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A multivariate approach to assessing landscape structure effects on wildlife crossing structure use

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Abstract

Background Complexity in landscape structure is often assessed using individual metrics related to ecological processes. However, this rarely incorporates important relationships among metrics and may miss landscape structure effects. Multivariate statistics provide techniques for assessing overall landscape structure effects. We assessed how multivariate statistics could be used to connect landscape structure with an ecological process [bobcat (*Lynx rufus*) wildlife crossing structure (WCS) use]. We tested how landscape structure at WCS sites compared to the surrounding landscape and how structure affected detections at WCS sites. Our study was conducted in Cameron County, Texas, USA where WCSs are in various stages of construction and monitoring. We used a classified land use/land cover map and aerial LiDAR to calculate configuration and density metrics at WCS and random sites. We created indices for configuration and density using principal components analysis to assess landscape structure effects on camera trap detections at WCSs.

Results Landscape structure at WCSs did not differ from random locations. Wildlife crossing structure use increased with greater woody cover and decreased with increasing vegetation density. Our indices allowed identification of differences in how configuration and density impacted WCS use. Ordination methods helped identify individual contributions of landscape metrics to the overall landscape structure effect.

Conclusions Wildlife crossing structures are permanent fixtures on landscapes, so selecting appropriate locations using broad-scale landscape structure likely increases target species use. Using indices of landscape structure provides planners with a more holistic approach to WCS placement and provides a more comprehensive picture of landscape pattern and process relationships.

Keywords Wildlife crossing structure, Multivariate statistics, Landscape structure, LiDAR, Landscape metrics, Bobcat

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Introduction

At broad spatial scales, heterogeneity in landscape structure can have strong effects on ecological processes (Turner 1989), but measuring heterogeneity is a complex process (With 2019). Landscape pattern analyses based on classification of remotely sensed imagery is commonly used to quantify landscape metrics (Forman and Godron 1981; Uuemaa et al. 2009; With 2019). Landscape metrics measure unique characteristics of landscape structure and can provide a glimpse into how landscape structure and complexity influences ecological processes (Hesselbarth et al. 2019; McGarigal et al. 2012). Effects of overall landscape heterogeneity and structure on ecological processes are often of interest. However, an individual class-level metrics approach may mask complex interrelationships between landscape patterns and ecological processes (Frazier and Kedron 2017; Topaloğlu et al. 2022). Landscape metrics provide useful information about certain aspects of landscape structure, but using individual metrics to examine relationships between overall landscape patterns and ecological processes is a misuse of landscape metrics (Li and Wu 2004; With 2019) because individual metrics only represent snippets of these patterns. One solution is to develop a landscape structure index by combining individual class-level metrics into a composite variable which can then be used to assess the overall impact of a landscape pattern on an ecological process (Olsen et al. 2018; Toosi et al. 2022). Additionally, many commonly used landscape metrics are derived from the number of patches and number of edges (Frazier and Kedron 2017), leading to high correlation among metrics and subsequent statistical issues.

Combining landscape metrics to examine landscape structure is not new in landscape ecology. The gradient concept of landscape structure (McGarigal and Cushman 2005) coupled with the concept of slack (Guthery 1999) to define the optimal range of values for a set of landscape metrics for a particular species can be used to identify suitable habitat across a range of landscape metrics (Lombardi et al. 2021; Mata et al. 2018). However, determining suitability inherently requires identifying habitat/non-habitat locations (Lombardi et al. 2021), which limits its predictive power to explain effects of overall landscape structure on ecological processes. An alternative method utilizes multivariate statistics to create indices of landscape structure based on individual metrics (Fig. 1).

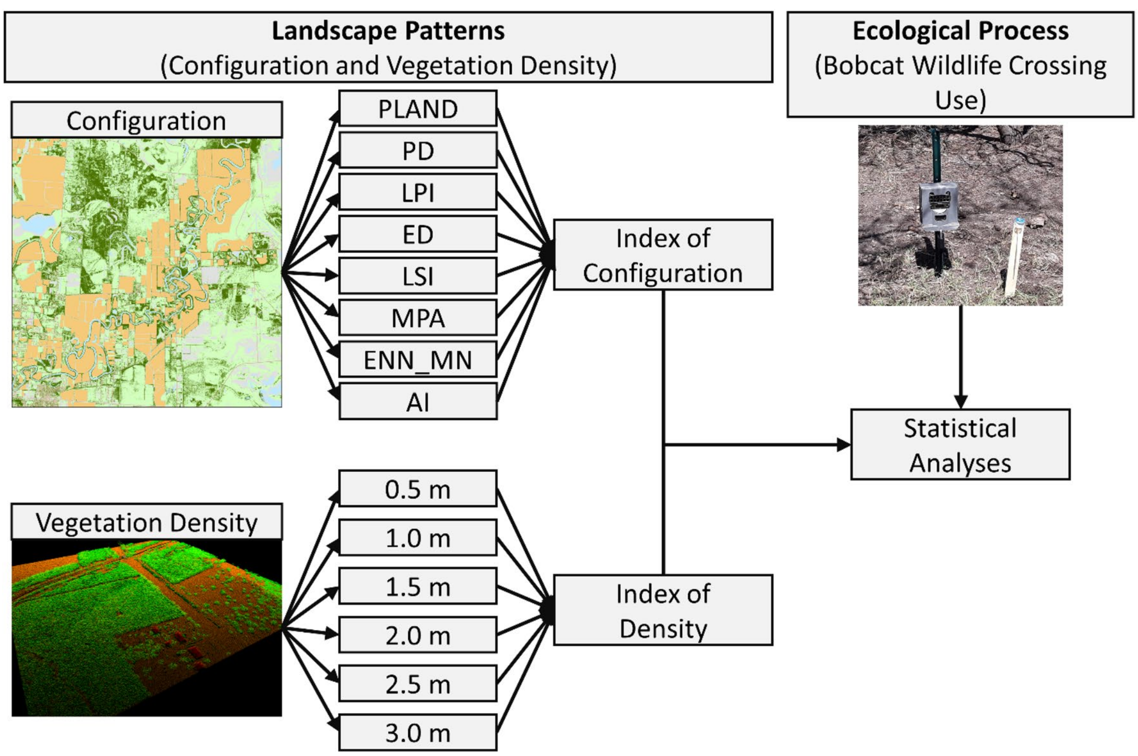

Fig. 1 Workflow describing how to relate landscape structure as described by landscape metrics derived from multiple sources with an ecological process such as bobcat (*Lynx rufus*) wildlife crossing structure (WCS) use along various high-speed roadways in Cameron County, Texas, USA. In this study, eight metrics of landscape configuration [percent land cover (PLAND), patch density (PD), largest patch index (LPI), edge density (ED), landscape shape index (LSI), mean patch area (MPA), mean Euclidean nearest neighbor distance (ENN_MN), and aggregation index (AI)] and six metrics of vegetation density (0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m above the ground) were used to create two indices of landscape patterns

Combining correlated landscape metrics into a single measure of overall landscape structure using multivariate statistics provides greater statistical power to detect relationships between landscape pattern and process (Grafius et al. 2018; Johnson and Wichern 2007; Lamine et al. 2018). However, landscape pattern analysis is often conducted using no statistical analyses (Liu and Yang 2015; Magidi and Ahmed 2019; Sertel et al. 2018) or multiple univariate analyses (Blackburn et al. 2021a, 2022; Miller et al. 2019; Vizzari and Sigura 2013). Although these approaches can provide information on landscape change or how individual metrics may relate to ecological processes, performing many tests lends itself to the multiple testing problem in statistics (Bender and Lange 2001). Additionally, univariate methods cannot incorporate correlation among predictors into analyses, a process that often increases statistical power (Johnson and Wichern 2007).

Multivariate statistics and indices of landscape structure allow researchers to examine the relative effects of different sets of metrics or metrics derived from different sources on ecological processes (Grafius et al. 2018; Peng et al. 2010; Yang and Liu 2005). Remote sensing technology is rapidly growing and evolving so there is increased interest in incorporating metrics derived from different platforms into analyses (Kuras et al. 2021). Incorporating metrics from multiple sources may also enhance our ability to examine ecological processes from landscape patterns (Zhou 2013). While metrics derived from different remote sensing platforms may explain similar aspects of landscape structure, they may also be complementary rather than replacements. Incorporating metrics derived from multiple platforms allows researchers to better understand how landscape structure impacts ecological processes.

Light detection and ranging (LiDAR) uses a laser mounted to an aerial- or terrestrial-based platform to map the three-dimensional structure of vegetation, buildings, and other hard surfaces (Ebrahim 2015; Eitel et al. 2016). This unique model of vegetation structure can provide powerful new metrics that cannot be estimated by other remote sensing tools. One metric that is easily estimated from LiDAR, likely plays an important role in habitat use, and cannot otherwise be estimated from categorical land cover data is vegetation density (Roussel et al. 2020). Vegetation density is the amount of vegetation per unit volume and can be estimated from a LiDAR point cloud using point density as a proxy for vegetation density (Knapp et al. 2018). Each return (laser pulse) in the point cloud represents a light particle reflecting off a solid object (e.g., leaf, stem, trunk, branch) so the absolute number of returns within a voxel (three-dimensional pixel) can represent vegetation density (Kamoske et al. 2019; Popescu and Zhao 2008; Putman and Popescu 2018).

Landscape metrics are often used to inform habitat management and species conservation and selecting appropriate metrics for the system of interest is critical (Lombardi et al. 2020b; With 2019). In the United States, the ocelot (*Leopardus pardalis*) is a federally endangered species that relies on dense woody cover (Sergeyev et al. 2023b) but is heavily threatened by roads through vehicle collisions and fragmentation (Blackburn et al. 2021b; Haines et al. 2005). Therefore, the Texas Department of Transportation (TxDOT) has installed wildlife crossing structures (WCSs) on several highways near known ocelot populations based on ocelot-vehicle collision sites, telemetry data, or the presence of woody cover in the vicinity (Blackburn et al. 2022; Schmidt et al. 2021). Broader-scale landscape structure has rarely been considered in WCS placement in Texas because it has been assumed that transient or dispersing ocelots are most at-risk from road-related mortality (Blackburn et al. 2021b; Schmidt et al. 2020). However, WCSs are novel structures, so it is unlikely that dispersing ocelots who may have never seen a WCS would use WCSs (Veals et al. 2022a). Resident individuals are more likely to use WCSs, so considering broad-scale land cover around WCSs likely better informs potential WCS use by resident ocelots (Veals et al. 2022a). While landscape structure at WCSs in the region has been compared to ocelot roadkill locations (Blackburn et al. 2022) and ocelot roadkill locations are known to have different landscape structure than successful crossing sites (Lombardi et al. 2023), it is unclear if the landscape structure at WCSs differs from the surrounding landscape. Landscape structure drives movement patterns and home range selection (Lombardi et al. 2021; Veals et al. 2022b), yet roads have a complex effect on landscape structure (McGarigal et al. 2001; Saunders et al. 2002) so it is essential to understand whether the landscape structure around a WCS will facilitate movement of target species across roads.

Due to relatively low population size, WCS use by ocelots is rare. However, sympatric and similar-sized bobcats (*Lynx rufus*) regularly use WCSs in the region. Bobcats also rely on woody cover in South Texas and overlap with ocelots both spatially and behaviorally (Lombardi et al. 2020a; Sergeyev et al. 2023a) making bobcats a good proxy for assessing potential effects of vegetation structure around WCSs on ocelots (Litvaitis et al. 2015; Schmidt et al. 2021).

In this study, we used multivariate methods to assess how landscape structure (metrics measuring landscape configuration and vegetation density) affects WCS use (an ecological process). We aimed to (1) compare the landscape structure (as represented by multiple metrics of landscape configuration and vegetation density) at WCSs to highways and the surrounding landscape and (2) assess how indices of landscape configuration and vegetation density can be used to predict WCS use by bobcats. We hypothesized (1) that WCSs would have a landscape configuration and vegetation density that represented greater amounts of dense woody cover that is highly connected, (2) including metrics of vegetation density would provide an additive effect on explaining bobcat WCS use, and (3) that bobcats would be detected more often at WCSs with larger patches of woody cover that are more connected and denser. We expected that using a more holistic measure of landscape structure would better explain how landscape structure affected WCS use than the traditional "individual metric" approach.

Methods

Study area

Our study area was Eastern Cameron County, Texas, encompassing an area with known ocelots. We focused our work on three highways where WCS construction has occurred since 2016: State Highway (SH) 100 (five WCS completed 2018), Farm-to-Market (FM) 106 (eight WCS completed 2020), and FM 1847 (five WCS completed 2022; Fig. 2). During the study period, the highways differed in annual average daily traffic, speed, and number of lanes (Table 1).

Land cover in our study site is diverse and consists of a mosaic of woody cover, herbaceous cover, bare ground, water, agriculture, wind energy development, and

Table 1 Road characteristics including name, average annual daily traffic in 2020 (AADT), surface type, road width (number of lanes), speed limit (km/h), and number of wildlife crossing structures (WCS) of the three study roads and other major paved roads in eastern Cameron County, Texas, including state highways (SH), Farm-to-Market (FM) roads, and county roads (CR)

Name	AADT	Road width	Speed limit	WCS
SH 100	6894–9465	4	105	5
FM 106	743–1732	2	88	8
FM 1847	2216–3233	2	88–105	5
FM 510	2671–3377	2	48–88	0
CR 3069	475–598	2	48–96	0
FM 2480	1474–4867	2	48–88	0
San Roman Road	111–1472	2	48–96	0

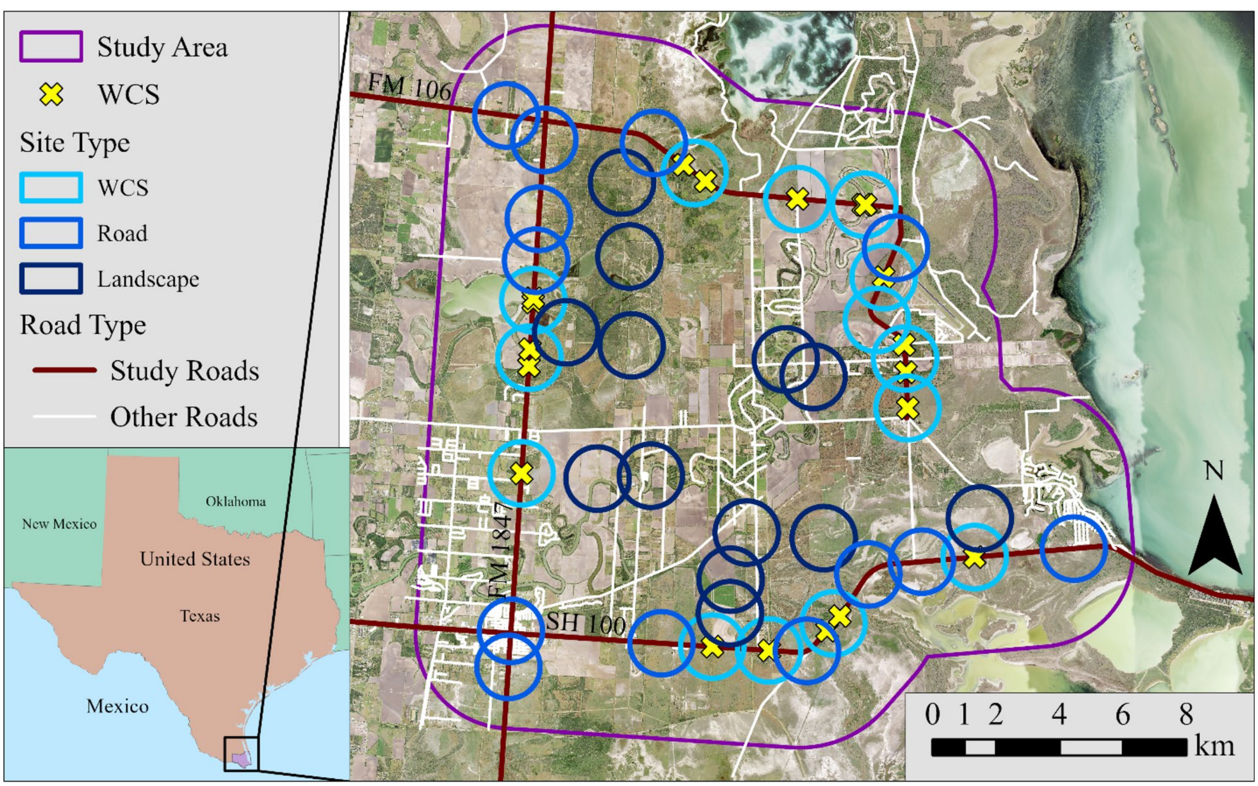

Fig. 2 Study area showing the locations of the three study roads (State Highway (SH) 100, Farm-to-Market (FM) 106, and FM 1847), other roads, the locations of wildlife crossing structures (WCS), the random road sites, and the surrounding landscape locations representing the surrounding landscape in eastern Cameron County, Texas, USA

Table 2 Description of wildlife crossing structures (WCS), including highway, completion date (month year), type (small, medium, or large box culvert or bridge), urbanization level (rural, peri-urban, or urban), and openness ratio ($\frac{Width \times Height}{Length}$)

Highway	WCS	Completion date	Type	Urbanization level	Openness ratio
State Highway 100	WCS 1	May 2018	Large box	Rural	0.44
	WCS 2	May 2018	Large box	Rural	0.39
	WCS 3	May 2018	Bridge	Rural	1.76
	WCS 3a	May 2018	Small box	Rural	0.21
	WCS 4	May 2018	Medium box	Rural	0.63
Farm-to-Market 1847	WCS 1	August 2022	Medium box	Urban	0.35
	WCS 2	August 2022	Bridge	Peri-urban	10.54
	WCS 3	August 2022	Medium box	Peri-urban	0.58
	WCS 4	August 2022	Medium box	Rural	0.51
	WCS 5	August 2022	Medium box	Rural	0.51
Farm-to-Market 106	FM 1	December 2019	Medium box	Rural	0.47
	FM 2	December 2019	Medium box	Rural	0.80
	FM 3	December 2019	Medium box	Rural	0.40
	FM 4	December 2019	Medium box	Rural	0.42
	FM 5	December 2019	Medium box	Rural	0.50
	FM 6	December 2019	Medium box	Rural	0.40
	FM 7	December 2019	Medium box	Rural	0.40
	FM 8	December 2019	Medium box	Rural	0.47
	FM Airport*	NA	Small box	Rural	0.20

* This location was not built as a WCS. The structure is a small box culvert that has no modifications for wildlife but was monitored during the study period for use by wildlife, therefore it was included in this study

developed areas. Woody vegetation in the study area is primarily Tamaulipan thornscrub, a vegetation community made up of short (<5 m), thorny trees and shrubs (Lombardi et al. 2020b; Veals et al. 2022a). Land use is primarily private ranchland, agriculture, residential areas, and protected areas. The climate in the region is generally hot and humid throughout the year with temperatures ranging from 10 °C in January to 36 °C in July (Palecki et al. 2020). The area receives highly variable rainfall, ranging from 313 to 529 mm per year, and experiences episodic droughts (Cooper and Wagner 2013).

Data collection

We focused data collection at the WCSs on SH 100, FM 106, and FM 1847. On FM 106, one small box culvert was also monitored for wildlife use in addition to the eight WCSs (Table 2). Of the 19 WCSs [five WCSs on SH 100, nine (eight WCSs and one non-WCSs box culvert) on FM 106, and five WCSs on FM 1847; hereafter WCS sites], 12 could not be considered spatially independent (at least 500 m from another WCS), so these WCSs were combined into single sites, leaving 13 WCS sites (four on SH 100, six on FM 106, and three on FM 1847; Fig. 2). We randomly sampled an equal number of locations, randomly located at least 1 km from a study highway and within the area bounded by the study highways. Landscape locations represented typical landscapes in the study area and included protected areas, rangelands, other roads, and low-intensity urban development. Additionally, we randomly sampled an equal number of locations along the study roads that were at least 1 km from a WCS to represent the landscape around the study roads that was away from WCSs. We created 1 km buffers around each location to measure landscape configuration and vegetation density.

Landscape structure metrics

We created a classified land cover map based on 1-m resolution National Agricultural Imagery Program (NAIP) aerial imagery captured in 2016; 2016 imagery was the most recently available imagery that encompassed the entire study area. NAIP imagery has four bands (red, green, blue, near infrared) and was collected in November 2016. We used ArcGIS Pro (Esri, Redlands, CA, USA) to conduct a supervised classification using a random forest model to classify our imagery into four land cover classes: bare, herbaceous, water, and woody (Sheykhmousa et al. 2020). We created a Normalized Difference Vegetation Index (NDVI) layer using ArcGIS Pro to aid in the classification. The bare class mostly represented unpaved roads (caliche, earthen soil) on ranchlands and areas near ephemerally flooded water bodies (wetlands and resacas). The herbaceous class was primarily cord grass (*Spartina spartinae*) prairie, sea-oxeye daisy (*Borrichia frutescens*) prairie, and salt flats. The water class represented freshwater canals, lakes, and saltwater estuaries and bays. The woody class was made up of Tamaulipan thornscrub, honey mesquite (*Prosopis glandulosa*) woodland, and various ornamental trees in residential and urban areas.

To assess the accuracy of the classified map, we hand classified 500 random points selected from a simple random sample of the landscape (Foody 2002; Stehman and Foody 2019) using multiple high resolution images (< 1.0 m; Pulighe et al. 2016). These points were representative of the landscape based on a χ^2 analysis ($\chi^2_{df=3}=2.657$, $p=0.448$) and had an estimated 95% confidence interval of 0.029 (Stehman and Foody 2019). We then created a confusion matrix to assess overall accuracy and class accuracy. An overall accuracy of 85% with individual class accuracies of 70% has been recommended as a standard for accuracy of fine scale imagery (Thomlinson et al. 1999). Following the recommendation of Thomlinson et al. (1999), we added training samples and reclassified our map until we achieved the desired accuracy. When adding training samples, we ensured that no training samples overlapped with accuracy assessment samples. Our final classified map exceeded this threshold with an overall accuracy of 87.0% (producer and user accuracies of 83.8% and 81.7% respectively for bare, 89.6% and 88.9% for herbaceous, 86.3% and 93.6% for water, and 83.2% and 83.2% for woody) so we were comfortable proceeding with the analysis.

We also included two human land use classes in our final classified map: agriculture and developed. Initially, we attempted to classify these using the random forest model but we could not achieve the desired accuracies for either of these classes due to the variety of different spectral signatures of each, so we manually digitized agricultural and developed land uses within the study area to include in our classified land cover map. Agricultural areas in the study area included fallow fields (appear as bare ground), row crops (appear as herbaceous cover), and citrus groves (appear as woody cover). Developed areas within the study area were primarily low-density urban so we defined the developed land cover type as buildings (appear as any class depending on the spectral signature) and paved roads (appear as bare or water cover) within the study area. We used the TxDOT Roadway Inventory database to identify paved roads (Texas Department of Transportation 2022) and created 10 m buffers around each to account for the width of the road and right-of-way. To identify buildings, we classified an aerial LiDAR point cloud obtained in 2018 (nominal point spacing = 0.7) into building, vegetation, and other points using the program LP360 (GeoCue, Madison, AL, USA). We used software-based tools within LP360 to create polygons and distinguished buildings from dense vegetation using discriminant analysis of building, vegetation, and ground points (Yamashita et al. 2023). We combined building polygons with the road buffers to create a developed layer.

We rasterized the agricultural and developed land uses then combined them with the land cover map using the raster calculator in ArcGIS Pro to produce a land use/land cover map with six classes: agriculture, bare, developed, herbaceous, water, and woody (Fig. 3). Overlap between the agriculture and developed classes could occur as a result of the vector-based classification, not raster-based classification of these classes. When agricultural and developed land uses overlapped, we gave priority to developed, opting for the more intensive land use.

We used Fragstats v4.2 to calculate eight class-level metrics within each buffer around the WCS and random locations: percent land cover (PLAND; %), patch density (PD; # patches/100 ha), largest patch index (LPI; %), edge density (ED; m/ha), landscape shape index (LSI; no units), mean patch area (MPA; ha), mean Euclidean nearest neighbor distance (ENN_MN; m), and aggregation index (AI; %; McGarigal et al. 2012; Table 3, Supplementary material). The selected metrics are known to effectively describe the configuration of woody cover in southern Texas and have been used previously to assess ocelot and bobcat resource selection, road mortality patterns, habitat suitability, and landscape connectivity (Blackburn et al. 2021a; Jackson et al. 2005; Lombardi et al. 2021, 2020b, 2023; Schmidt et al. 2020).

We used the same LiDAR point cloud as above to calculate vegetation density (LiDAR returns/voxel; Table 3). Using only points classified as vegetation, we defined a voxel size of 1.5 m × 1.5 m × 0.5 m, the smallest horizontal cell size possible with the available point cloud. We calculated point density within each voxel as a proxy for vegetation density using the *lidR* package in Program R (Roussel et al. 2020). Ocelots and bobcats are known to respond to horizontal and vertical cover up to 3 m above the ground (Lombardi et al. 2022; Sergeyev et al. 2023a), so we limited our analyses to the first 3 m of vegetation (Fig. 4). Within each height bin, we calculated an average vegetation density within each buffered area to create six metrics of vegetation density, based on height above the ground: 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m (Table 3). Finally, we calculated canopy height from the LiDAR point cloud by calculating the difference between a 1.5 × 1.5 m resolution digital terrain model and digital elevation model using ArcGIS Pro.

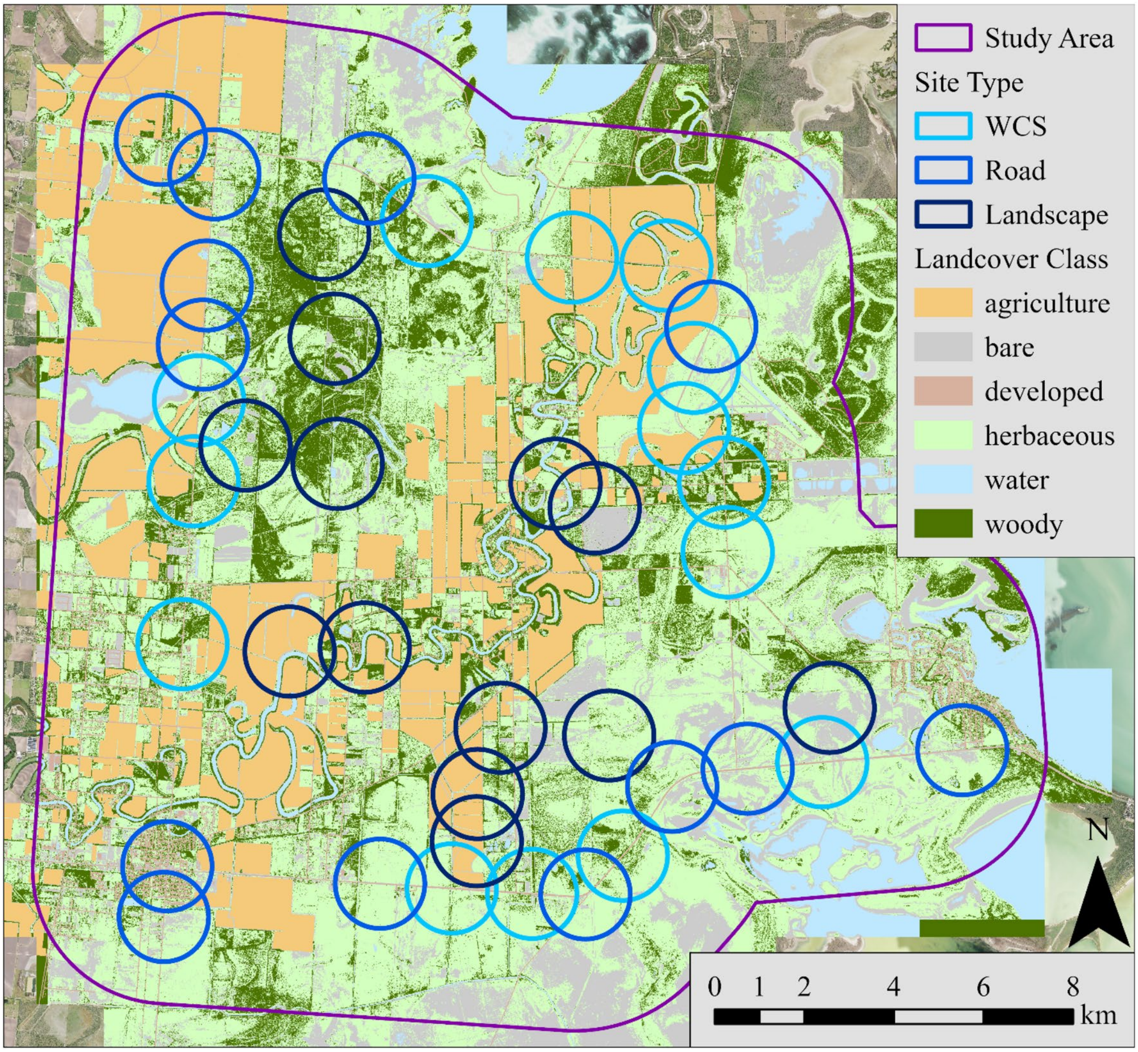

Fig. 3 Land cover classification map showing the four natural cover classes (bare, herbaceous, water, and woody) and two human land use types (agriculture and developed) and the locations of the wildlife crossing structure (WCS), random road sites, and surrounding landscape sites in eastern Cameron County, Texas, USA

Bobcat wildlife crossing structure use

To assess bobcat WCS use, we used camera traps set up at each of the 19 WCS sites to monitor mammal populations and assess WCS effectiveness in multiple concurrent studies (Kline et al. 2020, 2022; Tewes et al. 2020). Because WCSs were in different stages of construction at the time of this study, camera setup varied slightly across highways. All cameras were either Reconyx PC900 or Hyperfire 2 (Reconyx Corp., Holmen, WI, USA), set at a height of 30–50 cm above the ground, set to record 1–5 photographs per trigger, and set to high sensitivity. Due to differences in WCS size, shape, and construction stage, 4–12 cameras were set up at each WCS site. At completed WCS sites (SH 100 and FM 106), an active infrared trigger system was also set up to aid in capture of WCS use (Cogan 2018). These systems were not used at under-construction WCS sites (FM 1847) because they work best when there is a clearly defined path (Cogan 2018).

For completed WCSs, we defined independent events based on animal behavior at WCSs. Using a 30-min interval, we determined whether an animal crossed through a WCS or was just seen in the area. Occasionally, animals crossed in both directions within the 30 min interval, or multiple individuals were seen having different interactions with WCSs so these were considered to be separate events creating potentially multiple independent events within a single 30 min period (Kintsch et al. 2018; Kline et al. 2020, 2022). At under-construction WCSs, we used a 30 min interval to define independent events (Kelly 2003; Kelly and Holub

Table 3 Description of the landscape metrics used in this study, including their units, data source and software for calculation, and the mean ± standard deviation for wildlife crossing structure locations (WCS) and random locations

	Metric	Description	Units	Data source	WCS	Landscape	Road
Configuration	Percent land cover (PLAND)	Percentage of landscape taken up by a class	%	Classified imagery, Fragstats	14.14 ± 11.7	20.6 ± 16.57	12.23 ± 6.83
	Patch density (PD)	Number of patches of each class on a landscape	Patches/100 ha	Classified imagery, Fragstats	1188.79 ± 678.88	1362.91 ± 776.06	1359.92 ± 401.62
	Largest patch index (LPI)	Percentage of the landscape made up of the largest patch of a particular class	%	Classified imagery, Fragstats	2.63 ± 2.64	6.2 ± 7.85	1.96 ± 1.35
	Edge density (ED)	The amount of edge between two classes	m/ha	Classified imagery, Fragstats	566.81 ± 367.83	755.08 ± 484.18	620.03 ± 272.08
	Landscape shape index (LSI)	A standardized measure of edge length	None	Classified imagery, Fragstats	67.43 ± 24.37	75.49 ± 25.02	79.53 ± 15.31
	Mean patch area (MPA)	Average size of each patch of a particular class	ha	Classified imagery, Fragstats	0.01 ± 0.01	0.02 ± 0.01	0.009 ± 0.004
	Mean Euclidean nearest neighbor distance (ENN_MN)	Average distance between two patches of the same class	m	Classified imagery, Fragstats	5.37 ± 1.31	4.64 ± 0.59	5.07 ± 0.86
	Aggregation index (AI)	Percentage of pixels of a given class that are adjacent to another class	%	Classified imagery, Fragstats	86.92 ± 6.1	88.94 ± 4.85	84.92 ± 5.70
Density	Point density at 0.5 m (m0.5)	Average LiDAR returns from 0.0 to 0.05 m above the ground	Returns/voxel	Aerial LiDAR, lidR package	0.63 ± 0.33	0.75 ± 0.21	0.66 ± 0.25
	Point density at 1.0 m (m1.0)	Average LiDAR returns from 0.5 to 1.0 m above the ground	Returns/voxel	Aerial LiDAR, lidR package	0.11 ± 0.1	0.14 ± 0.07	0.08 ± 0.05
	Point density at 1.5 m (m1.5)	Average LiDAR returns from 1.0 to 1.5 m above the ground	Returns/voxel	Aerial LiDAR, lidR package	0.16 ± 0.11	0.25 ± 0.17	0.15 ± 0.09
	Point density at 2.0 m (m2.0)	Average LiDAR returns from 1.5 to 2.0 m above the ground	Returns/voxel	Aerial LiDAR, lidR package	0.18 ± 0.12	0.31 ± 0.24	0.18 ± 0.12
	Point density at 2.5 m (m2.5)	Average LiDAR returns from 2.0 to 2.5 m above the ground	Returns/voxel	Aerial LiDAR, lidR package	0.18 ± 0.13	0.33 ± 0.29	0.19 ± 0.14
	Point density at 3.0 m (m3.0)	Average LiDAR returns from 2.5 to 3.0 m above the ground	Returns/voxel	Aerial LiDAR, lidR package	0.17 ± 0.14	0.33 ± 0.31	0.18 ± 0.14

A full description of the landscape metrics used in this study is provided in the supplementary material

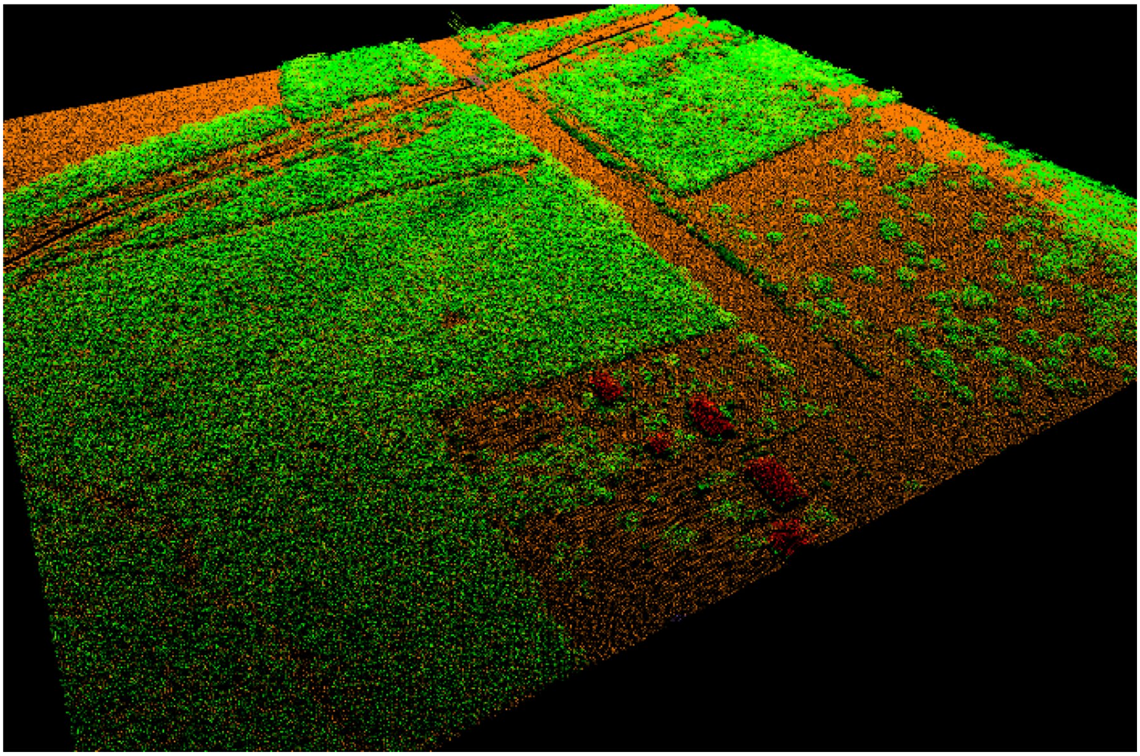

Fig. 4 Example of the classified Light Detection and Ranging (LiDAR) point cloud used to describe vegetation density. Ground points (orange), vegetation points (green), and buildings (red) are shown

2008; Silver et al. 2004). However, because there was no possibility of interacting with a WCS, each 30 min period was always made up of one event. For analyses, we used the total number of events, as defined above for completed and under-construction WCSs, because WCS interactions could not be determined at under-construction WCSs. When multiple WCSs made up a site, the average number of events, rounded to the nearest whole number was used for that site. Camera trapping was limited to December 2019 to November 2020 to ensure that cameras were active on all three highways at the same time.

Statistical analysis

For analysis, we exclusively examined the woody class because it is the class most associated with ocelots and bobcats in South Texas (Lombardi et al. 2022; Sergeyev et al. 2023b). The other land cover classes were not included in analyses but help to provide a visually, more complete picture of the landscape structure and can be used in other studies in the region. To determine if the landscape structure (defined as landscape configuration plus vegetation density metrics) at WCSs was different from other road sites and the surrounding landscape, we used a permutational multivariate analysis of variance (PERMANOVA) to test the hypothesis that WCSs, the landscape around highways, and the surrounding landscape did not differ with respect to a suite of eight landscape configuration metrics (PLAND, PD, LPI, ED, LSI, MPA, ENN_MN, and AI) and six vegetation density metrics (0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m). PERMANOVA is a semi-parametric multivariate analysis of variance that compares the dissimilarity in response variables (metrics) among experimental units (sites) to identify differences in treatment (WCS, road, or random; Anderson 2001). Because PERMANOVA, like other multivariate analyses, simultaneously considers all response variables in the analysis, it is ideal for testing whether there are overall differences in landscape structure. We used Euclidean distance to calculate a dissimilarity matrix because it is most appropriate for non-count interval and ratio data (Legendre and Legendre 2012, Ch. 7). PERMANOVA is sensitive to differences in both location and dispersion (Anderson 2017), so we also tested for differences in multivariate dispersion using a permutational distance-based test for differences in dispersion (PERMDISP; Anderson 2006).

Finally, coupling PERMANOVA with an appropriate ordination technique is recommended for aiding in interpretation and visualization of the result (Anderson 2017).

Therefore, we ran Principal Component Analysis (PCA) using the *prcomp* function in Program R (Abdi and Williams 2010). Correlation between the landscape metrics and the principal component axes (PCs) was used to aid in interpretation of the relationship between individual metrics and site types.

To examine how bobcat WCS use related to landscape structure, we analyzed a generalized linear mixed model (GLMM) to assess how monthly bobcat detections at WCSs were affected by landscape configuration, vegetation density, and canopy height (m). Canopy height was included as a covariate in the models because it is known to influence bobcat and ocelot habitat use (Sergeyev et al. 2024), is generally tied to woody cover, and can have an effect on vegetation density (Pervin et al. 2022). Therefore, canopy height is likely an important source of variation in models of woody cover. To account for high multicollinearity and to assess overall relationships between bobcat WCS use and configuration and density, we employed a principal components regression (PCR) approach (Massy 1965). Principal components regression is a well-documented technique to eliminate multicollinearity in regression and when all PCs are included, the results are identical to regression on the original predictors (Legendre and Legendre 2012, Ch. 10). By interpreting fewer axes, however, PCR can help alleviate the issues of multicollinearity, as long as the selected axes reasonably explain the variation in the response variable (Artigue and Smith 2019; Hadi and Ling 1998). When the selected PCA axes are interpreted instead of the original predictors, they can represent an index of the original predictors.

In our analyses, we aimed to assess overall effects of configuration (PLAND, PD, LPI, ED, LSI, MPA, ENN_MN, and AI) and density (0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m), so we used PCA to develop separate indices of these two measures of landscape structure to assess how overall landscape structure impacts bobcat WCS use. Landscape metrics were centered and scaled before calculation of the PCA to ensure that the predictors contribute equally to the computation of the PCA (Legendre and Legendre 2012, Ch. 10). These indices represent the relative contribution of each set of metrics (configuration and density; Table 3) to the variation in bobcat detections at each site through time. The use of PCA to develop indices is well documented in both ecology (Ewaid et al. 2020; Olsen et al. 2018) and the social sciences (Bucherie et al. 2022). This technique mirrors partial linear regression which is used to assess the relative contribution of sets of predictors to the variation in a response variable (Borcard et al. 1992; Legendre and Legendre 2012, Ch. 10; Mood 1971). In PCR, the dropping of PCs can occur before or after regression (Hadi and Ling 1998) so to assess overall structure effects and reduce multicollinearity effects, we only included PCs that explained > 85% of the variation in each suite of metrics. Relationships between all PCA axes and bobcat detections were also examined to determine whether another axis might represent a significant source of variation in bobcat detections. We analyzed a GLMM using a negative binomial error distribution using *Proc Glimmix* in SAS v9.4 (SAS Institute, Cary, NC, USA) with bobcat WCS detections as the response variable and the configuration index, density index, and canopy height as fixed effects and site as a random effect. We were also interested in determining if including LiDAR-derived vegetation density metrics explained additional variation than a model including just configuration metrics, so we used a likelihood-ratio test to compare the global model to a model that only included configuration and canopy height.

We accounted for repeated measures within a site by modeling the within-error correlation structure (Stroup 2013, Ch. 14). We modeled nine plausible correlation structures: variance components, compound symmetry, heterogeneous compound symmetry, first-order autoregressive, heterogeneous first-order autoregressive, Toeplitz, heterogenous Toeplitz, first-order autoregressive moving average, and unstructured. We chose the best correlation structure based on AICc. This was done separately for each model (global model and reduced model) to ensure that the best error structure represented each model. A model including interactions among factors was also tested but the interaction effects were not statistically significant, so these were excluded from the global model.

Once we determined our global model, we were interested in assessing how our PCA axes compared to known relationships between bobcat space use and landscape metrics. We calculated the relative contributions to the regression equations for each landscape configuration and density metric using by multiplying the matrix of eigenvectors produced from PCA and the vector of beta coefficients of the selected PC axes to assess how each metric affected bobcat detections (Legendre and Legendre 2012, Ch. 10). The computed relative contributions represent the beta coefficients of the original metrics in reduced PCA space so we could use these values to assess the directionality and magnitude of the individual relationships between each metric and bobcat WCS use.

Results

Our PERMANOVA results revealed that landscape structure at WCSs, random road sites, and the surrounding landscape did not differ (pseudo-$F = 2.075$, $p = 0.083$, unique permutations = 9938). PERMDISP revealed an overall difference in dispersion

($F_{2,36}=4.542$, P(perm) = 0.030). Post-hoc pairwise tests revealed that there was only a difference between the random road sites and surrounding landscape sites ($t=2.986$, P(perm) = 0.012) where random road sites had a lower dispersion than the surrounding landscape. Wildlife crossing structure sites were not different from either random road sites ($t=2.050$, P(perm) = 0.075) or surrounding landscape sites ($t=1.074$, P(perm) = 0.332). While not statistically significant, WCSs and random road sites generally had lower vegetation density and lower PLAND, LPI, and ED, and higher ENN_MN than the surrounding landscape (Fig. 5).

We detected bobcats 2,773 times at the 19 WCSs during the study period. Two PCs explained 87.1% of the variation in landscape configuration metrics and one PC explained 90.2% of the variation in vegetation density so our global model included two indices for configuration; one index for density, and average canopy height. Landscape configuration metrics were highly correlated with the first PC axis of configuration (− 0.81 for ENN_MN to 0.93 for ED; Fig. 6A, Table 4) and with the second PC axis of configuration (− 0.80 for MPA to 0.73 for LSI; Fig. 6A, Table 4). Vegetation density metrics were only highly correlated with the first PC axis of vegetation density (0.89 for 0.5 m to 0.98 for 2.0 m; Fig. 6B, Table 5).

For the global model, six correlation structures converged with the Toeplitz structure having the best fit (AIC = 505.61; supplementary material). For the configuration-only model, eight correlation structures converged with the Toeplitz structure having the best fit (AICc = 466.72; supplementary material). Including vegetation density in the model explained significantly more of the variation in monthly bobcat detections than a model that did not include density ($\chi^2=38.89$, $p<0.0001$). Based on our global regression model, we documented a 211.8% increase in bobcat detections with a one-unit increase in the first axis of the configuration index ($p=0.005$) and a 32.9% decrease in detections with a one-unit increase in the density index ($p=0.027$; Fig. 7; supplementary material). There were no significant relationships between bobcat detections and the second configuration axis (beta = − 5.192%, $p=0.767$) or mean canopy height (beta = − 93.66%, $p=0.191$).

There was a positive relationship between bobcat detections and centered and scaled versions of PLAND (0.461), PD (0.381), LPI (0.410), ED (0.485), LSI (0.369),

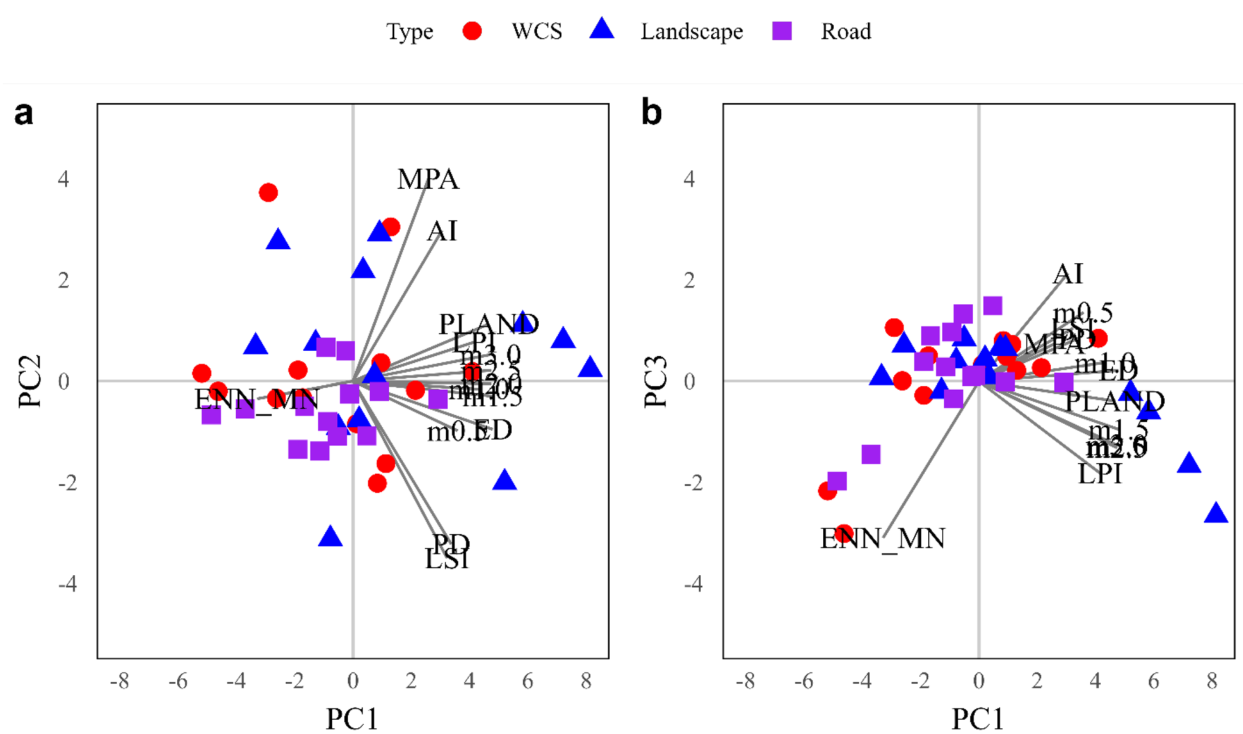

Fig. 5 Principal components (PC) analysis of eight metrics of landscape configuration [percent land cover (PLAND), patch density (PD), largest patch index (LPI), edge density (ED), landscape shape index (LSI), mean patch area (MPA), mean Euclidean nearest neighbor distance (ENN_MN), and aggregation index (AI)] and six metrics of vegetation density (0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m above the ground), showing differences between wildlife crossing structure (WCS) sites, the surrounding landscape (Landscape), and the random road (Road) locations. Relationships between the first and second (**a**), and first and third (**b**) PC axes are shown. Lines represent the relative correlation between each metric and PC axis

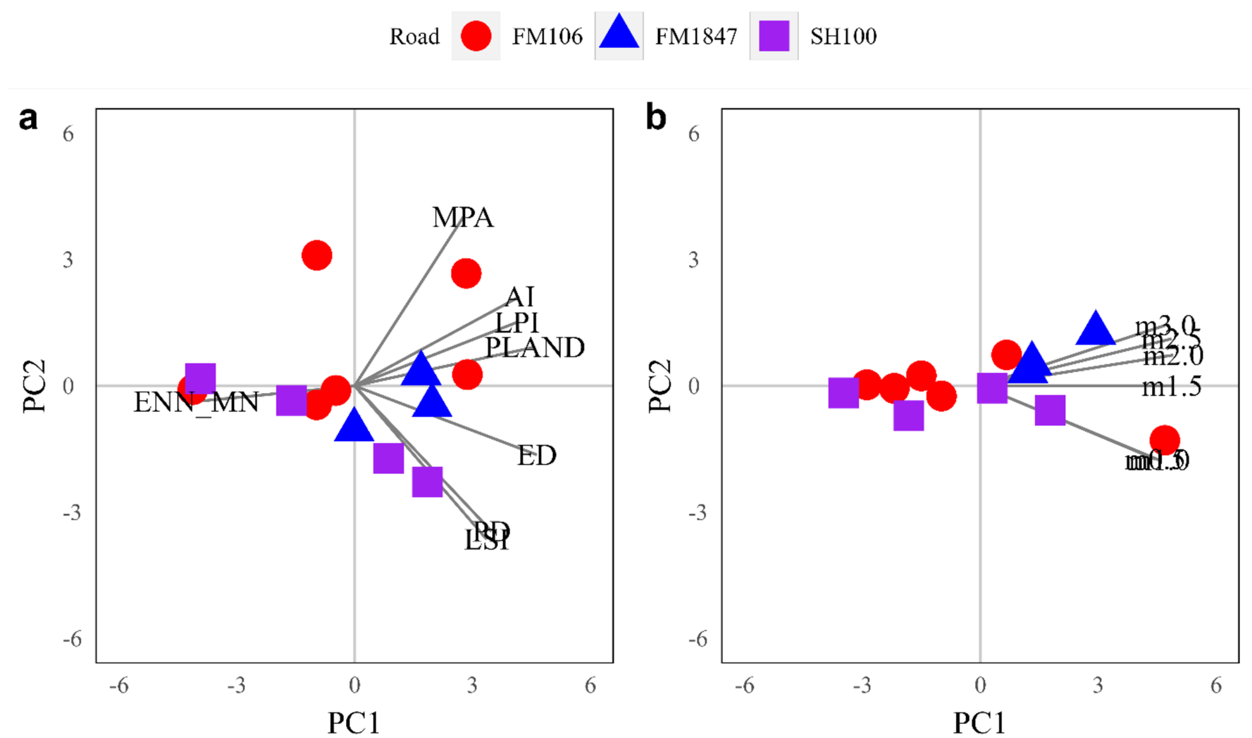

Fig. 6 Principal components (PC) analysis of (**a**) eight metrics of landscape configuration [percent land cover (PLAND), patch density (PD), largest patch index (LPI), edge density (ED), landscape shape index (LSI), mean patch area (MPA), mean Euclidean nearest neighbor distance (ENN_MN), and aggregation index (AI)] and (**b**) six metrics of vegetation density (0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m above the ground), showing differences among wildlife crossing structure sites on each highway (State Highway [SH] 100, Farm-to-Market [FM] 106, and FM 1847) in eastern Cameron County, Texas). Only the first two PC axes are shown. Lines represent the relative correlation between each metric and each PC axis

Table 4 Correlation between the first two principal components (PC) axes of landscape configuration and eight metrics of landscape configuration: percent land cover (PLAND; %), patch density (PD; # patches/100 ha), largest patch index (LPI; %), edge density (ED; m/ha), landscape shape index (LSI; no units), mean patch area (MPA; ha), mean Euclidean nearest neighbor distance (ENN_MN; m), and aggregation index (AI; %)

Configuration Metric	PC 1	PC 2	Contribution to regression
PLAND	0.918	− 0.183	0.461
PD	0.696	0.691	0.381
LPI	0.826	− 0.301	0.410
ED	0.927	0.327	0.485
LSI	0.672	0.729	0.369
MPA	0.553	− 0.802	0.252
ENN_MN	-0.805	0.074	− 0.408
AI	0.838	− 0.423	0.412

The relative contribution of each metric to the regression was also calculated by multiplying the matrix of eigenvectors from principal components analysis and the beta coefficients of the included PCs

Table 5 Correlation between the first principal components (PC) axis of vegetation density and six metrics of vegetation density: 0.5 m, 1.0 m, 1.5 m, 2.0 m, 2.5 m, and 3.0 m above the ground

Density Metric	PC 1 (density)	Contribution to regression
0.5 m	0.889	− 0.153
1.0 m	0.910	− 0.157
1.5 m	0.977	− 0.168
2.0 m	0.982	− 0.169
2.5 m	0.973	− 0.168
3.0 m	0.941	− 0.162

The relative contribution of each metric to the regression was also calculated by multiplying the matrix of eigenvectors from principal components analysis and the beta coefficients of the included PC

MPA (0.252), and AI (0.412; Table 4). Mean Euclidean nearest neighbor distance (− 0.408; Table 4) and density at all levels (− 0.169 to − 0.153; Table 5) had a negative relationship with bobcat detections.

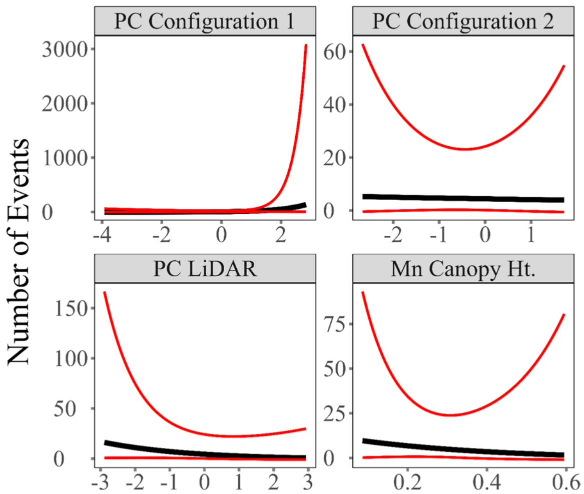

Fig. 7 Regression lines (black) and confidence bands (red) between bobcat detections and the first principal components (PC) axis of configuration (PC Configuration 1; unitless), the second PC axis of configuration (PC Configuration 2; unitless), the first PC axis of density (PC LiDAR; unitless), and mean canopy height (Mn Canopy Ht.; m)

Discussion

Wildlife crossing structure sites generally represented the available woody cover on the landscape; however, landscape configuration and vegetation density were slightly smaller at WCS than in the surrounding landscape. Landscape structure at WCSs did not correspond with greater woody cover in larger patches that are close together therefore the hypothesis that WCSs would have greater amounts of woody cover than the available landscape was rejected. Including an index of vegetation density provided an additive benefit for predicting bobcat WCS use over a model including only an index of landscape configuration and canopy cover. Finally, bobcats preferred WCSs with greater amounts of less dense woody cover providing mixed validity for our hypothesis that bobcats would be detected more often at WCSs with greater amounts of connected and dense woody cover. By using PCA to develop indices of configuration and density, we were able to incorporate all known and important woody cover metrics for bobcats, allowing us to assess the relationship between bobcat detection and overall landscape structure.

We were able to assess the effect of overall landscape structure on bobcat detections by utilizing PCA to create indices of landscape configuration and vegetation density. The suite of metrics we selected for both indices have been well documented to be important to both bobcats and ocelots in South Texas (Blackburn et al. 2021a, 2022; Harveson et al. 2004; Jackson et al. 2005; Lombardi et al. 2021, 2022, 2023; Schmidt et al. 2020; Sergeyev et al. 2023a), allowing us to create informative measures of overall landscape structure (Cushman et al. 2008; Grafius et al. 2018; Kupfer 2012). Our selected PCA axes generally agreed with these previous results with PC1 being associated with associated with greater levels of PLAND, AI, and LPI and lower ENN_MN, indicating that the positive relationship that we saw between PC1 and bobcat detections was likely driven by increases in unfragmented, large patches of woody cover (Branney et al. 2024; Lombardi et al. 2021, 2020c). Our density results showing a negative relationship between vegetation density and WCS use contradict some previous results that showed that bobcats generally select for areas of dense canopy cover below 2 m (Sergeyev et al. 2024). That study did show high levels of variation among individuals and areas with dense cover tend to be used as denning or rest sites while bobcats will move through and forage in more open areas (Sergeyev et al. 2023b). Therefore, it is likely that WCSs are being used for their intended purpose as movement corridors where dense cover is less important for bobcats. Ocelots are more dependent on dense cover than bobcats in South Texas (Sergeyev et al. 2023a), so the general agreement between our results based on indices of woody cover and previous studies on bobcat and ocelot resource selection and space use indicate that using indices of cover based on PCA provides a useful metric for assessing landscape structure impacts on WCS use.

Using a regression approach, it would otherwise have been impossible to examine the individual effects of all 14 metrics of interest (a GLMM using all 14 metrics or all PCA axes as would be done in a full PCR approach does not converge even with the simplest representations of the error correlation). While separate models for individual or suites of metrics may have allowed us to look at some aspects of landscape structure, we would not have been able to examine overall impacts of woody cover on bobcat WCS use or whether vegetation density was additive or not. Metrics derived from different sources are regularly compared (see Carrasco et al. 2019; Hagar et al. 2020), however, these studies often neglect the potential additive effects of incorporating all metrics, especially when they represent different aspects of landscape structure. Our study demonstrates the importance of examining the potential additivity of new metrics when comparing suites of metrics. Other approaches, such as maximum entropy, may allow one to examine several metrics at once (Elith et al. 2011; Habel et al. 2016; Schmidt et al. 2020), but these are limited to non-correlated predictors and should not be used for assessing specific relationships between landscape pattern and process (Phillips et al. 2006).

Landscape configuration metrics are often highly correlated with each other which complicates our ability to examine independent effects of different aspects of landscape structure (Grafius et al. 2018; Uuemaa et al. 2009). This was true in our study as well with correlations ranging from – 0.68 to 0.96. Although assessing individual effects of metrics has a place in landscape pattern analysis, this approach has several flaws that make it impractical for examining effects of landscape structure on WCS use. First, high correlation among predictors makes it impossible to assess independent effects of each predictor. A commonly recommended solution is to drop a highly correlated variable (Grafius et al. 2018; Herzog et al. 2001; Peng et al. 2010). However, dropping important predictors leads to model specification errors (relevant variable omission, Gujarati and Porter 2009, Chapter 13) and risks losing interpretability of models. When a predictor is significant but correlated with a variable that was excluded from the model, it is impossible to determine if the identified relationship was due to the included or excluded variable.

Second, with 14 predictors with 14 individual tests, the Type I experiment-wise error rate is inflated (Bender and Lange 2001). Although it may be useful to understand how individual aspects of structure impact WCS use, especially in wildlife management, the individual metric approach may lead to improper long-term management decisions due to mistaken interpretations of the significance of particular metrics. Wildlife crossing structure placement is an expensive, long-lasting, and difficult to modify management decision so it is critical that WCS placement be properly informed by appropriate landscape-level variables (Blackburn et al. 2022). Accounting for the correlations among multiple metrics is at the heart of multivariate statistics (Johnson and Wichern 2007). The relative importance of individual metrics is then assessed using ordination techniques such as PCA, multidimensional scaling, or correspondence analysis (Legendre and Legendre 2012, Ch. 9) or other multivariate analyses, such as similarity percentages (Jongman et al. 1995) making this approach ideal for accurately assessing landscape structure around WCSs.

Ocelots were the target species for WCSs in our study area, with WCS locations primarily derived from known road mortality locations and limited telemetry data. However, the landscape structure around these WCSs was not distinguishable from the surrounding landscape. This may have been due to the use of road mortality locations to place WCSs. Road mortality patterns may not accurately reflect successful road crossing locations (Ascensão et al. 2019). Additionally, road mortality locations may differ in surrounding landscape structure from successful road crossing locations (Lombardi et al. 2023). Non-migratory species are more likely to use WCSs when they are placed in areas with known individuals living around roads, so it is important to monitor roadside areas before placing WCSs to ensure that they will provide the greatest benefit to target species. Using road mortality locations to inform WCS placement can lead to WCS placement in heterogenous landscapes, potentially reducing their effectiveness in target species conservation (Lombardi et al. 2023). However, increased heterogeneity at WCSs may provide benefits to the broader animal community (Andis et al. 2017; Clevenger 2005).

Although our study does not determine where new WCS locations should be placed, it does provide insights into the effectiveness of constructed WCSs. Our study indicated that bobcats used WCSs with less fragmented, but more complex woody cover, an expected result given that bobcats select areas with more woody cover in South Texas (Lombardi et al. 2020a; Sergeyev et al. 2023a). However, bobcat detections were negatively associated with the vegetation density index, indicating that bobcats may prefer WCSs with lower vegetation density between 0.5 and 3.0 m above the ground. This may indicate that bobcats prefer WCSs where dense woody cover makes up a small proportion of the woody cover in the area. Roads that have large portions of woody cover around them may encourage crossings of the road surface, increasing risks from vehicle collisions. While dense vertical and horizontal cover (> 75%) is used by both bobcats and ocelots as rest sites (Harveson et al. 2004; Horne et al. 2009; Sergeyev et al. 2023b), both species regularly move through more open areas to forage (Lombardi et al. 2020a; Sergeyev et al. 2023b). Because WCSs are often used as movement corridors, locations with less dense woody cover may be preferable to bobcats.

Time since a WCS was constructed has been shown to be important in predicting WCS use (Clevenger and Waltho 2005; Huijser et al. 2011). However, temporal differences in WCS use may also be explained by temporal differences in environmental conditions which may have stronger impacts on WCS use than temporal WCS effects (Clevenger and Waltho 2005; van der Grift et al. 2013). To account for temporal variation in environmental conditions, we utilized bobcat data collected during the same time period at all locations rather than data collected at the same time since construction. We tested for the effect of highway (and therefore time since construction) in preliminary analyses which showed a small effect of highway on WCS use, however this may be due to differences in disturbance and human activity rather than differences in time since construction. This identified effect warrants future study on time-since-construction effects on WCS use.

Bobcats are often used as surrogates for ocelots and broader road effects on carnivores in parts of North America (Litvaitis et al. 2015; Schmidt et al. 2020). While ocelots and bobcats in South Texas differ in habitat preference (Lombardi et al. 2020a; Sergeyev et al. 2023b), both species rely on woody cover. By using indices of woody cover, we believe that WCSs that are frequently used by bobcats are also likely to be used by ocelots. While it was not assessed in this study, ocelot use of WCSs have been documented on FM 106 and these correspond with WCSs with high bobcat use (Kline et al. 2022).

We assessed the effect of the overall structure of woody cover on bobcat WCS use using multivariate statistics. Creating indices of configuration and density allowed us to incorporate the relatedness among individual metrics into our analyses giving us a powerful assessment of the relationship between landscape structure and bobcat WCS use. Multivariate techniques such as those used in this study will not only allow researchers to better assess overall effects of landscape structure on ecological processes but also parse out effects of individual metrics and better incorporate additional, additive landscape metrics, such as those derived from aerial LiDAR.

Abbreviations

LiDAR	Light detection and ranging
TxDOT	Texas department of transportation
WCS	Wildlife crossing structure
SH	State highway
FM	Farm-to-Market road
PLAND	Percent land cover
PD	Patch density
LPI	Largest patch index
ED	Edge density
LSI	Landscape shape index
MPA	Mean patch area
ENN_MN	Mean Euclidean nearest neighbor distance
AI	Aggregation index
PERMANOVA	Permutational multivariate analysis of variance
PERMDISP	Distance-based test for homogeneity of multivariate dispersions
PCA	Principal components analysis
GLMM	Generalized linear mixed model
PC	Principal component
PCR	Principal component regression

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-024-00555-z.

Supplementary Material 1.

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Author contributions

Conceptualization: TJY, HLP, JVL; Data Curation: TJY, KWR, RJK, JVL; Formal Analysis: TJY, DBW; Funding Acquisition: JHY, MET, JVL; Investigation: TJY; Methodology: TJY, HLP, DBW, JVL; Project Administration: MET, JVL; Resources: JHY, KWR, RJK, MET; Software: TJY; Supervision: JVL, MET; Validation: TJY; Visualization: TJY; Writing – Original Draft Preparation: TJY; Writing – Review and Editing: All authors.

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Data availability

Original 1 m NAIP imagery and 0.7 nominal point spacing LiDAR imagery are freely available through the Texas Natural Resources Institute online webservice (https://data.tnris.org, accessed 1 March 2021). Locations of wildlife crossing structures are publicly available through Texas Department of Transportation. Bobcat detection data available upon reasonable request, if interested please contact John H. Young, john.young@txdot.gov. All code and landscape metrics are available on GitHub at https://github.com/tomyamashita/LandscapeStructureBobcats.

Declarations

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare no conflict of interest.

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