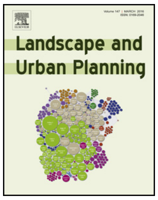
Landscape and Urban Planning 147 (2016) 50–58

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan



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.

ARTICLE INFO

Article history:
Received 28 August 2014
Received in revised form 7 May 2015
Accepted 13 November 2015
Available online 13 December 2015

Keywords:
California
Carnivore
Connectivity
Road ecology
Santa Cruz
Land-use

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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http://dx.doi.org/10.1016/j.landurbplan.2015.11.009

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_{ROADS}; Forman & Deblinger, 1998) and median patch size (y_{PATCH}; Reed, 2007). We calculated each