ELSEVIER

Contents lists available at ScienceDirect

Landscape and Urban Planning



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

Integration of landscape fragmentation analysis into regional planning: A statewide multi-scale case study from California, USA

Evan H. Girvetz^{a,b,*}, James H. Thorne^b, Alison M. Berry^{a,c}, Jochen A.G. Jaeger^{a,d}

^a Road Ecology Center, University of California, One Shields Avenue, Davis, CA 95616, USA

^b Information Center for the Environment, University of California, One Shields Avenue, Davis, CA 95616, USA

^c Department of Plant Sciences, University of California, One Shields Avenue, Davis CA 95616, USA

^d Concordia University, Department of Geography, Planning and Environment, 1455 de Maisonneuve Boulevard West, Suite H1255, Montréal, Quebec, Canada H3G 1M8

ARTICLE INFO

Article history: Received 29 August 2007 Received in revised form 18 December 2007 Accepted 20 February 2008 Available online 2 May 2008

Keywords: Effective mesh size Landscape connectivity Habitat fragmentation Wildlife movement Road ecology Transportation planning

ABSTRACT

Landscape fragmentation due to urban development, transportation infrastructure, and agriculture poses a threat to environmental integrity. There is a need to quantify the level of landscape fragmentation in an ecologically meaningful way for inclusion in planning and decision-making. Effective mesh size $(m_{\rm eff})$ is an ecologically relevant metric that quantifies landscape fragmentation based on the probability that two randomly chosen points in a region are located in the same non-fragmented patch. We investigated variation in $m_{\rm eff}$ measured by transportation districts, municipal counties, and six spatial levels of watersheds within the state of California. Four fragmentation geometries were developed by overlaying highways, roads, urbanized areas, agricultural areas, and natural fragmenting features. Two meet calculation methods were compared: one where planning unit boundaries fragment the landscape (CUT), the other allowing for cross-boundary connections (CBC). The CUT procedure always produced lower $m_{\rm eff}$ values than CBC, with greater differences occurring in smaller planning units, confirming the bias introduced using boundaries with landscape metrics. Calculated metrics values varied from 0 to 20 885 km² across 6994 units in California. Roads contributed the most to fragmentation, while agriculture contributed little, as California's agricultural areas are already heavily fragmented by roads. This paper provides a systematic, quantitative, and intuitive method for transportation, land use and environmental planners to analyze cumulative impacts of multiple fragmenting features across a range of spatial scales within a variety of planning units. This approach could be used for analyzing the impact of future land development scenarios, and integrated into regional planning processes.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Landscape fragmentation due to roads, urbanization, and other human development has major impacts on wildlife, including many species of concern (Forman et al., 2003; Trombulak and Frissell, 2000). These impacts include direct mortality (Mazerolle, 2004; Riley et al., 2003), behavioral changes (Mazerolle et al., 2005), reduced dispersal capacity (Forman and Alexander, 1998), impediment to gene flow (Epps et al., 2005; Riley et al., 2006), disturbance effects such as traffic noise affecting breeding birds (Reijnen and Foppen, 1995; Reijnen et al., 1995), and lack of recolonization of depopulated habitats. With the recognition of these impacts has come a renewed focus on quantifying land-

* Corresponding author. Present address: University of Washington, College of Forest Resources, Box 352100, Seattle, WA 98195-2100, USA. Tel.: +1 206 543 5772; fax: +1 206 543 3254.

E-mail address: girvetz@u.washington.edu (E.H. Girvetz).

scape fragmentation for use in environmental and conservation planning.

Analytical approaches are needed that can quantify habitat fragmentation at multiple spatial scales, and can be easily used by planners. Many measures of landscape fragmentation have been proposed (Gustafson, 1998; McGarigal et al., 2002). Such metrics have evolved from those that simply quantify landscape patterns to metrics that also relate to ecological processes (Li and Wu, 2004). Landscape ecologists consider the identification of relationships between metrics of landscape structure and ecological processes a major current research topic (Turner, 2005; Vos et al., 2001). Although dozens of landscape metrics have been proposed, most fail to correlate with ecological processes (Girvetz et al., 2007; Tischendorf, 2001).

Recently, landscape metrics have been proposed that explicitly incorporate ecological processes into their definitions. One such metric is the effective mesh size, which is an expression of the probability that any two locations in the landscape are connected, i.e., not separated by barriers such as roads (Jaeger, 2000). Effective

^{0169-2046/\$ –} see front matter 0 2008 Elsevier B.V. All rights reserved. doi:10.1016/j.landurbplan.2008.02.007

mesh size can also be interpreted as the average size of the area that an animal placed randomly in the landscape will be able to access without crossing barriers. This metric addresses the ecological process of animal dispersal and can be related to a wide range of animal movement processes. Jaeger (2002) compared effective mesh size with 21 other metrics with regard to their reliability for quantifying landscape fragmentation. He systematically investigated the eight most promising metrics using a set of suitability criteria including: intuitive interpretation, mathematical simplicity, modest data requirements, low sensitivity to small patches, monotonous reaction to different fragmentation phases (Forman, 1995), detection of structural differences, mathematical homogeneity, and additivity. Effective mesh size ranked highest according to these criteria (Jaeger, 2000, 2002).

Landscape fragmentation is caused by many different fragmenting elements. In order to quantify landscape fragmentation, it is first necessary to identify which landscape elements are relevant to the ecological process or organism affected by the fragmentation (Gontier et al., 2006). The specific choice of fragmenting elements defines a so-called "fragmentation geometry". Common fragmenting elements that define fragmentation geometries include, but are not limited to: roads, railroads, areas of urban development, industrial zones, and agricultural fields. Large rivers and other water bodies, and high mountains may also act as barriers to animal movement (Gerlach and Musolf, 2000), and can be included in order to detect the combined barrier effect of the relevant natural and anthropogenic landscape elements.

Landscape metrics must be calculated in relation to defined spatial units (Gulinck and Wagendorp, 2002). Spatial unit boundaries often are based on political boundaries or ecological criteria such as ecoregions and watersheds (Omernik and Bailey, 1997; Padoa-Schioppa et al., 2006). Watershed-based analyses are becoming a standard used by regulatory agencies, such as the United States Federal Highway Administration watershed-based 'Eco-logical' program (Brown, 2006). However, most planning is done using human-defined areas such as counties or transportation districts. Moreover, these reporting units occur at a range of spatial scales, and are often hierarchically organized. For example, in the state of California, the Department of Transportation (Caltrans) districts are formulated along county boundaries, and contain from one to several counties. Thus, counties are nested within Caltrans districts, which are nested within the state of California. Similarly, watersheds are nested hierarchical entities with major watersheds containing multiple sub-watersheds, which themselves nest watersheds at finer spatial scales, and so on (Fig. 1). Accordingly, a multi-scale assessment framework is needed that can analyze both watershed units and administrative units (e.g., transportation planning districts and municipal counties).

The boundaries of reporting units often do not coincide with the location of fragmenting elements in the landscape. Therefore, patches crossing the boundaries of reporting units need to be attributed to the reporting units in some suitable, unambiguous way. This requirement causes a problem in calculating landscape fragmentation metrics, because methods for these metrics often cut habitat patches off at the boundaries of the reporting unit being analyzed (a cut-out procedure). Such analyses produce a potentially biased assessment of habitat fragmentation. This is the case with the original method for calculating the effective mesh size landscape metric (Jaeger, 2000). However, recent advances in landscape metric theory have led to a modified effective mesh size calculation that accounts for cross-boundary connections (Moser et al., 2007).

This paper presents an analysis of the effective mesh size landscape fragmentation metric (m_{eff}) for the entire state of California, USA, using two different procedures for calculating the effective mesh size—the original cutting-out procedure (Jaeger, 2000) and the more recent cross-boundary connection procedure (Moser et al., 2007). The two procedures were compared to evaluate the negative bias introduced by not accounting for cross-planning unit boundary connections, causing a systematically lower calculated m_{eff} value. A user-friendly geographic information system (GIS) tool for calculating the effective mesh size was developed to address relevant questions about the differences among regions and their degree of landscape fragmentation. The ranges and frequency distributions of m_{eff} values were analyzed for various reporting units (planning districts, counties, watersheds) with respect to adding



Fig. 1. Administrative and watershed boundaries used as planning units to calculate effective mesh size for the state of California. Two spatial scales of administrative boundaries are shown on the left: counties (thin grey lines) nested within Caltrans districts (dark lines). Six spatial scales of watershed used in this analysis are shown on the right: hydrologic regions (thick black lines) and hydrologic units (thinner grey lines) zoomed-in to show hydrologic areas (medium thickness grey lines) and hydrologic sub-areas (thin grey lines), and zoomed-in finer to show super-planning watersheds (thinner grey lines) and planning watersheds (dashed lines).

and removing different fragmenting elements such as minor roads, agricultural areas, and natural fragmenting elements.

California is an ideal location to study habitat fragmentation in the context of regional planning because it is a globally ranked biodiversity hotspot and is currently undergoing a rapid increase in human population density with associated development of urban areas and transportation infrastructure. As with many other places in the world, agencies and organizations working in the state of California are actively engaged in regional planning efforts that attempt to resolve conflicts between development and environmental needs. Federal regulations mandate regional planning for threatened and endangered species protection in the form of United States Fish and Wildlife Service administered habitat conservation plans (USFWS, 1996), and provision 6001 of the Federal Highways Administration's SAFETEA-LU program (United States Congress, 2005). Regional planning efforts within the state include the California state Governor's San Joaquin Valley partnership (Schwarzenegger, 2005), the California Transportation Plan, and the California Department of Fish and Game administered natural communities and conservation plans (California State Legislature, 2003). These regional planning efforts frequently require multiagency collaboration. For these efforts to be successful, systematic, quantitative, and intuitive assessment tools are needed, which can be agreed upon by all stakeholders.

2. Methods

2.1. The "effective mesh size" landscape metric

The effective mesh size landscape metric (m_{eff}) expresses the likelihood that any two randomly chosen points in the region under observation may or may not be connected. The more barriers (e.g., roads, railroads, urban areas) erected in the landscape, the less chance that the two points will be connected. It can also be interpreted as the ability of two animals of the same species - placed randomly in a landscape - to find each other. In this study, simple rules of polygon connectivity were used to define the unfragmented patched bounded by roads, urban areas, and/or agricultural areas. The encountering probability is converted into the size of an area called the effective mesh size. The more barriers in the landscape, the lower the probability that the two locations will be connected, and the lower the effective mesh size. If a landscape is fragmented evenly into patches all of size $m_{\rm eff}$, then the probability of two randomly chosen points in the landscape being connected is the same as for the fragmentation pattern under investigation.

The effective mesh size calculation for a given planning unit *j* is calculated using the following formula (Jaeger, 2000):

$$m_{\rm eff}(j) = \frac{1}{A_{tj}} \sum_{i=1}^{n} A_{ij}^2$$
(1)

where *n* is the number of unfragmented patches in planning unit *j*, A_{ij} is size of patch *i* within planning unit *j*, and A_{ij} is the total area of planning unit *j*.

One problem with this definition, as pointed out by Moser et al. (2007), is that it assumes the patches of land stop at the boundary of the planning unit (i.e., county, Caltrans district, or watershed), when in fact, a patch may extend far beyond the boundary of the planning unit. Accordingly, the cutting-out (CUT) procedure cuts patches at the edge of a given planning unit (like a cookie cutter), and ignores contiguous parts of patches located outside the unit boundary. If these patch parts are large, this approach can generate considerable negative bias in the results, constituting the so-called boundary problem (Moser et al., 2007). An alternative implementation of the effective mesh size calculation is the cross-boundary connec-

tion (CBC) procedure, which accounts for connected unfragmented areas that extend beyond the boundaries of a given planning unit that the effective mesh size is being calculated for. Therefore, this study carried out a comparison of the CUT and CBC procedures to evaluate how different the results from the two procedures were for planning units in California and to analyze which procedure is more suitable for being used in the context of regional planning.

The CBC effective mesh size calculation for a given planning unit j is calculated using the following formula modified from Eq. (1) above (Moser et al., 2007):

$$m_{\rm eff}^{\rm CBC}(j) = \frac{1}{A_{tj}} \sum_{i=1}^{n} A_{ij} A_{ij}^{\rm cmpl}$$
⁽²⁾

where *n* is the number of patches intersecting planning unit *j*, A_{ij} is the total area of planning unit *j*, A_{ij} is the area of patch *i* inside of planning unit *j*, and A_{ij}^{cmpl} is the complete area of patch *i* including the area outside the boundaries of planning unit *j*.

2.2. Automated effective mesh size calculation tool

A geographic information system (GIS) automated tool for calculating effective mesh size was developed for use in ArcGIS 9.1 (ESRI, 2005). This tool calculates the effective mesh size for both CUT and CBC procedure based on GIS maps of a given fragmentation geometry and planning unit boundaries. This tool was written as a Visual Basic 6.0 dll using the ArcObjects programming library, and can be obtained from the authors upon request.

The tool calculates the effective mesh size by first calculating the area of each planning unit from the planning unit layer and the area of each patch from the fragmentation geometry layer (described below). These two layers are then intersected while retaining the information about the area of each original planning unit and the unfragmented patches bounded by the fragmenting elements. The area of each unfragmented patch that is located within each planning unit was calculated, as was the area of each unfragmented patch located outside of the planning unit (i.e., located in an adjacent planning but still connected to the unfragmented patch). From this information, the $m_{\rm eff}$ CUT and $m_{\rm eff}$ CBC are calculated based on Eqs. (1) and (2).

2.3. GIS database

This section describes the database of GIS layers that represent fragmenting elements and planning units. The fragmenting elements were combined together using GIS overlay techniques (as described below) to create a suite of four fragmentation geometries. These fragmentation geometries and the planning units were used as inputs to the automated effective mesh size calculation tool for running the various analyses presented in this paper.

2.3.1. Fragmentation geometries

A 1:100000 scale GIS dataset of all roads for the state of California in 2005 was obtained from the California Department of Transportation (Caltrans). This dataset included attributes distinguishing between divided highways/expressways, major connector/artery roads, and minor local roads. The minor local road category contains roads used for local traffic and usually has a single lane of traffic in each direction. These minor local roads may be paved or unpaved, however, this category does not include non-paved roads/trails intended for off-highway vehicles, nor does it include non-paved logging or fire access roads. For the fragmentation geometries, major highways were buffered by 10 m (on either side), major roads were buffered by 5 m, and minor roads were

Table 1

Summary of the fragmenting elements used to define each fragmentation geometry

Fragmentation geometry	Fragmenting elements included				
FG 1	Highways, major roads, railroads, urbanized areas				
FG 2	FG 1 and minor roads				
FG 3	FG 2 and agricultural areas				
FG 4	FG 3 and lakes, major rivers, alpine areas above 3000 m				

Note that each higher level of fragmentation geometry builds on the previous fragmentation geometry by adding additional fragmenting elements, as signified in the table.

buffered by 3 m. A 1:100000 scale GIS dataset of railroads was obtained from the California Spatial Information Library (CASIL, http://gis.ca.gov), which were buffered by 3 m for the fragmentation geometries.

A GIS layer of urbanized areas was created by combining two datasets: (1) A statewide map called "Footprint of Development", derived from 2000 Census blocks (housing density), and developed by the California Department of Forestry and Fire Protection, Forest Resources Assessment Program (4 ha minimum mapping unit, CDFFP, 2002); and (2) the California Farmlands Mapping and Monitoring program map layer dataset (CDC, 2006), which identifies urbanized areas for agricultural counties. These two datasets were overlaid using a spatial union in ArcGIS 9.1 and any area identified as urban in either of the datasets was so assigned in fragmentation geometry calculations.

A layer of naturally fragmenting areas was assembled that included lakes, major rivers, and high elevation alpine areas. Lakes and major rivers were identified from the National Hydrologic Dataset. All lakes and permanently flooded areas were included in the fragmentation geometries, while only rivers greater than approximately 10 m wide were included. Areas above 3000 m elevation were identified using a 30 m digital elevation model, the approximate elevation at which alpine areas begin in California.

Four fragmentation geometries for California were created using the spatial union overlay functions in ArcGIS 9.1. Each fragmentation geometry builds on the previous with fragmentation geometry (FG) 1 containing the least number of fragmenting elements and FG 4 containing the most (Table 1). FG 1 includes highways, major connector/arterial roads, railroads, and urban areas. FG 2 includes all fragmenting elements in FG 1 plus all minor roads. FG 3 includes all elements from FG 2 plus agricultural areas. FG 4 includes all elements from FG 3 plus the natural fragmenting elements described above. These fragmentation geometries delineate unfragmented patches whose patch area is calculated (as described below). The unfragmented patches contain a range of land cover types, including different plant communities, rural development, resource extraction, and agriculture (for FG 1 and 2 only). The actual mix of these land cover types that will be in a given unfragmented patch greatly depends on the location of the patch in the state of California; see Barbour et al. (1993) for a good discussion of the spatial distribution of plant communities and landcover in California.

2.3.2. Planning units

County boundaries, transportation district boundaries, and five nested spatial scales of watershed boundaries for California were obtained from CASIL. These layers were used as the reporting units for which the effective mesh size was calculated. Both the CUT and CBC procedure were used to calculate the effective mesh size ($m_{\rm eff}$) landscape metric for each of the four fragmentation geometries within each Caltrans district (12 total), county (58 total), and five spatial scales of watersheds: river basin (RB, nine total), hydrologic unit (HU, 189 total), hydrologic area (HA, 577 total), hydrologic subarea (HSA, 1036 total), super-planning watersheds (SPWS, 2305 total), and planning watersheds (PWS, 6994 total).

2.4. Analysis of effective mesh size

The CUT and CBC procedures were graphically compared using a box and whisker plot of the effective mesh sizes calculated using each procedure. This plot shows the median, and 5%, 25%, 75%, and 95% quantiles as well as outliers beyond the 5% and 95% quantiles for each spatial scale of watershed. The CBC effective mesh size procedure was used for all subsequent analyses because it is the preferred method for assessing the degree of habitat fragmentation since it does not introduce a negative bias into the calculation (see Sections 3 and 4 for more details).

The effective mesh size for each county, Caltrans district, and watershed was mapped out to identify spatial patterns of fragmentation and connectivity in the state. The minimum, maximum, and median effective mesh size for each of the four fragmentation geometries within each county. Caltrans district, and watershed (at all six scales) were summarized in tabular format. Counties were then analyzed by graphing the contribution of each fragmentation geometry to the combined effective mesh size and by identifying the hydrologic sub-area watershed within each county that had the largest effective mesh size (lowest fragmentation). Finally, one county (Merced) was chosen to map in greater detail to show how the fragmenting elements contribute to the effective mesh size calculated. Merced county was selected because it is rapidly growing, has many regional planning efforts occurring within it, and is impacted by all of the fragmenting elements included in this analysis.

3. Results

3.1. Fragmentation geometries

Maps of the four fragmentation geometries show the spatial distribution of patch sizes bounded by fragmenting elements throughout California (Fig. 2). Some similarities among the four maps can be seen, such as the Sierra Nevada mountain range (east/north-east) and north coastal mountains, and south eastern desert areas having larger patch sizes, and the large metropolitan areas having consistently smaller patch sizes. However, many differences exist among the fragmentation geometries. The largest difference throughout the state can be seen in patch size reduction between the FG 1 and FG 2, due to the addition of minor roads to the fragmenting elements. In contrast, the addition of agricultural areas only impacted the patch sizes at very specific locations within the state where there is extensive agricultural development, such as the Central Valley, the Imperial Valley (southern boarder) and other smaller agricultural valleys. Similarly, the addition of natural fragmenting elements in FG 4 caused decreases in patch sizes in the more rural and high elevation areas, especially along the southern spine of the Sierra Nevada mountain range in the central-eastern portion of California.

3.2. Comparison of m_{eff} CBC and CUT procedures

The complete results of effective mesh size calculated using both the CBC and CUT procedure for each fragmentation geometry within each of the eight sets of planning units are massive, so they are provided as supplementary material (online). Only summary graphs and tables of the calculated effective mesh sizes are provided in the paper.

Examining the box plots of the effective mesh size calculated using both the CBC and CUT procedure shows striking differences for all levels of planning units except river basins (rb, Fig. 3). As the size of the planning unit decreases (from left to right in the







Fig. 3. Box and whisker plots showing the distribution of effective mesh sizes (m_{eff}) calculated using the cross-boundary connection method (CBC, left graph) and CUT procedure (right graph), based on fragmentation geometry (FG) 4, for the six nested spatial scales of watersheds in the state of California (from largest to smallest watersheds): river basins (rb), hydrologic units (rbu), hydrologic areas (rbua), hydrologic sub-areas (rbua), super-planning watersheds (rbuasp), and planning watersheds (rbuaspw). The dark line in the middle of the boxes represent the median, the edge of the boxes represent the 25% and 75% quantiles, the whiskers represent the 5% and 95% quantiles, and the circles represent outliers beyond the 5% and 95% quantiles. The dashed line represents the effective mesh size for the entire state for fragmentation geometry 4. The CBC procedure identifies the unbiased distribution of effective mesh sizes, in contrast to the CUT procedure which shows a strong negative bias in m_{eff} . Also note that the strength of the single smaller (toward the right).

graphs) the range of the CBC $m_{\rm eff}$ increases, while the range of the CUT stays constantly at some rather low value. The median CBC $m_{\rm eff}$ fluctuates between planning units, but shows no trend as the planning units get smaller. However, the CUT procedure shows a decreasing trend in the $m_{\rm eff}$ quantiles as the planning units get smaller (Fig. 3). This can be seen by the statistical range of $m_{\rm eff}$ increasing with decreasing size of the planning unit. For example, for FG 4, the range of $m_{\rm eff}$ for large river basins is 1138 km², while the range for the much smaller planning watersheds is 10 175 km² (Table 2). This effect is due to the cutting off of patches by the boundaries of the planning units which act as artificial fragmenting elements, resulting in lower $m_{\rm eff}$ CUT values for smaller planning

units. This pattern was found to hold true for all fragmentation geometries.

3.3. Effective mesh size for administrative and watershed planning units

The $m_{\rm eff}$ (CBC procedure) within the state as a whole for FG 1 is 2962 km². By including minor roads in the fragmenting elements, FG 2 results in $m_{\rm eff}$ decreasing to 1128 km² (63.0% decrease from FG 1). The addition of agricultural areas to the fragmenting elements in FG 3 resulted in only a slight decrease in $m_{\rm eff}$ to 1116 km² (1.1% decrease from FG 2). This slight decrease is due to the fact

Table 2

Planning unit area and effective mesh size (CBC) summary statistics for the two nested administrative planning unit boundaries – Caltrans districts and municipal counties – and six nested watershed planning unit boundaries – river basins (RB), hydrologic units (HU), hydrologic areas (HA), hydrologic sub-areas (HSA), super planning watersheds (SPWS), and planning watersheds (PWS) in California. For each of the boundaries the median, minimum, and maximum planning unit area, and effective mesh size for the four fragmentation geometries (FG) are given. The $m_{\rm eff}$ for the state as a whole for FG 1 is 2962 km², for FG 2 is 1128 km², for FG 3 is 1116 km², and for FG 4 is 789 km². Note that some planning units have an area of zero because they are located at the edge of the state and have an area less than 0.5 km².

		Caltrans district (km ²)	County (km ²)	RB (km ²)	HU (km ²)	$HA(km^2)$	$HSA(km^2)$	SPWS (km ²)	PWS (km ²)
Number of units (n)		12	58	9	189	577	1036	2305	6994
Planning unit area	Median	28541	4017	29715	1129	422	193	109	32
	Min	2052	118	7235	28	0	0	0	0
	Max	72240	52061	153699	18219	8282	7871	6692	6692
FG 1	Median	1604	920	1619	1143	673	502	830	1,256
	Min	171	0	259	0	0	0	0	0
	Max	6620	12092	5401	18436	20885	20885	20885	20885
FG 2	Median	470	242	394	354	153	103	143	181
	Min	50	0	84	0	0	0	0	0
	Max	2829	5064	1638	10447	14891	14891	14900	14900
FG 3	Median	455	221	376	332	133	94	134	173
	Min	43	0	78	0	0	0	0	0
	Max	2813	5058	1629	10445	14889	14889	14898	14898
FG 4	Median	420	175	366	258	117	74	112	147
	Min	43	0	78	0	0	0	0	0
	Max	1722	2615	1216	4821	7883	9097	10137	10175



Fig. 4. Effective mesh size within six different planning units for the four fragmentation geometries. (a) The two administrative planning units and four levels of watershed maps are shown and labeled across the top. The effective mesh size CBC metric is calculated for the different planning units based on: (b) fragmentation geometry 1, (c) fragmentation geometry 2, (d) fragmentation geometry 3, and (e) fragmentation geometry 4.

that the agricultural areas are covered by a dense network of minor roads, which are already included in FG 2. Finally, by adding natural fragmenting elements in FG 4, $m_{\rm eff}$ decreased to 789 km² (29.3% decrease from FG 3).

California counties showed a wide range of effective mesh sizes across all four fragmentation geometries (Figs. 4 and 5, Table 3). San Francisco county had the smallest effective mesh size across all fragmentation geometries because it is almost entirely urbanized, while Tulare county had the largest effective mesh size across all fragmentation geometries because much of the county is located along the southern spine of the Sierra Nevada Mountain range where very large unfragmented areas exist (Fig. 5). There is clearly a break in the county effective mesh size for all fragmentation geometries, in that one group of counties had effective mesh sizes greater than all the rest (the 10 counties not included in the zoom in graph in Fig. 5). Although there was a significant correlation (p < 0.01)between the effective mesh sizes for all fragmentation geometries, there were certain counties with disproportionately higher or lower effective mesh sizes for specific fragmentation geometries. For instance, Ventura county has a relatively low effective mesh size for FG 1, with relatively high values of $m_{\rm eff}$ for FG 2, 3 and 4, showing that it is more affected by major roads than other counties with similar effective mesh sizes for FG 2, 3 and 4 (Fig. 4, Table 3). Similarly Lassen and San Luis Obispo counties have fairly high effective mesh sizes for fragmentation geometry 1, but have low effective mesh sizes for fragmentation geometries 2, 3, and 4, showing that those counties are more affected by minor roads than other counties (Fig. 4, Table 3). It can be seen that the natural fragmenting features of FG 4 have a much greater effect (relative to FG 3) on the counties that have higher effective mesh sizes for all geometries (i.e., those not in the zoomed section of Fig. 5). Similarly, the addition of agriculture to the fragmenting elements did not affect the effective mesh size much for most counties, although a moderate effect can be seen in some counties including Mono, Kern, Imperial, Merced, Napa, Yolo, and Solano.

The detailed single-county analysis for Merced county shows a pattern of fragmentation similar to that of many counties located in the central valley of California (Fig. 6). Most of the urbanization and associated fragmentation due to roads (FG 1 and 2) is located in the lower elevation valley floor areas. As with most counties in California, $m_{\rm eff}$ drops substantially from FG 1–2. Although a majority of this county is in agriculture, the addition of agricultural areas to the fragmenting elements only decreased $m_{\rm eff}$ by 16.6%, because the agricultural areas are located in the low elevation valley floor which is already fragmented by roads and urban areas (Fig. 6). Thus, the higher-elevation more-montane areas located in the eastern portion of the county tend to contribute strongly to the overall county $m_{\rm eff}$ value, because they are large unfragmented areas. The addition of naturally fragmenting elements decreased $m_{\rm eff}$ moderately, but in this case, the decrease by 14.5% was fairly large considering that the natural fragmenting elements make up a small proportion of the landscape as compared with agricultural areas (Fig. 6). Since these natural fragmenting elements tend to be located in the less fragmented higher-elevation areas, they have a greater effect on $m_{\rm eff}$.

4. Discussion

4.1. Overview

The effective mesh size landscape metric $(m_{\rm eff})$ provides an easy-to-use and informative method for quantifying landscape fragmentation that is useful for regional planning. The metric produces a map of the spatial distribution of fragmentation levels

Table 3

Effective mesh sizes (CBC) in km² of all four fragmentation geometries (FG) for all counties sorted from highest to lowest for FG 1

County	Area (km ²)	Effective mesh size (km ²)					
		FG 1	FG 2	FG 3	FG 4		
Tulare	12543	12092	5064	5058	2615		
Fresno	15583	8332	4721	4716	2034		
Madera	5575	7558	3767	3761	2129		
Inyo	26480	7444	2863	2861	1959		
San Bernardino	52061	5130	1579	1577	1549		
Mariposa	3786	4792	3241	3238	2104		
Mono	8098	3927	2295	2246	950		
Tuolumne	5899	3857	2100	2077	1256		
Del Norte	2618	3805	1521	1518	1281		
Trinity	8307	3027	1321	1321	1306		
Santa Barbara	7093	2049	535	503	469		
Imperial	11595	1978	688	648	563		
Alpine	1917	1854	1015	1010	923		
Lassen	12219	1816	171	158	143		
Humboldt	9268	1725	701	697	577		
Siskiyou	16431	1721	598	594	573		
Kern	21130	1714	336	302	278		
Riverside	18907	1694	611	604	592		
San Luis Obispo	8588	1687	113	106	100		
Monterey	8574	1628	268	260	259		
Modoc	10874	1398	188	176	156		
Tehama	7660	1332	394	385	313		
Ventura	4803	1301	854	821	810		
San Benito	3599	1168	268	261	253		
Plumas	6769	1115	111	110	93		
Mendocino	9085	1080	375	371	368		
Calaveras	2682	1030	107	106	93		
Placer	3884	980	399	398	349		
Glenn	3436	952	/1	61	5/		
Shasta Santa Clana	9976	888	252	248	219		
Sdiita Cidia	3303	845	319	307	295		
Lake San Diana	3444	839	232	223	195		
Sali Diego	10958	697	318 111	31Z	310		
Amador	2524	667	160	111	99 140		
Fl Dorado	1509	620	102	101	2/1		
Siorra	24055	612	202	202	241 75		
Marcad	5105	612	100	166	1/2		
Stanielaue	3026	5/3	327	307	300		
Coluca	2006	/28	08	79	75		
Kings	3605	414	27	17	17		
Rutte	4343	404	84	76	46		
Los Angeles	10548	343	112	102	90		
Nana	2047	309	254	220	143		
Yolo	2644	295	183	128	107		
Sonoma	4108	271	73	65	62		
Yuba	1667	266	39	33	21		
Alameda	1920	262	88	85	82		
Solano	2196	190	112	53	24		
Orange	2052	171	50	43	43		
San Joaquin	3693	161	91	46	45		
Santa Cruz	1153	160	29	27	27		
Contra Costa	1943	158	61	25	24		
San Mateo	1164	119	26	25	24		
Sutter	1576	89	15	4	4		
Sacramento	2574	84	29	7	6		
Marin	1344	76	33	31	30		
San Francisco	118	0.04	0.02	0.02	0.01		
Entire State	400145	2062	1128	1116	780		

present in different planning units on multiple scales that are relevant to planners. Such analytical techniques and tools are needed to improve and support the regional environmental planning process.

The results presented here illustrate potential uses of the effective mesh size metric, and raise questions about how best to incorporate estimates of habitat degradation due to fragmentation into regional land use planning. The analytical approach presented here can be used to identify contiguous suitable habitats split by



Fig. 5. Effective mesh sizes (CBC) given in km² for each of the four fragmentation geometries with each county in California. Because the fragmentation geometries are building on each other, the values of m_{eff} are ordered: m_{eff} (FG 1) > m_{eff} (FG 2) > m_{eff} (FG 3) > m_{eff} (FG 4). The inset shows more details which in the complete graph are difficult to distinguish. The value of m_{eff} for the state as a whole for FG 1 is 2962 km², for FG 2 is 1128 km², for FG 3 is 1116 km², and for FG 4 is 789 km².



Fig. 6. Patch sizes for each of the four fragmentation geometries (FG) within Merced county shown in a color gradient from yellow (small) to blue (large). Developed areas and roads are shown in red, agricultural areas are shown in orange (FG 2 and 3), and naturally fragmenting elements are shown in grey (FG 4 only). Effective mesh sizes (CBC) for all fragmentation geometries are shown in the bar graph.

urban areas, roads and other fragmenting elements and help prioritize locations for conservation and management. This methodology represents an important step forward in analyzing and interpreting the current situation in California and could be applied to other states or for comparative analyses of ecoregions. The results of this research are being provided to the California Department of Transportation for incorporation in a statewide database intended to identify potential biological impacts of planned future transportation projects (Thorne et al., 2007). Effective mesh size analysis provides a straightforward metric for assessing the impact of future transportation projects on habitat fragmentation and connectivity. This analysis took a multi-scale approach to assessing habitat fragmentation in order to account for the range of scales that both transportation projects and ecological processes work across. That is, a small road improvement project may only affect a fraction of a hectare of the landscape, but a major road project may affect tens to hundreds of hectares, while regional transportation plans and policies may affect thousands to millions of hectares. Likewise, different organisms respond to landscape characteristics at different spatial scales (Kotliar and Wiens, 1990). A mountain lion will respond to habitat fragmentation at a much broader scale than will a small mammal. We recommend that tools developed for envi-



Fig. 7. Map of the 58 counties in California showing the watershed (hydrologic subarea) with highest effective mesh size for each county (in fragmentation geometry 4), i.e., the least fragmented watershed. The watershed must have at least half of its area located within the county to be considered for this analysis.

ronmental assessment should be flexible enough to allow for the analysis of potential fragmentation impacts at a range of spatial scales. The method described here allows for the flexibility to identify and analyze habitat fragmentation at scales that are relevant to a wide range of transportation planning efforts and animals that may be impacted.

By calculating $m_{\rm eff}$ in an integrated GIS database for eight different administrative and watershed planning units, cross-unit queries can be carried out. For example, the watershed within each county with the highest effective mesh size for any fragmentation geometry of interest can be identified, as in Fig. 7 for FG 4. This indicates the priority watershed that conservation planners in each county could focus on for large-scale habitat fragmentation and connectivity. Note that in many cases the priority watershed may cross county borders, leading to the need for cross-county planning.

4.2. Cross-boundary connections and ecological realism of landscape metrics

The cross-boundary connection procedure for calculating effective mesh size allowed for an assessment of landscape structure that incorporates a high level of ecological complexity by explicitly including connections to the neighboring reporting units, leading to a more ecologically realistic measure of landscape structure. We note that we could not account for landscape patch connections at the edge of the overall study area (the entire state of California in this case), because patches that intersect with the state boundary were cut off at the state boundary due to limitations in the base data. The loss of accuracy introduced by such state boundaries is fairly small when the effective mesh size is being calculated at the state scale because in this case the size of the planning unit is much larger than the size of the patches being cut off by the state borders. However, our analysis shows that as the planning units get smaller, the boundary effect generally increases, thus suggesting that when smaller planning units are located at or near the edge of the larger analysis area the effective mesh sizes will be underestimated to a higher, but unknown degree.

These results corroborate the findings of Moser et al. (2007), who demonstrated by empirical evidence and mathematical proof, that the CUT procedure was always smaller than the size of the respective municipality, while the CBC procedure was independent of municipality size. We found a similar pattern across multiple spatial scales, and further have now shown that as the size of the planning unit decreases, the effect of the bias introduced by the CUT procedure increases. Thus, the strength of the bias is a function of the spatial scale of the planning unit used in relation to the size of the unfragmented habitat patches being analyzed.

Although there are many landscape metrics available for use, few have been shown to be relevant to ecological processes. The effective mesh size calculated using the CBC procedure is an ecologically relevant measure of landscape fragmentation because it is explicitly based on the probability that an organism can move between two randomly chosen locations in the landscape without encountering a fragmenting element. This metric directly relates to the ecological process of functional connectivity which can be defined as "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al., 1993).

Such ecological processes in a landscape can be described as having first-order and second-order statistical characteristics. Firstorder statistics describe the variation in process at individual locations in a given study area, whereas second-order characteristics summarize all point-to-point relationships in the study area (Wiegand and Moloney, 2004). In general, second-order properties describe the spatial dependence between events at any two locations, i.e., they "examine the correlations or covariances between events occurring in two distinct points or regions" (Fotheringham et al., 2000, p. 140). Landscape connectivity is by definition a secondorder property because it relates to the possibility of movement of organisms among resource patches or points in a landscape (Taylor et al., 1993).

Both first-order and second-order statistics offer the potential of detecting patterns across spatial scales. Most landscape metrics calculate first-order statistics, e.g., road density, patch area, patch shape metrics (McGarigal et al., 2002). However, this use of firstorder statistics to assess the second-order processes of landscape connectivity is likely a reason why Tischendorf (2001) found that most landscape metrics correlate poorly with ecological processes related to landscape connectivity. Similarly, the newly proposed landscape metric roadless volume is a first-order metric (Watts et al., 2007), which has also been shown to produce results that do not relate to the ecological process of connectivity (Girvetz et al., 2007).

As such, the second-order ecological processes of landscape connectivity should be measured and quantified using second-order landscape metrics, such as $m_{\rm eff}$. In the case of $m_{\rm eff}$, the points (or events) are uniformly distributed over the landscape, and the underlying process can be thought of as identifying for each point all accessible other points in the landscape, and as movement of animals between these points. Several other landscape metrics have been proposed that have second-order properties. These include the ecologically scaled landscape index average patch connectivity (Vos et al., 2001), which is the probability that a patch is colonized based on species-specific movement distances and the spatial configuration of habitat patches. Other examples are Ripley's K and the O-ring statistic (Wiegand and Moloney, 2004).

The m_{eff} CBC procedure takes the approach of using a secondorder metric and extends it across the boundaries of the reporting unit, making the metric even more ecologically realistic. Therefore, the application of the CBC procedure is a logical implication of the effective mesh size being a second-order metric, and could also be successfully applicable to other second-order metrics.

An additional convenient asset of the CBC procedure is that $m_{\rm eff}$ is area-proportionately additive (Moser et al., 2007), which implies that the values of $m_{\rm eff}$ for aggregations of reporting units can be calculated directly from the values of the reporting units, e.g., within the set of nested watersheds in California or other nested reporting units. The value of $m_{\rm eff}$ of the aggregated reporting unit is the areaweighted sum of the $m_{\rm eff}$ values of the individual reporting units (for details see Moser et al., 2007). This is not the case for the CUT procedure because of the bias introduced through the boundaries of the reporting units.

4.3. Implications for wildlife management and land use planning

Systematic, objective and quantitative landscape metrics are needed for use in regional environmental planning efforts and impact assessments (Geneletti, 2006). This has been widely recognized, including in the national report "The State of the Nation's Ecosystems - Measuring the Lands, Waters, and Living Resources of the United States", which aims at using seven indicators of fragmentation and landscape pattern, but suffers from the lack of data on these indicators (Heinz Center, 2002; O'Malley et al., 2003). This lack of useful indicators for assessing habitat fragmentation could be addressed using $m_{\rm eff}$. For example, effective mesh size could be used to identify areas that are prone to wildlife-vehicle collisions. Areas with very high $m_{\rm eff}$ would be expected to exhibit little or no fragmentation effects on deer populations, and would not be prone to wildlife-vehicle collisions. Now that methods for quantifying effective mesh size have been developed, many research questions in road ecology can be revisited using this landscape fragmentation index.

More explicitly, the method of effective mesh size serves as an analytical tool in regional planning for the following purposes: (1) Quantitative assessments of the degree to which planned future transportation and urban development scenarios will increase landscape fragmentation in a given planning unit. Such an approach can also be used retrospectively, to assess the rate of fragmentation in a planning unit over time. This approach permits quantification of the cumulative effects of several projects combined. (2) It is possible to determine how much each category of fragmenting elements (e.g., different types of roads and urban areas), adds to the total degree of landscape fragmentation. (3) The method can be applied to identify and test future scenarios for the removal of roads or installation of wildlife crossing structures that would have the greatest positive effect on the effective mesh size. (4) The level of fragmentation of regions can be analyzed in relation to their human population density and economic productivity and other relevant factors.

This paper provides a yardstick for further investigations and assessment of the degree of landscape fragmentation. Historical, current and future values of $m_{\rm eff}$ for California, or other regions, could be compared to determine the degree of landscape fragmentation. Observing, understanding and documenting changes in the environment are important goals of environmental monitoring. Our findings on the degree of landscape fragmentation are relevant not only in relation to wildlife populations but also for the scenery, noise pollution, and recreational value of landscapes. The study's data should therefore be integrated into the existing monitoring, management and planning programs on the national, state, and county levels. Such programs typically require new indicators to meet a set of criteria before the indicators can be integrated into the system. The effective mesh size has been shown to meet such criteria well and is therefore suitable for being used in environmental monitoring systems (Esswein et al., 2003; Jaeger, 2007).

4.4. Future directions

One long-term goal of this research is to create a basis for comparative assessment within and across states and countries around the world. These applications could serve as a foundation for drawing up agreements about environmental standards such as limits, norms, and targets to limit landscape fragmentation. For this purpose, it would also be useful to establish a time series of effective mesh size for making comparisons with previous conditions, including comparisons with/without increase in traffic volume, and for identifying changes in trends. An effective mesh size analysis of this type could be useful for planners elsewhere who have access to a time series of fragmenting elements. Spatially-explicit urban growth model outputs could be used to project a time series of fragmenting elements into the future (Thorne et al., 2006), and the effective mesh size metric could inform planners about the impact of future fragmentation due to different urban and transportation development scenarios. These results can be used to inform land use and conservation planning policies, including potential impacts of fragmentation on bird flight corridors and nature conservation areas.

Further refinements made to the effective mesh size could improve its ecological relevance and the range of it applicability for management decisions. In particular, adding a permeability value for each different type of fragmenting element (e.g., different road traffic volumes) would allow this model to incorporate more realistic and complex abilities of organisms to cross roads (Jaeger, 2007). This could include separate parameters for traffic volume, road width, and estimates of the larger road effect zone of environmental impacts. Simple rules of contiguity were used here to delineate habitat patches, however other more sophisticated patch delineation techniques could be used to improve the ecological relevance of the delineated habitat patches (Girvetz and Greco, 2007). In addition, the qualities of the various habitat patches could be included in the effective mesh size calculated by weighing each patch by its quality as measured, for example, by a speciesspecific habitat suitability index (HSI, Bender et al., 1996; Hein et al., 2007) or by the more general Kaule's conservation value classes for ecosystems (Kaule, 1991). Addition of these types of details and refinements to the effective mesh size statistic could also permit assessment of the location for road crossing structures (Forman et al., 2003; Jaeger, 2007; van der Grift, 2005) and design of wildlife corridors (Crooks and Sanjayan, 2006; Hilty et al., 2006) using the effective mesh size metric.

5. Conclusions

Analyses of the degree of landscape fragmentation can provide valuable information for land use, transportation, conservation, and urban planning efforts. Studies correlating such fragmentation relationships with the absence or population decline of species, especially listed species, may indicate to what degree the amount and loss of unfragmented areas reflect the condition of species populations (e.g., Roedenbeck and Köhler, 2006). Population viability may respond to critical thresholds of fragmentation, above which populations are prone to a much higher risk of extinction (Jaeger and Holderegger, 2005; With and King, 1999). Empirical determination of these fragmentation thresholds in real landscapes is difficult to achieve due to long time lags in population dynamics, current lack of information about, and research methodologies for, measuring population responses. Better decision-making procedures and planning tools are needed that are based on the precautionary principle, population models, and quantitative assessment landscape fragmentation. The methods and results presented here provide a tool for assessing the effects of different landscape elements on habitat fragmentation and connectivity at the regional scale.

It has been called a cruel irony in road ecology that "the more important the question, the more uncertainty is associated with the answers that road science will be able to provide" (Roedenbeck et al., 2007). This implies that very important decisions need to be made, requiring large-scale environmental assessment on the strategic level, for which we lack scientific information and analytical techniques. While there is a rather large body of experience on how to study local-level effects, cumulative effects at broader scales are much more difficult to analyze and assess. Since indicators of landscape integrity are presently still scarce in environmental monitoring, impact assessment and regional planning, the tool presented here allows for an assessment of habitat fragmentation and connectivity on multiple scales, including the level of strategic environmental assessments.

Acknowledgments

This research was supported by a UC Davis Sustainable Transportation Center faculty grant (A.M.B.). We thank Katie Benouar (Road Ecology Center, UC Davis) for project coordination and Mike McCoy (Information Center for the Environment, UC Davis) for technical support.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.landurbplan.2008.02.007.

References

- Barbour, M., Pavlik, B., Drysdale, F., Lindstrom, S. (Eds.), 1993. California's changing landscape: diversity and conservation of California vegetation. California Native Plant Society, Sacramento, CA.
- Bender, L.C., Roloff, G.J., Haufler, J.B., 1996. Evaluating confidence intervals for habitat suitability models. Wildlife Society Bulletin 24, 347–352.
- Brown, J.W., 2006. Eco-logical: An Ecosystem Approach To Developing Infrastructure Projects. United States Federal Highways Administration, Office of Project Development and Environmental Review, Washington, DC.
- California Department of Conservation, 2006. California Farmland Conversion Report, 2002–2004 (online). California Department of Conservation, Division of Land Resource Protection, Farmland Mapping and Monitoring Program, Sacramento, CA.
- California Department of Forestry and Fire Protection, 2002. Multi-source Land Cover Dataset. California Department of Forestry and Fire Protection, Fire Resources Assessment Program, Sacramento, CA.
- California State Legislature, 2003. Natural Community Conservation Planning (NCCP) Act.
- Crooks, K.R., Sanjayan, M., 2006. Connectivity Conservation. Cambridge University Press, New York, NY.
- Epps, C.W., Palsboll, P.J., Wehausen, J.D., Roderick, G.K., Ramey, R.R., McCullough, D.R., 2005. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8, 1029–1038.
- ESRI, 2005. ArcGIS 9.1. Environmental Systems Research Institute, Redlands, CA.
- Esswein, H., Jaeger, J., Schwarz-von Raumer, H.-G., 2003. Der Grad der Landschaftszerschneidung als Indikator im Naturschutz: unzerschnittene verkehrs arme Räume (UZR) oder effektive Maschenweite (m_{eff})? Naturschutz-Indikatoren/Neu Wege im Vogelschutz. NNA-Berichte 16, 53–68.
- Forman, R.T.T., 1995. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge, MA.
- Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29, 207–231.
- Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2003. Road Ecology: Science and Solutions. Island Press, Washington, DC.
- Fotheringham, A.S., Brunsdon, C., Charlton, M., 2000. Quantitative Geography: Perspectives on Spatial Data Analysis. Sage Publications, London.

- Geneletti, D., 2006. Some common shortcomings in the treatment of impacts of linear infrastructures on natural habitat. Environmental Impact Assessment Review 26, 257–267.
- Gerlach, G., Musolf, K., 2000. Fragmentation of landscape as a cause for genetic subdivision in bank voles. Conservation Biology 14, 1066–1074.
- Girvetz, E.H., Greco, S.E., 2007. How to define a patch: a spatial model for hierarchically delineating organism-specific habitat patches. Landscape Ecology 22, 1131–1142.
- Girvetz, E.H., Jaeger, J.A.G., Thorne, J.H., 2007. Comment on "Roadless space of the conterminous United States". Science 318, 1240b.
- Gontier, M., Balfors, B., Mörtberg, U., 2006. Biodiversity in environmental assessment – current practice and tools for prediction. Environmental Impact Assessment Review 26, 268–286.
- Gulinck, H., Wagendorp, T., 2002. References for fragmentation analysis of the rural matrix in cultural landscapes. Landscape and Urban Planning 58, 137–146.
- Gustafson, E.J., 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1, 143–156.
- Hein, S., Voss, J., Poethke, H.J., Schroder, B., 2007. Habitat suitability models for the conservation of thermophilic grasshoppers and bush crickets – simple or complex? Journal of Insect Conservation 11, 221–240.
- Heinz Center, 2002. State of the Nation's Ecosystems: Measuring the Lands, Waters, and Living Resources of the United States. Cambridge University Press, New York (available online at http://www.heinzctr.org/ecosystems/report.html).
- Hilty, J.A., Lidicker, W.Z., Merenlender, A.M., 2006. Corridor Ecology. Island Press, Washington, DC.
- Jaeger, J., 2002. Landscape fragmentation: A transdiciplinary study according to the concept of environmental threat (in German: Landschaftszerschneidung. Eine transdisziplinäre Studie gemäß dem Konzept der Umweltgefährdung). Verlag Eugen Ulmer, Stuttgart, Germany.
- Jaeger, J., Holderegger, R., 2005. Thresholds of landscape fragmentation (in German: Schwellenwerte der Landschaftszerschneidung). GAIA 14, 113–118.
- Jaeger, J.A.G., 2000. Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landscape Ecology 15, 115–130.
- Jaeger, J.A.G., 2007. Effects of the configuration of road networks on landscape connectivity. In: Proceedings of the 2007 International Conference on Ecology and Transportation (ICOET), Little Rock, AR. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC, pp. 267–280.
- Kaule, G., 1991. Arten und Biotopschutz, 2nd ed. Ulmer, Stuttgart, Germany.
- Kotliar, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure – a hierarchical framework for the study of heterogeneity. Oikos 59, 253– 260.
- Li, H.B., Wu, J.G., 2004. Use and misuse of landscape indices. Landscape Ecology 19, 389–399.
- Mazerolle, M.J., 2004. Amphibian road mortality in response to nightly variations in traffic intensity. Herpetologica 60, 45–53.
- Mazerolle, M.J., Huot, M., Gravel, M., 2005. Behavior of amphibians on the road in response to car traffic. Herpetologica 61, 380–388.
- McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS: Spatial Pattern Analysis Program For Categorical Maps. University of Massachusetts, Amherst, MA, USA (www.umass.edu/landeco/research/fragstats/fragstats.html).
- Moser, B., Jaeger, J.A.G., Tappeiner, U., Tasser, E., Eiselt, B., 2007. Modification of the effective mesh size for measuring landscape fragmentation to solve the boundary problem. Landscape Ecology 22, 447–459.
- O'Malley, R., Cavender-Bares, K., Clark, W.C., 2003. Providing "better" data: not as simple as it might seem. Environment 45, 8–18.
- Omernik, J.M., Bailey, R.G., 1997. Distinguishing between watersheds and ecoregions. Journal of the American Water Resources Association 33, 935–949.
- Padoa-Schioppa, E., Poggesi, M.C., Bottoni, L., 2006. River basins as ecological units to evaluate landscape fragmentation. In: Davies, B., Thompson, S. (Eds.), Water and the Landscape – The Landscape Ecology of Freshwater Ecosystems. IALE-UK, pp. 77–84.
- Reijnen, R., Foppen, R., 1995. The effects of car traffic on breeding bird populations in Woodland.4. Influence of population-size on the reduction of density close to a highway. Journal of Applied Ecology 32, 481–491.
- Reijnen, R., Foppen, R., Terbraak, C., Thissen, J., 1995. The effects of car traffic on breeding bird populations in Woodland.3. Reduction of density in relation to the proximity of main roads. Journal of Applied Ecology 32, 187–202.
- Riley, S.P.D., Pollinger, J.P., Sauvajot, R.M., York, E.C., Bromley, C., Fuller, T.K., Wayne, R.K., 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. Molecular Ecology 15, 1733–1741.
- Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C., Wayne, R.K., 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17, 566–576.
- Roedenbeck, I.A., Fahrig, L., Findlay, C.S., Houlahan, J.E., Jaeger, J.A.G., Klar, N., Kramer-Schadt, S., Van der Grift, E.A., 2007. The Rauischholzhausen agenda for road ecology. Ecology and Society 12, 11.
- Roedenbeck, I.A., Köhler, W., 2006. Effekte der Landschaftszerschneidung auf die Unfallhäufigkeit und Bestandsdichte von Wildtierpopulationen. Zur Indikationqualität der effektiven Maschenweite. Naturschutz und Landschaftsplanung 38, 314–322.
- Schwarzenegger, A., 2005. California Partnership for the San Joaquin Valley: Executive Order S-5-05. Office of the Governor, State of California.
- Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. Oikos 68, 571–573.

- Thorne, J.H., Gao, S.Y., Hollander, A.D., Kennedy, J.A., McCoy, M., Johnston, R.A., Quinn, J.F., 2006. Modeling potential species richness and urban buildout to identify mitigation sites along a California highway. Transportation Research Part D Transport and Environment 11, 277–291.
- Thorne, J.H., Girvetz, E.H., McCoy, M.C., 2007. A multi-scale and context sensitive state-wide environmental mitigation planning tool for transportation projects in California. In: Proceedings of the 2007 International Conference on Ecology and Transportation (ICOET), Little Rock, AR. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC, pp. 88–99.
- Tischendorf, L., 2001. Can landscape indices predict ecological processes consistently? Landscape Ecology 16, 235–254.
- Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14, 18–30.
- Turner, M.G., 2005. Landscape ecology: what is the state of the science? Annual Review of Ecology Evolution and Systematics 36, 319–344.
- United States Congress, 2005. Public Law 109-59. Safe, Accountable, Flexible, Efficient Transportation Equity Act: A Legacy for Users (SAFETEA-LU).
- United States Fish and Wildlife Service, 1996. Habitat Conservation Planning and Incidental Take Permit Processing Handbook. United States Department of the Interior, Fish and Wildlife Service, Washington, DC.
- van der Grift, E.A., 2005. Defragmentation in the Netherlands: a success story? GAIA Ecological Perspectives for Science and Society 14, 144–147.
- Vos, C.C., Verboom, J., Opdam, P.F.M., Ter Braak, C.J.F., 2001. Toward ecologically scaled landscape indices. American Naturalist 157, 24–41.
- Watts, R.D., Compton, R.W., McCammon, J.H., Rich, C.L., Wright, S.M., Owens, T., Ouren, D.S., 2007. Roadless space of the conterminous United States. Science 316, 736–738.
- Wiegand, T., Moloney, K.A., 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104, 209–229.
 With, K.A., King, A.W., 1999. Extinction thresholds for species in fractal landscapes.
- With, K.A., King, A.W., 1999. Extinction thresholds for species in fractal landscapes. Conservation Biology 13, 314–326.

Evan H. Girvetz is currently a postdoctoral research associate in the College of Forest Resources at the University of Washington. His research focuses on using geographic information systems (GIS) integrated with quantitative analysis

techniques to provide decision-support for answering real-world questions faced by land use planners and decision makers. He received his PhD from the Graduate Group in Ecology at the University of California (UC) Davis (2007). This research was conducted while he was a research fellow at the Road Ecology Center (UC Davis), and at the Information Center for the Environment (UC Davis).

James H. Thorne is a research scientist at the Information Center for the Environment, UC Davis. He got his PhD in Ecology at UC Davis in 2003, and has a masters in geography from the UC Santa Barbara. His research interests include the integration of ecological data into planning, development and deployment of large datasets, and estimating the impacts of climate change.

Alison M. Berry is a plant scientist and professor in the Department of Plant Sciences, and the director of the Road Ecology Center at UC Davis. As director of the Road Ecology Center she develops key research issues in road ecology, and builds graduate education and training opportunities. The UC Davis Road Ecology Center aims to facilitate interactions among UC Davis researchers and agency stakeholders that will lead to a new framework for research and technology transfer in road ecology.

Jochen A. G. Jaeger is an assistant professor in the Department of Geography, Planning and Environment at Concordia University in Montréal, Canada, since July 2007. He received his PhD from the Department of Environmental Sciences at the Swiss Federal Institute of Technology (ETH) in Zurich, Switzerland. He was at the Center of Technology Assessment in Baden-Württemberg in Stuttgart, Germany, and at Carleton University in Ottawa, Canada, as a postdoctoral fellow with Dr. Lenore Fahrig. In 2003, he came back to ETH Zurich to work as a research associate in the Department of Environmental Sciences in the Group for Ecosystem Management. From April to June 2007 he was a visiting scholar at the Road Ecology Center at UC Davis. His publications include the book Landschaftszerschneidung (Landscape Fragmentation) (2002, Verlag Eugen Ulmer, Stuttgart). His research interests are in landscape ecology, road ecology, the quantification and assessment of landscape structure and landscape change, assessment of the suitability of landscape metrics, environmental indicators, ecological modeling, environmental impact assessment, urban sprawl, and novel concepts of problem-oriented transdisciplinary research.