RESEARCH ARTICLE

Scale-dependent seasonal habitat selection by jaguars (*Panthera onca*) and pumas (*Puma concolor*) in Panama

Kimberly Craighead [ORCID] · Milton Yacelga · Ho Yi Wan [ORCID] · Robert Vogt ·
Samuel A. Cushman

Abstract

Context Few habitat modeling studies consider multiple spatial or temporal scales; less identify the operative scale of an organism's response to predictor variables. Optimizing habitat suitability models yields robust, reliable inferences about species-habitat relationships that can inform conservation efforts for species, such as jaguars (*Panthera onca*) and pumas (*Puma concolor*).

Objectives We provide one of the first examples of evaluating temporal nonstationarity between seasons while simultaneously evaluating the effects of spatial and temporal scales on habitat selection. We sought insight into the predictor variables and associated scales determining seasonal distribution.

Methods We selected predictor variables known to affect felid occurrence, then identified the optimal scale for each variable. We calculated the focal mean at spatial scales ranging from 500 m to 15,000 m. We then developed habitat suitability models and evaluated the effects of temporal scale on species co-occurrence.

Results Patterns of jaguar and puma habitat selection varied. For jaguars, primary forest and its resources at fine scales were dominant predictors. For pumas, primary forest, secondary forest, and agropecuary lands at broad scales drove habitat selection. We observed divergent seasonal habitat selection, particularly for jaguars. Models confirmed that these sympatric predators might engage in spatial coordination to facilitate coexistence, as increased spatial overlap at a given scale in each season was associated with a diversification of landcover types.

Conclusions Our results highlight the importance of considering spatial and temporal scales and temporal nonstationarity in habitat modeling. We suggest habitat modeling studies evaluate and optimize spatial and temporal scale relationships.

K. Craighead (✉) · M. Yacelga · R. Vogt
Kaminando Habitat Connectivity Initiative, Oakland, USA
e-mail: kcraighead@kaminando.org

Ho Yi Wan
Humboldt State University, Arcata, USA

S. A. Cushman
US Forest Service Center for Landscape Science, Flagstaff, USA

Introduction

Accurate descriptions of spatiotemporal patterns of species-specific, optimal habitat, are fundamental to forecasting the impacts of anthropogenic landscape change on natural communities and ecosystems (Pearson et al. 2004; Guisan et al. 2006). Currently, the application of habitat suitability models (HSMs) shows promise for understanding both the association of the geographic location of a species with a set of environmental variables (Guisan and Zimmermann 2000), and assessing the biogeographical relationships between ecologically interacting species, such as potential competitors (Acevedo et al. 2010; Espinosa et al. 2018; Hearn et al. 2018).

Central to HSM is the effect of spatial scale, how the scale of analysis affects the quantification of species-habitat relationships (Wiens 1989; Levin 1992; Wheatley and Johnson 2009). Species-habitat relationships are fundamentally scale-dependent and inherently spatial processes (Thompson and McGarigal 2002; Wasserman et al. 2012; Mateo Sánchez et al. 2014; McGarigal et al. 2016). Each species will experience its environment at a range of scales relative to its life history traits and ecological requirements (Johnson 1980; Wiens 1989). Since we often have no a priori knowledge about the scales at which a species responds to environmental heterogeneity, the characteristic scale (or scales in the cases of multi-modal scale relationships) of response must be identified empirically (Jackson and Fahrig 2015; McGarigal et al. 2016; Timm et al. 2016; Wan et al. 2017; Atzeni et al. 2020). Describing how the contribution of each environmental variable varies across scales produces more accurate, organism-centered models that are biologically more meaningful, and statistically, often more powerful than a fixed scale framework (McGarigal et al. 2016; Atzeni et al. 2020).

Herein, we examine the role of environmental interactions and anthropogenic pressures at multiple scales in shaping the spatial distribution of two sympatric, apex predators, the jaguar (*Panthera onca*), and puma (*Puma concolor*), by conducting a scale-optimized habitat selection analysis (sensu McGarigal et al. 2016). Although each species' geographic range is relatively well known (e.g., Jędrzejewski et al. 2018), there are major knowledge gaps regarding the contribution of environmental factors to range

configuration, occupied habitats, and fragmentation, especially in tropical montane cloud forests.

To fill this gap, we used detection-nondetection data from camera traps to develop seasonal maps of habitat suitability in Panama. The models utilized Random Forests (RF) (Breiman 2001), a machine-learning algorithm based on an ensemble of predictor variables. RF has frequently produced stronger predictive models compared to other methodologies (e.g., linear discriminant analysis, logistic regression) (Cutler et al. 2007; Evans et al. 2011; Cushman and Wasserman 2018).

In this study, our goals were (1) to determine the spatial scale at which each variable most strongly influenced jaguar and puma detection, (2) evaluate the variability of prediction across seasons, (3) map and assess patterns of suitable habitat for each species, and (4) describe the differences in predicted habitat suitability and overlap between species seasonally and annually. We hypothesized that the habitat of pumas is broader and more general, while the habitat of jaguars is more specialized and restrictive, and associated with extensive forest cover and proximity to water. Also, we expected that correlations would be higher between models for the same species than for models between the species, and within species, we expected correlations between annual-wet and annual-dry to be higher than between wet-dry.

We aimed to understand the mechanisms behind each felid species' distribution in this region of Central America. The modeling efforts carried out in this study bolster our understanding of jaguar and puma habitat selection in Panama and provide valuable baseline predictions that drive future investigations to evaluate the accuracy of our models. Collectively, the models can be used to make informed land management decisions to protect these species from habitat deterioration. To our knowledge, this is the first HSM study on jaguars and pumas in Central America to adopt a multi-scale optimized approach.
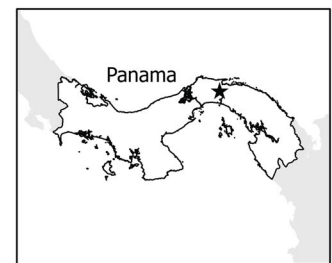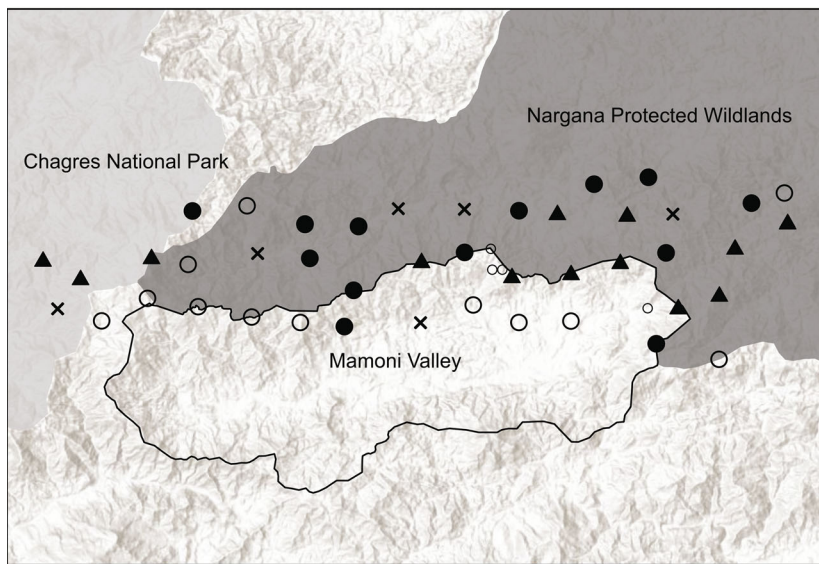
Methods

Study area

The Republic of Panama (9° N, 80° W) spans about 75,717 km^2 on an east–west axis, acting as a land bridge between North and South America (Stehli and Webb
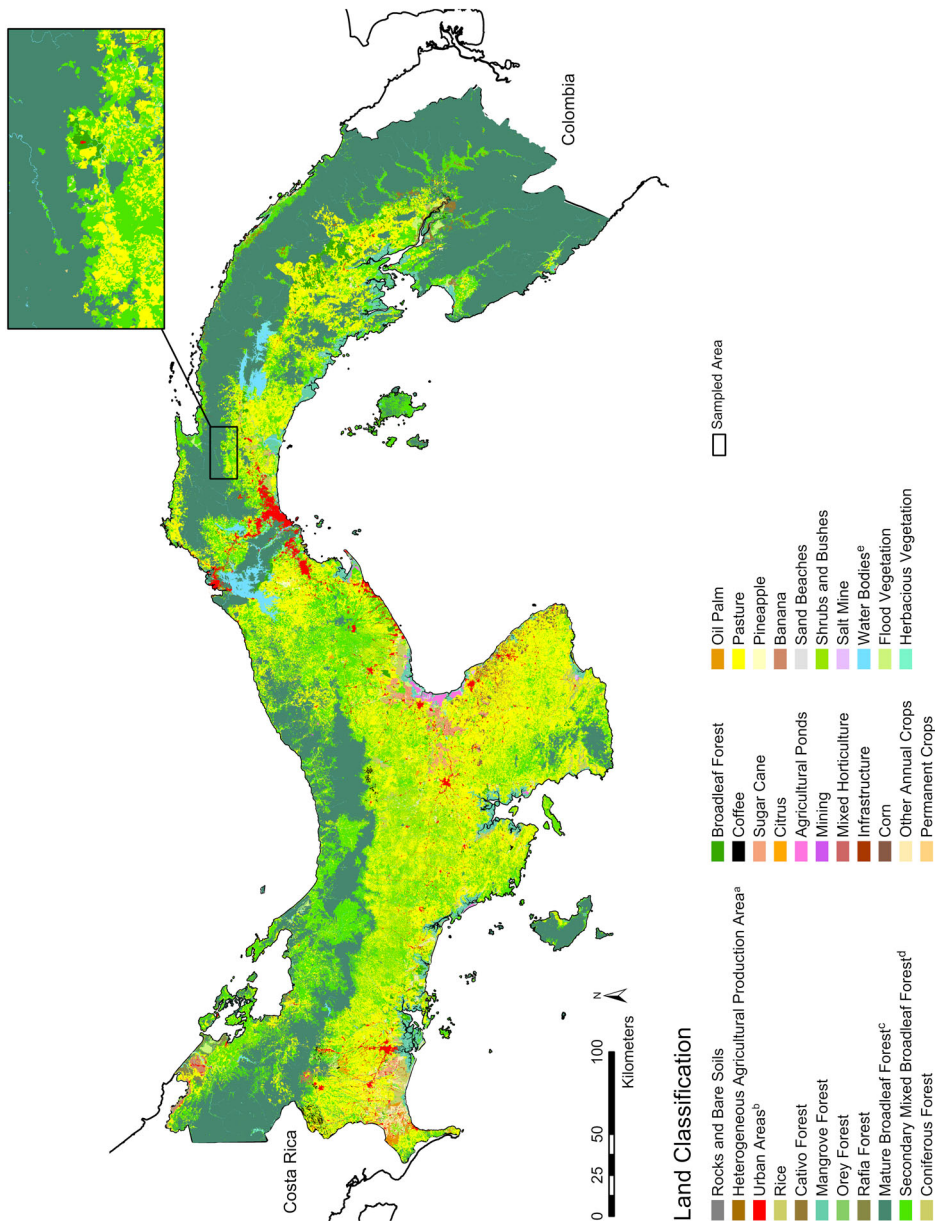
Fig. 1 The map depicts all land classifications found in Panama and indicates the location of the sampled area. The superscripts refer to landcover types renamed for the analyses: Heterogeneous Agricultural Production Area[a] (Agropecuary), Urban Areas[b] (Human Settlement), Mature Broadleaf Forest[c] (Primary Forest), Secondary Mixed Broadleaf Forest[d] (Secondary Forest), Water Bodies[e] (Hydrologic Feature). Source: MiAmbiente, Cobertura Boscosa y Uso de Tierra (2012)

Land Classification

- Rocks and Bare Soils
- Heterogeneous Agricultural Production Area[a]
- Urban Areas[b]
- Rice
- Cativo Forest
- Mangrove Forest
- Orey Forest
- Rafia Forest
- Mature Broadleaf Forest[c]
- Secondary Mixed Broadleaf Forest[d]
- Coniferous Forest

- Broadleaf Forest
- Coffee
- Sugar Cane
- Citrus
- Agricultural Ponds
- Mining
- Mixed Horticulture
- Infrastructure
- Corn
- Other Annual Crops
- Permanent Crops

- Oil Palm
- Pasture
- Pineapple
- Banana
- Sand Beaches
- Shrubs and Bushes
- Salt Mine
- Water Bodies[e]
- Flood Vegetation
- Herbacious Vegetation

- Sampled Area

(a)

(b)
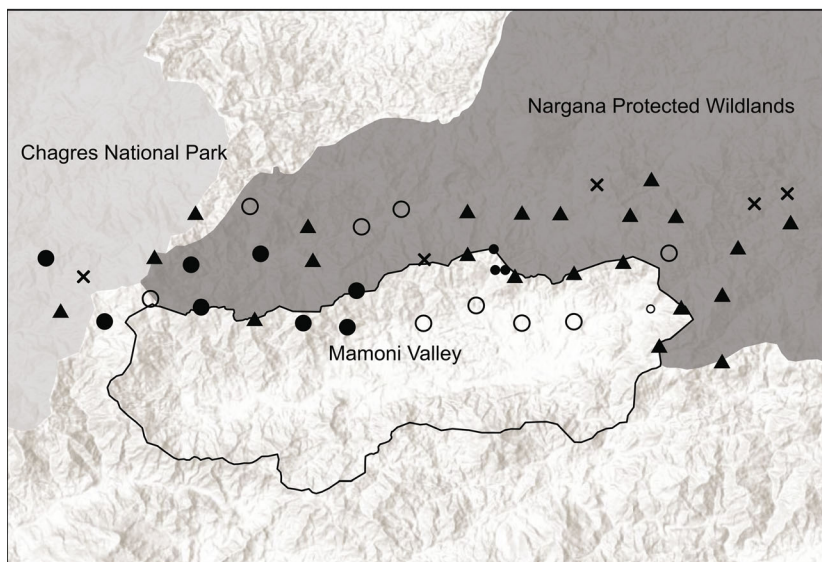
Fig. 2 The sampled area indicating camera trap locations with jaguar (**a**) and puma (**b**) detection and nondetection within the three land tenures of the Nargana Protected Wildlands, Chagres National Park, and Mamoni Valley

1985; Woodburne et al. 2006; Weir et al. 2009) (Fig. 1). The physiographic features that characterize the country include the Talamanca mountains, which abut the Serrania de Tabasara to the west, and the Cordillera de San Blas and Serrania del Darien mountains to the east (Myers 1969). Panama's elevation ranges from 0 to ca. 3475 m a.s.l. Mean annual temperatures range from 30 °C in the valleys to 20 °C in the mountains. The wet season occurs from May to November and the dry season from December to April. Annual rainfall amounts range between 1700 mm and 4000 mm on the Pacific and Atlantic coasts, respectively (Condit et al. 2001; Ibáñez et al. 2002). Elevational differences with associated temperature and precipitation patterns

produce distinct vegetative regimes that contribute to the country's rich biodiversity (Myers 1969). Humid tropical and premontane forests dominate the lower reaches of the mountains. Panama also boasts tropical montane cloud forests, one of the world's most imperiled ecosystems (Aldrich et al. 1997).

Sampled area

The sampled area was selected for its ecological significance and strategic location at the convergence of three important protected areas in eastern Panama: the Nargana Protected Wildlands, Chagres National Park, and the Mamoni Valley. Together, the sampled area comprised ~ 200 km^2. Despite its limited size, the sampled area is representative of the landscape and resources used by jaguars and pumas in Panama (Figs. 1, 2a, b).

The Nargana Protected Wildlands falls within the semi-autonomous territory of the Indigenous Guna Yala people. It includes the Caribbean side of the Cordillera de San Blas, which has a very wet climate owing to showers spawned by moisture-laden trade winds. Most of the forest within this area is largely undisturbed by human activities, but patches of fallow (locally known as rastrojo) (pioneer forests 40–50 yrs. old fallow) and secondary mature forest are apparent (Fig. 2a, b).

Chagres National Park is part of the Panama Canal Watershed (Condit et al. 2001), it borders the southwestern end of the Nargana Protected Wildlands. Communities that live within the park rely on agriculture and subsistence hunting for their livelihoods. Old-growth forest dominates the upper ridges. Its topography is rugged with permanent and intermittent streams, steep rock walls along ridgelines, and ravines with clear, fast-flowing, rocky streams (Fig. 2a, b).

The Mamoni Valley is located on the leeward side of the Cordillera de San Blas facing the Pacific slope. With most of the upper reaches still forested, the Mamoni Valley acts as a buffer zone, protecting the eastern border of Chagres National Park and the southwestern border of the Nargana Protected Wildlands. The valley includes 115 km^2 of privately-owned and protected lands. There are four villages within the valley with an estimated population of 400 people whose economy is largely agricultural, and ranching based. The land cover is composed of a mixed matrix that includes secondary forest, fallow (with various stages of maturity), tree farms, pasture, and agropecuary practices (e.g., agriculture and livestock) (Fig. 2a, b).

Data collection

We obtained detection-nondetection data on jaguar and puma habitat use from systematic camera trap surveys in three contiguous areas under different tenure regimes: (1) Nargana Protected Wildlands, (2) Chagres National Park, and (3) the Mamoni Valley (Fig. 2a, b). Camera trapping data were collected from July 2016–September 2018. We established 48 camera stations throughout the ~ 200 km^2 sampled area. Cameras were deployed year-round (through wet and dry seasons), producing 16,583 trap nights. We obtained a total of 153 detections of jaguars and 218 detections of pumas. A single jaguar or puma detection was considered one photographic capture per hour.

Data analysis and predictor variables

We selected twenty-one predictor variables for modeling the potential habitat of jaguars and pumas based on their relevance to the species' ecology (Table S1). We used a 30 m resolution digital elevation model to derive topographic covariates from Aster Global DEM V002 (NASA). We applied the Gradient & Geomorphometry Metrix Toolbox (Evans et al. 2014) in ArcGIS (ESRI, Redlands, CA) to calculate both the topographical roughness and relative slope position. We determined the landscape composition variables, water body, and land use features by interpreting the Cobertura Boscosa y Uso de Tierra 2012 land cover map, the latest version provided by the Ministry of Environment of Panama (MiAmbiente). We derived the percent tree cover from the USGS Global Tree-Canopy Cover Circa 2010, the most accurate data at the spatial resolution and extent relevant to the study area. These layers, despite being a few years apart from our camera trap data, represent the best available layers at the spatial grain and extent relevant to this study. Also, no major disturbance had significantly altered the sampled landscape between those years. We obtained climate variables from Global Climate Data—WorldClim.org (annual average past 30 years). We resampled all landcover variables from a spatial resolution of 5 m to 30 m with nearest neighbor interpolation in the Resample tool in ArcGIS. To resample the climate variables to a 30 m spatial

Table 1 Optimal scales for the most important variables found in the annual, wet season, and dry season jaguar and puma models

Species	Season (model accuracy)[a]	Variable Name	Code	Optimal scale (m)
Jaguar (Panthera onca)	Annual (k,0.53; OOB, 0.22)	Secondary forest	Foremix	10,500[b]
		Coniferous forest	Forconi	14,000[b]
		Human settlement	People	4000
		Aspect	Aspect_cos	6000
		Fallow	Rastrojo	3500
		Primary forest	Mix_forest	10,500[b]
	Wet (k,0.63; OOB, 0.18)	Hydrologic feature	Hydro	4500
		Aspect	Aspect_cos	3500
		Slope	Slope	3000
		Fallow	Rastrojo	1500
		Elevation	Dem	3500
		Broadleaf forest	Forlatif	11,000[b]
		Coniferous forest	Forconi	12,500[b]
	Dry (k,0.40; OOB, 0.28)	Fallow	Rastrojo	3500
		Secondary forest	Foremix	10,500[b]
		Elevation	Dem	7000
Puma (Puma concolor)	Annual (k,0.61; OOB, 0.11)	Primary forest	Mix_forest	500
		Coniferous forest	Forconi	13,500[b]
		Elevation	Dem	5500
		Aspect	Aspect_cos	11,000[b]
		Hydrologic feature	Hydro	500
		Agropecuary	Agropec	10,500[b]
		Secondary forest	Foremix	2000
	Wet (k,0.39; OOB, 0.22)	Primary forest	Mix_forest	500
		Agropecuary	Agropec	14,000[b]
		Elevation	Dem	6000
		Hydrologic feature	Hydro	15,000[b]
		Aspect	Aspec_cos	11,000[b]
		Coniferous forest	Forconi	13,500[b]
		Slope	Slope	1500
	Dry (k,0.56; OOB, 0.20)	Primary forest	Mix_forest	500
		Aspect	Aspect_cos	1000
		Secondary forest	Foremix	11,000[b]

[a] Model accuracy indicated by k, Cohen's kappa, and OOB error (refer to text for definitions)

[b] Variable importance at broad scales (over 7500 m)

resolution we used bilinear interpolation. Other variables were not resampled given their original form at 30 m. The spatial grain was held constant at 30 m in the multi-scale analyses.

Habitat suitability modeling: random forests

RF is based on a classification and regression tree-based bootstrap method that provides well-supported predictions with large numbers of independent variables and relatively small sample sizes (Breiman 2001; Cutler et al. 2007). This nonparametric approach is suitable for modeling nonlinear data such as environmental data and sparse data on occurrence, particularly for rare, threatened, or endangered species (Farrell et al. 2019). We used the "randomForest" package (Liaw and Wiener 2002) in R statistical software.

Scale optimization and variable selection

To identify the optimized scale for each predictor variable that was most related to felid response, we calculated the focal mean of each predictor variable around each camera location across 30 spatial scales (Wasserman et al. 2012), ranging from 500 m to 15,000 m radii at 500 m increments. For summarizing our results, we categorized the 500 m–7500 m scales as fine scale, and the 8000 m–15,000 m scales as broad scale. We first utilized the Focal Statistic tool in ArcGIS (ESRI, Redlands, CA) to conduct a moving window analysis using a circular neighborhood and the 30 spatial scales as search radii for each variable to obtain an output raster. We then extracted the raster values around each camera trap location for each scale and each variable. The full set of candidate variables was reduced from twenty-one to seventeen (Table 1; Table S1).

Multi-scale optimized multivariate modeling

Following Cushman et al. (2017) and Cushman and Wasserman (2018), we developed multi-scale optimized models of jaguar and puma occurrence in three stages. First, we conducted univariate scaling analyses to identify the spatial scale at which each variable was most strongly related to felid occurrence using the total number of detections as the response variable. Univariate scaling is a well-established method to identify the characteristic scale (also known as scale of effect, scale domain, optimal scale, etc.) in habitat relationship modeling (Mateo-Sánchez et al. 2014; Zeller et al. 2014; Jackson and Fahrig 2015; Laforge et al. 2015; McGarigal et al. 2016; Vergara et al. 2016; Wan et al. 2017). The RF classifier includes two random processes that improve the predictive power of the classification. When building each decision tree in the forest (ensemble), at each tree branching node a subset of potential predictor variables is randomly selected on which the data is split (creating a child node), thereby reducing the correlation between the trees, resulting in a lower error rate (Horning 2010; Smith 2010; Duro et al. 2012; Puissant et al. 2014; Ashrafzadeh et al. 2020). In addition, the RF algorithm randomly selects a bootstrap sample from a subset of the total training data available to build each tree. A third of this subset is left out-of-bag (OOB) and not used to construct the tree. This OOB subset is then run through a constructed tree to cross-validate the classification, thereby deriving an unbiased estimate of the test-set error (Breiman and Cutler 2003). We selected the best-supported scale from each variable based on the model with the lowest OOB error rate (OOB; see Breiman 2001). Second, we applied the multicollinear function in the rfUtilities R package (Evans and Cushman 2009) to assess potential multicollinearity among all possible pairs of scale-optimized variables identified in the univariate scaling step, and removed variables that were significantly correlated ($p < 0.05$). Third, we ran RF with the remaining variables (17) to model the probability of jaguar and puma occurrence. We developed three final RF models for each species: annual, wet season, and dry season. Further, we acknowledge that the predictions outside of the sampled area might not be as accurate as within the sampled area (as described in the limitation section).

Model validation

To assess the final models' performance, we conducted random permutations, cross-validation using a resampling approach with the rf.crossValidation function in the rfUtilities package in R (Evans and Murphy 2018). We performed a total of 99 permutations. The cross-validation produced a suite of performance metrics including model error variance, Cohen's kappa statistics, and the cross-validated OOB error rate. We calculated the mean square error ("%IncMSE") as a measure of variable importance. The %IncMSE plot shows the mean increase of MSE in nodes that use a predictor in the model when the predictors' values are randomly permuted. Additionally, we produced partial dependency plots that display how the RF model predictions are influenced by each predictor when all other predictors in the model are being controlled (Evans et al. 2011). They graphically characterize the relationship between variables and the predicted probabilities of felid presence obtained by RF.

Correlation and average absolute difference between models

We conducted pixel-pixel correlations of the predicted probability between each pair of predicted maps (15 pairs of maps at 30 m pixel size). The correlations

provide a value that ranges from 0 to 1, in which 1 indicates a stronger correlation between the two predicted occurrence probability maps compared. We hypothesized that (1) correlations would be higher between models for the same species than for models between the species, and (2) within species, we expected correlations between annual-wet and annual-dry to be higher than between wet-dry.

While the pixel-pixel correlation between maps indicates the degree to which habitat suitability values covary linearly between maps (measures how linearly related suitability values are), the average absolute difference measures the degree to which pixel-pixel values differ quantitatively across pairs of maps (total difference in predicted suitability across maps). Together, they provide a full picture of the covariation and total difference in predicted suitability (Hearn et al. 2018). We hypothesized that (1) the average absolute difference would be lowest for model pairs of the same species, and (2) within species, we expected the absolute average difference between wet-annual and dry-annual to be lower than between wet-dry.

Results

The final optimized multi-scale seasonal models indicated that jaguar and puma occurrence probabilities differed in their respective relationships to the spatial scale at which each predictor variable was measured. The metrics related to jaguar and puma habitat suitability were more influential at fine scales (68.7% and 52.9%, respectively) than at broad scales (31.2% and 47.0%, respectively) (Table 1), with variables in the jaguar models concentrated at fine scales and variables in the puma models relatively evenly balanced between fine and broad scales.

Variable importance varied seasonally in the jaguar models (Fig. 3a). In the annual model, the top predictors were secondary and coniferous forests and human settlement. Hydrologic and topographic features were the most important determinants of jaguar habitat selection during the wet season, whereas fallow, secondary forest, and elevation were most important in the dry season. The puma seasonal models revealed similar influential predictor variables throughout seasons, including primary and secondary forests and agropecuary, followed by topographic features (Fig. 3b).

For the jaguar models, the cross-validated OOB error indicated relatively high predictive performance for annual, wet, and dry seasons (0.22, 0.18, 0.28, respectively), with the wet season model showing the highest performance, followed by the annual and dry season models. In contrast, for the puma models, the cross-validated OOB error indicated the highest predictive performance was the annual model (0.11), followed by the dry (0.20) and wet (0.22) season models (Table 1; Tables S2–S7).

Further, the Cohen's kappa coefficient (Landis and Koch 1977) for the jaguar models indicated reliable predictions ranging from a moderate agreement (0.53), a substantial agreement (0.63), and a fair agreement (0.40) for the annual, wet, and dry season models, respectively. In the puma models, the kappa coefficient showed a relatively high level of accuracy with a substantial agreement (0.61), just below the threshold for a moderate agreement (0.39), and a moderate agreement (0.56) for the annual, wet, and dry season, respectively (Table 1).

According to the annual partial dependency plots (Evans et al. 2011), the highest probability of jaguar occurrence was associated with a low degree of secondary forest and a high amount of primary forest (Fig. 4). Jaguar occurrence decreased drastically as the extent of the human-inhabited area, coniferous forest, and fallow increased in the landscape. Proximity to hydrologic features was associated with higher jaguar detections, while a non-linear relationship with elevation indicated a selection of altitudes ranging between 250 m–500 m during the wet season and 250 m–350 m in the dry season (Figures S1 and S2, respectively).

The puma model's partial dependency plots showed the probability of its occurrence increased with a greater extent of primary forest and decreasing extent of secondary forest (Fig. 5). Puma presence was negatively associated with coniferous forest and elevations above 250 m and showed little association with hydrologic features. Pumas had a positive relationship with agropecuary lands in the annual model, but not in the wet or dry season models (Figures S3 and S4, respectively).

Predictive suitability maps

Overall, our habitat suitability maps showed a high predicted occurrence probability (> 0.5) for both
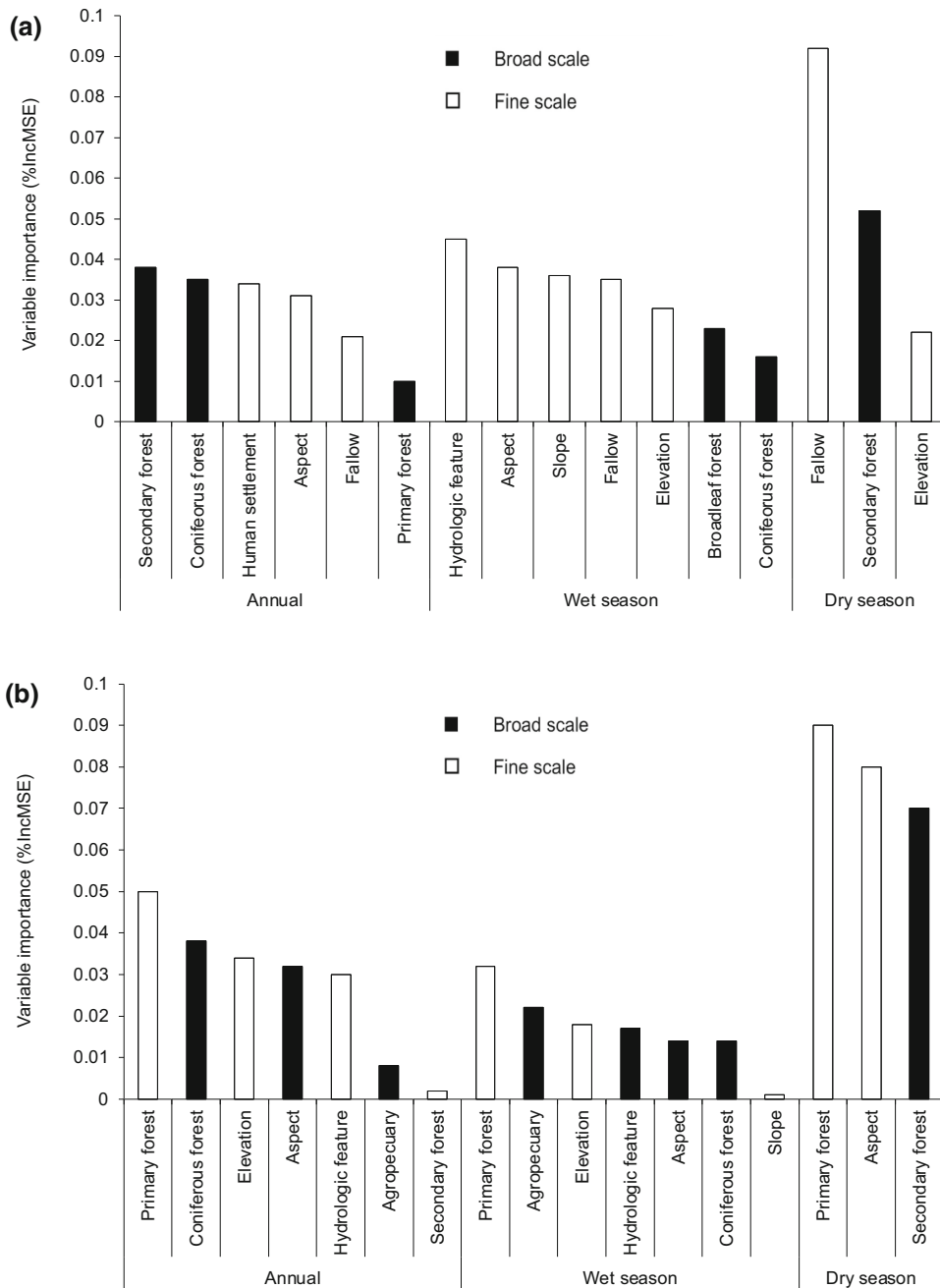
Fig. 3 The plots show the variable importance for jaguars (**a**) and pumas (**b**) by season, measured as the increases mean square error (%IncMSE), representing the deterioration of the model's predictive ability when each predictor is replaced in turn by random noise. Higher %IncMSE values indicate variables that are more important to the classification

jaguars and pumas in sizeable contiguous forest blocks that stretch along the northern part of the country from east to west, suggesting that this is the stronghold for the two felid species, and highlights the importance of protected areas and indigenous lands. While eastern

Panama boasts three major protected areas concurrent with high-quality habitat (Darien National Park, Guna Yala territory, and Chagres National Park), habitat suitability declined west of the Panama Canal. Low quality and highly fragmented habitat may limit the
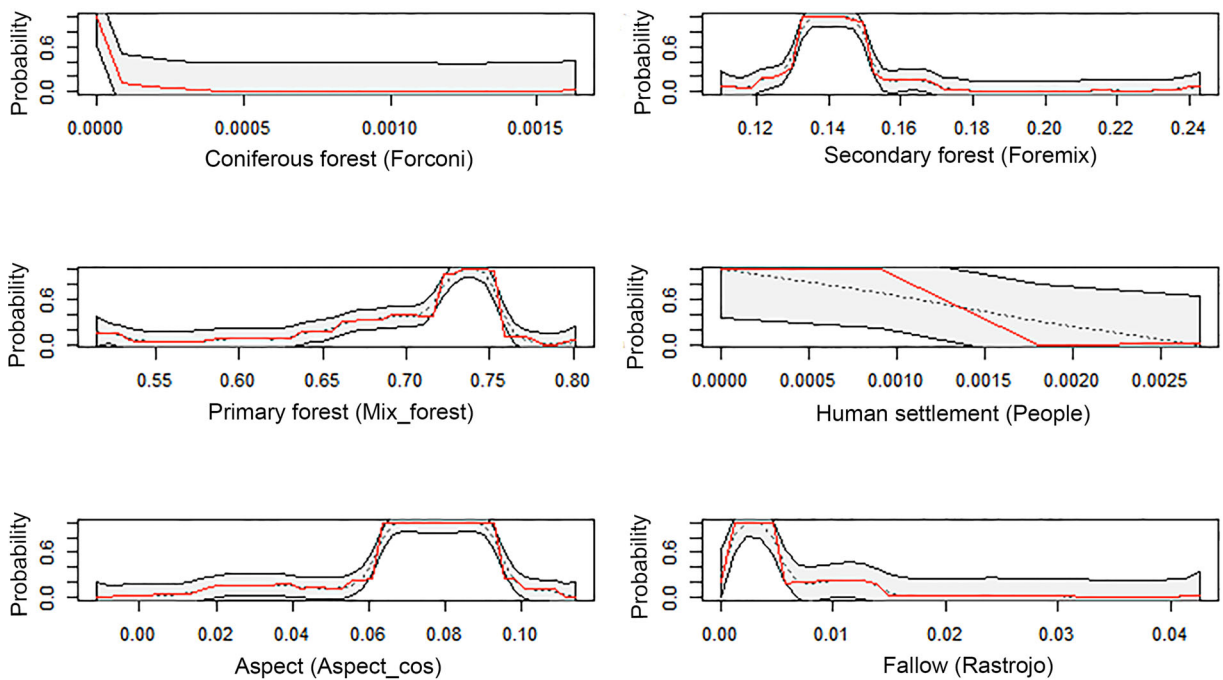
Fig. 4 Partial dependency plots representing each variable's marginal effect in the annual RF jaguar model. In a partial plot of marginal effects, only the range of values (and not the absolute values) can be compared between plots of different variables (Cutler et al. 2007). The gray area indicates the 95% confidence interval, and the red line indicates the mean average. The x and y axes range from 0 to 1

regional connectivity of felid populations, especially for jaguars, whose presence is linked to extensive forest cover at broad scales (Fig. 6).

Correlation and average absolute difference between models

Consistent with our first hypothesis, the average correlation for pairs of maps that were puma-puma (0.52833) was much higher than pairs of maps that were puma-jaguar (0.31591) (Fig. 7). However, the correlation for jaguar-jaguar maps (0.31007) was approximately the same as for puma-jaguar maps. These results suggest that the puma's predicted habitat suitability was relatively stable across the year and did not significantly differ between wet and dry seasons; while the annual model across the full year was highly correlated with the wet season and moderately correlated with the dry season. However, for jaguars, the results implied strong seasonality in habitat suitability, showing a relatively low correlation between wet and dry seasons (r = 0.2735) and

between the annual and dry seasons (r = 0.2348). For both species, the wet season models were more correlated to the annual model than with the dry season model, or the dry season model correlated with the annual model. The correlation results imply that the dry season's habitat suitability is quite different from what would be predicted from the wet season or analysis across the full extent of the year.

Our results did not strongly support our hypothesis that the average absolute difference would be lowest for model pairs of the same species; nor that within species, the absolute average difference between wet-annual and dry-annual would be lower than between wet-dry. The average absolute difference between puma-puma models and jaguar-jaguar models was higher than the differences between puma-jaguar models (r = 0.25667, 0.22697, 0.21844, respectively). The results suggest large differences in the predicted suitability values between seasonal models for each species, and these are as big or bigger than the quantitative differences in pixel-pixel probability values between puma-jaguar models.
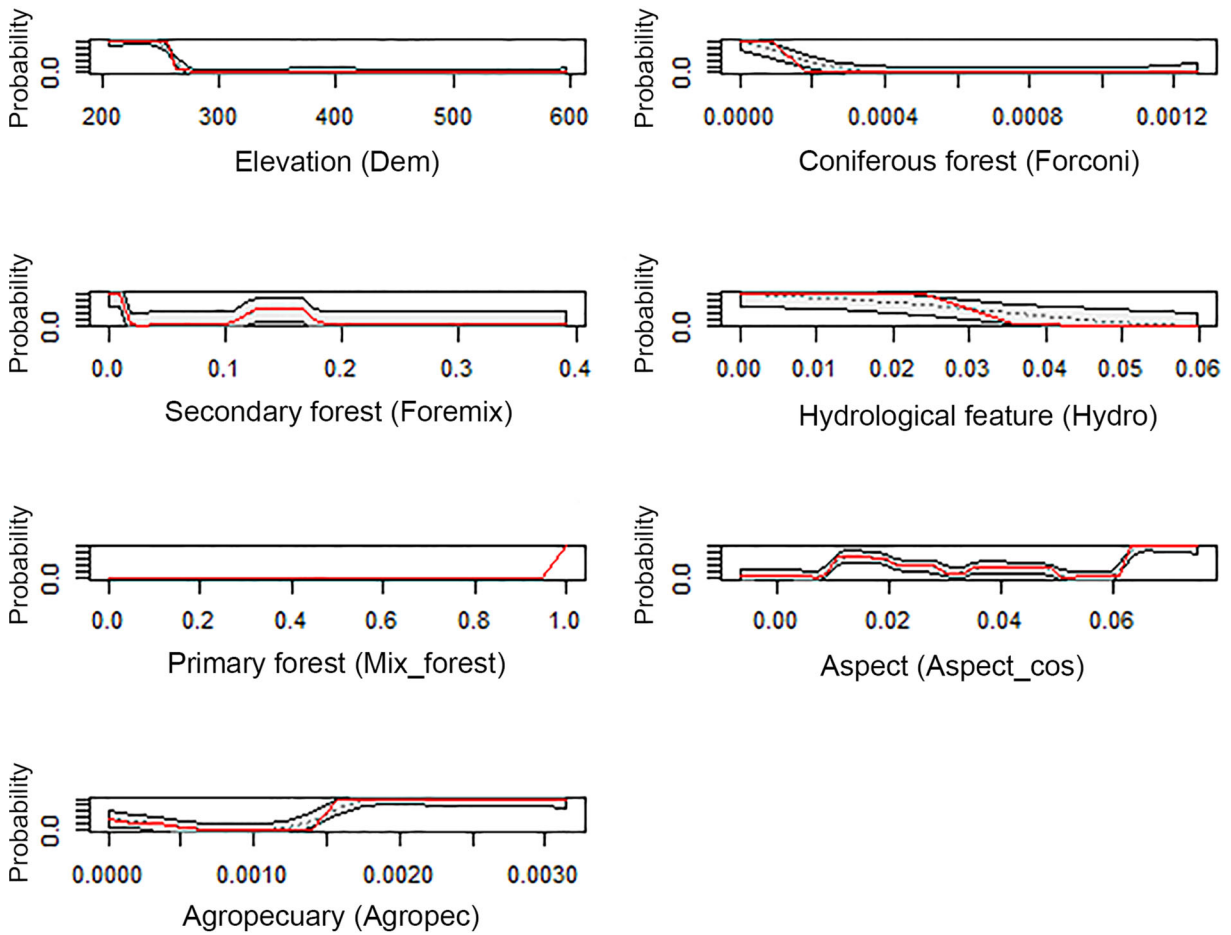
Fig. 5 Partial dependency plots representing each variable's marginal effect in the annual RF puma model. In a partial plot of marginal effects, only the range of values (and not the absolute values) can be compared between plots of different variables (Cutler et al. 2007). The gray area indicates the 95% confidence interval, and the red line indicates the mean average. The x and y axes range from 0 to 1

Discussion

Our study adds to the knowledge provided by prior studies on sympatric jaguar and puma habitat selection (Schaller and Crawshaw 1980; Crawshaw and Quigley 1991; Scognamillo et al. 2003; Silveira 2004; Cullen Jr et al. 2005; Cullen Jr 2006; Foster 2010; Sollmann et al. 2012; Palomares 2016; de la Torre et al. 2017; Alvarenga et al. 2021). These previous studies documented positive associations of both species with forest cover and negative associations with human land use but did not employ multi-scale optimization or formally compare seasonal habitat selection differences. The multi-scale optimized analyses provided insight into the range of habitats used in Panama's structurally complex tropical montane

cloud forest. Further, we identified the optimal scale for each habitat characteristic selected by each species. Our analyses revealed the unique combination of environmental variables and corresponding scales important to defining the differences among seasonal habitat associations for jaguars and pumas. We observed strong temporal nonstationarity in habitat suitability patterns, particularly for jaguars. Models confirmed that these sympatric predators might engage in spatial coordination to facilitate coexistence, as increased spatial overlap at a given scale in each season was associated with a diversification of landcover types. Our models indicated that jaguars exhibit divergent seasonal habitat use. Wet season habitat selection was driven by hydrology and topography, whereas in the dry season, jaguars primarily
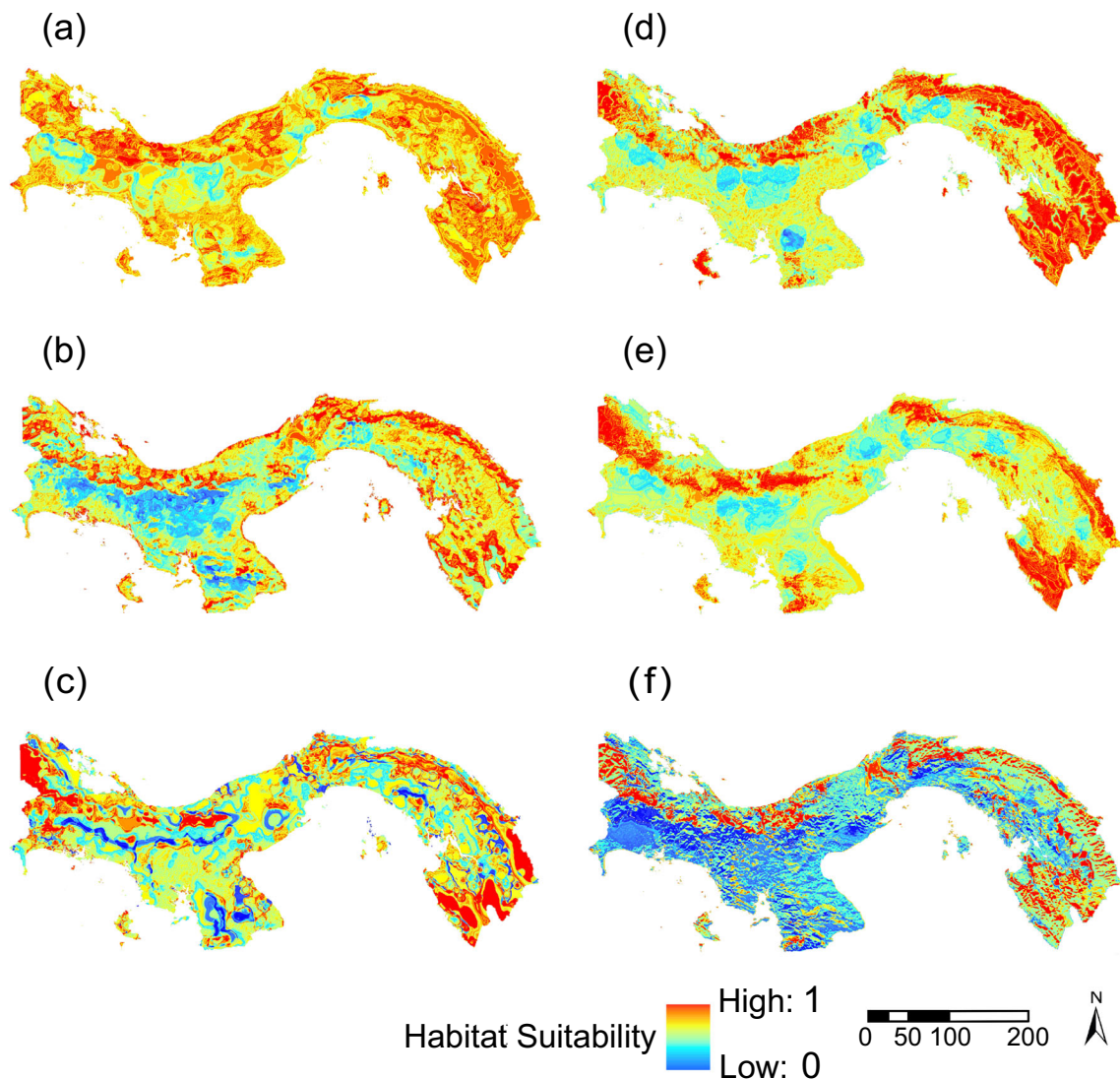
Fig. 6 Seasonal habitat suitability maps showing the predicted occurrence of jaguars and pumas in Panama derived from multiscale optimized models. Prediction maps **a**–**c** are for jaguars and maps **d**–**f** are for pumas (top row is annual, middle row is the wet season, and the bottom row is the dry season)

select areas of extensive forest cover and low human impact. Puma habitat selection across the year is tied to the extent of forest cover and degree of human impact.

Effects of scale optimization on predicted habitat suitability

The multi-scale optimization results identified the main drivers of jaguar and puma habitat suitability more often at fine scales than broad scales, especially

for jaguars. The variables retained in the puma models were relatively well balanced between fine and broad scale. These results were somewhat surprising given the pattern observed in past work, in which large carnivores were frequently associated with habitat features at broad spatial scales (e.g., Mateo-Sanchez et al. 2014; Rostro-Garcia et al. 2016; Hearn et al. 2018; Macdonald et al. 2018).

Overall, for both species, the most influential and consistent predictors of habitat selection at a fine scale were hydrologic and topographic features. Most

	PA	PD	PW	JA	JD	JW
PA		0.498	0.654	0.3561	0.2605	0.3993
PD	0.3606		0.433	0.2698	0.2288	0.4028
PW	0.1688	0.2406		0.3	0.3246	0.3013
JA	0.1534	0.3989	0.2022		0.2348	0.4219
JD	0.2653	0.2128	0.1534	0.2796		0.2735
JW	0.2426	0.1986	0.1388	0.2544	0.1469	

Fig. 7 Correlation (upper triangle), and average absolute difference (lower triangle) for all pairs of predicted probability of occurrence maps. Pairs of maps that are both for puma (PA, PD, PW) are shaded medium grey, both jaguar (JA, JD, JW) are light grey, and pairs that are jaguar-puma (JA, JD, JW, PA, PD, PW) comparisons are dark grey

notably, as shown by numerous studies, jaguars were more associated with hydrologic features (i.e., rivers and streams) (Sollmann et al. 2012; Nuñez-Perez and Miller 2019) than were pumas (Zeller et al. 2017). Selectively, these features may confer advantages for top predators, offering cover and hunting opportunities or dispersal and escape pathways. Additionally, given that the presence of cliffs and steep slopes were determinants of jaguar and puma habitat, the differential of preferred elevation for jaguars (200 m–500 m) and pumas (250 m–300 m)–in the wet season–is indicative of a selection of resources in areas with high productivity. During the resource-limited dry season, jaguars preferred lower elevations, suggesting a concentration in areas of extensive forest surrounding permanent water bodies (Nowell and Jackson 1996; Sollmann et al. 2012; de la Torre and Rivero 2019; Nuñez-Perez and Miller 2019; Alvarenga et al. 2021). This preference may explain the much larger seasonal habitat displacement of jaguars than pumas, with jaguars shifting habitat selection in the dry season to areas highly proximal to permanent water, while pumas remained more widely distributed in upland areas.

At fine scales, jaguars, unlike pumas, exhibited a stronger avoidance of human settlements, indicating the higher vulnerability to human disturbance and land-use change as compared with pumas (Sunquist and Sunquist 2002; Scognamillo et al. 2003; Silveira 2004; Foster 2008). Our habitat models indicated that forest edges, highlighted by the cordilleras in Talamanca and San Blas, were strong predictors of habitat selection by jaguars. Forest edges are known to provide food availability for carnivores in the tropics, including pumas, ocelots, margays, and jaguarundis (Magioli et al. 2014, 2019; Guerisoli et al. 2019). Therefore, edge habitat may be of great importance to this felid population; combined with extensive use of continuous forest, it may provide a matrix of food and source of cover (Cullen Jr et al. 2013; de la Torre et al 2017; Nuñez-Perez and Miller 2019). Notably, the edges predicted to be most important for jaguars in our models were natural edges driven by topographical features, not anthropogenic edges, which the jaguar, due to its high sensitivity to human disturbance, likely avoid (e.g., Foster et al. 2010; Morato et al. 2016; Jędrzejewski et al. 2018).

At a broad scale, extensive primary forest cover was more related to jaguar habitat suitability than for puma. Pumas incorporated agropecuary and secondary forest features into their habitat selection, while these land cover types were not selected by jaguars. The selection of vegetation cover types at a broad scale, as reported for other large carnivores (e.g., Elliot et al. 2014; Zeller et al. 2017; Hearn et al. 2018), provides critical insight into species' home range limitations (Rettie and Messier 2000). In turn, it reflects the distribution of suitable habitat and exemplifies species' ecological attributes (e.g., diet, temporal activity patterns) on co-occurrence patterns (Davis et al. 2018), implying broad scale spatial partitioning among these top predators.

Spatiotemporal change in habitat among carnivores

The habitat selection models and the resulting habitat suitability maps show that jaguar and puma habitat selection was strongly influenced by seasonality and spatial heterogeneity of resources. Our analysis suggests that the puma's predicted habitat suitability remains relatively stable across the year, while the correlation results for the jaguar suggest seasonality in the predicted habitat suitability. The degree of ecological plasticity that these species have evolved to exploit the available resources in a heterogeneous landscape may be allowed by substantial seasonal changes in resource availability. The degree of species segregation at broad scales may increase with seasonal precipitation. Since precipitation is positively linked to plant productivity, distribution, and diversity in

tropical rainforests, we argue that seasonal spatial segregation and the degree of precipitation during the wet season are intimately linked to a seasonal distribution and abundance of prey. Specifically, the association of jaguars with water, especially in the dry season, and spatial shift to lower elevations more closely tied to water availability in the dry season, are the main drivers of the seasonal spatial shift of jaguars, suggesting a high dependence on water, particularly in seasons of scarcity.

Despite being sympatric, jaguars present a narrower habitat preference than pumas (Astete et al. 2017). In line with this assertion, our models showed that pumas were more versatile in their resource exploitation and had the most extensive and connected suitable habitat in both wet and dry seasons. In contrast, the extent of suitable habitat for jaguars was smaller and largely overlapped with the puma. Of the two species, the jaguar is likely more vulnerable to habitat loss and fragmentation because comparatively, it is a habitat specialist in Panama. Also, two of its most important habitat components–water bodies and extensive forest–are vulnerable to recent land-use change, which is likely to continue to spike.

Species segregation is generally expected to increase with increasing competitive interactions for limiting resources. Our results point to the association of specific habitat components at fine spatial scales as additional drivers of species segregation, leading to the felids' adjustment of their spatiotemporal position to avoid aggressive encounters (de la Torre et al. 2017). Palomares (2016) pointed out that under the subordinate (puma) and dominant (jaguar) scenario, at small scales, pumas could avoid jaguars by "fine-shifting micro-habitat use." Shifting is evident in our study, as jaguars and pumas exhibited fine scale spatial overlap with topographic features (elevation and slope) (Table 1; Fig. 2). Therefore, while using the same (micro) habitat, species may segregate along the fine scale temporal or dietary axis to successfully avoid or decrease competition and thus maintain coexistence (Foster et al. 2010; Santos et al. 2019). Our results indicated that the puma is more of a generalist than the jaguar, which is more vulnerable to anthropogenic landscape change, particularly deforestation in lower elevations near permanent water, where deforestation is most concentrated in Latin America (Hansen et al. 2010).

Temporal nonstationarity in habitat selection

One of the frontiers in habitat modeling is understanding the temporal nonstationarity of habitat relationships and model predictions (e.g., Kaszta et al. 2021). There has been considerable attention paid to spatial nonstationarity, in which metareplicated studies are conducted to understand differences in habitat relationships and limiting factors in different study areas (e.g., Short Bull et al. 2011; Shirk et al. 2014; Wan et al. 2019). In contrast, there has been less attention paid to temporal nonstationarity, except in terms of comparing seasonal habitat models (e.g., Shirk et al. 2014) or post-disturbance changes in limiting factors (e.g., Cushman et al. 2011). Our results identified temporal nonstationarity in jaguar habitat selection, but not in puma habitat selection (Fig. 5). In tropical regions, food and water availability are subject to spatial and temporal variations, and habitat selection needs to be interpreted in that context. Thus, in systems with high seasonality of habitat use (e.g., Shirk et al. 2014), models developed from occurrence data across the full year may fail to accurately reflect habitat selection in any season within the year. These results suggest that for large felids in Mesoamerica, considering temporal nonstationarity is important for some species but might not be relevant for others. Scale has emerged as a focal area of habitat ecology work, but few studies have evaluated the effects of temporal scale on predictions (McGarigal et al. 2016), and we encourage future research to evaluate further temporal scale relationships in habitat selection.

Overall, our results highlight the importance of considering the temporal scale and temporal nonstationarity in habitat modeling and spatial scaling. Given the high sensitivity of model predictions to temporal periods and temporal scales, we strongly suggest habitat modeling studies evaluate and optimize temporal relationships, as has recently become standard for spatial scale relationships (McGarigal et al. 2016).

Limitations

Though our data were collected from a relatively small area (Figs. 1, 2a, b), its geographical location is critical to range-wide connectivity for the species

(Rabinowitz and Zeller 2010). Thus, information on the factors affecting jaguar and puma occurrence in this landscape is relevant at scales much larger than our study. However, it is unknown how well our models would extrapolate to other parts of the species' ranges. It would be valuable to compare these model predictions to those from other parts of the species' ranges using the same methods (Short Bull et al. 2011; Shirk et al. 2014; Wan et al. 2018), applying multi-model combined inferences (e.g., Wan et al. 2019).

The study area contains broad ecological, topographical, and land cover gradients that are characteristic of each species' Central American range, so we conjecture that our models would have predictive and heuristic value in that part of the range of both species. This study serves as a baseline for habitat assessment of the two studied species, and we recommend future studies to expand into a broader region and to sample beyond the range of conditions examined in our sampling area (see Table S1 for the range of sampled values for each variable). Despite the limited sampling area and relatively small data set, our models provide highly accurate and robust predictions of habitat suitability for jaguars and pumas. The use of HSMs with machine learning to derive distribution estimates of rare, difficult to detect species has been underutilized. The application of these tools to predict a distribution area beyond the sample range is a recent development in the literature (Mi et al. 2017). Nevertheless, models with few detection samples can generate accurate species predictive distributions using the RF method (Mi et al. 2017).

Further, the extrapolation of data from the sampled area across the country was warranted because of the urgent need among local agencies to identify potential locations for future monitoring efforts. We acknowledge that the prediction outside of the sampled area might not be as accurate as within the sampled area, though it establishes a starting point to guide these efforts.

A final potential limitation to the interpretation of our results relates to the scale optimization. The approach taken here uses model optimization based on an objective function based on predictive performance (OOB). It is intended to identify the operative range of scales that are relevant to the organism or process being examined. However, it is not always clear if this metric successfully identifies the true operative scales. For example, two recent papers (Atzeni et al. 2020; Chiaverini et al. 2021) used simulation modeling to evaluate the ability of scale optimization approaches such as those used here to correctly identify the variables and scales at which those variables influence species occurrence. The results showed the high ability of the models to predict the probability of occurrence correctly, but less ability to identify the correct variables and scales out of a pool of correlated alternatives. This suggests that future work should be conducted using a simulation approach that allows explicit control over the stipulated pattern process relationships to investigate the performance of different modeling methods and approaches to scale dependence and temporal nonstationarity.

Author contributions KC and MY acquired the funding, conceived of the study design, methodology, performed the investigation, and analyzed the data. The first draft of the manuscript was written by KC and MY with input from all authors. KC, MY, RV, and HW designed the visualization. HW and SC directed and supervised the formal analysis and data interpretation and contributed to the review and editing of the manuscript.

Data availability All data generated or analyzed during this study are included in this published article (and its supplementary information files).

Code availability Unavailable.

Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

Informed consent Publication has been approved by all co-authors and responsible authorities.

References

Acevedo P, Ward AI, Real R, Smith GC (2010) Assessing biogeographical relationships of ecologically related species using favourability functions: a case study on British deer. Divers Distrib 16:515–528

Aldrich M, Billington C, Edwards M, Laidlaw R (1997) Tropical montane cloud forests: an urgent priority for conservation. WCMC Biodivers Bull 2:1–16

Alvarenga GC, Chiaverini L, Cushman SA, Dröge E, Macdonald DW, Kantek DLZ, Morato RG, Thompson J, Oscar RBLM, Abade L, de Azevedo FCC, Ramalho EE, Kaszta Z (2021) Multi-scale path-level analysis of jaguar habitat use in the Pantanal ecosystem. Biol Conserv 253:108900

Ashrafzadeh MR, Khosravi R, Adibi MA, Taktehrani A, Wan HY, Cushman SA (2020) A multi-scale, multi-species approach for assessing effectiveness of habitat and connectivity conservation for endangered felids. Biol Conserv 245:108523

Astete S, Marinho-Filho J, Kajin M, Penido G, Zimbres B, Sollmann R, Jácomo ATA, Tôrres NM, Silveira L (2017) Forced neighbours: coexistence between jaguars and pumas in a harsh environment. J Arid Environ 146:27–34

Atzeni L, Cushman SA, Bai D, Wang J, Chen P, Shi K, Riordan P (2020) Meta-replication, sampling bias, and multi-scale model selection: a case study on snow leopard (*Panthera uncia*) in western China. Ecol Evol 10:7686–7712

Breiman L (2001) Random Forests. Mach Learn 45:5–32

Breiman L, Cutler A (2003) Manual-setting up, using, and understanding random forests v4. 0. Statistics Department, University of California Berkeley, CA, USA 1(58)

Chiaverini L, Wan HY, Hahn B, Cilimburg A, Wasserman TN, Cushman SA (2021) Effects of non-representative sampling design on multi-scale habitat models: flammulated owls in the Rocky Mountains. Ecol Modell 450:109566

Condit R, Robinson WD, Ibanez R, Aguilar S, Sanjur A, Stallard RF, Garcia T, Angehr GR, Petit L, Wright SJ, Robinson TR, Heckadon S (2001) The status of the Panama Canal watershed and its biodiversity at the beginning of the 2lst century. Bioscience 51:389–398

Crawshaw PG, Quigley HB (1991) Jaguar spacing, activity, and habitat use in a seasonally flooded environment in Brazil. J Zool Soc Lond 223:357–370

Cullen L Jr, Abreu KC, Sana D, Nava AFD (2005) Jaguars as landscape detectives for the upper Paraná River corridor, Brazil. Nat Conserv 3:124–146

Cullen L Jr, Sana DA, Lima F, de Abreu KC, Uezu A (2013) Selection of habitat by the jaguar, Panthera onca (Carnivora: Felidae), in the upper Paraná River, Brazil. Zoologia (curitiba) 30:379–387

Cullen L Jr (2006) Jaguars as landscape detectives for conservation in the Atlantic Forest of Brazil. University of Kent

Cushman SA, Wasserman TN (2018) Landscape applications of machine learning: comparing Random Forests and logistic regression in multi-scale optimized predictive modeling of American marten occurrence in Northern Idaho, USA. In: Humphries G, Magness D, Huettmann F (eds) Machine learning for ecology and sustainable natural resource management. Springer, New York, pp 185–203

Cushman SA, Raphael MG, Ruggiero LF, Shirk AS, Wasserman TN, O'Doherty EC (2011) Limiting factors and landscape connectivity: the American marten in the Rocky Mountains. Landsc Ecol 26:1137–1149

Cushman SA, Macdonald EA, Landguth EL, Malhi Y, Macdonald DW (2017) Multiple-scale prediction of forest loss risk across Borneo. Landsc Ecol 32:1581–1598

Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ (2007) Random Forests for classification in ecology. Ecology 88:2783–2792

Davis CL, Rich LN, Farris ZJ, Kelly MJ, Di Bitetti MS, Di BY, Albanesi S, Farhadinia MS, Gholikhani N, Hamel S, Harmsen BJ, Wultsch C, Kane MD, Martins Q, Murphy AJ, Steenweg R, Sunarto S, Taktehrani A, Thapa K, Tucker JM, Whittington J, Widodo FA, Yoccoz NG, Miller DAW (2018) Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide. Ecol Lett 21:1401–1412

de la Torre JA, Rivero M (2019) Insights of the movements of the Jaguar in the tropical forests of Southern Mexico. In: Reyna-Hurtado R, Chapman C (eds) Movement ecology of neotropical forest mammals. Springer, New York, pp 217–241

de la Torre JA, Núñez JM, Medellín RA (2017) Habitat availability and connectivity for jaguars (Panthera onca) in the Southern Mayan Forest: conservation priorities for a fragmented landscape. Biol Conserv 206:270–282

Duro DC, Franklin SE, Dubé MG (2012) Multi-scale object-based image analysis and feature selection of multi-sensor earth observation imagery using random forests. Int J Remote Sens 33:4502–4526

Elliot NB, Cushman SA, Loveridge AJ, Mtare G, Macdonald DW (2014) Movements vary according to dispersal stage, group size, and rainfall: the case of the African lion. Ecology 95:2860–2869

Espinosa S, Celis G, Branch LC (2018) When roads appear jaguars decline: Increased access to an Amazonian wilderness area reduces potential for jaguar conservation. PLoS ONE 13:e0189740

Evans JS, Cushman SA (2009) Gradient modeling of conifer species using Random Forests. Landsc Ecol 24:673–683

Evans JS, Murphy MA, Holden ZA, Cushman SA (2011) Modeling species distribution and change using Random Forest. In: Drew AC, Wiersma Y, Huettmann F (eds) Predictive species and habitat modeling in landscape ecology. Springer, New York, pp 139–159

Evans JS, Murphy MA (2018) Package 'rfUtilities': R package version 2.1–3. https://cran.r-project.org/package=rfUtilities. Accessed 15 Dec 2019

Evans JS, Oakleaf J, Cushman SA, Theobald DM (2014) An ArcGIS toolbox for surface gradient and geomorphometric modeling. https://evansmurphy.wixsite.com/evansspatial/arcgis-gradient-metrics-toolbox. Accessed 15 Dec 2019

Farrell A, Wang G, Rush SA, Martin JA, Belant JL, Butler AB, Godwin D (2019) Machine learning of large-scale spatial distributions of wild turkeys with high-dimensional environmental data. Ecol Evol 9:5938–5949

Foster RJ, Harmsen BJ, Doncaster CP (2010) Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. Biotropica 42:724–731

Foster RJ, Harmsen BJ, Doncaster CP (2008) The ecology of jaguars (Panthera onca) in a human-influenced landscape. Dissertation, University of Southampton

Guerisoli MDLM, Caruso N, Luengos Vidal EM, Lucherini M (2019) Habitat use and activity patterns of Puma concolor in a human-dominated landscape of central Argentina. J Mammal 100:202–211

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Modell 135:147–186

Guisan A, Lehmann A, Ferrier S, Austin M, Overton JMC, Aspinall R, Hastie T (2006) Making better biogeographical predictions of species' distributions. J Appl Ecol 43:386–392

Hansen MC, Stehman SV, Potapov PV (2010) Quantification of global gross forest cover loss. Proc Natl Acad Sci USA 107:8650–8655

Hearn AJ, Cushman SA, Ross J, Goossens B, Hunter LTB, Macdonald DW (2018) Spatio-temporal ecology of sympatric felids on Borneo. Evidence for resource partitioning? PLoS ONE 13:1–25

Horning N (2010) Random Forests: an algorithm for image classification and generation of continuous fields data sets. In: Proceedings of the international conference on geoinformatics for spatial infrastructure development in Earth and Allied Sciences. Osaka, Japan, vol 911, pp 1–6

Ibáñez R, Condit R, Angehr G, Aguilar S, García T, Martínez R, Sanjur A, Stallard R, Wright SJ, Rand AS, Heckadon S (2002) An ecosystem report on the Panama Canal: monitoring the status of the forest communities and the watershed. Environ Monit Assess 80:65–95

Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? Global Ecol Biogeogr 24:52–63

Jędrzejewski W, Robinson HS, Abarca M, Zeller KA, Velasquez G, Paemelaere EAD, Goldberg JF, Payan E, Hoogesteijn R, Boede EO, Schmidt K, Lampo M, Viloria ÁL, Carreño R, Robinson N, Lukacs PM, Nowak JJ, Salom-Pérez R, Castañeda F, Boron V, Quigley H (2018) Estimating large carnivore populations at global scale based on spatial predictions of density and distribution—application to the jaguar (Panthera onca). PLoS ONE 13:1–25

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Kaszta Ż, Cushman SA, Slotow R (2021) Temporal non-stationarity of path-selection movement models and connectivity: an example of African Elephants in Kruger National Park. Front Ecol Evol 9:553263

Nowell K, Jackson P (eds) (1996) Wildcats: status survey and conservation action plan. IUCN/SSC Cat Specialist Group, IUCN, Gland

Laforge MP, Brook RK, van Beest FM, Bayne EM, McLoughlin PD (2015) Grain-dependent functional responses in habitat selection. Landsc Ecol 31:855

Landis JR, Koch GG (1977) The measurement of observer agreement for categorical data. Biometrics 33:159–174

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Liaw A, Wiener M (2002) Classification and regression by Random Forest. R News 2:18–22

Macdonald DW, Bothwell HM, Hearn AJ, Cheyne SM, Haidir I, Hunter LT, Kaszta Ż, Linkie M, Macdonald EA, Ross J, Cushman SA (2018) Multi-scale habitat selection modeling identifies threats and conservation opportunities for the Sunda clouded leopard (Neofelis diardi). Biol Conserv 227:92–103

Magioli M, Moreira MZ, Ferraz KMB, Miotto RA, de Camargo PB, Rodrigues MG, da Silva Canhoto MC, Setz EF (2014) Stable isotope evidence of Puma concolor (Felidae) feeding patterns in agricultural landscapes in southeastern Brazil. Biotropica 46:451–460

Magioli M, Moreira MZ, Fonseca RCB, Ribeiro MC, Rodrigues MG, de Barros KMPM (2019) Human-modified landscapes alter mammal resource and habitat use and trophic structure. Proc Natl Acad Sci USA 116:18466–18472

Mateo Sánchez MC, Cushman SA, Saura S (2014) Scale dependence in habitat selection: the case of the endangered brown bear (Ursus arctos) in the Cantabrian Range (NW Spain). Int J Geogr Inf Sci 28:1531–1546

McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA (2016) Multi-scale habitat selection modeling: a review and outlook. Landsc Ecol 31:1161–1175

Mi C, Huettmann F, Guo Y, Han X, Wen L (2017) Why choose Random Forest to predict rare species distribution with few samples in large undersampled areas? Three Asian crane species models provide supporting evidence. PeerJ. https://doi.org/10.7717/peerj.2849

Morato RG, Stabach JA, Fleming CH, Calabrese JM, De Paula RC, Ferraz KMPM, Kantek DLZ, Miyazaki SS, Pereira TDC, Araujo GR, Paviolo A, De Angelo C, Di Bitetti MS, Cruz P, Lima F, Cullen L, Sana DA, Ramalho EE, Carvalho MM, Soares FHS, Zimbres B, Silva MX, Moraes MDF, Vogliotti A, May JA, Haberfeld M, Rampim L, Sartorello L, Ribeiro MC, Leimgruber P (2016) Space use and movement of a neotropical top predator: the endangered jaguar. PLoS ONE 11:1–17

Myers CW (1969) The ecological geography of cloud forest in Panama. The American Museum of Natural History, New York

Nuñez-Perez R, Miller B (2019) Movements and home range of jaguars (Panthera onca) and mountain lions (Puma concolor) in a tropical dry forest of western Mexico. In: Reyna-Hurtado R, Chapman CA (eds) Movement ecology of neotropical forest mammals. Springer, New York, pp 243–262

Palomares F, Fernández N, Roques S, Chávez C, Silveira L, Keller C, Adrados B (2016) Fine-scale habitat segregation between two ecologically similar top predators. PLoS ONE 11:1–16

Pearson RG, Dawson TP, Liu C (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography 27:285–298

Puissant A, Rougier S, Stumpf A (2014) Object-oriented mapping of urban trees using Random Forest classifiers. Int J Appl Earth Obs Geoinf 26:235–245

Rabinowitz A, Zeller KA (2010) A range-wide model of landscape connectivity and conservation for the jaguar, panthera onca. Biol Conserv 143:939–945

Rettie WJ, Messier F (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466–478

Rostro-García S, Tharchen L, Abade L, Astaras C, Cushman SA, Macdonald DW (2016) Scale dependence of felid predation risk: identifying predictors of livestock kills by tiger and leopard in Bhutan. Landsc Ecol 31:1277–1298

Santos F, Carbone C, Wearn OR, Rowcliffe JM, Espinosa S, Moreira MG, Ahumada JA, Gonçalves ALS, Trevelin LC, Alvarez-Loayza P, Spironello WR, Jansen PA, Juen L, Peres CA (2019) Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. PLoS ONE 14:1–23

Schaller GB, Crawshaw PG Jr (1980) Movement patterns of jaguar. Biotropica 12:161–168

Scognamillo D, Maxit IE, Sunquist M, Polisar J (2003) Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. J Zool 259:269–279

Shirk AJ, Raphael MG, Cushman SA (2014) Spatiotemporal variation in resource selection: insights from the American marten (*Martes americana*). Ecol Appl 24:1434–1444

Short Bull RA, Cushman SA, Mace R, Chilton T, Kendall KC, Landguth EL, Schwartz MK, McKelvey K, Allendorf FW, Luikart G (2011) Why replication is important in landscape genetics: American black bear in the Rocky Mountains. Mol Ecol 20:1092–1107

Silveira L (2004) Ecologia comparada e conservacão da onca-pintada (*Panthera onca*) e onca-parda (*Puma concolor*), no Cerrado e Pantanal. Dissertation, Universidade de Brasília

Smith A (2010) Image segmentation scale parameter optimization and land cover classification using the Random Forest algorithm. J Spat Sci 55(1):69–79

Sollmann R, Furtado MM, Hofer H, Jácomo ATA, Tôrres NM, Silveira L (2012) Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. Mamm Biol 77:41–46

Stehli FG, Webb SD (1985) The great American biotic interchange. Topics in geobiology. Plenum Press, New York

Sunquist M, Sunquist F (2002) Wild cats of the world. The University of Chicago Press, London

Thompson CM, McGarigal K (2002) The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). Landsc Ecol 17:569–586

Timm BC, McGarigal K, Cushman SA, Ganey JL (2016) Multi-scale Mexican spotted owl (Strix occidentalis lucida) nest/roost habitat selection in Arizona and a comparison with single-scale modeling results. Landsc Ecol 31:1209–1225

Vergara M, Cushman SA, Urra F, Ruiz-González A (2016) Shaken but not stirred: multiscale habitat suitability modeling of sympatric marten species (*Martes martes* and *Martes foina*) in the northern Iberian Peninsula. Landsc Ecol 31:1241–1260

Wan HY, McGarigal K, Ganey JL, Lauret V, Timm BC, Cushman SA (2017) Meta-replication reveals nonstationarity in multi-scale habitat selection of Mexican Spotted Owl. Condor 119:641–658

Wan HY, Cushman SA, Ganey JL (2018) Habitat fragmentation reduces genetic diversity and connectivity of the mexican spotted owl: a simulation study using empirical resistance models. Genes. https://doi.org/10.3390/genes9080403

Wan HY, Cushman SA, Ganey JL (2019) Improving habitat and connectivity model predictions with multi-scale resource selection functions from two geographic areas. Landsc Ecol 34:503–519

Wasserman TN, Cushman SA, Wallin DO, Hayden J (2012) Multi scale habitat relationships of martes americana in northern Idaho, U.S.A. USDA For Serv-Res Pap RMRS-RP 1–21

Weir JT, Bermingham E, Schluter D (2009) The great American biotic interchange in birds. Proc Natl Acad Sci USA 106:21737–21742

Wheatley M, Johnson C (2009) Factors limiting our understanding of ecological scale. Ecol Complex 6:150–159

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397

Woodburne MO, Cione AL, Tonni EP (2006) Central American provincialism and the Great American Biotic Interchange. In: Carranza-Castañeda Ó, Lindsay EH (eds) Advances in late Tertiary vertebrate paleontology in Mexico and the Great American Biotic Interchange: Universidad, vol 4. Nacional Autónoma de México, Instituto de Geología and Centro de Geociencias, Publicación Especial, pp 73–101

Zeller KA, McGarigal K, Beier P, Cushman SA, Vickers TW, Boyce WM (2014) Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study. Landsc Ecol 29:541–557

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 12:1–20