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# Landscape feature-based permeability models relate to puma occurrence

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## HIGHLIGHTS

- Landscape permeability estimates based on roads and patch size relate to puma occurrence.
- Pumas readily used low-density residential areas.
- Pumas rarely used the most heavily urbanized areas or the least disturbed steeper sloped terrain.
- Landscape permeability estimates support planning where species information is unavailable.
- Permeability models may be the best approach to habitat connectivity in the absence of focal species.

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## ABSTRACT

Habitat fragmentation in human-dominated landscapes is seen as a major threat to biodiversity persistence. Nearly all corridor conservation plans designed to restore habitat connectivity are based on modeled data, and are rarely tested with empirical field data. Here we describe landscape permeability models derived from an estimated linear relationship between specific landscape features related to human land use (e.g. traffic volume, housing density) and bird and mesocarnivore detection levels from empirical field studies. We compare these model estimates with existing occurrence data for pumas (*Puma concolor*), a generalist predator commonly used as a focal species for connectivity analysis, in the Santa Cruz Mountains. Our results show that pumas were observed to readily use moderately disturbed habitats, and rarely were detected in the most heavily disturbed areas. This comparison of a more generic connectivity model estimate with animal field observations shows that while generic models can be useful for corridor designs in highly disturbed environments they may be less useful in moderately impacted rural to semi-natural landscapes, where more detailed studies of species behavior may be required to delineate functional corridors. Mapping the level of landscape permeability that surrounds the built environment, as measured by distance to roads and housing density, offers a spatially explicit way to identify areas important wildlife movement. This approach provides a tool to help managers and land-use planners prioritize habitat corridors for biodiversity conservation across fragmented landscapes.


## 1. Introduction

One of the primary threats to biodiversity is human-induced habitat fragmentation (IUCN, 2013; Tilman et al., 2001), which is on the rise worldwide (Butchart et al., 2010; Nilsson, Reidy, Dynesius, & Revenga, 2005; Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). A fragmented landscape is characterized by patches of natural habitat surrounded by a matrix of human-modified land cover (McIntyre & Hobbs, 1999). Protection of habitat connectivity is crucial for biodiversity conservation to facilitate movement through the matrix (Bennett, 1999), especially for wide-ranging mammalian carnivores (Crooks, Burdett, Theobald, Rondinini, & Boitani, 2011; Hilty, Lidicker, & Merenlender, 2006). Specifically, to conserve biodiversity we must identify and preserve core habitat patches supporting the persistence of species assemblages and ecosystems, and ensure connectivity among such patches with habitat linkages and/or a permeable matrix (Crooks et al., 2011; Noss, 2001).

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Increasingly, habitat corridors are being planned and established to mitigate habitat fragmentation (Hilty et al., 2006) at multiple scales. For example, large-scale projects focusing on entire ecosystems are underway to connect forest communities from southern México into Panamá (Kaiser, 2001) and linking the Yellowstone area in Wyoming north to Alaska (Walker & Craighead, 1998). Similarly, local-scale projects to protect wildlife movement are happening worldwide (Klar et al., 2012; Underwood, Francis, & Gerber, 2011). Connectivity endeavors are often custom projects that depend upon species- and landscape-specific information (LaRue & Nielsen, 2008), a practice that is expensive and time-consuming. Yet, land use and conservation planners often need connectivity assessment methods that can be rapidly developed and adapted into local and regional planning (Huber, Shilling, Thorne, & Greco, 2012).

Connectivity metrics for biodiversity conservation differ in data requirements and informational yield across a spectrum that ranges from strictly structural connectivity at one extreme and biologically-informed functional connectivity at the other (Rayfield, Fortin, & Fall, 2011; Rudnick et al., 2012). Structural connectivity is derived from landscape attributes such as the shape, size, and configuration of habitat patches, but does not account for animal dispersal ability. This approach requires less input data and generates relatively crude estimates of connectivity (Calabrese & Fagan, 2004). Similarly, simple estimates of "naturalness levels" have been used to coarsely model landscape permeability across the entire United States (Theobald, Reed, Fields, & Soulé, 2012). On the other hand, functional connectivity is a measure of the ability of organisms to move among patches of suitable habitat in a fragmented landscape (Fahrig, 2003; Hilty et al., 2006; Taylor, Fahrig, Henein, & Merriam, 1993). Ideally, measures of functional connectivity are derived from actual data about landscape composition, habitat use, and movement by wildlife. Such detailed data is uncommon at the landscape level because it is costly to collect.

When empirical field data on species movement are unavailable, connectivity estimates can be derived from mathematical models. Models may be based on empirical studies of species' abundance or occurrence among different land cover types, or on expert opinion of species' habitat associations (Rocchini et al., 2011). Given the major influence the matrix has on connectivity among habitat fragments (Ricketts, 2001), several models based on matrix connectivity have been developed including habitat resistance (friction; Joly, Morand, & Cohas, 2003; Ray, Lehmann, & Joly, 2002), least-cost paths (Adriaensen et al., 2003), circuit theory (McRae, Dickson, Keitt, & Shah, 2008), habitat permeability (Merenlender & Feirer, 2011, report; Theobald et al., 2012), and linkage designs (Beier & Brost, 2010).

Here we describe landscape permeability models derived from an estimated statistical relationship between specific landscape features related to the built environment and species detections from empirical studies (Forman & Deblinger, 1998; Merenlender, Reed, & Heise, 2009; Reed, 2007). Permeability models are an extension of the resistance concept (Ray et al., 2002); model output often is in the form of a grid-based map with a value assigned to each cell that represents its permeability to an organism's movement. The permeability models were developed for linkage analysis by the Santa Cruz Land Trust (Merenlender & Feirer, 2011) and designed to make biologically informed approximations of community assemblage response to habitat quality (Metzger & Décamps, 1997). The built environment, especially roads, and urban development can reduce the ability for wildlife to move across the landscape (Fu, Liu, Degloria, Dong, & Beazley, 2010; Tannier, Foltête, & Girardet, 2012). Santa Cruz County, California, harbors some of the world's most majestic redwood and mixed confer coastal forestlands; however, residential development is wide spread at urban to exurban densities. The Santa Cruz Land Trust and other environmental organizations in the area are actively trying to conserve open space and biodiversity (Press, Doak, & Steinberg, 1996). Conservation and land use planners in the region face challenges commonly encountered in areas with sprawling development, including how to maintain wildlife movement across an increasingly developed landscape (Girvetz, Thorne, Berry, & Jaeger, 2008). To this end, there is a need for methods that are readily available, straightforward, and spatially explicit to examine landscape permeability and help land use planners prioritize land conservation.

We compare model estimates with occurrence data for pumas (*Puma concolor*), a generalist predator commonly used as a focal species for connectivity analysis (Beier, 2009; Cardillo et al., 2005; Crooks, 2002; Terborgh et al., 2001), in the Santa Cruz Mountains. Pumas are the largest predator in the study area, and are known to travel long distances (Dickson & Beier, 2002). The question guiding our analysis is: How well do our model estimates of landscape permeability derived from simplified, biologically-informed connectivity models compare with actual occurrence of a generalist predator across a gradient of land use?

## 2. Methods

### 2.1. Study area

The Santa Cruz Mountain range is in central California, adjacent to the San Andreas Fault (122° 7′ to 121° 50′ W, 37° 21′ to 36° 53′ N). Forming a ridge along the San Francisco peninsula, the mountains separate the Pacific Ocean from the Santa Clara Valley. The study area (217,375 ha) is an island of relatively undeveloped land within the Santa Cruz Mountains, situated between the Pacific Ocean on the west, and the metropolitan centers of San Francisco, San Jose, and Santa Cruz to the north, east, and south, respectively. The four primary land cover types within the study area were (1) forest and woodland, (2) shrubland and grassland, (3) agricultural land, and (4) land that is developed or otherwise of human use (US Geological Survey, Gap Analysis Program, 2011). The study area was bounded to represent assumed puma occurrence in the region (Fig. 1).

Our study area faces encroachment by development as the populations of surrounding San Francisco, Santa Clara, and Santa Cruz counties steadily increase. The annual population growth for each county between 1980 and 2008 ranged between 0.7% and 1.29% (U.S. Census Bureau, Population Division, 2011). The study area was surrounded and intersected by highways, such as California State Route 17 that bisects the study area and connects the cities of San Jose and Santa Cruz.

Climate in the Santa Cruz Mountains is Mediterranean with mild, wet winters and cool, dry summers. The average summer and winter temperatures were 20 °C and 10 °C, respectively. Heavy summer fog provided moisture to the western, ocean-facing part of the range, creating a cool coastal habitat supporting coast redwoods (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*). At higher elevations and on sunny south slopes, the microclimate is warm and dry with drought-resistant chaparral vegetation including manzanita (*Arctostaphylos* spp.) and California scrub oak (*Quercus berberidifolia*).

### 2.2. Landscape permeability maps

We used regression models derived from mesocarnivore and bird assemblage response to human-modified land cover and landscape configuration as inputs to construct potential permeability maps (Fig. 2). For each permeability map, we used as input a regression model derived these two indices of habitat fragmentation: distance to roads ($y_{\mathrm{ROADS}}$; Forman & Deblinger, 1998) and median patch size ($y_{\mathrm{PATCH}}$; Reed, 2007). We calculated each

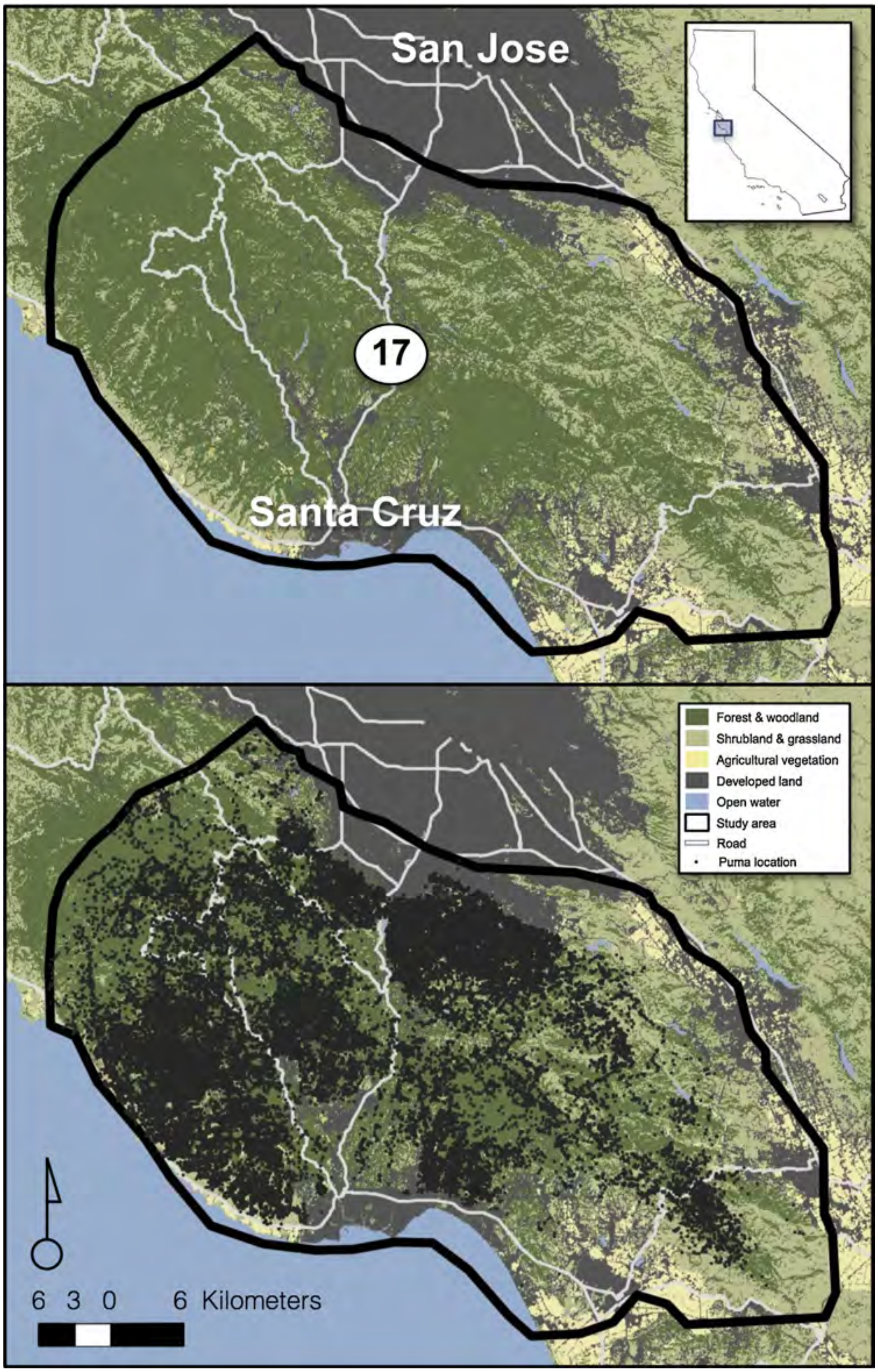


**Fig. 1.** (A) A map of the study area depicting the major land types in the Santa Cruz Mountains in California, USA: forest/woodland, shrubland/grassland, agricultural land, and developed land. Our study area was a 217,375 ha island of relatively undeveloped land within the Santa Cruz Mountains, situated between the Pacific Ocean on the west, and metropolitan centers of San Francisco, San Jose, and Santa Cruz to the north, east, and south, respectively. (B) The study area overlaid with the 115,384 puma points we sampled from 2008 to 2013. Coordinates for center of study area are: (37.106, −121.946).

permeability map with ArcGIS 9.3.1 software (ESRI, Redlands, CA, USA). We applied each regression model to create a map using both the permeability value and the geographical position and orientation of all relevant landscape elements in the study area (per Safner et al., 2011). All permeability values ranged between 0.0 and 1.0 with a cell size of 30 m × 30 m (900 m$^2$).

*2.2.1. Distance to roads*

There is overwhelming evidence of the effects of roads on natural communities (Fahrig & Rytwinski, 2009), and thus we use distance from road, scaled by traffic volume ($y_{ROADS}$), as an index of animal response to transportation infrastructure. We calculated $y_{ROADS}$ based on empirical data from several prior studies

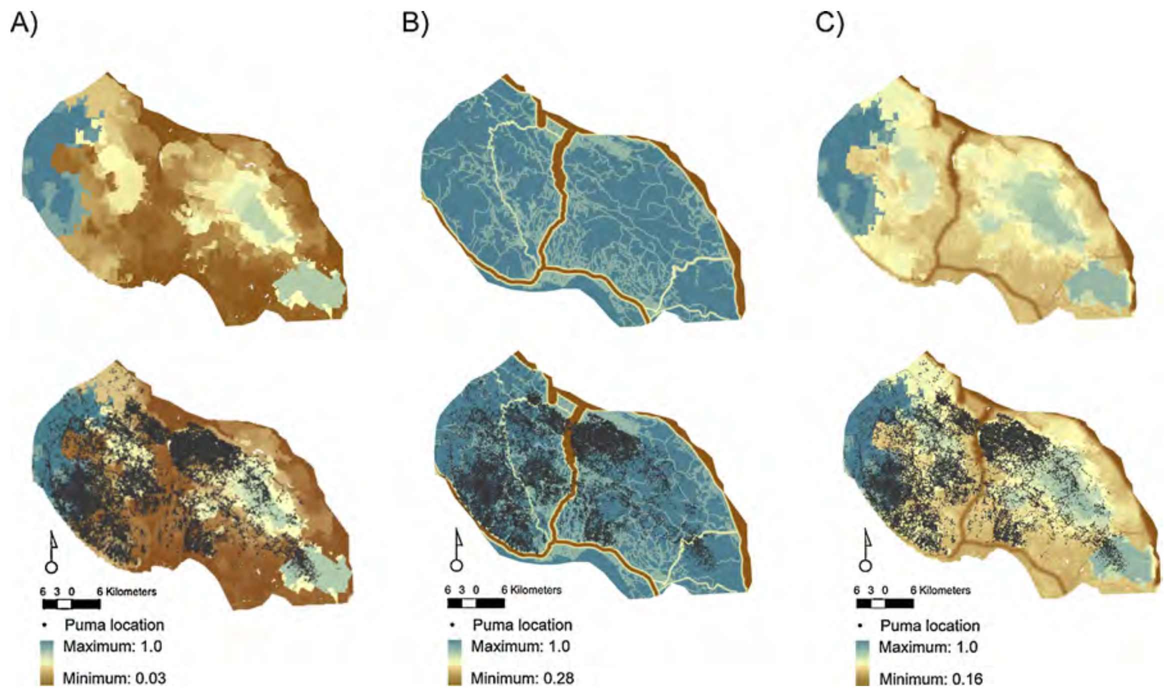


**Fig. 2.** Distribution of permeability values for landscape (above), and with puma points overlaid (below), across the study area. (A) Median patch size layer ($y_{\text{PATCH}}$). (B) Distance to roads layer ($y_{\text{ROADS}}$). (C) Combined distance to roads and median patch size layer ($y_{(\text{PATCH+ROADS})}$).

that evaluated the impact of roads on wildlife (Forman, 2000; Forman & Deblinger, 1998; Reijnen, Foppen, Braak, & Thissen, 1995; Reijnen, Foppen, & Meeuwsen, 1996). Forman and Deblinger (1998) described the correlation between the distance to a road and bird species abundance and diversity; the closer a location is to a road, and the greater the road's traffic level, the larger the road effect, resulting in a corresponding decrease in abundance and diversity of urban avoiding birds. This approach assumes that the maximum magnitude of the road effect and effect-distance are proportional to the volume of traffic along the road.

We applied the effect-distance relationships for sensitive bird species described by Forman and Deblinger (1998) to calculate the maximum effect-distance for each road in the study area as a function of mean traffic volume, measured as annual average daily traffic:

$$x_{\text{ED}} = 0.0126 w_{\text{TV}} + 178.75,$$

where $w_{\text{TV}}$ is the annual average daily traffic volume of the road, and $x_{\text{ED}}$ is the road effect-distance.

We then assumed that the magnitude of effect of any given road would be proportional to the maximum effect and would decline linearly with increasing distance from the road. Thus, the road effect of each cell was calculated using the following equation:

$$y_{\text{ROADS}} = -\left(\frac{1}{\max(x_{\text{ED}})}\right) z_{\text{ROADS}} + \frac{x_{\text{ED}} - \max(x_{\text{ED}})}{\max(x_{\text{ED}}) + 1}$$

where $z_{\text{ROADS}}$ is the Euclidean distance from the nearest road and $y_{\text{ROADS}}$ is the magnitude of the road effect. We calculated the permeability map for $y_{\text{ROADS}}$ with ArcGIS 9.3.1 software using road effect values from $y_{\text{ROADS}}$ and the geographical position and orientation of all relevant landscape elements in the study area (per Safner et al., 2011) (Fig. 2B). The traffic volume data came from the California Department of Transportation (http://traffic-counts.dot.ca.gov). In our study area, the maximum effect-distance $\max(x_{\text{ED}})$ for all roads was 2812 m.

### 2.2.2. Median patch size

We used median patch size ($y_{\text{PATCH}}$) as a landscape-scale, area-informed index of habitat integrity calculated using the contiguity and relative size of proximate habitat patches. There is increasing recognition that area-informed metrics are useful to explain variation in wildlife abundances and movement capacity (Magle, Theobald, & Crooks, 2008) and perform well in analyses of landscape connectivity (Bender, Tischendorf, & Fahrig, 2003). We defined a patch as a contiguous area of habitat with natural vegetation cover and whose land uses were compatible with the establishment of mesocarnivore home ranges, based on information from prior space use studies. The model for $y_{\text{PATCH}}$ was derived from a study (Reed, 2007) investigating the correlation between patch size and mesocarnivore (e.g. coyote, bobcat, gray fox) occurrence in northern California, which found that the frequency of mesocarnivore detections increased with the size and contiguity of adjacent patches. $y_{\text{PATCH}}$ was calculated as the median area of habitat patches within a fixed buffer radius. In exploratory analyses, Reed (2007) found that $y_{\text{PATCH}}$ measured at a buffer distance of 2500 m explained the most variation in detections of the greatest number of mammalian carnivores. This work also revealed 'median patch size' to be a better predictor than buffered radius indices or proximity metrics (Reed, 2007).

Per Reed (2007), we calculated $y_{\text{PATCH}}$ using the equation:

$$y_{\text{PATCH}} = \frac{0.2356(x_{\text{PATCH}})^{1/2} + 1.385}{\max(y_{\text{PATCH}})}$$

where $x_{\text{PATCH}}$ is the median patch size in hectares (ha) within a 2500 m radius buffer, and $y_{\text{PATCH}}$ is the effect of habitat integrity on landscape resistance, measured as the density of native mesocarnivore detections along a survey transect.

As input data for $y_{\text{PATCH}}$, we used a map of terrestrial vegetation cover from existing land cover data (Farmland Mapping and Monitoring Program, 2008) and removing roads (Research and Innovative Technology Administration, Bureau of Transportation Statistics, 2011), mines and quarries, water bodies, and all land parcels less than 2 ha. Selecting which patches should be analyzed as part of a habitat connectivity network is very difficult in a landscape where privately owned wild lands exist outside the protected areas, as is the case in Santa Cruz County. We began by selecting the larger patches in the landscape, which we defined to be any patch greater than 250 acres (101 ha). In addition to these larger patches, smaller patches found in the more fragmented parts of the study area were included if they were the largest patch within a fixed kernel distance ranging between 1 km from any given point in the landscape – a range of median dispersal distances expected for terrestrial vertebrates found in the area. We used the $y_{PATCH}$ equation to calculate the patch size effect for each grid cell in the permeability map (Fig. 2A).

### 2.3. Puma GPS data

We used location point data for 30 ($F$ = 15, $M$ = 15) pumas (*P. concolor*) collected between October 2008 and January 2013 (Wilmers et al., 2013), for a total of 115,384 georeferenced points overall. We visualized puma point location data in the ArcGIS 9.3.1 Geographic Information System (GIS) using the WGS1984 geographic coordinate system and an Albers projection. The Institutional Animal Care and Use Committee at UC Santa Cruz approved all animal-handling procedures (Wilmc1101). Roughly 53% of the puma occurrence locations in the study area were in forest or woodland, 20% in shrubland or grassland, 20% in developed land, and 4% in agricultural land (US Geological Survey, Gap Analysis Program, 2011).

### 2.4. Data analysis

To evaluate whether puma occurrence corresponded with landscape permeability, we compared expected land use with observed landscape use by pumas. We calculated the relative frequency of landscape permeability values across the entire study area and the relative frequency of landscape permeability values for only the puma points. We made these comparisons for $y_{ROADS}$, $y_{PATCH}$, and $y_{ROADS+PATCH}$ to assess the relative effect of each factor in influencing in habitat use. To determine the level of difference between the puma points and all the points in the study area we created a frequency distribution table for each data set, calculated an odds ratio between the two data sets, and used a Monte Carlo simulation method to generate a confidence interval estimate.

To determine the relative frequency of landscape permeability values, we extracted the cell values for the 2.37 M cells, created a frequency distribution table with 20 intervals (from 0.0 to 1.0 in 0.05 landscape permeability unit increments), and calculated the abundance of expected points ($A_E$) by interval. We repeated this calculation for each permeability map to create the relative distributions of landscape permeability for each regression model with which to compare with puma occurrence. We defined $A_E$ as:

$$A_E = \frac{\#\,\text{points in interval}}{2,372,749}$$

To determine the relative frequency of the landscape permeability values for only the puma points, we extracted the permeability values at all puma point locations ($N$ = 115,384), created a frequency distribution table with 20 intervals (from 0.0 to 1.0 in 0.05 landscape permeability unit increments) for the 115,384 values for the puma, and calculated the abundance of observed points ($A_O$) by interval. We repeated this calculation for each permeability map to summarize the relative distribution of permeability values for puma for each regression model. We defined $A_O$ as:

$$A_O = \frac{\#\,\text{points in interval}}{115,384}$$

To determine the level of difference between the puma points and all the points in the study area we calculated an odds ratio between the expected ($A_E$) and observed ($A_O$) abundance (Bland & Altman, 2000). To calculate the odds ratio (OR), we compared the distribution of landscape values (E) with that of puma point locations (O) for each regression model. We calculated odds (ODDS) of occurrence by interval for $A_E$ ($ODDS_E$) and $A_O$ ($ODDS_O$) using the following two equations:

$$ODDS_E = \frac{A_E}{(1 - A_E)}$$

$$ODDS_O = \frac{A_O}{(1 - A_O)}$$

Next, we calculated the odds ratio (OR) by interval between $A_E$ and $A_O$ using the following equation:

$$OR = \frac{ODDS_O}{ODDS_E}$$

Finally, we transformed OR using a log 10 transformation and plotted the distribution. When there was no difference between $A_E$ and $A_O$, OR values were between 1 and 0; when $A_E > A_O$, OR values were <1 (negative); and when $A_E < A_O$, OR values were >1 (positive).

To approximate a confidence interval for distribution of permeability values in the study area we used a Monte Carlo simulation approach (Manly, 2007) with 1000 iterations to extract landscape permeability values for 115,384 random grid locations from each permeability map. We separated the randomly subsampled points in a similar fashion (20 intervals from 0.0 to 1.0) and calculated the abundance of subsampled points ($A_S$) by interval. We defined $A_S$ as:

$$A_S = \frac{\#\text{points in interval}}{115,384}$$

We visualized the results as a boxplot and used the boxplot as a confidence interval estimate.

Examining the location data at the population level could potentially mask sampling bias, such as the number of data points per puma or where pumas had been caught for collaring. Each puma had variable detection times – ranging from once per day to once every 15 min – and differing numbers of total collection days. The median collection time across all puma detections was once every 3.95 h (once every 237 min). The data was not corrected for autocorrelation, nor standardized for collection time in order to take advantage of all the known detections. Behaviorally correlated features in the environment may be overrepresented in the distribution of puma point locations – a known issue for home range or utilization distribution estimates for individual animals (Swihart & Slade, 1985). However there is no a priori reason to expect a bias in levels of permeability and higher number of points collected. To explore the importance of study area delineation and potential false absences on the final results, we compared the study area at two different geographic extents: (1) the full study area and (2) a constrained study area cropped closely around the puma occurrence data.

The odds ratio results showed distinct differences between the availability of permeability values and the detection of pumas for all three models (Fig. 3).

## 3. Results

We compared the puma occurrence data with each of the three models independently as well as in various multi-model combinations. Our results show much of the landscapes in the Santa Cruz Mountains is of intermediate permeability for $y_{PATCH}$, and high permeability for $y_{ROADS}$. Specifically, 88.50% of the study area had a landscape permeability value for $y_{ROADS}$ between 0.9 and 1.0. For $y_{PATCH}$, 87.90% of the study area had a landscape permeability value

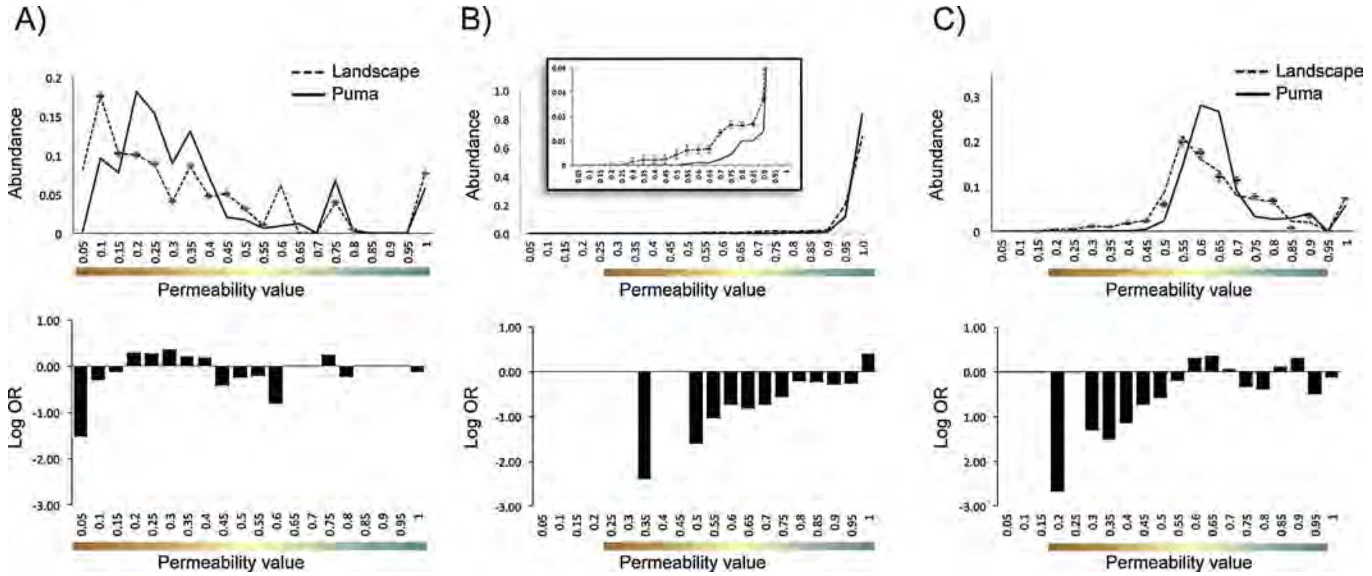


**Fig. 3.** Relative abundance of permeability values for landscape and puma points across the study area, with Monte Carlo results visualized as a confidence interval estimate above, and log OR results below. (A) Median patch size layer ($y_{PATCH}$). (B) Distance to roads layer ($y_{ROADS}$), with inset showing detailed abundance for landscape permeability values <0.95. (C) Combined distance to roads and median patch size layer ($y_{(PATCH+ROADS)}$).

for $y_{PATCH}$ between 0.0 and 0.6, corresponding to a median patch size of 0–21.21 ha (Fig. 3). The distribution of puma location points was similar, with 86.05% of puma locations found at points with a $y_{PATCH}$ permeability value between 0.0 and 0.6, and 97.03% of puma locations found at points with a $y_{ROADS}$ permeability value between 0.9 and 1.0 (Fig. 3).

The log OR distribution for the lowest $y_{PATCH}$ permeability values showed a distinct difference between the availability of habitat with very low permeability values and the distribution of puma detections (interval 0–0.15; average log OR = −0.66). However, for habitat with intermediate and high permeability values, log OR was alternately positive and negative (interval 0.2–1.0). Specifically, log OR was positive between 0.2 and 0.4, and negative between 0.4 and 0.6. There were no cells in the study area with a value between 0.65 and 0.7 nor between 0.85 and 0.95.

For $y_{ROADS}$, the log OR interval between the minimum landscape permeability value of 0.28–0.95 was negative (average log OR = −0.82). Log OR was most negative for the most disturbed habitat (interval 0.28–0.35; log OR = −2.40). It was only for the least disturbed regions that log OR was positive (interval 0.95–1.0; log OR = 0.39).

As expected of a combined model, the log OR distribution for the lowest $y_{ROADS+PATCH}$ permeability values was similar to the trends shown for $y_{PATCH}$ and $y_{ROADS}$. The log OR values were negative for low permeability habitat (interval 0.16–0.55; average log OR = −1.17), and was smallest for the most disturbed regions (interval 0.16–0.2; log OR = −2.67). As with the $y_{PATCH}$ model, log OR alternated between positive and negative values for habitat with intermediate and high permeability values (interval 0.55–1.0). Specifically, log OR was positive between 0.55–0.6 and 0.85–0.9, and negative between 0.75–0.8 and 0.95–1.0.

## 4. Discussion

By measuring landscape permeability associated with human development, this research offers an easy to calculate spatially explicit method to examine landscape permeability that can help land-use planners prioritize habitat corridors for improved wildlife movement.

Pumas in the Santa Cruz Mountains were not found in areas with low permeability scores as compared with the availability of this type of disturbed habitat, and they were found in landscapes with moderate to high permeability in proportion to its availability. Pumas used areas with estimated moderate landscape disturbance, in the form of nearby low traffic volume roads, as well as land with intermediate median habitat patch size. There appeared to be a possible threshold beyond which pumas begin avoiding disturbed landscapes, equivalent to a permeability score of ≤0.2 for $y_{PATCH}$ and ≤0.90 for $y_{ROADS}$ (Fig. 3).

Pumas were not commonly observed in highly disturbed areas far from large core habitat patches or adjacent to major roads. California pumas are known to more frequently use areas farther away from paved roads (Dickson & Beier, 2002) and other carnivores have shown aversion to roads such as the wolf which is know to respond negatively to increased levels of human activity on roads (Lesmerises, Dussault, & St-Laurent, 2013). However, they readily used moderately disturbed habitat with mid-range permeability scores. The fact that pumas roam and feed in and near rural residential developments is well documented in Alberta (Knopff, Knopff, Boyce, & Clair, 2014) and California (Burdett et al., 2010; Dickson & Beier, 2002; Wilmers et al., 2013). Pumas may use moderately disturbed areas due to abundance and ease of catching of prey. Forest on a patch edge can provide adequate cover for pumas to stalk prey in adjacent open habitat (Elbroch, Lendrum, Newby, Quigley, & Craighead, 2013; Laundré & Loxterman, 2007). In this sense, habitat patches of medium size could be more amenable to hunting given their ratio of intact habitat to edge. However, because of risks associated with hunting near housing, female pumas living adjacent to humans have decreased prey consumption time and altered hunting patterns (Smith, Wang, & Wilmers, 2015).

Surprisingly, pumas did not preferentially occupy the least disturbed areas close to large core habitat patches or far from major roads. This finding might reflect an avoidance of habitat with steeper slopes. Pumas have been shown to avoid land with steep slopes (Beier, 1995; Dickson & Beier, 2006; Dickson, Jenness, & Beier, 2005), possibly for energetic reasons (Dickson et al., 2005), or to preferentially utilize bottom canyons and gentle terrain where available (Dickson & Beier, 2006). Because human activity tends to decrease on steep slopes, when pumas do travel on steep slopes they travel more closely to houses present there (Wilmers et al., 2013). Slope tends to correlate with high permeability for sites within the Santa Cruz Mountains. For example, 5.6% of $y_{\text{ROADS+PATCH}}$ values over 0.7 in our study area have a slope >50%. Because our study area includes very steep slopes and sheer cliffs, these locations could be the least disturbed because they are topographically unsuitable for development.

Across all models, pumas appear to avoid areas with very low permeability. Species avoidance of habitat with low permeability values may be even stronger for other carnivores, herbivores, and bird species than we observed for pumas. To explore the importance of taxonomic differences between the species under consideration and the modeled species assemblage – such as dissimilar sensitivity (Crooks, 2002) or scale of response to environmental variables – the model predictions could be compared to occurrence data for animals that avoid anthropic development like the gray fox (*U. cinereoargenteus*) (Hilty & Merenlender, 2004) or a migratory songbird (Merenlender, Reed, & Heise, 2009). Such a comparison would likely show a different habitat use pattern than that of a large, generalist carnivore like the puma, and perhaps result in clearer trends between moderate and undisturbed landscapes.

For our analysis, we pooled all data points and examined the location data set as a whole at the population level. All puma observations were taken from contiguous home ranges within the study area and are assumed to represent the entire resident population during the sampling period, although there could have been migrating non-resident individuals in the area that were not collared. Imperfect detection is a known issue with sampling an elusive carnivore like the puma that can negatively bias occupancy estimates (Karanth et al., 2011) and in this case could mean that pumas may be present in the study area that were not detected or collared. The number of individual pumas within the study area was limited and there is inherent selection bias as to the home range location of each individual. For this reason, we pooled the observations rather than analyzing each puma's location points separately. We found no difference between the results from our comparison of the study area delineation, and so we based our conclusions on the entire study area.

Because landscapes are increasingly urban in nature (US: Alig, Kline, & Lichtenstein, 2004; Europe: Antrop, 2004), and becoming more so globally (McDonald, 2008), it is important to identify social–ecological processes and land use patterns – such as patch size and distance to roads – that impact a variety of wildlife in a similar way. The permeability maps were designed to make a general, community-level habitat quality assessment based on linear regression models derived from species assemblages in northern California, developed for linkage analysis as requested by the Land Trust of Santa Cruz County (Merenlender & Feirer, 2011, report). The original linkage exercise for Land Trust of Santa Cruz County was coarse, completed in response to managers' desire for generalized permeability maps of places lacking species data and modeling capacity. In this analysis, we evaluated how community-level habitat permeability maps compared with existing occurrence data for a focal species of conservation concern in the area. To that end, this analysis presents a simple comparison of permeability maps based on land cover and noted responses by entire assemblages of species rather than detailed research on puma habitat selection. See Wilmers et al. (2013) for details about behavioral responses of pumas to human development using mixed effects modeling. Others have shown how the behavioral features of the focal species can change the dynamic permeability of the studied landscape (Dickson, Roemer, McRae, & Rundall, 2013; Stoner et al., 2013) and therefore warrants further study.

Our work shows that biologically-informed, structural permeability models do reflect puma habitat use – and thus functional connectivity – on the ground to some extent. While the puma is an important species of conservation concern, the use of any sole focal species to assess landscape adequacy cannot fully capture the needs of other integral species in the landscape. Instead, this evaluation supports the use of a structural permeability model for conservation planning efforts. For example, this approach was used to identify potential habitat linkages for inclusion in the Conservation Blueprint for Santa Cruz County.

Our models were derived from mesocarnivore and bird species detections from empirical studies, but compared to data set from a large-bodied apex predator often used for connectivity planning (Beier, Vaughan, Conroy, & Quigley, 2006). While our roads model was originally developed for bird community response to traffic volume in a geographically distant environment from our study area, it showed a reasonably strong relationship with the empirical puma data. However, the model's utility may vary by location, environment, and species of interest. We included this response to roads model based on bird community assemblage data, despite obvious differences between the environments and study animals, because this was the best data on traffic impacts on wildlife available when we applied these models.

Although both mesocarnivores and carnivores are predators, their diets differ in terms of prey size and composition (Elbroch et al., 2013; Robinette, Gashwiler, & Morris, 1959). Thus, an evaluation of functional connectivity based on data from a smaller-bodied organism with a correspondingly reduced home range size and distinct diet composition may show different results. Future landscape-level evaluations of habitat permeability could be enhanced by including organisms of differing sizes and from multiple trophic levels (e.g. mesocarnivores, migratory birds).

## 5. Conclusions

The comparison of the permeability model described and the animal field observations shows that a model constructed using information about animal response to human land use can be an informative component for reserve design, land management, and conservation planning. Specifically, landscape planners and conservation organizations should focus on conserving the most permeable core areas and linkages while taking care to avoid landscapes with steep slopes. Steeper areas are also at lower risk for development, and, hence, do not require conservation action.

Land use planners can employ our approach to conservation planning in fragmented landscapes even when species data are unavailable. For example, this research was used to identify potential habitat linkages for inclusion in the Conservation Blueprint for Santa Cruz County. The priority linkages, comprised of the most natural land cover types that facilitate wildlife movement among core natural areas, were identified in the Santa Cruz Mountains Connectivity Report, which is available from the Santa Cruz Land Trust.

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