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RESEARCH ARTICLE

Aiming for the optimum: examining complex relationships among sampling regime, sampling density and landscape complexity to accurately model resource availability

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Abstract
Context Obtaining accurate and precise maps of landscape features often requires intensive spatial sampling and interpolation. The data required to generate reliable interpolated maps varies with sampling density and landscape heterogeneity. However, there has been no rigorous examination of sampling density relative to landscape characteristics and interpolation methods.
Objectives Our objective was to characterize the 3-way relationship among sampling density, interpolation method, and landscape heterogeneity on interpolation accuracy and precision in simulated and in situ landscapes.
Methods We simulated landscapes of variable heterogeneity and sampled at increasing densities using gridded and random strategies. We applied three local interpolation methods (i.e., Inverse Distance Weighting, Universal Kriging, and Nearest Neighbor) to the sampled data and estimated accuracy (slope and intercept) and precision (R^2) between interpolated surfaces and the original surface. Finally, we applied these analyses to in situ data using a normalized difference vegetation index raster collected from pasture with various resolutions.
Results In our simulations, all interpolation methods and sampling strategies yielded similar accuracy and precision except in the case of Universal Kriging with random sampling. Additionally, low heterogeneity and increasing sample density improved both accuracy and precision, with cross-validation slopes and R^2 values approaching optimal values. In situ analysis demonstrated that heterogeneity decreased with resolution. Nearest Neighbor under both sampling strategies and Universal Kriging using the gridded sampling strategy had the highest accuracy and precision. Decreased heterogeneity and increased sampling density improved accuracy and precision for all combinations of interpolation method and sampling strategies.
Conclusions Heterogeneity of the landscape is a major influence on the accuracy and precision of interpolated maps. There is a need to create structured tools to aid in determining sampling design

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most appropriate for interpolation methods across landscapes of various heterogeneity.

Keywords Optimal sampling · Landscape interpolation · Heterogeneity · Kriging · Inverse distance weighting · Nearest neighbor

Introduction

Measurement of ecological processes at a landscape level requires a thorough understanding of spatial relationships of the target resource across landscape gradients. Originally focused within landscape ecology or biogeography (Turner and Gardner 2015), measuring landscape heterogeneity has emerged as an important research front in movement ecology, agroecology, disturbance ecology, precision agriculture, and other landscape-level sciences focused on ecological processes and the spatial configuration of resources (Carlile et al. 1989). For example, spatial configuration of forage mass and quality influence landscape utilization and grazing pressure by cattle (*Bos taurus*) and bison (*Bison*; Kohl et al. 2013) and browse selection by moose (*Alces*; Balluffi-Fry et al. 2020; Leroux et al. 2017). Further, spatial sampling is commonly used in agricultural fields to identify areas which may need alternative management strategies, such as increased nutrient inputs (Franzen 1995), or designate wildlife habitat and conservation areas (Burger 2019), which can result in economic and environmental improvements (Sun and Brus 2021). As such, a common objective of landscape-level studies is the creation of data layers or maps that accurately portray the distribution forage biomass, nutrient density, species distribution, habitat, soil quality or landscape condition (Turner and Gardner 2015).

Given that complete measurement of resources across the landscape is virtually impossible, the full landscape of resource availability is often approximated by sampling predetermined locations and performing spatial interpolation to estimate resource values at unobserved locations (Li and Heap 2008). Accuracy and precision of estimated resource values generally depend upon: (1) the sampling strategy employed (Cobby et al. 1985); (2) number of samples collected (Tsutsumi et al. 2007); (3) the degree of variability among samples across the landscape (Sun and Brus 2021); (4) the interpolation method used (Li and Heap 2008); and (5) the spatial scale under investigation (Wu 2004; Turner and Gardner 2015). These effects have been individually examined, often in detail. For example, ecologists have utilized gridded, random, stratified random, and cyclic sampling strategies in hopes of identifying some optimum strategy that efficiently and accurately describes a landscape variable (Burrows et al. 2002; Turner and Gardner 2015). Additionally, the minimum number of samples required to accurately model the landscape must be considered given that sample collection is often labor and cost intensive (Burrows et al. 2002; Tsutsumi et al. 2007; Turner and Gardner 2015). Spatial heterogeneity is driven by underlying biotic and abiotic processes and their interactions. For instance, the heterogeneity of available forage can be driven by interactions between grazing patterns of herbivorous animals, soil type, moisture availability and infiltration, slope gradient, plant species distribution, and soil microbe populations (Barthram et al. 2005; Hirata et al. 2012). Interpolation methods provide a means of creating a continuous surface from point processes; however, selection of the best method for a specific process and sample strategy is difficult (Li and Heap 2008). Finally, defining the appropriate spatial scale matched with the correct sampling strategy and sample number is required to accurately and precisely model landscape resources (Wiens 1989; Fryxell et al. 2008; Turner and Gardner 2015; Sun and Brus 2021).

Clearly there has been substantial attention to each of these components regarding spatial sampling; however, there is not yet a comprehensive demonstration of how these factors interact to determine the accuracy and precision of common interpolation strategies. In keeping with recent calls for critical utilization of currently existing metrics of landscape structure and scale (Turner and Gardner 2015), herein we use well-defined metrics with clear application to examine the relationship among sampling strategy, sampling density, and landscape heterogeneity within the context of scale (Wu 2004). Particularly, we focus on systematic and random sampling strategies because these are commonly used techniques for landscape sampling in agriculture and forestry (e.g., Burrows et al. 2002; Jordan et al. 2003; Clark et al. 2008; Sun and Brus 2021). We generate multiple simulated landscapes representing a gradient of landscape heterogeneity and perform interpolation using 3 common geostatistical techniques (i.e., Nearest Neighbor, Universal Kriging, Inverse Distance Weighting) to estimate continuous surfaces from derived samples (Li and Heap 2008). We then explicitly consider how landscape heterogeneity interacts with sample size and the interpolation method itself to determine the accuracy (i.e., a 1-to-1 relationship) and precision (i.e., goodness-of-fit; R^2) between predicted and observed surfaces (Fig. 1). Finally, we repeat these procedures using in situ data to validate our findings from simulation with empirical data, and to evaluate interpolation accuracy as spatial resolution decreases.

Methods

Simulated landscapes

We simulated a series of landscapes, similar to, Matthiopoulos et al. (2015), using the *bkde2D* kernel density function in the `kernsmooth` package in program R (Wand, 2021). Landscape dimensions and average resource availability were held at 600 × 600 pixels and 50 units, respectively. Resources were distributed across the landscape around one resource epicenter and smoothed outward according to unique bandwidths (analogous to the extent to which resources were spread) ranging from 30 to 740. This created a landscape dataset of 300 unique landscape simulations with a broad representation of heterogeneity. Then, we measured landscape heterogeneity for each simulated landscape using rho (Tsutsumi et al. 2007), with higher rho values indicating greater landscape similarity and autocorrelation structure. Rho was calculated as the squared mean divided by the squared standard deviation of the landscape resource (μ^2/σ^2; Tsutsumi et al. 2007).

We created sampling densities ranging from 0.28 to 2.8 samples per 10,000 pixels, which equate to 10 to 100 locations increased in 1-step increments (range = 10 – 100 samples), resulting in 91 unique sampling densities. Sampling points were created via regular gridded and uniform spatial random sampling using the *spsample* function from R package `sp` (Hijmans et al. 2021). Gridded sampling points were set a specified distance apart at the intersection of evenly spaced gridlines laid across the landscape. For both gridded and random sampling strategies, and for each simulated landscape × sample number combination, we extracted resource values from simulated landscape surfaces at each sampling location and used extracted values to create predicted landscape surfaces using each of 3 interpolation methods. First, we used Universal Kriging by implementing the *autokrige* function within the `automap` R package (Hiemstra 2013; Gräler et al. 2016) to create a kriged surface. Next, we created an Inverse Distance Weighting interpolated surface with the *idw* function available within the `gstat` R package (Gräler et al. 2016). Finally, we created a Nearest Neighbor interpolated surface using Thiessen polygons and identifying the closest observed point from which to interpolate using the *whichmin* function (Brunson 2019; R Core Team 2021). Interpolated landscape surfaces created from each combination of interpolation method, sampling strategy, and sampling density were then compared to their original simulated landscape using simple linear regression between the interpolated and true landscape surface with the *lm* function (R Core Team 2021). This is a common cross-validation technique whereby performance of a defined model (here, an interpolation method and sampling density) is evaluated based on 1-to-1 agreement between the predicted (interpolated) and observed (true) surface (Harrell, 2001; Tedeschi 2006). Accuracy of the interpolation model is indicated when the intercept of the regression equals 0 and the slope equals 1, and precision when the R^2 value approaches 1 (Harrell 2001; Tedeschi 2006). This provided a robust framework from which to make comparisons among

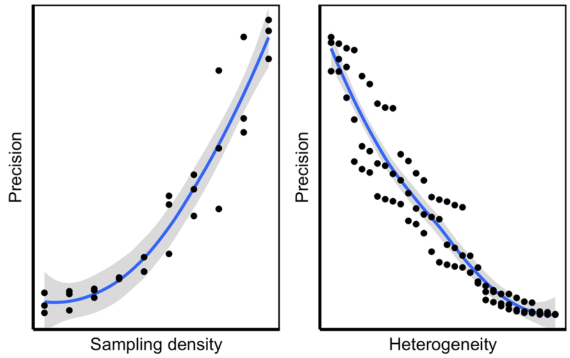

Fig. 1 Conceptual representation of the expected precision (R^2) due to sampling density (left) and an increase in landscape heterogeneity (right)

interpolation method, sampling strategy, and sampling density given decreasing levels of landscape heterogeneity.

To see whether methods performed similarly, we compared R^2 values for each sampling strategy and interpolation method using Pearson Correlation Coefficients calculated via the *cor* function and pairwise comparisons via the *t.test* function, in the `base` R package (R Core Team 2021). For Pearson Correlation Coefficients we determine high correlation with a coefficient > 0.70 (Nettleton, 2014) and for t-tests, we adjusted significance for multiple comparisons using the Bonferroni correction given the number of comparisons (Ott & Longnecker 2016). We then examined the effect of landscape surface heterogeneity (rho), interpolation method (Inverse Distance Weighting, Nearest Neighbor, or Universal Kriging), sampling strategy (gridded or random), and sampling density (n) on accuracy and precision of interpolated landscape surfaces using generalized linear regression with the *glm* function (R Core Team 2021). We tested post-hoc mean differences using the *emmeans* function in the `emmeans` R package (Lenth et al. 2018). Effect comparisons were demonstrated using density and line plots with the *geom_density* and *geom_line* functions in the `ggplot2` package (Wickham et al. 2019). Finally, we ran a series of beta regression models using the `betareg` R package (Cribari-Neto and Zeileis 2010) to evaluate the effect of landscape heterogeneity (rho), sampling strategy and density, and interpolation method on the precision (R^2) value obtained from interpolated versus true surface cross validations (values fell between 0 and 1, range = 0.001–0.98). Given the large variation in raw values (Figure S1), we used beta regression model to create 3-dimensional plot using *wireframe* within the `lattice` R package (Sarkar 2008).

Application to in situ *data from pastoral landscape*

Following our simulation exercise, we applied the same approach to remotely sensed data collected from an experimental grazing facility in Starkville, Mississippi, USA (33 26′07 N 88 48′03 W; Fig. 2) in June 2019. The pasture was ~ 9.35 ha and consisted of a mixture of tall fescue (*Festuca arundinacea*), bermudagrass (*Cynodont dactylon*), and annual ryegrass (*Lolium multiflorum*), which was inter-seeded across one-half of the pasture in fall 2018. Remotely sensed imagery was collected using a Red Edge MX hyperspectral camera (MicaSense®, Seattle, WA, USA) mounted on a Matrice 100 unmanned aerial system (DJI, Shenzhen, Guangdong, China). The camera collected reflectance in the green, blue, red, near-infrared, and red-edge spectral bands at 8.5 cm resolution from a flight altitude of 122 m above ground level with 80% overlap. After imagery was collected, individual pictures were mosaiced utilizing Pix 4D

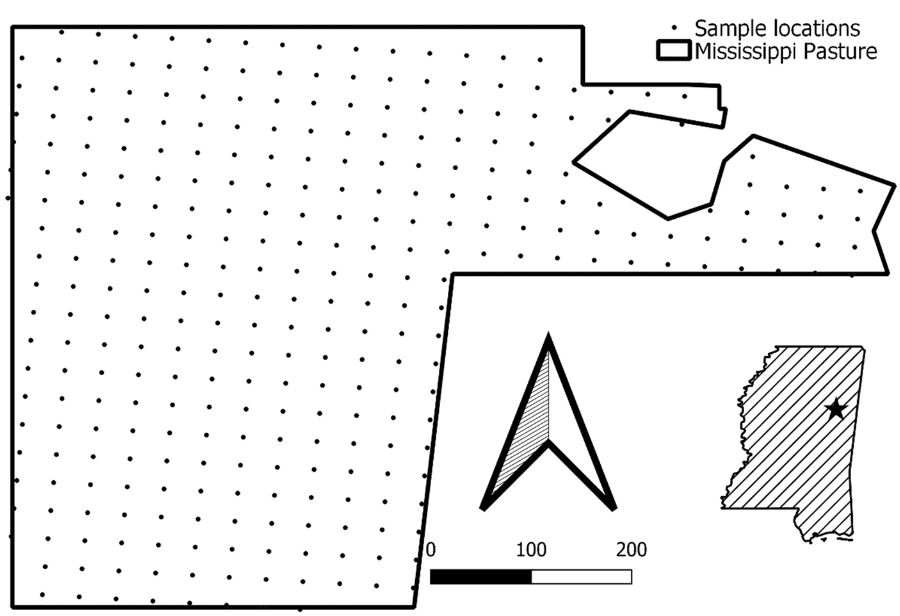

Fig. 2 The 307 forage sampling locations (equating to a sampling density of 32 samples/ha) used to collect forage samples during an 11-month grazing study in 2019 in a pasture in Starkville Mississippi, USA (inset)

software (Pix 4D Inc. Prilly, Switzerland). Last, we calculated the normalized difference vegetation index (NDVI) at each pixel following standard procedure (Huete et al. 2002).

We conducted an identical analysis to that used in the simulated landscapes, increasing resolution from 0.085 to 100 m at 1 m increments and measured accuracy and precision metrics (cross-validation model intercepts, slope, and R^2) to observe the consequences of decreasing heterogeneity on the landscape (Wu 2004). At each resolution, resampling was conducted at increasing rates of sample density, ranging from 1 to 185 samples per hectare (equating to 0.003 to 0.49 samples/10,000 pixels at a 0.085 m resolution and 26 to 261,515 samples/10,000 pixels at 100 m resolution) with a minimum of 9 and maximum 1726 actual samples collected at each resolution. Sampling points were identified using gridded and random sampling designs identical to the simulated procedures outlined above. Interpolation techniques, identical to those used for simulated landscapes, were applied to each combination of landscape resolution (i.e., heterogeneity measured with rho), interpolation method, sampling strategy, and sampling density, and then compared to the original landscape to measure interpolation accuracy and precision, resulting in 111,000 interpolation attempts. All simulations and applications of simulation methods to in situ data were performed in R version 3.6.3 (R Core Team 2021).

Results

Simulated landscapes

We depict the expected relationship of the predictive accuracy and precision for each interpolation method (Fig. 1) as landscape complexity decreases across simulated landscapes (Fig. 3). Across simulated landscapes, average values of rho were 98 and ranged from 0 (most heterogeneous) to 333 (least heterogenous; Figure S2). In total, 163,800 interpolations were attempted but 163,292 were successful because 508 simulation attempts using original kriging failed to fit a variogram when using the grid sampling strategy. This provided a robust dataset from which to make inference for each combination of interpolation method, sampling strategy, sampling density, and landscape heterogeneity.

To evaluate the effect of interpolation method, sampling strategy, sampling density, and landscape heterogeneity on precision and accuracy of interpolated surfaces, we conducted both Pearson correlations, a generalized linear model, and paired t-tests. Pearson correlation tests between interpolated and true surfaces demonstrated substantial differences among combination of interpolation method and sampling strategy for metrics of accuracy and precision (Table S1 –S6). For accuracy, correlation coefficients indicated that only Inverse Distance Weighting and Nearest Neighbor gridded sampling intercepts were similar (i.e., $r \geq 0.70$, Table S1), while there were no slopes across interpolation method and sampling strategies that were similar (Table S3). However, pairwise t-test demonstrated varying and significant differences between both cross-validation intercepts and slopes across both interpolation method and sampling strategy (Table S2 and S4), with Universal Kriging paired with random points showing the greatest divergence in accuracy from all other methods. For precision (i.e., R^2 values), 5 interpolation methods and sampling strategies performed similarly according to both correlation coefficients and paired differences (Table 1. Pearson correlations between linear model intercept values for 3 interpolation methods (Inverse Distance Weighting, Nearest Neighbor, or Universal Kriging) and 2 sampling strategies (gridded or random points).S5 and S6).

Generalized linear regressions for accuracy (cross-validation intercept and slope) and precision (cross-validation R^2) revealed that interpolation method combined with sampling strategy provided the largest effect on both the accuracy and precision of the interpolated landscape surface, (Fig. 4) compared to landscape heterogeneity (Fig. 5 and 7). Universal Kriging paired with random sampling strategy over-predicted resource availability and provided the least accurate and precise interpolation sampling strategy as demonstrated by a positive intercept greater than 0, slope less than 1 (Fig. 4 a, c), and the lowest R^2 values (Fig. 4e). At greater sampling densities, Universal Kriging with random sampling intercepts were closer to 0, slopes were closer to 1, and precision increased, though values were always well below idealized values (Fig. 4b, d, f). Conversely, for both sampling strategies, Inverse Distance Weighting under-predicted resource availability, with cross-validation model intercepts and

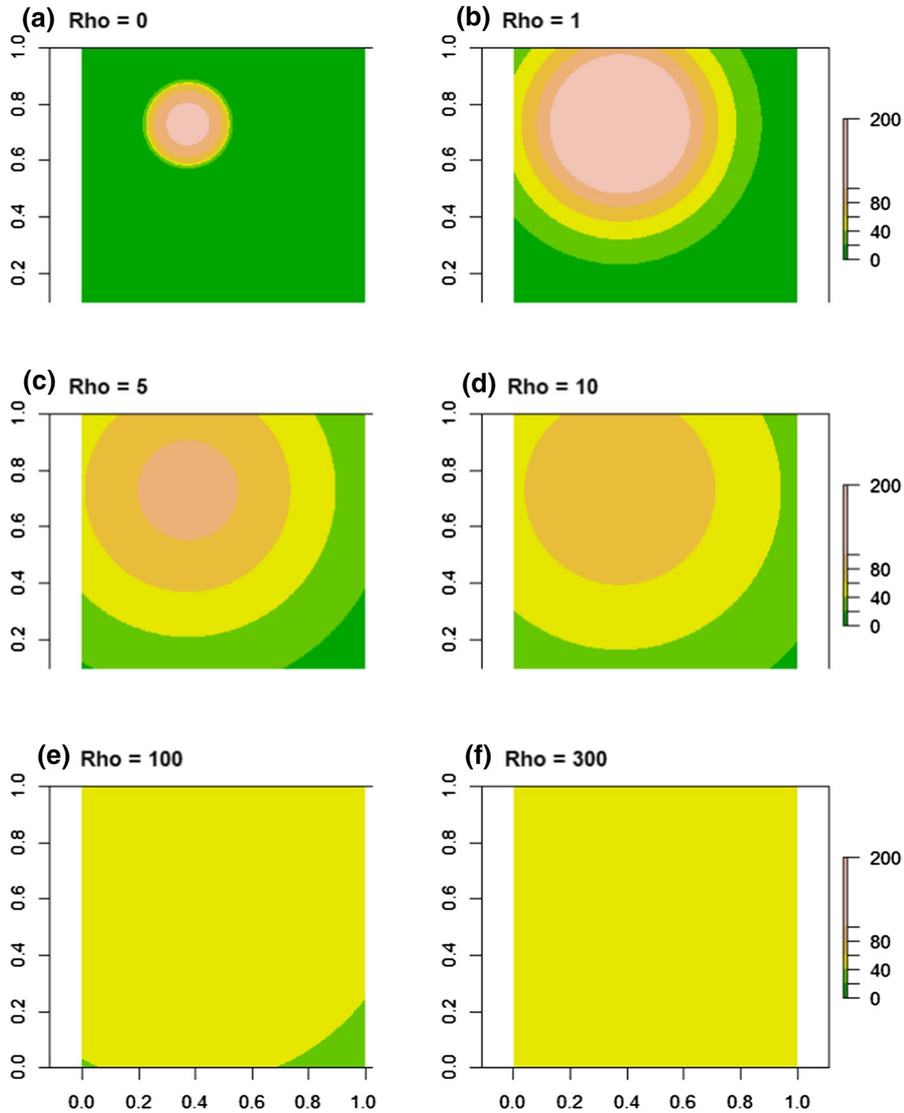

Fig. 3 Examples of simulated landscapes, each containing the same volume of resources, but with varying gradients around the resource epicenter, resulting in heterogeneities ranging from 0 (most heterogeneous) to 300 (least heterogeneous)

slopes ranging from -10 to -40, and slopes 1.0 to 1.8, respectively (Fig. 4 a, c). Intercepts and slopes for Inverse Distance Weighting did get closer to 0 and 1, respectively, as sampling density increased although these changes were marginal (Fig. 4b, d). However, Inverse Distance Weighting predicted with similar precision as other interpolation methods and sampling strategies across sampling densities other than random sampling with Universal Kriging (Fig. 4e, f). Both sampling strategies with Nearest Neighbor produced the most accurate predictions across all sampling densities (Fig. 4). All pairs of interpolation methods and sampling strategies interacted in a positive manner with increasing sampling density and lower landscape heterogeneity demonstrated in Fig. 4 (panels b, d, and f). The positive interaction is most pronounced in Universal Kriging paired with random sampling, and Inverse Distance Weighting where both gridded and random sampling strategies demonstrated increased accuracy and precision (approached 0 and 1 for cross-validation model intercept and slope, respectively) as sample density increased. In all instances, we see cross-validation model intercept, slope, and R^2 approach theoretical perfect agreement between interpolated and original landscape surfaces (0, 1, and 1 for cross-validation model intercept, slope, and R^2, respectively).

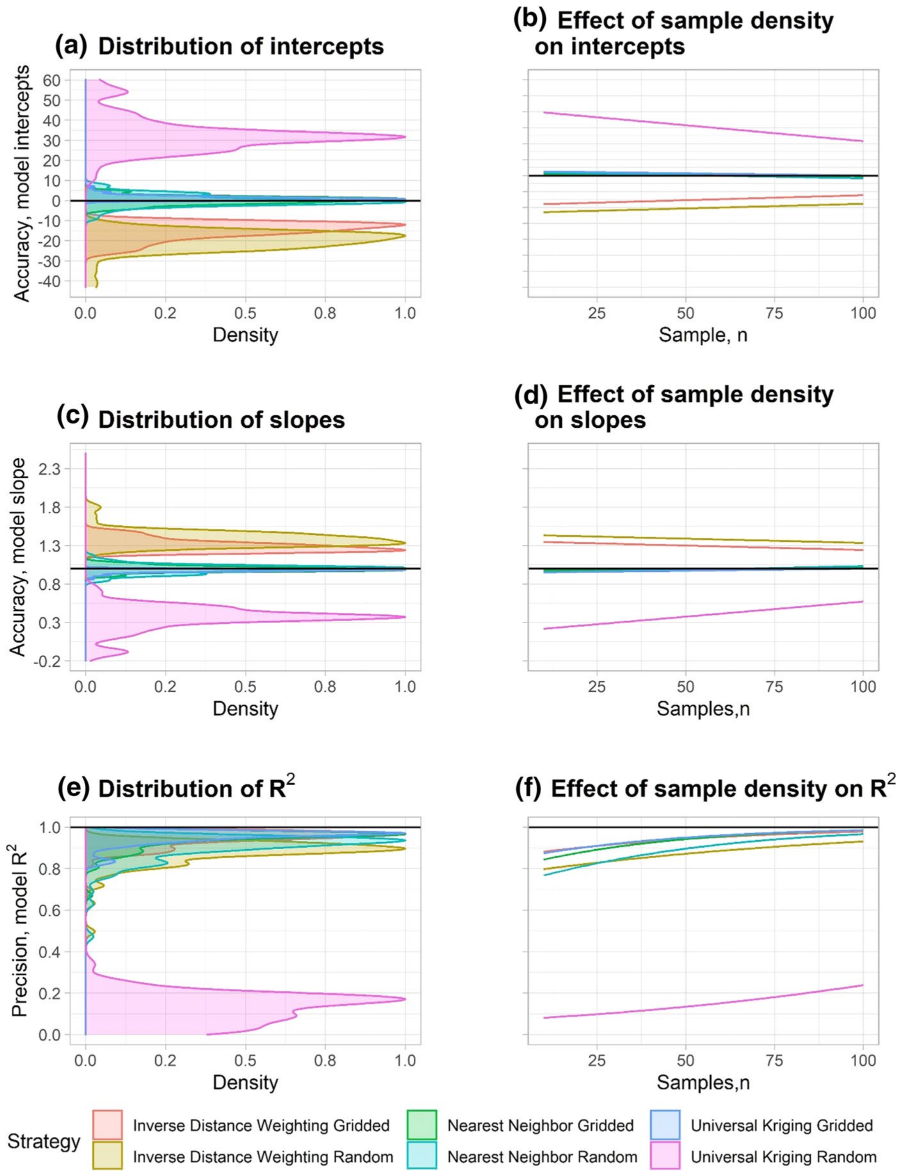

Fig. 4 Effects of interpolation method (Inverse Distance Weighting, Nearest Neighbor, or Universal Kriging), sampling strategy (Gridded or Random) and sampling density (n) on the accuracy (cross-validation model intercepts and slopes) and precision (R^2 values) for simulated landscapes. Perfect accuracy of 0 and 1 for intercepts and slopes, respectively, and perfect precision of 1 for R^2 values are indicated by solid horizontal black lines. Density distributions of model a) intercepts, c) slopes, and e) R^2 values, along with the change in b) intercepts, d) slopes and f) R^2 as sampling density increases is provided

Finally, we focused on the effect of landscape heterogeneity and its interaction with interpolation method, sampling strategy, and sample density on interpolation precision (R^2) using beta-regression model. Results from simulated landscapes indicated that all combinations of interpolation methods and sampling strategies had similar levels of precision (values between 0.8 and 1.0) except for Universal Kriging combined with random sampling strategy (Fig. 4 and 5). The greatest precision for these interpolation-sampling combinations occurred at low levels of landscape heterogeneity regardless of sampling density and values beyond 10 approached a 1:1 relationship (Fig. 5). In contrast, Universal Kriging under a random sampling strategy yielded a convex relationship with consistently low precision before increasing markedly as sampling density increased; landscape heterogeneity had no effect on precision (Fig. 5).

Application to in situ *pastoral landscape*

We decreased the resolution of the pasture (Figure S3) in 1-m increments from 0.085 to 100 m, which resulted in moderate levels of heterogeneity (rho = 34

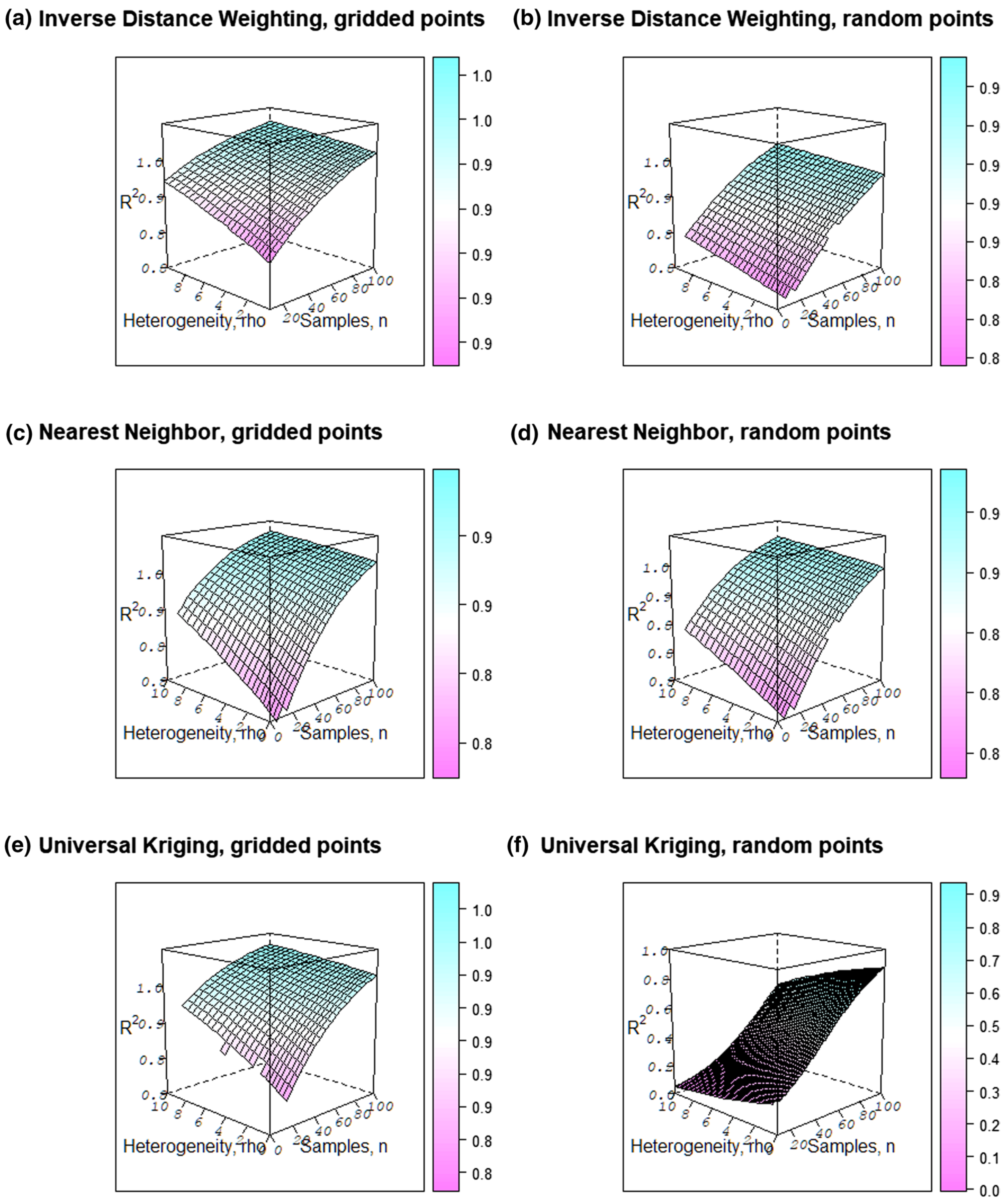

Fig. 5 Precision (R^2) of Inverse Distance Weighting, Nearest Neighbor, and Universal Kriging interpolation applied to simulated landscapes at increasing sample densities and landscape heterogeneities (with 0 being more heterogeneous) using a systematic or random sampling strategy. Raw values are provided in Supplementary Fig. 3 and values for some heterogeneities < 10 (given the rates of change at these values of rho) are provided in Supplementary Tables 4–9

– 111) compared to simulated landscapes. Again, there were large deviations for intercepts, slopes, and R^2 values for most interpolation methods and sampling techniques, although Nearest Neighbor under both sampling strategies and gridded Universal Kriging had distributions of values closest to idealized values (Fig. 6). Increased sampling density allowed the intercepts and slopes of these interpolation-sampling combinations to get closer to 0 and 1, respectively, although Universal Kriging with gridded sampling obtained the best precision (Fig. 6). Decreased landscape heterogeneity and increasing sample density were associated with increased precision from all interpolation techniques, although the level of precision was again highest for Universal Kriging with gridded sampling (Fig. 6 and 7). In this case, there was a greater effect of landscape heterogeneity on precision compared to sampling density (Fig. 7). Gridded sampling resulted in the highest accuracy values for Universal Kriging, and this performance was matched in random sampling for Nearest Neighbor and Inverse Distance Weighting (Fig. 6 and 7). Decreasing landscape heterogeneity increased the accuracy and precision of both Inverse Distance

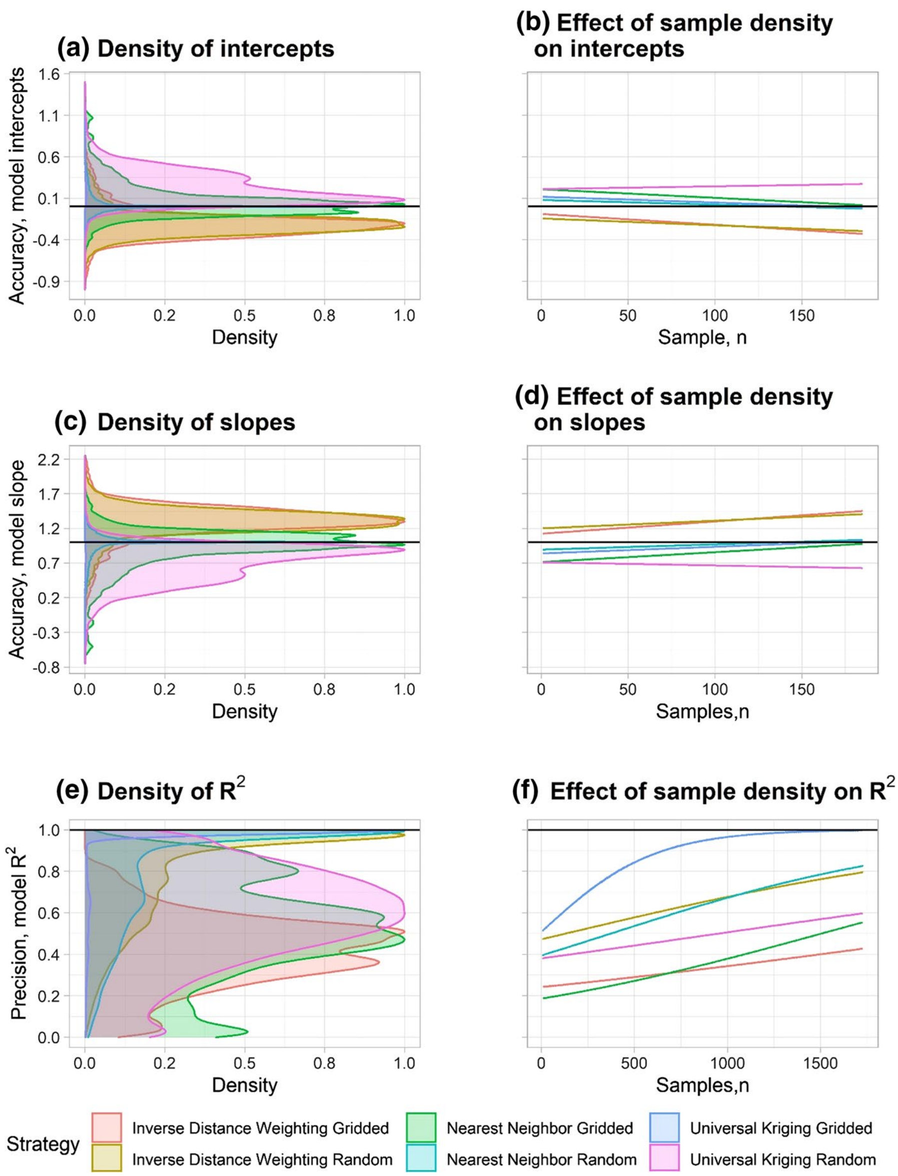

Fig. 6 Effects of interpolation method (Inverse Distance Weighting, Nearest Neighbor, or Universal Kriging), sampling strategy (Gridded or Random) and sampling density (n) on the accuracy (cross-validation model intercepts and slopes) and precision (R^2) values of interpolated landscapes applied to NDVI values collected via remote sensing, controlling for the effect of landscape heterogeneity (rho). Perfect accuracy of 0 and 1 for intercepts and slopes, respectively, and perfect precision of 1 for R^2 values are indicated by solid horizontal black lines

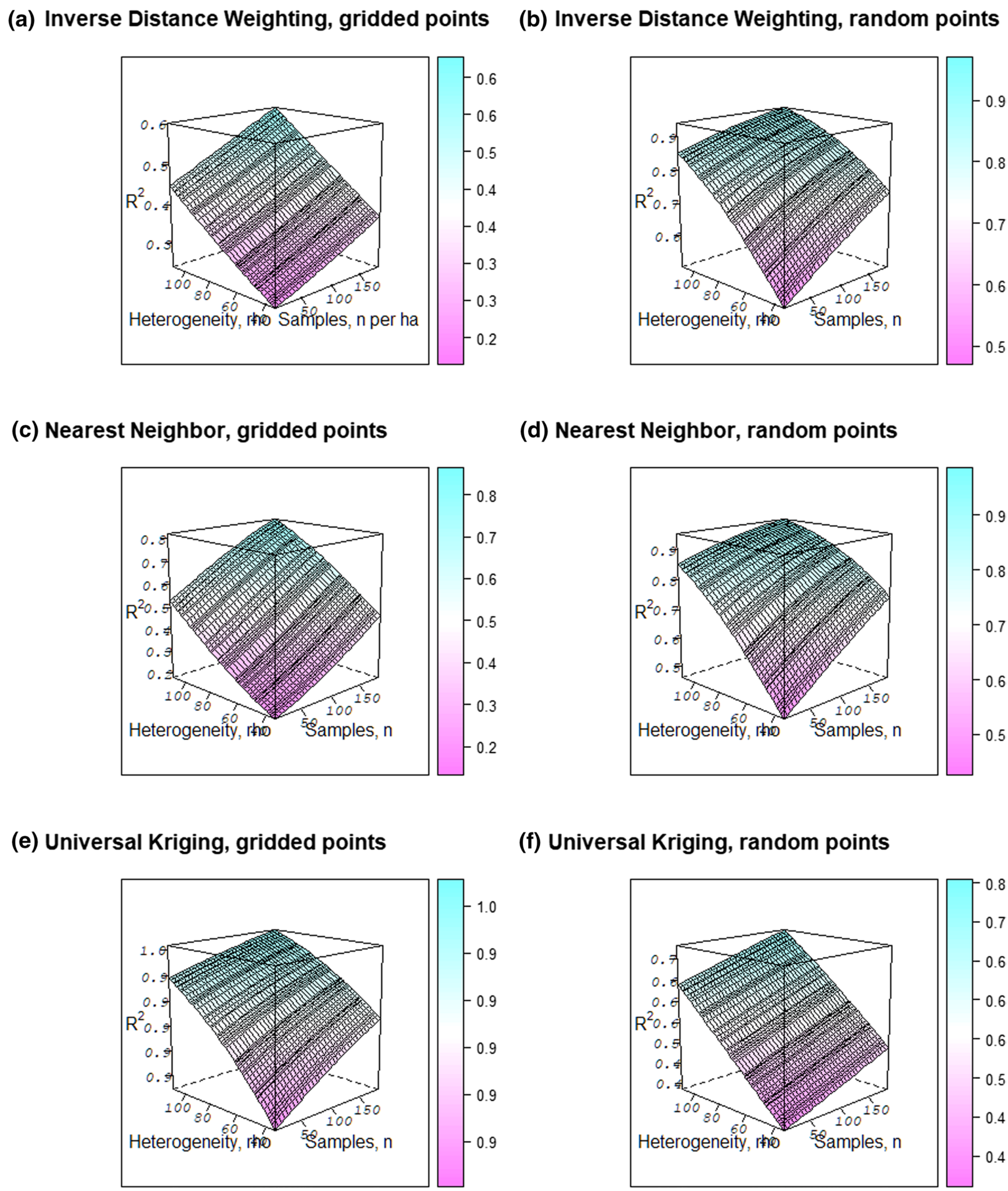

Fig. 7 Precision (R^2) of Inverse Distance Weighting, Nearest Neighbor, and Universal Kriging interpolation applied to NDVI values collected via remote sensing at increasing sample densities and decreasing landscape resolution to reduce heterogeneity (with 0 being more heterogeneous) using a gridded or random sampling strategy

Weighting and Nearest Neighbor interpolation (Fig. 7). We observed qualitative agreement between our simulation analysis and our application to in situ pastoral landscapes except in the case of Universal Kriging with random sampling.

Discussion

Our objective was to evaluate the ability of different interpolation methods to produce accurate and precise representations of a known landscape under variable landscape heterogeneity, sampling strategies, sample densities, and spatial scales. Our simulations and use of in situ pastoral NDVI data showed that both accuracy and precision are strongly affected by the interpolation method and sampling density (Fig. 4 and 6), and that the choice of interpolation method, sampling strategy and sampling density interact with landscape heterogeneity to have substantial influence on the precision and accuracy of interpolated landscapes (Tsutsumi et al. 2007). Accuracy and precision are affected negatively by increased landscape heterogeneity, with decreased heterogeneity substantially improving the accuracy and precision of interpolated landscape surfaces. However, in the case of simulated data, the effect of landscape heterogeneity could be overcome by employing gridded sampling strategies, increasing sample density, and carefully selecting the interpolation method (Fig. 5). In contrast, while careful consideration of the interpolation method and sampling strategy also applied to NDVI data, there was a strong effect of landscape heterogeneity, which would likely not be overcome by sampling density across interpolation methods (Fig. 7). For both datasets, trends in sampling density and heterogeneity indicate there are threshold levels of sampling given the heterogeneity encountered (Fig. 5 and 7).

We demonstrated that random sampling strategies, especially when paired with the Universal Kriging method for interpolation, provides the least accurate and precise interpolated surface. This is surprising given it has been shown in other landscape simulations that random sampling is superior for estimating forage biomass on the landscape (Tsutsumi et al. 2007) and better captures the necessary lag distance within a pine wood stands (Burrows et al. 2002). As such, it is suggested that a systematic approach to landscape sampling better captures landscape structure than does a random sampling strategy. While there has been use of other sampling strategies including transect sampling, stratified random sampling, and cyclic sampling (Sun and Brus 2021), transect and stratified random sampling combine methods inherent to both grid and completely random strategies, and likely would have similar results to the ones obtained in this study. In contrast, cyclic sampling strategies attempts to match the sampling distance to the expected spatial autocorrelation pattern across the landscape and reduce the number of redundant points sampled; however, implementation requires prior knowledge of the landscape to inform the expected autocorrelation of landscape structure (Sun and Brus 2021), which cannot be easily obtained. Further strategies should be explored if they are believed to be of value in improving interpolations.

In addition to demonstrating the importance of selecting the appropriate sampling strategy, we also showed variation in accuracy, but not necessarily precision, across interpolation methods (Fig. 4 and 6, Tables S1 – S6). We note that while pairwise differences between accuracy and precision varied between combinations of interpolation methods and sampling strategy were statistically significant, we would expect these results given the high n used in comparisons and thus caution should be used when interpreting those results. This is consistent with other studies where it has been shown that Nearest Neighbor and Universal Kriging can have a greater ability to capture landscape heterogeneity, particularly at lower sampling densities within more heterogenous landscapes compared to other interpolation methods (Coelho et al. 2008). Our use of random sampling with no prior attention given to matching sampling point distance to an expected variogram inhibited Universal Kriging as we failed to capture the appropriate lag distance. Under these conditions, we would recommend a systematic sampling strategy, such as gridded, paired with Universal Kriging if the sample point distance captured the appropriate lag as demonstrated by the variogram.

There were increases in accuracy and precision with increasing sample density, but this effect was dependent on the interpolation method (Fig. 4 and 6). While it is known that sampling density can increase precision (Tsutsumi et al. 2000; Jordan et al. 2003), this relationship is often described as asymptotic, which assumes that ever increasing numbers of samples will continue to push accuracy and precision ever closer to a 1:1 match at some diminishing rate. In our case, sampling never achieved a perfect asymptote, which is most likely due to the low sampling densities explored within our simulations given the size of the simulated landscape. A moderate sampling strategy is typically sufficient to accurately create interpolated maps of forage quality (Jordan et al. 2003), and simulation exercises within grasslands of varying levels of heterogeneity demonstrated a similar phenomenon (Tsutsumi et al. 2007).

Like sample density, we observed a positive relationship between precision and landscape heterogeneity for most sampling strategies and interpolation methods. This is in line with our predictions, given that as the landscapes became more heterogenous, the distance over which self-similarity occurs increases; therefore, decreasing the total variability within the landscape while increasing the number of samples required to detect small or spatially isolated differences. These relationships were further emphasized when we applied the same techniques to in situ pastoral data where we observed a decrease in the rate of return as heterogeneity diminished (Fig. 7). While adequately measuring heterogeneity can be a complex endeavor in both cases, it is worthy of increased attention given its influence on precision.

We demonstrated the influence of sampling strategy on accuracy and precision estimates across sampling densities and heterogeneities in our simulations (Fig. 4 and 5). As the resolution decreased, the measured heterogeneity of the NDVI landscape also decreased, which indicates a loss of information (Supplementary Figure S3). Indeed, decreased resolution caused dominant values on the landscape to become more predominant with continued aggregation (Turner et al. 1989), effectively causing a reduction in the total observed plant productivity. This effect is driven by how dispersed the variation is across the landscape (Turner et al. 1989). Clearly, changing the resolution has dramatic impacts on the information available at that scale (Turner et al. 1989), and should be carefully considered with respect to meeting the needs and objectives of the analysis (Reynolds et al. 2016).

Our results indicate that it is important to carefully consider interpolation method, sampling density, sampling strategy, and landscape heterogeneity and understand how heterogeneity is influenced by landscape-level processes to construct a useful sampling design. While we showed that capturing landscape-level heterogeneity can occur irrespective of most sampling regimes and interpolation methods, exploring how sampling density and heterogeneity perform under other sampling regimes may be useful. Further, it is also expected that relationships between sampling density and heterogeneity may change with different landscape metrics. This was demonstrated in the wide variation of samples required to predict within crop variation in nitrogen, phosphorous, potassium, and sulfur (Jordan et al. 2003). Thus, spatial sampling should be structured to capture the most heterogenous variable of interest to ensure adequate sampling of all variables. Finally, while we look at the spatial relationships among interpolation method, sampling density and strategy, and landscape heterogeneity, it is likely that these relationships also change temporally. Indeed, we examined these relationships at the height of the growing season, a time when factors affecting landscape heterogeneity, such as resource restriction and grazing pressure, are likely less influential (Cid and Brizuela 1998). We would also expect sampling requirements to vary based on plant phenology and abiotic factors such as rainfall. For example, the sample number required to precisely measure silage production and plant nutrient values varies between cuttings over the summer and by metric of nutrient density (Jordan et al. 2003). As a result, more work on temporal changes in resource distribution is needed to precisely and accurately predict the level of heterogeneity expected within a given landscape; such an investigation is likely critical to target areas of rapid change.

Conclusion

Landscape ecology requires mapping resource distribution across the landscape. Thus, a thorough understanding of spatial relationships allows for selection of the appropriate sampling structure and interpolation method to arrive at accurate and meaningful results (Reynolds et al. 2016), though landscape heterogeneity may be an underlying driver of mapping accuracy for in situ pastoral data. The current body of knowledge offers less than desired guidance for selection between methods. This and future work should lay foundations for a structured decision-making process which will allow researchers and managers to clearly identify sampling strategies and interpolation prediction methods to meet their specific objectives in a resource efficient manner.

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Declarations

Conflict of interest The authors declare no conflict or competing interests.

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