



Machine learning allows for large-scale habitat prediction of a wide-ranging carnivore across diverse ecoregions

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Abstract

Context Resource selection functions are powerful tools for predicting habitat selection of animals. Recently, machine-learning methods such as random forest have gained popularity for predicting habitat selection due to their flexibility and strong predictive performance.

Objectives We tested two methods for predicting continental-scale, second-order habitat selection of a wide-ranging large carnivore, the mountain lion (*Puma concolor*), to support continent-wide

conservation management, including estimating abundance, and to predict habitat suitability for re-colonizing or reintroduced animals.

Methods We compared a generalized linear model (GLM) and a random forest model using GPS location data from 476 individuals across 20 study sites in the western USA and Canada and remotely-sensed landscape data. We internally validated models and examined their ability to correctly classify used and available points by calculating area under the receiver operating characteristics (AUC). We performed

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leave-one-out (LOO) out-of-sample tests of predictive strength on both models.

Results Both models suggested that mountain lions select for steeper slopes, areas closer to water, and with higher normalized difference vegetation index (NDVI), and against variables associated with human impact. The random forest model (AUC=0.94) demonstrated that mountain lion habitat can be accurately predicted at continental scales, outperforming the traditional GLM model (AUC=0.68). Our LOO validation provided similar results ($\bar{x}$ =0.93 for the random forest and $\bar{x}$ =0.65 for the GLM).

Conclusions We found that the added flexibility of the random forest model provided deeper insights into how individual covariates impacted habitat selection across diverse ecosystems. Our LOO analyses suggested that our model can predict mountain lion habitat selection in unoccupied areas or where local data are unavailable. Our model thus provides a tool to support discussions and analyses relevant to continent-wide mountain lion conservation and management including estimating metapopulation abundance.

Keywords Conservation · Habitat suitability · *Puma concolor* · Random forest · Machine learning · Resource selection function

Introduction

In ecological modeling, we choose between the distinct goals of inference or prediction (James et al. 2013; Bzdok

and Ioannidis 2019). The goal of inference is to differentiate between alternative a priori hypotheses, which requires low variance to determine coefficients that are non-zero. In contrast, prediction seeks to minimize mean squared errors to best forecast new observations (James et al. 2013; Tredennick et al. 2021). When modeling animal habitat relationships, for example, the difference can be expressed as “what” or “why” versus “where”. Inference seeks to understand “what” constitutes habitat (i.e., what features of the landscape do animals select) or “why” an animal uses a particular habitat. In contrast, prediction seeks to understand “where” habitat occurs (i.e., where on the landscape do animals prefer to live). The question of where is fundamental to numerous ecological and conservation management activities. For example, predicting species distribution might be the basis for estimating abundance (Jędrzejewski et al. 2018), predicting future use by recolonizing or reintroduced species (Winkel et al. 2023), or guiding strategic investment for species conservation management or interventions (Li et al. 2017). Generally, models with high flexibility exhibit lower interpretability but are more suited to prediction (Bzdok and Ioannidis 2019). When the goal is prediction, Westphal and Brannath (2020) recommend comparing multiple models and then choosing the one with the highest predictive strength, rather than the most parsimonious, as is characteristic when the goal is inference.

Resource selection functions (RSF) are a common approach to predicting the probability of an animal's use of different landscape traits, such as elevation, terrain ruggedness, or variations in vegetation (Manly

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et al. 2002). Typically, RSFs are performed using generalized linear models (GLM) but more recently, ecologists are increasingly turning to machine-learning algorithms, namely, a popular technique known as random forest (Breiman 2001; Shoemaker et al. 2018; Bohnett et al. 2020). Random forest models are not bound by linearity, are well suited to include a large numbers of covariates, and can detect complex relationships and interactions. In addition, the bootstrapped structure of random forest models decreases the problematic issue of correlated data commonly associated with wildlife movement data (Breiman 2001; Fleming et al. 2015). Random forest models should apply well to the habitat selection behavior of wild animals (Shoemaker et al. 2018); however, their performance appears to suffer with unbalanced presence-absence datasets in which absences outnumber detections (Chiaverini et al. 2023).

Mountain lions (*Puma concolor*) are a generalist carnivore that occupy diverse habitats ranging from mountains, to jungles, to deserts. Historically, they ranged from central Canada to the southern tip of South America, but following range contraction due to intense persecution, they remain absent in what was historic range in the eastern USA and Canada (Yovovich et al. 2023) as well as portions of Latin America (Nielsen et al. 2015). Mountain lions are predominantly managed as a game species in the USA and Canada at the state or provincial level, hindering our ability to estimate their abundance or any fitness metric that might support conservation strategies or management decisions at larger scales (Elbroch et al. 2022). Nevertheless, mountain lions have seen recovery into new and historic range in the USA and Canada over the last 50 years (Papouchis 2004), resulting in significant interest in mapping their potential use of historic range as well as novel habitats like desert and boreal ecosystems where they were previously absent or at very low density but are now colonizing due to changes in human attitudes (Benson et al. 2023) habitat and prey distributions (e.g., bighorn sheep (*Ovis canadensis*), Berger and Wehausen 1991; woodland caribou (*Rangifer tarandus caribou*), White et al. 2020). As an obligate carnivore, the foremost resource that mountain lions depend on is ungulate prey (Logan and Sweanor 2001; Lendrum et al. 2014), but there may also be abiotic landscape traits that affect mountain lion fitness, such as

rugged terrain important for rest and thermoregulation (Kusler et al. 2017), or specific habitat where preferred ungulate prey is hunted (Cristescu et al. 2019). As such, analysis of mountain lion resource selection should include abiotic landscape traits alongside metrics that may indicate prey distribution and abundance such as primary productivity (Walters 2001).

As a wide-ranging species, mountain lions occupy large areas where no data has been collected making habitat modeling in those areas difficult. Our aim was to compare two methodologies for projecting mountain lion habitat in areas where no data exists. We created a classical GLM alongside a random forest model and tested both for predictive strength using out-of-sample validation. Our first goal was to test which method created the best predictive map of second order habitat selection by mountain lions across North America. This map could be used as a basis for estimating local and continental-scale abundance (Jędrzejewski et al. 2018) or to inform conservation strategies, such as corridor mapping (Winkel et al. 2023), determining the likeliness of successful recolonization (Yovovich et al. 2023), or predicting interactions with rare prey species such as woodland caribou as they expand northward due to climate change and new distributions of the mountain lion's primary prey, deer (*Odocoileus* spp.; White et al. 2020). By sampling multiple study areas across diverse ecoregions, we aimed to identify the most robust effects that different landscape traits have on mountain lion resource selection. Our second goal was to determine whether mountain lion habitat selection is consistent across ecoregions at the continental scale. We employed out-of-sample validation to test whether our model could be used to accurately identify habitat in un-sampled regions where intensive studies have not occurred, due to costs or other feasibility, or in areas of historic but currently unoccupied mountain lion range (i.e., the eastern USA; Winkel et al. 2023, Yovovich et al. 2023).

Study area

We compiled mountain lion global positioning system (GPS) location data from multiple state and federal agencies, universities, and non-governmental organizations (NGOs) across the USA and Canada. These data span the desert southwest, coastal

chaparral, montane, and alpine zones of the Rocky Mountains, and the temperate rain forests of the Pacific Northwest. Our study area is thus best represented as current North American mountain lion range excluding Mexico (Fig. 1; Hornocker and Negri 2010; Nielsen et al. 2015). Elevations in the study area ranged from sea level to over 4,200 m, annual precipitation ranged from 13 cm in southern California to > 500 cm in the Pacific Northwest, and land-use varied from highly urban areas to remote wilderness. As such, they cover much of the variability likely to be encountered by mountain lions across North America.

Methods

Overview

Both GLM and random forest compare actual animal locations to available or pseudo absence locations at relevant spatial scales to predict habitat use based on the variables contained in the model. At small scales, an RSF may show how an animal uses areas within its home range, but a small analytical scale may not be appropriate in predicting a species' first or second order selection (i.e., selection by all animals across its full range, or selection of an entire population of

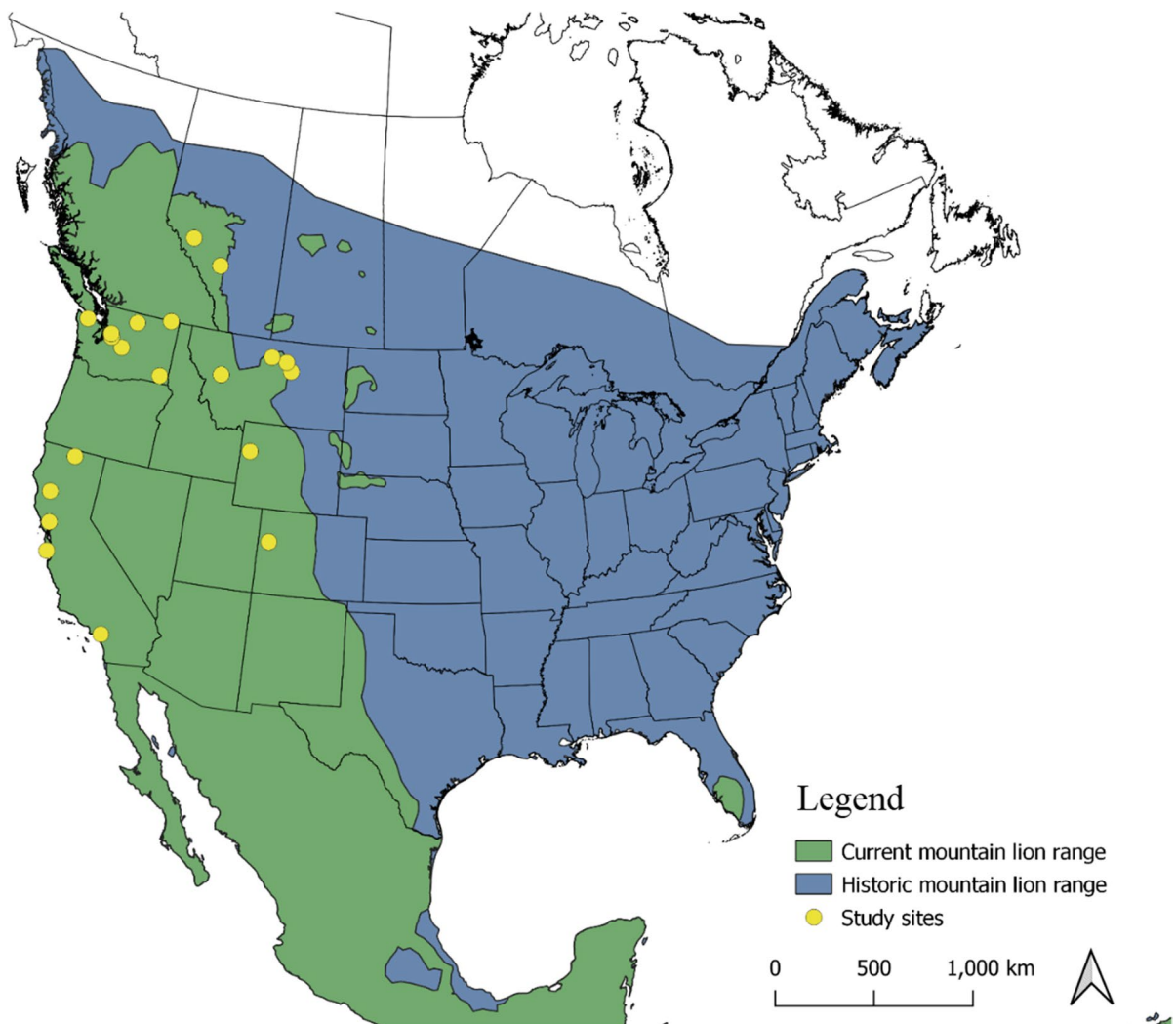


Fig. 1 The study area, defined by historic mountain lion range in the USA and Canada (Nielsen et al. 2015; Hornocker and Negri 2010). Study sites represent areas where GPS location data was collected between 2002 to 2020

animals; Johnson 1980) (Boyce 2006, DeCesare et al. 2014).

Both GLM and random forest methods can be used to map the predicted probability of use based upon disproportionate selection for habitat characteristics. GLMs employ the maximum likelihood method of logistic regression to compare use to availability, whereas random forest classification tallies votes from bootstrapped decision trees. First, a number of trees are created from bootstrapped data (commonly 500 trees), then an observation is predicted by each tree. The number of trees predicting “used” points is divided by the number of trees predicting “available” points to achieve a probability (e.g., 50 votes for “use” of a particular point and 450 votes for non-use, or “available” point, would produce an 11% probability of use; Shoemaker et al. 2018) (Table 1).

Data

From 2002 onwards, researchers have deployed GPS collars on mountain lions which provide accurate locations and typically cover the diel period with multiple fixes per animal per day. For our analyses, we compiled 1.3 million location points from 476 collared animals from 20 different study sites across the USA and Canada (Table 2), and restricted the data to GPS collar locations from independent, resident adults using the CTMM package in R (Calabrese et al. 2016; R core team 2021). Most data did not include position dilution of precision or other measures of precision and we therefore did not remove points based on these metrics. We did, however, remove some locations we judged as clearly erroneous (i.e., with single point data errors > 100 miles from the previous point in < 4 h).

Table 1 Candidate landscape and human impact variables and hypothesized effects on mountain lion resource selection. A positive sign indicates a greater probability of selection asso-

ciated with that variable while negative sign indicates a lesser probability of selection associated with that variable

Covariate	Data source (resolution)	Hypothesized effect on resource selection	Published support of hypothesized effect
Biotic/landscape (bottom-up)			
Distance to water	JRC Global Surface Water (30 m)	-	Dellinger et al. 2020
Normalized difference vegetation index	Landsat 8 (30 m)	+	Logan and Sweanor 2001, Walters 2001
Gross primary productivity	Landsat 8 (30 m)	+	Logan and Sweanor 2001, Walters 2001
Precipitation	PERSIANN-CDR	+	Logan and Sweanor 2001, Walters 2001
Slope	U.S. Geological Survey (30 m)	+	Zeller et al. 2017
Forest cover	MOD44Bv006 (250 m)	+	Robinson et al. 2015, Dellinger et al. 2020
Shrub cover	MOD44Bv006 (250 m)	+	Robinson et al. 2015, Dellinger et al. 2020
Non-vegetation	MOD44Bv006 (250 m)	-	Zeller et al. 2017, Dellinger et al. 2020
Elevation	U.S. Geological Survey (30 m)	+	Robinson et al. 2015, Dellinger et al. 2020
Aspect	U.S. Geological Survey (30 m)	South preferred	Robinson et al. 2015
Human impact/competition (top-down)			
Roads impact	Wildlife Conservation Society	-	Zeller et al. 2017, Dellinger et al. 2020
Land-use impact	Wildlife Conservation Society (100 m)	-	Robinson et al. 2015, Zeller et al. 2017
Infrastructure impact	Wildlife Conservation Society (100 m)	-	Robinson et al. 2015, Zeller et al. 2017
Population density	U.S. Census Bureau (100 m)	-	Dellinger et al. 2020

Advances in technology have led to decreasing fix intervals in GPS data which increases autocorrelation and can bias parameter estimates (Alston et al. 2023). However, large sample sizes and external validation counteract the problem of autocorrelation, especially in cases where the goal is prediction rather than inference (Northrup et al. 2013). Therefore, we did not filter the data for the purpose of counteracting autocorrelation but instead relied on the large sample size and a rigorous method of external validation. In addition, the bootstrapping step of the random forest acts as a thinning mechanism to decorrelate autocorrelated data (Breiman 2001).

Spatial covariates

Our goal was to create a predictive resource selection model as opposed to a more traditional test of competing hypotheses in a multi-model context. A complete list of all variables considered is shown in Table 1. Following ecological theory (Power 1992), we categorized covariates into two broad categories, which we called “bottom-up” or “top-down” effects.

Mountain lions depend on their prey which are tied to primary productivity (Walters 2001) so a main bottom-up driver will be primary productivity as represented by the normalized difference vegetation index (NDVI; Pettorelli et al. 2005). NDVI is calculated from the ratio of red to near-infrared (NIR) reflectance ($NDVI = (NIR - RED) / (NIR + RED)$) (Myneni et al. 1995) and measures “greenness” of vegetation which is tied to digestible energy for herbivores (Garrouette et al. 2016). As an ambush predator that utilizes cover for hunting, structural habitat traits are important to a mountain lion’s ability to catch prey (Cristescu et al. 2019, Coon et al. 2020). We used several layers from MODIS (DiMiceli et al. 2015) including forest, shrub cover, and non-vegetated areas. These layer values represent the proportion of the pixel at 250 m resolution covered by that vegetation type. We acquired these data from satellite imagery using the Google Earth Engine platform (Gorelick et al. 2017). We also included other bottom-up covariates representing abiotic landscape traits that might impact hunting success and other fitness, such

Table 2 Summary table of GPS location data collected from 476 mountain lions from 20 study sites between the years 2002–2020. County and state or province abbreviation provided in parentheses

Study site	Average fix interval (hours)	Number of animals	Number of fixes	Average fixes per animal	Data timespan
1 (Santa Cruz, CA)	4.97	63	193,265	3067.7	2009–2020
2 (Teton, WY)	9.35	12	97,543	8128.58	2012–2016
3 (Clallam, WA)	4.92	8	26,311	3288.88	2018–2020
4 (Garfield, CO)	2.05	12	56,682	4723.5	2011–2013
5 (Orange, CA)	3.13	91	338,739	3722.41	2002–2016
6 (Sonoma, CA)	2.23	14	54,174	3869.57	2016–2020
7 (Mendocino, CA)	2.13	5	14,714	2942.8	2010–2012
8 (Siskiyou, CA)	0.78	14	228,249	16,303.5	2017–2020
9 (Columbia, WA)	NA	29	39,514	1362.55	2009–2014
10 (Stevens, WA)	7.38	20	23,064	1153.2	2004–2008
11 (Okanogan, WA)	NA	47	48,881	1040.02	2006–2014
12 (King, WA)	5.38	30	68,554	2285.13	2012–2017
13 (King, WA)	6.09	24	19,360	806.67	2003–2009
14 (Chouteau, MT)	7.26	5	3804	760.8	2006–2009
15 (Phillips, MT)	NA	3	2369	789.67	2008–2009
16 (Phillips, MT)	5.23	7	8049	1149.86	2011–2015
17 (Kittitas, WA)	10.66	25	40,220	1608.8	2002–2008
18 (Powell, MT)	NA	16	34,021	2126.31	2002–2006
19 (Yellowhead, AB)	1.52	7	27,924	3989.14	2017–2018
20 (Clearwater, AB)	4.76	49	47,864	976.82	2005–2017

as aspect (converted from degrees to a continuous measure using a cosine transformation), slope (degrees) and elevation.

Mountain lions are also impacted by top-down effects such as human values, impact and alterations of the landscape (Dickson et al. 2005, Wilmer et al. 2013, Wolfe et al. 2015, Benson et al. 2019, 2023) although some human-altered landscapes may be to their benefit (Coon et al. 2019). Therefore, we included covariates measuring potential human impact (Table 1).

We used human density and several human impact layers produced by the Wildlife Conservation Society (2022) including roads, land-use, and infrastructure. These layers are a weighted calculation of impact based on multiple factors and utilize an exponential decay function to decrease the value of the impact at distance to the feature. For instance, the roads impact layer included weighted values scaled from the lowest impact which includes footpaths and cycle-ways to higher impact values for motorized roads and major highways (Wildlife Conservation Society 2022).

We standardized all variables using a Z transformation. To reduce the total number of candidate variables and to produce a single candidate set, we first screened variables for significance ($p < 0.05$) in univariate models (Hosmer Jr et al. 2013). We then screened covariates for collinearity, removing correlated variables $|r| > 0.8$ from the candidate set based on lower relative univariate r^2 value. We chose a high correlation threshold because overfitting is less of an issue in cases of prediction, especially when sample size is sufficient (Hawkins 2004; Steyerberg 2019). The result of this screening process was a set of candidate variables that we then used to model resource selection using the two methods (see below).

Resource selection modeling

To model second order selection, habitat traits within an animal's home range are compared to the surrounding landscape (Johnson 1980). In our model, used points were GPS locations for each mountain lion while available points were randomly generated pseudo absences. We used the *adehabitatHR* package in R for the following tasks (Calenge 2006; R core team 2021): 1) We set the spatial extent of available points specific to each study site by creating 99% adaptive kernel polygons using the combined GPS

locations from all independent mountain lions that were marked with GPS collars in each research project. Because research projects define study sites differently and often in non-biologically relevant ways, it was important to create standardized available habitat for each site. 2) We matched used and available points from each study site at a 1:1 ratio. We used the raster package in R to extract landscape (i.e., covariate) values from the used and available points (Hijmans 2022; R core team 2021).

Generalized linear mixed model

To account for individual and geographical variation, we included individual animals and study sites as random effects (Gillies et al. 2006). The model took the form for location i , animal j , and study area k :

$$\text{Logit}\{Pr(y_{ij} = 1 | x_{ijk}, \zeta_{jk})\} = \beta_1 + \beta_2 x_{2ij} + \beta_3 x_{3ij} + \zeta_{jk}$$

where β_1 , β_2 , and β_3 are covariate fixed effects and ζ_{jk} accounts for random variation at the intercept for individual animals and study areas. We used the *lme4* package in R to fit this model (Bates et al. 2015; R core team 2021).

Random forest model

We used the *randomForest* package in R (Liaw and Wiener 2002; R core team 2021) to build a random forest model using the same pool of habitat variables and used and available points as for the GLM above. Although random forest is well suited for large numbers of highly correlated variables (Breiman 2001), we chose to use the same pool of variables for greater comparability to the GLM. Following guidance in Probst et al. (2019), we tuned the model to 1000 trees and 6 variables at each split using the *tuneRF* function from the *randomForest* package.

Model validation and method comparison

We validated both models using internal and external methods. We internally validated the models and examined their ability to correctly classify used and available points by calculating area under the receiver operating characteristic (AUC) curve in R (Spackman 1989; R core team 2021). An AUC score of > 0.7 is

generally considered acceptable and a score of >0.8 is considered excellent (Hosmer Jr et al. 2013). We tested the variable inflation factor (VIF) to ensure no two variables were excessively correlated (i.e., $VIF < 5$). Ecological data often contain dependence structures (i.e., correlations within individual animals or study sites), therefore non-random, blocked, cross-validation approaches should be used to validate the models more rigorously (Roberts et al. 2017). To accomplish this, we performed a leave-one-out (LOO) external validation by excluding each study site from the model and projecting the model to that same site to measure its predictive ability. We first reclassified the RSF into 10 equal area bins based on probability of use, and then summed the number of used points in each of 10 bins. We then conducted a Spearman's rank correlation test to see if used points fell in the higher probability bins (Fielding and Bell 1997; Boyce et al. 2002). We examined the output of the two models by comparing the variable importance for the random forest model and scaled and centered effect size for the GLM. Finally, we used the raster package in R to project the top model to all of the historic mountain lion range to create a probability map of mountain lion habitat (30 m cells; Hijmans 2022; R core team 2021).

Results

Candidate covariates

After initial screening, our final candidate set of covariates included: distance to water, NDVI, slope, forest cover, shrub cover, non-vegetation, elevation, aspect, roads impact, land-use, infrastructure, and human density. Gross Primary Productivity was removed due to excessive correlation to NDVI.

Generalized linear model

In the final multivariate GLM, NDVI, slope, and shrub cover had positive effects on mountain lion resource selection while forest cover, elevation, road impact, infrastructure, non-vegetation, land-use, and population density had negative effects (Table 3). Distance to water also showed a negative effect, indicating a higher probability of use closer to water sources.

Random forest model

The random forest variable plots show similar effects to the GLM with habitat covariates exhibiting positive responses, and human-influence covariates generally exhibiting negative responses (Fig. 5). Interpreting the variable plots from the random forest model is more complex as compared to the GLM beta estimates, due to the inherent non-linearity of random forest. For example, mountain lions generally showed higher probability of use for areas at low elevations, but probability declines at very low elevations (i.e. at 0 elevation or sea level). Mountain lions exhibited a lower probability of use for areas lacking footpaths or trails, higher probability of use for low-impact roads (i.e. footpaths and dirt roads), and then again a lower probability of use for high-impact roads (i.e. paved roads and highways), aligning well for what is known about their behavior (e.g. Dickson et al. 2005). Most variables exhibited a “humped” shape (e.g. NDVI, slope, forest, non-vegetated area, and shrub cover), indicating that mountain lions varied their probability of use across the range of values for these variables, rather than exhibited a single consistent relationship and probability of use.

Table 3 Beta estimates, standard error, z value and p value for the final general linear model of resource selection of mountain lions from 476 individuals and 20 study sites from years 2002–2020

	Est	S.E	z val	p
(Intercept)	-0.212	0.102	-2.070	<0.039
Normalized-difference vegetation index	0.652	0.003	217.272	<0.000
Slope	0.100	0.002	65.405	<0.000
Distance to water	-0.160	0.002	-101.574	<0.000
Aspect	-0.078	0.001	-57.857	<0.000
Elevation	-0.568	0.003	-170.234	<0.000
Roads impact	-0.032	0.002	-19.049	<0.000
Forest	-0.093	0.002	-45.160	<0.000
Infrastructure	-0.054	0.002	-29.284	<0.000
Non-vegetated area	-0.163	0.003	-61.577	<0.000
Shrub cover	0.117	0.003	45.634	<0.000
Human population density	-0.395	0.007	-57.760	<0.000
Land-use impact	-0.535	0.002	-238.894	<0.000

Comparative analysis of GLM and random forest models

The random forest outperformed the GLM, with AUC values of 0.68 for the GLM and 0.94 for the random forest (Fig. 2). The mean Spearman's rho score from our LOO validation was 0.65 for the GLM and 0.93 for the random forest (Fig. 3). Within the GLM framework, we found support for all hypothesized effects except elevation and forest (Table 3). We predicted elevation and forest cover would show positive effects on mountain lion selection however both showed negative effects on probability of use. Random forest partial dependency variable plots show similar responses

of our selected variables (Fig. 5). Probability of use declines overall with increased elevation in both models. Probability of use increases slightly with forest cover but declines near the maximum values of percent forest per pixel. This is corroborated by the negative effect for forest cover in the GLM.

Variable importance and effect sizes

The random forest and GLM show similar ranking of variable importance and effect size (Fig. 4). Both show elevation and NDVI as the most important variables. A notable separation between the models occurs

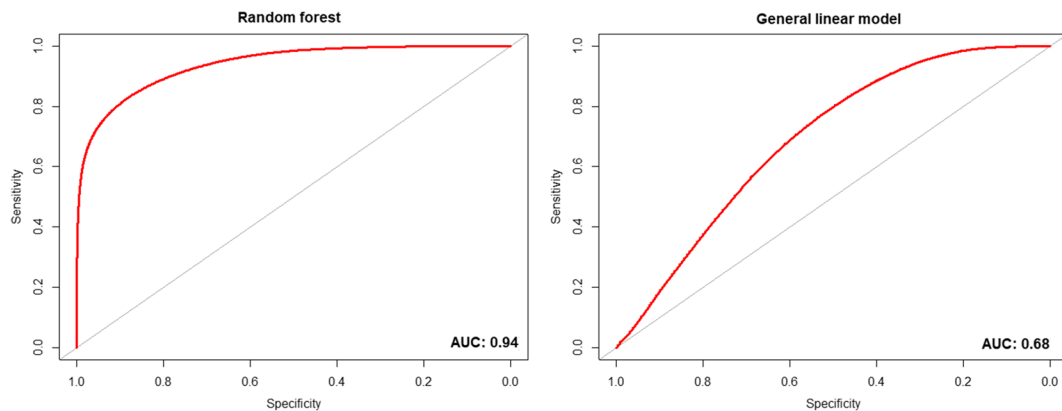
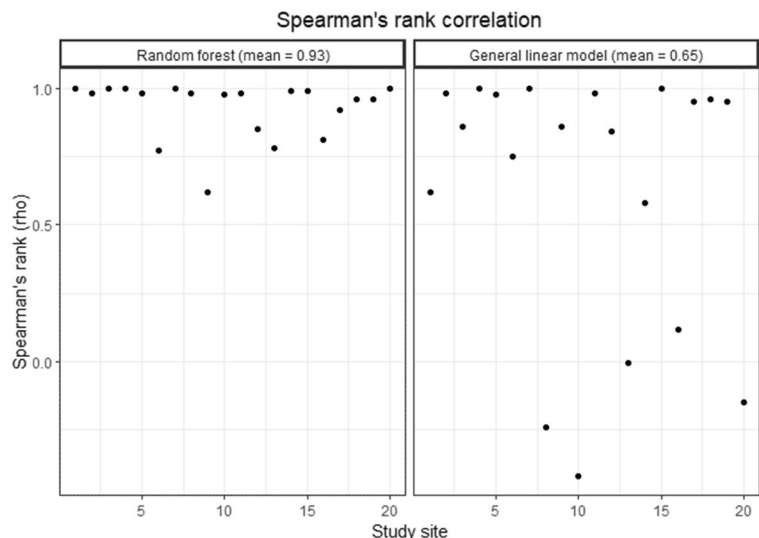


Fig. 2 A comparison of internal validation method using ROC curves for the GLM and random forest resource selection models for 476 mountain lions from data collected across 20 study sites in the USA and Canada between 2002 and 2020

Fig. 3 Comparison of leave-one-out external validation of GLM and random forest mountain lion resource selection models from 20 separate sites (see also Fig. 1) between 2002 to 2020



with the variables, land-use impact and human population density. These variables exhibit the third and fourth largest effect sizes in the GLM but are ranked much lower (i.e. tenth and eleventh) by the random forest (Fig. 5).

Model projection

We projected the random forest model to create a map depicting probable mountain lion use or occurrence (Fig. 6). Higher probability areas appear closely tied to rugged, wilderness areas and away from flat farmland and urban areas. The eastern U.S. is characterized by an abundance of high-probability habitat.

Discussion

In predicting continental-scale second-order resource selection of a cryptic carnivore, random forest models (AUC=0.94) outperformed GLM models (AUC=0.68), highlighting the strength of random forest methods in predicting non-linear, complex interactions characteristic of animal habitat use and selection. Mountain lion resource selection was positively associated with bottom-up factors such as NDVI and shrub cover, and negative associations with all top-down, anthropogenic factors, including human population density, land-use and infrastructure. Our

LOO analyses highlighted the strength of our model in predicting mountain lion habitat selection across ecoregions and in novel areas into which they are expanding, as well as their potential use of historic range currently unoccupied. Our model provides a powerful tool to aid conservation practitioners in transcending the current limitation of state- or provincial-scale assessments of the species, and one that supports discussions and analyses of continent-wide, cross-jurisdictional conservation and management of mountain lions (Elbroch et al. 2022).

Discrepancies between GLM and random forest models

We found general agreement between the random forest and GLM models, with regards to the relative importance of the various covariates tested (Fig. 4). The added flexibility of random forest models, however, provided deeper insights when interpreting the influence of covariates on habitat selection. For example, where the GLM only revealed a small negative effect associated with roads, the random forest showed a stronger and more complex relationship; mountain lions increased their selection for low-impact roads such as footpaths but decreased selection for high-impact roads, such as paved motorways and highways (Fig. 5). The random forest also showed slightly increased selection for forest cover with decreased selection for the maximum values of forest cover. This is likely due to mountain

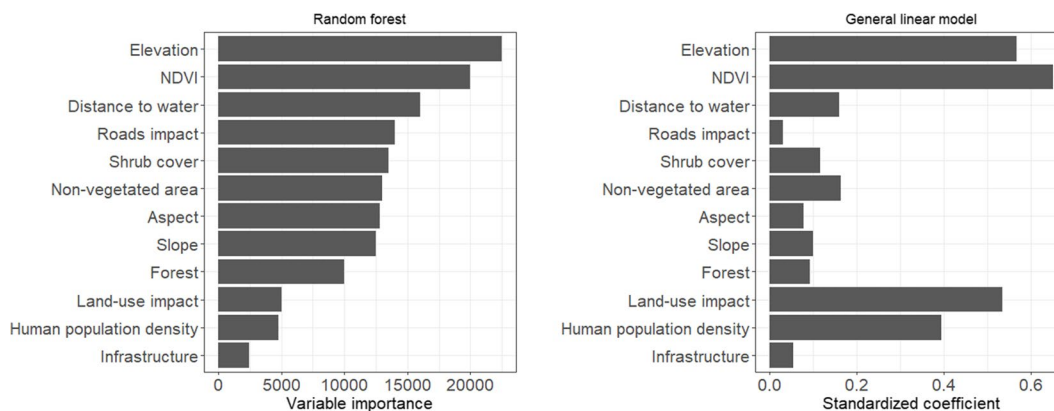


Fig. 4 A comparison of variable importance from the random forest model with standardized, absolute value, effect size from the GLM for 476 mountain lions collared across 20 sites

between 2002–2020. The ordering of the variables in the GLM is matched to the random forest for comparison

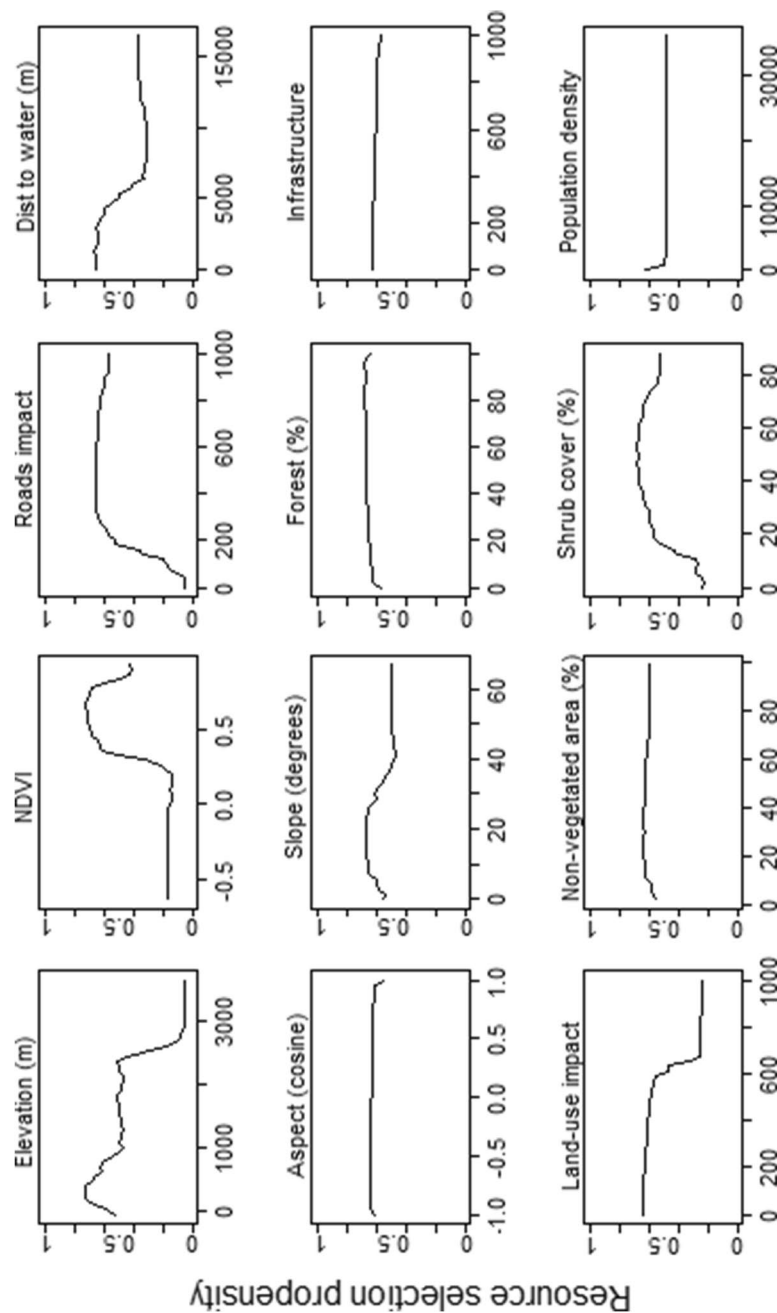


Fig. 5 Random forest partial dependence variable plots depicting mountain lion resource selection in North American for years between 2002–2020. Impact factor variables (roads impact, infrastructure, land-use impact) are unit-less. Population density is people per km.²

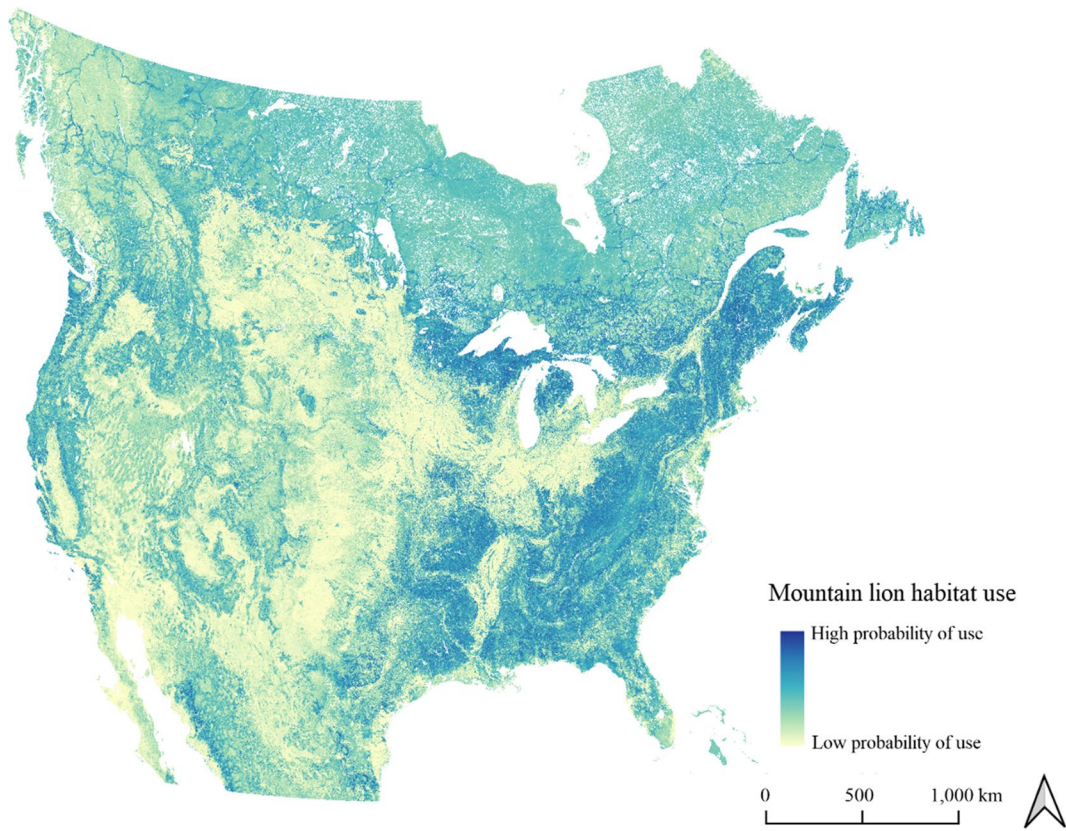


Fig. 6 Random forest derived resource selection function depicting predicted continent-wide mountain lion habitat suitability in North America from data collected from 476 mountain lions between 2002–2020

lions favoring mixed vegetation and partially open canopies where prey and hunting opportunities are higher.

Nevertheless, when comparing the effect sizes of the GLM with the variable importance ranking of the random forest, land-use impact and human population density ranked very differently (Fig. 4). These variables showed large effect sizes in the GLM but low importance in the random forest, due to differences in model structure. The GLM is bound by linearity and requires interaction effects between predictors to be specified, whereas random forest allows for non-linear relationships and inherently accounts for interactions among features in the construction of decision trees. A variable that appears less important in a GLM might be identified as more important in random forest due to its contribution to reducing prediction error when used in conjunction with other variables.

Addressing model overfitting and external validation

As with other complex models, there is risk of random forest overfitting predictive models. This can be examined with rigorous external validation as performed here with the “leave-one-out” method. As stated previously, ecological data often contain dependence structures so “blocked” external validation is needed; in this case, leaving out each study site, some of which represented entire ecoregions. For example, the model performed well at predicting mountain lion habitat use in the desert southwest, even when data from the desert southwest was omitted from model building. This suggests that the model did not overfit and is transferable to regions where no data are available. In addition, an advantage of a large-scale analysis such as this is that the problem of overfitting is mitigated by using data spanning a range of environmental conditions. An RSF built from one

study site may overfit to unique aspects of that region whereas an RSF built from multiple sites will better capture the true habitat selection behavior of the species and can more confidently be extrapolated to other areas once externally validated.

Implications for conservation and management

Our model predicted an abundance of high-quality mountain lion habitat in their historic range in the eastern USA and Canada. In fact, our predictive map would suggest that portions of the eastern USA are superior habitat in comparison to the west. This is likely due to NDVI being the strongest driver of mountain lion habitat selection in our model and that the eastern USA contains very high relative NDVI values. Nevertheless, even considering the current human footprint in the more densely populated eastern USA, our model supports other analyses based on expert opinion (e.g., Winkel et al. 2023, Yovovich et al. 2023) which predict significant mountain lion habitat beyond their current range today.

Limitations and future directions

Our analysis lays the groundwork for population prediction, utilizing a habitat-based approach to estimate mountain lion densities (e.g. Boyce and McDonald 1999). By establishing a correlation between habitat and densities, this model can be used to create defensible assessments of current mountain lion populations and holds the potential to project future densities in regions where mountain lions may recolonize. Moreover, this understanding of habitat can be utilized in formulating effective management plans tailored to specific jurisdictions (e.g. harvest setting when determined by habitat-based abundance estimates; Beausoleil et al. 2013). Leveraging the habitat map, hunted areas can be strategically categorized into low, medium, and high habitat quality zones, facilitating the development of targeted management strategies for conservation.

Our model does not assess the impacts of landscape connectivity on potential habitat selection. Large highways are an impediment for mountain lion movement (Ernest et al. 2014; Yovovich et al. 2023), and the eastern U.S., with its dense highway system may prove to be an obstacle for mountain lions trying to reach potential habitat. Although our projected model does not measure connectivity explicitly, it

can be used as a base layer for connectivity modeling (Chetkiewicz and Boyce 2009). Zeller et al (2018) showed that RSF models outperform other layers when converted to resistance layers from relative probability of use.

Conclusion

Our study represents an advancement in the field of habitat selection modeling, particularly in the context of large carnivore conservation. By comparing the performance of GLM and random forest models in predicting habitat selection of mountain lions at a continental scale, we demonstrated the superiority of machine learning techniques in capturing the complexity of habitat selection behavior. The higher predictive accuracy of the random forest model underscores its potential utility in predicting habitat for mountain lions in unoccupied areas or regions lacking local data. These findings contribute to our understanding of mountain lion ecology and have broader implications for wildlife management and conservation efforts on continental scales. Our model can serve as a valuable tool for informing conservation strategies, estimating metapopulation abundance, and facilitating habitat restoration efforts for mountain lions and other wide-ranging carnivores. Additionally, our study highlights the importance of collaborative data sharing and integrating advanced machine-learning techniques into ecological research.

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Author contributions CO, HR, ME, KZ and PB contributed to the study conception and design. Data collection was performed by CO, ME, MB, RB, BK, KK, BM, QM, MM, CW, HW, and WV. Data processing and analysis was performed by CO. Majority of writing and editing was performed by CO, ME, KZ, HR and HW. All authors read and edited multiple versions of the manuscript.

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Data availability The datasets generated during analysis may be made available upon reasonable request.

Declarations

Ethical approval Our research adhered to the guidelines outlined by the American Society of Mammologists (Sikes et al. 2011).

Competing interests The authors declare no competing interests.

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References

- Alston JM, Fleming CH, Kays R, Streicher JP, Downs CT, Ramesh T, Calabrese JM (2023) Mitigating pseudoreplication and bias in resource selection functions with autocorrelation-informed weighting. *Methods Ecol Evol* 14:643–654
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1):1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beausoleil RA, Koehler GM, Maletzke BT, Kertson BN, Wielgus RB (2013) Research to regulation: cougar social behavior as a guide for management. *Wildl Soc Bull* 37:680–688
- Benson JF, Mahoney PJ, Vickers TW, Sikich JA, Beier P, Riley SP, Ernest HB, Boyce WM (2019) Extinction vortex dynamics of top predators isolated by urbanization. *Ecol Appl* 29:e01868
- Benson JF, Dougherty KD, Beier P, Boyce WM, Cristescu B, Gammons DJ, Garcelon DK, Higley JM, Martins QE, Nisi AC, Riley SP (2023) The ecology of human-caused mortality for a protected large carnivore. *Proc Natl Acad Sci* 120:e2220030120
- Berger J, Wehausen J (1991) Consequences of a mammalian predator-prey disequilibrium in the Great Basin Desert. *Conserv Biol* 5:243–248
- Bohnett E, Hulse D, Ahmad B, Hootor T (2020) Multi-level, multi-scale modeling and predictive mapping for jaguars in the Brazilian Pantanal. *Open J Ecol* 10:243
- Boyce MS (2006) Scale for resource selection functions. *Divers Distrib* 12:269–276
- Boyce MS, McDonald LL (1999) Relating populations to habitats using resource selection functions. *Trends Ecol Evol* 14:268–272
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FK (2002) Evaluating resource selection functions. *Ecol Model* 157:281–300
- Breiman L (2001) Random forests. *Mach Learn* 45:5–32
- Bzdok D, Ioannidis JP (2019) Exploration, inference, and prediction in neuroscience and biomedicine. *Trends Neurosci* 42:251–262
- Calabrese JM, Fleming CH, Gurarie E (2016) ctmm: An R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol Evol* 7:1124–1132
- Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519
- Chetkiewicz CLB, Boyce MS (2009) Use of resource selection functions to identify conservation corridors. *J Appl Ecol* 1036–1047
- Chiaverini L, Macdonald DW, Hearn AJ, Kaszta Z, Ash E, Bothwell HM, Can OE, Channa P, Clements GR, Haidir IA, Kyaw PP (2023) Not seeing the forest for the trees: Generalised linear model out-performs random forest in species distribution modelling for Southeast Asian felids. *Eco Inform* 75:102026
- Coon CA, Mahoney PJ, Edelblutte E, McDonald Z, Stoner DC (2020) Predictors of puma occupancy indicate prey

- vulnerability is more important than prey availability in a highly fragmented landscape. *Wildlife Biol* 2020:1–12
- Coon CA, Nichols BC, McDonald Z, Stoner DC (2019) Effects of land-use change and prey abundance on the body condition of an obligate carnivore at the wildland-urban interface. *Landsc Urban Plan* 192:103648
- Cristescu B, Bose S, Elbroch LM, Allen ML, Wittmer HU (2019) Habitat selection when killing primary prey versus alternative prey species supports prey specialisation in an apex predator. *J Zool* 309(4):259–268
- DeCesare NJ, Hebblewhite M, Bradley M, Hervieux D, Neufeld L, Musiani M (2014) Linking habitat selection and predation risk to spatial variation in survival. *J Anim Ecol* 83:343–352
- Dellinger JA, Cristescu B, Ewanyk J, Gammons DJ, Garcelon D, Johnston P, Martins Q, Thompson C, Vickers TW, Wilmers CC, Wittmer HU (2020) Using mountain lion habitat selection in management. *J Wildl Manag* 84:359–371
- Dickson BG, Jenness JS, Beier P (2005) Influence of vegetation, topography, and roads on cougar movement in southern California. *J Wildl Manag* 69:264–276
- DiMiceli C, Carroll M, Sohlberg R, Kim D, Kelly M, Townsend J (2015) MOD44B MODIS/terra vegetation continuous fields yearly L3 global 250m SIN Grid V006. NASA EOSDIS land processes DAAC. <https://doi.org/10.5067/MODIS/MOD44B.006>. Accessed 2022-07-07
- Elbroch LM, Petracca LS, O'Malley C, Robinson H (2022) Analyses of national mountain lion harvest indices yield ambiguous interpretations. *Ecol Sol Evid* 3:12150
- Ernest HB, Vickers TW, Morrison SA, Buchalski MR, Boyce WM (2014) Fractured genetic connectivity threatens a southern California puma (*Puma concolor*) population. *PLoS One* 9:107985
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ Conserv* 24:38–49
- Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM (2015) Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* 96:1182
- Garrouette EL, Hansen AJ, Lawrence RL (2016) Using NDVI and EVI to map spatiotemporal variation in the biomass and quality of forage for migratory elk in the Greater Yellowstone Ecosystem. *Remote Sensing* 8:404
- Gillies CS, Hebblewhite M, Nielsen SE, Krawchuk MA, Aldridge CL, Frair JL, Saher DJ, Stevens CE, Jerde CL (2006) Application of random effects to the study of resource selection by animals. *J Anim Ecol* 75:887–898
- Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R (2017) Google earth engine: planetary-scale geospatial analysis for everyone. *Remote Sens Environ* 202:18–27
- Hawkins DM (2004) The problem of overfitting. *J Chem Inf Comput Sci* 44:1–12
- Hijmans RJ (2022) raster: geographic data analysis and modeling. R package version 3.5–21. <https://CRAN.R-project.org/package=raster>. Accessed 1 June 2020
- Hornocker MG, Negri S (2010) Cougar: ecology and conservation. The University of Chicago Press, Chicago
- Hosmer DW Jr, Lemeshow S, Sturdivant RX (2013) Applied logistic regression, vol 398. Wiley
- James G, Witten D, Hastie T, Tibshirani R (2013) An introduction to statistical learning. Springer, New York
- Jędrzejewski W, Robinson HS, Abarca M, Zeller KA, Velasquez G, Paemelaere EA, Goldberg JF, Payan E, Hoogesteijn R, Boede EO, Schmidt K (2018) Estimating large carnivore populations at global scale based on spatial predictions of density and distribution—application to the jaguar (*Panthera onca*). *PLoS One* 13:3
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71
- Kusler A, Elbroch LM, Quigley H, Grigione M (2017) Bed site selection by a subordinate predator: An example with the cougar (*Puma concolor*) in the Greater Yellowstone Ecosystem. *PeerJ* 5:e4010
- Lendrum PE, Elbroch LM, Quigley H, Thompson DJ, Jimenez M, Craighead D (2014) Home range characteristics of a subordinate predator: selection for refugia or hunt opportunity? *J Zool* 294:58–66
- Li J, Alvarez B, Siwabessy J, Tran M, Huang Z, Przeslawski R, Radke L, Howard F, Nichol S (2017) Application of random forest, generalised linear model and their hybrid methods with geostatistical techniques to count data: Predicting sponge species richness. *Environ Model Softw* 97:112–129
- Liaw A, Wiener M (2002) Classification and regression by randomforest. *R News* 2:18–22
- Logan KA, Sweanor LL (2001) Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington D. C., USA
- Manly BF, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Introduction to resource selection studies. Resource selection by animals: statistical design and analysis for field studies. pp 1–15
- Myneni RB, Hall FG, Sellers PJ, Marshak AL (1995) The interpretation of spectral vegetation indexes. *IEEE Trans Geosci Remote Sens* 33:481–486
- Nielsen C, Thompson D, Kelly M, Lopez-Gonzalez CA (2015) Puma concolor. The IUCN red list of threatened species. <https://doi.org/10.2305/IUCN.UK.20154.RLTS.T1886.8A50663436.en>. Accessed 20 Feb 2021
- Northrup JM, Hooten MB, Anderson CR Jr, Wittemyer G (2013) Practical guidance on characterizing availability in resource selection functions under a use–availability design. *Ecology* 94:1456–1463
- Papouchis CM (2004) Conserving mountain lions in a changing landscape. People and predators: from conflict to coexistence, pp 219–239
- Pettorelli N, Vik JO, Myrsterud A, Gaillard JM, Tucker CJ, Stenseth NC (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol Evol* 20:503–510
- Power ME (1992) Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology* 73:733–746
- Probst P, Wright MN, Boulesteix AL (2019) Hyperparameters and tuning strategies for random forest. Wiley interdisciplinary reviews: data mining and knowledge discovery, 9:1301

- R Core Team (2021) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. <https://R-project.org/>. Accessed 1 August 2021
- Roberts DR, Bahn V, Ciuti S, Boyce MS, Elith J, Guillerá-Arroita G, Hauenstein S, Lahoz-Monfort JJ, Schröder B, Thuiller W, Warton DI (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* 40:913–929
- Robinson HS, Ruth T, Gude JA, Choate D, DeSimone R, Hebblewhite M, Kunkel K, Matchett MR, Mitchell MS, Murphy K, Williams J (2015) Linking resource selection and mortality modeling for population estimation of mountain lions in Montana. *Ecol Model* 312:11–25
- Shoemaker KT, Heffelfinger LJ, Jackson NJ, Blum ME, Wasley T, Stewart KM (2018) A machine-learning approach for extending classical wildlife resource selection analyses. *Ecol Evol* 8:3556–3569
- Sikes RS, Gannon WL, Use Committee of the American Society of Mammalogists (2011) Guidelines of the American society of mammalogists for the use of wild mammals in research. *J Mammal* 92:235–253
- Spackman KA (1989) Signal detection theory: valuable tools for evaluating inductive learning. Proceedings of the sixth international workshop on machine learning, Morgan Kaufmann, pp 160–163
- Steyerberg, E.W. 2019. Overfitting and optimism in prediction models. In *clinical prediction models*, vol 95. Springer, Cham 112
- Tredennick AT, Hooker G, Ellner SP, Adler PB (2021) A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology* 102:e03336
- Walters S (2001) Landscape pattern and productivity effects on source-sink dynamics of deer populations. *Ecol Model* 143:17–32
- Westphal M, Brannath W (2020) Evaluation of multiple prediction models: A novel view on model selection and performance assessment. *Stat Methods Med Res* 29:1728–1745
- Wildlife Conservation Society (2022) Species conservation landscapes. Available at: [Github.com/SpeciesConservationLandscapes](https://github.com/SpeciesConservationLandscapes). Accessed 1 June 2020
- Wilmers CC, Wang Y, Nickel B, Houghtaling P, Shakeri Y, Allen ML, Kermish-Wells J, Yovovich V, Williams T (2013) Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS One* 8:e60590
- Winkel BM, Nielsen CK, Hillard EM, Sutherland RW, LaRue MA (2023) Potential cougar habitats and dispersal corridors in Eastern North America. *Landsc Ecol* 38:59–75
- White SC, Shores CR, DeGroot L (2020) Cougar (*Puma concolor*) predation on northern mountain caribou (*Rangifer tarandus caribou*) in central British Columbia. *Can Field-Nat* 134:265–269
- Wolfe ML, Koons DN, Stoner DC, Terletzky P, Gese EM, Choate DM, Aubry LM (2015) Is anthropogenic cougar mortality compensated by changes in natural mortality in Utah? Insight from long-term studies. *Biol Cons* 182:187–196
- Yovovich V, Robinson N, Robinson H, Manfredo MJ, Perry S, Bruskotter JT, Vucetich JA, Solórzano LA, Roe LA, Lesure A, Robertson J (2023) Determining puma habitat suitability in the Eastern USA. *Biodivers Conserv* 32:921–941
- Zeller KA, Jennings MK, Vickers TW, Ernest HB, Cushman SA, Boyce WM (2018) Are all types of connectivity models created equal? Validating common connectivity approaches with dispersal data. *Divers Distrib* 24:868–879
- Zeller KA, Vickers TW, Ernest HB, Boyce WM (2017) Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: pumas as a case study. *PLoS One* 12:e0179570

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