*	GR	H	DEC	2000	3250	X	X		X
Carex	*heteroneura*	GR	H	DEC	2000	3500		X		X
Carex	*illota*	GR	H	DEC	2400	3200	X		X	X
Carex	*leporinella*	GR	H	DEC	2500	3500	X			X
Carex	*luzulina*	GR	H	DEC	2600	3200		X		X
Carex	*multicostata*	GR	H	DEC	2200	3100				X
Carex	*nigricans*	GR	H	DEC	2900	3500	X	X	X	X
Carex	*praeceptorum*	GR	H	DEC	2500	3400		X		
Carex	*scopulorum* var. *bracteosa*	GR	H	DEC	2500	3100	X	X		X
Carex	*spectabilis*	GR	H	DEC	2600	3500	X	X	X	X
Carex	*subnigricans*	GR	H	DEC	2600	3800	X	X		
Carex	*utriculata*	GR	H	DEC	1800	3100				X
Carex	*vernacula*	GR	H	DEC	2900	3800	X	X	X	X
Cassiope	*mertensiana*	SS	F	EVG	2650	3550		X		
Castilleja	*lemmonii*	PH	H	DEC	2500	3500	X	X	X	X
Castilleja	*miniata*	PH	H	DEC	1200	3400		X		X
Chamerion	*angustifolium* ssp. *circumvagum*	PH	H	DEC	2000	3000				X
Danthonia	*intermedia* ssp. *intermedia*	GR	H	DEC	3000	3500	X			X
Deschampsia	*cespitosa*	GR	H	DEC	2000	3700	X			X
Dodecatheon	*alpinum*	PH	H	DEC	2400	3700	X	X	X	X
Draba	sp.	PH	H	DEC				X	X	
Eleocharis	sp.	GR	H	DEC					X	
Eleocharis	*acicularis*	GR	H	DEC	1000	3100				X
Eleocharis	*macrostachya*	GR	H	DEC	500	2700	X	X		X
Eleocharis	*quinqueflora*	GR	H	DEC	2000	3450	X			
Epilobium	*oregonense*	PH	H	DEC	2100	3500	X	X	X	X
Erigeron	*aphanactis*	PH	H	DEC	1500	2850		X	X	
Erigeron	*coulteri*	PH	H	DEC	2100	3500				X
Erigeron	*glacialis* var. *glacialis*	PH	H	DEC	2000	3400				X
Erigeron	*glacialis* var. *hirsutus*	PH	H	DEC	1500	3100				X
Festuca	sp.	GR	H	DEC			X			
Gentiana	*newberryi*	PH	H	DEC	2000	3350	X	X	X	X
Gentianella	*amarella*	PH	H	DEC	2500	3000	X			
Gentianopsis	*holopetala*	PH	H	DEC	2000	3500	X			
Hypericum	*anagalloides*	PH	H	DEC	2500	3300				X
Ivesia	sp.	PH	H	DEC					X	
Ivesia	*lycopodioides* var. *megalopetala*	PH	H	DEC	2500	3700	X			
Juncus	*balticus*	GR	H	DEC	2000	2800	X			
Juncus	*drummondii*	GR	H	DEC	2400	3600		X	X	X
Juncus	*mertensianus*	GR	H	DEC	2200	3550	X	X	X	X
Juncus	*orthophyllus*	GR	H	DEC	2000	3100	X			
Juncus	*parryi*	GR	H	DEC	2400	3600				X
Kalmia	*polifolia*	SS	SFCS	EVG	2500	3500	X	X	X	X
Lewisia	*glandulosa*	PH	H	DEC	2000	3600			X	
Lewisia	*pygmaea*	PH	H	DEC	2000	4000	X	X		
Lupinus	*lepidus* var. *ramosus*	PH	H	DEC	2500	3900				X
Luzula	*divaricata*	GR	H	DEC	2700	3100		X		
Luzula	*orestera*	GR	H	DEC	2700	3100		X		X
Luzula	*subcongesta*	GR	H	DEC	2000	3500				X
Luzula	sp.	GR	H	DEC			X			
Micranthes	*aprica*	PH	H	DEC	2000	3500		X		
Micranthes	*odontoloma*	PH	H	DEC	2500	3400				X
Mimulus	*primuloides*	PH	H	DEC	1500	3500	X	X	X	X
Mimulus	*tilingii*	PH	H	DEC	1400	3500	X		X	X
Minuartia	*obtusiloba*	PH	H	DEC	3100	3600		X		
Mosses		BR	H	EVG			X	X	X	X
Muhlenbergia	*richardsonis*	GR	H	DEC	1500	3600	X			
Muhlenbergia	*filiformis*	GR	H	DEC	1500	3100	X	X		X
Oreostemma	*alpigenum* var. *andersonii*	PH	H	DEC	2000	3500	X	X	X	X

Table 5 (*continued*)

Genus	Species	Plant functional traits			Elev range (m)		Wetland forefield taxa			
		Life form	Woodiness	Leaf trait	Lower	Upper	Virginia talus	Green-stone talus	Kuna RG	Barney RG
Oxyria	*digyna*	PH	H	DEC	2500	3400		X	X	
Packera	*pauciflora*	PH	H	DEC	2500	3900				X
Packera	*subnuda*	PH	H	DEC	1500	3000	X	X	X	X
Parnassia	*palustris*	PH	H	DEC	1900	3300				X
Pectiantia	*breweri*	PH	H	DEC	2200	3000				X
Pedicularis	*groenlandica-attollens*	PH	H	DEC	2000	4000	X			X
Pedicularis	*groenlandica*	PH	H	DEC	2000	3500		X		X
Pedicularis	*attollens*	PH	H	DEC	2000	4000		X		X
Penstemon	*heterodoxus*	PH	H	DEC	1200	3400	X	X	X	
Perideridia	*parishii*	PH	H	DEC	1800	3300				X
Phleum	*alpinum*	GR	H	DEC	2000	3500	X	X	X	X
Phyllodoce	*breweri*	SS	SFCS	EVG	2500	3700	X	X	X	X
Pinus	*albicaulis*	T	AR	EVG	2600	3700	X			
Pinus	*contorta*	T	AR	EVG	2000	3200				X
Platanthera	*dilatata* var. *leucostachys*	PH	H	DEC	1400	3200				X
Poa	*fendleriana* ssp. *longiligula*	GR	H	DEC	1700	3700				X
Poa	*glauca* ssp. *rupicola*	GR	H	DEC	3000	4100	X	X	X	X
Poa	*pratensis* ssp. *pratensis*	GR	H	DEC	1100	3500	X			
Poa	*secunda*	GR	H	DEC	200	3800		X		X
Poa	*wheeleri*	GR	H	DEC	2000	3800				X
Potentilla	*breweri*	PH	H	DEC	2500	3500	X	X		X
Potentilla	*flabellifolia*	PH	H	DEC	2400	3700		X	X	X
Potentilla	*glaucophylla* var. *glaucophylla*	PH	H	DEC	2500	3500	X	X		X
Ranunculus	*alismifolius* var. *alismifolius*	PH	H	DEC	2200	3800				X
Ranunculus	*eschscholtzii*	PH	H	DEC	2900	4000	X	X		X
Rhododendron	*columbianum*	SH	F	EVG	2500	3600	X			X
Ribes	*montigenum*	SH	F	DEC	2500	3500		X		X
Salix	*eastwoodiae*	SH	F	DEC	2000	3700				X
Salix	*orestera*	SH	F	DEC	2100	3700	X	X	X	X
Salix	*planifolia*	SH	F	DEC	2400	3900	X	X	X	
Salix	sp.	SH	F	DEC				X		
Salix	*petrophila*	SS	SFCS	DEC	3000	3500	X	X	X	
Senecio	*aronicoides*	PH	H	DEC	500	3000		X		
Senecio	*scorzonella*	PH	H	DEC	2000	3600		X		
Senecio	*triangularis*	PH	H	DEC	2000	3300				X
Sibbaldia	*procumbens*	PH	H	DEC	3000	3700	X	X	X	
Silene	*sargentii*	PH	H	DEC	2900	3800			X	
Solidago	*multiradiata*	PH	H	DEC	2500	4000	X	X	X	X
Sphenosciadium	*capitellatum*	PH	H	DEC	2000	3450				X
Stellaria	*crispa*	PH	H	DEC	2000	3100		X	X	X
Stellaria	*longipes* ssp. *longipes*	PH	H	DEC	1200	3500	X		X	
Stellaria	*umbellata*	PH	H	DEC	2200	3500				
Stipa	*kingii*	GR	H	DEC	2500	3500	X	X	X	X
Trichophorum	*clementis*	GR	H	DEC	2750	3150	X	X		
Trifolium	*monanthum*	PH	H	DEC	1500	3750	X			X
Trisetum	*spicatum*	GR	H	DEC	2100	3750	X	X	X	X
Tsuga	*mertensiana*	T	AR	EVG	2300	3500				X
Isoetes	sp.	PH	H	DEC			X			
Vaccinium	*cespitosum*	SS	SFCS	DEC	2400	3600		X	X	X
Veratrum	*californicum* var. *californicum*	PH	H	DEC	1500	3200				X
Veronica	sp.	PH	H	DEC					X	
Veronica	*wormskjoldii*	PH	H	DEC	2500	3500	X	X	X	X
Woodsia	sp.	FFL	H	DEC	2100	3500		X		
Total							**65**	**65**	**48**	**84**

The species assemblages associated with scree, talus, or rocky environments at the SJRA and HRNA reference sites were distinctly different from those on the rock glaciers. Seventy-seven species were described for HRNA and 26 for SJRA (Supplemental Table 1). Only 12 taxa were in common between at least one of the rock glaciers and one of the reference sites. Canonical correspondence analysis distinguished the rock-glacier flora from the flora at the two reference sites in the first two vectors (Fig. 5C). Only seven species of the rock glacier list were not aligned with this vector (*Athyrium distentifolium* var *americanum*, *Cirsium scariosum*, *Holodiscus discolor* var *microphyllus*, *Hulsea algida*, *Monardella odoratissima*, *Phacelia hastata* and *Poa secunda*). Sørensen similarity indices between the rock glaciers and the reference sites were much lower (HRNA, 0.22; SJRA, 0.17) than the value between the two rock glaciers. The species elevation distribution ranges for taxa at the rock glaciers had low, middle, and high median values that were 500 m higher than the respective ranges of taxa occurring in rocky environments at HRNA and SJRA.

3.2. Rock glacier/talus wetland vegetation

Talus wetlands were smaller in area (mean, 0.6 ha) than rock-glacier wetlands (mean, 4.3 ha), although the two rock glacier wetlands differed considerably in area as well (Table 1). Despite that the rock glaciers were much larger features than the talus slopes, their wetlands were proportionately much smaller. On average, the wetlands were 17% the area of the rocky landform that supported them (Table 2). By contrast, the talus wetlands were

larger than the talus slopes above them; on average 122% their extent. We identified 133 taxa overall in the wetland floras of these landforms, with 65 taxa on each of the talus wetlands and a mean of 67 on the rock glacier wetlands (Tables 2 and 5). The large wetlands below Barney rock glacier supported the largest number of taxa (84) and Kuna rock glacier wetland the least (48). Only four taxa were in common with species observed on the rock-glacier surfaces (*Pinus albicaulis*, *Poa secunda*, *Silene sargentii*, and *Solidago multiradiata*). Of the total species observed on the wetlands, there were about equal numbers of perennial, deciduous herbs (48%) as graminoids (40%), primarily *Carex* species, with the remainder being evergreen and deciduous shrubs (8%), coniferous trees (2%), and bryophytes, ferns and allies (2%). The median species elevation range for the taxa growing at the four wetland locations was 100–330 m lower than the elevation of the sites. Species at Greenstone wetland had the highest median elevation ranges among species of the four sites.

Diversity was high within patches and among patches within sites (Table 4B). In non-parametric analysis of variance, significant differences among patches overwhelmed site differences, which were non-significant. The first two vectors of the canonical ordination show the relationships of species diversity and cover at the four sites, with little systematic distinction between the classes of rock-glacier vs. talus wetlands in the first vector, but with slightly ordered differences in the second (Fig. 5B). In the contingency analysis of interspecific proportional cover, differences among site were significant ($p < 0.0001$). Sørensen similarity indices differed little among the pairwise comparisons, and were moderate in value, ranging from 0.44 (Barney and Gibbs rock glaciers) to 0.61 (Greenstone and Virginia talus), showing no evidence for the wetland types (rock glacier vs. talus) to be distinguished (Table 4D).

Species associated with wetland environments at the two reference sites had considerable overlap with the rock-glacier and talus wetland floras. The HRNA was most diverse, with 108 species and SJRA had 87 species (Supplemental Table 2). Of these, 79 taxa were found in at least one of the rock- glacier or talus wetlands as well as one of the reference sites. Based on presence-absence data, canonical correspondence ordination distinguished the rock-glacier/talus wetlands flora from species at the two reference sites, and the references sites from each other, in the first two vectors (Fig. 5D). The elevation ranges for taxa at the rock glacier and talus wetlands had low, mid, and high median values 100–300 m higher than the comparable values for wetland species growing at the HRNA and SJRA. Sørensen similarity indices corroborated these patterns. Reference site HRNA had a similarity coefficient of 0.59 to the rock-associated wetlands, whereas SJRA had a lower value of 0.36.

3.3. Rock glacier/talus wetland arthropods

Apparent trends in vegetation structure at the arthropod sites indicated nominally greater litter depth and lower percent senescent vegetation and shoot density at the rock glacier wetlands relative to talus wetlands, although these differences were not significant (Table 6). Abundances and the composition of the arthropod assemblages differed between the rock-glacier/talus and reference wetlands. Overall abundance was three times higher in the rock-associated wetlands than in reference meadows ($p = 0.012$; Table 7). Forty-seven of the 60 collected families were more abundant in rock glacier and talus wetlands than in reference meadows (sign test, $p = 0.00053$). The fauna of the rock-associated wetlands was dominated by cicadellid leafhoppers (mean, 26 per 50 sweeps; standard error [SE], 6.1) and aphids (mean, 25; SE, 13). Other common taxa included mirids (Hemiptera), muscid, chloropid, ephydrid, and anthomyiid flies, chironomid midges, and thomisid and araneid spiders. Chloropid flies were the most abundant family on the reference sites (mean 9.1; SE, 8.4), and cicadellids, muscids, and thomosids were the only other families with abundances in the same range as that of the common fauna from the rock-associated wetlands. The disparate nature of the faunal composition was apparent from a low Sørensen similarity index of 0.29. The influences of the high abundance and richness at the rock-associated sites, the latter nominally as much as twice that of the reference sites, had a self-canceling effect on diversity, yielding $E(S_3)$, PIE, and dominance metrics that were that almost identical between the rock-associated wetlands and reference sites (Table 7). These patterns of high abundance and nominally greater richness at the rock glacier sites, combined with similar overall diversity, are underscored by rank-abundance plots (Fig. 6). The curves for the two sets of sites are both almost congruent, yet distinct ($p = 0.0049$, Kolmogorov–Smirnov two-sample tests).

Table 6
Means (SE) for vegetation structural parameters in rock-glacier and talus wetlands with *p* values from two-tailed, independent *t*-tests.

Indicator	Rock glacier wetlands	Talus wetlands	*p* Value
Canopy height (cm)	12.0 (1.1)	8.82 (1.8)	0.17
Litter depth (cm)	0.938 (0.33)	0.0625 (0.063)	0.04
Litter cover (%)	1.88 (1.2)	0.625 (0.63)	0.44
Bare ground (%)	6.88 (2.6)	5.63 (2.6)	0.79
Brown cover (%)	9.38 (5.4)	20.6 (5.7)	0.17
Green cover (%)	80.0 (6.0)	70.0 (7.4)	0.33
Complexity	6.44 (1.4)	11.5 (2.9)	0.2
Shoot density/m^2	1498 (109)	2752 (576)	0.054

Table 7
Means (SE) for arthropod assemblage metrics (per 50 sweeps) and *p* values resulting from two-tailed, independent *t*-tests that contrasted the rock-associated wetlands with reference wet meadow sites.

Indicator	Rock-glacier/talus wetlands	Reference wetlands	*p* Value
Total individuals	87.9 (23)	28.8 (13)	0.012
Species richness	20.5 (4.4)	11.1 (2.4)	0.1
Family richness	14.6 (3.0)	8.75 (1.7)	0.14
Expected number of species	2.42 (0.14)	2.56 (0.12)	0.47
Probability of interspecific encounter	0.757 (0.064)	0.767 (0.059)	0.9
% Species dominance	39.8 (7.4)	36.4 (7.1)	0.72

Assemblage metrics were more divergent between the rock glacier and talus-associated wetlands (Table 8). Richness and diversity measures were higher in the rock glacier wetlands than those associated with the talus slopes; there were significant differences for species and family richness, $E(S_3)$, and PIE. Although overall abundance was not significantly different, family abundances were lower in talus wetlands than in rock glacier wetlands (sign test, $p < 0.0001$); 34 of forty families were more abundant near rock glaciers than near talus. Thirty families that were present in rock glacier wetlands were absent from the talus wetlands, whereas the inverse held for only two families. The Sørensen similarity index for the two rock-associated habitats was 0.61. Rank abundance plots provide further indication that richness and evenness were greater for the rock glacier habitats than those below talus fields (Fig. 6). The curves for these two habitats were clearly separate distributions ($p < 0.0001$, Kolmogorov–Smirnov two-sample tests).

Table 8
Means (SE) for arthropod assemblage metrics (per 50 sweeps) and *p* values resulting from two-tailed, independent *t*-tests that contrasted rock glacier versus talus wetland habitat.

Indicator	Rock glacier wetlands	Talus wetlands	*p* Value
Total individuals	113 (37)	63.3 (24)	0.24
Species richness	30.0 (4.8)	11.0 (2.6)	0.013
Family richness	21.3 (3.3)	8.00 (1.5)	0.0087
Expected number of species	2.70 (0.076)	2.15 (0.18)	0.03
Probability of interspecific encounter	0.882 (0.030)	0.632 (0.089)	0.041
% Species dominance	27.5 (5.0)	52.1 (11)	0.096

The multivariate analysis further supported the distinctness of the assemblages. The MRPP was highly significant ($p = 0.0030$) with a modest effect of size ($A = 0.22$). Pairwise tests within the MRPP analysis indicated that compositional differences between rock glacier and talus wetlands were marginally non-significant (0.066), but that both rock-dominated habitats differed from reference meadows ($p = 0.021$ and $p = 0.011$, respectively). The overall analyses of dispersion were assessed in multiple ways and all were insignificant. Analyses were based upon both deviations from centroids and from spatial medians (each in turn from both ANOVA tables and permutation of residuals), and *p*-values ranged from 0.38 to 0.97. The significant results from the MRPP combined with the non-significant dispersion results indicate that there were compositional differences between both types of rock-associated habitats and reference meadows and that these two groups did not simply exhibit differing levels of variability.

4. Discussion and conclusions

4.1. Biodiversity associated with rock glacier and talus ecosystems

We report the first assessment of biotic diversity associated with rock glaciers and periglacial taluses and their forefield wetlands in the Sierra Nevada. Despite the abundance and widespread distribution of these rocky landforms throughout alpine and arctic regions of the world (Giardino and Vitek, 1988; Barsch, 1996), they have been mostly overlooked as mountain ecosystems or potential refugia for plants and animals under warming conditions. Flora associated with rock glaciers have been surveyed primarily to assess rock-glacier movement, and as indicators of persistent internal ice and permafrost. In rock glaciers of the Swiss Alps, for instance, active rock glaciers (i.e., ice-cored) were thought to maintain no or little plant cover due to movement (Barsch, 1996). Subsequent studies, however, showed that active rock glaciers in mesic regions such as the Alps can develop vegetative cover up to 10% (Burga et al., 2004). Cold-adapted and movement-resilient plants, characterized by low stature, creeping shoots and roots, extension growth, caespitose life form, and cushion plant strategy, were also associated with active features (Burga et al., 2004). By contrast, relict rock glaciers in the Swiss Alps (no permanent ice remaining) supported up to 80% vegetation cover, and were characterized by growth on their surfaces of subalpine conifers, dwarf shrubs, and grass communities. Prior assessments of the rock glaciers in the current study indicate that these landforms contain embedded ice and are likely active (Millar et al., 2013). If so, our results suggest that in regions of dry, Mediterranean climates such as the Sierra Nevada, plant cover on active rock-glaciers remains low (<2%), approaching Barsch's (1966) estimates. The only other study of vegetation related to rock glaciers in the Sierra Nevada has been conducted by Franklin (2012). In studies focused on herbchronology, she documented the dominance of *Linanthus pungens* at Barney rock glacier, and the value of this species for herbchronological assessment (Franklin, 2013).

Although primarily descriptive, our plant surveys on two rock glaciers of the central eastern Sierra Nevada suggest that these landforms constitute a distinct mountain habitat. On the mantles of rock glaciers, patches of thin, rocky soils are scattered as small islands, yet support a diversity of perennial herb and shrub species. An area effect is possible in that species richness on the larger and more complex Barney rock glacier was twice that of Gibbs rock glacier. Possibly also the larger rock glacier has more stable and/or better developed soil patches. Ordination results and Sørensen similarity values also suggest a capacity of the larger site to capture and maintain more species. Each of the two reference sites and the rock glaciers were separated in ordinal space and had few species in common. The low similarity values further corroborated the difference relative to the rock-glacier floras despite the large areal extent of the reference areas and inclusion of a wide range of rocky habitats. Relative to other rock environments in the Sierra, the rock-glacier taxa derived from cooler-adapted, more alpine distributions, as inferred from relative elevation ranges.

Whereas the sparse, thin-soiled islands of vegetation scattered on the mantles of the Sierra Nevada rock glaciers supported a small but distinct flora, the wetlands at their forefields contained large numbers of plant species with high diversity within and between sites. Mosaics of distinct vegetation characterized these wetlands, and, despite overall taxonomic similarity, each site had unique combinations of taxa, patch types and species abundance, and cover relationships. Perennial herbs and grasses, especially sedges, with deciduous foliage, were dominant. No obvious patterns distinguished the flora of the talus wetlands from the rock glacier wetlands. This result might be expected, given that many wetland species are circumboreal and adapted to multiple substrates, with limits driven primarily by moisture and temperature regime. Despite high differentiation among the sites, the small talus wetlands (~0.6 ha) supported more than 60 species each. The high diversity of the Barney rock glacier forefield wetland potentially relates to the heterogeneous nature of the large forefield environment, with slopes, benches and flat terraces, rocky intrusions, and aspects from southeast to northeast. These variable environments support a range of wetland types from sloping shrublands to bottomland saturated vegetation. Further, the setting of the large Barney rock-glacier forefield is such that it extends from the alpine into the subalpine zone. Thus it may be more accessible than the other three rock glaciers, set in alpine context, for colonization from diverse wetland taxa of both zones.

Taxonomic diversity of flora at the rock-glacier and talus wetlands was comparable to the SJRA reference wetlands and less similar to the HRNA reference site. The two reference sites were distinct compositionally and neither site clustered with the rock glacier wetlands, although there was a high proportion of shared taxa with the talus-associated wetlands. The reference species list derived from surveys conducted in multiple wetland sites across large areas of HRNA and SJRA, and included wetland communities from a wider range of contexts than the present study. Considering this, overall diversity and richness of species contained in the small rock-glacier wetlands were remarkably high, and had considerable overlap with the reference sites, indicating that a wide range of Sierra Nevada wetland-adapted taxa could be found in individual rock-associated wetlands. Species at the rock glacier wetlands supported a cooler-adapted set of species than the reference sites, again as inferred from relative elevation ranges.

Here we report also the first assessment of arthropod diversity focused on rock glacier and talus wetlands for the Sierra Nevada. Available wetland reference sites from a similar drought year and

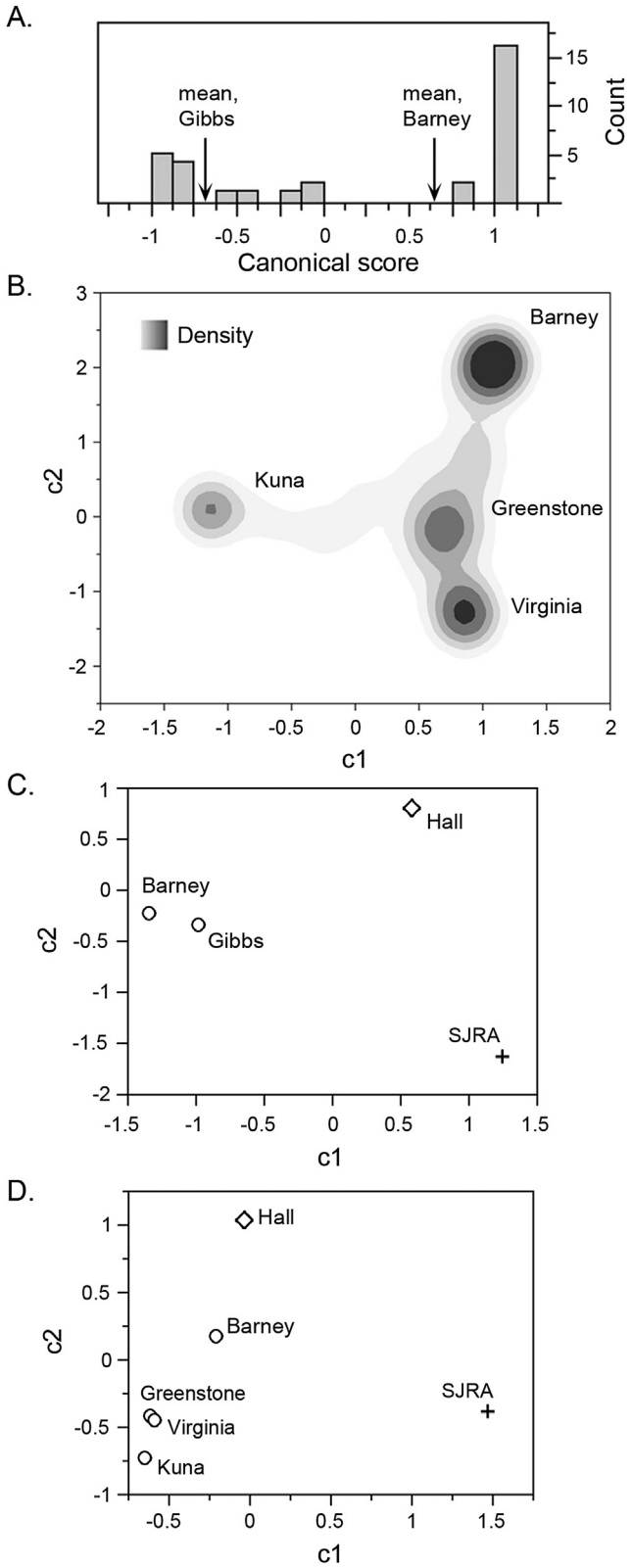

Fig. 5. Canonical correspondence ordinations. A. Rock-glacier floras. Frequency distribution of plant species diversity and cover data; histograms show frequencies of species' scores in one dimension (100% of variation). Means for Gibbs and Barney rock glacier scores are indicated. B. Wetland floras. Ordination of plant-species diversity and cover data, vectors 1 and 2 (78% of total variation). Density of species' scores for each site are shown as contour intervals (darker shade is denser). C. Rock-glacier floras. Rock-glacier versus reference (Hall and SJRA) sites, presence-absence data only, vectors 1 and 2 (58% of total variation). D. Wetland floras. Wetland versus reference (Hall and SJRA) sites, presence-absence data only, vectors 1 and 2 (58% of total variation). Vectors 1 and 2 are noted as c1 and c2.

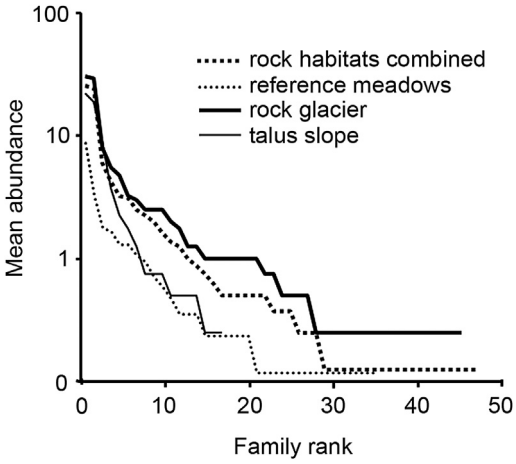

Fig. 6. Rank abundance plot (log scale) comparing combined forefield meadows versus reference wetlands as well as rock-glacier versus talus wetlands. Note that the differing sample sizes for the two sets of comparisons result in differing asymptotes and preclude four-way comparisons.

consistent survey methods enabled useful comparisons, although caution is nonetheless required due to the differing survey years. The combined data from the rock-associated wetlands indicated differing composition and higher overall population and total abundances relative to reference meadows, and there were higher population abundances and diversity in the rock glacier wetlands versus those near taluses. These significant differences are of note given the low power of these analyses due to small sample size. Arthropod assemblages are structured by a broad array of influences, including plant assemblages, vegetation structure, and soil moisture (Reid and Hochuli, 2007; Holmquist et al., 2011, 2013b), and all of these factors may have had a role in creating the patterns observed. Responses to these influences can shift as a function of the temporal (Holmquist et al., 2013a) and spatial (Hatfield and LeBuhn, 2007) scales of assessment. Our study of forefield wetlands emphasizes effects during late season and at the meadow scale, and these habitats may have different influences at patch and landscape scales and over different or longer time periods. It appears nonetheless that these wetlands, particularly those associated with rock glaciers, support a diverse and abundant fauna.

4.2. Rock glacier and talus ecosystems as refugia under warming climates

Prior studies have drawn attention to potentially unique elements associated with rock glacier and talus landforms that, considered together, constitute distinct mountain ecosystems (Růžička, 1993; Kubat, 2000). Common elements related to the cool and wet nature of these rock-dominated habitats relative to ambient conditions include 1) occurrence of assemblages of cold-adapted plant species growing on rock-glacier surfaces (Burga et al., 2004; Fickert et al., 2007) and in rock-glacier and talus forefields (Sasaki, 1986; Gude et al., 2003; Freppaz et al., 2008) significantly below typical altitudinal limits; 2) occurrence of unique micro-faunal assemblages of cold-adapted arthropod taxa and microbes living within the rocky matrices of rock glaciers and taluses displaced below their expected altitudinal range (Molenda, 1996; Williams et al., 1997; Zacharda et al., 2005); and 3) cold-

buffered thermal regimes partially decoupled from ambient climatic processes that are critical for survival and persistence of high mountain mammals including pikas, small rodents (Millar and Westfall, 2010; Millar et al., in press), and large carnivores (Inman et al., 2012).

A Pleistocene refugial role was proposed to explain the occurrence of diverse alpine plants growing below their late Holocene altitudinal niche on debris-covered glaciers (Fickert et al., 2007). In all cases, the features were large piedmont (ice) glaciers whose margins and snouts had become mantled with transported soil and rock debris. On the soil-covered portions, plant taxa were growing that appear to be relict from Pleistocene distributions. These taxa included conifer species with understories of alpine shrubs and herbs. In all cases these assemblages occurred in regions with climates characterized by high precipitation, heavy snowfall, and short, cool summers, conditions quite unlike those typifying the Sierra Nevada.

The current study extends investigation of high elevation refugia to Sierra Nevada rock-glacier and talus ecosystems. Our findings of high diversity in this environment suggest that rock-glacier and talus habitats in the Sierra Nevada are capable of supporting important components of regional biotic diversity in very small areas. A refugial role for these environments implies that, even with warming, Sierra Nevada biodiversity associated with cool, wet conditions could persist in these rocky environments. The potential for rock glaciers and taluses to remain buffered and resist warming in the future is indicated by a combination of characteristics. Unique thermal regimes maintain cooler than ambient conditions (Harris and Pedersen, 1998; Juliussen and Humlum, 2008; Millar et al., 2013, in press) and enable internal ice to build up and be maintained (Haeberli, 2005; Lambiel and Pieraccci, 2008; Millar et al., in press). Deep rock mantling covers the entire surface, and insolates the interior from solar radiation and resists ice melting (Clark et al., 1994; Hauck and Kneisel, 2008). Thermal conditions create cool environments on rock-glacier surfaces and venting of cool air at snouts onto the forefields (Sawada et al., 2003; Zacharda et al., 2007; Millar et al., in press). Persistent and stable seeps and springs issuing from the embedded ice maintain wetland forefields (Clow et al., 2003; Millar and Westfall, 2008; Leopold et al., 2011; Millar et al., 2013). Finally, an assumption emerges that embedded ice will lag in melt relative to exposed snow and ice fields under future warming, hence continuing to maintain cold and mesic environments (Millar and Westfall, 2008, in press). Thus, although other sources of warm-season water in the Sierra Nevada — snowfields and ice glaciers—are already disappearing with the warming climates (Stewart et al., 2004; Maurer, 2007; Basagic, 2008), rock glaciers are likely to retain cool temperatures and serve as hydrologic reservoirs. These rock glacier and talus ecosystems exemplify the class of climatic micro-refugia that depends for their occurrence and persistence on complexities of topography and thermal regime (Dobrowski, 2010).

Our arthropod results in particular suggest that forefield wetlands could function as biotic refugia in a warmer and drier future environment. Wetlands not closely associated with persistent water sources in the central Sierra Nevada typically senesce during mid-August, even in average snow years, with accompanying sharp declines in arthropod diversity and abundance at this time (Holmquist et al., 2011, 2013a). These temporal patterns were accelerated during drought years such as 2007 and 2012, and many nearby wet meadows not associated with rocky landforms in the region senesced by late July of that year (Holmquist and Schmidt-Gengenbach, unpublished). Rock-associated wetlands had significantly higher arthropod abundances than reference meadows during late season, although abundances were not greater than those observed in reference meadows at mid-season (Holmquist et al., 2011, 2013a). Thus forefield wetlands may not currently serve as refugia for arthropods throughout the growing season, but likely serve this function during late season. The strong influence of these late-season refugia is likely a result of faunal mobility. Unlike plants, arthropods can move rapidly to more hospitable conditions (e.g., Humbert et al., 2012), and as a result, abundances in refugia are not only maintained during disturbances, but rather are often increased (Lake, 2000). The high biodiversity of the forefield wetlands sampled during late season of this particularly dry year is consistent with the projection that these sites might persist and act as mesic refugia even as climates warm and dry in the future. In turn, the higher diversity and population abundances in the rock glacier wetlands suggest that these habitats may be particularly valuable, even relative to the talus wetlands. Similar observations of rock glacier springs persisting through summer and into autumn of 2007, following one of the driest water years on record in the Sierra Nevada, contrasted with other types of spring-fed wetlands not associated with rocky springs that dried by mid-August in that year (Millar et al., 2013; Millar, unpublished).

The implications of this preliminary study would benefit from corroboration by further research, including systematic assessment of plant and animal diversity and abundance at additional rock-glacier and talus locations, and comparison to appropriate reference sites through the same growing season. Given findings in other parts of the world of unusual arthropod diversity within the matrices of these rocky landforms (Růžička and Zacharda, 1994; Molenda, 1996), a similar exploration of rock glaciers and high-elevation taluses in the Sierra Nevada might reveal additional biodiversity roles of the internal environment. Indeed, Cokendolpher and Krejca (2010) recently described a new species of pseudoscorpion from talus caves in Yosemite, albeit at a lower elevation than our area of interest. Finally, repeat measurements of rock glacier and talus ecosystems and references sites, especially in association with thermal and hydrological monitoring, would allow assessment of the future refugial capacity of these environments as climates change.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2013.11.003.

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