Ecosystems (2023) 26: 1670–1684
https://doi.org/10.1007/s10021-023-00857-x
ECOSYSTEMS

A Cosmic View of 'Tundra Gardens': Satellite Imagery Provides a Landscape-Scale Perspective of Arctic Fox Ecosystem Engineering

Sean M. Johnson-Bice,* James D. Roth, and John H. Markham

Department of Biological Sciences, Faculty of Science, University of Manitoba, 50 Sifton Rd, Winnipeg, Manitoba R3T 2N2, Canada

Abstract

Most animal ecology studies using remote sensing data have assessed how environmental characteristics shape animal abundance, distribution, or behavior. But the increasing availability of high-resolution data offers new opportunities to study how animals, in turn, shape ecosystems at diverse scales. We evaluate the efficacy of using Sentinel-2 satellite imagery to quantify the effects of Arctic fox (*Vulpes lagopus*) denning activity (nutrient accumulation, bioturbation) on vegetation. Using an imagery-derived metric (NDVI), we compared maximum plant productivity and plant phenology patterns on 84 Arctic fox dens vs. reference sites, i.e., points generated within preferred denning habitat areas (predicted from a habitat selection analysis). We show that high-resolution imagery can be used to measure the effects of Arctic fox denning activity on vegetation. Plant productivity and the rate of green up were both greater on fox dens compared to reference (preferred-habitat) sites. Productivity on reference sites was lower than average productivity on the tundra (i.e., random sites), indicating foxes primarily establish dens in low-productivity areas. Plant productivity on dens was also unrelated to recent occupancy patterns, indicating fox denning activity has long-term legacy effects on plants that last beyond the lifetime of foxes. Our findings support Arctic foxes being classified as ecosystem engineers in low-Arctic tundra ecosystems by converting low-productivity sites into relatively high-productivity sites through their denning activity. We demonstrate the efficacy of using remote sensing technologies to study how predators increase landscape heterogeneity and influence ecosystem dynamics through patch-scale mechanisms, and ultimately advance our understanding of animal functional roles.

Key words: ecosystem function; landscape heterogeneity; NDVI; nutrient cycling; predator behavior; remote sensing; Sentinel-2; *Vulpes lagopus*.

Received 19 February 2023; accepted 21 May 2023;
published online 27 June 2023

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-023-00857-x.

S.M. Johnson-Bice led the conception of the ideas, designed the methodology, collected the data, analyzed the data, and led the writing of the manuscript. J.D. Roth and J.H. Markham helped conceive the study ideas and design the methodology. All authors contributed critically to the drafts and gave final approval for publication.

**Corresponding author; e-mail:* s.johnsonbice@gmail.com

Highlights

- Remote sensing data offers opportunities to understand how animals shape ecosystems
- We used satellite imagery to quantify effects of

Arctic fox den activity on plants
- Our study provides a novel, spaceborne perspective of predator functional roles

Introduction

Technological and methodological advancements in remote sensing in recent decades have provided novel insights into relationships between animals and their environment. For instance, researchers can use airborne and satellite-based light detecting and ranging (LiDAR) data to remotely quantify and describe the influence of ecosystem 3D structure on animals (Davies and Asner 2014). Satellite imagery is similarly used to evaluate the influence of environmental factors like precipitation, temperature, and land cover type on animals (Pettorelli and others 2014). In particular, satellite-derived metrics such as the normalized difference vegetation index (NDVI)—a metric frequently used to approximate vegetation and ecosystem productivity—have been used to assess animal-habitat relationships across space and time (Pettorelli and others 2005; Pettorelli and others 2011). Most studies using satellite-derived metrics to advance animal ecology have been conducted on large spatial scales, including revealing how herbivores track vegetation green-up throughout migration corridors (Sawyer and Kauffman 2011; Bischof and others 2012; van Moorter and others 2013; Merkle and others 2016; Aikens and others 2017), how ecosystem productivity drives the structure of herbivore communities across the Arctic tundra (Speed and others 2019), and modeling the distribution, abundance, and richness of animal species (e.g., Hurlbert and Haskell 2003; Tognelli and Kelt 2004; Bartoń and Zalewski 2007; Evans and others 2008; Nieto and others 2015).

More recently launched satellites capable of capturing imagery at higher resolutions, such as the Sentinel series launched by the European Space Agency, offer the potential to decipher animal-habitat relationships at finer spatial scales (Pettorelli and others 2014). Compared to 30 m resolution data from current Landsat satellites, 10 m resolution imagery captured by the Sentinel-2 satellite was a better predicter of bird richness patterns across the continental United States (Farwell and others 2021). Integrating these high-resolution data sources can also improve the performance of species distribution models (Koma and others 2022) and help identify microhabitat selection and suitability for small animals (Valerio and others 2020; Alessandrini and others 2022). Many remote sensing data sources are also freely available and easily accessible via platforms like Google Earth Engine. With advancements in the availability and accessibility of these data, we can expect researchers to use them to address a diversity of ever-evolving ecological questions (Turner and others 2015; Schulte to Bühne and Pettorelli 2018). In particular, finer-scale data sources may help unravel not only how environmental conditions affect animals, but how animals, in turn, influence ecosystem dynamics.

Predators are widely recognized for their ecological influence on prey abundance and behavior but they also alter ecosystems through localized, patch-scale pathways that contribute to landscape heterogeneity across space and time (Johnson-Bice and others 2023). These pathways include distributing carcasses across the landscape (Bump and others 2009; Schmitz and others 2010; Risch and others 2020; Monk and Schmitz 2022) and killing ecosystem engineers that create landscape patches (e.g., beaver [*Castor canadensis*] ponds; Gable and others 2020), as well as concentrating nutrients derived from prey into discrete locations such as foraging (Holtgrieve and others 2009), scent-marking (Ben-David and others 1998; Crait and Ben-David 2007), and social aggregation sites (Fariña and others 2003; Bokhorst and others 2019). Through each of these pathways, predators alter or create patches that influence landscape heterogeneity by indirectly affecting other species in a localized manner (Johnson-Bice and others 2023). For instance, predators that perennially reuse home sites may indirectly affect local plant and soil communities by concentrating prey-derived nutrients there. Soil nutrient levels and plant growth are greater at ground-nesting eagle owl (*Bubo bubo*) nests compared to reference sites (Fedriani and others 2015), whereas the combination of bioturbation (from digging burrows) and nutrient deposition by badgers (*Meles meles*) and red foxes (*Vulpes vulpes*) benefits plants around their dens (Kurek and others 2014; Kucheravy and others 2021; Lang and others 2021). To date, few studies have looked at these patch-scale predator effects from a landscape-scale perspective (but see Bump and others 2009; Gable and others 2020).

Arctic foxes (*Vulpes lagopus*) are important terrestrial predators that occupy multiple functional roles in low-Arctic tundra ecosystems. Although often recognized for their role in regulating the abundance (Angerbjörn and others 1999; Bêty and others 2001; Iles and others 2013) and altering the behavior (Bêty and others 2002; Clermont and others 2021) of their prey, their distinctive dens have also garnered considerable scientific and public interest. Throughout parts of their range, Arctic fox dens are characterized by unique vegetation compared to the surrounding area (Figure 1) (Chesemore 1969), earning them the nickname of the 'gardens of the tundra'.

Arctic foxes are thought to be the main driver of these changes in plant composition in the tundra, but due to the longevity of Arctic fox dens—one study estimated the average lifespan of a den to be 330 years (Macpherson 1969) —it has been difficult to attribute the unique vegetation to the foxes. Nonetheless, the enhanced vegetation on fox dens aligns with other similar observations of predator home sites noted earlier (Kurek and others 2014; Fedriani and others 2015; Kucheravy and others 2021; Lang and others 2021), supporting the hypothesis that the predators are the cause of the enhanced vegetation. Most likely, the combination of disturbance from digging burrows (bioturbation) and the accumulation of nutrients from prey remains and nutrients from predator excrement alters local vegetation. Arctic foxes, and other predators, have accordingly been classified as ecosystem engineers—organisms that benefit other species through physical modifications of their environment (Jones and others 1994). In the case of Arctic foxes, their denning activity indeed positively affects both plant and wildlife species. Arctic fox dens have greater soil and plant nutrient content, greater plant biomass, and unique plant assemblages compared to nearby areas (Garrott and

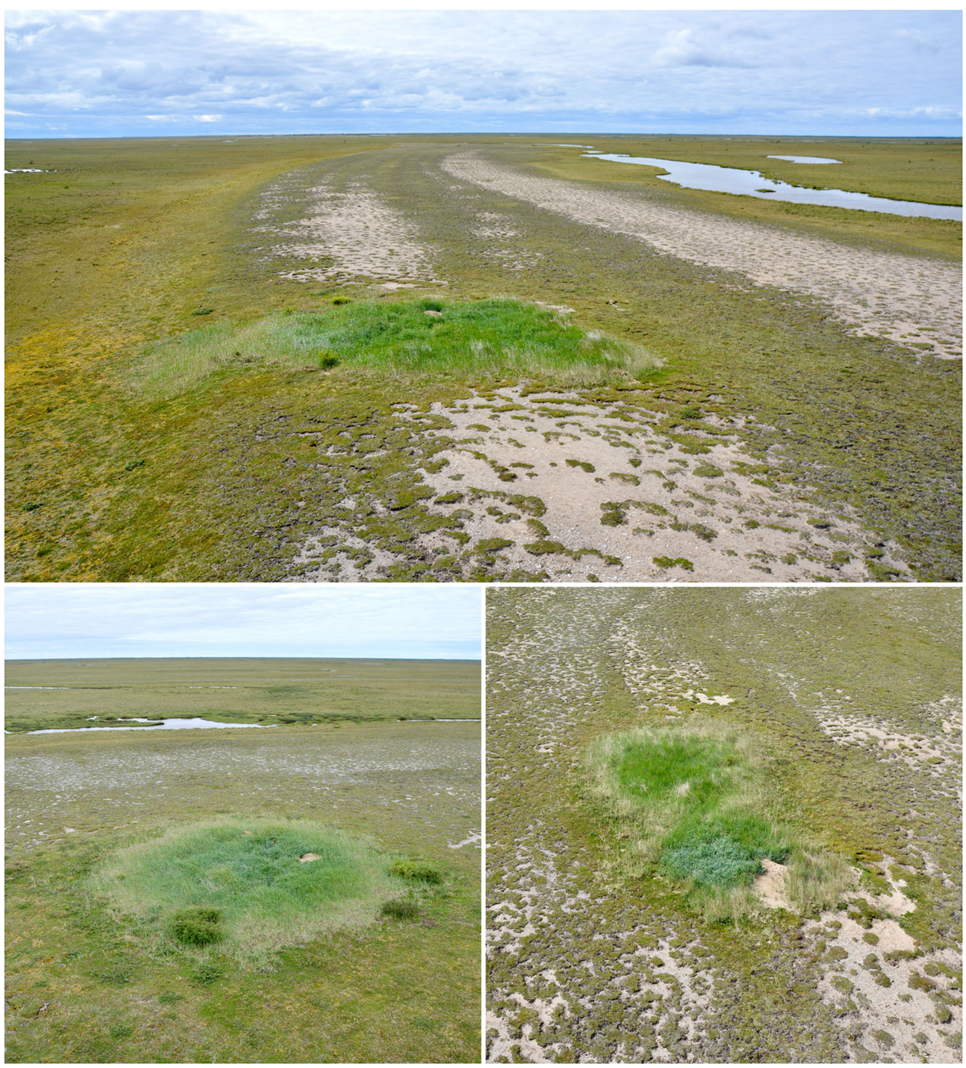

Figure 1. Photos of typical Arctic fox dens in Wapusk National Park, Manitoba, Canada taken during an aerial survey. Dens are generally constructed on relatively elevated ancient beach ridges and are characterized by unique plant characteristics relative to the surrounding landscape.

others 1983; Smith and others 1992; Bruun and others 2005; Gharajehdaghipour and others 2016; Gharajehdaghipour and Roth 2018; Fafard and others 2020). These plant and soil traits are thought to be influenced by the fact that the tundra is nutrient-limited, indicating that nutrients concentrated in a given location may induce large ecological effects (Ostertag and DiManno 2016). Tundra wildlife also adjust their space use towards dens, likely attracted there by the prospect of food subsidies—herbivores being attracted to the enhanced vegetation, and predators being attracted by the prey remains littered on the dens (Zhao and others 2022). Despite this accumulation of evidence supporting Arctic foxes being classified as ecosystem engineers, these analyses were conducted on smaller spatial scales using comparisons with directly adjacent areas that were assumed to be representative of suitable denning habitat. Without explicitly accounting for den selection preferences across the full landscape, it has remained difficult to directly attribute fox activity to the plant characteristics found on their dens as opposed to alternative explanations.

Here, we apply a novel application of remote sensing data towards advancing our understanding of the ecological impacts of Arctic fox denning activity on the low-Arctic tundra. Specifically, we used freely available, high spatial and temporal resolution satellite imagery to quantify vegetative characteristics on Arctic fox dens, and ultimately unravel the role of Arctic foxes as ecosystem engineers through a landscape-scale analysis. We first developed a habitat selection model for fox dens to create *reference* sites, which are sites that effectively represent areas suitable for denning based on factors influencing current fox den locations (i.e., preferred-habitat sites). By quantifying factors contributing to fox den selection patterns, this approach allowed us to at least partially account for alternative explanations to the plant patterns on dens, namely that the den sites were already high-productivity patches. Then, using NDVI data derived from Sentinel-2 satellite imagery, we compared (1) maximum plant productivity and (2) plant phenology patterns on (i) Arctic fox dens compared to (ii) reference sites on the tundra. We also compared plant productivity and phenology on fox dens and reference sites with (iii) fully *random* sites on the tundra (i.e., sites that represent all terrestrial habitats) to provide insight into how vegetation patterns on den and reference sites compare with average (random) tundra sites. We predicted plant productivity would be greater and plant green up would start earlier and progress faster on fox dens compared to reference sites, supporting the hypothesis that Arctic foxes act as ecosystem engineers by altering local vegetation. Our study demonstrates the potential of using high-resolution remote sensing data to advance our understanding of the functional role(s) of predators in ecosystems.

Methods

Study Area

We conducted our study within a ~ 1200 km^2 tundra region of Wapusk National Park in northeastern Manitoba, Canada along the western coastline of Hudson Bay (Figure 2A). Wapusk is part of the Hudson Bay Lowlands, one of the largest wetland ecosystems in the world. Monthly average temperature ranges from −26.0°C in January to 12.7°C in July (ECCC 2022). There is an average of 87 frost-free days (Jun. 19 to Sept. 15) annually in the area.

Arctic fox dens in Wapusk are predominantly located on ancient beach ridges formed from isostatic rebound after the melting of the Keewatin ice sheet (Ritchie 1956; Roth 2003; Sella and others 2007). The ridges are relatively elevated and run roughly parallel to the Hudson Bay shoreline, with ponds, lakes, and wetland habitats between the ridges. Beach ridges are thought to be suitable denning habitats for foxes due to the low soil moisture levels and greater depth to permafrost layer, which allows for easier burrow digging (Chesemore 1969; Smits and others 1988; Dalerum and others 2002). Our study area included all 84 known Arctic fox dens that were used for the NDVI analysis (density: ~ 7 dens/100 km^2), but in the habitat selection analysis we excluded two dens that were misclassified as 'open water' according to the 2015 Canada Land Cover data set. On these beach ridges, essentially the only patches of high-productivity vegetation are associated either with fox dens or spruce tree islands. Otherwise, these ridges are characterized with barren ground or prostrate shrub communities (Fafard and others 2020). The vast majority of Wapusk dens were well-established prior to 1997 and most have been at least periodically occupied by foxes. The average size of Arctic fox dens in our study area is ~ 560 m^2 (Gharajehdaghipour and Roth 2018).

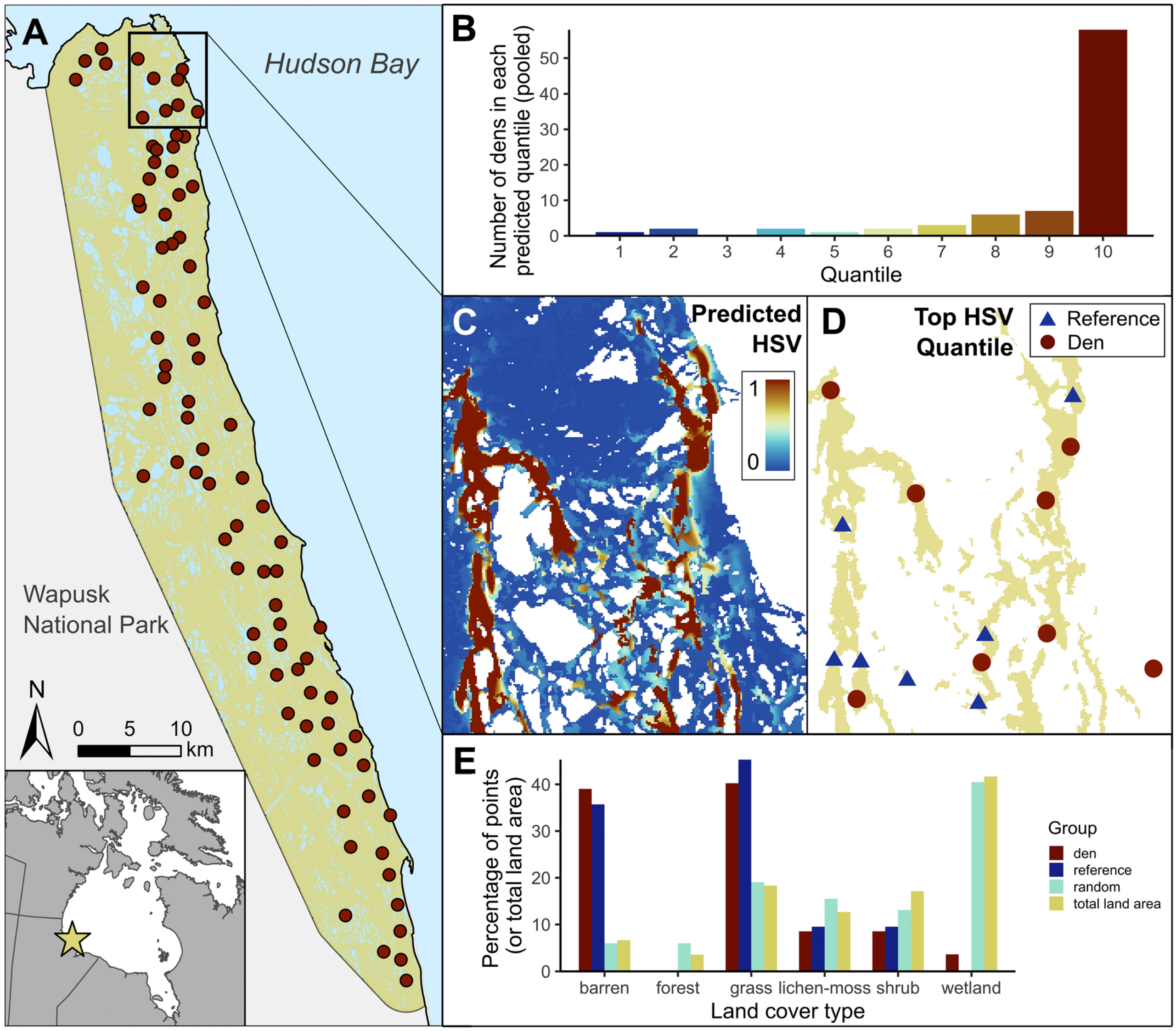

Figure 2. Map of the study area in Wapusk National Park, Manitoba, Canada, and results related to our den habitat selection analysis. Panel (**A**) shows the study area and all 84 known Arctic fox den locations therein. Panel (**B**) shows the number of Arctic fox dens predicted to be within each quantile (1–10) pooled across all five folds of the cross-validation procedure; Spearmans's rank correlation (r) on the pooled quantiles was 0.86 ($p = 0.002$). Panel (**C**) shows the predicted habitat selection map generated from the den selection model fit to the full data set, where habitat selection values (HSV) closer to 1 (red) represent areas more likely to be selected by Arctic foxes for denning. Panel D shows the same region with only the reclassified top quantile (10%) of cells present, overlaid with den (red circles) and randomly generated reference sites (blue triangles) used in this study. The study area region shown in Panels (**C**) and (**D**) is depicted within Panel (**A**). Panel (**E**) shows the percentage of den, reference, and random points categorized by each of the six land cover types, along with the percentage of the total study area comprised of each cover type (not pictured: percent 'open water', which comprises ~ 15% of the total study area).

Arctic Fox Den Habitat Selection Analysis

To evaluate how Arctic foxes select denning locations, we first delineated the area available for possible denning sites by creating a minimum convex polygon around all known fox dens and then applying a 3 km buffer (clipped to the shoreline; Figure 2A). This approach restricted the habitat selection analysis to only areas near known dens. Next, we generated 8200 random points (100 per den) within terrestrial habitats in the study area after removing all areas identified as 'open water' from the 2015 Canada Land Cover data set (Natural Resources Canada 2019).

We performed the habitat selection analysis by comparing den and random sites (input as 1 and 0, respectively) using a binomial generalized additive model with a logit link function. We used four variables for the analysis: elevation, land cover type, and the latitude and longitude of each point. Latitude and longitude were included to control for spatial autocorrelation in the landscape data preemptively. Elevation data was obtained from the 30 m resolution FABDEM data set (Hawker and others 2022). We reclassified the 2015 Land Cover data (Natural Resources Canada 2019) into six categories: 'forest' (comprised of all forest cover types); 'shrub' (comprised of polar and non-polar shrub cover types); 'grass' (comprised of polar and non-polar grass cover types); 'lichen-moss'; 'wetland'; and 'barren'. We used 'wetland' as the reference level, as it is the most abundant habitat type in the study area. The habitat selection model is defined as:

$$\text{logit}(Y) = \text{Land Cover} + f_1(\text{elevation}) + f_2(\text{latitude, longitude})$$

where Land Cover is the point's land cover type (categorical variable), f_1(elevation) is the point's elevation (in meters) fit with a smoothing component f_1 using a cubic regression spline, and f_2(latitude, longitude) is the interaction between the point's latitude and longitude (in UTM units) fit with a smoothing component f_2 using a Gaussian process spline.

Habitat Selection Model Validation

Creating 'reference' points for the NDVI analysis relied upon having a habitat selection model that could adequately predict known Arctic fox den locations, as this model would be used to generate new points in locations where foxes are likely to create dens but may not have done so yet. We therefore validated the habitat selection model performance using fivefold cross-validation (detailed in Boyce and others 2002; Roberts and others 2017). Briefly, this process involved: (1) fitting 80% of the data to the habitat selection model, (2) creating a predictive habitat selection map (30 m resolution) of the study area from the model, (3) binning the map into 10 equal-sized quantiles, (4) identifying which quantile each den from the withheld (testing) data set was predicted to be in, and (5) performing a Spearman's rank correlation test (R version 4.2.0; R Core Team 2022) on the withheld dens and their predicted quantile score. This process was repeated four more times until each 20% of data was withheld as a testing fold. Because the dens in our area are well-dispersed (Figure 2A) and landscape configuration does not differ substantially, we were comfortable using a random cross-validation approach. We also performed a Spearman's rank correlation on the predicted quantile data pooled across all five folds (Figure 2B).

After model validation, which determined if the habitat selection model performed adequately in predicting Arctic fox denning locations, we fit the full data set to the habitat selection model. We then created a predictive habitat selection map from this model (Figure 2C), reclassified the map into 10 equal-sized quantiles, and generated 84 random points within cells of the top quantile more than 250 m from another reference site and from the nearest den (Figure 2D). These 'reference' points effectively represent the 10% of terrestrial areas Arctic foxes are most likely to select for denning. All habitat selection models were fit using the 'gam' function from the *mgcv* package (Wood 2011) in R.

Plant Productivity and Phenology Analyses

Evaluating Maximum Plant Productivity

We compared maximum plant productivity between 84 each of (1) 'den' locations, (2) 'reference' locations representing preferred but unused denning habitat (described earlier), and (3) 'random' locations, which represent the total terrestrial habitat availability in the study area (Figure 2E). 'Random' points were randomly generated in ArcGIS Pro (version 2.8; Esri 2022) within terrestrial habitats in the study area more than 250 m from every other point (den, reference, and random), a distance that would ensure sampled locations would not influence one another.

We assessed maximum plant productivity by creating a greenest pixel mosaic of 2A surface reflectance Sentinel-2 imagery (captured every 2–4 days in our study area) across the full growing season for 2019, 2020, and 2021 using Google Earth Engine (2019 is the earliest year 2A imagery is available for our study area). We defined the growing season as Jun. 16–Sept. 30, which was based on the average dates of last and first frost (Jun. 19 and Sept. 15) and suitable satellite image availability (cloud and snow coverage interference is high outside of this date range). Though essentially all greenest pixels would be from the middle/peak of the growing season, we chose to create the greenest pixel mosaic from across the full season to match the phenology analysis (see next section). This process involved first extracting all satellite images within the growing season, applying the 's2cloudless' (Zupanc 2017) algorithm to mask clouds and shadows from each image, calculating NDVI values for each image pixel, and then using the 'qualityMosaic' tool in Google Earth Engine to create a greenest pixel mosaic raster. This mosaic raster represents the maximum NDVI value on a pixel-by-pixel basis across the growing season. We exported the mosaic raster to ArcGIS Pro, excluded all cells with NDVI values < 0.1 (as these cells corresponded to open water features or noise in the data), and calculated the mean NDVI value within a 20 m buffer of each point using the 'Zonal Statistics as Table' tool. Notably, since the average den size in our study area is ~ 560 m^2, the 20 m radius (1257 m^2) includes area beyond many dens; NDVI estimates for dens should therefore be conservative. We compared 20 m maximum NDVI values between dens, reference points, and random points using a linear mixed effects model with 'point ID' and 'year' as random intercept terms (*lme4* package; Bates and others 2015). Tukey's Honest Significant Difference pairwise comparisons were conducted using the 'pairs' function from the *emmeans* package (Lenth 2022).

We were also interested in quantifying how prominent Arctic fox dens are on the landscape relative to the other locations used in the productivity analysis (reference and random groups). We therefore compared the difference in mean NDVI values within a 20 m buffer versus mean NDVI values within a 250 m buffer for each point, each year (2019–2021). We averaged the mean maximum NDVI for each point across the 3 years and used Wilcoxon signed rank tests in R to assess differences in average productivity between the two buffer distances for each group.

Finally, we assessed how recent fox reproductive success affected maximum plant productivity on dens. For each year spanning 2011–2021, we assessed the reproductive success of dens using on-the-ground and aerial surveys (details in McDonald and others 2017). Briefly, we examined each den for signs of reproductive success, such as abundant prey remains on dens, fresh digging in burrows, and presence of fresh pup scats. To evaluate whether recent fox reproduction patterns influenced plant productivity, we used a Spearman's rank correlation test to evaluate the relationship between percent reproductive success (defined as the number of years each den produced pups divided by the number of years the den was surveyed) and maximum growing season NDVI averaged over the three years of imagery. We included only dens that had been surveyed at least 9 times for this analysis (n = 78 dens).

Evaluating Patterns of Plant Phenology

To understand whether plant phenology patterns on Arctic fox dens differed from other areas on the tundra, we examined whether dens start green-up earlier or stay green longer, and when, during the growing season, any differences in plant productivity may arise. For this analysis, we used a similar 'greenest pixel mosaic' approach as described for the plant productivity analyses. We divided the growing season into seven equal time periods (Jun. 16–30, Jul. 1–15, Jul. 16–31, Aug. 1–15, Aug. 16–31, Sep. 1–15, Sep. 16–30) and generated greenest pixel NDVI mosaics for each time period spanning 2019–2021. Because of issues with cloud and shadow interference in the mosaics generated from the shorter time periods of this analysis, we manually inspected each mosaic raster and retained only the points where NDVI values could be satisfactorily calculated. Across all seven time periods spanning 2019–2021 we acquired 3779 useable NDVI data points (71.4% total success rate in acquiring data to calculate NDVI, with a range across the seven time periods of 23.8 to 97.2%).

For each time period raster mosaic, we calculated mean NDVI within a 20 m buffer of each point using the methods described earlier. We evaluated plant NDVI phenology using a hierarchical generalized additive model with a Gaussian distribution:

$$\mathrm{NDVI}_{ijk} = f_{\mathrm{Group}}\left(\mathrm{Time\ Period}_{ijk}\right) + \mathrm{Group}_{ijk} + \mathrm{Point\ ID}_{i} + \mathrm{Year}_{j}$$

where NDVI_{ijk} is the mean 20 m NDVI value of the kth observation for point i in year j, and Point ID (categorical variable with unique values for point) and Year are random intercept terms that were assumed to be normally distributed with a mean of 0. $f_{\mathrm{Group}}\left(\mathrm{Time\ Period}_{ijk}\right)$ is the time period of the kth observation for point i in year j (coded as an integer from 1 to 7, representing the seven equal time periods) fit with a smoothing component f_{Group} using a thin plate regression spline comprised of seven basis functions. The spline varied by group level (den, reference, random) and had individual penalties (i.e., group-level factor smooth interactions with no shared penalty; Pedersen and others 2019). The use of a smoother on time period was done to control for temporal autocorrelation in NDVI levels at the various time periods. The phenology model was fit using the 'gam' function in the *mgcv* package (Wood 2011). We quantified pairwise differences among each of the factor smooth groups at each of the seven time periods using the 'difference_smooths' function from the *gratia* R package (Simpson 2022).

Results

Fox Den Habitat Selection

Arctic foxes predominantly constructed dens in 'barren' or 'grass' land cover types and avoided 'wetland' areas (Figure 2E). The smoothing components of elevation (effective degrees of freedom [edf] = 4.90, Chi-square = 66.4, $p < 0.001$) and the interaction between latitude/longitude parameters (edf = 18.79, Chi-square = 84.4, $p < 0.001$) were both significant (edf values > 1.0 indicate a non-linear relationship), with fox dens occurring more frequently in elevated areas nearer to the coast than random sites.

Model Validation Results

Results from our five-fold cross-validation procedure indicated the den habitat selection model adequately characterized Arctic fox den locations. Spearman's rank correlation (r) results ranged from 0.43 ($p = 0.22$) to 0.81 ($p = 0.005$), with an average r of 0.67. Variation in r values may have been due in large part to the low sample size of dens used for each testing fold ($n = 16$ or 17), whereby 1–2 dens categorized into low quantiles can greatly influnce r values. When pooled across all five folds, the Spearman's rank correlation test on the binned quantiles was significant ($r = 0.86$, $p = 0.002$), with 71% (58/82) and 87% (71/82) of dens predicted to be within the top one and three quantiles, respectively (Figure 2B). When fit to the full data set the habitat selection model explained 31.8% of deviance in Arctic fox den charactersistics. We interpreted these results to indicate the habitat selection model had a moderate to good ability to explain current fox den characteristics and could be used to adequately characterize other areas foxes may select for when constructing new dens (i.e., could be used to generate 'reference' sites). The similarity in land cover types between den and reference sites within the top quantile supports this interpretation (Figure 2E).

Maximum Plant Productivity

Maximum growing season plant productivity was significantly greater on Arctic fox dens compared to reference sites ($p < 0.001$, $T = 4.89$; Figure 3A). The estimated marginal mean annual NDVI was 0.66 (95% confidence interval [CI]: 0.62–0.70) on dens compared to 0.59 (95% CI: 0.54–0.63) for reference sites (Figure 3B). Plant productivity at random sites was significantly greater than productivity at reference sites ($p < 0.001$, $T = -3.94$; Figure 3A-B), suggesting that Arctic fox dens are typically constructed in relatively low-productivity areas. There was no difference in plant productivity between den and random sites ($p = 0.61$, $T = 0.94$).

Plant productivity was significantly greater on Arctic fox dens compared to the surrounding area, such that average maximum NDVI values within a 20 m buffer around Arctic fox dens were greater than average NDVI values within a 250 m buffer ($T = 8.07$, $p < 0.001$, $df = 83$; Figure 3C). As expected, plant productivity at reference and random sites did not differ from their surrounding areas ($p = 0.58$ and 0.33, respectively; Figure 3C).

Average fox den reproductive success (number of years pups were produced at each den divided by the number of years surveyed) over the last 11 years was 0.25 (SD = 0.20). We found no relationship between recent fox reproduction and plant productivity on dens (Spearman's $r = -0.076$, $p = 0.51$; Figure 3D).

Plant Phenology

We found Sentinel-2 imagery can be used to detect and visualize plant phenology patterns on Arctic fox dens (Figure 4A). As expected, the temporal trends in plant productivity (NDVI) across the growing season were all statistically significant and non-linear for each group (den [edf = 5.89, $p < 0.001$], reference [edf = 5.87, $p < 0.001$], and random sites [edf = 5.92, $p < 0.001$]). Specifically, plant productivity increased from mid-June until a peak around mid-July, where it remained at peak productivity until the end of August (Figure 4B). We found den NDVI values were significantly greater than reference NDVI values at time periods 2–6 (Jul. 1–Sept. 15), and greater NDVI values at random sites compared to reference sites at all time periods except the first (Figure 4B-C). No difference in NDVI between den and reference sites at time periods 1 and 7 implies plants on dens do not start green-up earlier or stay green longer; however, judging by the slope of the increase in NDVI from time period 1 to 3, it appears that the rate of plant green-up is greater on dens (Figure 4B).

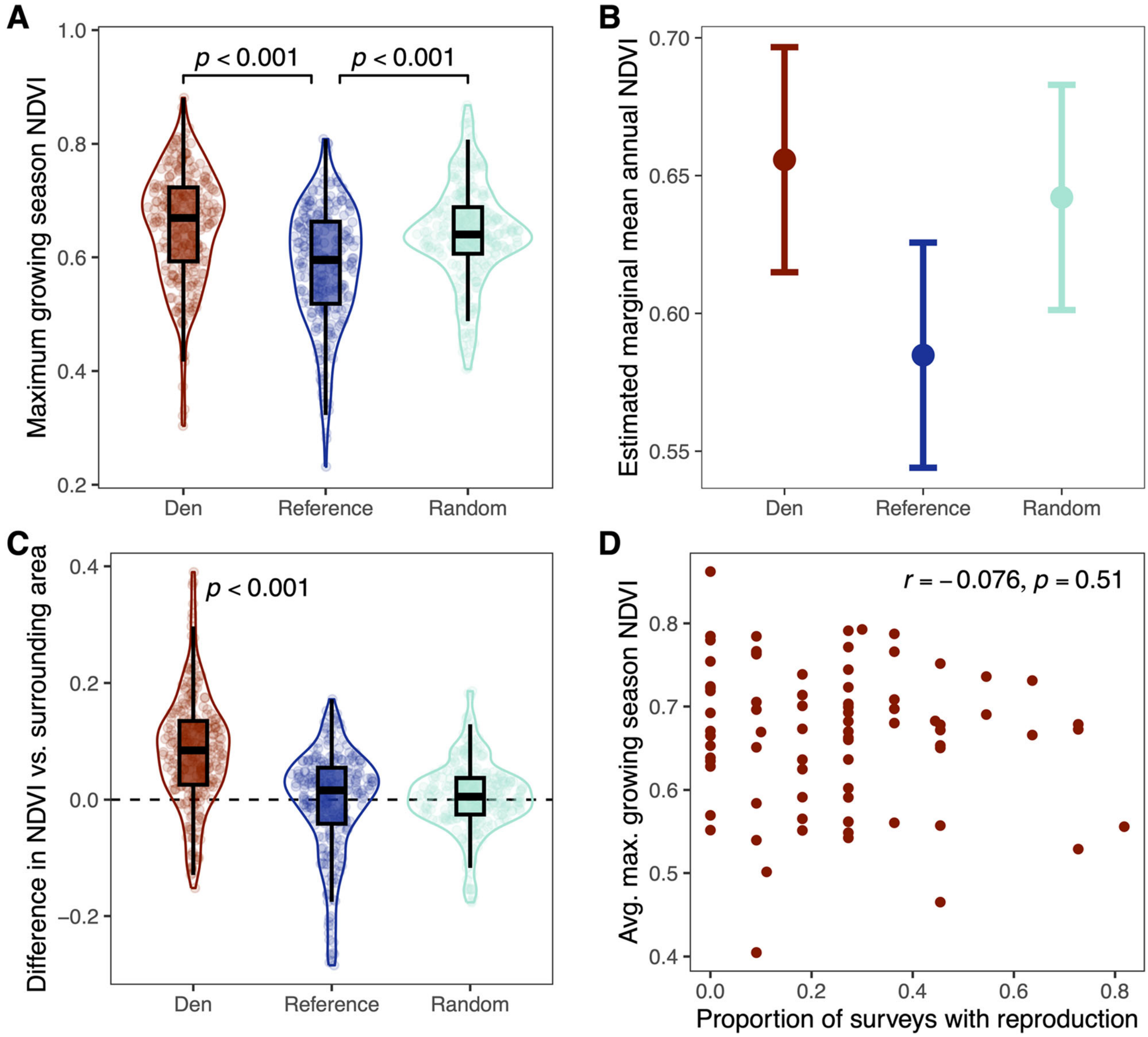

Figure 3. Results related to maximum plant productivity analyses on Arctic fox dens in Wapusk National Park, Manitoba, Canada. Panels A and B show the observed values (**A**) and estimated marginal mean (± 95% confidence intervals; **B**) of maximum growing season NDVI for dens, reference sites, and random sites, where reference sites represent preferred denning habitats based on a habitat selection model and random sites are representative of total habitat availability in the study area. Panel (**C**) shows the observed difference between annual average NDVI values within 20 and 250 m buffers, with differences only found for dens. Panel (**D**) shows the lack of relationship between fox reproductive success and average maximum growing season NDVI on dens.

Discussion

Using freely available software and high-resolution satellite imagery, our study provides a novel, landscape-scale perspective on the effects of Arctic fox denning activity on plant productivity and phenology. We demonstrated that plant productivity on Arctic fox dens is significantly greater than other areas in similar habitats, which are generally limited to relatively elevated but low-productivity areas. By using a habitat selection analysis to generate reference points, we were able to control for certain ecological factors that Arctic foxes select for when creating dens and thus help disentangle the relative effects of habitat vs. fox denning activity on plants. Our results provide further evidence that Arctic foxes are ecosystem engineers in low-Arctic tundra ecosystems.

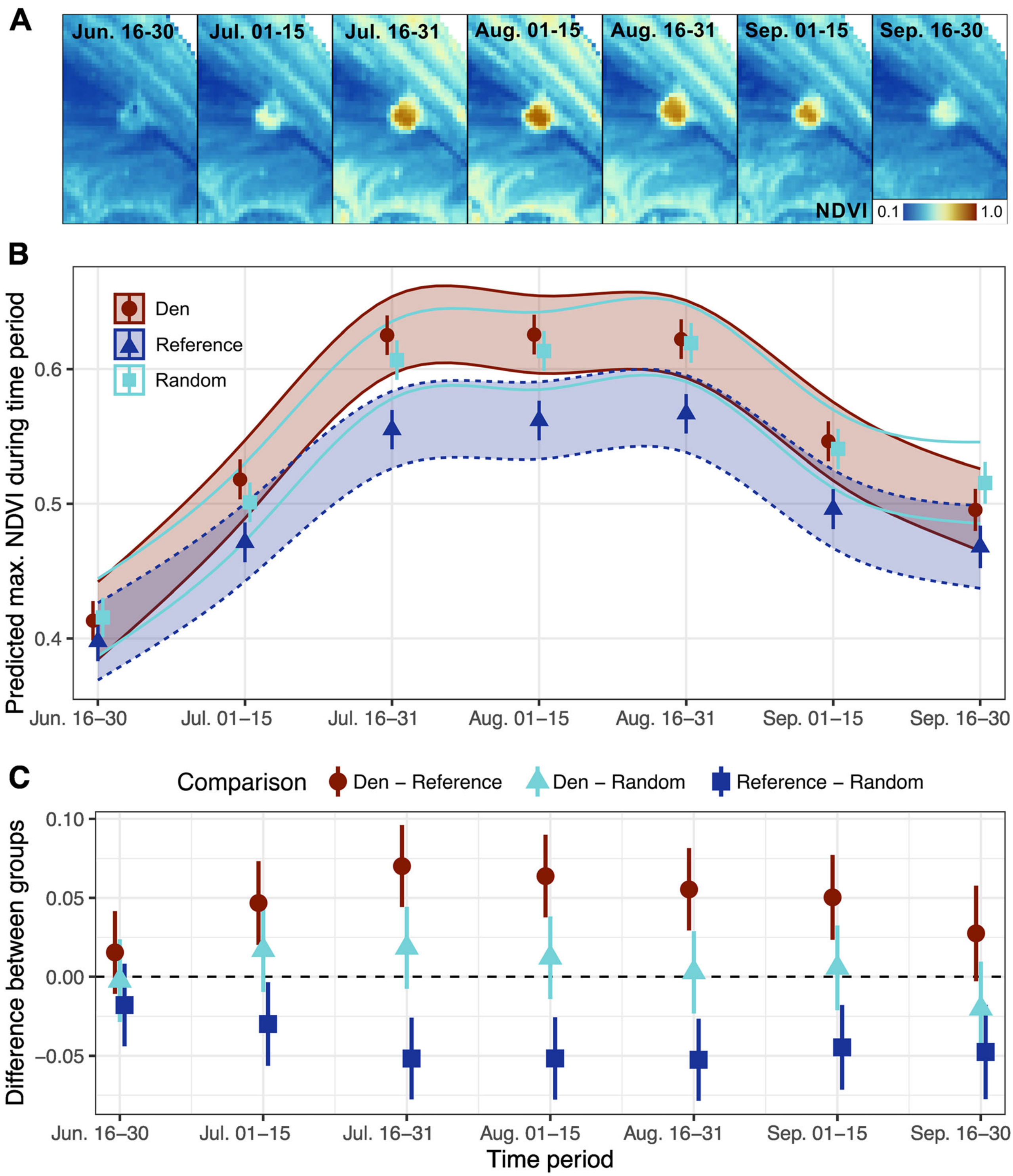

Figure 4. Results related to the plant phenology analysis on Arctic fox dens in Wapusk National Park, Manitoba, Canada. Panel (**A**) shows the intra-annual change in plant productivity (assessed from NDVI values) across seven time periods on a single Arctic fox den. Each subpanel shows the NDVI values created from the greenest pixel mosaic from each time period. The den is at the center of each panel, the outline of which can be most clearly seen in the middle subpanels. Panel (**B**) shows the point and standard error NDVI estimates for den, reference, and random sites predicted from the generalized additive model. The ribbons are the predicted NDVI 95% confidence intervals (CI) for each group. Panel (**C**) shows the pairwise differences (point ± 95% CI) in smooth estimates between each group at each time period. Comparisons where the 95% CIs do not overlap 0 (the dashed horizonal line) are considered significant.

Which Came First: The Foxes or The Plants?

One of the lingering questions related to vegetation patterns on Arctic fox dens is whether their denning activity converts unproductive sites into productive sites through nutrient deposition and bioturbation, or whether they select for preexisting high-productivity sites to build their dens. The easiest way to address this question is to monitor newly-created dens to see whether they (1) are created in pre-existing lush vegetation patches, or (2) are created in low-productivity areas that, through time, develop into lush vegetation patches. Although on the surface this seems straightforward, it is in fact far more challenging when the longevity of Arctic fox dens is factored in (estimated average lifespan of 330 years; Macpherson 1969). In our study area, we know of only 2 dens that have been created since 1994 and both of these dens started in low-productivity areas with prostrate shrub vegetation typical of the elevated beach ridges (Fafard and others 2020). Our approach to evaluate whether we can attribute plant characteristics on dens to fox activity was to use a quantitative method (habitat selection model) to develop paired reference sites that could be used to compare plant productivity. Despite the coarse variables included in our habitat selection model, our cross-validation results indicated it performed well in characterizing den site locations and could therefore be used to generate these matching 'reference' sites for comparison. The fact that the top quantile from the habitat selection model contained the habitat type the vast majority of dens are located on, elevated beach ridges, provides more support for its use in characterizing den characteristics. When comparing plant productivity between dens, reference sites, and random sites, we found that productivity on dens was much greater than reference sites, and that reference sites had lower productivity on average than random sites on the tundra (Figure 3A-B). In other words, the results collectively indicate Arctic foxes select for low-productivity areas when digging dens (i.e., reference sites are less productive than average tundra sites), which likely turn into relatively high-productivity areas through their denning activity (i.e., dens have greater productivity than matching reference sites).

Moreover, our analysis also provided quantitative evidence that Arctic fox dens are in fact high-productivity patches that contrast strongly with the landscape, as we found plant productivity is significantly greater on Arctic fox dens compared to the immediately surrounding area (Figure 3C). This result is not surprising given how visually prominent the dens are on the landscape (Figure 1). Nonetheless, our objective with this portion of the analysis was to derive an index of 'prominence' that could quantify what our eyes perceive when viewing these dens. Given the fact that high-productivity patches on beach ridges in our area are essentially only associated with fox dens or tree islands (at which we have never documented denning activity), when we collate all available lines of evidence, the most parsimonious explanation for the vegetation found on fox dens in the area is that Arctic fox denning activity is the cause of these vegetative patterns as suggested previously in research from our study area (Gharajehdaghipour and others 2016; Gharajehdaghipour and Roth 2018; Fafard and others 2020; Zhao and others 2022).

Our approach from the present study thus provides greater evidence that Arctic foxes act as ecosystem engineers by converting sites of low productivity into sites of relatively high productivity. The fact that fox reproduction patterns spanning a decade were unrelated to maximum plant productivity on dens indicates the effects of fox denning behavior on plants are long-lasting—well beyond the lifetime of foxes. Indeed, the effects from nutrient deposition and bioturbation seem to compound through many generations of fox occupancy and reproduction. And once the changes to plant assemblages occur on dens, these legacy effects likely last for a long time. When comparing the spatial scale and temporal longevity of Arctic fox dens against other ecosystem engineers (reviewed by Hastings and others 2007), Arctic fox dens are considerably larger (> 500 m^2) and longer lasting (hundreds of years) than the vast majority of patches engineered by animals. Continued monitoring of plant productivity and assemblages may reveal greater information about how plant dynamics change through time on Arctic fox dens in relation to occupancy patterns (see *Future directions and concluding remarks* section for more discussion).

Harnessing High-Resolution Remote Sensing Data to Assess Animal-Habitat Relationships

Our first objective when planning this study was to conduct a ''proof of concept'' analysis evaluating whether satellite imagery could actually detect vegetation on Arctic fox dens. Prior to the launch of the Sentinel-2 satellite, freely available, high-temporal frequency imagery was available only on a coarser scale (e.g., 30 m resolution of the LANDSAT satellites). Arctic fox dens are represented by 1 pixel at this resolution (900 m^2), making it challenging to distinguish dens. Sentinel-2 imagery clearly provides a fine enough spatiotemporal scale to detect and quantify plant productivity and phenology patterns on Arctic fox dens (Figures 3, 4). Although plants on dens do not appear to start green-up earlier or stay green longer than other tundra areas, we found green-up rates were higher on dens than reference sites and were able to assess when, during the growing season, plant productivity begins to differ between these areas (July 1–15; Figure 4B-C). Assessing plant phenology patterns on these dens at a similar spatiotemporal scale using field-based methods would have been prohibitively costly and time intensive, as the majority of the dens in our 1200 km^2 study area (~ 65–70%) are accessible only via helicopter during the growing season.

As remote sensing data further increases in availability and spatiotemporal resolution, it will continue to offer new perspectives and insights on animal functional roles within ecosystems at diverse spatial scales. Most animal ecology studies using remote sensing data have applied it towards understanding how environmental conditions affect animals. But as we demonstrated, remote sensing data can also be used to understand how animals shape ecosystems themselves. Our study is not alone in applying remote sensing methods towards evaluating animal impacts on ecosystems. For instance, satellite imagery has been used to identify how spatiotemporal fluctuations in spawning salmon abundance influences forest productivity (Kieran and others 2021), how beaver-modified environments buffer riparian ecosystems against wildfire (Fairfax and Whittle 2020), and how grazing pressure from migrating bison (*Bison bison*) alters the quality and phenology of the grasses they forage upon (Geremia and others 2019). Airborne LiDAR has revealed the effects of elephant (*Loxodonta africana*) foraging on the structural diversity, rates of treefall, and vegetation height of savanna woodlands (Asner and others 2009; Asner and Levick 2012; Asner and others 2016; Davies and others 2018). We add to these studies by demonstrating high-resolution satellite imagery can provide a landscape-scale perspective of animal ecological effects that function at smaller, patch-level scales.

Future Directions and Concluding Remarks

By demonstrating that satellite imagery can be used to detect vegetation patterns on Arctic fox dens, there are several ways this study can be built upon for future research and monitoring efforts. First, we propose satellite-derived information could be used to identify and locate previously unknown dens with similar vegetation characteristics. In particular, the prominence index we employed may be used to identify vegetation hotspots that, in tandem with region-specific den selection preferences, may guide search efforts for dens. Second, as we continue to assess fox occupancy and reproductive success at dens, we will likely gain a better understanding of how fox denning behavior affects plants across space and time. For instance, how long do the changes to plant communities last once a den is abandoned for good? After a new den is constructed, how long until major changes to plants are detectable? Finally, as Sentinel-2 and other comparable satellites continue to collect high-resolution spatiotemporal imagery, these data can be used to regularly monitor temporal patterns in plant productivity and phenology on dens and assess how climate change may affect these patterns across multiple spatial scales.

Effective species conservation and management often requires employing efficient ways to monitor and measure animal-habitat relationships. This is especially true when resources are limited, when studies are conducted across large spatial or temporal scales, or when the species are imperiled or have important ecological effects, like top predators do. Remote sensing data offer unique avenues to advance these objectives (Pettorelli and others 2014; Schulte to Bühne and Pettorelli 2018), provided the data remain affordable and accessible (Turner and others 2015). Our study validates the utility of such data by demonstrating how free and easily accessible satellite imagery can provide a cosmic view of animal ecological effects, and ultimately advance our understanding of the intricate functional role predators play in ecosystems.

ACKNOWLEDGEMENTS

We acknowledge salary and stipend support provided by the University of Manitoba. Support in locating and monitoring Arctic fox dens was provided by the Natural Sciences and Engineering Research Council of Canada, Natural Resources Canada Polar Continental Shelf Program, University of Manitoba Fieldwork Support Program, the

Churchill Northern Studies Centre Northern Research Fund, and the many students that hiked out to dens as part of the Churchill Fox Project long-term research and monitoring efforts. Finally, we thank comments from two anonymous reviewers that improved the manuscript.

DATA AVAILABILITY

Due to the sensitive nature of Arctic fox dens, specific location data is only available upon request from the authors. Otherwise, all other data and code used in this study are available as supplementary information files.

REFERENCES

Aikens EO, Kauffman MJ, Merkle JA, Dwinnell SPH, Fralick GL, Monteith KL. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecology Letters 20:741–750.

Alessandrini C, Scridel D, Boitani L, Pedrini P, Brambilla M. 2022. Remotely sensed variables explain microhabitat selection and reveal buffering behaviours against warming in a climate-sensitive bird species. Remote Sensing in Ecology and Conservation 8:615–628.

Angerbjörn A, Tannerfeldt M, Erlinge S. 1999. Predator-prey relationships: arctic foxes and lemmings. Journal of Animal Ecology 68:34–49.

Asner GP, Levick SR. 2012. Landscape-scale effects of herbivores on treefall in African savannas. Ecology Letters 15:1211–1217.

Asner GP, Levick SR, Kennedy-Bowdoin T, Knapp DE, Emerson R, Jacobson J, Colgan MS, Martin RE. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. Proceedings of the National Academy of Sciences 106:4947–4952.

Asner GP, Vaughn N, Smit IPJ, Levick S. 2016. Ecosystem-scale effects of megafauna in African savannas. Ecography 39:240–252.

Bartoń KA, Zalewski A. 2007. Winter severity limits red fox populations in Eurasia. Global Ecology and Biogeography 16:281–289.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Ben-David M, Bowyer RT, Duffy LK, Roby DD, Schell DM. 1998. Social behavior and ecosystem processes: river otter latrines and nutrient dynamics of terrestrial vegetation. Ecology 79:2567–2571.

Bêty J, Gauthier G, Giroux J-F, Korpimäki E. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos 93:388–400.

Bêty J, Gauthier G, Korpimäki E, Giroux J-F. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. Journal of Animal Ecology 71:88–98.

Bischof R, Loe LE, Meisingset EL, Zimmermann B, Van Moorter B, Mysterud A. 2012. A migratory Northern ungulate in the pursuit of spring: jumping or surfing the green wave? The American Naturalist 180:407–424.

Bokhorst S, Convey P, Aerts R. 2019. Nitrogen inputs by marine vertebrates drive abundance and richness in Antarctic terrestrial ecosystems. Current Biology 29:1721–1727.

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Bruun HH, Österdahl S, Moen J, Angerbjörn A. 2005. Distinct patterns in alpine vegetation around dens of the Arctic fox. Ecography 28:81–87.

Bump JK, Peterson RO, Vucetich JA. 2009. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. Ecology 90:3159–3167.

Chesemore DL. 1969. Den ecology of the Arctic fox in Northern Alaska. Canadian Journal of Zoology 47:121–129.

Clermont J, Grenier-Potvin A, Duchesne É, Couchoux C, Dulude-de Broin F, Beardsell A, Bêty J, Berteaux D. 2021. The predator activity landscape predicts the anti-predator behavior and distribution of prey in a tundra community. Ecosphere 12:e03858.

Crait JR, Ben-David M. 2007. Effects of river otter activity on terrestrial plants in trophically altered yellowstone lake. Ecology 88:1040–1052.

Dalerum F, Tannerfeldt M, Elmhagen B, Becker D, Angerbjörn A. 2002. Distribution, morphology and use of arctic fox *Alopex lagopus* dens in Sweden. Wildlife Biology 8:185–192.

Davies AB, Asner GP. 2014. Advances in animal ecology from 3D-LiDAR ecosystem mapping. Trends in Ecology & Evolution 29:681–691.

Davies AB, Gaylard A, Asner GP. 2018. Megafaunal effects on vegetation structure throughout a densely wooded African landscape. Ecological Applications 28:398–408.

Environment Climate Change Canada (ECCC). 2022. Climate normals 1981–2010 for the Churchill, MB station. Accessed 4 Aug 2022.

ESRI. 2022. ArcGIS Pro version 2.8. Redlands, CA.

Evans KL, Newson SE, Storch D, Greenwood JJD, Gaston KJ. 2008. Spatial scale, abundance and the species–energy relationship in British birds. Journal of Animal Ecology 77:395–405.

Fafard PM, Roth JD, Markham JH. 2020. Nutrient deposition on Arctic fox dens creates atypical tundra plant assemblages at the edge of the Arctic. Journal of Vegetation Science 31:173–179.

Fairfax E, Whittle A. 2020. Smokey the Beaver: beaver-dammed riparian corridors stay green during wildfire throughout the western USA. Ecological Applications 30:e02225.

Fariña JM, Salazar S, Wallem KP, Witman JD, Ellis JC. 2003. Nutrient exchanges between marine and terrestrial ecosystems: the case of the Galapagos sea lion *Zalophus wollebaecki*. Journal of Animal Ecology 72:873–887.

Farwell LS, Gudex-Cross D, Anise IE, Bosch MJ, Olah AM, Radeloff VC, Razenkova E, Rogova N, Silveira EMO, Smith MM, Pidgeon AM. 2021. Satellite image texture captures vegetation heterogeneity and explains patterns of bird richness. Remote Sensing of Environment 253:112175.

Fedriani JM, Garrote PJ, Delgado MdM, Penteriani V. 2015. Subtle gardeners: inland predators enrich local topsoils and enhance plant growth. PLoS ONE 10:e0138273.

Gable TD, Johnson-Bice SM, Homkes AT, Windels SK, Bump JK. 2020. Outsized effect of predation: wolves alter wetland creation and recolonization by killing ecosystem engineers. Science Advances 6:abcd5439.

Garrott RA, Eberhardt LE, Hanson WC. 1983. Arctic fox den identification and characteristics in Northern Alaska. Canadian Journal of Zoology 61:423–426.

Geremia C, Merkle JA, Eacker DR, Wallen RL, White PJ, Hebblewhite M, Kauffman MJ. 2019. Migrating bison engineer the green wave. Proceedings of the National Academy of Sciences USA 116:25707–25713.

Gharajehdaghipour T, Roth JD. 2018. Predators attract prey through ecosystem engineering in the Arctic. Ecosphere 9:e02077.

Gharajehdaghipour T, Roth JD, Fafard PM, Markham JH. 2016. Arctic foxes as ecosystem engineers: increased soil nutrients lead to increased plant productivity on fox dens. Scientific Reports 6:24020.

Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG. 2007. Ecosystem engineering in space and time. Ecology Letters 10:153–164.

Hawker L, Uhe P, Paulo L, Sosa J, Savage J, Sampson C, Neal J. 2022. A 30 m global map of elevation with forests and buildings removed. Environmental Research Letters 17:024016.

Holtgrieve GW, Schindler DE, Jewett PK. 2009. Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. Ecological Research 24:1125–1135.

Hurlbert Allen H, Haskell JP. 2003. The effect of energy and seasonality on avian species richness and community composition. The American Naturalist 161:83–97.

Iles DT, Rockwell RF, Matulonis P, Robertson GJ, Abraham KF, Davies JC, Koons DN. 2013. Predators, alternative prey and climate influence annual breeding success of a long-lived sea duck. Journal of Animal Ecology 82:683–693.

Johnson-Bice SM, Gable TD, Roth JD, Bump JK. 2023. Patchy indirect effects of predation: predators contribute to landscape heterogeneity and ecosystem function via localized pathways. Oikos. (In press).

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Kieran CN, Obrist DS, Muñoz NJ, Hanly PJ, Reynolds JD. 2021. Links between fluctuations in sockeye salmon abundance and riparian forest productivity identified by remote sensing. Ecosphere 12:e03699.

Koma Z, Seijmonsbergen AC, Grootes MW, Nattino F, Groot J, Sierdsema H, Foppen RPB, Kissling WD. 2022. Better together? Assessing different remote sensing products for predicting habitat suitability of wetland birds. Diversity and Distributions 28:685–699.

Kucheravy CE, Roth JD, Markham JH. 2021. Red foxes increase reproductive output of white spruce in a non-mast year. Basic and Applied Ecology 51:11–19.

Kurek P, Kapusta P, Holeksa J. 2014. Burrowing by badgers (*Meles meles*) and foxes (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest. Ecological Research 29:1–11.

Lang JA, Roth JD, Markham JH. 2021. Foxes fertilize the subarctic forest and modify vegetation through denning. Scientific Reports 11:3031.

Lenth R. 2022. Emmeans: estimated marginal means, aka least-squares means. R package version 1.7.5. https://CRAN.R-project.org/package=emmeans.

Macpherson AH. 1969. The dynamics of Canadian arctic fox populations. Ottawa, CA: Canadian Wildlife Service Report Series. p 52.

McDonald RS, Roth JD, Baldwin FB. 2017. Goose persistence in fall strongly influences Arctic fox diet, but not reproductive success, in the Southern Arctic. Polar Research 36(sup1):5.

Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, Oates BA, Sawyer H, Scurlock BM, Kauffman MJ. 2016. Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society B: Biological Sciences 283:20160456.

Monk JD, Schmitz OJ. 2022. Landscapes shaped from the top down: predicting cascading predator effects on spatial biogeochemistry. Oikos 2022:e08554.

Natural Resources Canada. 2019. 2015 Land cover of Canada. Canada Centre for Remote Sensing, Natural Resources Canada. Government of Canada.

Nieto S, Flombaum P, Garbulsky MF. 2015. Can temporal and spatial NDVI predict regional bird-species richness? Global Ecology and Conservation 3:729–735.

Ostertag R, DiManno NM. 2016. Detecting terrestrial nutrient limitation: a global meta-analysis of foliar nutrient concentrations after fertilization. Frontiers in Earth Science 4:23.

Pedersen EJ, Miller DL, Simpson GL, Ross N. 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. PeerJ 7:e6876.

Pettorelli N, Laurance WF, O'Brien TG, Wegmann M, Nagendra H, Turner W. 2014. Satellite remote sensing for applied ecologists: opportunities and challenges. Journal of Applied Ecology 51:839–848.

Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jedrzejewska B, Lima M, Kausrud K. 2011. The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15–27.

Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker CJ, Stenseth NC. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

R Core Team. 2022. R: a language and environment for statistical computing [Version 4.2]. Vienna, Austria: R Foundation for Statistical Computing.

Risch AC, Frossard A, Schütz M, Frey B, Morris AW, Bump JK. 2020. Effects of elk and bison carcasses on soil microbial communities and ecosystem functions in Yellowstone, USA. Functional Ecology 34:1933–1944.

Ritchie JC. 1956. The native plants of Churchill, Manitoba, Canada. Canadian Journal of Botany 34:269–320.

Roberts DR, Bahn V, Ciuti S, Boyce MS, Elith J, Guillera-Arroita G, Hauenstein S, Lahoz-Monfort JJ, Schröder B, Thuiller W, Warton DI, Wintle BA, Hartig F, Dormann CF. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40:913–929.

Roth JD. 2003. Variability in marine resources affects arctic fox population dynamics. Journal of Animal Ecology 72:668–676.

Sawyer H, Kauffman MJ. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80:1078–1087.

Schmitz OJ, Hawlena D, Trussell GC. 2010. Predator control of ecosystem nutrient dynamics. Ecology Letters 13:1199–1209.

Schulte Bühne H, Pettorelli N. 2018. Better together: integrating and fusing multispectral and radar satellite imagery to inform biodiversity monitoring, ecological research and conservation science. Methods in Ecology and Evolution 9:849–865.

Sella GF, Stein S, Dixon TH, Craymer M, James TS, Mazzotti S, Dokka RK. 2007. Observation of glacial isostatic adjustment in ''stable'' North America with GPS. Geophysical Research Letters. https://doi.org/10.1029/2006GL027081.

Simpson GL. 2022. Gratia: Graceful ggplot-based graphics and other functions for GAMS fitted using mgcv. R package version 0.7.3.18. https://gavinsimpson.github.io/gratia/.

Smith CAS, Smits CMM, Slough BG. 1992. Landform selection and soil modifications associated with Arctic fox (*Alopex lagopus*) den sites in Yukon Territory, Canada. Arctic and Alpine Research 24:324–328.

Smits CMM, Smith CAS, Slough BG. 1988. Physical characteristics of Arctic Fox (*Alopex lagopus*) dens in Northern Yukon Territory, Canada. Arctic 41:12–16.

Speed JDM, Skjelbred IÅ, Martin MD, Berteaux D, Bueno CG, Christie KS, Forbes BC, Forbey J, Fortin D, Grytnes J-A, Hoset KS, Lecomte N, Marteinsdóttir B, Mosbacher JB, Pedersen ÅØ, Ravolainen V, Rees EC, Skarin A, Sokolova NA, Thornhill AH, Tombre I, Soininen EM. 2019. Trophic interactions and abiotic factors drive functional and phylogenetic structure of vertebrate herbivore communities across the Arctic tundra biome. Ecography 42:1152–1163.

Tognelli MF, Kelt DA. 2004. Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. Ecography 27:427–436.

Turner W, Rondinini C, Pettorelli N, Mora B, Leidner AK, Szantoi Z, Buchanan G, Dech S, Dwyer J, Herold M, Koh LP, Leimgruber P, Taubenboeck H, Wegmann M, Wikelski M, Woodcock C. 2015. Free and open-access satellite data are key to biodiversity conservation. Biological Conservation 182:173–176.

Valerio F, Ferreira E, Godinho S, Pita R, Mira A, Fernandes N, Santos SM. 2020. Predicting microhabitat suitability for an endangered small mammal using Sentinel-2 data. Remote Sensing 12:562.

van Moorter B, Bunnefeld N, Panzacchi M, Rolandsen CM, Solberg EJ, Sæther B-E. 2013. Understanding scales of movement: animals ride waves and ripples of environmental change. Journal of Animal Ecology 82:770–780.

Wood SN. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B (statistical Methodology) 73:3–36.

Zhao S-T, Johnson-Bice SM, Roth JD. 2022. Foxes engineer hotspots of wildlife activity on the nutrient-limited Arctic tundra. Global Ecology and Conservation 40:e02310.

Zupanc A. 2017. Improving cloud detection with machine learning. https://medium.com/sentinel-hub/improving-cloud-detection-with-machine-learning-c09dc5dgfcx7cf13. Accessed 7 May 2022.