Exploring the role of vegetation fragmentation on aquatic conditions: Linking upland with riparian areas in Puget Sound lowland streams

Vivek Shandas [a,b,*], Marina Alberti [c,d]

[a] *Toulan School of Urban Studies and Planning, Portland State University, 506 SW Mill Street, Portland, OR 97207, United States*
[b] *Center for Urban Studies, Portland State University, 506 SW Mill Street, Portland, OR 97207, United States*
[c] *Urban Design and Planning, University of Washington, 410 Gould Hall, Seattle, WA 98207, United States*
[d] *Urban Ecology Research Lab, University of Washington, 410 Gould Hall, Seattle, WA 98207, United States*

ARTICLE INFO

ABSTRACT

A controversial issue in managing urbanizing watersheds is determining the scale at which conservation measures should be implemented. Current "best practices" suggest establishing riparian buffers along stream corridors and limiting impervious surfaces to prevent degradation of instream biological conditions. While there is increasing evidence that the amount of land covers (e.g., impervious surface, vegetation) has an impact on instream aquatic conditions, the effect of upland vegetation fragmentation on aquatic conditions requires further study. By using landscape metrics to quantity vegetation amount and distribution at the riparian and watershed scales, and a macroinvertebrate index to describe aquatic conditions, this study presents empirical evidence about the interactions between riparian and upland vegetation as they affect instream biological condition of 51 nested watersheds in the Puget Sound lowland. We ask if the fragmentation of vegetation within a watershed helps predict instream biological condition. In addition, we hypothesize that the fragmentation of vegetation at the riparian and watershed scales affects instream biological condition. Using parametric and non-parametric statistical analyses to test relationships, our findings suggest that the fragmentation of upland vegetation and the total amount of riparian vegetation explain the greatest amount of variation in aquatic conditions. These results help frame a management approach for conserving upland areas of vegetation through the use of land use planning techniques.

Published by Elsevier B.V.

1. Introduction

Evidence is mounting that the way humans use the land has dramatic consequences on land cover, and that land cover change impacts ecological systems (Dale et al., 1994; Chapin et al., 2000; Foley et al., 2005). Vitousek et al. (1997) estimate that between one-third and one-half of the earth's land cover has been transformed by human action. By altering land cover patterns and the use of land, humans have impacted the hydrologic cycle to provide fresh-water for irrigation, industry, and domestic consumption (Postel et al., 1996; Vörösmarty et al., 2000). Land use and land cover changes threaten biodiversity through loss, modification, fragmentation of habitats, degradation of soil and water; and overexploitation of native species (Pimm and Raven, 2000).

The role of land cover as it affects aquatic systems is well documented in the literature, and watershed management approaches have attempted to reflect scientific understandings. Since Klien (1979) seminal work established that "stream quality impairment is first evidenced when watershed imperviousness reaches 12%, but does not become severe until imperviousness reaches 30%", dozens of regional investigations have confirmed a relationship between the amount of a specific land cover and aquatic conditions (Osborne and Wiley, 1988; Schueler, 1994; Roth et al., 1996; Richards et al., 1996; Morley and Karr, 2002; Alberti et al., 2007). Accordingly, land use planning has applied "Best Management Practices" (BMPs) at the riparian and watershed scales to mitigate the impact of urban development. At the watershed scale, detention/retention pond ordinances and limits to the amount of allowable impervious surface are BMPs for reducing the amount and velocity of runoff entering stream systems. At the riparian scale, jurisdictions across the U.S. have adopted riparian vegetation ordinances – including critical areas, riparian buffers, and no-touch zones – to prevent reductions in streamside vegetation.

While the application of BMPs at the watershed and riparian scales helps to regulate hydrological, chemical, and trophic condi-

* Corresponding author at: Toulan School of Urban Studies and Planning, Portland State University, 506 SW Mill Street, Portland, OR 97207, United States.
Tel.: +1 503 725 5222.
E-mail address: vshandas@pdx.edu (V. Shandas).

tions occurring within the stream system (Gore, 1996; Stauffer et al., 2000; Konrad and Booth, 2002; Strayer et al., 2003; Stewart et al., 2001; Boyer et al., 2002; Tockner et al., 2002), several issues remain unresolved. First, in watersheds with similar types and amounts of land cover along the riparian corridor, considerable variability in aquatic conditions exists. For example, Booth et al. (2004) show that biological metrics for Little Bear creek (Washington State) almost doubled in value (Benthic Index of Biotic Integrity (B-IBI) change from 16 to 30) from one sampling point to the next downstream point. Second, there is the interaction between riparian and watershed BMPs. While it is commonplace to establish riparian buffers in urbanizing areas, models used to estimate BMP specifications do not differentiate cumulative versus incremental effects of aquatic degradation and rarely consider the presence of other BMPs in the watershed. Accordingly, BMPs are often applied incrementally with little regard to the interaction across scales (Booth and Jackson, 1997; Gergel et al., 2002). We do not know the extent to which BMPs interact to affect aquatic condition.

Finally, and perhaps connected to the inter-relationship among BMPs in the watershed, is that previous studies have produced mixed conclusions about the importance of riparian-scale versus coarse-scale physical factors in affecting aquatic condition (Richards and Host, 1994; Allan et al., 1997; Lambert and Allan, 1999; Wang et al., 2001, 2002; Dovciak and Perry, 2002; Fausch et al., 2002; Roy et al., 2003, 2007; Snyder et al., 2003). For example, Roth et al. (1996) examined the relationship among land use, land cover and instream biological conditions at various spatial scales in southeastern Michigan. While they found that watershed-scale land use is the strongest predictor of instream biological condition, a similar study in the same region by Lambert and Allan (1999) found that riparian-scale land cover characteristics explained more of the variation of instream biology. Although differences in study designs and changes in watershed conditions from one year to the next (i.e., development, removal of riparian land cover) may have influenced the results, both studies examined identical streams, used similar measures of land cover characteristics, as well as metrics for instream biological conditions (IBI). In another study, Roy et al. (2003) report that values of a macroinvertebrate IBI were strongly correlated with both catchment and riparian land cover over a range of 5–61% total urban area and 34–95% forest area in 100-m buffers. However, macroinvertebrate indices were more strongly correlated with environmental factors quantified at the reach-scale, including variation in substrate size and ion concentrations (Roy et al., 2003).

Several possible explanations may be offered to address the aforementioned variability of results when linking riparian and watershed conditions to instream biological measures. First, "landscape legacies" (Allan, 2004) may have a lasting impact on the condition of stream systems. Wang et al. (2001) found that values of IBI varied strongly along an urbanization gradient. This was interpreted as the legacy of similar habitat degradation at all sites under the common, prior influence of agriculture. Second, minor changes in land use may have an impact on the geomorphic features within a watershed and affect localized hydrological regimes across watersheds (Booth and Jackson, 1997; Trimble, 1997). Modifications in watershed hydrology impact instream biota through changes in the quantity and quality of water in the stream channel (Paul and Meyer, 2001). In addition, land use and land cover conditions are generally recognized as instrumental in affecting energy sources, habitat structures, chemical constituents, and biotic interactions within the stream system (Karr and Rossano, 2001), and have lasting consequences on instream conditions. Due to the mechanistic pathways through which these environmental characteristics influence aquatic biota, understanding the structure and dynamics of macroinvertebrate communities in streams, including their responses to human disturbance, can be enhanced by examining environmental and anthropogenic effects at multiple spatial and temporal scales (Peterjohn and Correll, 1984; Vannote et al., 1980; Allan and Johnson, 1997; Malmqvist, 2002; Weigel et al., 2003; Alberti, 2005).

Another possible explanation, and the topic explored in this study, is that previous research has largely relied on the composition of land cover in watersheds, such as percent of agricultural land and total amount of impervious or vegetated surface, disregarding the role of configuration or fragmentation of the land cover within the watershed (previous studies have examined separate scales – the riparian zone and whole watershed – but these studies do not explicitly consider the role of fragmentation of vegetation as it affects instream aquatic conditions). Watershed metrics that quantify spatial fragmentation of the land cover add important information to those that simply quantify landscape composition to help explain the variability in stream conditions (Alberti et al., 2007). Because configuration metrics are spatially explicit (Herzog and Lausch, 2001; Turner et al., 2001; Gergel et al., 2002), they account for the distributional effects of land uses or land covers on stream conditions. This is an important element since the distribution of land cover can be affected by land use planning activities, and spatial configuration may link more explicitly to management activities aimed at reducing the impact of urban development on aquatic systems.

This study explores the role of watershed vegetation patterns in explaining variations in aquatic conditions in the Puget Sound lowland. Vegetation patterns are defined as both the amount and the spatial distribution of vegetation cover in a watershed. By building upon previous studies examining the relationship between composition and configuration of vegetation and instream biological conditions, we examine this relationship across scales (riparian corridor and whole watershed). Specifically, we ask how vegetation patterns at the riparian and watershed scales help to explain instream biological conditions. To address this question we test two null hypotheses: (1) no significant relationship exists between riparian vegetation patterns and instream biological conditions that are not already explained by watershed vegetation patterns; and (2) fragmentation (a measure of configuration) of upland vegetation is not related to instream biological conditions. By explicitly describing the linkages between vegetation amount and distribution, and instream biological conditions, this research aims to expand scientific understanding of the role of vegetation in explaining instream biotic conditions. This study will also attempt to provide urban and regional watershed management agencies with tools for systematically describing and monitoring watershed conditions from the riparian to the watershed scales.

2. Methods

2.1. Study site selection

The Puget Sound region covers an area of more than 41,440 km^2 and comprises about 80% land and 20% water (Lasmanis, 1991). Puget Sound is an estuary—a semi-enclosed, glacial fjord where saltwater from the ocean is mixed with fresh water draining from the surrounding watersheds. Fresh water inflow from rivers amounts to a yearly mean of 41,000 cubic feet per second (ft^3/s), ranging between a peak of about 367,000 ft^3/s to a minimum of about 14,000 ft^3/s. Dense coniferous forests dominate the Puget Sound Lowland (here on Puget lowland), which are interspersed with a variety of deciduous woodlands, wetlands, and grass and shrub prairies. Prior to the 1800s' the vegetation was primarily old-growth conifer forests of western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Douglas fir (*Pseudotsuga*
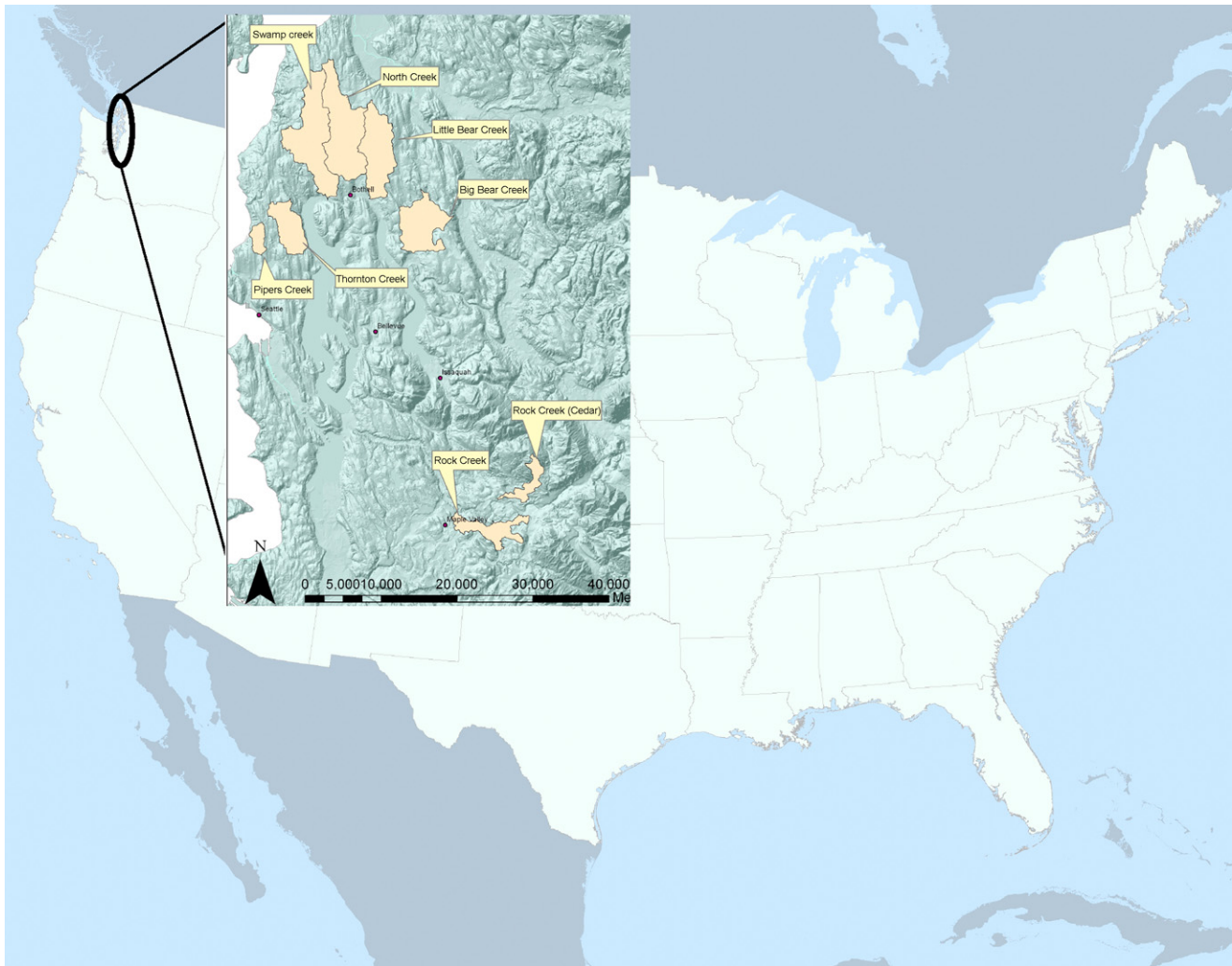
Fig. 1. Study location with study watersheds.

menziesii) (Omernik and Gallant, 1986). Today, the greater Puget Lowland's 3.2 million people account for a majority of the state's population (PSRC, 2002), which has increased by 20% since 1990 and 180% since 1950 (PSRC, 2002). It is expected that an additional one million residents will live in the Puget Lowland by 2025 (PSRC, 2005).
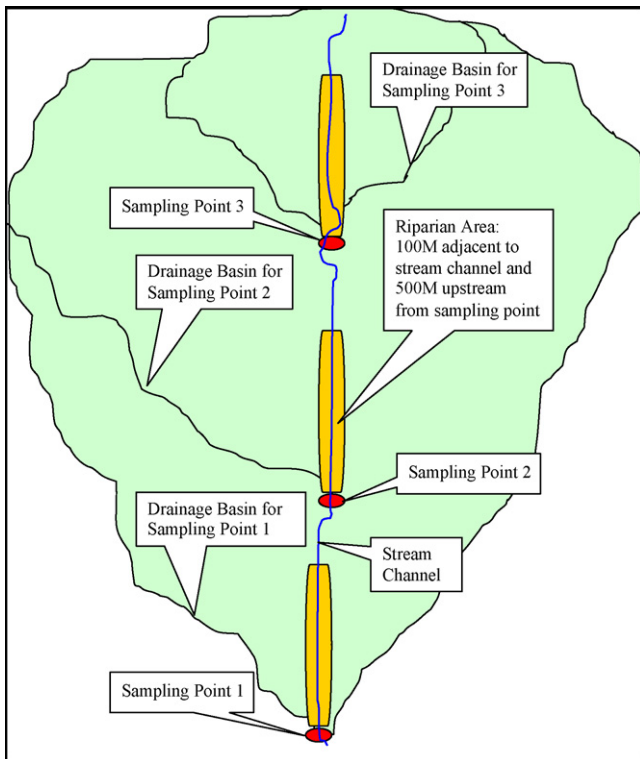
We selected eight watersheds, from a database of 57 sampled between 1992 and 2000 (Kleindl, 1995; May, 1996; Morley, 2000), to include in our study. Each watershed had data on instream macroinvertebrates assemblages using the same protocol (see Section 2.3 methods), contained salmon species listed under the Endangered Species Act (ESA), representing a range of urban development conditions (e.g., from highly urbanized core of Seattle to completely forested areas in the hinterlands), and information on the second and third order streams within each watershed (Fig. 1). All basins were located in the Puget Sound physiographic region, which contain relatively immature soils with shallow accumulations of organic material (Lasmanis, 1991).

2.2. Vegetation amounts and distribution

While past studies have focused on the relationship between impervious surfaces and aquatic conditions, we use an alternative approach, and one that we argue is more suitable for managing urban watersheds. It is well understood that changes in the

amount of urban development affect the configuration of vegetation (Dorney et al., 1984; McDonnell et al., 1993; Simpson et al., 1994), therefore, by examining differences in vegetation conditions across an urban to rural gradient we capture the process through which urban development changes landscape conditions. Unlike the total impervious area (TIA) metric often used to characterize land cover conditions, vegetation amounts and configurations can be modified and manipulated in terms of amount or location in the watershed. As a result, by examining vegetation amount and distribution we aim to provide urban planners and natural resource managers with information about how to manipulate vegetation amounts and distribution as one mechanism to mitigate the impact of urban development on stream systems.

Using geographic information system (GIS) software (ArcGIS 9.1) we characterized vegetation amounts and distribution in three steps. The first step involved delineating watersheds using a 10-m digital elevation model (DEM). While urbanized watersheds may not conform to the topographical form of a DEM, when this study was conducted, limited data on stormwater infrastructure and other artificial drainage systems were available. We classified land cover conditions for each watershed using a year 2000 Landsat Thematic Mapper® (TM) image (30 m resolution). The data were preprocessed to mosaic the two image swaths (path 46: rows 26–27, and path 47: rows 26–27) and corrected for the effects of atmosphere and topography (Alberti et al., 2004). The

grid cell into four land cover categories to match the watershed land cover classification. Once digitized, we compared our land cover classification to a high-resolution photograph of the same region and ensured at least a 95% accuracy assessment in our localized classification scheme. For each study basin, we calculated the percent of riparian and watershed vegetation (Table 1).

In our third and final, step we quantified the fragmentation of vegetation in the riparian zones and watersheds using FRAGSTATS (McGarigal et al., 2002). Studies in the field of landscape ecology offer several metrics for quantifying the fragmentation of land cover, and based on prior analysis we identified two landscape metrics that accurately describe the total amount and fragmentation of vegetation. Accordingly, we selected the composition metric "percent land" to describe the amount of vegetation relative to other land cover categories. For describing the fragmentation of vegetation, we used the aggregation index (AI; Turner and Gardner, 1991; Jaeger, 2000). AI of vegetation measures the number of adjacent pixels in relation to the maximum possible adjacencies, assuming vegetation would constitute a single aggregated patch (He et al., 2000; Jaeger, 2000). We applied the two metrics to all land cover categories in order to provide a quantitative description of watershed and riparian vegetation.

2.3. Sampling macroinvertebrates and B-IBI development

We conducted instream biological sampling at several points along the riparian corridor of the eight study streams, totaling 51 monitoring sites (see Table 1 for sampling intensity). The sampling occurred between August and September in 2003 and 2004, when stream flows were stable and low, taxa richness was high, and the field crew had relatively easy access to sites (Fore et al., 1996; Morley and Karr, 2002). We used standard protocols for monitoring macroinvertebrates in Puget Lowland streams (Karr and Chu, 1999; Morley, 2000). At each site a Surber sampler (500-μm mesh, 0.1 m^2 frame) was used to collect three samples along the midline of a single riffle (all three samples for each instream sampling site occurring no more than 10 m apart). In the field, each sample was strained through a 500-μm soil sieve, mineral material picked through and discarded, and the remaining sample preserved in a solution of 70/30 ethanol/water.

When samples were taken to the lab for identification, invertebrates were separated from the mineral and organic debris, identified, and counted. In this manner, each sample was processed and identified separately without compositing or sub-sampling (following Kearns and Karr, 1994; Karr and Chu, 1999; Doberstein et al., 2000). Insect nymphs and larvae, the majority of benthic samples, were identified to genus where practical (exceptions: *Capnidae*, *Ceratopogonidae*, *Chironomidae*, *Dolichopodidae*, *Dystiscidae*, *Leucridae*, *Phoridae*, and *Sciomyzidae*). Non-insect taxonomic identification varied from family to phylum. Other non-benthic invertebrates, pupae, and terrestrial adults were excluded from sample analysis. Across all study sites, the average abundance among replicates was 783 and median abundance 704.

Fig. 2. Characterizing riparian areas and drainage areas for each watershed— provided example has three B-IBI points.

classification procedure created a four-class land cover system – vegetation, grass/bare soil, impervious surface, or water – which we assessed for consistency using high-resolution digital orthophotos. We defined vegetation as containing canopied trees, and grass/bare soil as shrubs, cleared soil and grass.

The second step involved use of a high-resolution digital orthophoto (1 m resolution) (King County, 2000), and the same year 2000 Landsat Thematic Mapper® image (30 m resolution) to characterize riparian land cover. This localized riparian zone consisted of a 100 m buffer adjacent to the stream channel (Washington State Department of Ecology's recommended 'buffering' distance) and an upstream reach length of 500 m from the sampling point. Although this uniform approach does not reflect differences in the size of the watersheds, the distances upstream and adjacent to the sampling point are consistent with theories that describe river systems as hydrologically connected through longitudinal, lateral, and vertical dimensions (Vannote et al., 1980; Ward and Elliot, 1995; Naiman and Decamps, 1997; Strayer et al., 2003). Each drainage basin is hierarchically nested, containing multiple sampling points per stream channel with the lowest sampling point capturing all upstream points (Fig. 2). Each localized riparian zone was classified using a 5 m by 5 m grid (ArcInfo 8). We then hand-digitized each

Table 1
Name of study basins with respective attributes, including basin area, amount of riparian and watershed vegetation and sampling intensity.

Study basin	Area (km^2)	Amount of riparian vegetation (%)	Amount of watershed vegetation (%)	Number of sampling sites
Pipers Creek	10	70	27	3
Thornton Creek	25	28	24	4
Swamp Creek	20	40	38	9
North Creek	55	15	46	9
Little Bear Creek	40	43	69	9
Big Bear Creek	61	84	69	7
Rock (Cedar) Creek	35	87	96	5
Rock Creek	31	67	85	5

Table 2
Puget lowland B-IBI scoring criteria. Scoring criteria are based on protocol first described by Karr and Chu (1999).

	Metric		
	1	3	5
Taxa richness and composition			
Total number of taxa	[0, 20)	[20, 40]	>40
Number of Ephemeroptera (mayfly) taxa	[0, 4]	(4, 8]	>8
Number of Plecoptera (stonefly) taxa	[0, 3]	(3, 7]	>7
Number of Trichoptera (caddisfly) taxa	[0, 5)	[5, 10)	>10
Number of long-lived taxa	[0, 2]	(2, 4]	>4
Tolerance			
Number of intolerant taxa	[0, 2]	(2, 3]	>3
% of individuals in tolerant taxa	>50	(19, 50)	[0, 19]
Feeding ecology			
% of predator individuals	[0, 10)	[10, 20)	>20
Number of clinger taxa	[0, 10]	(10, 20]	>20
Population attributes			
% dominance (top 3 taxa)	>75	[50, 75)	[0, 50]

The taxonomic analysis provides the information for developing a multi-metric called the Benthic Index of Biotic Integrity (Karr, 1991). Taxa richness, relative abundance, tolerance, and invertebrate life history information were used to calculate B-IBI scores for each study site. Following procedures first outlined for fish (Karr et al., 1986), and later for invertebrates (Fore et al., 1996; Kearns and Karr, 1994; Kleindl, 1995; Morley, 2000), raw scores from the three replicates were averaged for each of the 10 metrics. While averaging the three replicates reduces the total information available in the site, this approach allowed us to compare across all sites. Based on deviation from reference conditions and previously established scoring criteria for Puget Lowland streams, metric scores of one, three, or five were then assigned to the raw metric values (Table 2). The 10 metrics scores were summed to provide a site and time specific B-IBI score, ranging from 10 to 50. One advantage of the B-IBI is that it provides a single number describing the biological condition of the stream at a given location that can be used by urban planners and natural resource managers for long-term monitoring and management of stream systems.

2.4. Data analysis

We used Pearson's correlation coefficient (r) to analyze relationships between watershed and riparian vegetation for all 51 sub-basins in the study region. Although these are not independent variables (i.e., smaller spatial units are incorporated within larger spatial units), we used correlation as a descriptive measure of the relative strengths of relationships. Correlation analysis was also used to determine relationships between vegetation pattern variables and B-IBI scores. Since we know that percent watershed vegetation is an important variable, we developed a hierarchical model starting with percent watershed vegetation and tested the significance of entering the fragmentation variable. Once added, we compared it to the percent vegetation metric using adjusted R^2 and the akaike information criterion (AIC). We then calculated the partial correlation coefficient for both the composition and fragmentation metric to see how much additional variance it explains over percent vegetation alone. To address issues of multicollinearity we performed a correlation analysis among the variables and estimated the variance inflation factor (VIF). While VIF values were high, they were still under the generally acceptable limits (max < 10). Since high multicollinearity leads to high covariance between regression coefficients of the related variables,

it is difficult to separate out the effects of each variable and can create unstable coefficients. This requires particular caution in interpreting the results. All independent variables were normally distributed, and the percent vegetation cover and AI values were transformed using arcsin square root.

Since whole-watershed vegetation amount and fragmentation may provide a dominant influence on macroinvertebrate assemblages, we asked how strong the evidence was that the amount and fragmentation of riparian vegetation influenced B-IBI, and whether that influence was dependent on the amount and fragmentation at the watershed scale. To address this question, we removed (or masked) the riparian areas from the larger contributing watershed when analyzing the relative contribution of riparian and watershed land cover. We also examined separate plots of percent vegetation in local riparian zones versus percent of watershed vegetation to determine if we had sufficient data (e.g., sites with high and low percent vegetation in watershed and riparian areas). A similar diagnostic analysis was also conducted using vegetation fragmentation indices for riparian and watershed areas.

We used a parametric regression and non-parametric analysis to examine the role of riparian and watershed vegetation in explaining instream biological conditions. To reduce the effects of multicollinearity, simple and multiregression models were developed with minimal correlation across all studied watersheds ($r < 0.7$, $P > 0.1$). Several diagnostics (see description below) were also employed to ensure independence of observations. We used an additive and interactive combination of watershed and riparian vegetative cover to create several multiple regression models. We plotted regressions for the best supported models for each vegetation pattern variable and B-IBI.

To ensure that the strongest model sufficiently addressed the assumptions of a regression model, we examined two additional relationships. The first relationship measured the unstandardized residuals of independent variables against the B-IBI values and the second relationship measured residuals versus predicted values. Examining the residuals provided information on assumptions about error terms and on the appropriateness of the model.

To prevent effects from spatial autocorrelation in the vegetation pattern variables we used a partial regression technique based on non-parametric statistical procedures to examine the relationships among. Several methods have been identified to assess spatial autocorrelation in data, including Mantel's r-test (Urban et al., 2002), Moran's I-test, and other methods (see Legendre and Legendre, 1998; Dutilleul et al., 2000). Mantel's r-test is frequently used (Smouse et al., 1986; Legendre and Legendre, 1998; Legendre, 2000; Fortin and Payette, 2002; Urban et al., 2002), and is particularly useful in testing spatial autocorrelation in stream systems (King et al., 2005). We employed the approach used by King et al. (2005) using R-Statistical Package (R Development Core Team, 2007) to asses the independence of observations and the level of spatial autocorrelation on the sample sites. The Mantel's r-test is a partial regression technique the uses the residuals of the independent variables and the spatial [Euclidian] distance of sampling sites to calculate the overall level of spatial autocorrelation among sampling sites. In this study we employed a partial Mantel test which allows a comparison to be made among two variables while controlling for the third. Accordingly, our approach allowed us to remove the variation in the B-IBI values and all independent variables expected due to similarity in inter-site distances, and compare the unexplained residuals of the B-IBI (that variation unrelated to spatial location) with variation in residuals of the independent variables. As a result, we assessed the associational relationship among the independent variables and B-IBI while controlling the Euclidian distance between sampling sites.
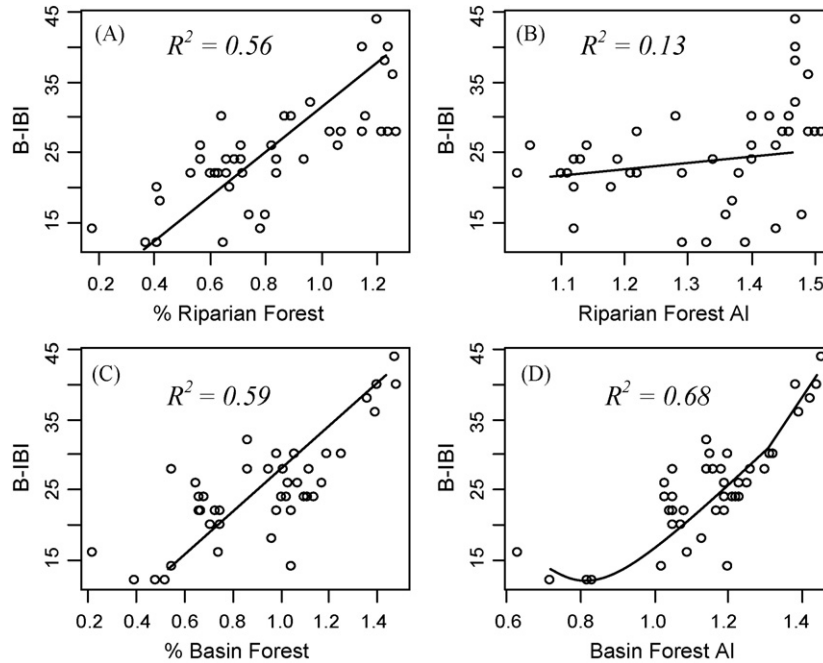
Fig. 3. Scatter plots of each landscape metric (ArcSin Transformed) and B-IBI using bi-variate correlation, (A) percent riparian forest, (B) riparian forest aggregation index (AI), (C) percent basin forest and (D) basin forest aggregation *index* (*AI*).

3. Results

Results of the Pearson's correlation analysis provided the basis for examining the relationship between the amount and fragmentation of watershed and the amount and fragmentation of riparian vegetation conditions. The amount of watershed vegetation and the fragmentation of that vegetation was highly correlated ($r = 0.88$, $P < 0.01$), and the relationship between the amount of watershed and riparian vegetation, while weak, was significant ($r = 0.28$, $P < 0.01$). Because of the high correlation between these watershed-wide variables, we developed seven distinct statistical models for testing against the B-IBI: (1) percent of riparian forest; (2) fragmentation of riparian vegetation; (3) percent and fragmentation of riparian vegetation; (4) percent of watershed vegetation; (5) fragmentation of watershed vegetation; (6) percent of riparian and watershed vegetation; (7) percent of riparian vegetation and fragmentation of watershed vegetation. The seven distinct models allow a separation of variables that are correlated, and provide a robust measurement of the impact of each independent variable on B-IBI (Braak and Van Tongeren, 1995).

Scatter plots provided clues about the relationship between independent variables and B-IBI (Fig. 3A–D). The *x*-axis on the plots reflects transformed landscape metric values, while the *y*-axis represents the raw B-IBI scores which were used to develop seven distinct statistical models. The results indicate a linear relationship between independent vegetation pattern variables and B-IBI. The percent of riparian forest had the strongest correlation ($R^2 = 0.56$, $P < 0.001$), while at the watershed scale the fragmentation of watershed vegetation contained the strongest ($R^2 = 0.68$, $P < 0.001$). The percent of watershed forest also suggested a strong relationship ($R^2 = 0.59$) with the fragmentation of riparian vegetation indicating an insignificant relationship to B-IBI ($R^2 = 0.13$, $P = 0.12$).

The seven statistical models varied in their indication concerning which vegetation metric most affect instream biological condition (Table 3). Of the two riparian forest variables used to predict the B-IBI score in Models 1–3 (Table 3), the riparian forest amount and the riparian aggregation index were both significant when taken individually (adjusted $R^2 = 0.56$, $P < 0.001$; adjusted $R^2 = 0.13$, $P < 0.001$). When combined (Model 3, Table 3), however, the riparian fragmentation metric (AI) was no longer significant

Table 3
Seven distinct models for the relationship between riparian and watershed vegetation patterns and instream biological conditions (B-IBI).

Model	Model number	Parameters	Standardized beta coefficient	T-value	Significance	Adjusted R^2
Riparian	1	Percent riparian forest	0.22	7.48	***	0.56
	2	Aggregation riparian forest	19.63	7.14	**	0.13
Combined riparian	3	Percent riparian forest	23.86	3.51	***	0.58
		Aggregation riparian forest	−1.70	6.67	0.12	
Landscape	4	Percent watershed forest	19.46	2.45	***	0.59
	5	Aggregation watershed forest squared	16.41	1.71	***	0.68
Riparian and landscape	6	Percent riparian forest	13.09	2.23	***	0.77
		Percent watershed forest	13.22	2.11	***	
	7	Percent riparian forest	11.11	2.24	***	0.79
		Aggregation watershed forest squared	11.60	1.68	***	

*** Significance is <0.001.

Table 4
Non-parametric analysis using Mantel's test to describe the relationship between riparian and watershed vegetation conditions and B-IBI.

	Dependent variable			
	No controls	Control Distance of sampling sites[a]	Percent riparian forest[a]	Basin forest aggregation index[a]
Mantel's r	0.49	0.44	0.45	0.45
Significance	**	**	**	**

[a] B-IBI.
** $P < 0.001$.

(adjusted $R^2 = 0.58$, $P = 0.12$) for any model including the fragmentation of riparian vegetation. In the latter case the results were not responsive possibly due to a minimum number of representative pixels. Since FRAGSTATS examines the adjacency of land cover pixels to describe the degree of fragmentation, the fewer pixels available in a study location, the higher the probability of unresponsive or erroneous results (He et al., 2000; Jaeger, 2000). The watershed alone and watershed combined with the riparian vegetation (Models 4–7, Table 3) were all significant, with the aggregation of watershed forest having the strongest relationship (adjusted $R^2 = 0.67$). Together the percent riparian vegetation and watershed fragmentation of vegetation (Model 7, Table 3) explained the greatest amount of variability in B-IBI across all study basins (adjusted $R^2 = 0.79$, $P < 0.001$).

Neither of the diagnostics measuring the sufficiency of the model or the independence of errors exhibited a systematic pattern, suggesting that the model fits the data well. However, the high degree of collinearity between watershed vegetation metrics (e.g., percent of basin forest and basin forest aggregation index) prevented, as in the previous regression analysis, the application of a Mantel's test that would include both variables at the watershed scale. When controlling for the watershed-level influences separately from the spatial distribution of sampling sites, the percent of riparian forest remained significant with only a minor change in the partial correlation value (Table 4). The correlation between the amount and distribution of riparian and watershed vegetation described by the Mantel's test corroborates results from the parametric regression analysis.

4. Discussion

Our study emphasized the measurement of spatial vegetation patterns – as defined by amount and fragmentation of vegetation – across riparian and watershed scales. We can reject our first null hypothesis because the percent of riparian vegetation was significantly correlated to instream biological conditions, while controlling for amount of watershed vegetation. Alternatively, the distribution of riparian vegetation, as characterized here by riparian AI, did not remain significant when considered with watershed vegetation. In addition, results from Model 7 (Table 3) and the Mantel's test (Table 4) suggest that the percent of riparian forest was significant, even when holding both the amount of basin vegetation and aggregation of watershed vegetation constant.

The second null hypothesis stated that fragmentation of upland vegetation is not related to instream biological conditions. Since both the simple regression between the fragmentation of vegetation (as described by AI and B-IBI) and the multiregression, consisting of riparian vegetation amounts and fragmentation, provided the strongest correlation with instream biological conditions, we can reject the second hypothesis. However, the high level of collinearity in the relationship between the percent of watershed vegetation and the aggregation of vegetation did not allow confirmation of the relationship between fragmentation and B-IBI. To assess unequivocally whether the fragmentation of vegetation

explained instream biological conditions would have required comparing watersheds with equal amounts of vegetation and variable levels of aggregation—a phenomenon that is difficult to find due to the spatial patterning of urban developments.

Our findings confirm a strong relationship between the amount of riparian and watershed vegetation and instream biological condition as demonstrated in previous studies (Richards and Host, 1994; Allan et al., 1997; Lambert and Allan, 1999; Wang et al., 2001; Dovciak and Perry, 2002; Fausch et al., 2002; Roy et al., 2003, 2007). Our results also suggest a need to further explore the role of vegetation fragmentation as it affects macroinvertebrate assemblages, and that the combination of the amount of riparian vegetation and contiguity of upland vegetation best explains the greatest variation of B-IBI scores in the study region. While other authors have suggested extending the reach of BMPs to include watershed-wide measures such as impervious surface limits on development (Schueler, 1994; May et al., 1997), little attention has been given to the role of the aggregation of forest patches by land use planners.

Current watershed management relies on BMP approaches, including containment of runoff from roads and bridges, stormwater detention systems, and riparian buffers. These strategies involve isolated conservation measures where areas are considered localized 'hot-spots' or environmentally sensitive areas (Francis et al., 2004). Land use regulations in upland areas of the watershed continue to permit activities which fragment forest patches—practices that are not allowed along riparian corridors (Randolph, 2004). Even with large buffers along all portions of a stream, an absence of contiguous forest in the upland areas may not be sufficient in protecting instream biology from urban development. For example, decisions about the placement of road networks can impact the configuration of forest patches in upland areas by fragmenting previously contiguous forest patches (Forman et al., 2002). Addressing multiple scales of management may allow land use regulations to move beyond the piece-meal, parcel-based approach that currently governs urban landscapes to one that considers regional (or ecological boundary-based) approaches to managing watersheds (Linehan et al., 1995; Johnson et al., 1999). Watershed management regulations that target the configuration of upland forests (e.g., distribution, location) may provide a means to begin examining a broader-scale approach to managing urban watersheds.

While our study does not address mechanisms through which the fragmentation of upland vegetation affects instream biological conditions, these results do suggest that multiple mechanisms may be operating at the different scales to affect aquatic conditions. Urban development has the twofold effect of breaking formerly contiguous patches of forest and introducing impervious surfaces. As a result, runoff frequency, volumes, and peak flow rates increase, while stream channels respond by increasing their cross-sectional area to accommodate the higher flows—through widening their stream channels, down-cutting their streambeds, or both (Lenat and Crawford, 1994; Boyer et al., 2002). In turn, changes to the benthic substrates, dissolved oxygen levels, sediment loading and bank erosion, and pollutant loading impact aquatic biota (Naiman

and Decamps, 1997; Naiman and Bilby, 1998; Hession et al., 2003; Palmer et al., 2000). Moreover, due to the loss of upland tracts of forest, flows are concentrated and less likely to be dispersed within the riparian area greatly reducing the potential for pollutant removal by riparian vegetation (Dillaha et al., 1989). Explicitly exploring which mechanisms explain these results could add important insight to this research.

Because environmental characteristics influence the aquatic systems through mechanistic pathways operating at multiple spatial and temporal scales, understanding the structure and dynamics of macroinvertebrate communities in streams, including their responses to human disturbance, requires caution when interpreting results. Vegetation pattern is one of five factors (Karr, 1999) associated with instream biological integrity and cannot account fully for the complexity of factors that explain the variability in biota. For example, streams with greater percentage of forest are likely to also have channel morphology that dictates improved habitat for benthic invertebrates. Since watershed and riparian forests is partially related to channel form (Naiman and Decamps, 1997; Allan, 2004), further research is required to assess the extent of the affect of channel form and the other factors on instream biological conditions.

In addition, in urban watersheds riparian vegetation is often difficult to increase due to the fact that these areas are predominately in private land holdings, and land owners are varied in their preferences for increasing vegetation amounts (Shandas, 2007). Associational studies are limited because they cannot exclude potential confounding variables or prove causation, nor can they explicitly identify what mechanisms operate at multiple scales. We can only suggest that known hydrologic, geomorphologic, and chemical mechanisms can explain the relationship between vegetation and macroinvertebrate assemblages (Pratt et al., 1981; Poff and Ward, 1989; Lenat and Crawford, 1994; Quinn and Hickey, 1994; Clausen and Biggs, 1997; Dole-Olivier et al., 1997). Also, we do not consider other biological interactions occurring within the stream or adjacent riparian areas, such as which specific vegetation characteristics (e.g., species composition, age) impact aquatic condition.

In heavily urbanized and urbanizing watersheds, removal of impervious surfaces may pose formidable challenges, and be prohibitively expensive (Kaiser et al., 1995). As an alternative watershed management approach, manipulation of vegetation by connecting fragmented patches of forest may help regulate runoff frequency, volumes, and peak flow rates across the whole watershed, and, as a result, provide a means for improving watershed health without the formidable challenges associated with removal of impervious surfaces. While the amount of vegetation and impervious surface may be correlated at the watershed scale, by focusing on the vegetation in watershed, environmental planners work at the parcel scale and can affect the location of vegetation through numerous land use planning tools. Several mechanisms in environmental planning enable connecting fragmented patches of vegetation if the land is owned by a private party, including: outright purchase, conservation easements, purchase of land with leaseback, lease, or undivided interest (Trust for Public Land, 2002).

5. Conclusions

A result of the urbanization process is the fragmentation of previously contiguous patches of vegetation (Paul and Meyer, 2001). Much of our understanding of the impact of vegetation fragmentation on ecosystems has focused on the demographic effects on bird and mammal populations (Ambuel and Temple, 1983; Freemark and Collins, 1992; Robinson et al., 1995; Tewksbury et al., 1998).

By building on such research, this study examines the role of forest fragmentation on aquatic conditions. Quantifying the role of both the riparian and upland areas of 51 nested watersheds in the Puget Lowland, we identified the role of vegetation amount and distribution that may have adverse affects on aquatic condition.

This study provides empirical evidence for the joint influence of upland and riparian conditions on stream biotic conditions. While we cannot provide watershed managers with specific standards and thresholds for developing policies aimed at protecting urban watersheds, these findings indicate: (1) the further research into the hydrologic relationship between upland and riparian areas; and (2) the need for urban and regional planning agencies to account for both the vegetation amount and distribution within the watershed. We hope that these results provide a critical lens to view current watershed planning practices in urbanizing regions by demonstrate the importance of linking watershed management with land use planning at the local and regional scale. Future studies should closely examine the mechanisms linking whole-watershed with riparian vegetation distribution so that a better understanding of how and where to emphasize aquatic protection measures can emerge.

References

Alberti, M., 2005. The effects of urban patterns on ecosystem function. International Regional Science Review 28 (2), 168–192.
Alberti, M., Booth, D., Hill, K., Coburn, B., Avolio, C., Coe, S., Spirandelli, D., 2007. The impact of urban patterns on aquatic ecosystems: an empirical analysis in Puget lowland sub-basins. Landscape and Urban Planning 1, 345–361.
Alberti, M., Weeks, R., Coe, S., 2004. Urban land-cover change analysis in central Puget Sound. Photogrammetric Engineering & Remote Sensing 70, 1043–1052.
Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on river ecosystems. Annual Reviews of Ecology, Evolution and Systematics 35, 257–284.
Allan, J.D., Johnson, L.B., 1997. Catchment-scale analysis of aquatic ecosystems. Freshwater Biology 37, 107–111.
Allan, J.D., Erickson, D.L., Fay, J., 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology 37, 149–161.
Ambuel, B., Temple, S.A., 1983. Area-dependent changes in bird communities and vegetation of southern Wisconsin forests. Ecology 64, 1057–1068.
Booth, D.B., Jackson, C.R., 1997. Urbanization of aquatic systems-degradation thresholds, stormwater detention, and limits of mitigation. Journal of American Water Resources Association 33 (5), 1077–1090.
Booth, D.B., Karr, J.R., Schauman, S., Konrad, C.P., Morley, S.A., Larson, M.G., Burges, S.J., 2004. Reviving urban streams: land use, hydrology, biology, and human behavior. Journal of the American Water Resources Association 40 (5), 1351–1364.
Boyer, E.W., Goodale, C.L., Jaworski, N.A., Howarth, R., 2002. Anthropogenic nitrogen sources and relationships to riverine nitrogen export in the northeastern U.S.A. Biogeochemistry 57–58, 137–169.
Braak, C.J.F., Van Tongeren, O.F.R., 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press.
Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Sala, O.E., Reynolds, H.L., Hooper, D.U., Mack, M., Diaz, S.E., Hobbie, S.E., Lavorel, S., 2000. Consequences of changing biodiversity. Nature 405, 234–242.
Clausen, B., Biggs, B.J.F., 1997. Relationships between benthic biota and hydrological indices in New Zealand Streams. Freshwater Biology 38, 327–342.
Dale, V.H., Offerman, H., Pearson, S., O'Neill, R.V., 1994. Effects of forest fragmentation on neotropical fauna. Conservation Biology 8, 1027–1036.
Dutilleul, P., Stockwell, J.D., Frigon, D., Legendre, P., 2000. The Mantel test versus Pearson's correlation analysis: assessment of the differences for biological and environmental studies. Journal of Agricultural, Biological and Environmental Statistics 5, 131–150.
Dillaha, T.A., Renear, R.B., Mostaghimi, S., Lee, D., 1989. Vegetative filter strips for agricultural nonpoint source pollution control. Transactions of the American Society of Agricultural Engineers 32 (2), 513–519.

Doberstein, C.P., Karr, J.R., Conquest, L.L., 2000. The effect of fixed-count sub-sampling on macroinvertebrate biomonitoring in small streams. Freshwater Biology 44, 355–371.

Dole-Olivier, M.J., Marmonier, P., Beffy, J.L., 1997. Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium? Freshwater Biology 37, 257–276.

Dorney, J.R., Guntenspergen, G.R., Keough, J.R., Stearns, F., 1984. Composition and structure of an urban woody plant community. Urban Ecology 8, 69–90.

Dovciak, A., Perry, J.A., 2002. In search of effective scales for stream management: does agroecoregion, watershed, or their intersection best explain the variance in stream macroinvertebrate communities? Environmental Management 30 (3), 365–377.

Fausch, K.D., Torgersen, C.E., Baxter, C.V., Li, H.W., 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52, 483–498.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.K., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574.

Fore, L.S., Karr, J.R., Wisseman, R.W., 1996. Assessing invertebrate responses to human activities: evaluating alternative approaches. Journal of North American Benthological Society 15 (2), 212–231.

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., 2002. Road Ecology: Science and Solutions. Island Press, Washington.

Fortin, M.J., Payette, S., 2002. How to test the significance of the relation between spatially autocorrelated data at the landscape scale: a case study using fire and forest maps. Ecoscience 9, 213–218.

Francis, T.B., Whittaker, K.A., Shandas, V., Mills, A., Graybill, J., 2004. Incorporating science into the environmental policy process: a case study from Washington State. Ecology and Society 10 (1), 35–42.

Freemark, K., Collins, B., 1992. Landscape ecology of birds breeding in temperate forest fragments. In: Hagan, J.M., Johnson, D.W. (Eds.), Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press, Washington, DC, pp. 443–454.

Gergel, S.E., Turner, M.G., Miller, J.R., Melack, J.M., Stanley, E.H., 2002. Landscape indicators of human impacts to riverine systems. Aquatic Sciences 64, 118–128.

Gore, J.A., 1996. Responses of aquatic biota to hydrological change. In: Petts, G.E., Calow, P. (Eds.), River Biota: Diversity and Dynamics. Blackwell Science.

He, H.S., DeZonia, B.E., Mladenoff, D.J., 2000. An aggregation index (AI) to quantify spatial patterns on landscapes. Landscape Ecology 15, 591–601.

Herzog, F., Lausch, A., 2001. Supplementing land-use statistics with landscape metrics: some methodological considerations. Environmental Monitoring and Assessment 72, 37–50.

Hession, W.C., Pizzuto, J.E., Johnson, T.E., Horowitz, R.J., 2003. Influence of bank vegetation on channel morphology in rural and urban watersheds. Geology 31 (2), 147–150.

Jaeger, J., 2000. Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landscape Ecology 15 (2), 115–130.

Johnson, K.N., Swanson, F., Herring, M., Greene, S. (Eds.), 1999. Bioregional Assessments—Science at the Crossroads of Management and Policy. Island Press, Washington.

Kaiser, E.J., Godschalk, D.R., Stuart, C.F., 1995. Urban Land Use Planning. University of Illinois Press, Chicago.

Karr, J.R., 1991. Biological integrity: a long-neglected aspect of water resource management. Ecological Applications 1, 66–84.

Karr, J.R., 1999. Defining and measuring river health. Freshwater Biology 41, 221–234.

Karr, J.R., Chu, E.W., 1999. Restoring Life in Running Waters: Better Biological Monitoring. Island Press.

Karr, J.R., Fausch, K.D., Angermeirer, P.L., Yant, P.R., Schlosser, I.J., 1986. Assessing Biological Integrity in Running Waters: A Method and Its Rationale. Illinois Natural History Survey Special Publication 5.

Karr, J.R., Rossano, E.M., 2001. Applying public health lessons to protect river health. Ecology and Civil Engineering 4 (1), 3–18.

Kearns, B.L., Karr, J.R., 1994. A Benthic Index of Biotic Integrity (B-IBI) for rivers of the Tennessee Valley. Ecological Applications 4, 768–785.

King County, 2000. King County Spatial Data Warehouse (KCSDW), high resolution satellite image, EMERGE dataset. Available at: http://www.metrokc.gov/gis/sdc/raster/ortho/ (accessed on April 20, 2003).

King, R.S., Baker, M.E., Whigham, D.F., Weller, D.E., Jordan, T.E., Kazyak, P.F., Hurd, M.K., 2005. Spatial considerations for linking watershed land cover to ecological indicators in streams. Ecological Applications 15 (1), 137–153.

Kleindl, W.J., 1995. A benthic index of biotic integrity for Puget Sound lowland streams, Washington, USA. MS Thesis. University of Washington, Seattle.

Klien, R.D., 1979. Urbanization and stream quality impairment. Journal of the American Water Resources Association 15 (4), 1211–1219.

Konrad, C.P., Booth, D.B., 2002. Hydrologic Trends Resulting from Urban Development in Western Washington Streams. U.S. Department of the Interior. Investigation Report, Water-Resources 02-4040. U.S. Geological Survey.

Lambert, M., Allan, J.D., 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environmental Management 23, 257–270.

Lasmanis, R., 1991. The geology of Washington. Rocks & Minerals 66, 262–276.

Legendre, P., Legendre, L., 1998. Numerical Ecology, second edition. Elsevier.

Legendre, P., 2000. Comparison of permutation methods for the partial correlation and partial Mantel tests. Journal of Statistical Computation and Simulation 67, 37–73.

Lenat, D.R., Crawford, K.J., 1994. Effects of land use on water quality and aquatic biota of three North Carolina Piedmont streams. Hydrobiologia 294, 185–199.

Linehan, J., Gross, M., Finn, J., 1995. Greenway planning: developing a landscape ecological network approach. Landscape and Urban Planning 33 (1–3), 179–193.

Malmqvist, B., 2002. Aquatic invertebrates in riverine landscapes. Freshwater Biology 47, 679–694.

May, C.W., Horner, R.R., Karr, J.R., Mat, W.B., Welch, E.B., 1997. Effects of urbanization on small streams in the Puget Sound Lowlands Ecoregion. Watershed Protection Techniques 2, 485–494.

May, C.W., 1996. Assessment of cumulative effects of urbanization on small streams in the Puget Sound Lowland ecoregion: implications for salmonid resource management. Ph.D. Dissertation. University of Washington, Department of Civil Engineering, Seattle.

Morley, S.A., 2000. Effects of urbanization on the biological integrity of Puget Sound lowland streams: restoration with a biological focus. M.S. Thesis. University of Washington, Seattle.

Morley, S.A., Karr, J.R., 2002. Assessing and restoring the health of urban streams in the Puget Sound Basin. Conservation Biology 16, 1498–1509.

McDonnell, M.J., Pickett, S.T.A., Pouyat, R.V., 1993. The application of the ecological gradient paradigm to the study of urban effects. In: McDonnell, M.J., Pickett, S.T.A. (Eds.), Humans as Components of Ecosystems. Springer-Verlag, New York, NY, pp. 175–189.

McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS: spatial pattern analysis program for categorical maps, Accessed no November 10, 2008 at www.umass.edu/landeco/research/fragstats/fragstats.html.

Naiman, R.J., Decamps, H., 1997. The ecology of interfaces: riparian zones. Annual Review of Ecological Systems 28, 621–658.

Naiman, R.J., Bilby, R.E., 1998. River Ecology and Management. Springer Verlag, New York.

Omernik, J.M., Gallant, A.L., 1986. Ecoregions of the Pacific Northwest, EPA/600/3-86/033. Environmental Research Lab, Corvallis, OR, USA.

Osborne, L.L., Wiley, M.J., 1988. Empirical relationships between land use/cover and stream water quality in an agricultural watershed. Journal of Environmental Management 26, 9–27.

Palmer, M.A., Swan, C.M., Nelson, K., Silver, P., Alvestad, R., 2000. Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. Landscape Ecology 15, 563–576.

Paul, M.J., Meyer, J.L., 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32, 333–365.

Peterjohn, W.T., Correll, D.L., 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology 65, 1466–1475.

Pimm, S.L., Raven, S.L., 2000. Extinction by numbers. Nature 403, 843–845.

Poff, L.N., Ward, J.V., 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46, 1805–1817.

Postel, S.L., Daily, G.C., Ehrlich PR, 1996. Human appropriation of available fresh water. Science 271, 785–788.

Pratt, J.M., Coler, R.A., Godfrey PJ, 1981. Ecological effects of urban stormwater runoff on benthic macroinvertebrates inhabiting the Green River, Massachusetts. Hydrobiologia 83, 29–42.

PSRC (Puget Sound Regional Council), 2002. Puget Sound Milestones: Population, Employment and Housing, 1995–2000. Accessed on September 18, 2008 at http://www.psrc.org/projects/monitoring/peh.htm.

PSRC (Puget Sound Regional Council), 2005. Growth Management By the Numbers: Population, Household, and Employment Growth Targets in the Central Puget Sound Region. Accessed on Sept 18, 2008 at: http://www.psrc.org/projects/monitoring/growthtargets/index.htm.

Quinn, J.M., Hickey, C.W., 1994. Hydraulic parameters and benthic invertebrate distributions in two gravelbed New Zealand rivers. Freshwater Biology 32, 489–500.

R Development Core Team, 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Randolph, J., 2004. Environmental Land Use Planning and Management. Island Press, Washington, DC.

Richards, C., Host, G.E., 1994. Examining land use influences on stream habitats and macroinvertebrates: a GIS approach. Water Resources Bulletin 30, 729–738.

Richards, C., Johnson, L.B., Host, G.E., 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences 53, 295–311.

Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R., Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267, 1987–1990.

Roth, N.E., Allan, J.D., Erickson, D.L., 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11, 141–156.

Roy, A., Rosemond, A.D., Paul, M.J., Leigh, D.S., Wallace, J.B., 2003. Stream macroinvertebrate response to catchment urbanization (Georgia, USA). Freshwater Biology 48, 329–346.

Roy, A.H., Freeman, B.J., Freeman, M.C., 2007. Riparian influences on stream fish assemblage structure in urbanizing streams. Landscape Ecology 22 (3), 385–402.

Schueler, T.R., 1994. The importance of imperviousness. Watershed Protection Techniques 1 (3), 100–111.

Shandas, V., 2007. An empirical study of streamside landowners' interest in riparian conservation. Journal of the American Planning Association 72 (2), 173–184.

Simpson, J.W., Boerner, R.E.J., DeMers, M.N., Berns, L.A., Artigas, F.J., Silva, A., 1994. Forty-eight years of landscape change on two contiguous Ohio landscapes. Landscape Ecology 9, 261–270.

Smouse, P.E., Long, J.C., Sokal, R.R., 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Systemic Zoology 35, 627–632.

Snyder, C.D., Young, J.A., Villella, R., Lemarié, D.P., 2003. Influences of upland and riparian land use patterns on stream biotic integrity. Landscape Ecology 18 (7), 647–664.

Stauffer, J.C., Goldstein, R.M., Newman, R.M., 2000. Relationship of wooded riparian zones and runoff potential to fish community composition in agricultural streams. Canadian Journal of Fisheries and Aquatic Science 57, 307–316.

Strayer, D.L., Beighley, R.E., Tompson, L.C., Brooks, S., Nilsson, C., Pinay, G., Naiman, R., 2003. Effects of land cover on stream ecosystems: roles of empirical models and scaling issues. Ecosystems 6 (5), 407–423.

Stewart, J.S., Wang, L.Z., Lyons, J., Horwatich, J.A., Mannerman, R., 2001. Influences of watershed, riparian-corridor, and reach-scale characteristics on aquatic biota in agricultural watersheds. Journal of American Water Resources Association 37, 1475–1487.

Tockner, K., Ward, J.V., Edwards, P.J., Kollmann, J., 2002. Riverine landscapes: an introduction. Freshwater Biology 47, 497–500.

Trimble, S.J., 1997. Contribution of stream channel erosion to sediment yield from an urbanizing watershed. Science 278, 1442–1444.

Trust for Public Land, 2002. Local Greentprinting for Growth, vol. 1. http://www.tpl.org/tier3_cd.cfm?content_item_id=10648&folder_id=175 (accessed January 20, 2005).

Turner, M.G., Gardner, R.H., O'Neil, R.V., 2001. Landscape Ecology in Theory and Practice: Pattern and Process. Springer.

Turner, M.G., Gardner, R.H., 1991. Quantitative methods in landscape ecology: an introduction. In: Turner, M.G., Gardner, R.H. (Eds.), Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity. Springer-Verlag.

Tewksbury, J.J., Hejl, S.J., Martin, T.E., 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79 (8), 2890–2930.

Urban, D.L., Goslee, S., Pierce, K.B., Lookingbill, T.R., 2002. Extending community ecology to landscapes. Ecoscience 9, 200–212.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37, 130–137.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, H., 1997. Human domination of Earth's ecosystems. Science 277, 494–499.

Vörösmarty, C.J., Green, P., Salisbury, J., Lammers, R.B., 2000. Global water resources: vulnerability from climate change and population growth. Science 289, 284–288.

Wang, L., Lyons, J., Kanehl, P., 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management 28, 255–266.

Wang, L., Lyons, J., Kanehl, P., 2002. Effects of watershed best management practices on habitat and fish in Wisconsin streams. Journal of the American Water Resources Association 38, 663–680.

Ward, A.D., Elliot, W.J. (Eds.), 1995. Environmental Hydrology. CRC Press.

Weigel, B.M., Wang, L., Rasmussen, P.W., Butcher, J.T., Stewart, P.M., Simon, T.P., Wiley, M.J., 2003. Relative influence of variables at multiple spatial scales on stream macroinvertebrates in the Northern Lakes and Forest Ecoregion, USA. Freshwater Biology 48, 1440–1461.

Vivek Shandas is an assistant professor in the Nohad A. Toulan School of Urban Studies and Planning and a research associate in the Center for Urban Studies at Portland State University.

Marina Alberti is an associate professor of Urban Design and Planning and the director of the Urban Ecology Research Lab at the University of Washington.