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Sixty-five years of change in montane plant communities in western Colorado, U.S.A.

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ABSTRACT

Documenting and predicting patterns of vegetation change over time are challenging due to a lack of sufficiently detailed historical data for comparison. Montane plant communities are expected to respond to anthropogenic disturbance, including climate change, in complex ways dependent on component species' responses to changing abiotic and biotic conditions. To investigate the patterns and possible causes of temporal changes in montane plant communities, we resampled 121 transects surveyed by Jean Langenheim from 1948 to 1952 in the East River Basin near Crested Butte, Colorado, U.S.A. Langenheim quantified the composition of the four predominant community types (sagebrush, spruce-fir, upland-herbaceous, and alpine) at sites ranging from 2600 to 4100 m in elevation. Our resurvey of the same sites 65 years later revealed that all four communities currently have much higher levels of heterogeneity among sites and have experienced significant changes in species composition and dominance. Compositional changes include significant increases in bare ground, graminoid and shrub abundance, and loss of forbs, at higher elevations. Species' mean elevations shifted upward 41 m, and many species expanded their ranges into new communities. Elevation shifts were most pronounced from lower elevation communities, while many alpine species shifted their ranges into lower subalpine meadow communities.

INTRODUCTION

Documenting patterns of vegetation change over time is challenging due to the general lack of baseline historical data of sufficient accuracy and resolution to allow rigorous comparison (Harrison et al., 2010). Nonetheless, analyzing these changes is increasingly important as global climate change and other anthropogenic disturbances are projected to have pronounced effects on plant populations and communities (Hellmann et al., 2008). Potential vegetation changes in response to climate warming include alterations in community composition (Damschen et al., 2010), local extinction of species (Hellmann et al., 2008), and overall loss of diversity (Currie et al., 2004; Sproull et al., 2015). While these types of vegetation changes have been documented across a variety of landscapes worldwide, different environments do not respond to climate change identically (Breshears et al., 2005; Damschen et al., 2010). Additional environment-specific factors, both abiotic (e.g., elevation, substrate, and precipitation regime) and biotic (plant life-history strategies, competition, predation, and mutualisms) may all contribute to the variability in vegetation response to climate warming (CaraDonna et al., 2014; Venn et al., 2014). Disentangling these multiple factors affecting temporal changes in vegetation is essential for understanding how global climate change differentially affects plant communities on a regional scale (Hellmann et al., 2008; Chase et al., 2011).

Vegetation in water-stressed environments, especially at low to moderate elevations, may decrease in diversity and abundance under climate change. For instance, Breshears et al. (2005) found that drought, coupled with recent higher mean annual temperatures, increased mortality of piñon-juniper woodlands and their associated under-story species. The same pattern of species loss was not detected during periods of drought in the cooler 1950s. Another long-term study (1977–2012) of vegetation change in the semiarid Santa Rosa Mountains of southern California found that the 10 dominant species all shifted their distribution upward, reducing their abundance at the lower, drier portions of their elevational range (Kelly and Goulden, 2008). Loss of species, or reduced abundance, in response to climate warming is therefore expected in more water-limited environments (Harrison et al., 2010). Conversely, moist subalpine forests and meadows and insular alpine regions may increase in species richness as some plant growth forms readily colonize now suitable areas and other herbaceous species expand upward (Kammer et al., 2007). For example, increasing species richness at mountain summits in the European Alps has been documented since surveys began as early as 1835 (Pauli et al., 2003; Wipf et al., 2013). Modeled vegetation responses to temperature increases in the White and Inyo Mountains of eastern California showed an upward migration and distinct clustering of formerly mid-elevation species at mountain peaks (Van de Ven et al., 2007). Species richness is therefore expected to increase at higher elevations, while overall species elevational ranges are expected to move upward (Harrison et al., 2010).

Historical data sets can provide new insights when reexamined in novel ways (Price and Waser, 2000; Kelly and Goulden, 2008; Wipf et al., 2013; Rudgers et al., 2014). For instance, Harrison et al.'s (2010) revisitation after a 50-year interval to Whittaker's sites in the Siskiyou Mountains described altered species composition caused in part by a decrease in vegetation cover at lower elevations and an increase of shade-tolerant species in the forest understory (Damschen et al., 2010). We were fortunate to have access to a similar historical data set that allowed examination of changes in plant community composition and diversity over a 65-year interval for the East River Basin of Western Colorado (Langenheim, 1953; Zorio, 2015). Revisiting Langenheim's study is of particular interest because of the wide range in elevation and historically distinct community assemblages across habitat types that were sampled, ranging from arid sagebrush to high mountain summits (Langenheim, 1962). The mean annual temperature in the study area has increased from 36 to 38 °C between 1950 and 2014 (NOAA, 2014), similar to patterns reported globally (Pauli et al., 2003; Harrison et al., 2010). In addition, changes in recreation, agriculture, grazing, wildlife management, and other human impacts may have affected vegetation patterns in the region.

In order to document vegetation change over the past 65 years, we revisited and compared the species composition of 121 sites originally surveyed between 1948 and 1952 (Langenheim, 1953; 1962), representing four major community types: sagebrush, spruce-fir forest, upland-herbaceous (subalpine) meadow, and alpine. We examined site- and community-level changes in species diversity and abundance to consider four questions: (1) Has species diversity changed in the four community types? (2) Have alterations in community composition and structure occurred, and have the community types changed in different ways? (3) Have species distributions shifted in elevation? (4) Have the species composition and dominant plant functional groups of communities changed?

METHODS

Study Area

Plant community surveys were conducted in the East River Basin, a headwater tributary of the Gunnison River, located in Gunnison County near Crested Butte, Colorado, U.S.A. (38.8697°N, 106.9878°W; elevation 2400 m) and the Rocky Mountain Biological Laboratory (RMBL). Surveys were performed over an approximately 249 km^2 area ranging from 2600 to 4100 m in elevation on the east side of the upper East River

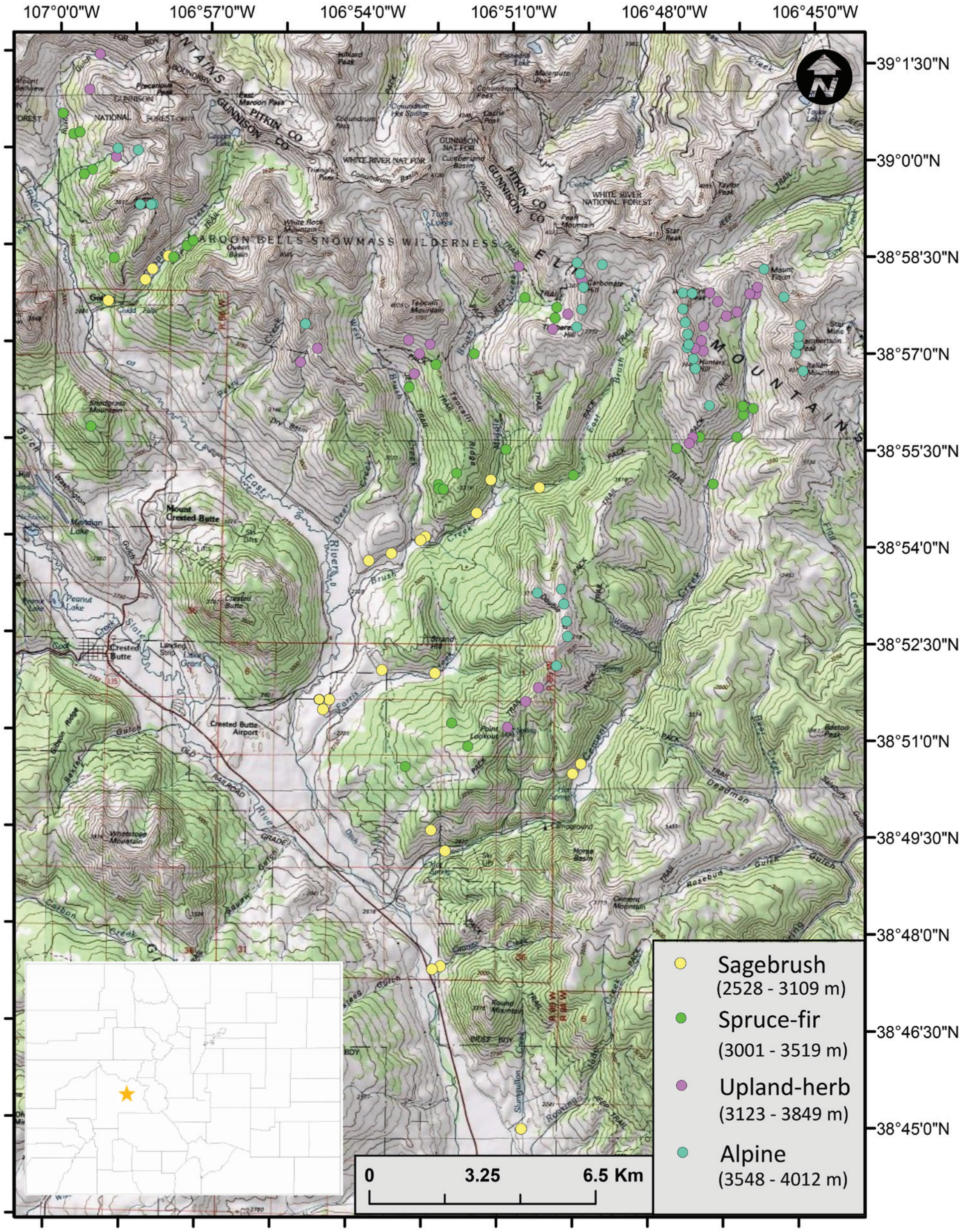

FIGURE 1. **Topographic map of the 236 km² study area in the upper Gunnison Basin, Colorado. Range in elevation (m) is given below each community type. Base map source: ©2014 National Geographic Society, i-cubed.**

drainage (Fig. 1). The annual average maximum and minimum temperatures are 10.8 °C and –7.8 °C, respectively. Average total precipitation is 59.9 cm yr^{-1}, and average snowfall is 502.7 cm yr^{-1}, with an average snow event depth of 25.4 cm (NOAA, 2014).

Site Relocation and Mapping

The primary focus of our study was to resurvey sites and community types sampled by Langenheim between 1948 and 1952 and to evaluate vegetation change at those locations. Langenheim's Ph.D. thesis (1953) contained quantitative species abundance data from transect sampling at 125 sites in four community types—sagebrush, spruce-fir, upland-herbaceous (often termed subalpine meadow), and alpine. These site-specific data were not included in Langenheim's published work (1962), and to our knowledge the sites had not previously been revisited. Exact coordinates for sampled sites were not included in Langenheim's dissertation or published work (Langenheim, 1953, 1962). Thus, approximate locations for sites were determined from descriptions included in the dissertation, personal correspondence with Dr. Jean Langenheim and

Dr. Ralph Langenheim, and site descriptions on Langenheim's plant voucher specimens. The CU-Boulder Herbarium (COLO; cumuseum.colorado.edu/research/botany/databases) and the Southwest Environmental Information Network (SEINet; swbiodiversity.org) herbarium databases were used to access Langenheim's digitized voucher information.

ArcGIS 10.2 was used to map and analyze sites in the four communities. Orthoimagery from Bing was used to configure a 10–30 m resolution basemap for the study sites. Several steps were employed to further increase the likelihood of resampling Langenheim's original sites and remove bias from choosing site centerpoints. We digitized polygons on the basemap that contained the habitat patches of each community type within the study area based on the most likely locations of the original sampling sites. Next, we generated random points within each polygon to serve as center points for sites. Buffers of 50 m were placed around each of the randomly generated points to avoid potential overlap. In this way, we were able to assign the most likely sampling points corresponding to 121 of Langenheim's 125 original sites (sagebrush: 27, spruce-fir: 31, upland-herbaceous: 30, alpine: 33; Fig. 1). A ⅓ arc second (10 m resolution) National Elevation Dataset (NED) from the U.S. Geological Survey (earthexplorer.usgs.gov) provided the basis for calculating elevation, slope, and aspect for each site.

Field Methods

Our resurvey methods were comparable to those used by Langenheim (1953, 1962), but we updated them to reflect current practices and to increase the likelihood of resampling the same sites she surveyed. Langenheim (1953, 1962) used the "step-point method" (Levy and Madden, 1933): she walked 100 paces of ~1 m each in a straight line, recording all plants that touched the toe of her boot at each step. We instead laid out a 100 m tape and sampled plants at 1 m intervals along it, a comparable point-intercept approach. Rather than a single straight transect, we established four 75-m transects at 90-degree angles from the site's center point. Two transects ran along the elevational contour, and two ran up- and downslope from the contour. Plant species intercepting transects at each meter (= 300 data points) were recorded.

Data Preparation

Langenheim's (1953) relative species abundance data (relative frequency) in each community were based on 100 sample points per site. The relative abundance of each species and bare area at a site was calculated as the count of a species (or bare area) divided by the summed total of all species' (and bare area) counts for that site (Langenheim, 1953, 1962). In Langenheim's data, total species abundance for a site was often greater than 100, suggesting that multiple, overlapping species were recorded at some sample points. We likewise recorded multiple, overlapping species at a sample point when encountered. In some cases, total species counts for a site were less than 100, suggesting that infrequently occurring species were dropped from Langenheim's data set. Species present at low frequency (<1%) within a site were denoted as "x" (Langenheim, 1953). We replaced those values with frequencies of 0.5%, to allow quantitative analysis. Species difficult to identify and grouped by genus by Langenheim were also consolidated at the genus level in the resurvey. The original survey limited analyses to species occurring with ≥14% constancy, where constancy is the proportion of sites within a community in which a species was recorded (Langenheim, 1953). For comparability, species with <14% constancy in the new survey were also dropped from analyses. Because our sampling procedure (300 points per site) was more intensive than Langenheim's (100 points per site), we randomly subsampled our resurvey data set to reflect Langenheim's maximum effort of 131 observations per site and to reduce artificial inflation of species richness. Procrustes comparisons of several nonmetric multidimensional scaling (NMDS) ordinations based on random 131 observations-per-site subsamples insured that using any of these multivariate data sets led to similar inferences ($R^2 > 0.9$, $p < 0.001$). A single, subsampled random data subset was used for all subsequent analyses. We updated the species names from the original survey using Weber and Wittmann (2012) to be comparable to our resurvey data. Vouchers collected during the resurvey are deposited at the RMBL Herbarium and are available through SEINet. The full new survey (nonsubsampled) data set, and the original data set of Langenheim (1953) with nomenclatural updates are archived at the RMBL.

Tests of Community Diversity and Species Distributions

Alpha-diversity within community types was described using species richness and the Shannon-Weiner index (cf. Magurran, 2013). We used the Raup-Crick dissimilarity index (Chase et al., 2011) to measure heterogeneity among sites (β-diversity) within communities, and between paired sites across the two survey periods. This adaptation uses presence/absence data to compare the observed number of shared species in a community to those of a null model (Chase et al., 2011; Oksanen et al., 2013). The probability of adding species to the null model assemblages is proportional to the species frequencies, thereby accounting for the confounding effect of α-diversity (Chase et al., 2011). Resultant values range between 0 (low dissimilarity) and 1 (high dissimilarity), similar to Bray-Curtis dissimilarities (Bray and Curtis, 1957). Paired *t*-tests were used to test for differences within community type between surveys in richness per site and α-diversity. Repeated measures ANOVA (with blocking by paired sites) of distance-to-centroid values for Raup-Crick dissimilarities was used to test for differences in β-diversity (Anderson et al., 2011; Oksanen et al., 2013).

We also examined the average proportion of growth forms (forb, shrub, graminoid, and bare ground) among community types and tested whether these proportions changed between the two surveys using paired *t*-tests. Finally, we tested for changes in the mean elevation at which species occurred between the two surveys. We calculated the mean elevation for each species present in both surveys. Elevations of sites at which a species occurred were weighted by its relative abundance at that site. Differences in abundance-weighted mean elevations of species between surveys were tested using a paired *t*-test.

Ordination and Multivariate Hypothesis Testing

To depict the dissimilarity of sites and community types, and their changes between the two surveys we used NMDS (Legendre and Legendre, 2012). Bray-Curtis dissimilarity (Bray and Curtis, 1957) was used as the underlying resemblance metric in NMDS because of its propensity to effectively represent dissimilarity structures in zero-inflated data sets (Magurran, 2013). An NMDS ordination using all data from both surveys and ordinations for each community type were used to examine pairwise shifts of Bray-Curtis dissimilarity values for sites between sampling periods. Vector fitting (Oksanen et al., 2013) was used to overlay environmental variables (elevation, slope, aspect) and growth forms on the ordinations, and to test null hypotheses of no association with the NMDS projections. Repeated measures permutational ANOVA (PERMANOVA; Anderson, 2005) was used to determine whether the communities outlined by Langenheim were distinct in the multivariate species space of both the original and new survey, and to test for community-level changes over time. The statistical program R was used for all analyses (R Core Team, 2015), with heavy reliance on the package *vegan* (Oksanen et al., 2013) for β-diversity, ordination, PERMANOVA, and other community-level analyses.

RESULTS

A total of 286 species from 45 families was documented from the 121 sites in the new survey. In the original study, Langenheim (1953) reported 157 species from 27 families. A reduced data set including only species with >14% constancy (see Methods) consisting of 198 species from 35 families was used for comparative statistical analyses.

Changes in Richness and Diversity

Based on the presence/absence of the 198 species with >14% constancy retained in the comparative data set, average species richness per site decreased significantly between the two surveys in the sagebrush ($t_{(26)} = 2.45$, $p = 0.021$), and alpine ($t_{(32)} = 9.20$, $p < 0.001$) communities. Richness increased significantly over time in paired upland-herbaceous sites ($t_{(29)} = -2.17$, $p < 0.038$; Table 1). Likewise, Shannon-Weiner diversity decreased significantly at alpine sites ($t_{(32)} = 5.95$, $p < 0.001$) and increased in upland-herbaceous sites ($t_{(29)} = -2.23$, $p = 0.033$) between 1950 and 2014 (Table 1). Heterogeneity in species composition among sites (β-diversity) increased significantly in all community types as shown by the Raup-Crick index (sagebrush, $F_{(1,52)} = 55.60, p < 0.001$; spruce-fir, $F_{(1,60)} = 105.22, p < 0.001$; upland-herbaceous. $F_{(1,58)} = 50.58, p < 0.002$; alpine, $F_{(1,64)} = 50.26, p < 0.003$; Table 1).

Changes in Community Composition

NMDS ordinations of sites surveyed in both 1950 and 2014 (three dimensions, stress = 14.7; Kruskal and Wish, 1978) further suggest that sites within community types became more heterogeneous in species composition, and in some cases that community types are now less distinct (Fig. 2). Compared to 2014, the community centroids for the 1950 survey are more widely separated in species space. The size of the 95% confidence ellipses around community centroids also tend to be smaller in 1950, indicating lower dispersion of sites around their community centroids, than in 2014. Confidence ellipses grew appreciably larger for upland-herb and sagebrush communities between surveys, while shrinking somewhat for spruce-fir and alpine communities (Fig. 2).

PERMANOVA analyses show that communities in both the original and new surveys were compositionally distinct from each other ($F_{(3,241)} = 42.61, R^2 = 0.329, p < 0.001$). These analyses also confirmed that communities in the original survey were more distinct and well-defined than in the resurvey, based on a higher F-ratio and R^2 value for that analysis (original survey: $F_{(3,120)} = 40.39, R^2 = 0.508, p < 0.001$; new survey: $F_{(3,120)} = 18.65, R^2 = 0.323, p < 0.001$). Species composition *within* community types changed significantly between sampling periods for all four community types (sagebrush, $F_{(1,53)} = 9.10, R^2 = 0.146, p < 0.001$; spruce-fir, $F_{(1,61)} = 14.45, R^2 = 0.193, p < 0.001$; upland-herbaceous, $F_{(1,59)} = 14.62, R^2 = 0.198, p < 0.001$; and alpine ($F_{(1,65)} = 20.92, R^2 = 0.236, p < 0.001$).

Changes in Species Dominance Between Surveys

The relative abundance and rank order of the dominant species in each community changed markedly between 1950 and 2014 (Table 2, parts a–d). Overall, the relative abundance of the most common species in each community type declined, reducing dominance and increasing evenness, while the proportion of bare area increased in all communities. Communities also become more heterogeneous in species composition as indicated by the lower constancy (presence at fewer sites) of most species in 2014 versus 1950 (Table 2, parts a–d). Notable shifts in the most abundant/dominant species occurred between 1950 and 2014 in each community type, as outlined below.

In the sagebrush community (Table 2, part a), big sage (*Seriphidium tridentatum*) and Thurber's fescue (*Festuca thurberi*) remained the characteristic dominant species, although at much lower abundances. Several shrubs (*Chrysothamnus* spp., *Symphoricarpos rotundifolius, Amelanchier alnifolia,* and *Rosa woodsii*) declined sharply in abundance. Two weedy, herbaceous species of sage (*Oligosporus dracunculus* and *Artemisia frigida*) became much more abundant. Grasses (particularly *Bromopsis* spp. and *Elymus* spp.) were all much more abundant in 2014 than 1950 (Table 2, part a). Although the native *Bromopsis frondosus* declined somewhat in abundance (mean relative abundance, 1950 = 1.69; 2014 = 1.11), the introduced smooth brome (*Bromopsis inermis*) changed from unobserved in 1950 to the 25th most abundant species at sagebrush sites in 2014 (mean relative abundance = 0.67, constancy = 40.74). The spruce-fir community (Table 2, part b) experienced a decrease in overall understory vegetation cover (increased bare ground) between 1950 and 2014. *Vaccinium myrtillus* and *Arnica cordifolia* remained among the most abundant species. Lousewort (*Pedicularis* spp., particularly *P. racemosa*) declined dramatically in abundance, as did *Lupinus* spp. and *Polemonium pulcherrimum*. The sedge, *Carex geyeri*, as well as *Ligusticum porteri*, became more abundant and widespread in spruce-fir sites.

The upland-herb (subalpine meadow) community (Table 2, part c) saw a dramatic decrease in vegetation cover (bare ground increased from 3.5% to 28.6%) between surveys. The formerly dominant plant species all declined in both relative and rank abundance. A few species normally associated with wetter meadow habitat, such as *Delphinium barbeyi*, *Sibbaldia procumbens*, and *Acomastylis rossii* all decreased in abundance between 1950 and 2014. Conversely, willows (*Salix* spp.) and grasses became much more abundant in upland-herb sites between surveys. *Bromopsis* spp. and *Bromelica spectabilis* increased almost 10-fold in abundance between 1950

TABLE 1

Summary statistics of average richness, Shannon-Weiner diversity, and Raup-Crick dissimilarity among sites in four community types. Original data (Langenheim, 1953) are named 1950, and the resurvey is 2014. The total number of sampled sites in each community is listed. Site means and standard errors are shown for each metric. Asterisks denote significant difference between study periods via paired *t*-tests for richness and Shannon-Weiner diversity, and repeated measures ANOVA (with blocking by paired sites) of distance-to-centroid values for Raup-Crick dissimilarities (see Results).

		Richness		Shannon-Weiner		Raup-Crick	
Community	Sites	1950	2014	1950	2014	1950	2014
Sagebrush	27	22.56 (± 3.3)	18.33* (± 8.4)	2.32 (± 0.32)	2.22 (± 0.70)	0.256 (± 0.27)	0.325* (± 0.30)
Spruce–fir	31	16.32 (± 5.3)	15.39 (± 6.1)	2.09 (± 0.52)	2.02 (± 0.52)	0.189 (± 0.22)	0.298* (± 0.03)
Upland–herb	30	22.1 (± 4.6)	24.9* (± 5.4)	2.6 (± 0.28)	2.77* (± 0.11)	0.34 (± 0.32)	0.366* (± 0.29)
Alpine	33	20.6 (± 3.5)	12.6* (± 3.8)	2.38 (± 0.37)	1.73* (± 0.50)	0.296 (± 0.30)	0.367* (± 0.31)

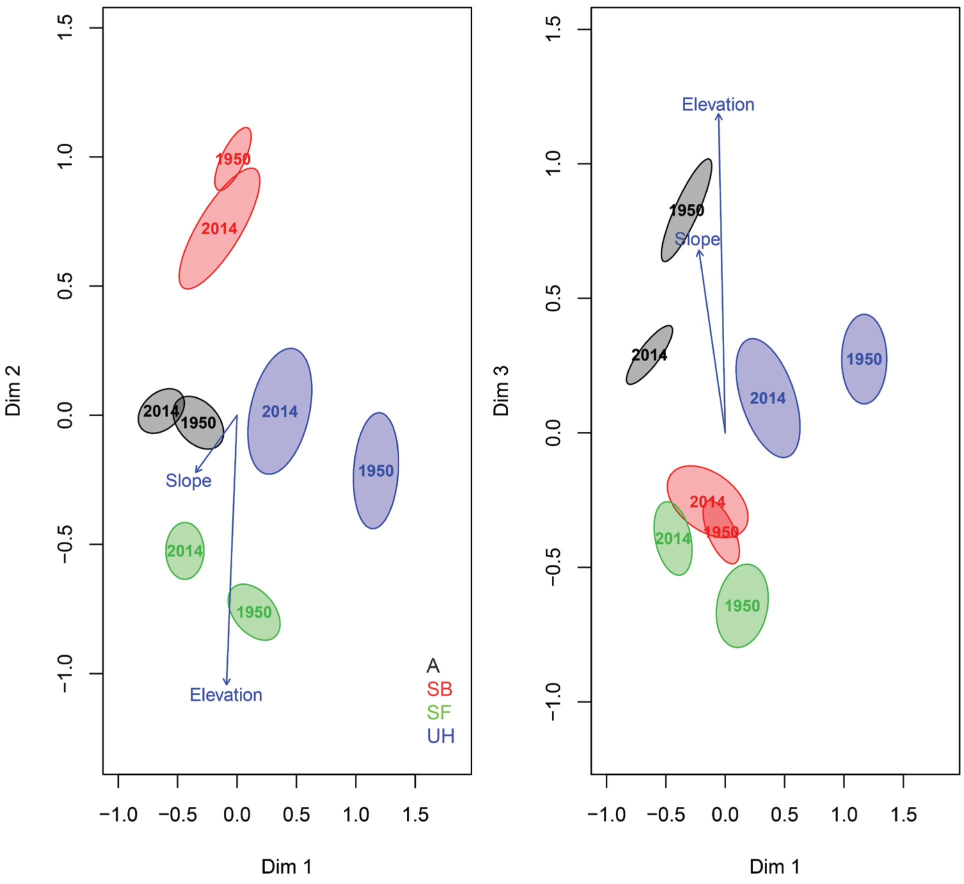

FIGURE 2. Non-metric multidimensional scaling (NMDS) ordinations of dimensions 1 and 2, dimensions 1 and 3, and regression vectors for environmental variables for Langenheim (1953) and new survey data (2014) showing 95% confidence ellipses for community centroids. Arrows indicate increasing slope and elevation, and western-facing aspects. Final stress for 3D NMDS solution = 0.13. A = Alpine, SB = Sagebrush, SF = Spruce-fir, and UH = Upland-herb.

TABLE 2

The 15 most abundant species for each community in the original (1950) and new (2014) surveys. Species are ranked by their mean relative abundance in 1950. The range of relative abundances among sites and constancy (percentage of sites in which species is present) are given for each species. Some difficult to distinguish species are lumped at the genus level.

TABLE 2a

Sagebrush Community (n = 27 sites).

Species	Rank abundance 1950	Relative abundance (range) 1950	Constancy 1950	Rank abundance 2014	Relative abundance 2014	Constancy 2014
Bare ground	N/A	12.26 (2.19–36.17)	N/A	N/A	22.72 (0.76–86.67)	N/A
Seriphidium tridentatum	1	33.56 (9.14–60.61)	100	1	15.02 (0.00–46.56)	66.67
Festuca thurberi	2	6.21 (0.00–20.20)	96.3	2	4.87 (0.00–27.48)	44.44
Arenaria congesta	3	4.44 (0.00–18.97)	81.48	35	0.48 (0.00–6.87)	18.52
Chrysothamnus spp.[1]	4	4.26 (0.00–13.11)	81.48	12	2.35 (0.00–9.92)	62.96
Potentilla spp.[2]	5	3.36 (0.00–14.49)	92.59	3	3.70 (0.00–19.08)	62.96
Eriogonum umbellatum	6	2.61 (0.00–10.84)	92.59	13	2.32 (0.00–12.21)	51.85
Lupinus spp.	7	2.35 (0.00–11.11)	59.26	10	2.60 (0.00–11.45)	55.56
Symphoricarpos rotundifolius	8	2.27 (0.00–13.71)	44.44	30	0.54 (0.00–5.38)	22.22
Rosa woodsii	9	2.23 (0.00–10.29)	66.67	55	0.25 (0.00–2.29)	18.52
Erigeron spp.[3]	10	1.73 (0.00–6.86)	85.19	6	3.10 (0.00–14.51)	66.67
Bromopsis spp.[4]	11	1.69 (0.00–14.29)	51.85	8	2.66 (0.00–8.40)	62.96
Achillea millefolium	12	1.61 (0.00–4.48)	92.59	7	2.94 (0.00–9.92)	70.37
Lathyrus leucanthus	13	1.59 (0.00–6.06)	81.48	11	2.47 (0.00–11.45)	55.56
Agastache urticifolia	14	1.54 (0.00–10.12)	51.85	31	0.54 (0.00–8.40)	14.81
Amelanchier alnifolia	15	1.53 (0.00–9.47)	29.63	24	0.72 (0.00–6.11)	33.33
Oligosporus dracunculus	>40	0.00	0.00	4	3.42 (0.00–26.72)	37.04
Elymus spp.[5]	30	0.53 (0.00–3.43)	55.56	5	3.15 (0.00–13.74)	62.96
Artemisia frigida	34	0.39 (0.00–2.07)	40.74	9	2.60 (0.00–33.59)	18.52
Castilleja linariaefolia	17	1.48 (0.00–5.49)	74.07	14	1.61 (0.00–11.63)	55.56
Koeleria macrantha	36	0.31 (0.00–1.93)	25.93	15	1.53 (0.00–7.63)	40.74

[1] Including *Chrysothamnus nauseosus* and *C. parryi*.

[2] Including *Potentilla pulcherrima* (only species identified in 1950), *Pentaphylloides floribunda*, and other unidentified *Potentilla* spp.

[3] Including *Erigeron speciosus* (only species identified in 1950), *E. glabellus*, and *E. subtrinervis.*

[4] Including *Bromopsis frondosa* (only species identified in 1950), *B. ciliata, B.inermis, B. richardsonii*, and *Anisantha tectorum*.

[5] Including *Elymus trachycaulus* (only species identified in 1950), *E. glaucus, E. lanceolatus,* and *E. elymoides.*

TABLE 2b

Spruce–Fir Community (*n* = 31 sites).

Species	Rank abundance 1950	Relative abundance (range) 1950	Constancy 1950	Rank abundance 2014	Relative abundance 2014	Constancy 2014
Bare ground	N/A	10.53 (2.29–46.49)	N/A	N/A	28.56 (0.76–51.91)	N/A
Vaccinium spp.[1]	1	24.25 (0.00–70.90)	96.77	1	21.32 (0.00–80.15)	74.19
Pedicularis spp.[2]	2	10.03 (0.00–35.98)	93.55	15	0.96 (0.00–3.82)	41.94
Arnica cordifolia	3	8.37 (0.00–21.26)	96.77	2	11.50 (0.00–32.06)	87.10
Lupinus spp.	4	6.14 (0.00–27.40)	61.29	14	1.03 (0.00–12.21)	32.26
Polemonium pulcherrimum ssp. *delicatum*	5	4.61 (0.00–19.89)	74.19	19	0.86 (0.00–6.11)	35.48
Ribes montigenum	6	4.24 (0.00–17.75)	70.97	8	1.53 (0.00–8.40)	45.16
Fragaria virginiana	7	3.03 (0.00–16.22)	96.77	4	2.68 (0.00–9.16)	64.51
Mertensia spp.[3]	8	2.27 (0.00–12.50)	74.19	12	1.31 (0.00–7.63)	32.26
Paxistima myrsinites	9	2.16 (0.00–33.51)	29.03	5	2.07 (0.00–11.45)	41.94
"Senecio" spp.[4]	10	1.57 (0.00–9.46)	58.06	27	0.64 (0.00–4.58)	32.26
Koeleria macrantha	11	1.65 (0.00–15.54)	38.71	>65	0.00	0.00
Carex spp.[5]	12	1.58 (0.00–8.28)	61.29	3	4.06 (0.00–17.56)	77.42
Pseudocymopterus montanus	13	1.44 (0.00–5.88)	67.74	6	1.77 (0.00–11.45)	41.93
Ribes wolfii	14	1.40 (0.00–12.29)	61.29	34	0.44 (0.00–5.34)	22.58
Osmorhiza depauperata	15	1.28 (0.00–6.09)	48.39	9	1.43 (0.00–5.34)	61.29
Lathyrus leucanthus	21	0.96 (0.00–9.80)	25.81	10	1.38 (0.00–12.21)	38.71
Erigeron spp.[6]	36	0.23 (0.00–2.12)	19.35	11	2.60 (0.00–33.59)	18.52
Ligusticum porteri	>40	0.00	0.00	13	1.18 (0.00–7.63)	38.71

[1] Mostly *Vaccinium myrtillus* and some *V. caespitosum*.

[2] Mostly *Pedicularis racemosa* ssp. *alba* and occasional *P. bracteosa* and *P. procera*.

[3] Mostly *Mertensia ciliata* (only species identified in 1950) and *M. brevistyla*.

[4] Including *Ligularia amplectens* (only species identified in 1950*), S. integerrimus, S. serra,* and *S. triangularis.*

[5] Mostly *Carex geyeri* (only species identified in 1950).

[6] Including *Erigeron glabellus, E. glacialis,* and *E. speciosus*.

TABLE 2c

Upland–herb (subalpine meadow) Community (n = 30 sites).

Species	Rank abundance 1950	Relative abundance (range) 1950	Constancy 1950	Rank abundance 2014	Relative abundance 2014	Constancy 2014
Bare ground	N/A	3.49 (2.29–16.30)	N/A	N/A	28.56 (0.76–51.91)	N/A
Ligusticum porteri	1	12.03 (0.00–48.19)	90.00	5	3.92 (0.00–27.48)	50.00
Lupinus spp.	2	10.71 (0.00–26.88)	83.33	8	3.04 (0.00–12.21)	60.00
Senecio spp.[1]	3	7.66 (0.00–22.66)	96.67	11	2.67 (0.00–15.27)	70.00
Carex spp.[2]	4	5.45 (0.00–16.22)	86.67	10	2.74 (0.00–8.40)	73.33
Delphinium barbeyi	5	4.79 (0.00–14.86)	66.67	14	2.13 (0.00–12.98)	46.67
Poa spp.[3]	6	4.43 (0.00–13.87)	90.00	26	1.10 (0.00–9.16)	40.00
Helianthella quinquenervis	7	3.94 (0.00–17.91)	63.33	9	2.80 (0.00–10.69)	63.33
Bistorta bistortoides	8	3.82 (0.00–15.22)	63.33	41	0.61 (0.00–7.63)	26.67
Erigeron spp.[4]	9	3.80 (0.00–11.43)	93.33	13	2.44 (0.00–21.37)	53.33
Vaccinium spp.[5]	10	3.01 (0.00–33.11)	43.33	17	1.63 (0.00–10.69)	36.67
Achillea millefolium	11	2.46 (0.00–14.86)	73.33	6	3.23 (0.00–9.16)	76.67
Sibbaldia procumbens	12	2.15 (0.00–12.09)	46.67	>65	0.00	0.00
Festuca thurberi	13	2.14 (0.00–41.48)	26.67	12	2.64 (0.00–22.90)	50.00
Potentilla spp.[6]	14	2.12 (0.00–11.24)	76.67	2	4.68 (0.00–19.85)	93.33
Acomastylis rossii	15	1.94 (0.00–24.00)	36.67	31	0.92 (0.00–6.11)	30.00
Bromopsis spp.[7]	41	0.50 (0.00–3.75)	26.67	1	5.22 (0.00–12.98)	80.00
Bromelica spectabilis	44	0.28 (0.00–3.10)	25.81	3	4.35 (0.00–20.61)	23.33
Salix spp.	>50	0.00	0.00	4	4.24 (0.00–29.77)	53.33
Fragaria virginiana	37	0.66 (0.00–4.49)	40.00	7	3.10 (0.00–12.21)	70.00
Mertensia spp.[8]	>50	0.00	0.00	15	2.01 (0.00–16.79)	46.67

[1] Including *Senecio crassulus* (the only species identified in 1950), *S. integerrimus, S. triangularis,* and *S. wootonii*.

[2] Indvidual sedge species not recorded in 1950, includes *Carex aquatilis, C. microptera,* and *C. siccata* in 2014.

[3] *Poa* not identified to species in 1950, includes *Poa fendleriana* and *Poa pratensis* in 2014.

[4] Including *Erigeron coulteri, E. elatior,* and *E. glacialis* (in 1950*),* plus *E. glabellus, E. leiomerus,* and *E. speciosus* added in 2014.

[5] Mostly *Vaccinium caespitosum*.

[6] Including *Potentilla pulcherrima* and *P. rubricaulis.*

[7] Including *Bromopsis ciliata* (only species identified in 1950), *B. inermis,* and *B. frondosa*.

[8] Primarily *Mertensia ciliata* in 2014.

TABLE 2d

Alpine Community (*n* = 33 sites).

Species	Rank abundance 1950	Relative abundance (range) 1950	Constancy 1950	Rank abundance 2014	Relative abundance 2014	Constancy 2014
Bare ground	N/A	25.33 (3.05–79.52)	N/A	N/A	48.72 (5.71–83.02)	N/A
Carex spp.[1]	1	8.45 (0.00–52.07)	87.88	4	2.63 (0.00–12.70)	63.64
Rydbergia grandiflora	2	5.00 (0.00–14.57)	84.85	29	0.72 (0.00–00.81)	21.21
Dryas octopetala	3	4.91 (0.00–45.59)	42.42	13	1.31 (0.00–12.50)	24.24
Artemisa scopulorum	4	4.74 (0.00–24.36)	81.81	21	0.92 (0.00–5.00)	33.33
Ivesia gordonii	5	4.21 (0.00–26.09)	48.48	16	1.16 (0.00–7.84)	30.30
Silene acaulis	6	3.94 (0.00–15.49)	75.76	10	1.67 (0.00–8.08)	51.52
Erigeron spp.[2]	7	3.92 (0.53–11.29)	63.33	3	3.37 (0.00–12.50)	69.70
Poa spp.	8	3.89 (0.00–17.74)	93.94	20	0.94 (0.00–9.52)	21.21
Polemonium viscosum	9	3.60 (0.00–16.88)	75.76	18	1.09 (0.00–8.06)	27.27
Acomastylis rossii	10	3.43 (0.00–30.00)	66.67	5	2.35 (0.00–23.53)	39.39
Potentilla spp.[3]	11	3.41 (0.00–11.70)	93.94	2	3.41 (0.00–13.48)	66.67
Elymus spp.[4]	12	2.40 (0.00–8.54)	81.82	1	5.19 (0.00–24.36)	63.64
Trisetum spicatum	13	2.22 (0.00–12.21)	84.85	27	0.75 (0.00–7.69)	24.24
Festuca spp.[5]	14	2.06 (0.00–10.60)	75.76	6	2.01 (0.00–10.94)	39.39
"Senecio" spp.[6]	15	1.78 (0.00–8.70)	63.64	15	1.24 (0.00–6.02)	45.46
Achillea millefolium	25	0.88 (0300–7.32)	51.52	7	1.82 (0.00–9.38)	33.33
Salix spp.[7]	16	1.76 (0.00–23.31)	51.52	8	1.82 (0.00–13.95)	36.36
Astragalus spp.	>35	0.00	0.00	9	1.73 (0.00–7.50)	39.39
Trifolium dasyphyllum	>35	0.00	0.00	11	1.42 (0.00–10.48)	33.33
Oxytropis deflexa ssp. *sericea*	>35	0.00	0.00	12	1.40 (0.00–5.00)	60.61
Oxytropis podocarpa	>35	0.00	0.00	14	1.25 (0.00–6.02)	42.42

[1] Includes unidentified *Carex* spp. plus *Kobresia myosuroides*.

[2] Including *Erigeron glacialis* and *E. pinnatisectus,* plus *E. leiomerus* added in 2014.

[3] Including *Potentilla nivea* and *P. uniflora*.

[4] Including *Elymus trachycaulus* and *E. scribneri*.

[5] Predominantly *Festuca brachyphylla*.

[6] Including *Ligularia soldanella, Packera cana,* and *P. werneriifolia*.

[7] Primarily *Salix petrophila, S. nivalis,* and *S. brachycarpa*.

and 2014. The introduced *Bromopsis inermis* went from undetected in 1950 to the 18th most abundant species surveyed in 2014 (mean relative abundance = 1.58, constancy = 43.33).

Bare ground almost doubled, from 25.3% to 48.7% of sample points, between 1950 and 2014 in alpine sites (Table 2, part d). Some of the most well recognized alpine species, such as *Dryas octopetala*, *Ivesia gordonii*, and *Silene acaulis*, were all less abundant and widespread in the resurvey than in 1950. Several species in the pea family, which were not recorded in 1950, increased in alpine sites, including milk-vetches (*Astragalus* spp.), locoweeds *(Oxytropis* spp.), and clovers (particularly *Trifolium dasyphyllum*). A number of fleabanes (*Erigeron* spp.), as well as *Achillea millefolium*, also became more abundant. Grasses increased dramatically in abundance between surveys, particularly *Elymus* spp. and *Festuca* spp., while sedges declined.

Shifts in Dominant Growth Forms

Intracommunity ordinations (Fig. 3) revealed consistent shifts in community composition for paired sites over time (two dimensions, stress <20). In general, sites within communities generally became more dispersed in species space as communities became more heterogeneous in species composition. However, alpine sites appear to have become compositionally *less heterogeneous* between 1950 and 2014. Notably, sites within communities tended to change along similar vectors (in the same way), although there appear to be two dominant directions of change in sagebrush and spruce-fir communities. Community changes are correlated with changes in the three growth forms and bare area (Figs. 3 and 4). Bare area increased significantly in all community types between surveys (sagebrush: $t_{(26)} = -2.32$, $p = 0.03$; spruce-fir: $t_{(30)} = -5.93$, $p < 0.001$; upland-herbaceous: $t_{(29)} = -4.75$, $p < 0.001$; and alpine: $t_{(32)} = -7.35$, $p < 0.002$). Graminoids significantly increased in the sagebrush ($t_{(26)} = -4.16$, $p < 0.001$), and decreased in the alpine ($t_{(32)} = 2.60$, $p = 0.014$) communities. Shrubs decreased in the sagebrush ($t_{(26)} = 5.19$, $p < 0.001$), but increased in the spruce-fir ($t_{(30)} = -5.96$, $p < 0.001$) and alpine communities ($t_{(32)} = -3.01$, $p < 0.001$). Sites shifted strongly toward lower forb abundance in the spruce-fir ($t_{(30)} = 2.87$, $p = 0.007$), upland-herbaceous ($t_{(29)} = 5.95$, $p < 0.001$), and alpine ($t_{(32)} = 4.85$, $p < 0.001$) communities.

Species' Elevation and Range Shifts

Abundance-weighted mean elevations were calculated for 83 species that could be identified with certainty and that were observed in ≥5 sites in both the 1950 and 2014 surveys (mean number of sites occupied = 19.6 per survey period; Table 3). Overall, the mean elevation at which species occurred in 2014 was significantly higher than in 1950 (mean elevation difference = +41.1 m; $t_{(82)} = 2.14$, $p = 0.018$). Mean elevation changes, however, ranged widely among species, from –466 m to +471 m. Species characteristic of different elevations and community types had different patterns of mean elevation change as described below.

Species that predominantly occurred in the low elevation sagebrush community in 1950 (mean elevation <3000 m; Table 3) showed a strong pattern of upward movement between surveys (mean elevation difference = +151.5 m; $t_{(21)} = 4.29$, $p < 0.001$). Many species expanded into a wider range of community types. Several formerly low elevation species dramatically shifted their elevational range upward, including: *Maianthemum stellatum* (+471 m), *Boechera stricta* (+447 m), *Ipomopsis aggregata* (+462 m), and *Linum lewisii* (+346 m). Two shrubs, *Symphoricarpos rotundifolius* and *Rosa woodsii*, increased their mean elevations between surveys (+260 m and +223 m, respectively), while the dominant shrub *Seriphidium tridentatum* shifted downward slightly (–14 m).

Species occupying mid-elevation sites (mean elevation = 3000–3300 m), particularly spruce-fir forest, in 1950 (Table 3) also significantly shifted their distributions upward by 2014 (mean elevation difference = +70.7 m; $t_{(19)} = 2.99$, $p = 0.004$). Several spruce-fir understory specialists showed little change in mean elevation, remaining predominantly in the forest understory (e.g., *Paxistima myrsinites*, *Aquilegia elegantuala*, *Arnica cordifolia*, *Carex geyeri*; mean elevation difference = +10.1 m). A few species expanded upward into new communities, including *Thalictrum fendleri, Mertensia ciliata, Fragaria virginiana,* and *Polemonium pulcherrimum* (mean elevation difference = +188.8 m). *Heterotheca villosa*, one of the most wide-ranging composites, appears to have contracted its range, but increased its mean elevation by over 200 m.

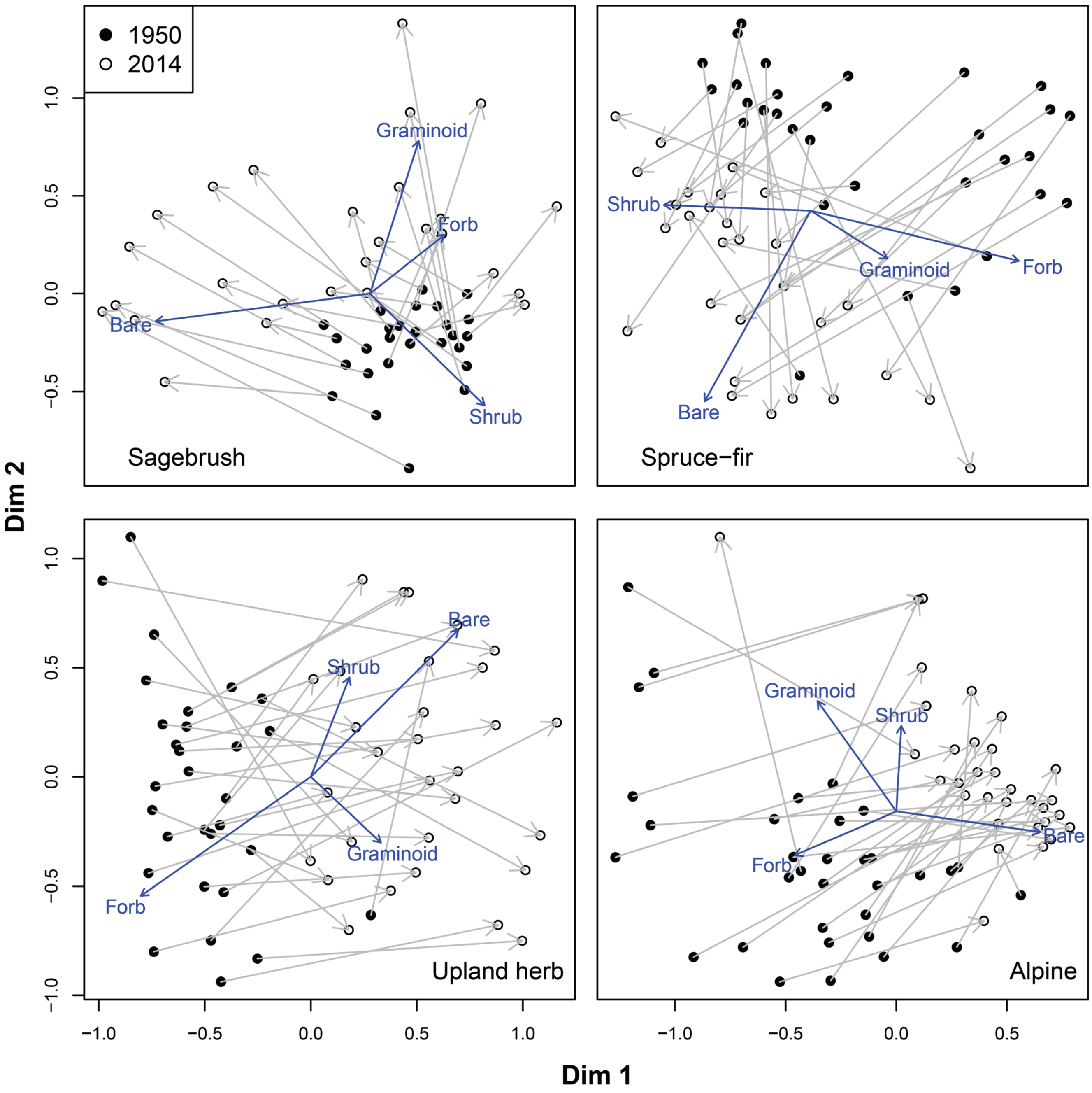

FIGURE 3. NMDS ordinations of paired sites in the two sampling periods for each community type. Vector fits for the proportion of three growth forms (forbs, graminoids, and shrubs) and bare area for each community from the resurvey are fit on each ordination. Arrow direction indicates increasing proportions of growth forms and bare area. Faint arrows connect paired sites between sampling periods. Final stress for the 3D NMDS solutions ranged from 0.12 to 0.18.

Species characteristic of upland-herbaceous subalpine meadows (mean elevations = 3300–3700 m; Table 3) showed wide variation in mean elevation and range shifts (–466 to +268 m) between 1950 and 2014. Overall these species occurred at slightly lower elevations in the recent survey (mean elevation difference = –38.6 m; $t_{(26)} = 2.12$, $p = 0.02$). Many of these species expanded their ranges into new community types, but there was no clear pattern to the direction of movement. Species typical of alpine communities, with mean elevations >3700 m (Table 3) did not significantly shift their mean elevations between surveys (mean elevation difference = –21.0 m; $t_{(13)} = 1.21$, $p = 0.123$). Most of these species were found exclusively in alpine communities in 1950, but expanded their ranges downward to include upland-herb communities, and were found at somewhat lower mean elevations in 2014 (Table 3).

DISCUSSION

Dramatic vegetation shifts have occurred over the past 65 years in four Rocky Mountain plant communities originally described by Langenheim (1962). We found significant changes in species richness, diversity, relative abundance of species and growth forms, and shifts in species elevational ranges that are largely consistent with patterns expected with a warmer, drier climate. Sites within communities followed similar trajectories of compositional change (Fig. 3), suggesting that the observed community changes are driven by common underlying causes. Changes in diversity and species' distributions were largely consistent with other studies showing that climate change results in the upward movement of species, and that diversity changes most dramatically in water-limited areas at lower elevations (Kelly and Goulden, 2008; Harrison et al., 2010) and temperature-limited, subalpine and alpine zones (Pauli et al., 2003; Sproull et al., 2015). Large increases in the proportion of bare ground in all communities suggest decreases in productivity and vegetative cover over time (cf. Currie et al., 2004).

Changes in Richness and Diversity

In contrast to our prediction based on other studies (Kammer et al., 2007; Wipf et al., 2013), we did not detect an increase in average species richness or diversity in the alpine community (3700–4000 m; Table 1). In fact, α-diversity declined significantly between 1950 and 2014. This loss of alpine plant diversity coincides with a large loss of vegetative cover and consequent reduction in the abundance of dominant species at alpine sites (Table 2, part d). Few species extended their ranges upward into alpine sites, but many typical alpine species extended their ranges downward into the upland-herb community (Table 3). A lack of increased alpine diversity could be caused by snow and nutrient-limited growing conditions that stall upward species expansion (Kammer et al., 2007). Alternatively, lower snowpack and earlier snowmelt in the region (Inouye and Mcguire, 1991; CaraDonna et al., 2014) could cause exposed alpine sites on ridges and unstable slopes to become warmer and more water-limited during the growing season, more like low elevation sites.

The sagebrush and spruce-fir communities saw a reduction in species richness and diversity as might be expected for lower elevation, water-limited sites (Kelly and Goulden, 2008; Harrison et al., 2010; Table 1). The relative abundance of the dominant species declined (Table 2), and a number of species shifted their elevational distributions upward into new habitats (Table 3). This supports the prediction that climate change will cause lower montane species to expand upward while alpine specialists decline due to increased competition from migrants or loss of suitable habitat (Pauli et al., 2003; Harrison et al., 2010). An increase in introduced and weedy species, such as *Bromopsis inermis* and *Oligosporus dracunculus* at sagebrush sites may reflect effects of range management practices as well as a warmer, drier climate. Vertebrate herbivores may also reduce the abundance and diversity of highly palatable species, such as *Pedicularis* spp. in the spruce-fir understory (Table 2, part b).

Only the upland-herb community saw significant increases in species richness and diversity over time (Table 1). This community was also associated with the greatest changes in dominant species and species elevation shifts, both up and down. A number of species common to the alpine sites in 1950 actually became more abundant in lower elevation, upland-herb sites by 2014, while other species moved out of forested sites and became more common in subalpine meadows (Table 3). Grasses, including smooth brome, assumed greater dominance in upland-herb communities, while sedges declined over time (Table 2, part c).

Because of changes in diversity, species' abundance, reduced vegetative cover, and species' elevational shifts, sites within all four community types have become more heterogeneous in composition, and communities less distinct than those described by Langenheim (1953, 1962; Table 1). When the effect of variation in species richness was omitted, all four communities became significantly more heterogeneous over time (Table 1), suggesting that differences in species richness is not the main driver of increased heterogeneity. The topographical isolation and high elevation (>2500 m) of the study area may somewhat limit the introduction of new species (Damschen et al., 2010). Instead, species distributions are reshuffling within the regional species pool as increased temperatures increase mortality (possibly indicated by lower relative abundance and constancy) and alter microhabitats within communities (Kelly and Goulden, 2008; Venn et al., 2014).

Changes in Community Composition

The observed shifts in the community centroids (Fig. 2) and sites within communities (Fig. 3) between surveys reflect the underlying changes in the species composition of sites and communities. These changes correspond to the gain and loss of species, and rank order changes in species abundance. There was an overall decrease in the relative abundance and constancy of the most common species in each community (Table 2). This had the effect of decreasing dominance, while increasing the heterogeneity among sites within communities.

A competitive advantage of graminoid and shrub growth forms is predicted in some climate change scenarios for montane environments (Bahre and Shelton, 1993; Harte and Shaw, 1995; Rudgers et al., 2014), while large declines in herbaceous (forb and grass) cover and richness have been documented in other studies (Damschen et al., 2010; Harrison et al. 2010). We found that the relative abundance of forbs decreased significantly between surveys in all but the sagebrush community. Conversely, shrub abundance increased in all but the lowest elevation (sagebrush) community (Fig. 4). The significant increase of shrubs in the spruce-fir community (Fig. 4) and movement of sites toward increasing shrub abundance in the intracommunity ordinations (Fig. 3) may indicate that this community is moving toward a more typical conifer understory assemblage dominated by shrubs and shade-tolerant vegetation such as *Arnica cordifolia* (Table 2; Coop et al., 2014). Increased shrub abundance in the alpine community is mainly due to the greater abundance and dominance of *Salix* spp. (Table 2). Graminoids increased in abundance in the sagebrush community between surveys (Fig. 4, Table 2, part a). In the spruce-fir community, sedges became more abundant (Table 2), while grasses increased slightly in abundance over time. Sedge abundance declined in both the upland-herb and alpine communities, while grasses tended to increase (Fig. 4, Table 2, parts c and d). This outcome accords with a climate-warming experiment conducted near our study sites at the RMBL (Rudgers et al., 2014). Those investigators found that, under ambient conditions, the frequency of sedges decreased and grasses increased over a 20-year period in control plots compared to warming plots.

Besides climate warming, several alternative causes could underlie changes in community composition over the past 65 years at our sites. These include logging, fire, introduced/invasive species, herbivory by native and nonnative ungulates, and timing of censuses (Bahre and Shelton, 1993; Coop et al., 2014). No substantial wildfires or logging activities have occurred in the study area since mining operations ceased in the early 1900s (Langenheim, 1962; Coop et al., 2014), although postdisturbance succession may be slow in high-elevation and/or water-limited habitats (Pauli et al., 2003). Livestock grazing has decreased since the original study (Coop et al., 2014), yet historical grazing could have contributed to the increased abundance of grasses within the sagebrush community (Table 2, Fig. 4). The increase in *Bromopsis inermis* probably results from its intentional introduction as a forage grass in sagebrush and upland-herb communities in western North America. In contrast to livestock, populations of wild ungulates have increased over time (Coop et al., 2014). Herbivory, from nondomesticated species, may have driven substantial decreases of highly palatable genera like *Pedicularis* in spruce-fir sites (Table 2). Given the constraints of our data, however, it is challenging to ascertain if grazing is having an appreciable impact on community composition (Damschen et al., 2010; Coop et al., 2014). Aside from *B. inermis* and perhaps *Poa pratensis*, introduced species (nine total, see Appendix Tables A1 and A2) were uncommon, occurred with low abundance, and probably had a minor effect on altering community composition.

TABLE 3

Abundance–weighted mean elevations (m) for species observed at ≥5 sites (mean = 19.6 sites per survey period) in both the original (1950) and new (2014) surveys. Positive (+) and negative (–) change (Δ) in elevation between surveys; the range of site elevations, and occupancy of species in each community are indicated (SB: sagebrush (mean elevation = 2827 m, range = 2528–3110 m); SF: spruce–fir, (mean = 3231 m, range = 3001–3520 m); UH: upland–herbaceous (mean = 3506 m, range = 3124–3850 m); AL: alpine (mean = 3765 m, range = 3549–4013 m) for both surveys.

	Mean elevation (m)			Elevation range (community occupancy)	
Species	1950	2014	Δ	1950	2014
Maianthemum stellatum	2663	3134	+471	2584–3110 (SB)	2684–3410 (SB,SF)
Symphoricarpos rotundifolius	2751	3011	+260	2528–3110 (SB)	2542–3301 (SB,SF)
Rosa woodsii	2757	2981	+223	2758–3110 (SB)	2529–3429 (SB,SF,UH)
Castilleja linariaefolia	2774	2803	+30	2542–3081 (SB)	2542–3081 (SB)
Ipomopsis aggregata	2798	3259	+462	2529–3110 (SB)	2684–3735 (SB,UH,A)
Vicia americana	2798	3106	+308	2584–2962 (SB)	2584–3850 (SB,SF,UH)
Chrysothamnus spp.	2807	2835	+28	2542–3052 (SB)	2584–2929 (SB)
Mahonia repens	2815	2915	+100	2529–3110 (SB)	2584–3219 (SB,SF)
Penstemon strictus	2818	3096	+278	2542–2962 (SB)	2599–3606 (SB,UH)
Amelanchier alnifolia	2820	2788	–32	2529–3110 (SB)	2529–2929 (SB)
Linum lewisii	2820	3166	+346	2542–3052 (SB)	2684–3441 (SB,SF,UH)
Campanula parryi	2822	2873	+51	2751–2976 (SB)	2792–2976 (SB)
Seriphidium tridentatum	2823	2809	–14	2529–3110 (SB)	2529–2976 (SB)
Agastache urticifolia	2837	3026	+189	2542–3110 (SB)	2599–3652 (SB,UH)
Phleum pratense	2840	2863	–113	2529–2962 (SB)	2684–2873 (SB)
Bromus frondosus	2855	2855	+23	2542–3110 (SB)	2542–3110 (SB)
Eriogonum umbellatum	2854	2874	+21	2529–3110 (SB)	2529–3658 (SB,UH,A)
Boechera stricta	2877	3324	+447	2542–3110 (SB)	2587–3872 (SB,SF,UH,A)
Erigeron speciosus	2878	3079	+201	2529–3110 (SB)	2542–3672 (SB,SF,UH,A)
Artemisia frigida	2884	2803	–80	2542–3110 (SB)	2587–2910 (SB)
Galium septentrionale	2932	2964	+33	2584–3110 (SB)	2542–3653 (SB,SF,UH)
Festuca thurberi	2972	3073	+101	2529–3530 (SB,UH)	2736–3850 (SB,SF,UH,A)
Eremogone congesta	3068	3158	+90	2529–3840 (SB,UH,A)	2584–3831 (SB,SF,UH,A)
Lathyrus leucanthus	3089	3087	–2	2529–3530 (SB,SF,UH)	2542–3672 (SB,SF,UH)
Taraxacum officinale	3090	3133	+43	2542–3627 (SB,UH)	2684–3658 (SB,SF,UH)
Koeleria macrantha	3103	3020	–83	2835–3273 (SB,SF)	2529–3667 (SB,UH,A)
Paxistima myrsinites	3112	3175	+63	2529–3273 (SB,SF)	3039–3317 (SF)
Senecio triangularis	3160	3401	+240	3042–3520 (SF)	3053–3672 (SF,UH)
Heterotheca villosa	3167	3384	+217	2761–3850 (SB,SF,UH,A)	2599–3658 (SB,UH)
Thalictrum fendleri	3190	3416	+226	3114–3434 (SF)	2834–3735 (SB,SF,UH,A)
Aquilegia elegantula	3192	3178	–14	3042–3410 (SF)	3042–3398 (SF)
Campanula rotundifolia	3199	3387	+188	2587–3627 (SB,UH)	2801–3672 (SB,UH)
Mertensia ciliata	3227	3509	+282	3039–3520 (SF)	3271–3850 (SF,UH)
Ribes wolfii	3232	3249	+17	3002–3520 (SF)	3154–3520 (SF)
Arnica cordifolia	3234	3217	–17	3002–3520 (SF)	3039–3619 (SF,UH)
Chamerion danielsii	3234	3211	–23	3053–3410 (SF)	3039–3436 (SF)
Moneses uniflora	3254	3251	–3	3039–3436 (SF)	3132–3165 (SF)
Geranium richardsonii	3256	3226	–33	3042–3520 (SF)	2792–3436 (SB,SF)
Ribes montigenum	3256	3256	0	3041–3520 (SF)	2599–3520 (SF)
Polemonium pulcherrimum	3258	3342	+84	3002–3520 (SF)	3042–3850 (SF,UH)

TABLE 3

Continued

	Mean elevation (m)			Elevation range (community occupancy)	
Species	1950	2014	Δ	1950	2014
Fragaria virginiana	3265	3378	+113	3002–3672 (SF,UH)	2856–3751 (SB,SF,UH,A)
Carex geyeri	3269	3294	+25	3039–3520 (SF)	3039–3627 (SF,UH)
Achillea millefolium	3317	3217	–100	2542–3898 (SB,SF,UH,A)	2542–3850 (SB,SF,UH,A)
Bromelica spectabilis	3328	3124	+120	3124–3554 (UH)	2801–3672 (SB,SF,UH)
Pseudocymopterus montanus	3366	3498	+132	3002–3850 (SF,UH)	2751–3872 (SB,SF,UH,A)
Bromopsis ciliata	3392	3291	–101	3132–3658 (SF,UH)	2792–3672 (SB,SF,UH)
Helianthella quinquenervis	3398	3326	–72	2529–3850 (SB,UH)	2542–3672 (SB,SF,UH)
Penstemon whippleanus	3414	3682	+268	3042–3627 (SF,UH)	3371–3850 (UH,A)
Aquilegia coerulea	3420	3341	–79	3124–3619 (UH)	3132–3695 (SF,UH,A)
Psychrophila leptosepala	3434	3348	–86	3042–3672 (SF,UH)	3053–3658 (SF,UH)
Castilleja rhexiifolia	3447	3342	–105	3039–3850 (SF,UH)	2751–3671 (SB,SF,UH,A)
Delphinium barbeyi	3462	3469	+7	3042–3850 (SF,UH)	2873–3672 (SB,SF,UH)
Agoseris glauca	3463	2997	–466	3361–3672 (UH)	2529–3627 (SB,SF,UH)
Ligusticum porteri	3468	3436	–43	3002–3850 (SF,UH)	2599–3615 (SB,SF,UH)
Anticlea elegans	3480	3273	–207	3052–3850 (SF,UH)	2929–3872 (SB,SF,UH,A)
Castilleja miniata	3482	3376	–106	3039–3850 (SF,UH)	2839–3735 (SB,SF,UH,A)
Elymus trachycaulus	3493	3682	+189	2529–4013 (SB,UH,A)	2835–4004 (SB,UH,A)
Erigeron elatior	3504	3457	–48	3124–3658 (UH)	3053–3850 (SF,UH)
Frasera speciosa	3520	3375	–145	3371–3627 (UH)	2873–3612 (SB,SF,UH)
Senecio crassulus	3532	3573	+41	3124–3850 (UH)	3124–3672 (SF,UH)
Erigeron glacialis	3558	3582	+24	3042–4004 (SF,UH,A)	3368–3898 (SF,UH,A)
Trollius albiflorus	3560	3400	–161	3370–3672 (UH)	3053–3652 (SF,UH)
Erigeron coulteri	3564	3569	+4	3366–3850 (UH)	3124–3850 (UH)
Tolmachevia integrifolia	3568	3430	+31	3430–3672 (UH)	3368–3850 (UH,A)
Sibbaldia procumbens	3575	3615	+40	3361–3898 (UH,A)	3361–3840 (UH,A)
Erythronium grandiflorum	3577	3439	–138	3361–3850 (UH)	3132–3627 (SF,UH)
Calamagrostis purpurascens	3578	3580	+3	3366–3850 (UH)	3366–3850 (UH)
Bistorta bistortoides	3654	3639	–14	3361–3898 (UH,A)	2929–3839 (SB,SF,UH,A)
Sedum lanceolatum	3682	3655	–27	3430–3672 (UH,A)	3530–3840 (UH,A)
Acomastylis rossii	3712	3730	+18	3363–4013 (UH,A)	3362–3898 (UH,A)
Potentilla nivea	3726	3661	–64	3549–4013 (A)	3124–3898 (UH,A)
Oreoxis alpina	3732	3803	+72	3629–4013 (A)	3629–4013 (A)
Dryas octopetala	3756	3791	+35	3549–3898 (A)	3645–3874 (A)
Silene acaulis	3759	3770	+11	3549–4013 (A)	3409–4013 (UH,A)
Polemonium viscosum	3762	3867	+105	3629–4013 (A)	3740–4004 (A)
Anemone multifida	3767	3719	–49	3629–4013 (A)	3408–3875 (UH,A)
Phacelia sericea	3768	3677	–91	3629–3898 (A)	3436–3875 (UH,A)
Smelowskia calycina	3786	3815	+29	3549–4013 (A)	3409–3898 (UH,A)
Erigeron pinnatisectus	3794	3726	–68	3629–4013 (A)	3764–4013 (UH,A)
Ivesia gordonii	3795	3702	–93	3642–4004 (A)	3409–3850 (UH,A)
Rydbergia grandiflora	3798	3747	–51	3629–4013 (A)	3592–3898 (UH,A)
Elymus scribneri	3807	3715	–93	3629–4013 (A)	3124–4004 (UH,A)
Artemisia scopulorum	3814	3759	–55	3629–4013 (A)	3591–4004 (UH,A)

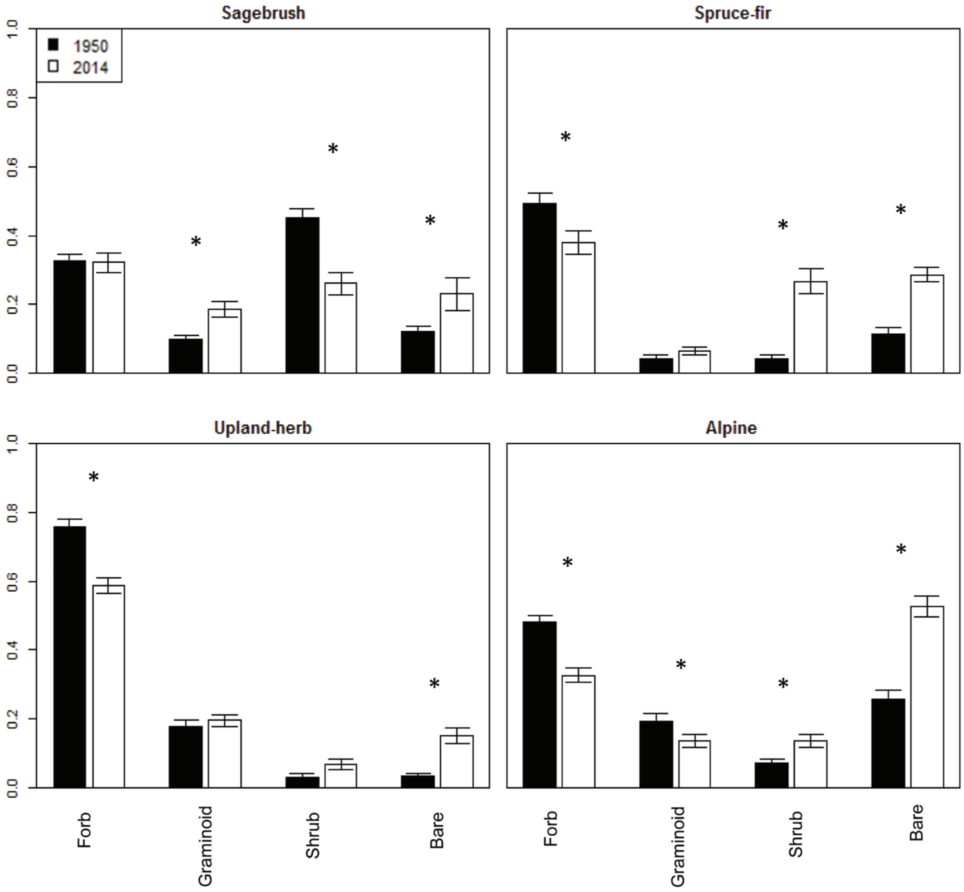

FIGURE 4. Average relative proportions of forb, shrub, and graminoid (grasses, rushes, and sedges) species and bare area in each community type from both the original and the new survey. Errors are standard errors of the mean. Asterisks denote significant ($\alpha = 0.05$) differences between surveys using paired *t*-tests.

The timing of the censuses could also affect differences in community composition between survey periods (Price and Waser, 2000). To address this issue, we note that (1) early- and late-flowering species occurred in both surveys, and (2) we observed almost all the species found in the original survey in our resurvey. In addition, increased length and advanced start of the growing season have been reported in long-term studies of flowering phenology in the East River Basin (Inouye and Mcguire, 1991; CaraDonna et al., 2014). As a result, early-flowering species in this study could be especially vulnerable to frost damage and asynchrony with pollinators and consequently become less well represented over time (CaraDonna et al., 2014).

Shifts in Species' Elevational Distributions

As predicted for many climate-warming scenarios (Wipf et al., 2013; Venn et al., 2014), we observed a general upward shift in mean elevation for the 83 species that could be compared between surveys (Table 3), although the magnitude and direction of elevation change differed among species characteristic of different community types and elevational zones. Plants from lower elevations tended to shift their distributions upward more strongly than species from higher elevation sites and communities. This is in agreement with other studies noting large upward shifts of species from low-elevation, water-limited sites in response to climate warming (Van de Ven et al., 2007; Kelly and Goulden, 2008). Species from mid-elevation upland-herb communities showed a net reduction in mean elevation (–39 m), but also saw the highest degree of in- and out-migration of species to different community types (Table 3). These meadow communities occur over a wide range of elevations, which may provide a wide array of suitable microhabitats for migrants from other elevations and communities. Species characteristic of alpine communities above 3700 m did not shift their distributions upward as expected (Pauli et al., 2003; Wipf et al., 2013). Rather, many taxa noted only in the alpine in 1950 expanded their ranges downward into upland-herb communities (Table 3). Although growing season may be extended in alpine communities, earlier snowmelt and warmer, drier conditions on alpine ridges and scree slopes could drive species distributions downward into appropriate microhabitats in subalpine meadows.

CONCLUSIONS

The patterns of vegetation change over a 65-year period, identified in this study—for example, loss of species diversity, reduced species abundance, reduced vegetation cover, upward shifts in species ranges and mean elevations, loss of forbs and increases of grasses and shrubs—are all indicative of the effects of climate warming in montane environments (Van de Ven et al., 2007; Rudgers et al., 2014; Sproull et al., 2015). However, multiple nonclimatic factors and species interactions that could not be considered in our analyses can also lead to vegetation change over time (Kammer et al., 2007). Thus, our results should not be ascribed solely to the effects of climate change (Currie et al., 2004). That the four communities were not affected equally suggests that other spatially heterogeneous factors such as microclimatic conditions, substrate, slope, and aspect further drive changes in species diversity and abundance among sites and communities (Price and Waser, 2000; Sproull et al., 2015). Species from the low-elevation, water-limited sagebrush community saw the greatest upward shift in species elevational ranges (cf. Kelly and Goulden, 2008; Harrison et al., 2010). The alpine community did not experience the predicted increase in species richness noted in other alpine regions (Pauli et al., 2003; Wipf et al., 2013). The alpine zone of the East River Basin is characterized by narrow ridges and steep, unstable slopes that may respond differently to climate warming than alpine tundra of other regions. The movement of many alpine species' ranges downward into upland-herb meadows suggests that the alpine may not be a refuge for lower elevation species with continued climate warming. The use of historical ecological data for comparative studies is a valuable tool for assessing and predicting effects of climate change and other factors on species and communities (Kammer et al., 2007; Sproull et al., 2015). We hope that future studies will continue to monitor Langenheim's sites in the East River Basin to document changes in plant communities within the study area or apply these data, for comparative purposes, to similar ecosystems worldwide.

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