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RESEARCH ARTICLE

Mapping foodscapes and sagebrush morphotypes with unmanned aerial systems for multiple herbivores

Peter J. Olsoy · Jennifer S. Forbey · Lisa A. Shipley · Janet L. Rachlow · Brecken C. Robb · Jordan D. Nobler · Daniel H. Thornton

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Abstract

Context The amount and composition of phytochemicals in forage plants influences habitat quality for wild herbivores. However, evaluating forage quality at fine resolutions across broad spatial extents (i.e., foodscapes) is challenging. Unmanned aerial systems (UAS) provide an avenue for bridging this gap in spatial scale.

Objectives We evaluated the potential for UAS technology to accurately predict nutritional quality of sagebrush (*Artemisia* spp.) across landscapes. We mapped seasonal forage quality across two sites in Idaho, USA, with different mixtures of species but similar structural morphotypes of sagebrush.

Methods We classified the sagebrush at both study sites using structural features of shrubs with object-based image analysis and machine learning and linked this classification to field measurements of phytochemicals to interpolate a foodscape for each phytochemical with regression kriging. We compared fine-scale landscape patterns of phytochemicals between sites and seasons.

Results Classification accuracy for morphotypes was high at both study sites (81–87%). Forage quality was highly variable both within and among sagebrush morphotypes. Coumarins were the most accurately mapped ($r^2 = 0.57$–0.81), whereas monoterpenes were the most variable and least explained. Patches with higher crude protein were larger and more connected in summer than in winter.

Conclusions UAS allowed for a rapid collection of imagery for mapping foodscapes based on the phytochemical composition of sagebrush at fine scales but relatively broad extents. However, results suggest that a more advanced sensor (e.g., hyperspectral camera) is needed to map mixed species of sagebrush or to directly measure forage quality.

Keywords Crude protein · Landscape patterns · Plant secondary metabolites · Regression kriging · Spatial patterns · Unmanned aerial systems

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P. J. Olsoy (✉) · L. A. Shipley · D. H. Thornton
School of the Environment, Washington State University,
Pullman, WA 99164, USA
e-mail: peterolsoy@gmail.com

J. S. Forbey · B. C. Robb · J. D. Nobler
Department of Biological Sciences, Boise State
University, Boise, ID 83725, USA

J. L. Rachlow
Department of Fish and Wildlife Sciences, University of
Idaho, Moscow, ID 83844, USA

Introduction

Wild herbivores must acquire sufficient nutrients while avoiding or minimizing ingestion and absorption of potentially toxic plant secondary metabolites (PSMs) (Hebblewhite and Merrill 2009; Camp et al. 2015; Crowell et al. 2018). These phytochemicals vary within and among plant species and thus are patchily distributed across the landscape. Distributions of nutrients and PSMs influence diet quality of herbivores and interact with other aspects of habitat quality, such as refuge from predators or thermal stress, to affect habitat use and distribution of herbivores. Although most herbivores are relatively mobile, they also make foraging decisions related to forage quality at fine spatial scales (Moore et al. 2010; Frye et al. 2013) that can have demographic consequences (DeGabriel et al. 2008). Thus, mapping different aspects of forage quality (e.g., nutrients, digestibility, or toxicity) at fine spatial resolutions across broad extents (i.e., creating foodscapes) could advance understanding of factors influencing foraging behavior, movement, spatial distributions, and population dynamics of herbivores. Despite this importance, mapping forage quality at meaningful scales is largely limited by costly, time-intensive fieldwork and chemical analyses. Currently, ecologists rely on proxies for forage quality such as the normalized difference vegetation index (NDVI) from coarse-resolution remote sensing data (e.g., Landsat or MODIS satellites) or ignore forage quality altogether in place of more generalizable structural metrics. These proxies index “greenness” and may track phenological changes in forage over time and space (Pettorelli et al. 2006, 2011), but they do not always capture functional traits that herbivores select or avoid, particularly at finer spatial scales such as individual plants where foraging decisions are made (Moore et al. 2010; Frye et al. 2013; McArthur et al. 2019).

Unmanned aerial systems (UAS) offer a remote sensing platform for gathering fine-scale environmental data across relatively broad spatial extents, fitting a niche between fine-resolution field data collected at few locations and coarse-resolution but broad-extent satellite systems. UAS have emerged as a viable platform for rapid, continuous, and relatively inexpensive collection of fine-resolution imagery (Anderson and Gaston 2013). Part of the registration and processing of UAS imagery uses structure from motion (SfM) photogrammetry to produce 2.5-dimensional point clouds and structural models of the landscape (Dandois and Ellis 2013; Olsoy et al. 2018). These structural models have been used to measure shrub height and canopy cover (Olsoy et al. 2018), biomass (Cunliffe et al. 2016), vegetation diversity (Getzin et al. 2012), and forage quantity (Forsmoo et al. 2018), but have not yet captured forage quality. One potential avenue to map forage quality with UAS, including those that only collect color imagery, is to use the metrics generated from SfM to scale up limited field-based measures of phytochemicals.

The sagebrush (*Artemisia* spp.) ecosystem in North America lends itself to mapping foodscapes because its structural complexity is relatively simple with discrete patches with one dominant shrub species, big sagebrush (*Artemisia tridentata*), that provides both cover and food for multiple specialist (e.g., pygmy rabbits [*Brachylagus idahoensis*], and greater sage-grouse [*Centrocercus urophasianus*]) and generalist (e.g., mountain cottontail [*Sylvilagus nuttallii*]) herbivores. Sagebrush-dominated areas are characterized by patches of sagebrush plants with phenotypically distinct structures, or morphotypes, which vary within species based on micro-topography, soil temperature, and soil moisture (Rosentreter 2005; Dumroese et al. 2015). These morphotypes have distinct structural differences that are detectable with UAS SfM (Olsoy et al. 2018). Although some morphological variation can be caused by environmental conditions, it can also arise from genetic variation including hybridization and introgression of sagebrush species and subspecies (McArthur et al. 1988). Phytochemicals, particularly the concentration of volatile compounds such as monoterpenes and the presence or absence of coumarins, are traits that also vary based on environmental conditions (Jaeger et al. 2016) and taxonomy of sagebrush. In addition, phytochemical characteristics can differ seasonally. Concentrations of monoterpenes are highest during summer and lowest during winter (Cedarleaf et al. 1983; Kelsey 1984; Rosentreter 2005). Monoterpenes and coumarin may influence palatability for some herbivores (Rosentreter 2005; Forbey et al. 2013; Ulappa et al. 2014) and also respond to damage by herbivores (Karban et al. 2014). Given the high spatio-temporal variability in forage quality in sagebrush ecosystems (Miller and Shultz 1987), mapping such variability and patchiness is an essential component of understanding how forage quality changes relative to climate, management by humans, and interactions with herbivores. A better understanding of sagebrush communities is increasingly critical given that sagebrush systems have decreased by over half from their historic extent, and many species rely on management activities related to sagebrush cover and nutritional quality (Rowland et al. 2006).

Pygmy rabbits are a species of conservation concern that depend on sagebrush for both cover and food, with sagebrush comprising 99% of their diet in winter and up to 50% in summer (Thines et al. 2004). Greater sage-grouse are also sagebrush specialists that consume diets of up to 100% sagebrush in winter (Wallestad et al. 1975). Mountain cottontails are generalist herbivores that opportunistically forage on sagebrush (MacCracken and Hansen 1984), but often discard the leaves and consume the less toxic stems (Crowell et al. 2018). All three herbivore species select diets based on trade-offs between nutritional constituents (e.g., crude protein, plant fiber) and PSMs (e.g., coumarins, monoterpenes) (Frye et al. 2013; Ulappa et al. 2014; Camp et al. 2015, 2017; Crowell et al. 2018; Nobler et al. 2019), generally selecting for higher crude protein and lower concentrations of PSMs. However, herbivores may trade-off phytochemicals differently. Pygmy rabbits tolerate higher concentrations of monoterpenes relative to concentrations of fiber than mountain cottontails (Crowell et al. 2018), whereas mountain cottontails will consume higher fiber to avoid monoterpenes (Crowell et al. 2018).

In this study, our objectives were to (1) evaluate the spatial pattern of phytochemicals known to influence forage quality at scales that are relevant to herbivores; (2) compare landscape patterns of phytochemicals between summer and winter when the foraging conditions for herbivores differ; and (3) determine how the structural morphotype and species classification of sagebrush influence our ability to map phytochemicals. To achieve these objectives, we used UAS to map phytochemicals and create foodscapes across two contrasting sagebrush-dominated landscapes that contained similar structural morphotypes, but differed in sagebrush species composition.

Materials and methods

Study sites

We created foodscapes at two sites in Idaho, USA. The “Camas” site (43° 14′ 28″ N, 114° 19′ 4″ W, elevation 1465–1480 m) was a 55-ha area located in south-central Idaho in the higher plain region bordering the Snake River Plain. Average temperatures were − 7.6 °C in January and 12.8 °C in June, and the site received 23.5 cm precipitation annually (WRCC 2016). The “Cedar Gulch” site (44° 41′ 57″ N, 113° 17′ 12″ W, elevation 1890–1940 m) was a 200-ha area in east-central Idaho west of the Continental Divide, approximately 180-km northeast of Camas. Average temperatures were − 6.9 °C in January and 14.9 °C in June, and the site received 32.8 cm precipitation annually (WRCC 2016). Both of our study landscapes were occupied to some extent by pygmy rabbits, greater sage-grouse, and mountain cottontails. The landscapes were characterized by mima mounds (Tullis 2005), which are earthen mounds with taller shrubs and deeper soils used by pygmy rabbits to dig their burrow systems that are also used secondarily by mountain cottontails. Both study sites had similar structural morphotypes with the dominant vegetation at both study sites being Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*), which occurs both on mima mounds (hereafter, on-mound), and off mima mounds (hereafter, off-mound), and off-mound dwarf (hereafter, dwarf) where the specific species of dwarf plants varied between sites. At Camas, the dwarf patches were composed of a different species of sagebrush (low sagebrush [*A. arbuscula*]), whereas at Cedar Gulch the dwarf patches were primarily low-growing Wyoming big sagebrush mixed with black sagebrush (*A. nova*). These dwarf species could be identified on the ground morphologically, but from the air they were indistinguishable and grouped together based on structural similarity.

Collecting and analyzing phytochemicals in sagebrush

To quantify the phytochemicals in sagebrush leaves known to influence foraging by herbivores and that vary among plants, patches (i.e., morphotypes) and landscapes, we first selected patches for sampling using a stratified random design to distribute samples evenly among the three structural morphotypes of sagebrush: on-mound, off-mound, and dwarf. Patches were defined as a single morphotype with a radius 3–6 m and at least 20 m away from another patch (n = 70 at Camas and n = 95 at Cedar Gulch). At each patch, we sampled three (single-species patches) to six (multi-species patches) plants at random. We clipped plant samples to collect about 3 g (wet weight, WW) of stems and leaves, but no more than 25% of the overall biomass, of each plant. We collected only the parts of the plant that an animal (e.g., pygmy rabbit or greater sage-grouse) could consume, and clipped representative sprigs from all sides of the plant. Plant material was stored on ice during transport to the lab where they were stored at − 20 °C for later analysis. Leaves and stems were ground in liquid nitrogen (∼ 2 mm) and immediately subsampled for crude protein, coumarin, and monoterpene analysis (Frye et al. 2013; Ulappa et al. 2014).

For crude protein, a subset of 1–2 g (WW) of each ground sample was dried at 64 °C to a constant dry weight (at least 48 h) and analyzed for total nitrogen content at Dairy One Forage Labs (Ithaca, NY) using the combustion method. Total nitrogen (%) values were converted to crude protein by multiplying each value by 6.25, which controls for non-protein nitrogen (Robbins 1983).

For coumarins, a subset of 50 mg (WW) of each ground sample was extracted in 1.0 mL 70% EtOH and the filtered extract was stored at − 20 °C. Total coumarin content was measured from the extract using a colorimetric assay in clear flat-bottomed 96-well plates run on a spectrophotometric plate reader set to measure fluorescence at an excitation wavelength of 350 nm and emission wavelength of 469 nm (Fremgen 2015). We used a standard curve of scopoletin to quantify coumarin content for each sample in micromoles, and we standardized samples by their dry weight (μmol/mg DW) (Fremgen 2015). Sagebrush varies in concentrations of coumarins, a subclass of phenolic compounds, depending on species and growing conditions (e.g., mountain big sagebrush [*A. t. vaseyana*], black sagebrush, and low sagebrush) (McArthur et al. 1988; Rosentreter 2005; Richardson et al. 2018), and act as an indicator of palatability for some sagebrush-obligate species, such as greater sage-grouse (Rosentreter 2005).

For monoterpenes, a subset of 100 mg (WW) of each ground sample was transferred to a headspace vial for monoterpene analysis and stored at − 20 °C. We quantified individual and total monoterpene content through the use of headspace gas chromatography (GC) (Agilent 7694 Headspace Sampler, Agilent 6890 Series GC). We analyzed the individual monoterpenes detected prior to the retention time of 24 min. After 24 min, the baseline begins to drift and individual peaks and areas cannot reliably be quantified. Using external standards, we identified the compounds 1,8-cineole, 3-carene, α-phellandrine, α-pinene, β-pinene, borneol, camphene, camphor, p-cymene, and terpinolene. For the purpose of this study, we only examined the concentrations of 1,8-cineole, camphor, and ß-pinene because of their effect on diet selection in previous studies of pygmy rabbit, greater sage-grouse, and mountain cottontail (Frye et al. 2013; Ulappa et al. 2014; Crowell et al. 2018; Nobler et al. 2019). We also quantified total monoterpene content and total number of compounds (i.e., separate peaks in the chromatogram) detected per sample before 24 min retention time. Concentration was calculated as area under the curve (AUC) for each chemical peak detected. For each sample, peaks less than 1% of the total AUC were discarded. All samples were standardized for their dry weight (AUC/mg DW), and we converted these concentrations to percentages of DW plant material using the average mg/AUC from 7 to 9 known standards that were quantified during each GC run where we the exact amount of monoterpene (mg) added to the vial and resulting AUC of that monoterpene are known. Overall phytochemical diversity was calculated as the Shannon diversity index of all individual monoterpene compounds present at greater than 1% of the total AUC (Fremgen 2015).

Collecting and analyzing UAS imagery

We conducted UAS flights in June 2013 at Camas and in June 2015 at Cedar Gulch with fixed-wing systems. For a detailed account of both flights, see Olsoy et al. (2018). Briefly, each flight was performed at approximately 100 m above ground level and resulted in more than 1000 color (RGB) photos. Photos were taken with a 10-MP Olympus E-420 camera (Olympus Corporation, Japan) on a University of Florida Nova 2.1 customized UAS (Burgess 2017) at Camas and a

12-MP Canon PowerShot S11 camera (Canon, USA) on a sensefly eBee (senseFly, Lausanne, Switzerland) at Cedar Gulch. We mosaicked the photos together in Agisoft PhotoScan v1.1.6 (Agisoft LLC, St. Petersburg, Russia) for Camas and Pix4D v3.4.21 (senseFly, Lausanne, Switzerland) for Cedar Gulch to produce a single seamless georeferenced orthomosaic (2.5–2.7 cm ground sampling distance) for each study site. We collected ground control points (84 at Camas and 49 at Cedar Gulch) with a sub-centimeter accuracy, survey-grade TopCon Hiper V receiver (Topcon, Livermore, California), which were used to improve image registration. During the image processing stage, we used structure from motion (SfM) (Dandois and Ellis 2013) to generate a dense point cloud and digital surface model representing the landscape surface height with horizontal accuracies of 0.027 m at Camas and 0.021 m at Cedar Gulch. Further processing details, including a complete list of processing parameters for both study sites is described in Olsoy et al. (2018). This processing resulted in a dense, high-resolution SfM-derived point cloud (148 points m^{-2} at Camas and 81 points m^{-2} at Cedar Gulch). The point cloud was classified into ground and vegetation points with the BCAL LiDAR Tools (https://www.boisestate.edu/bcal/tools-resources/bcal-lidar-tools; Streutker and Glenn 2006), and used to generate a 5-cm canopy height raster.

To classify the patches of each morphotype at each study sites (on-mound, off-mound, and dwarf), we used object-based classification with a machine learning classifier. First, we calculated a texture raster from the UAS canopy height raster. We aggregated the canopy height raster by a factor of five to more closely match the scale of a single shrub (25-cm pixel resolution), and generated the raw texture image by calculating the standard deviation in a 5-m circular moving window, the average radius of a mima mound. We removed high values by running a 2.5-m circular moving window minimum filter, and smoothed the texture raster with a 5-m circular moving window. Next, we segmented the texture image with Segment Mean Shift in ArcGIS 10.3 (ESRI, Redmond, CA) with spectral detail of 20, spatial detail of 3, and a minimum segment size of 20 pixels. We selected the highest level of spectral detail to discriminate between spectrally similar patches, but selected a low level of spatial detail to return a smoother output with larger patches and reduce "salt and pepper" noise. We performed a supervised classification with a support vector machine that was trained with 300 polygons at Camas and 650 polygons at Cedar Gulch. We generated training polygons by outlining areas of continuous, visibly distinguishable patches of each morphotype. We performed external validation with known morphotype locations from our field data collection patches at Camas (n = 70) and Cedar Gulch (n = 90), and we reported the classification accuracy in a confusion matrix including errors of omission, errors of commission, and overall accuracy.

To map phytochemicals across the landscape, we took advantage of differences in forage quality among morphotypes, and linked that with our UAS classification of morphotypes, while accounting for unmodeled variability in forage quality, to interpolate a foodscape with regression kriging (also called universal kriging of kriging with external drift; Hengl et al. 2004). A regression kriging model contains both a deterministic and stochastic component. The deterministic component of our model was a generalized least square (GLS) regression with morphotype as the predictor variable and explicitly accounted for a spherical correlation structure (corSpher) within the GLS model (Zuur et al. 2009). We extracted the residuals from the GLS model and checked assumptions for normality, homoscedasticity of variance, and stationarity. For the stochastic part of the model, we fitted a semivariogram to the residuals with a spherical covariance model using Cressie weights, and report the nugget, range, and partial sill. Semivariograms for all models are provided in Online Appendix A. Finally, we combined the GLS model with the semivariogram model to interpolate each forage quality variable across the study site with regression kriging. We assessed accuracy of our forage quality predictions with leave-one-out cross-validation (LOOCV) and reported the coefficient of determination (r^2) and root-mean-square error (RMSE). Regression plots for LOOCV prediction accuracy are provided in Online Appendix A.

To analyze the spatial patterning of forage quality, we determined relative high and low quality patches across the UAS landscape maps using threshold values based on the average values across the entire landscape in both summer and winter for each study site. Then, we calculated landscape metrics for the high and low-quality areas for each phytochemical in both summer and winter to evaluate spatial patterns of forage quality. In Fragstats 4.2 (McGarigal et al. 2012), we calculated patch density, largest patch index, mean patch size, standard deviation of patch size, area-weighted mean radius of gyration, and mean Euclidean nearest neighbor. The area-weighted mean radius of gyration, also called the correlation length, is the traversability of the map or the average distance an animal could travel from a random starting location (Keitt et al. 1997) and can be interpreted as the connectedness of the landscape along with largest patch index. We assessed overall fragmentation with patch density, mean patch size, and Euclidean nearest neighbor. Landscape metrics for high and low-quality patches were compared between seasons to identify possible patterns affecting forage quality, and therefore herbivore diets and predicted use of the foodscape by herbivores.

Results

Overall, phytochemistry of sagebrush was highly variable both within and among sagebrush morphotypes at both study sites (Table 1, Figs. 1 and 2). Crude protein was higher at Cedar Gulch than Camas in both summer and winter (Table 1, Fig. 1). In contrast, coumarins were higher at Camas than Cedar Gulch in both seasons, with most of the higher values found in the dwarf patches containing low sagebrush (Fig. 1). Concentrations of total monoterpenes, 1,8-cineole and camphor were also higher at Camas than Cedar Gulch, with the largest differences occurring in summer (Table 1, Figs. 1 and 2), whereas ß-pinene and phytochemical diversity were higher at Cedar Gulch than Camas in both seasons and across all morphotypes (Fig. 2).

We classified sagebrush morphotypes with the UAS imagery and assessed classification accuracy with external validation (Table 2). Camas had an overall classification accuracy of 81% (Table 2), whereas at Cedar Gulch the overall accuracy was 87% (Table 2). At both sites, classification errors occurred between off-mound and the other two morphotypes, but dwarf was never misclassified as on-mound, and on-mound was never misclassified as dwarf (Table 2). This misclassification could be due to off-mound patches being intermediate in structure between the other two morphotypes (Olsoy et al. 2018). The dominant morphotype at both sites was off-mound, but dwarf was more prevalent at Cedar Gulch than Camas (42% vs. 28%; Fig. 3). Also, much of the off-mound habitat at Cedar Gulch was on the east side of the site, whereas the rest of the study site was dominated by dwarf patches (Fig. 3).

When kriging across the landscape at the Camas site (Fig. 4), crude protein was predicted moderately well ($r^2 = 0.36$–0.38) (Table 3), whereas the kriging model predicted coumarins more accurately than other PSMs in both summer ($r^2 = 0.81$) and winter ($r^2 = 0.57$) (Table 3, Fig. 4), largely due to high separation among morphotypes in this variable (Table 3, Fig. 1). Total monoterpenes ($r^2 = 0.37$ and 0.51) (Fig. 4) and camphor ($r^2 = 0.53$ and 0.50) were also predicted moderately well at Camas. The phytochemical diversity index was predicted poorly ($r^2 = 0.28$ and 0.27), and 1,8-cineole showed no spatial autocorrelation and could not be kriged (Table 3). Coumarins showed the greatest amount of spatial autocorrelation with a range of 100–124 m, whereas most other variables had ranges of 50 m or less (Table 3).

At Cedar Gulch, morphotype explained little variation in forage quality of sagebrush, where only crude protein in summer and winter, and coumarins and monoterpenes in winter, had r^2 values of 0.1 or higher (Table 3). The semivariograms for 1,8-cineole and camphor in both seasons and coumarins in summer also demonstrated little to no spatial autocorrelation (Online Appendix A), so regression kriging was only performed for crude protein, coumarins in winter, total monoterpenes, and ß-pinene (Table 3).

The spatial patterns of forage quality at Camas differed between summer and winter, with summer having more high-quality patches that were more connected than winter. At Camas, we used a threshold of 10.0% crude protein, whereas Cedar Gulch had higher crude protein values during both seasons and had an average landscape value of 13.3%. For coumarins, the landscape average was 0.81 µmol/mg DW at Camas across both seasons, and at Cedar Gulch the landscape average was 0.46 µmol/mg DW in winter. The landscape averages for total monoterpenes were 0.92% for Camas and 0.45% for Cedar Gulch. In summer, patches of high nutritional quality (i.e., crude protein > 10.0%) made up 73% of the landscape with a mean patch size of 0.37 ha (± 0.38 SE), but declined to 27% of the landscape and 0.08 ha (± 0.01 SE) mean patch size in winter (Table 4, Fig. 5). The

Table 1 Summary statistics for phytochemicals including the nutrient crude protein, and plant secondary metabolites coumarins, total and individual (1,8-cineole, camphor, and ß-pinene) monoterpenes and phytochemical diversity index in sagebrush (*Artemisia* spp.) in two study sites in Idaho, USA (Camas and Cedar Gulch) during summer and winter (2014–2015)

Phytochemicals	Season	Site	n	$\bar{x}$	σ	95% CI[a]	Range (min–max)
Crude protein (%)	Summer	Camas	201	10.7	1.51	(10.5–10.9)	(7.2–16.2)
		Cedar Gulch	229	13.6	2.29	(13.3–13.9)	(8.2–21.5)
	Winter	Camas	138	10.1	1.87	(9.8–10.4)	(6.0–15.5)
		Cedar Gulch	256	13.2	1.72	(13.0–13.4)	(8.3–17.7)
Coumarins (μmol/mg DW)	Summer	Camas	178	0.44	0.59	(0.36–0.53)	(0.00–2.17)
		Cedar Gulch	189	0.27	0.16	(0.24–0.29)	(0.07–0.94)
	Winter	Camas	206	1.08	0.82	(0.97–1.19)	(0.14–4.24)
		Cedar Gulch	257	0.44	0.24	(0.41–0.47)	(0.00–1.44)
Total monoterpenes (%)	Summer	Camas	195	1.21	0.45	(1.15–1.27)	(0.17–2.82)
		Cedar Gulch	240	0.46	0.26	(0.43–0.49)	(0.05–2.22)
	Winter	Camas	205	0.72	0.37	(0.66–0.77)	(0.10–2.21)
		Cedar Gulch	273	0.46	0.19	(0.43–0.48)	(0.11–1.44)
1,8-cineole (%)	Summer	Camas	198	0.16	0.11	(0.15–0.18)	(0.00–0.51)
		Cedar Gulch	252	0.02	0.03	(0.02–0.02)	(0.00–0.20)
	Winter	Camas	205	0.07	0.07	(0.06–0.08)	(0.00–0.33)
		Cedar Gulch	278	0.01	0.01	(0.01–0.01)	(0.00–0.11)
Camphor (%)	Summer	Camas	198	0.46	0.27	(0.43–0.50)	(0.00–1.09)
		Cedar Gulch	252	0.05	0.04	(0.05–0.06)	(0.01–0.39)
	Winter	Camas	205	0.33	0.23	(0.30–0.36)	(0.00–1.14)
		Cedar Gulch	278	0.03	0.03	(0.03–0.04)	(0.00–0.14)
ß-pinene (%)	Summer	Camas	198	0.03	0.02	(0.03–0.03)	(0.00–0.13)
		Cedar Gulch	252	0.11	0.05	(0.10–0.11)	(0.00–0.29)
	Winter	Camas	205	0.02	0.01	(0.02–0.02)	(0.00–0.08)
		Cedar Gulch	278	0.11	0.06	(0.11–0.12)	(0.00–0.34)
Phytochemical diversity index	Summer	Camas	198	1.38	0.236	(1.35–1.41)	(0.67–2.12)
		Cedar Gulch	252	2.04	0.255	(2.01–2.07)	(1.21–2.74)
	Winter	Camas	205	1.27	0.228	(1.24–1.30)	(0.76–2.02)
		Cedar Gulch	278	1.82	0.268	(1.79–1.85)	(1.10–2.73)

n = sample size, $\bar{x}$ = sample mean, σ = standard deviation

[a] The 95% confidence interval was calculated using the standard error of the mean with ($\bar{x} \pm 1.96 \times (\sigma/\sqrt{n})$)

Euclidean nearest neighbor distance between high-quality patches was lower in summer (4.4 m ± 0.34 SE) than in winter (7.5 m ± 0.26 SE), and patch density increased from 195 to 849 patches per 100 ha, and the correlation length decreased from 285 to 45 m (Table 4), suggesting an increase in fragmentation. The opposite pattern occurred for monoterpenes, for which higher quality patches (i.e., monoterpene percentage by DW $< 0.92\%$) increased from 28% of the landscape in summer to 98% in winter (Fig. 5), whereas patterns of coumarins remained consistent across both seasons (Table 4). At Cedar Gulch, patterns of crude protein, monoterpenes, and coumarins were similar in summer and winter (Table 5).

Discussion

Our study demonstrated that phytochemicals influencing resource use by herbivores can be mapped with UAS across the landscape to create foodscapes at scales relevant to small vertebrate herbivores. In sites

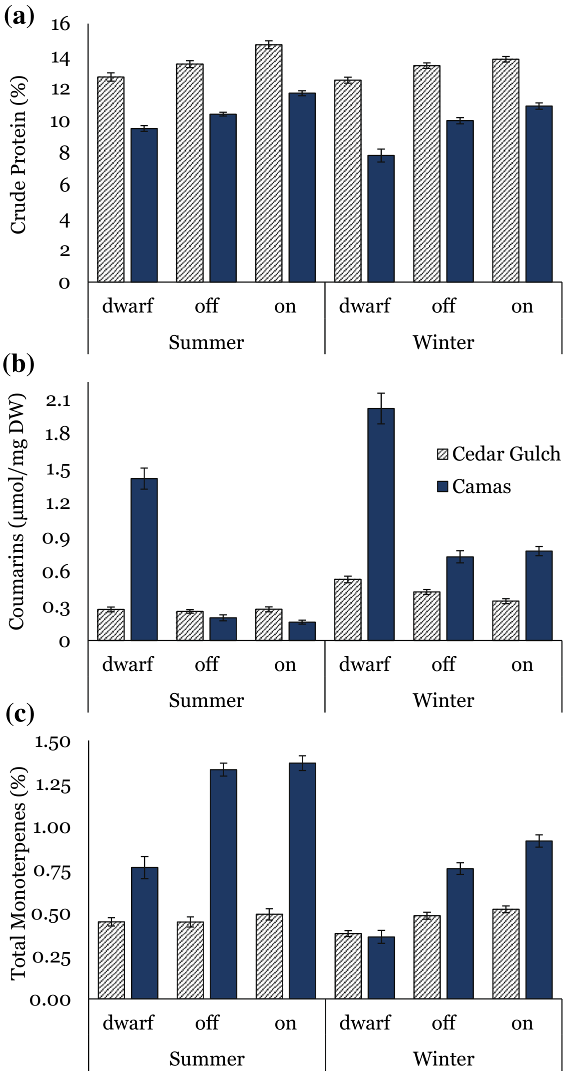

Fig. 1 Phytochemistry by sagebrush morphotype (dwarf sagebrush species [*Artemisia spp.*] [dwarf], off-mound Wyoming big sagebrush [*A. tridentata wyomingensis*] [off], on-mound Wyoming big sagebrush [on]) at the Camas and Cedar Gulch study sites in Idaho, USA, during summer and winter including **a** crude protein (%), **b** total monoterpenes (%), and **c** coumarins (μmol/mg DW)

where sagebrush morphotypes were chemically distinct (e.g., Camas, Figs. 1 and 2), our method was successful at mapping coumarins and moderately successful at mapping crude protein and total monoterpenes. In landscapes where sagebrush morphotypes contained multiple species and had relatively low concentrations of PSMs (e.g., Cedar Gulch, Fig. 1), our method was less successful. Accuracy of our mapping also depended on the particular phytochemical investigated. The high degree of variation in prediction accuracy of the different components of forage quality we measured might be driven by a variety of factors including micro-topography, ecological feedbacks, and genetics.

Applicability of method

Although not all sagebrush-dominated sites have mima mounds and interactions with pygmy rabbits, any biotic or abiotic condition that creates diverse morphotypes could benefit from our methods. Our methodology could be used to classify morphotypes and species associated with particular soil types that vary spatially (Rosentreter 2005) or that result from variation in the species and age of sagebrush from mixing of local and non-local seed sources after fires or other disturbances. Our results suggest that the more distinct the phytochemical concentration and composition is among morphotypes, the higher the accuracy. For example, the genetic basis for variation in coumarins (Richardson et al. 2018) may explain the higher prediction accuracy for coumarins at Camas where coumarin concentrations were dramatically higher in dwarf patches than in on- or off-mound patches (Fig. 1). Coumarin concentrations are linked to species or subspecies (Rosentreter 2005), and indicate that off-mound dwarf plants are genetically distinct from on-and off-mound Wyoming big sagebrush at Camas, but not at Cedar Gulch. Thus, the ability to classify morphotypes could assist in mapping both the chemical and genetic diversity and distribution of that diversity across entire landscapes. The phytochemicals that we had the least success in predicting were individual monoterpenes such as 1,8-cineole. This result could be caused by volatilization during collection and transport which may influence volatiles in relatively lower concentrations or associated with temporal dynamics of volatiles associated with induction by herbivore browsing (Karban et al. 2014). Camphor was the only individual monoterpene that was predicted well at the Camas site (r^2 = 0.50–0.53) (Table 3), perhaps because camphor was the highest concentration, least susceptible to volatilization (i.e., higher molecular weight), or had a stronger genetic link (Karban et al. 2014) than other monoterpenes. At Camas, camphor was much higher in on- and off-mound patches than in dwarf patches, but very low across all morphotypes at Cedar Gulch

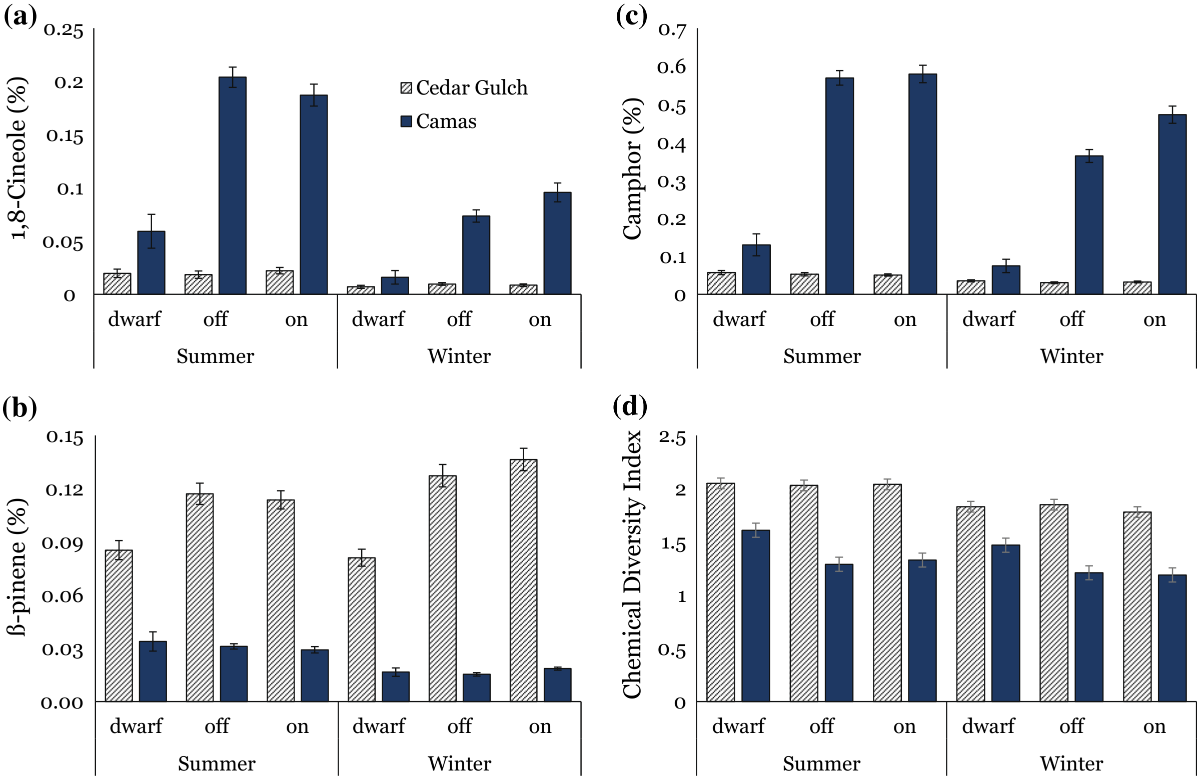

Fig. 2 Concentrations of individual monoterpenes by sagebrush morphotype (dwarf sagebrush species [*Artemisia spp.*] [dwarf], off-mound Wyoming big sagebrush [*A. tridentata wyomingensis*] [off], on-mound Wyoming big sagebrush [on]) at the Camas and Cedar Gulch study sites in Idaho, USA, during summer and winter including **a** 1,8-cineole (%); **b** camphor (%); **c** ß-pinene (%); and **d** phytochemical diversity index

Table 2 Confusion matrix for object-based image classification of unmanned aerial system imagery for two study sites (Camas and Cedar Gulch) in Idaho, USA, during summer

Study site	Morphotype	Classified			Omission error
	Reference	Dwarf	Off-mound	On-mound	
Camas	Dwarf	18	0	0	0.00
	Off-mound	7	17	1	0.32
	On-mound	0	5	22	0.19
	Commission error	0.28	0.23	0.04	
	Overall accuracy	0.81			
Cedar Gulch	Dwarf	31	0	0	0.00
	Off-mound	2	22	6	0.27
	On-mound	0	4	25	0.14
	Commission error	0.06	0.15	0.19	
	Overall accuracy	0.87			

(Fig. 2). Although 1,8-cineole, showed the same pattern as camphor, the absolute concentrations of 1,8-cineole were three times lower than camphor (Fig. 2). Monoterpenes at Cedar Gulch were more diverse (Fig. 2), but overall monoterpene concentration was much lower (Fig. 1) and phytochemicals were not as distinct as at Camas (Figs. 1 and 2).

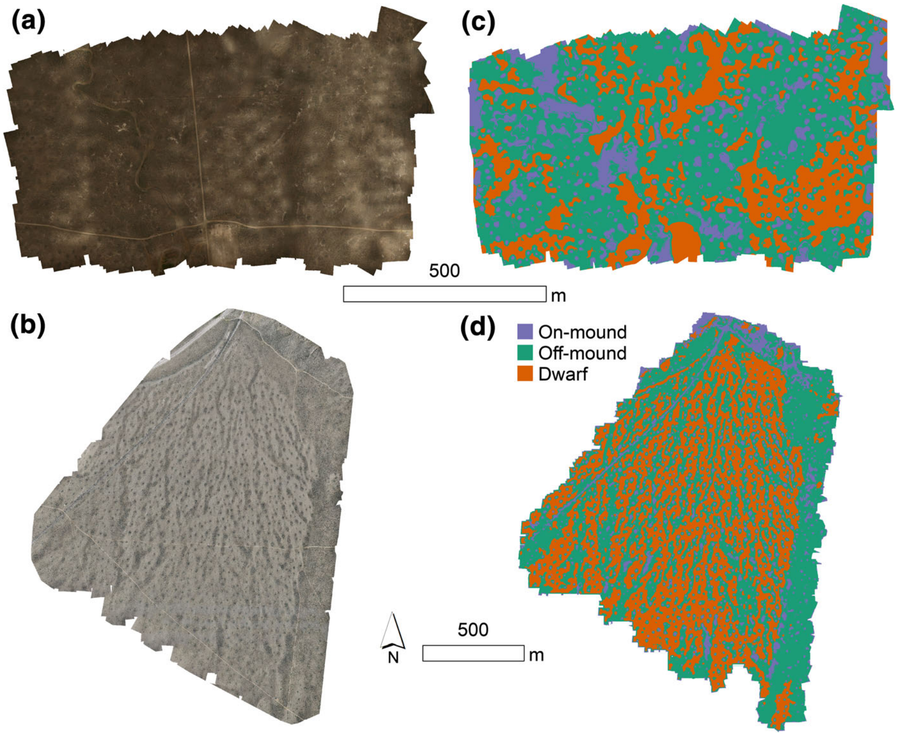

Fig. 3 Unmanned aerial system orthomosaics for the **a** Camas and **b** Cedar Gulch study sites in Idaho, USA in summer, and classified maps of sagebrush morphotypes (*Artemisia* spp.) for the **c** Camas and **d** Cedar Gulch study sites

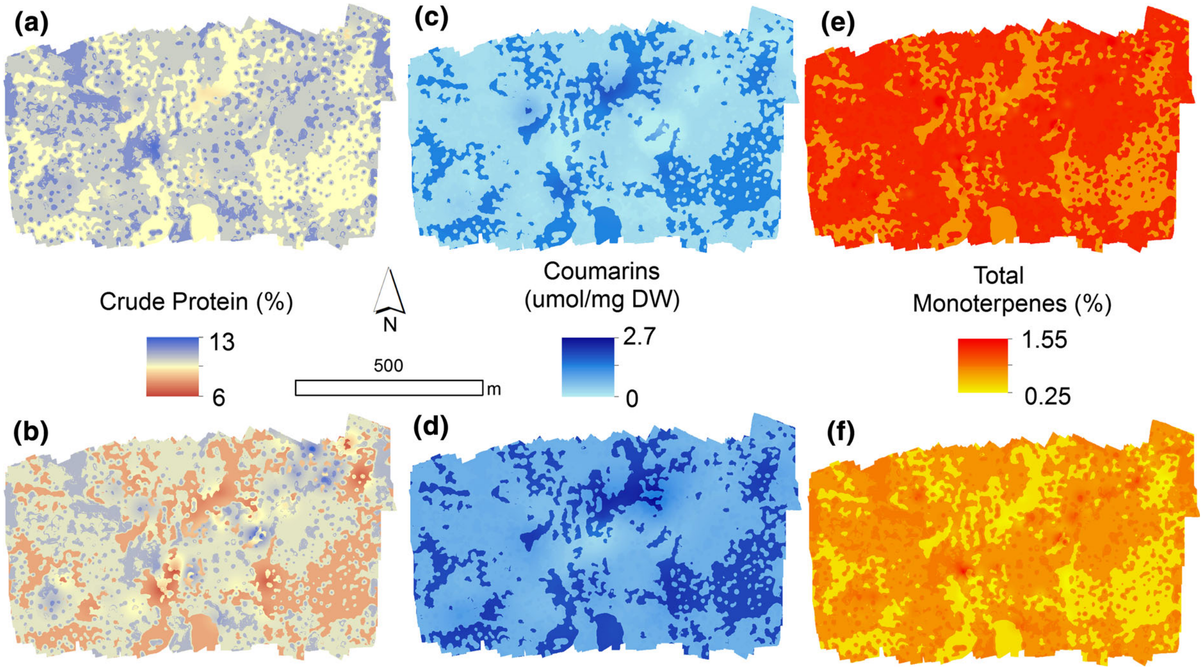

Fig. 4 Landscape-scale maps of crude protein (%) in **a** summer and **b** winter, coumarin concentrations (µmol/mg DW) in **c** summer and **d** winter, and total monoterpene concentrations (%) in **e** summer and **f** winter in sagebrush morphotypes (*Artemisia* spp.) at the Camas study site in Idaho, USA, generated with regression kriging

Table 3 Regression kriging prediction results at two study sites in Idaho, USA

Study site	Phytochemical	Season	*n*	Nugget	Range (m)	Partial sill	r^2	RMSE
Camas	Crude protein (%)	Winter	138	1.077	57	1.496	0.36	1.478
		Summer	201	1.245	50	0.240	0.38	1.188
	Coumarins (µmol/mg DW)	Winter	206	0.345	124	0.076	0.57	0.533
		Summer	178	0.050	100	0.066	0.81	0.254
	Total monoterpenes (%)	Winter	205	0.043	35	0.050	0.51	0.257
		Summer	195	0.087	25	0.054	0.37	0.351
	1,8-cineole (%)	Winter	205	–	–	–	–	–[a]
		Summer	198	–	–	–	–	–[a]
	Camphor (%)	Winter	205	0.019	28	0.009	0.50	0.160
		Summer	198	0.025	27	0.013	0.53	0.184
	ß-pinene (%)	Winter	205	–	–	–	–	–[a]
		Summer	198	–	–	–	–	–[a]
	Chemical diversity index	Winter	205	0.037	100	0.006	0.27	0.194
		Summer	198	0.039	100	0.007	0.28	0.200
Cedar Gulch	Crude Protein (%)	Winter	256	2.375	104	0.629	0.17	1.560
		Summer	229	1.562	35	2.403	0.20	2.036
	Coumarins (µmol/mg DW)	Winter	257	0.045	30	0.014	0.15	0.222
		Summer	189	–	–	–	–	–[b]
	Total monoterpenes (%)	Winter	273	0.026	10	0.009	0.09	0.181
		Summer	240	0.051	63	0.017	0.02	0.258
	1,8-cineole (%)	Winter	278	–	–	–	–	–[c]
		Summer	252	–	–	–	–	–[c]
	Camphor (%)	Winter	278	–	–	–	–	–[c]
		Summer	252	–	–	–	–	–[c]
	ß-pinene (%)	Winter	278	0.002	42	0.001	0.21	0.054
		Summer	252	0.002	30	0.001	0.09	0.050
	Chemical diversity index	Winter	278	–	–	–	–	–[c]
		Summer	252	–	–	–	–	–[c]

Accuracy was assessed using leave-one-out cross-validation (LOOCV). Regression plots for LOOCV prediction accuracy are provided in Online Appendix A

[a] At Camas, 1,8-cineole and ß-pinene did not show any spatial autocorrelation in the residuals, therefore a kriging model could not be fit for summer or winter

[b] At Cedar Gulch, coumarins in summer did not show any spatial autocorrelation in the residuals, therefore a kriging model could not be fit

[c] At Cedar Gulch, 1,8-cineole, camphor, and the chemical diversity index did not show any spatial autocorrelation in the residuals, therefore kriging models could not be fit in summer or winter

Spatial patterning of forage quality

The spatial patterns of forage quality varied seasonally, with a highly connected foodscape in summer and a more fragmented one in winter (Fig. 5). The isolated high-quality fragments in winter were mostly associated with on-mound patches, with some connectivity to high-quality off-mound patches (Figs. 3 and 5). This fine-scale fragmentation may not matter to more mobile herbivores, particularly greater sage-grouse that have large home ranges and can move > 1 km daily (Bruce et al. 2011), but for smaller herbivores such as pygmy rabbits and mountain cottontails, this scale of fragmentation may

Table 4 Landscape metrics for high and low quality sagebrush (*Artemisia* spp.) patches defined by whether they exceeded a threshold value derived from the mean value at the study site (high quality > 10.0% crude protein, high quality < 0.92% total monoterpenes, high quality > 0.81 µmol/mg DW coumarins) at the Camas study site in Idaho, USA for both summer and winter

Variable	Season	Quality	PLAND	NP	PD	LPI	AREA_MN	AREA_SD	GYRATE_AM	ENN_MN
Crude protein	Winter	Low	72.7	502	888	71.1	0.082	1.791	304	1.585
		High	27.3	480	849	5.0	0.032	0.198	45	7.519
	Summer	Low	28.0	193	342	8.0	0.082	0.396	66	8.468
		High	72.0	110	195	68.3	0.370	3.660	285	4.415
Total monoterpenes	Winter	Low	1.7	72	127	0.3	0.013	0.028	10	7.882
		High	98.3	31	55	98.3	1.793	9.815	307	0.992
	Summer	Low	72.3	108	191	68.6	0.378	3.710	285	4.396
		High	27.7	188	333	8.0	0.083	0.399	67	8.759
Coumarins	Winter	Low	63.4	139	246	60.2	0.258	2.872	289	3.288
		High	36.6	246	435	9.1	0.084	0.489	73	6.313
	Summer	Low	72.3	107	189	68.6	0.382	3.726	285	4.430
		High	27.7	188	333	8.0	0.083	0.400	67	8.648

PLAND Percentage of landscape, *NP* number of patches, *PD* Patch density (Patches per 100 ha), *LPI* largest patch index (percent of landscape), *AREA_MN* mean patch size (ha), *AREA_SD* standard deviation of patch size (ha), *GYRATE_AM* area-weighted mean radius of gyration, or correlation length, *ENN_MN* mean Euclidean nearest neighbor (m)

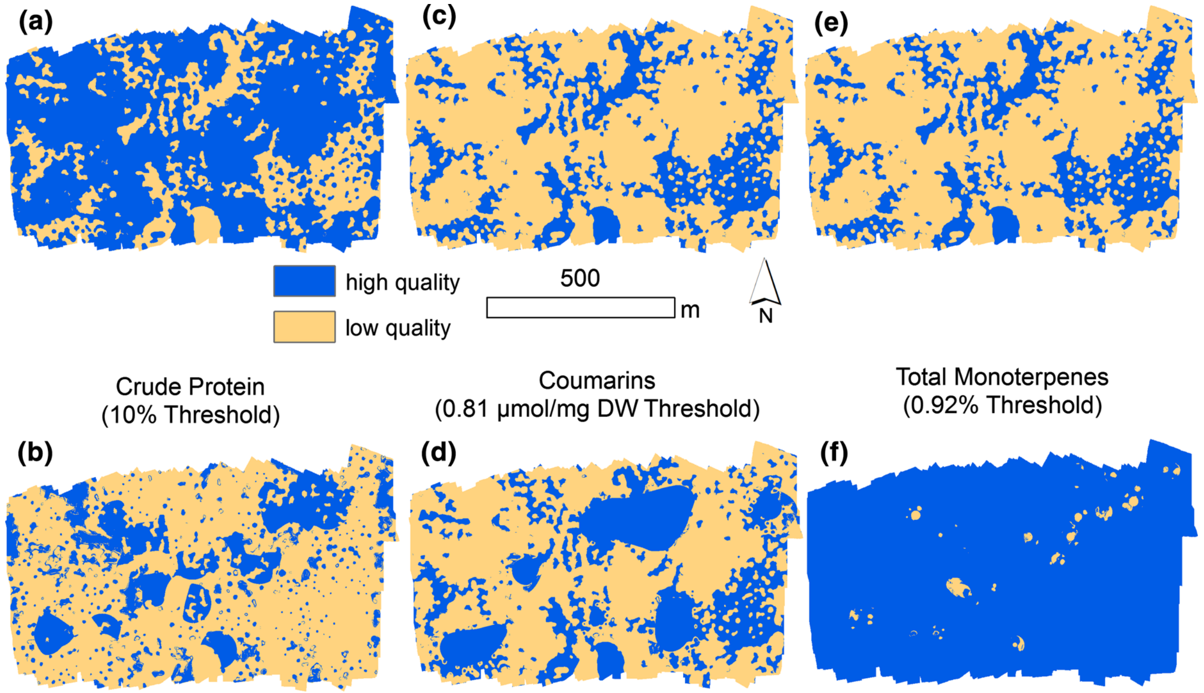

Fig. 5 Landscape-scale maps of sagebrush morphotypes (*Artemisia* spp.) with low quality (< 10%) or high quality (> 10%) concentration of crude protein in **a** summer and **b** winter, low quality (< 10%) or high quality (> 10%) concentration of coumarins in **c** summer and **d** winter, and low quality (> 0.92%) or high quality (< 0.92%) concentration of total monoterpenes in **e** summer and **f** winter at the Camas study site in Idaho, USA

Table 5 Landscape metrics for high and low quality sagebrush (*Artemisia* spp.) patches defined by whether they exceeded a threshold value derived from the mean value at the study site (high quality > 13.3% crude protein, high quality < 0.45% total monoterpenes, high quality > 0.46 µmol/mg DW coumarins) at the Cedar Gulch study site in Idaho, USA for both summer and winter

Variable	Season	Quality	PLAND	NP	PD	LPI	AREA_MN	AREA_SD	GYRATE_AM	ENN_MN
Crude protein	Winter	Low	47.4	196	100	41.2	0.476	5.771	405	8.427
		High	52.6	684	348	39.3	0.151	2.958	520	8.024
	Summer	Low	41.2	210	107	31.1	0.386	4.223	347	8.915
		High	58.8	549	279	44.0	0.211	3.697	512	6.826
Total monoterpenes	Winter	Low	58.3	525	267	42.6	0.218	3.658	497	6.346
		High	41.7	218	111	31.3	0.376	4.177	351	8.432
	Summer	Low	51.8	1433	729	33.7	0.071	1.765	321	4.154
		High	48.2	593	302	34.3	0.160	2.784	488	5.186
Coumarins	Winter	Low	58.1	537	273	41.8	0.213	3.554	493	6.205
		High	41.9	201	102	31.5	0.410	4.383	354	8.904

PLAND Percentage of landscape, *NP* number of patches, *PD* patch density (Patches per 100 ha), *LPI* largest patch index (percent of landscape), *AREA_MN* mean patch size (ha), *AREA_SD* Standard deviation of patch size (ha), *GYRATE_AM* area-weighted mean radius of gyration, or correlation length, *ENN_MN* mean Euclidean nearest neighbor (m)

influence habitat selection. During winter, pygmy rabbits dig subnivean tunnels when snow is deep enough (Katzner and Parker 1997), which helps maintain connectivity between higher quality patches of sagebrush while reducing predation risk. However, increasing temperatures under climate change leads to less snow (Pauli et al. 2013), and therefore exposes pygmy rabbits to more predation risk and potentially lower quality nutrition. Our maps suggest that in certain landscapes similar to Camas, loss of subnivean connectivity could be detrimental to foraging pygmy rabbits, because high-quality food patches are isolated and fragmented leading to poorer nutrition and potentially an increase in predation (Dwinnell et al. 2019). The differences in spatial patterning of nutrition that we documented between summer and winter may also be useful in explaining seasonal changes in movement trajectories, distribution, or trade-offs, and provide an example of how our methodology could be linked with species-level data to test ecological hypotheses.

Seasonal foodscapes

In addition to seasonal changes in forage quality, leaf phenology within a season affects concentration of volatile compounds such as monoterpenes, with higher concentrations occurring in the spring and summer with the addition of ephemeral leaves and new persistent leaves to deter herbivores (Kelsey 1984; Miller and Shultz 1987; Rosentreter 2005). The ephemeral leaves drop off in late summer, and the newer persistent leaves become less toxic as gland cells age and break open (Rosentreter 2005). Furthermore, the ratio of leaves to stems changes with more leaves produced in summer, likely leading to higher monoterpene concentrations and lower crude protein (Miller and Shultz 1987). This change is mirrored in our foodscape maps, with lower monoterpene concentrations in winter. However, the decrease in monoterpene concentrations seems to be relative because the same patches that had the highest concentration of monoterpenes in summer also had the highest concentrations in winter (Fig. 4). Additionally, crude protein concentrations were higher in summer. Although both pygmy rabbits and greater sage-grouse can consume diets of nearly 100% sagebrush, they consume considerably less sagebrush in summer (Thines et al. 2004; Gregg et al. 2008; Crowell et al. 2018). This could be due to the availability of other more nutritious plants or higher toxicity of sagebrush in summer because of an interaction between higher monoterpene concentrations (Figs. 1 and 2) and lower tolerance to those chemicals because of higher ambient temperatures (Gregg et al. 2008; Kurnath et al. 2016; Beale et al. 2018; Windley and Shimada 2020). In contrast, the colder temperatures and lower concentrations of monoterpenes during winter may facilitate greater intake of sagebrush during winter. The crude protein quality threshold (i.e., average landscape value) at Camas was 10.0%, which corresponded to 7.7% digestible protein (L.A. Shipley, unpublished data), and was the average amount consumed by captive pygmy rabbits during feeding trials (Crowell et al. 2018). Cedar Gulch had higher crude protein values during both seasons and had an average landscape value of 13.3%, which was similar to observations by Ulappa et al. (2014) at the same study site, where plants browsed by pygmy rabbits averaged 13.5% crude protein and unbrowsed plants averaged 12.5% crude protein. This finding suggests that even when the entire foodscape provides adequate crude protein, pygmy rabbits still select relatively more nutritious diets at a given site.

The quality of a foodscape is also defined by the herbivore. In addition to variation in mobility between species, species can also vary in their tolerance for specific phytochemicals. For example, mountain cottontails selected for total monoterpene concentrations in the diet less than 0.9% (Crowell et al. 2018), similar to our threshold value of 0.8% at Camas, whereas pygmy rabbits selected for monoterpene concentrations of 1.6% total monoterpenes (Crowell et al. 2018), much higher than our threshold values at either study site. Our maps, coupled with physiological knowledge of herbivores, allow us to test the hypothesis that Camas is less likely to support populations of mountain cottontails than Cedar Gulch.

Future directions in mapping foodscapes

Low prediction accuracy for phytochemicals at Cedar Gulch was most likely caused by morphotypes that consisted of the same sagebrush species but different structure, thus limiting the explainable variation both between and within patches. Color imagery and structural information from UAS SfM was unable to distinguish species or subspecies of sagebrush, only broader structural morphotypes. Therefore, at sites such as Cedar Gulch that have more complex plant phytochemistry that do not match the structural morphotypes, other types of camera sensors or methods may be required. For example, the added spectral information provided by hyperspectral sensors relative to color sensors (i.e., 10 + bands vs. 3 bands) might increase the ability for UAS-based imagery to classify plants to the species-level or more directly map phytochemicals, such as crude protein (Kokaly et al. 2009; Mitchell et al. 2012). Hyperspectral sensors have been getting smaller and cheaper, and have been recently deployed on UAS (Adão et al. 2017; Garzonio et al. 2017). Regardless, even with limited color imagery, our methods allowed us to make accurate, fine-resolution, landscape-level classifications of morphotypes that aided in mapping some important components of forage quality for herbivores.

Landscape-scale maps of forage quality from UAS will advance our ability to ask ecological questions about fundamental factors that shape foraging and patterns of space use by herbivores in diverse and heterogeneous environments. These maps are useful tools for management prioritization because they map functional features of habitats rather than standard land cover classifications. This knowledge is critical to understanding, monitoring and predicting how herbivores might respond to rapidly changing environments under climate change and increasing fire regimes that alter the distribution and quality of forage plants.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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