RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Monitoring ecological characteristics of a tallgrass prairie using an unmanned aerial vehicle

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Site-specific conditions, climate, and management decisions all dictate the establishment and composition of desired plant communities within grassland restorations. The uncertainty, complexity, and large size of grassland restorations necessitate monitoring plant communities across spatial and temporal scales. Remote sensing with unmanned aerial vehicles (UAVs) may provide a tool to monitor restored plant communities at various scales, but many potential applications are still unknown. In a tallgrass prairie restoration located in Franklin Grove, IL, we used UAV-based multispectral imagery to assess the ability of spectral indices to predict ecological characteristics (plant community, plant traits, soil properties) in the summer of 2017. Using 19 sites, we calculated the moments of 26 vegetation indices and four spectral bands (green, red, red edge, near infrared). Models based on each moment and a model with all moments were estimated using ridge regression with model training based on a subset of 15 sites. Each tested for significant error reduction against a null model. We predicted mean graminoid cover, mean dead aboveground biomass, mean dry mass, and mean soil K with significant reductions in cross-validated root mean square error. Averaged coefficients determined from cross-validation of ridge regression models were used to develop a final predictive model of the four successfully predicted ecological characteristics. Graminoid cover and soil potassium were successfully predicted in one of the sites while the other two were not successfully predicted in any site. This study provides a path toward a new level of ease and precision in monitoring community dynamics of restored grasslands.

Key words: drone, grassland restoration, remote sensing, ridge regression, unmanned aerial vehicle

Implications for Practice

- Unmanned aerial vehicle (UAV) imagery accurately predicted mean graminoid cover, mean dead aboveground biomass, mean dry mass, and mean soil K. This provides incentive to use ridge regression, a technique that allows for the incorporation of a large set of spectral indices and spectral diversity measures (i.e. standard deviation, coefficient of variation, skewness, kurtosis).
- UAV-based monitoring programs could provide managers with affordable quantitative information describing plant community characteristics and soil properties, and their relationships with restoration practices (e.g. prescribed fires, seeding, herbicide application) and/or climate across multiple spatial and temporal scales.

Introduction

Grasslands are one of the most diverse and productive ecosystems and cover roughly 40% of the earth's terrestrial surface (White et al. 2000). They also modulate ecosystem functioning worldwide, as evidenced by their pivotal role in the global carbon cycle (Andrade et al. 2015). However, grassland biodiversity and the services grasslands provide are also severely threatened, which makes conserving and restoring them a top priority (Henwood 1998; Andrade et al. 2015). Grassland restoration practices aim to restore diversity and functioning by improving degraded lands and reconverting historical grasslands from other land uses, primarily agriculture, to create a more heterogeneous landscape (Rowe 2010; Klopf et al. 2017).

The most common methods for restoration of tallgrass prairies in North America include seeding, reinstating disturbance regimes, hydrological restoration, and continued invasive species removal (Rowe 2010). These techniques create spatial variation dependent on when and how they are applied. For

Author contributions: RCB, HPJ, NAB, AKF conceived the project, designed the research, and collected the data; RCB, RB analyzed the data; RCB wrote the manuscript with input from all authors.

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doi: 10.1111/rec.13339
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13339/suppinfo

example, grazing and fire are both disturbances, but they have differing impacts on biotic and abiotic aspects of the ecosystem (Knapp et al. 1999; Anderson 2006) and can interact to have synergistic effects ("pyric herbivory") (Fuhlendorf et al. 2009). Further, restored grasslands undergo succession, so plant communities and functioning also can vary with time since restoration (Weber 1999). Spatial variations in the presence or timing of disturbances, time since restoration, and restoration techniques create a heterogeneous system with different patterns of variation at different spatial scales (e.g. one restoration vs. a landscape of restored sites). Monitoring the trajectory of restorations is already difficult with traditional on-ground methods and commonly never occurs (González et al. 2013; Holl 2017). The heterogeneity of grassland restorations increases the difficulty of monitoring vegetation, soil, and other ecosystem properties through the extrapolation of on-ground methods, especially across large spatial scales (Ali et al. 2016).

Remote sensing data allow researchers and land managers to address this issue of scale and heterogeneity, and restoration studies and monitoring programs have begun using these data more commonly within the last decade (Ali et al. 2016; Reif & Theel 2017). Since the launch of the first Landsat satellite in 1972, remotely sensed data have been incorporated into plant community monitoring to describe variation at large spatial scales (Holmgren & Thuresson 1998; Xie et al. 2008). The advancement of satellite and aerial sensor technology, and the development of vegetation indices (e.g. Normalized Difference Vegetation Index, NDVI), have provided information on plant communities, plant traits, and soil properties over large scales. These data have been incorporated into models to predict ecosystem metrics such as leaf area index, growth type, and total canopy nitrogen (Holmgren & Thuresson 1998; Xie et al. 2008; Ling et al. 2014; Reif & Theel 2017; Xu et al. 2018).

Recent trends in open source data have drastically lowered the cost of certain satellite imagery such as Landsat (Kelly & Di Tommaso 2015). Unfortunately, satellite and manned aerial based imagery still lack the high spatial and temporal resolution often necessary to describe the fine-grain heterogeneity present in tallgrass prairie restorations. High-resolution (spatial and temporal) multispectral satellite imagery, such as Worldview (spatial resolution of 1.34 m^2), does provide data that may help overcome the obstacles of lower resolution imagery but may be cost-prohibitive when repeated sampling is necessary to describe spatiotemporal variability (Reif & Theel 2017). Unmanned aerial vehicles (UAVs), on the other hand, provide even greater spatial resolution (1–10 cm^2) and can be flown on demand, yielding temporal resolutions equivalent to flight times (Anderson & Gaston 2013; Cordell et al. 2017). As a result, there has been a growing movement to experiment with UAV-acquired data in ecological studies.

The use of UAVs in environmental science and ecology has rapidly expanded over the last decade (Reif & Theel 2017; Nowak et al. 2019). Control of flight times, flight areas, and which sensors (e.g. lidar, multispectral, hyperspectral) are attached to the UAV provide users with an enormous range of potential applications, from counting wildlife to mapping individual plant populations. For example, Hodgson et al. (2018) found that counting the number of seabirds within colonies was more accurate when automated though UAV imagery than with trained field technicians. Mishra et al. (2018) tested the ability to identify individual tree species along a tree line ecotone in Nepal and found approximately 70% accuracy using UAV imagery alone. Grassland applications have largely been limited to quantifying the presence of a single species, landcover and vegetation types, biomass, and disturbances such as prescribed burns (Zweig et al. 2015; Cruzan et al. 2016; Lorah 2018; Lussem et al. 2019; Melville et al. 2019). However, Lu and He (2017) successfully mapped groupings of dominant species within a grassland using a modified RGB camera to incorporate a near infrared (NIR) band. These results show promise for the ability of UAVs to provide detailed information through a low-cost sensor (in comparison to costly hyperspectral or lidar sensors). However, the accuracy and precision of this approach is still uncertain in a highly heterogeneous habitat, such as restored tallgrass prairie. If low-cost UAV systems can accurately measure ecological characteristics, UAVs could massively expand the monitoring effort of tallgrass prairie restoration and provide insight into the effects of restoration practices through a much more timely and cost-effective approach.

In this article, we evaluate the potential applications of UAV-derived data within restored tallgrass prairies using an affordable sensor and UAV. We use penalized regression (Friedman et al. 2010) to predict the mean and standard deviation of 33 ecological characteristics across a chronosequence of prairie restorations. These characteristics fall within three types of ecological information (plant communities, plant traits, and soil properties) of interest to restoration practitioners. If plant communities, traits, and soil properties can be predicted using remote sensing technology, this would be an important advance in the ability to scale up from plot-scale measurements to large-scale landscapes, long considered an important goal in ecology (Underwood et al. 2005; Denny & Benedetti-Cecchi 2012).

Methods

Study Site

This study took place in summer 2017 at Nachusa Grasslands, a 1,400-ha preserve in Franklin Grove, IL, owned by The Nature Conservancy. Total annual precipitation for 2017 measured 804 mm, compared to an annual mean of 947 mm. Nachusa contains a mosaic of restored and remnant (never plowed but managed) tallgrass prairie sites with varying disturbance regimes. Along with these varying management activities, different plots of land at Nachusa have been restored since the 1980s, yielding a chronosequence of restoration ages (Fig. 1). These attributes create a heterogeneous landscape with varying plant community types and provide an ideal landscape to test the predictive capabilities of UAV imagery in a heterogeneous environment.

Managed disturbances allowed us to sample across a range of conditions within restored tallgrass prairie communities at the research site. Prescribed fires are applied frequently at Nachusa

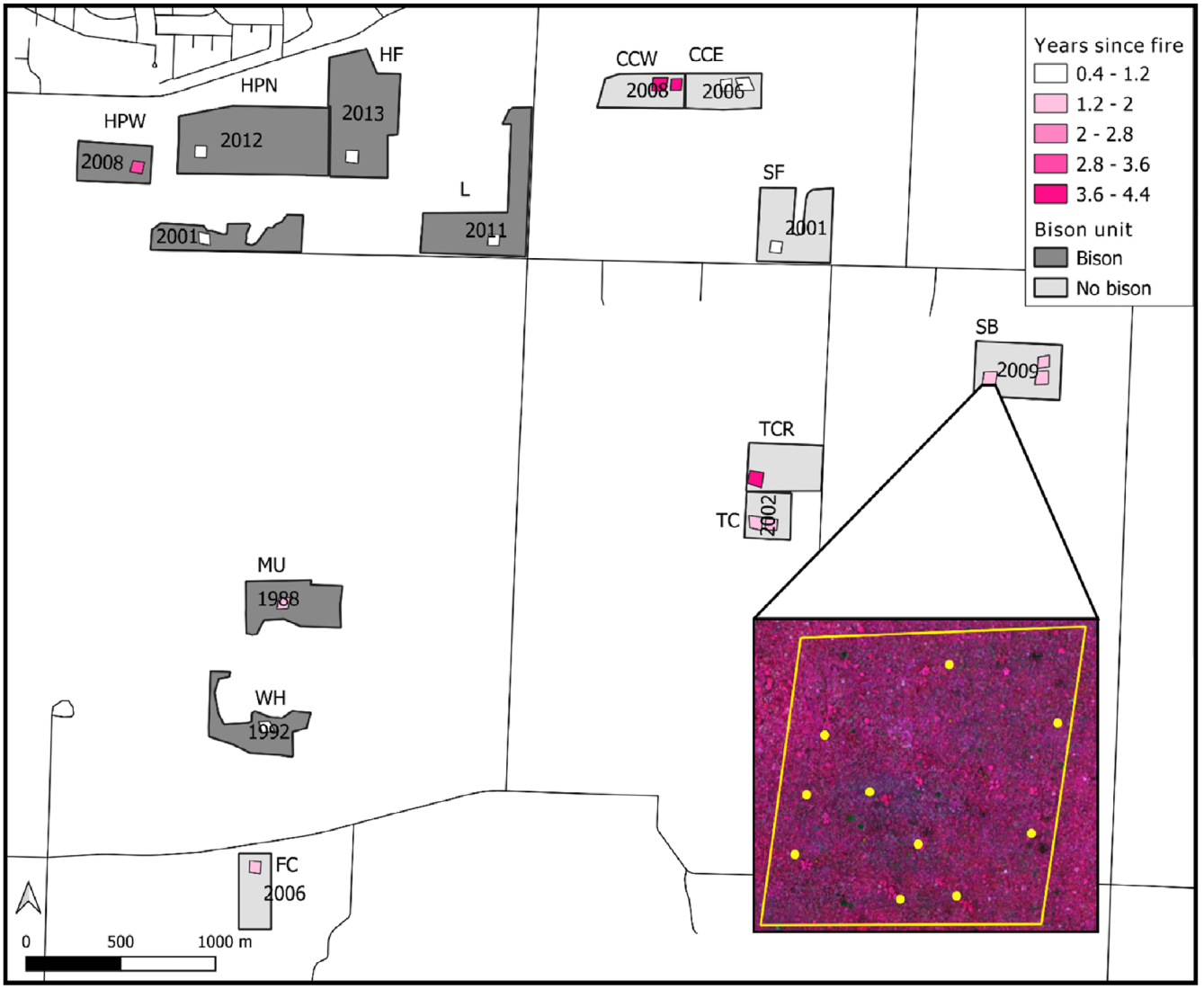

Figure 1. Study design of restoration sites representing different variations in disturbance and restoration history indicating a heterogeneous landscape. Planting boundaries are indicated by gray polygons while site boundaries are represented by polygons colored by a gradient of years since fire. The false color image was taken by the UAV with the site boundary and plant community quadrat locations shown in yellow.

to maintain ecosystem functioning with return intervals ranging from 1 to every 4 years. Bison were reintroduced to a large, fenced portion of the preserve (600 ha) in 2014 to provide grazing disturbance, with the goal of increasing plant diversity and heterogeneity. Our study used 18 restored sites and one remnant with seven sites in the bison unit and 12 sites outside of the bison unit, representing 4–31 years since restoration (Fig. 1). Overall, the sampling design represented the range of conditions within the typical restored tallgrass prairies found at Nachusa Grasslands.

Field Data

Plant Community Characteristics. Within each of the 19 sites, grids (60 × 60 m) were established with 25 points spaced 15 m apart. The 25-point grid was originally designed for studying small mammal communities. By randomly selecting 10 points per grid, we were still able to capture the variation in plant communities present at each site. A quadrat (0.25 m^2) was placed at each point for a total of 190 sampled quadrats. We identified vegetation and estimated cover to the species level between 15 and 17 August, 2017. Cover was estimated between 0 to 100% based on the stem basal area coverage per quadrat. Plants were identified using Williams (2010) and Wilhelm and Rericha (2017) guidelines. Plant cover by functional groups (i.e. C_3 grasses, C_4 graminoids, N-fixing forbs, non-N-fixing forbs, all forbs), Shannon diversity, richness, and a percent graminoid:forb ratio were calculated for each quadrat. The mean and standard deviation for each plant community characteristic were then determined based on all 10 quadrats for each site. These values represent the plant community characteristics we set forth to predict; standard deviations of site characteristics

were determined to assess the potential to predict differences in community variation within sites. Descriptions of all ecological characteristics can be found in Table S1.

We also collected biomass across the sampling grids from a 0.01 m^2 quadrat adjacent to each plant community survey quadrat (n = 10 per site) between 14 and 18 August, 2017. All plants within the smaller quadrat were clipped 2 cm above ground level. Aboveground biomass was sorted into dead, graminoids, and forbs prior to drying and weighing. A soil core (15 cm deep, 2 cm diameter) was collected from each aboveground biomass quadrat. Soil was rinsed from roots, and they were dried and weighed to determine belowground biomass. Mean and standard deviations of biomass were determined for each site and used as ecological characteristic responses.

Plant Trait Characteristics. Functional trait data were collected for the 10 most abundant species at each site between 17 and 28 July, 2017. A total of 10 individuals per species were selected randomly across the same sampling grid as the plant community data. When individuals of a species in the top 10 were unavailable, another common species was substituted so the sampled species comprised greater than 60% of plant cover. Leaf samples were chosen from mature individuals with little sign of damage and were taken from the highest point. Leaf samples were wrapped in moist paper towels, placed in a plastic bag, and kept in a cooler of ice to avoid desiccation. Some traits required immediate measurements and were analyzed within 4 hours (leaf toughness and fresh mass for leaf dry matter content). Other measurements (specific leaf area, leaf dry matter content, and leaf C and N content) were measured after the samples were pressed and dried. Community weighted means and standard deviations were calculated for each site using the R package lefse (Swenson 2014).

Soil Property Characteristics. Soil properties were measured across the same grid as all other measurements. Five locations within each site were randomly selected and soil was collected from the top 10 cm. Soil material was sent to Midwest Laboratories in Omaha, NE, for analysis. Mean and standard deviations for each soil property were calculated for each site.

UAV Data

Image Collection and Processing. UAV imagery covering the 19 sites across Nachusa was acquired between 15 and 25 July, 2017 using a Parrot Sequoia plus multispectral sensor (Parrot, SA, Paris, France). These dates overlapped with plant trait data collections. However, plant community data were collected after the drone acquisition followed by biomass. Tallgrass prairie biomass generally peaks in early August (Owensby et al. 1993), and we are assuming little plant growth occurred between flight and biomass data collection. Flight times were between 11:00 hours and 15:00 hours to maintain a relatively consistent sun angle. The Parrot Sequoia plus is a lower-cost multispectral sensor designed for agriculture and has a built-in GPS with approximately 1–3 m locational accuracy. Spectral information for this sensor is collected across four bands: green (550 nm), red (660 nm), red-edge (735 nm), and NIR (790 nm). This sensor was mounted on a Parrot Disco Pro AG fixed wing UAV and flown at 122 m. Automated drone piloting software (Pix 4D capture, Pix4D SA, Prilly, Switzerland) guided the UAV to collect images across a designated flight path with a minimum of 80% forward overlap and 75% side overlap. Orthomosaics for each site were created and converted to surface reflectance using Pix4D software. The resulting spatial resolution of each image was approximately 12.5 cm^2.

Extraction of Spectral Indices. For all sites, each corner location of the 60 × 60 m grid was recorded using a Garmin eTrex 20 with approximately 3 m locational accuracy (Garmin Inc., Olathe, Kansas, U.S.A.). We used these corner locations to create boundary shapefiles for each site (Fig. 1). Shapefiles were then visually assessed and confirmed to encompass each 60 × 60 m grid within the orthomosaics. Orthomosaics for each site were then cropped using the boundary shapefiles. The resulting orthomosaics were then assumed to represent the target area of inference. Any addition or subtraction of pixels from the study site during cropping were minimal. Additionally, these added or missing pixels were a part of the larger restoration (same time of establishment and subsequent management) and assumed to represent the sample area (Fig. 1). Twenty-six spectral indices were chosen based on relevant uses in the literature (Table S2). For each index, a function was created in R (R Core Team ;2019) that calculated the index for each pixel in the image. For each spectral index and band, we calculated several moments (mean, standard deviation, coefficient of variation, skew, kurtosis) within each site (i.e. index moments were estimated across the 60 × 60 m grid). This produced 150 independent variables (130 from spectral indices and 20 from the individual bands) determined from each of the 19 restoration sites. Predictors were subset based on each moment creating a total of six possible predictor sets per response: (1) mean subset, (2) standard deviation subset, (3) coefficient of variation subset, (4) skew subset, (5) kurtosis subset, and (6) full model (i.e. all predictors). We also included restoration age as a predictor to inform each model of known variations as a result of the chronosequence. Finally, a null model was created using only the intercept for comparison.

Statistical Analysis

To begin our analysis, 15 out of the 19 restoration sites were selected to represent the training data for model estimation. These 15 sites were used to establish predictive models for the mean or standard deviation of each of the restoration characteristics introduced in Table S1. The remaining four restoration sites not used during model estimation served as the testing data to evaluate the predictive performance of each final model. Twenty-four of the response variables were log transformed to meet assumptions of normality, and predictions were back transformed to validate models (Table S3). Penalized regression

Figure 2. Predicted ecological characteristics across a single UAV acquisition covering 55.8 ha. Multiple restorations fall within the single acquisition. Each pixel (60 m × 60 m) was predicted with the averaged coefficients from the cross-validated ridge regression model.

models were estimated using the 15 testing sites based on L2-penalization of coefficient magnitude, also known as ridge regression (Friedman et al. 2010). Estimation of ridge regression models was performed using *glmnet* (Friedman et al. 2010).

Ridge regression applies a penalty to the coefficient magnitudes providing stabilized estimation of linear coefficients under conditions of highly correlated predictors, which is expected when multiple indices are calculated from the same pixel. The effect of the penalty term is a shrinkage of the coefficient magnitude toward zero. Penalization also improves upon ordinary least squares in that stable solutions exist for the estimation of models with more predictors (p) than the collected sample size (n). Regularization methods, such as this approach, are an ideal case for this analysis because our sample size ($n = 15$) was much smaller than our predictors (p = 151 for full models and p = 31 for subset models) (Tibshirani 1996; James et al. 2013), typical

of restoration projects in which a limited number of management units are monitored. Ridge regression was chosen specifically due to the high correlation between predictors that commonly results from spectral indices (Fig. S1).

Ridge estimation requires the selection of a penalization parameter (λ) for effective shrinking of coefficient magnitudes and improved prediction. The magnitude of λ was established prior to final model estimation using cross validation (Friedman et al. 2010). Models were produced based on the seven distinct predictor subsets for the mean or standard deviation of each of the 33 ecological characteristics. Model estimation was validated using 10 × 5-fold cross validation. This provided 50 models per predictor set for each ecological characteristic of interest along with an assessment of the test set root mean square error (RMSE). RMSE provides a measure of error based on normalized sum of squared differences between the predicted and observed responses. The square root is then taken to convert the error back to the original unit of measure. The goal for effective predictive modeling is to minimize the resulting test set RMSE based on cross-validation. A model that produces a minimized test set RMSE will also have strong predictive performance (James et al. 2013). When the test set RMSE has been properly reduced, the predictive model is achieving an error rate on par to the variation that may be observed within the ecological setting (i.e. irreducible error). Final models were chosen based on significant reductions in RMSE in comparison to the null model using a corrected t value for repeated k-fold cross validation (Bouckaert & Frank 2004). To account for multiple comparisons, we adjusted the p values using false discovery rate (Benjamini & Hochberg 1995). Models were considered to have significantly reduced the error against the null model with a p value less than 0.2. We chose a larger threshold due to the loss of power from our small sample size. This allowed us to find potential relationships that would have been missed with a smaller threshold. If more than one model was significantly improved in comparison to the null, the model with the lowest mean RMSE (mRMSE) was chosen. Responses without models that outperformed the null model were left out of further analysis.

For the four characteristics in which models significantly reduced the error against the null model, we chose to further validate how well the ridge estimated models were performing by predicting the ecological characteristics of the four excluded sites. A final predictive model was then produced by averaging the coefficients of the 50 cross-validation iterations. The final models were used to predict the responses in the four sites excluded from the model estimation process. Using the predicted and observed ecological characteristics, we determined the magnitude of the deviations (absolute distance between prediction and observed) between the predictive model and the excluded site observed characteristics. We considered a prediction of a single site's characteristic to be acceptable if the deviation was less than the test set mRMSE. To provide an example of the use of such predictions, we used the same models for each of the four characteristics to predict them across an UAV acquisition.

Results

The results of cross-validation of ridge estimated linear models based on UAV image-derived vegetation indices are summarized for the mean and standard deviation of each ecological characteristic in Tables S3 and S4. Because there are no effective standards yet for acceptable error rates for predicting these characteristics, Table S3 and S4 represents novel testing error rates for the prediction of ecological characteristics based on UAV spectral indices.

Of the 66 responses evaluated in this work, four were found to have significantly reduced test set RMSE in comparison to the null model. Characteristics of two types (i.e. plant community and soil) were found to be significantly improved in comparison to the null including mean graminoid cover (p = 0.09), mean dead aboveground biomass (p = 0.09), mean dry mass (p = 0.08), and mean soil K (p = 0.14). These four characteristics only describe mean values. No variables describing plant traits or the standard deviation of the any characteristic were found to have significantly reduced RMSE in comparison to the null model. Additionally, three of the final models consisted of the predictors from the skew subset while mean graminoid cover consisted of the full model (Table 1). An example of the use of these four models in use with an UAV aquisition can be seen in Figure 2.

Table 1. Assessment of predicted mean ecological characteristics for each of the four excluded sites (CCWE, HPW, TCR, WH) during model estimation and the four characteristics for which models significantly reduced the error against the null model. The table gives the cross-validated test mean root mean square error (mRMSE), which represents the irreducible error determined during model estimation. The final four columns give the absolute deviation between the predicted characteristic and observed characteristic for each of the excluded sites. Predictions were assessed as having acceptable error if they fell within the mRMSE of the observed characteristic. Each acceptable deviation is bolded. Penalty values used during the ridge modeling are included for reproducibility.

Response	*Model*	*Penalty (λ)*	*mRMSE*	*CCWE*	*HPW*	*TCR*	*WH*
Plant community characteristics							
Mean graminoid cover (%)	Full	114.288	8.017	**7.789**	29.489	12.106	16.639
Mean dead aboveground biomass (g)	Skew	3.667	0.970	4.250	**0.836**	3.886	8.451
Mean dry mass (g)	Skew	2.549	0.038	0.176	0.169	0.161	0.190
Plant trait characteristics							
—	—	—	—	—	—	—	—
Soil property characteristics							
Mean K (ppm)	Skew	406.819	37.383	128.435	80.939	181.790	77.889

Validation of the final model performance showed two instances where the absolute deviation was within the test set mRMSE. Magnitudes of model coefficients for all 50 iterations are displayed in the supplemental materials (Figs. S2–S5). The models predicting mean graminoid cover and mean dead aboveground biomass both had one of four acceptable predictions. Mean dry mass and mean soil K models were unable to predict a site with a deviation below the test set mRMSE (Table 1).

Discussion

Our analysis has demonstrated the ability of a low-cost UAV monitoring system to predict four important ecological characteristics within a heterogeneous restored landscape, including characteristics that describe plant communities and soil properties. Even with a limited sample size, use of UAV-derived mean, standard deviation, skew, kurtosis, and coefficient of variation spectral indices as predictors of ecological characteristics can produce reliable models for managers to assess restorations at the landscape scale. Overall, we found that mean graminoid cover, mean dead aboveground biomass, mean dry mass, and mean soil K could be predicted with UAV imagery. Despite having few acceptable predictions for the left-out validation sites, the significant relationships found for the four characteristics should be further explored by reducing the limitations discussed below. Although these findings suggest UAV imagery may be unable to predict the wide array of characteristics we attempted here, they provide evidence that UAVs may be able to give managers important information about plant community and soil property characteristics.

The characteristics that could be successfully predicted with drone-obtained imagery underscores the potential uses of multispectral UAV imagery in heterogeneous grasslands. Most UAV imagery has been limited to quantifying landcover types, single-species cover, vegetation biomass, and disturbance regimes (Zweig et al. 2015; Cruzan et al. 2016; Lorah 2018; Lussem et al. 2019; Melville et al. 2019). Further, many studies use more advanced, higher-cost sensors (e.g. hyperspectral) and height-derived information (which requires on-ground measurements) to classify the landscape, or do not yet take advantage of spectral distributions through upscaling to predict characteristics of interest (Cruzan et al. 2016; Lorah 2018; Lussem et al. 2019; Pérez et al. 2019). Even studies using other types of remotely sensed data (e.g. satellite or ground sensors) still rely on more advanced sensors or the direct relationship of single indices to response variables such as the relationship of NDVI to species richness (Ling et al. 2014; Wang et al. 2016). Here, we successfully predicted characteristics that can provide a range of ecological insights by calculating all potentially influential spectral indices and the distribution of these indices over a given site. Further, ridge regression is rarely used in the remote sensing literature, but has been used to investigate soil moisture, land temperature, and plant traits (Fan et al. 2017; Kang et al. 2018; Moreno-Martínez et al. 2018). Our approach provides a framework for future studies to apply ridge regression to UAV imagery, to build on this type of modeling for grassland metrics, and to further refine the outcomes to better understand landscape-scale variation in community and ecosystem properties.

While this study provides insight into site-level (60 × 60 m) estimates, it is limited by both sample size and spatial scale. Due to the collection methods for field data and lack of submeter GPS, we were restricted to making site-level inferences which confined our sample size to the number of study sites for which we had collected field data. Nonetheless, this is a scale relevant to management decisions, as multiple sites (one site approximately 0.36 ha) often fit in an individual restoration which are commonly several hectares in size. This would allow managers to see variations of mean characteristics across a single management unit. Additionally, our results suggest that an increase in sample size may increase the accuracy of models for metrics that were both well and poorly predicted by our models. This is illustrated by the deviations of excluded sites TCR and WH, which produced zero acceptable predictions. Although we tried to evenly pair sites by restoration age, TCR and WH are unique in that TCR is the only remnant in the study and WH is the only restoration closely adjacent to savanna habitats, with some level of woody encroachment. Because these two were randomly chosen to be left out of the training data, they were not properly represented, and our models were unable to make good predictions given the site conditions. In contrast, CCWE and HPW contain site conditions well represented throughout the model and had at least one acceptable prediction given our condition of falling below the cross-validation mRMSE. Unsurprisingly, this means that sites that generally are more similar to those in the training set will be better predicted by resulting models. We thus hypothesize that model accuracy would increase with a larger, more representative training model sample size (James et al. 2013).

By calculating statistical summaries based on several moments (i.e. mean, standard deviation, coefficient of variation, skew, kurtosis) of spectral indices across sites, we have created more informative predictors but at a loss of spatial inference. Coefficient magnitudes represent how influential each spectral index statistic is on the given response. We found that the skew subset generally outperformed the other model sets except when modeling graminoid cover. Graminoid cover was largely driven by indices' standard deviations and means across the site. Wang et al. 2016; 2018 used the coefficient of variation as a measure of spectral diversity for a hyperspectral sensor and related this to plant diversity on the fine scale (<10 cm). Spectral diversity can be measured in a variety of ways and has been linked to various chemical and physical plant traits (Asner & Martin 2009; Schweiger et al. 2018). Because of the high spatial resolution of our UAV imagery (12.5 cm), our data capture the spectral diversity of each vegetation index. Here, we captured spectral diversity using a variety of moments. The influence of different moments on successfully predicted responses varied (i.e. skewness, standard deviation, mean) indicating that spectral diversity should be explored in a variety of ways when predicting plant or soil characteristics. Because this study is limited to the 60 × 60 m sites, we are unsure of how well these moments would work on a different scale. Future UAV studies should investigate the use of calculated dispersion statistics at finer

spatial scales such as averaging pixels within a vegetation quadrat when high-precision GPS is available.

Our findings suggest that UAV imagery produces data that can model tallgrass prairie characteristics that are useful in restoration monitoring at a landscape scale. Characteristics relating to plant communities and soil properties can provide restoration practitioners with insight into how these variables are impacted by management decisions. For example, in tallgrass prairies, bison reintroductions are being used to promote more heterogeneous and diverse restorations through increasing forb abundance thought to be driven by a decrease in graminoid cover (Biondini et al. 1999; Knapp et al. 1999; Eby et al. 2014). UAV-derived models could allow practitioners to quantify the "success" of bison reintroductions by monitoring changes in graminoid cover. Further, soil potassium has been shown to correlate with the distribution of C_3 and C_4 plant communities and some forb genera (Barnes et al. 1983; Parker et al. 1993). With regular monitoring using UAV-derived models, temporal trends of potassium could be accurately estimated and paired with other temporal trends of plant communities.

Bridging the gap between our study and the routine use of UAV-based monitoring in grassland restoration management is closer than it may seem. This research used a low-cost UAV platform that is accessible to many restoration practitioners, and the FAA has created a straightforward path to becoming a UAV pilot through the small UAV rule (Wallace et al. 2017). With additional research supporting this study, the modeling of UAV imagery could be autonomous through a future web platform much like those in agriculture today (Koptilina 2019). Cloud-based computations could produce mapped metrics in relation to plant communities, plant traits, and soil properties providing a cheaper landscape approach to restoration monitoring and planning. The future of grassland restoration will inevitably rely on advances in technology, and future research must try to link these advances to restoration monitoring and management.

Acknowledgments

We would like to thank the staff at Nachusa, specifically B. Kleiman and C. Considine for assisting in site selection and field arrangements. We are also grateful to the many undergraduate students and volunteers from the Jones and Barber labs that assisted in data collection. This project was funded through the Friends of Nachusa Grasslands, the National Science Foundation under Grant NSF-DEB 1647502, and Northern Illinois University. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

LITERATURE CITED

Ali I, Cawkwell F, Dwyer E, Barrett B, Green S (2016) Satellite remote sensing of grasslands: from observation to management. Journal of Plant Ecology 9: 649–671

Anderson RC (2006) Evolution and origin of the central grassland of North America: climate, fire, and mammalian grazers. Journal of the Torrey Botanical Society 133:626–647

Anderson K, Gaston KJ (2013) Lightweight unmanned aerial vehicles will revolutionize spatial ecology. Frontiers in Ecology and the Environment 11: 138–146

Andrade BO, Koch C, Boldrini II, Vélez-Martin E, Hasenack H, Hermann J-M, Kollmann J, Pillar VD, Overbeck GE (2015) Grassland degradation and restoration: a conceptual framework of stages and thresholds illustrated by southern Brazilian grasslands. Natureza & Conservação 13:95–104

Asner GP, Martin RE (2009) Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests. Frontiers in Ecology and the Environment 7:269–276

Barnes PW, Tieszen LL, Ode DJ (1983) Distribution, production, and diversity of C_3- and C_4-dominated communities in a mixed prairie. Canadian Journal of Botany 61:741–751

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 57:289–300

Biondini ME, Steuter AA, Hamilton RG (1999) Bison use of fire-managed remnant prairies. Journal of Range Management 52:454

Bouckaert RR, Frank E (2004) Evaluating the replicability of significance tests for comparing learning algorithms. Pages 3–12.In: Dai H, Srikant R, Zhang C (eds) Advances in knowledge discovery and data mining. Springer Berlin Heidelberg, Berlin, Heidelberg, Germany. http://link.springer.com/10.1007/978-3-540-24775-3_3 (accessed 7 Aug 2020)

Cordell S, Questad EJ, Asner GP, Kinney KM, Thaxton JM, Uowolo A, Brooks S, Chynoweth MW (2017) Remote sensing for restoration planning: how the big picture can inform stakeholders: remote sensing for restoration planning. Restoration Ecology 25:S147–S154

Cruzan MB, Weinstein BG, Grasty MR, Kohrn BF, Hendrickson EC, Arredondo TM, Thompson PG (2016) Small unmanned aerial vehicles (micro-UAVs, drones) in plant ecology. Applications in Plant Sciences 4:1600041

Denny M, Benedetti-Cecchi L (2012) Scaling up in ecology: mechanistic approaches. Annual Review of Ecology, Evolution, and Systematics 43:1–22

Eby S, Burkepile DE, Fynn RWS, Burns CE, Govender N, Hagenah N, et al. (2014) Loss of a large grazer impacts savanna grassland plant communities similarly in North America and South Africa. Oecologia 175:293–303

Fan C, Rey SJ, Myint SW (2017) Spatially filtered ridge regression (SFRR): a regression framework to understanding impacts of land cover patterns on urban climate. Transactions in GIS 21:862–879

Friedman J, Hastie T, Tibshirani R (2010) Regularization paths for generalized linear models via coordinate descent. Journal of Statistical Software 33: 1–24. http://www.jstatsoft.org/v33/i01/ (accessed 10 Jan 2020).

Fuhlendorf SD, Engle DM, Kerby J, Hamilton R (2009) Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conservation Biology 23:588–598

González E, Rochefort L, Boudreau S, Hugron S, Poulin M (2013) Can indicator species predict restoration outcomes early in the monitoring process? A case study with peatlands. Ecological Indicators 32:232–238

Henwood WD (1998) Editorial—the world's temperate grasslands: a beleaguered biome. Parks 8:1–2

Hodgson JC, Mott R, Baylis SM, Pham TT, Wotherspoon S, Kilpatrick AD, Raja Segaran R, Reid I, Terauds A, Koh LP (2018) Drones count wildlife more accurately and precisely than humans. Methods in Ecology and Evolution 9:1160–1167

Holl KD (2017) Restoring tropical forests from the bottom up. Science 355: 455–456

Holmgren P, Thuresson T (1998) Satellite remote sensing for forestry planning—a review. Scandinavian Journal of Forest Research 13:90–110

James G, Witten D, Hastie T, Tibshirani R (eds) (2013) An introduction to statistical learning: with applications in R. Springer, New York

Kang J, Jin R, Li X, Zhang Y, Zhu Z (2018) Spatial upscaling of sparse soil moisture observations based on ridge regression. Remote Sensing 10:192

Kelly M, Di Tommaso S (2015) Mapping forests with Lidar provides flexible, accurate data with many uses. California Agriculture 69:14–20

Klopf RP, Baer SG, Bach EM, Six J (2017) Restoration and management for plant diversity enhances the rate of belowground ecosystem recovery. Ecological Applications 27:355–362

Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG (1999) The keystone role of bison in North American tallgrass prairie. Bioscience 49:39

Koptilina DM (2019) IT-technologies in agriculture on the example of "drones". IOP Conference Series: Earth and Environmental Science 274:012082

Ling B, Goodin D, Mohler R, Laws A, Joern A (2014) Estimating canopy nitrogen content in a heterogeneous grassland with varying fire and grazing treatments: Konza prairie, Kansas, USA. Remote Sensing 6:4430–4453

Lorah P (2018) Using drones to generate new data for conservation insights. International Journal of Geospatial and Environmental Research 5:1–13

Lu B, He Y (2017) Species classification using Unmanned Aerial Vehicle (UAV)-acquired high spatial resolution imagery in a heterogeneous grassland. ISPRS Journal of Photogrammetry and Remote Sensing 128:73–85

Lussem U, Bolten A, Menne J, Gnyp ML, Schellberg J, Bareth G (2019) Estimating biomass in temperate grassland with high resolution canopy surface models from UAV-based RGB images and vegetation indices. Journal of Applied Remote Sensing 13:1

Melville B, Fisher A, Lucieer A (2019) Ultra-high spatial resolution fractional vegetation cover from unmanned aerial multispectral imagery. International Journal of Applied Earth Observation and Geoinformation 78:14–24

Mishra N, Mainali K, Shrestha B, Radenz J, Karki D (2018) Species-level vegetation mapping in a Himalayan treeline ecotone using unmanned aerial system (UAS) imagery. ISPRS International Journal of Geo-Information 7:445

Moreno-Martínez Á, Camps-Valls G, Kattge J, Robinson N, Reichstein M, van Bodegom P, et al. (2018) A methodology to derive global maps of leaf traits using remote sensing and climate data. Remote Sensing of Environment 218:69–88

Nowak MM, Dziób K, Bogawski P (2019) Unmanned aerial vehicles (UAVs) in environmental biology: a review. European Journal of Ecology 4:56–74

Owensby CE, Coyne PI, Ham JM, Auen LM, Knapp AK (1993) Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO2. Ecological Applications 3:644–653

Parker IM, Mertens SK, Schemske DW (1993) Distribution of seven native and two exotic plants in a tallgrass prairie in southeastern Wisconsin: the importance of human disturbance. American Midland Naturalist 130:43

Pérez DR, Pilustrelli C, Farinaccio FM, Sabino G, Aronson J (2019) Evaluating success of various restorative interventions through drone- and field-collected data, using six putative framework species in Argentinian Patagonia. Restoration Ecology 28:A44–A53

R Core Team (2019). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reif MK, Theel HJ (2017) Remote sensing for restoration ecology: application for restoring degraded, damaged, transformed, or destroyed ecosystems: remote sensing for restoration ecology. Integrated Environmental Assessment and Management 13:614–630

Rowe HI (2010) Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration. Restoration Ecology 18:253–262

Schweiger AK, Cavender-Bares J, Townsend PA, Hobbie SE, Madritch MD, Wang R, Tilman D, Gamon JA (2018) Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. Nature Ecology & Evolution 2:976–982

Swenson NG (2014) Functional and phylogenetic ecology in R. Springer UseR! Series, Springer, New York

Tibshirani R (1996) Regression shrinkage and selection via the Lasso. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 58:267–288

Underwood N, Hambäck P, Inouye BD (2005) Large-scale questions and small-scale data: empirical and theoretical methods for scaling up in ecology. Oecologia 145:176–177

Wallace RJ, Loffi JM, Ison AG, Courtney RM (2017) Evaluating methods of FAA regulatory compliance for educational use of unmanned aircraft systems (UAS). Collegiate Aviation Review International 35:25–51. https://ojs.library.okstate.edu/osu/index.php/CARI/article/view/7434/6834 (accessed 17 Dec 2019)

Wang R, Gamon JA, Cavender-Bares J, Townsend PA, Zygielbaum AI (2018) The spatial sensitivity of the spectral diversity–biodiversity relationship: an experimental test in a prairie grassland. Ecological Applications 28:541–556

Wang R, Gamon J, Montgomery R, Townsend P, Zygielbaum A, Bitan K, Tilman D, Cavender-Bares J (2016) Seasonal variation in the NDVI–species richness relationship in a prairie grassland experiment (Cedar Creek). Remote Sensing 8:128

Weber S (1999) Designing seed mixes for prairie restorations: revisting the formula. Ecological Restoration 17:196–201

White RP, Murray S, Rohweder M (2000) Pilot analysis of global ecosystems: grassland ecosystems. World Resources Institute, Washington D.C.

Wilhelm G, Rericha L (2017) Floar of the Chicago region: a floristic and ecological synthesis. Indiana Academy of Science, Indianapolis, Indiana

Williams D (2010) The Tallgrass Prairie Center guide to seed and seedling identification in the upper Midwest. 1st edition. University of Iowa Press, Iowa City, Iowa

Xie Y, Sha Z, Yu M (2008) Remote sensing imagery in vegetation mapping: a review. Journal of Plant Ecology 1:9–23

Xu Y, Smith SE, Grunwald S, Abd-Elrahman A, Wani SP, Nair VD (2018) Estimating soil total nitrogen in smallholder farm settings using remote sensing spectral indices and regression kriging. Catena 163:111–122

Zweig CL, Burgess MA, Percival HF, Kitchens WM (2015) Use of unmanned aircraft systems to delineate fine-scale wetland vegetation communities. Wetlands 35:303–309

Supporting Information

The following information may be found in the online version of this article:

Table S1. Ecological characteristics of interest for prediction based on UAV monitoring.
Table S2. Table of all spectral indices, their corresponding formulas, and references.
Table S3. Results of 10 × 5-fold cross validation using the 15 training restoration sites for prediction of mean ecological characteristics for each model.
Table S4. Results of 10 ×5-fold cross validation using the 15 training restoration sites for prediction of standard deviation ecological characteristics for each model.
Figure S1. Correlations between mean spectral indices.
Figures S2-S5. Coefficient magnitudes from repeated 10 × 5-fold cross validation for each successfully predicted ecological characteristic.

Guest Coordinating Editor: Jodi Price

Received: 8 September, 2020; First decision: 1 November, 2020; Revised: 10 December, 2020; Accepted: 10 December, 2020