

DISSERTATION

**LAND USE INFLUENCES ON ADJACENT ECOLOGICAL SYSTEMS:
IMPLICATIONS FOR CONSERVATION PLANNING**

Submitted by

Alisa Ann Wade

Department of Geosciences

In partial fulfillment of the requirements
for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, CO

Summer 2009

UMI Number: 3385185

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

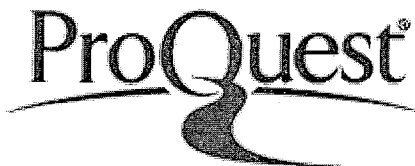
In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



UMI 3385185

Copyright 2009 by ProQuest LLC.

All rights reserved. This edition of the work is protected against unauthorized copying under Title 17, United States Code.



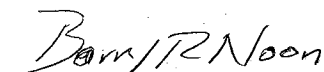
ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

COLORADO STATE UNIVERSITY

June 5, 2009

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER
OUR SUPERVISION BY ALISA A. WADE ENTITLED LAND USE INFLUENCES
ON ADJACENT ECOLOGICAL SYSTEMS: IMPLICATIONS FOR
CONSERVATION PLANNING BE ACCEPTED AS FULFILLING IN PART
REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

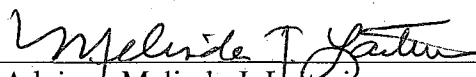
Committee on Graduate work



Barry R. Noon



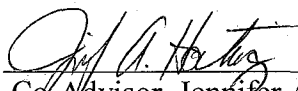
N. Thompson Hobbs



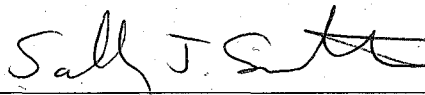
Advisor Melinda J. Lantieri



Co-Advisor David M. Theobald



Co-Advisor Jennifer A. Hoeting



Department Head Sally J. Sutton

ABSTRACT OF DISSERTATION

LAND USE INFLUENCES ON ADJACENT ECOLOGICAL SYSTEMS: IMPLICATIONS FOR CONSERVATION PLANNING

This research investigated the spatial relationships between land uses, primarily urbanization, and adjacent ecological systems. As anthropogenic stressors encroach on protected areas and aquatic systems, the ecological functioning of those systems is reduced, and this has implications for natural resource management and conservation. I conducted three separate studies to address different research questions relating to land use and land cover – ecological system linkages.

I assessed the vulnerability of conservation lands throughout the U.S. to adjacent anthropogenic threats and identified protected lands that are likely threatened by human activities as well as unprotected lands that offer opportunities for future conservation action. I also quantified the amount of residential development encroachment surrounding protected lands in the U.S., and I quantified how encroachment has altered the landscape structure around conservation lands nationally from 1970 through 2000, and forecast changes for years 2000 through 2030. Results from these two studies showed that there are a number of protected areas that are vulnerable to neighboring threats and that development has both reduced the buffer surrounding and the connectedness between protected areas. However, results also suggested that there are a number of options for future conservation action, although continued urbanization will limit these options.

These studies indicate that conservation planning must consider adjacent land uses. However, the final study presented in this dissertation illustrated that conservation scientists and land managers must recognize the limitations of their approach when modeling the relationships between ecological systems and adjacent land use. I used a conceptual model of how land cover at different upslope scales influences aquatic integrity to show how different modeling approaches can substantially alter resulting inference. Results suggest that a modeling approach that incorporates ecological knowledge may provide more relevant inference for management decisions. A finding applicable to all three studies is that a key conservation strategy will be to work cooperatively with adjacent land owners and managers to successfully manage both protected areas and aquatic systems.

Alisa A. Wade

Department of Geosciences

Colorado State University

Fort Collins, CO 80523

Summer 2009

DISCLAIMER

This research was supported in part by the U.S. Department of Agriculture (USDA) under National Needs Fellowship Grant 2002-38420-11713, the Environmental Protection Agency under the Science to Achieve Results (STAR) Fellowship Program, and the National Science Foundation under Integrative Graduate Education and Research Traineeship grant DGE-0221595. None of the supporting agencies have officially reviewed or endorsed this publication, nor do they endorse any products or commercial services mentioned in this dissertation. The views expressed here are solely those of the author.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my committee for their guidance, support, and encouragement through my doctoral studies. My advisor, Dr. Melinda Laituri, provided funding support, down-to-Earth advice, and a friendly ear, without which I could not have completed this work. My co-advisor, Dr. David Theobald, served as an inspiring mentor, with a cutting intellect and an easy personality, making collaboration a pleasure. Dr. Jennifer Hoeting, my second co-advisor, exhibited preternatural patience as I struggled through the statistics while making me feel at-ease with her laugh. There are not enough words of thanks for the encouragement provided by Dr. N. Thompson Hobbs; his dedication to teaching, mentorship, and science is truly inspiring. Finally, I thank Dr. Barry Noon for his time, interest, and questions which always challenged me and have made me a better scientist. It is a true honor to have worked with each of my committee members, and I am fortunate to have gathered such a spectacular group of scientists.

My research was supported through a National Needs Fellowship from the U.S. Department of Agriculture Grant #2002-38420-11713, the U.S. Environmental Protection Agency under the Science to Achieve Results (STAR) Fellowship Program, and the National Science Foundation Integrative Graduate Education and Research Traineeship (IGERT) Program Grant #DGE-0221595. I thank these funders for making this research possible.

Dr. Dan Kashian of Wayne State University, Nate Piekeliak and Dr. John Gross of the National Park Service, Dr. R. I. McDonald of The Nature Conservancy, Dr. Jodi Hilty of the Wildlife Conservation Society, and Dr. Andy Hansen of Montana State University all provided either helpful feedback on previous drafts of chapters in this dissertation or gave generously of their time in helping guide the research direction.

I am indebted to fellow-students John Norman, Sam Litschert, Pete Barry, Grant Wilcox, and Jeff Deems for their technical advice and friendship. Several members of my PRIMES cohort also provided valuable technical assistance.

Numerous friends deeply enriched my time in Fort Collins and went on the adventures with me that kept me sane, and I appreciate their friendship (and miss them all). Thanks also to my dear friends in California, Montana, and elsewhere.

My parents Jack and Norlyn Wade have provided a lifetime of support. Any successes in my life are because they taught me the values of tenacity, integrity, and hard work. A special thanks to my father for all those early years at the kitchen table helping me write book reports and making me look up the words in the dictionary.

Finally, my deepest thanks are to my family. Thank you to my husband, Andrew Wilcox, for his unflappable and steadfast support and his fearlessness in all things ranging from editing my work to washing the diapers. Thank you for being my best friend, biggest fan, and true love. I am especially grateful for my son, Peter Wilcox, for helping me keep everything in perspective. Thank you for your good-natured acceptance when I had to go to work and your cheery “it’s ok, mommy” when I felt overwhelmed. You are a superstar. And to Baby X, I hope you are not born too addicted to coffee.

TABLE OF CONTENTS

Chapter 1. Introduction to dissertation	1
1.1 Introduction.....	1
1.2 Research overview and objectives.....	3
1.3 Background	6
Chapter 2. Vulnerability of U.S. protected areas to local and adjacent threats	23
Abstract.....	23
2.1 Introduction.....	24
2.2 Methods.....	26
2.3 Results.....	34
2.4 Discussion and conclusions	36
Tables.....	41
Table 2.1. Threats to protected areas	41
Table 2.2. Values assigned to the four threat factors.....	42
Table 2.3. Assumed average speeds of travel by road type	43
Figures.....	44
Fig. 2.1. Schematic of the vulnerability matrix	44
Fig. 2.2. Map of threat factors.....	45
Fig. 2.3. Map of vulnerability categories.....	46

Fig. 2.4. Vulnerability category summary for the entire U.S. comparing protected vs. unprotected lands	47
Fig. 2.5. Vulnerability category summary for percent of area within 10 km of a national park.....	48
Chapter 3. Residential development encroachment on U.S. protected areas.....	49
Abstract.....	49
3.1 Introduction.....	50
3.2 Methods.....	52
3.3 Results.....	57
3.4 Discussion	62
Tables.....	68
Table 3.1. Method details for defining core, core edge, potential buffer, buffer zones, developed lands, clusters, and passageways	68
Figures.....	70
Fig. 3.1. Comparison of core, buffer area, and connectedness metrics for the 48 conterminous states.....	70
Fig. 3.2. Comparison of proportion of developable area between areas outside and within core edge that experienced development intensification.....	71
Fig. 3.3. Quadrants of encroachment	72
Fig. 3.4. Summary of change across or between study years 1970, 2000, and 2030	73
Chapter 4. How do hierarchal scales of upslope land cover interact to influence aquatic integrity?	75
Abstract.....	75

4.1 Introduction.....	76
4.2 Methods.....	79
4.3 Results.....	87
4.4 Discussion	89
Tables.....	96
Table 4.1. Adjusted R^2 and Akaike weights for single-scale regressions	96
Table 4.2. Models ranked by Akaike weights	97
Table 4.3. Model summary and analysis of variance for hierarchical multiple regression	98
Figures.....	99
Fig. 4.1. Gunpowder Hydrologic Unit, located in Maryland, USA.....	99
Fig. 4.2. Conceptual model of the interaction of urban and natural land cover at the catchment, riparian, and local scales.....	100
Chapter 5. Conclusions.....	101
5.1 Summary of research and conservation implications	101
5.2 Future research directions	103
Figures.....	109
Fig. 5.1. An example of a detailed conceptual model.....	109
Chapter 6. Reflections on my PhD experience	110
Literature cited.....	113
Appendix A. Logistic function for development threat factor.....	135
Appendix B. GIS analysis data and flowcharts.....	137

CHAPTER 1. INTRODUCTION TO DISSERTATION

1.1 Introduction

Understanding the spatial relationship between ecological stressors and ecological processes has emerged as a fundamental challenge for landscape ecologists (Wu & Hobbs 2002). This relationship is critical in the study of how anthropogenic land cover modification affects neighboring natural systems. Anthropogenic stressors, human activities that impair ecological processes (Salafsky et al. 2008), are likely the most important factor affecting ecological systems throughout the world (Vitousek et al. 1997; Terborgh 1999) and are the primary driver of species endangerment (Lande 1998; Wilcove et al. 1998; Czech et al. 2000). Research focusing on the interplay between human land cover modification and neighboring systems provides insight into pattern-process dynamics and assists land managers in gauging the potential impact from future modification of adjacent lands, helping them anticipate and manage for change (Clark et al. 2001).

In this dissertation, I consider several land uses, but focus on the impacts from urban development¹. Urbanization is particularly associated with decreased biodiversity and species richness (Harris & Silva-Lopez 1992; McKinney 2002; Walsh et al. 2005)

¹ I use the terms urban development and urbanization interchangeably, referring to increased number of housing units and associated intensification of infrastructure – including commercial development and transportation and utility infrastructure – regardless of the density of development. I use the terms urban density or urban housing density to refer to a specific density of residential development (units/ha).

and a reduction in ecological flows in both terrestrial and aquatic systems (Cole & Landres 1996; Weber et al. 2001; Hansen et al. 2002; Allan 2004). My research addresses human land use and land cover influences on two types of neighboring ecological systems, protected areas and aquatic systems. With urbanization often occurring most rapidly adjacent to protected areas (Frentz et al. 2004; McDonald et al. 2008) and river networks (Theobald et al. 1996), it is particularly important to understand the current spatial patterns of urbanization and likely relations with these neighboring ecological systems.

Protected areas, lands with formal, permanent protection from conversion of natural land cover and managed in whole or in part for conservation purposes (Jennings 2000), provide valuable ecosystem services and habitat (Millennium Ecosystem Assessment 2003; UNEP 2003). Because they increasingly represent the last large, contiguous, and relatively unmodified land areas, protected lands provide critical leverage points for future conservation actions (Margules & Pressey 2000). Protected areas also serve as optimal subjects for research into the spatial relationship between landscape modification and ecological impairment because they are relatively natural and open systems, whereby alterations in flows of biological, chemical, and physical matter and energy into the system produces significant effects (Cole & Landres 1996).

I also look at developed land uses in relation to aquatic systems because rivers serve as excellent indicators of broader system state, integrating conditions from throughout the watershed (Hynes 1975; Johnson & Gage 1997). Rivers and streams provide critical habitat for maintaining biodiversity, and they provide immeasurable ecosystem services for human health and well-being (Meyer et al. 2005). Anthropogenic

impacts have significantly altered both the structure and function of river systems (Postel & Richter 2003), and better defining the spatial relationship between land use and these systems is critical to conservation of aquatic species (Fausch et al. 2002; Wiens 2002).

1.2 Research overview and objectives

The research presented here investigates implications for conservation planning that arise from the spatial interactions between land use and land cover, primarily urbanization, and adjacent ecological systems. I explore three aspects of this dynamic relating to three primary research problems. The three studies include: a national assessment of landscape vulnerability to threats from human activities; a national summary of the potential impact to ecological processes on protected lands due to adjacent urbanization; and a study of how hierarchical spatial scales of land use influence aquatic integrity.

Assessing the vulnerability of an ecological system to threats from human activities requires consideration of both local and adjacent threats (Newmark 1985; Margules & Pressey 2000; Wilson et al. 2007). Threats are the human activities that degrade conservation targets (Salafsky et al. 2008). Yet most existing techniques focus solely on vulnerability to in-situ threats. In Chapter Two, I present a method to extend previous vulnerability assessments, creating an integrative vulnerability score that considers both local and adjacent threats. By using a novel conceptual model of the relationship between in-situ threats and contextual threats, I translate the vulnerability assessment into a spatially explicit evaluation of lands in the conterminous U.S. that have the capacity, or offer opportunities, for ecological conservation. The primary objective of this study is to explicitly map both where existing conservation lands are either

effectively buffered from surrounding human threats, or where adjacent land use likely threatens lands nominally considered protected. Further, I identify those lands that are not currently formally protected but that, because they are spatially disjoint from threatening human activities, may offer options for future conservation action. Chapter Two details a flexible, scalable tool to assist land managers in conducting more complete vulnerability assessments.

As human activities encroach on neighboring conservation lands, the ecological functioning of those lands is reduced (Noss 1983; Hansen & DeFries 2007). In Chapter Three, I look at residential housing development encroachment on lands formally protected for conservation purposes. Using a spatially explicit model of change in housing density for the years 1970-2030, I quantify the past impacts to existing conservation lands and forecast the implications for future conservation planning. This study's central objective is to provide a national summary of how, when, and where residential development affects the landscape context around conservation lands, likely altering the ecological integrity of the lands and limiting their capacity for conservation of natural resources and processes. This study provides conservation planners with a coarse-scale assessment of options for the eventual establishment of a national, comprehensive, conservation system, and assists land managers in identifying areas likely to become most threatened in the future.

Simple correlative studies of the spatial relationships between land use and land cover and neighboring systems fail to provide ecologically relevant insight (NRC 1995; Noon 2003). Instead, empirical analyses of ecological systems should be grounded in conceptual models based on first principles of ecology to better guide cause-effect

interpretation and to lead to statistical inference that is ecologically relevant (Lookingbill et al. 2007). Several past studies in aquatic ecology have sought to understand the spatial scale (extent) of upslope land use and land cover that most strongly influences aquatic integrity; yet, the statistical approaches employed have often ignored the known principles of aquatic spatial hierarchies. In Chapter Four, I apply a simple conceptual model of how land cover at different scales influences downstream aquatic integrity to inform different statistical approaches, and I trace how altering the focus from maximizing predictive power to partitioning influence between scales leads to different results and ecological inference. The objective of the study is to illustrate how incorporating ecological knowledge into the assessment of an ecological system may both advance our ecological understanding while also improving conservation management. The chapter suggests a general approach that may provide better guidance for today's management applications as well as for developing tomorrow's research questions.

All three research studies relied on Geographic Information Systems (GIS) to elucidate the spatial relationships between land use and land cover and neighboring ecosystems (Appendix A). In two of the studies (Chapters Two and Three), I use GIS to calculate travel time from an urban area (as opposed to a standard Euclidean distance) to provide a distance measure more relevant to assessing potential threats from human activities. In Chapter Four, I use GIS to calculate three scales of upstream accumulation from aquatic integrity sampling points. In all studies, GIS was used as the primary tool for organizing, extracting, and analyzing spatial data.

1.3 Background

This dissertation builds on a wide range of research areas in conservation planning, landscape ecology, vulnerability assessment, aquatic ecology, and ecological modeling. This section provides pertinent background information and reviews selected literature related to these topics.

1.3.1 Urban land use influences on adjacent ecological systems

A primary driver of land use and land cover change in the U.S. is the conversion of natural lands for residential housing development. In the United States, the increase in land area affected by residential development outpaced the population growth rate by 25 percent between 1980 and 2000, and it is estimated that in many regions of the U.S., this pace of development will continue or increase (Theobald 2005). The increasing ratio of land area consumed to population is partially explained by the recent explosion in residential development in exurban areas – areas of relatively low-density development outside of existing urban boundaries (Theobald et al. 2000).

Drawn to the “natural amenities” of scenery and nearby outdoor recreation, this low-density residential growth is often occurring in once distant landscapes, often near open lands and water features (Howe et al. 1997; Rasker & Hansen 2000). McGranahan (1999) found that rural population growth between 1970 and 1996 closely corresponded with a natural amenities index that included factors such as proximity to water, scenery, and recreational availability. While many previous studies have focused exclusively on impacts only from development in major urban areas, inclusion of exurban densities is critical as they cover five times the land area of urban areas (Theobald 2001) and are

particularly threatening to natural processes in relatively unaltered landscapes (Hansen et al. 2002).

Residential development and its associated infrastructure have been linked to alterations across a spectrum of ecological processes. Houses and roads fragment aquatic and riparian habitats, inhibiting species movement, isolating animals, and reducing the likelihood of recolonization of extirpated habitat areas (Theobald et al. 1996; Theobald 2000; McKinney 2002; Hansen et al. 2005). Urbanization is ranked as one of the foremost causes of species endangerment in the United States (Czech & Krausman 1997). Division of the landscape from roads and fences inhibits species movement, isolates animals, and reduces the likelihood of recolonization of extirpated habitat patches (Theobald et al. 1996; Trombulak & Frissell 2000). Residential development is further associated with increased introduction of non-native species of both plants and animals. Of particular concern is the introduction of ‘subsidized predators’, such as cats and dogs, that may reduce native wildlife populations far below the numbers that would be required to maintain native predator species (Soule et al. 1988). Housing in the wildland urban interface additionally alters disturbance processes, in part by encouraging fire suppression policies (Hobbs & Theobald 2001).

1.3.1.1 Urban land use influences on protected areas

Originally established in areas of low population density, protected areas are becoming islands in a sea of development, leading the National Park Service (NPS) to identify urban encroachment as a primary threat to park resources (GAO 1994). Protected areas serve as focal areas for habitat conservation and restoration efforts (Lathrop & Bognar 1998). Yet, many protected areas are threatened by shifts in the structure,

complexity, and fragmentation of their natural systems resulting from anthropogenic modifications of the landscape (Noss 1987).

Globally, human population growth near protected areas is expected to significantly degrade biodiversity by 2030 (McDonald et al. 2008). Hansen and Defries (2007) provide a review of the influences surrounding land uses have on protected areas, including reduction in the area for dynamic ecological processes, changes in the flows of information, genes, and biota in and out of protected areas, habitat loss and fragmentation, and increased edge effects from greater exposure to human activities. Of various land use types, urban land use is the most likely to affect all of these ecological processes (Hansen & DeFries 2007). These impacts to protected areas will be particularly detrimental under climate change, when species will require greater habitat area and connectivity (Hannah et al. 2007). Further, urban encroachment on protected areas may have a significantly negative impact on the availability of ecosystem services from protected areas, such as the production of foods and fibers (DeFries et al. 2007).

1.3.1.2 Residential development influences on aquatic systems

Allan (2004) provides a review of the influence of land use, including urban, on rivers, and both Booth and Reinelt (1993) and Walsh et al. (2005) review characteristics of the “urban stream syndrome” (as termed by Meyer et al. 2005). The associated increase in impervious surfaces from roads, parking lots, and rooftops is one of the best studied impacts from urbanization (see Schueler 1994; Brabec et al. 2002 for reviews), and stormwater runoff arising from imperviousness is likely the predominant driver of urban impacts to streams (Walsh et al. 2005). There may be a threshold at approximately 10% impervious cover where increased runoff and resulting modified peak discharge and

flood frequency strongly affect channel morphology, biota, vegetative succession, and water chemistry (Booth & Reinelt 1993; May et al. 1997).

Increased chemical pollutant loads are widespread in urban streams (Walsh et al. 2005), and increased concentrations of chemicals can be observed at relatively low levels of watershed urbanization (Hatt et al. 2004). Urban systems are designed to efficiently move stormwater out of developed areas, changing sediment supply and flow regime and resulting in morphological changes which in turn reduces channel complexity and thus stream and riparian habitat (Walsh et al. 2005). These chemical and morphological changes result in dominance by more tolerant aquatic species (Meyer et al. 2005). The growth of human populations further affects aquatic systems through increased demands for water, resulting in a greater number of channelizations, impoundments and lower water tables from aquifer pumping (Pringle 2000).

Roads and trails are associated with the spread of exotic species, increased sediment loading, and alterations in chemical composition of water resources, especially resulting from deicing salts and heavy metals, in addition to their contribution to flow regime alteration from imperviousness (Forman & Alexander 1998; Trombulak & Frissell 2000). Road dust may affect vegetation and nutrient cycling (Forman & Alexander 1998). Increased accessibility to open lands from roads and trails is associated with bank erosion, species disturbance, and fecal contamination of aquatic systems (Cole & Landres 1996; Forman & Alexander 1998). Greater numbers of housing units and roads are also directly related to increased air emissions from cars and home heating and cooling systems, and anthropogenic pollutants have been found in otherwise 'pristine' wildlands and water bodies, likely resulting from atmospheric transport and proximity to

developed areas (Heit et al. 1984). Nitrogen saturation may be occurring in wildlands via atmospheric pathways as well (Baron et al. 1985).

1.3.2 Measuring level of urbanization

The level of urbanization in an area can be measured in several ways. The U.S. Geological Survey created the Land Use and Land Cover data set, manually interpreting nine primary land-use categories from aerial photography. More recent techniques have been developed to automate urban land-cover detection from satellite imagery, although land use continues to be used as a general term. Theobald (2001) provides a listing of some of these techniques. The more recent National Land Cover Database (NLCD) (Vogelmann et al. 2001), obtained from classifying of 30-meter resolution Landsat satellite imagery from early- to mid-1990 into twenty-one land covers (Theobald 2001), is currently the most widely available and used means for identifying anthropogenic land cover. The U-Index (human use index) (O'Neill et al. 1988) is also commonly used, categorized by landscapes that have urban or agricultural land cover types. Data from the U.S. Census Bureau provide another source for urbanization data, often being used to measure population density at the county level, or more commonly, by metropolitan statistical areas (MSA) or urban areas (USCB 2000b).

Both of these methods tend to misestimate actual urbanization. Using urban land cover classifications tends to neglect large areas of low-density development not picked up in the imagery classification, while the use of MSAs may overbound metropolitan development while not including smaller developments outside the primary metropolitan areas (Theobald 2001). Theobald (2001) recommends the use of more fine-grained Census data, calculating housing density by census block groups. In the 2000 Census,

each census block contained approximately 250-550 housing units, with more than 250,000 block groups covering the (USCB 2000a). While population density data are used in some studies, housing density is a more robust indicator of land cover change from residential development as population counts are based on the primary place of residence and do not account for vacation and second homes (Theobald 2001).

Many studies also rely on road densities or “roaded area” (e.g., Stoms 2000), or percent impervious surfaces (see Brabec et al. 2002 for a review) to reflect human modification of the landscape. However, many of these measures of urbanization are collinear (King et al. 2005) so it is best to limit the number of urbanization measures used. There is some evidence that percent impervious surface is a more accurate measure across a wider range of urbanization (Center for Watershed Protection 1997), but the data is much more difficult to obtain and remote imagery classification errors can affect results. There are several indices that attempt to reflect the level of human-domination in a landscape as a single dimension as well (e.g., Aplet et al. 2000; Sanderson et al. 2002; Woolmer et al. 2008), and these may be of use for coarse-scale studies.

1.3.3 Assessing vulnerability of and impacts to ecological integrity

Evaluating the influences of surrounding land cover on the ecological integrity of neighboring natural systems can be done from a perspective of assessed vulnerability or measured impacts. Ecological integrity is defined as the characteristics that allow a natural system to remain stable in its capacity to self-repair and to maintain a balanced, adaptive community of organisms comparable to the region’s natural biota (Karr et al. 1986). In many instances, direct impacts to integrity are difficult to measure, or it is not even known how to measure the dimensions of integrity (Karr 1987). Further,

conservation planners often consider future scenarios of land cover change, and assessing vulnerability to forecast changes is often more tractable than modeling future impacts. Lastly, one of the most critical elements of conservation planning is to mitigate local and contextual activities that may threaten the conservation values and goals for a particular landscape (Sarkar et al. 2006).

Vulnerability is often defined as the likelihood of negative impacts to ecological systems caused by threatening processes (Pressey et al. 1996). Vulnerability assessments tend to measure one of three possible dimensions of vulnerability, imminence, intensity, and the impact of the threatening process or activity (Wilson et al. 2005), although most studies focus on imminence of the threat, because intensity and impact are more difficult to assess spatially (Wilson et al. 2005). Wilson et al. (2005) provide a review of vulnerability assessment methods, which generally consist of methods based on land use, environmental variables, threatened species, or expert opinion.

It is important to consider vulnerability throughout the planning process (Margules & Pressey 2000), but is particularly critical when designing conservation area networks and prioritizing conservation action (Wilson et al. 2005). Unfortunately, most conservation assessments methods for protected areas undervalue threats from external sources, despite a rising awareness of the need to consider external threats (Gaston et al. 2002; Reyers 2004). However, there has been a recent emphasis on how to better incorporate surrounding land use into conservation planning frameworks (Theobald et al. 2000; Cowling & Pressey 2003; Pierce et al. 2005; Pejchar et al. 2007), including by the IUCN (International Union for Conservation of Nature), where controversy has arisen over whether to expand IUCN categories to better incorporate working landscapes near

protected areas (Locke & Dearden 2005). One difficulty in including the multitude of external threats is in developing a method to combine information on different threatening processes (Sarkar et al. 2006). A second difficulty is the general inability to link threats to causal impacts, although this may only be viable in finer-scale studies (Gaston et al. 2002).

In studies that do not consider future scenarios or that are limited to a relatively narrowly defined ecological system, quantifiable metrics that serve as proxy indicators for ecological integrity can be used. Because aquatic systems tend to be relatively confined, proxy indicators have often been used in past research of land cover influences on aquatic integrity. While there is no consensus on the ideal indicator or suite of indicators for assessing aquatic ecology, relative consensus exists on an indicator's desired characteristics. Indicators should be easy to measure, have a fairly low error of measurement and stability over the measurement period, show a clear relationship with the processes of interest, rely on data that is not difficult to obtain, and provide mappable trends (Reuter 1998; Boulton 1999; Aspinall & Pearson 2000).

Older studies analyzing land cover impacts on aquatic resources have focused on chemical water parameters as indicators. Urbanization has been linked to nutrient loading of streams, particularly nitrogen and phosphorous (Osborne & Wiley 1988; Hunsaker & Levine 1995; May et al. 1997; Herlihy et al. 1998). Habitat indicators have also often been applied in studies of land cover influence on both aquatic and terrestrial systems, and the earliest studies considered physical characteristics, including catchment area and stream order for aquatic systems (Kuehne 1962; Hynes 1975).

Despite the difficulty of obtaining biotic parameters, many researchers believe that they better integrate all the processes that may affect aquatic systems across an entire watershed (Adams 2002). Karr (1999) stated that, as physical, chemical, evolutionary, and ecological processes have shaped local and regional biota, biotic indicators are the most integrative approach that account for watershed-scale effects. Because the biota is recognized as the usual endpoint for assessment of river degradation, there has been an increase in the use of biological measures (Norris & Thoms 1999).

Biotic indicators often rely on multimetric indices. By incorporating several measures that are responsive to a broad array of human actions, multimetric indices are believed to better reflect the intricate and composite interactions within an ecosystem (Karr 1993; Boulton 1999). The Index of Biotic Integrity (IBI) (Karr 1981) is a multimetric index that has become widespread in watershed assessments and studies. The IBI combines species richness, composition, trophic structure, and abundance into a single index. Originally developed to measure aspects of fish assemblages, the IBI has been more recently modified to consider benthic macroinvertebrate populations (BIBI), and macroinvertebrates are now used as one of the primary indicators of river health (Wallace et al. 1996). These multimetric indices are considered “rapid assessment” techniques, allowing for reduction in costs and a summary of results into a single score that can be understood across watershed comparisons and among non-specialists (Norris & Thoms 1999).

Land cover in the catchment has been shown to affect these indexes of biotic status (e.g., Wentz 2000; Snyder et al. 2003; Strayer et al. 2003). Numerous other studies have found similar relationships between urbanization and biotic indicators (e.g., Lenat &

Crawford 1994; Griffith et al. 2002; Davis et al. 2003; Gray 2004). Research has shown that less field-intensive and simpler biotic measures, such as the Ephemeroptera + Plecoptera + Tricoptera Index (EPTI, consisting of species considered highly sensitive to poor water quality), are equally effective in tracking changes in biotic health as compared to the more field-data intensive BIBI (Wallace et al. 1996). However, even the EPTI requires on-the-ground data collection; therefore availability of EPTI data is also limited.

Measures of habitat pattern and structure have become particularly popular as GIS and remote sensing technologies improve. These landscape ecological metrics attempt to quantify amount and arrangement of land cover in order to reflect land pattern change (Meyer & Turner 1994). It is unclear, however, whether landscape ecological metrics should be used as dependent or independent variables. Goodwin (2003) provides a review of studies using measures of landscape connectivity as dependent versus independent variables. He found that approximately 75 percent of the papers used a landscape connectivity measure as an independent variable to explain another ecological process. While indicative of trends, the use of landscape metrics as independent variables may fail to explain the underlying ecological mechanisms (Aspinall & Pearson 2000; Goodwin 2003). However, linking landscape metrics to biotic endpoints within an ecologically accepted conceptual model may avoid this problem to some degree (Noon 2003; Novotny et al. 2005).

Riparian structure is one example of a habitat characteristic that can be relatively easily calculated across broad areas using landscape structure metrics. Innis et al. (2000) summarize several potential riparian and floodplain indices obtained from remotely sensed imagery and other methods. Riparian cover is important for providing refugia

(Novotny et al. 2005), and Bunn et al. (1999) found that riparian connectivity and cover in Australian watersheds was a strong predictor of two stream ecological processes, benthic gross primary production and food web dynamics. Further, riparian cover influences water chemistry, controls stream temperature, and provides organic matter input (Pusey & Arthington 2003), and thus, the riparian structure can have a significant impact on biotic integrity (Rogers et al. 2002; Davis et al. 2003). Urbanization has been shown to reduce and fragment riparian vegetative cover (Sovern & Washington 1997; Davis et al. 2003), and urbanization and reduced riparian conditions often covary (Morley & Karr 2002; Walsh et al. 2005).

1.3.4 Ecological modeling concepts

1.3.4.1 Spatial propagation of influences in ecology

The analysis of how urbanization or land use influences neighboring systems implicitly assumes the physical transport of matter and processes across space. This is theoretically grounded in the discipline of ecosystem ecology, where systems are seen as open to flows of both energy and matter (Odum 1953), and the awareness that ecosystem dynamics are influenced by factors external to a system is now a predominant concept in ecology (Polis et al. 1997). While ecosystem ecology and biogeochemistry have tended to focus on vertical fluxes, recent attention has been given to lateral interactions in systems with ecological influences propagating via spatially mediated pathways (Reiners & Driese 2004). Polis et al. (1997) provide a useful review of studies and concepts of spatial transfer of biotic and abiotic factors in their paper on landscape influences on trophic dynamics, and Burke (2000) discusses approaches to assessing landscape influences on biogeochemistry.

Influence pathways can be modeled to represent the distance that matter and processes travel. Employing Euclidian straight-line distance assumes that space alone is the primary agent in impact modulation. However, failing to account for transport complexities, the over-simplicity of this approach may lead to spurious results (Wiley et al. 1997). The discipline of landscape ecology has probably applied the most advanced spatial treatments of flows and connectivity, reflecting an intrinsic concern with movement across landscapes (Reiners & Driese 2004). While studies of landscape ecology often focus on biotic movement, the role of intervening landscape heterogeneity in spatial transport is a concept with broader application. When distances are treated explicitly in landscape ecology, they are most often represented as percolation or diffusion processes across a heterogeneous habitat matrix. A common landscape ecology approach is the representation of effective connectivity (also called “functional distance”), which acknowledges that ecological processes respond to the physical components of the landscape (Berry 1993; Bennett 1999). For example, the distance between urbanization and a target indicator may be effectively shortened by steep channel slopes, erodable soils, and direct stream connectivity, while riparian zones and intervening vegetation serve as natural filters, thereby dampening propagation and increasing the effective distance (Naiman & Decamps 1990; Johnson & Gage 1997; Snyder et al. 2003). Theobald (2006) reviews methods for assessing effective distance and lists numerous recent examples of the application of effective distance in ecological studies. A frequently employed methodology draws on least-cost path analysis, which assigns a cost value to every cell in the landscape based on hypothesized levels of impedance arising from the underlying landscape structure, and then calculates the spatial path that accumulates the lowest cost

of travel, by traversing cells with the lowest assigned travel cost, when moving between two points (Theobald 2006).

1.3.4.2 Conceptual models incorporating ecological knowledge

Assessing the relationship between anthropogenic threats and measures of ecological condition is best conducted conceptual mechanistic model of the studied system in order to provide insight into cause-effect relationships (Barber 1994; NRC 1995; Noon et al. 1999; Busch & Trexler 2003). Yet, many previous studies fail to apply a priori, conceptual models, hindering our understanding of ecological processes (Schindler 1995; Johnson & Gage 1997; Pickett 2000; Noon 2003; Benda et al. 2004). Conceptual models provide a structured expression of the a priori hypotheses about system function, allowing formal testing about how components and processes are related even when knowledge of the system is sparse (Manley et al. 2004). These a priori hypotheses are necessary in order to use correlative study findings for targeted decision making and successful monitoring and planning (Lehman 1986; Noon 2003). Further, conceptual models built from foundations of ecological theory provide a tractable means of investigating concepts that cannot be approached experimentally (Jackson et al. 2000; Noon 2003). These models are well seated in the emergent field of biocomplexity, focusing not on decomposing a complex problem within controlled experiments, but on the creation of new, interdisciplinary, integrative frameworks for assessment of complex questions (Michener et al. 2001).

Lorenz et al. (1997) provide a useful list of conceptual frameworks in aquatic ecology and suggests potential indicators that are linked to each concept. An example is the River Continuum Concept (RCC) (Vannote et al. 1980), which posits a linear system

of changes to biotic communities from headwaters to confluence. While one of the most important and ubiquitous conceptual models for river ecologists, the RCC fails to consider the broader landscape's influence on aquatic systems (Fausch et al. 2002). More recent frameworks focus on the hierarchical nature of aquatic system processes and heterogeneity (e.g., Benda et al. 2004).

1.3.4.3 Hierarchies in ecological systems

One concept of hierarchy in ecological systems is that of cascading processes, with general, coarse-scale processes filtering down to affect specific, local biota and processes. Numerous researchers have explored the hierarchical spatial nature of aquatic systems from large basins to microhabitats (e.g., Frissell et al. 1986; Poff 1997; Montgomery 1999; Fausch et al. 2002). Frissell et al. (1986) posited one of the classic hierarchical views of aquatic systems, with microhabitat nested within reaches nested within segments, which are in turn nested in the catchment. Environmental filters determine the biota and processes found at each scale. Frissell et al.'s (1986) model focuses on the riverine system, yet it has been long recognized that streams are strongly influenced by the characteristics of the surrounding watershed (Hynes 1975). In response, Poff (1997) expanded the idea of filter scales to include the interactions between both the terrestrial and aquatic systems. Watershed scale filters such as terrestrial geology affect general species and assemblage traits, while finer-scale local filters define unique individual species traits such as body morphology. This concept has been supported quantitatively, with Richards et al. (1996) finding surficial geology serving as important an influence on macroinvertebrate habitat and assemblages as land-use patterns at finer scales, and at coarser scales, geology-structure variables had an even greater influence.

Other ecologists agree that factors operating at coarser-scales may be important in controlling local-scale effects and must be accounted for to avoid spurious results, especially when considering processes across an entire watershed (Norris & Thoms 1999). Novotny et al. (2005) emphasize the need for an a priori outline of the hierarchical linkages between initial anthropogenic stressors that ultimately impact biotic assessment endpoints. The initial stresses are transmitted spatially across the landscape, following various pathways where they are transformed into proximal stressors to the biota (Novotny et al. 2005). Burcher et al. (2007) present a specific, tested version of this conceptual model, identifying a land-cover cascade that illustrates how abiotic mechanisms mediate upstream land-cover disturbance.

The second, obviously related, type of hierarchy is hierarchy of spatial scale. Foundational to the fields of ecology and landscape ecology, spatial hierarchies are perhaps the single most important concept in ecology (Levin 1992). Hierarchically scaled process models illustrate the concept that processes show heterogeneity and exert varying influence on a range of spatial and organizational scales (Allen & Starr 1982; Wiens 1989; Levin 1992). In aquatic systems, for example, the moderately fine scale of the riparian buffer is thought to play an important role disproportionate to its total land area, and therefore the riparian buffer's regulation of aquatic systems has been studied intensively (e.g., Osborne & Kovacic 1993; Vought et al. 1995). Many studies have sought to understand which spatial scale, as represented by extent of accumulated upstream and upslope flow, is more important to aquatic resource condition, comparing how land use in the riparian zone versus the entire catchment influences indicators of aquatic condition. Results are ambiguous as some studies have found that the finer

riparian buffer scale had the greatest impact (e.g., Dillaha et al. 1989; Carpenter et al. 1998; Lammert & Allan 1999), while others demonstrate that the entire catchment had greater influence (e.g., Osborne & Wiley 1988; Roth et al. 1996; Allan et al. 1997; Snyder et al. 2003). Allan (2004) provides a more extensive review of these studies.

However, most previous studies consider each scale separately, comparing predictive power for each individual scale. Fausch et al. (2002) contend that this failure is one of the greatest hindrances to furthered understanding of stream biology, proposing instead a continuous view of “riverscapes” that includes the full terrestrial and aquatic heterogeneity of the watershed across a spectrum of spatial scales. Based in landscape ecology’s recognition that how pattern affects process is scale dependent, Fausch et al. (2002) call for a model framework that accounts for both the varying importance of processes across scales as well as the interaction amongst scales. Model designs that explicitly incorporate the multi-scale hierarchies of aquatic systems can overcome the limits on analysis imposed by a single spatial scale (Fausch et al. 2002). A nested hierarchy of analysis permits scale to be explicitly assessed and modeled, allowing effects from general constraints to be measured at larger spatial extents and signals from mechanistic processes to be identified at smaller extents (Allen & Starr 1982).

Spatial scale relates directly to indicator selection, as different indicators of ecological integrity will respond differently to land use changes in the catchment, depending on the spatial extent at which they are measured (Johnson et al. 1997; Strayer et al. 2003). Therefore, considering indicator response across a range of scales increases analysis accuracy (Boulton 1999; Norris & Thoms 1999). Additionally, a greater range of spatial extents furthers understanding of thresholds at which specific indicators no longer

respond to the signal of land use change. Allan (2004) identifies non-linearities in aquatic system response to urbanization as one of the primary challenges for future research.

Finally, because humans disturb landscapes at multiple scales, optimally indicators measuring this disturbance should also be assessed at multiple scales (Wiens et al. 2002).

CHAPTER 2. VULNERABILITY OF U.S. PROTECTED AREAS TO LOCAL AND ADJACENT THREATS²

Abstract

Protected areas are vulnerable to threats from human activities, and these threats limit conservation options. Ensuring effective conservation and leveraging future conservation actions requires assessing a location's vulnerability to threats. Previous protected area assessments have focused on vulnerability to in-situ threats despite a long-standing consensus on the importance of adjacent, contextual threats. We present a method to extend previous approaches by integrating both in-situ and contextual threats into vulnerability assessments. We assess the spatial patterns of human activities that may threaten biodiversity and natural process and quantify an integrated vulnerability score. Using a novel, yet simple, conceptual model of the relationship between in-situ threats, contextual threats, and the potential conservation value of an area, we translate our vulnerability assessment into a spatially explicit evaluation of lands in the conterminous U.S. that have the capacity, or offer opportunities, for ecological conservation. We find the least vulnerable areas tend to overlay existing protected areas, but we map numerous locations where existing protected areas are vulnerable or where currently unprotected lands provide opportunities for future conservation. We identify regional patterns where

² This chapter is a manuscript, co-authored with David M. Theobald and Melinda J. Laituri, in review at *Landscape and Urban Planning*.

western core conservation areas are larger and better buffered from surrounding threats, but that conservation planning in the South and Northeast must rely on creating networks of stepping-stone conservation islands.

2.1 Introduction

Protected areas, lands with formal, permanent protection from conversion of natural land cover and managed in whole or in part for conservation purposes (Jennings 2000), provide valuable ecosystem services and habitat (UNEP Millennium Ecosystem Assessment 2003; 2003) and serve as critical leverage points for future conservation actions (Margules & Pressey 2000). However, protected areas are vulnerable to threats from human activities, and these threats limit future conservation options (USGAO 1994; Cole & Landres 1996; McDonald et al. 2008). Here, we define threats as human activities that have caused or may cause the destruction or impairment of the ecological resources or processes a conservation project is trying to conserve (after Salafsky et al. 2008). Recently, a consortium of non-governmental organizations, the International Union for Conservation of Nature's Conservation Measures Partnership (IUCN-CMP; 2006), developed a comprehensive list of threats to protected areas, with most being human caused (Table 2.1).

Assessing an area's vulnerability to these threats is recognized as one critical component in both assessing protected area effectiveness (Ervin 2003; Hockings 2003; Parrish et al. 2003) and in conservation prioritization frameworks (e.g., Abbitt et al. 2000; Wilson et al. 2006; Murdoch et al. 2007). Yet, most techniques focus solely on vulnerability to in-situ threats despite a long-standing consensus that adjacent, contextual threats should also be accounted for (Newmark 1985; Margules & Pressey 2000; Reyers

2004; Wilson et al. 2005). For example, a small “island” protected area embedded within a highly urbanized landscape would be considerably less effective in maintaining ecosystem dynamics than a large protected area situated in a similar context. There has been a recent emphasis on how to better incorporate surrounding land use into conservation planning frameworks (Theobald et al. 2000; Cowling & Pressey 2003; Pierce et al. 2005; Pejchar et al. 2007), including by the IUCN, where controversy has arisen over whether to expand IUCN categories to better incorporate working landscapes near protected areas (Locke & Dearden 2005).

In this paper, we present a method to 1) assess the spatial patterns of human activities that may threaten biodiversity and natural processes and 2) quantify an integrated vulnerability score that accounts for vulnerability to both in-situ and adjacent threats. Our methods provide a means to expand recent in-situ only threat mapping efforts (e.g., Aplet et al. 2000; Sanderson et al. 2002; Woolmer et al. 2008) into more comprehensive vulnerability assessments for incorporation into conservation planning and prioritization efforts. Using a novel, yet simple conceptual model of the relationship between in-situ threats, adjacent threats, and the potential conservation value of an area, we translate our vulnerability assessment into a vulnerability matrix that suggests both strategies for managing existing protected areas and future conservation actions. We illustrate the method by providing a national-extent, spatially explicit comparison of lands in the United States (U.S.) that have the capacity to, or offer opportunities for, protecting natural resources versus those that, comparatively, may not perform as effectively because of their vulnerabilities. We summarize our findings nationally as well as by the area within 10 km of all terrestrial national parks in the conterminous U.S.

2.2 Methods

Our methods consisted of five steps to create an integrated assessment of vulnerability to both in-situ and adjacent threats.

Step 1. Identify threats to natural resources and conservation goals. For this demonstration, we chose four factors to serve as proxies for a multitude of threats: development (D), land cover (C), accessibility (A), and resource extraction (E). We defined development intensity based on housing densities. We categorized land cover by developed areas, agricultural uses, and remaining undeveloped lands. Accessibility was a proxy metric for impacts from roads and human disturbance including recreation and tourism. Resource extraction accounted for oil and gas wells and non-energy related mines.

We concentrated on these factors for three primary reasons. First, the factors serve as surrogates for many of the CMP identified threats, such as impacts from development, agriculture, oil and gas wells, roads, human caused disturbances to wildlife and other resources, wildfire suppression, introduction of invasive species, and pollution (Table 2.1). Second, residential development, roads and related accessibility, and land use change are among the primary threats to biodiversity and conservation (Czech et al. 2000; McKinney 2002; McKee et al. 2004), and land managers have identified those threats, along with mining, as the most threatening to federal protected area resources (USGAO 1994). Third, spatial data for these factors are easy to obtain, making them useful, accessible, and quantifiable proxies. We recognize that these factors do not provide a complete assessment of vulnerability; threats from climate change, water resource

development, and alternative energy development are among the noted exceptions in our approach.

Step 2. Quantify vulnerability to threats by assigning values that reflect the probability that a threat will negatively impact conservation values as well as the magnitude of that impact (Wilson et al. 2005). This approach follows other efforts to map the intensity of human influence across space (e.g., Aplet et al. 2000; Sanderson et al. 2002; Watts et al. 2007). Optimally, threat values are assigned based on empirical relationships (e.g., Leu et al. 2008), but for general assessments, species or system-specific derived functions are not applicable, and more often threat values are assigned based on subjectively estimated relationships (e.g., Lesslie & Malsen 1995; Aplet et al. 2000; Sanderson et al. 2002; Woolmer et al. 2008; generally, threat values are referred to as "scores", but we reserve that word for the combination of the four threat factor values). To assign threat values, we used our best judgment, guided by quantitative relationships based on published studies where available. We assigned values to each of the four threat factors ranging from 0 to 100, assigning the highest value of 100 to lands with the greatest capacity for conservation (least vulnerable to identified threats; Table 2.2). We assigned values to each 1-ha square of land within a grid representing the conterminous U.S. using a Geographic Information System (GIS) as detailed below. All analyses were conducted using Albers Equal Area Conic, North American Datum (NAD) 1983 projection in ArcGIS v.9.2 (ESRI, Redlands, CA).

Development (D). We used housing density as an indicator of the intensity of land use modification resulting from urbanization (defined here as intensification of housing density, regardless of the density per se; e.g., lands transitioning from open to rural would

be undergoing urbanization). We used housing density rather than population density because population data may underestimate landscape effects of vacation and second homes that are not reflected in population data. Housing densities were calculated from U.S. Census Bureau 2000 block level datasets (USCB 2000a). Block level housing units were spatially allocated to developable lands based on land cover, groundwater well density, and road accessibility (after Theobald 2005).

The relationship between population density and threats to ecosystems is complex and uncertain (Luck 2007), but empirical studies of impacts to species across an urban gradient suggest a logistic decline with increased housing density (assuming that impacts asymptote at high levels of development intensity; McKinney 2002; Hansen et al. 2005).

We rescaled normalized species richness and occurrence data across housing density categories from several studies for bees, birds, lizards, butterflies, plants, and carnivores (see studies summarized in Hansen et al. 2005; Randa & Yunger 2006) and used the data to parameterize a logistic function to weight vulnerability to threats from housing density

$$[D=100-\left(\frac{50}{1+100*e^{-0.03*d}}\right), \text{ where } d \text{ was the continuous housing density in (units/ha) } *$$

1000] so that median housing density values for five housing density categories matched the average empirical result for that density category (Table 2.2, Appendix A). Because the logistic function only asymptotically approached minimum and maximum values, we forced lands with zero housing density to a value of 100 and lands with urban housing densities to a value of 0. Although our approach did not account for the fact that some species benefit from intermediate housing densities (McKinney 2002), it also likely underestimates threats to many other species and processes (Hansen et al. 2005).

Land Cover (C). To assign land cover threat factor values, we grouped 2001 National Land Cover Dataset (NLCD, Vogelmann et al. 2001) data into three categories – “natural”, “agriculture”, and “urban/built up” – and assigned higher values to more natural land cover types (Table 2.2). We assigned threat values to the original 30-m resolution NLCD data and then aggregated to a 1-ha resolution (based on the mean factor value). Although the literature provides little guidance on how to quantify general threats from various types of land cover, it is generally assumed higher intensity urban development is a greater threat to ecological processes than agricultural activities (Marzluff & Ewing 2001).

Accessibility (A). To account for threats from roads and their use as well as for other difficult to measure human uses (e.g., recreation), we created a metric that measured accessibility. We calculated travel time (minutes) from urban areas (USCB 2000a), based on anticipated travel speeds for specific road types (ESRI 2005), with off-road walking times calculated based on slope according to Tobler’s (1993) equation (Table 2.3). Because private lands are generally not accessible to the public, we added an additional 10% slope to all private lands before calculating travel times. We weighted travel times based on the nearest urban area’s population, and we again applied a logistic function to reflect our assumptions about vulnerability to threats from human presence

$$A = \left(\frac{90}{1 + 2.5 * e^{-0.03 * t}} \right), \text{ where } t \text{ was the calculated weighted time from urban area). Again,}$$

because of the asymptotic nature of the logistic function, we forced travel times of 0 to a value of 0, and travel times over 5 hours to have a threat factor value of 100. Although more research is needed to empirically validate our estimates, estimating accessibility is a stronger surrogate for threats from roads and associated accessibility because it

differentiates the size of cities and roads and captures the topographic variability around roads as compared to simply measuring straight-line distance from roads (e.g., Sanderson et al. 2002; Riitters & Wickham 2003; Watts et al. 2007).

Extraction (E). Extraction of natural resources, such as oil and gas, tends to occur primarily near wildlands (Weller et al. 2002) and has substantial impacts, particularly on landscape connectivity (e.g., Berger 2004). Spatial data for extractive activities are sparse, and we were unable to locate comprehensive datasets for some energy related extraction (e.g., coal mines and uranium) or for timbering. However, because of the importance, we included the 1-ha footprints associated with oil and gas wells at densities greater than 5 wells per ha and for non-energy surface mines (data obtained from USGS 1995; 2003, respectively). Although most mines are larger than 1-ha in size, the data to reflect true mining footprints were unavailable.

Step 3. Calculate local threat vulnerability score by combining in-situ threat factor values. To calculate the local threat vulnerability score, we took the geometric mean of the four threat factors ($\sqrt[4]{DCAE}$), calculating a local score for every cell in the U.S. We used the geometric, as opposed to the arithmetic, mean because it better represents situations where a low value for one factor (significant vulnerability) cannot be compensated by higher values for other factors. The geometric mean also minimizes impacts from correlation between the four threat factors.

Step 4. Calculate context threat vulnerability score to assess how the spatial configuration of adjacent human activities influence neighboring areas. To compute the context threat vulnerability score, we passed a 5-km radius moving window over the local threat vulnerability score grid, calculating the arithmetic mean and the standard deviation

of the surrounding cell scores. We then subtracted the standard deviation from the mean to avoid undue influence from “outlier” scores and inconclusive results obtained from averaging both high and low vulnerability scores within the neighborhood. The 5-km neighborhood assesses the context over 7,850 ha, capturing broader scale landscape processes that can affect a given location, and may be an appropriate distance for contextual influences to internal dynamics (Janzen 1983). While some other studies have used buffers of one or two threats (e.g., roads) to indirectly consider adjacent threats (e.g., Aplet et al. 2000; Sanderson et al. 2002), a moving window analysis provides results for every cell in the analysis area and includes the context situation for all threats. We also ran the analysis using a 1-km neighborhood (314 ha) to assess sensitivity to the neighborhood used, but results were similar when viewed at the national scale and are therefore not included.

Step 5. Create an integrated vulnerability assessment by blending local and context threat vulnerability scores. We contend that consideration of both local and contextual threats results in a more comprehensive vulnerability assessment and provides a natural framework for assisting in conservation management decisions and conservation action prioritization. Our framework can be viewed as a two-dimensional matrix, where local vulnerability is on one axis (Y) of a matrix and context vulnerability is on the other axis (X; Fig. 1a). Comparing local and context threat vulnerability scores within the matrix suggests in-situ management strategies or future conservation actions to increase the capacity for natural resource conservation. We show four primary vulnerability categories in the matrix for simplicity, although results can be considered continuously across a two-dimensional space.

As categorized here, protected areas with both low local and context vulnerability, such as wilderness areas, would be considered “conservation cores” and would best be managed to maintain current levels of resource conservation. “Conservation islands” with low local but high context vulnerability could be continually managed as stepping-stone conservation refuges. Conservation actions (defined as interventions undertaken to achieve ultimate conservation goals per Salafsky et al. 2008) that reduced context threats could be considered to move the area into the conservation core category. “Modified islands” with high local vulnerability but low context vulnerability, such as a large protected area entrance parking lot, could be managed to contain local threats (e.g., parking lot designed to minimize runoff), or future conservation actions could restore the area to conservation core. The “modified cores” with both high local and context vulnerability could be managed to maximize conservation at finer scales (e.g., developed areas designed to provide fine-scale native plant and animal habitat) and minimize threats to neighboring areas at coarser scales (e.g., designed to minimize light or air pollution). In all instances, knowledge of threat vulnerability would assist in targeting management actions to minimize management costs and to set more realistic conservation goals and objectives (Pressey et al. 2007).

Adding a third dimension to the matrix that considers formal conservation protection (Z axis) suggests when protected areas might be considered for withdrawal from a conservation system if adjacent threats could not be overcome to achieve local conservation goals. The third axis also suggests currently unprotected lands that should be prioritized for formalized protection. Perhaps a protected area modified core could be exchanged for a conservation core area that was not yet formally protected.

For the national summary of the vulnerability matrix, we conducted a comparative assessment, using quantiles as thresholds to assign grid cells to vulnerability categories because it is difficult to map and summarize continuous results. We calculated the ten quantiles (deciles) for the entire local vulnerability score grid and the entire context vulnerability grid, and used combinations of extreme scores to place lands into the four primary vulnerability categories shown in matrix (Fig. 1b). For example, 1-ha cells in the U.S. grid that had local vulnerability scores in the lowest 20% and context vulnerability scores in the lowest 10% of all scores compared to the entire U.S. were considered modified cores. We also added a fifth “buffer” category for lands not at the extremes in the vulnerability matrix (Fig. 2.1a), but that could be important for providing a spatial buffer between modified and conservation areas.

To represent the Z axis in the vulnerability matrix, we further divided the five vulnerability categories based on whether they were protected area or non-protected area (henceforth, unprotected) lands. We defined protected areas with formalized conservation protection as lands listed as GAP (U.S. Geological Survey’s Gap Analysis Program) stewardship level 1 – 3. GAP stewardship level 1 and 2 lands are assumed to be perpetually protected from development and managed primarily for conservation purposes. GAP stewardship 3 lands are permanently protected but may be subjected to extractive uses. GAP stewardship level 4 lands (private, unprotected) have no formalized conservation protection (Jennings 2000). We refer to those lands as “unprotected” here, although we note that many of these lands are well stewarded, and may have higher capacity for conservation than some lands we define as “protected” area.

We obtained GAP stewardship level data from the Protected Area Database (PAD; CBI 2006). PAD tiles together spatial data from state or regional GAP projects. We updated PAD with more recent and detailed data in some instances. California lands were updated using data from the California Resource Agency's Legacy Project (2004). New England lands were updated using data from The Nature Conservancy (2006). We updated South Dakota using the South Dakota Gap Analysis Program (2002). Colorado lands were updated with data from CoMAP (Theobald et al. 2007). CoMAP does not include stewardship level information, therefore, for Federal or State owned lands, we selected parcels owned or managed by agencies with conservation or open-space preservation mandates and assigned these lands a stewardship level of 3. We then assigned either the PAD data stewardship level or level 3, whichever was the minimum (higher protection). All of these data sources included at least partial information on privately owned lands held in conservation easements and other perpetual protective covenants, and we assigned these lands a stewardship level of 3. After these updates to the original PAD vector data, we created a grid of 1-ha resolution. We converted any area of GAP stewardship level 1, 2, or 3 that was smaller than 10 ha to stewardship level 4 to remove noise from our analysis. To remove water bodies from the PAD, we assumed water bodies shared the stewardship level of their neighboring lands, expanding the adjacent lands until all water bodies were filled with some proportion of stewardship levels 1-4 based on the portion of shoreline in each level.

2.3 Results

Our choice and quantification of threat factors (Fig. 2.2 D, C, A) resulted in a local vulnerability score that illustrated vulnerability to threats throughout the majority of

the U.S., with a swath of relatively low vulnerability lands in Nevada and along the Rocky Mountain West (Fig. 2.2b). Mapping vulnerability categories from the vulnerability matrix (Fig. 2.3a), modified cores (8% of U.S.) were primarily collocated with urban areas, as would be expected, and the vast majority were on unprotected lands (Fig. 2.4). Modified islands (~1% of U.S.) were almost equally distributed between protected and unprotected lands, primarily representing roads and some mines and oil and gas wells because our methods did not include other more localized threats, such as campgrounds and parking lots. The effects of roads could be seen in the vulnerability category detail around Rocky Mountain National Park, CO (ROMO; Fig. 2.3b). In areas of low vulnerability, such as the area to the far west of ROMO, roads were identified as modified islands, separating blocks of conservation lands, but leaving large enough tracts that they remained conservation core. Within the boundaries of ROMO, the roads through the park and the areas surrounding them were categorized as undetermined because the context vulnerability within ROMO was relatively low (as a result of the vulnerability to threats emanating from the Front Range, visible as modified core along the eastern map border). Thus, within ROMO, roads both hindered conservation core and resulted in fragmented, smaller blocks of conservation island.

Conservation core made up 15% of the U.S. Most conservation core was in the West, where the majority of protected area lie, and about twice as much conservation core was found on protected land compared to unprotected land. However, of all protected lands, only about 40% was definitively categorized as conservation core, with the remaining being relatively vulnerable to either internal or contextual threats. We identified numerous opportunities for future conservation actions on unprotected lands,

however, with 20% of all unprotected lands being identified as conservation core, such as along the eastern Rocky Mountain front (Fig. 2.3a). Of the 14% of total area in the U.S. we identified as conservation island, the vast majority was on unprotected lands.

Because we relied on extreme scores when combining local and context threat vulnerability (based on deciles, see Fig. 2.1b), we did not determine integrated vulnerability scores for approximately 50% of the U.S. Most of the lands that with undetermined vulnerability categories were unprotected. Decile thresholds could be varied to increase the amount of area assigned to a vulnerability category, but we believe that assigning categories to moderately scored lands should be done at finer scales, using more detailed and locally appropriate data. Thus, we list lands that are not obviously within a category as “undetermined” (Fig. 2.3 and 2.4).

Summarizing results by national park arranged by census region (Fig. 2.5) illustrated that the area within 10 km of parks in the West and Midwest had greater amounts of conservation core (61% and 59%, respectively) compared to the South (35%). The southern parks had more conservation island (11%) than did the western and Midwestern parks (4% and 3% respectively). There was only one national park in the Northeast, which had no conservation core and 22% conservation island. Parks in the West were also much more likely to include buffer lands and much less likely to contain modified areas.

2.4 Discussion and conclusions

Although we relied on only four threat factors, the broad patterns of our local vulnerability results were similar to “human footprint” assessments across a range of scales that rely on a greater number of inputs (see Sanderson et al. 2002; Leu et al. 2008;

Woolmer et al. 2008). However, by incorporating contextual threats, our results expand on previous efforts and provide greater insight for conservation planning. By comparing local and context vulnerabilities, our approach allows for the assessment of the effectiveness of existing and potential future conservation areas, two key steps in systematic conservation planning (Margules & Pressey 2000; Pressey & Bottrill 2008). We also quantify “accessibility” to better approximate threats from the transportation system, providing a richer assessment beyond relying on simple buffers.

What we categorize as conservation or modified is relative to the existing situation across the entire U.S. This approach is common in conservation land identification or prioritization methods (e.g., Sanderson et al. 2002; Ricketts & Imhoff 2003). Previous studies have assumed that the pattern of human influence, or vulnerability as mapped here, is the inverse of the pattern of natural processes (Sanderson et al. 2002). If so, it would follow that conservation core and island areas would be expected to have the greatest capacity for maintaining ecological processes and biodiversity.

As applied, our framework indicated that despite much of the U.S. being internally or contextually vulnerable to human related threats, many areas with relatively low vulnerability remain. Of the protected areas for which we determined vulnerability categories, only 3% was modified core or island (compared to 27% for unprotected lands). The remainder of categorized protected area was either conservation core (54%), conservation island (12%), or buffer (32%), demonstrating that the majority of protected areas are greater than 5 km away from areas of high human influence (although, this does not speak to whether PA are ideally located for biodiversity conservation) (see Scott et al.

2001 and discussion below). However, our quantification methods tended to select conservation core because it overlaid a protected area (e.g., low housing density, predominantly natural land cover, and relatively distant from urban areas). Thus, comparative results within parks (Fig. 2.5) better suggest conservation implications.

We found that western parks provide better opportunities for abating threats via conservation core buffered by surrounding lands, although Crater Lake, Great Sand Dunes, Joshua Tree, Mount Ranier, Rocky Mountain, and Saguaro present examples of potentially vulnerable national parks. In the South and Northeast, conservation planning may need to rely more on creating networks of stepping-stone conservation islands on private lands. Formalized protection of the currently unprotected lands classified as conservation core (16% of the categorized unprotected area) should be considered, but establishing new legally mandated protected areas will be difficult as a result of U.S. ownership patterns and competition for natural resources (Shafer 1994, Margules and Pressey 2000). This highlights the need to engage private landowners in resource conservation (Theobald & Hobbs 2002; Maestas et al. 2003; Higgins et al. 2007). Beyond conservation partnerships with private landowners, public education of those living in communities that are near conservation areas may create an ecologically informed public, improving conservation in both protected and unprotected ecosystems (McKinney 2002).

It is important to acknowledge that our framework does not measure impact from threats directly, only potential vulnerability to threats. Our results may also be sensitive to errors in data, quantification of threat factors, or choice of deciles as thresholds (although the use of decile extremes tends to mitigate sensitivity to these choices), and, as with all broad-scale analyses, care should be used in interpreting the results. Most

importantly, our national assessment as applied here is primarily an assessment of wilderness qualities, and low vulnerability to human influence is only one part of biodiversity protection (Sarkar 1999). For prioritization of conservation actions for biodiversity protection, our vulnerability results would need to be combined with spatial data on biodiversity and conservation management effectiveness (Hockings 2003).

While our national example illustrates a coarse-scale application and provides an initial assessment of focal areas for finer-scale analyses, the vulnerability framework presented here can be applied locally to more accurately suggest conservation actions. An analysis applied at finer-scales (extent and grain), improved by the use of richer, more detailed data, would allow land managers and conservation planners to calibrate and apply the framework as necessary to achieve local conservation goals. For example, planners could include more proxy factors for locally important threats. Locally, both knowledge of and data for threats more directly linked to biological and process targets are likely available and should be used, and threat values should be assigned based on this knowledge. Detailed land use and land cover data could provide a very fine-scale assessment of conservation islands so that even within an intensely modified urban area, green park networks could be identified. Note that our method outputs continuous values for both local and context threat vulnerability scores. We combine and categorize them here using deciles for simplicity and ease of discussion, but at finer-scales, results could be represented continuously using three-dimensional graphic tools or vulnerability categories could be definitively calibrated using biologically determined thresholds. Further, vulnerability is often quantified based on predicted potential loss of habitat over time (e.g., Abbitt et al. 2000; Davis et al. 2006; Murdoch et al. 2007), and at local extents,

land managers could incorporate forecasted changes in threat status to provide an important temporal aspect to vulnerability assessment (Wilson et al. 2005). However, we contend that our contextual vulnerability score is a sufficient proxy for temporal change in residential development, given that urban growth models inevitably rely on surrounding development intensity to predict future growth (Theobald & Hobbs 1998). At any scale, we argue that our integrative vulnerability assessment can be used to extend and improve other approaches for either stand alone vulnerability assessment for identifying locations for appropriate management strategies depending on exposure to threats (Pressey et al. 2007) or for incorporation into other conservation planning and prioritization schemes (e.g., Ervin 2003; Parrish et al. 2003; Davis et al. 2006; Murdoch et al. 2007; Wilson et al. 2007).

Acknowledgements

We thank J. Hilty and N. Piekeliuk for comments on a previous draft of this paper. This research was supported in part by the USDA under National Needs Fellowship Grant #2002-38420-11713, the EPA under the Science to Achieve Results (STAR) Fellowship Program, the NSF under IGERT Grant #DGE-0221595 (to A.A.W.), and USDA National Research Initiative Award No. 2003-35401-13801 and NASA-DSS Award (to D.M.T.). None of the supporting agencies has officially endorsed this publication.

Tables

Table 2.1. Threats to protected areas as identified by the Conservation Measures Partnership (IUCN-CMP 2006), and the factors used in this study as proxy measures for the threats: development (D), land cover (C), accessibility (A), and resource extraction (E).

CMP Level 1 Threat Classification (Level 2 detail examples)	Proxy threat factors (D, C, A, E)
1. Residential & commercial development (housing & urban areas, commercial areas)	D, C
2. Agriculture & aquaculture (non-timber crops, livestock ranching)	C
3. Energy production & mining (oil and gas drilling, mining and quarrying)	E
4. Transportation & service corridors (roads & railroads, utility and service lines)	C, A
5. Biological resource use (hunting & collecting terrestrial animals)	A
6. Human intrusions & disturbance (recreational activities, work activities)	A
7. Natural system modifications (fire suppression, ecosystem modifications)	D, C
8. Invasive & other problematic species & genes (invasive non-native species, introduced genetic material)	A
9. Pollution (urban, industrial, and agricultural effluents, air-borne pollutants)	D, C, A, E
10. Geological events (volcanoes, avalanches)	Not considered
11. Climate change & severe weather (habitat shifts, droughts, flooding)	Not considered

Table 2.2. *Values assigned to the four threat factors: development (D) based on housing density; land cover (C) based on 2001 National Land Cover Dataset (NLCD) codes; accessibility (A) based on travel time from an urban area; and extraction (E) based on oil and gas well density and surface mines. We assigned values to each factor to reflect the vulnerability of natural resources to each threat, ranging from 0 to 100, with 100 representing highest capacity for conservation (lowest vulnerability to identified threats). The values for both Development and Accessibility were continuous; we categorize them in the table for summary only.*

Development (D) ^a		Land cover (C)		Accessibility (A)		Extraction (E)	
Housing density (units/ha)	Value	Land cover type (NLCD codes)	Value	Travel time	Value	Wells/ha	Value
Undeveloped (<=0.001)	100	Natural (11,12,31,41-43, 52,71, 90,95)	100	> 5 hours	100	< 4	100
Rural (0.0011 - 0.062)	97 - 99			3 hours	~ 90		
Exurban (0.0621 - 1.45)	50 - 96	Agriculture (81,82)	75	2 hours	~ 85	5 - 6	75
Suburban (1.451 - 4.12)	50	Urban/ built up (21,22,23,24)	50	30 minutes	~ 50	7 - 9 or mine	50
Urban (< 4.12)	0			0 minutes	0		

^a Weights were continuous, but median values for these five housing density categories were compared to previously studied relationships between housing density and species richness, and this comparison was used to parameterize the logistic function used to weight threat values.

Table 2.3. Assumed average speeds of travel by road type used to calculate travel time from urban areas. Off-road travel speeds were adjusted by slope according to Tobler's (1993) equation.

Road type	Average speed (km/hr)
Interstate highway	112
US Highway	88
Secondary (state and county)	64
Local	48
Four wheel drive	17
No roads (walking)	$6^{-3.5 \times slope + 0.05}$

Figures

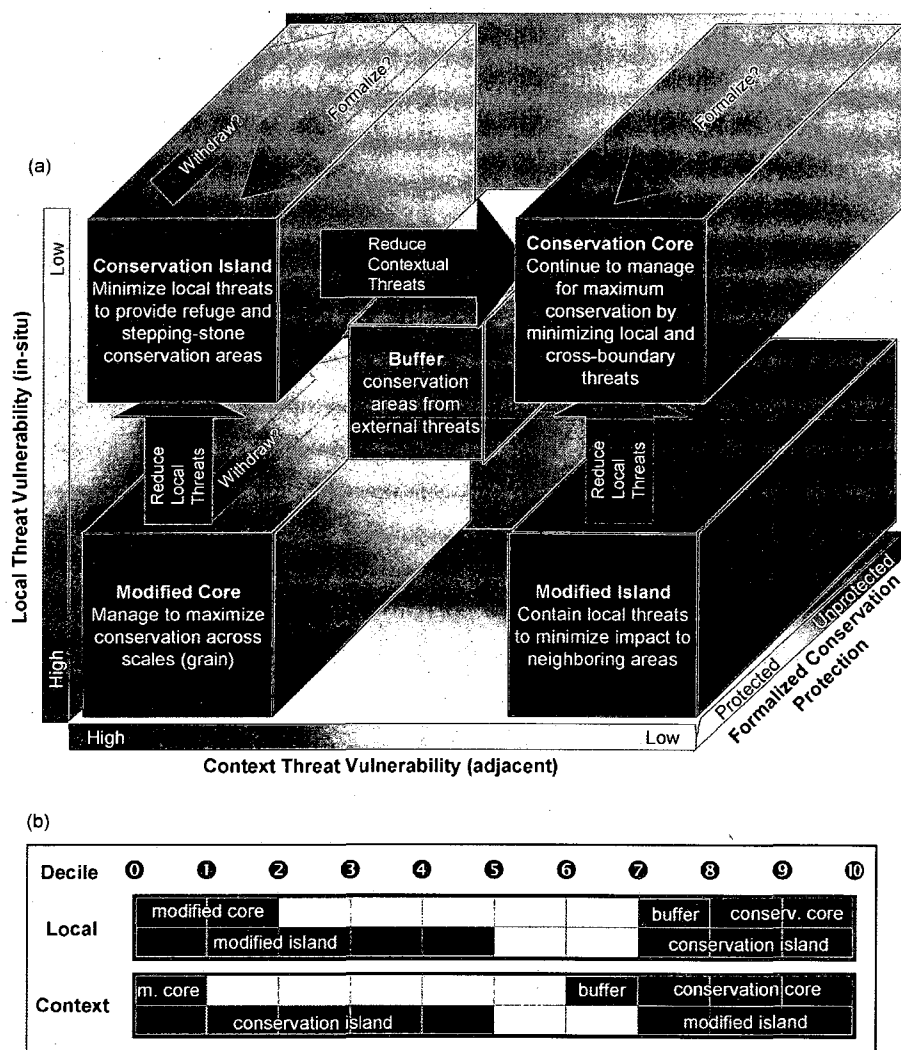
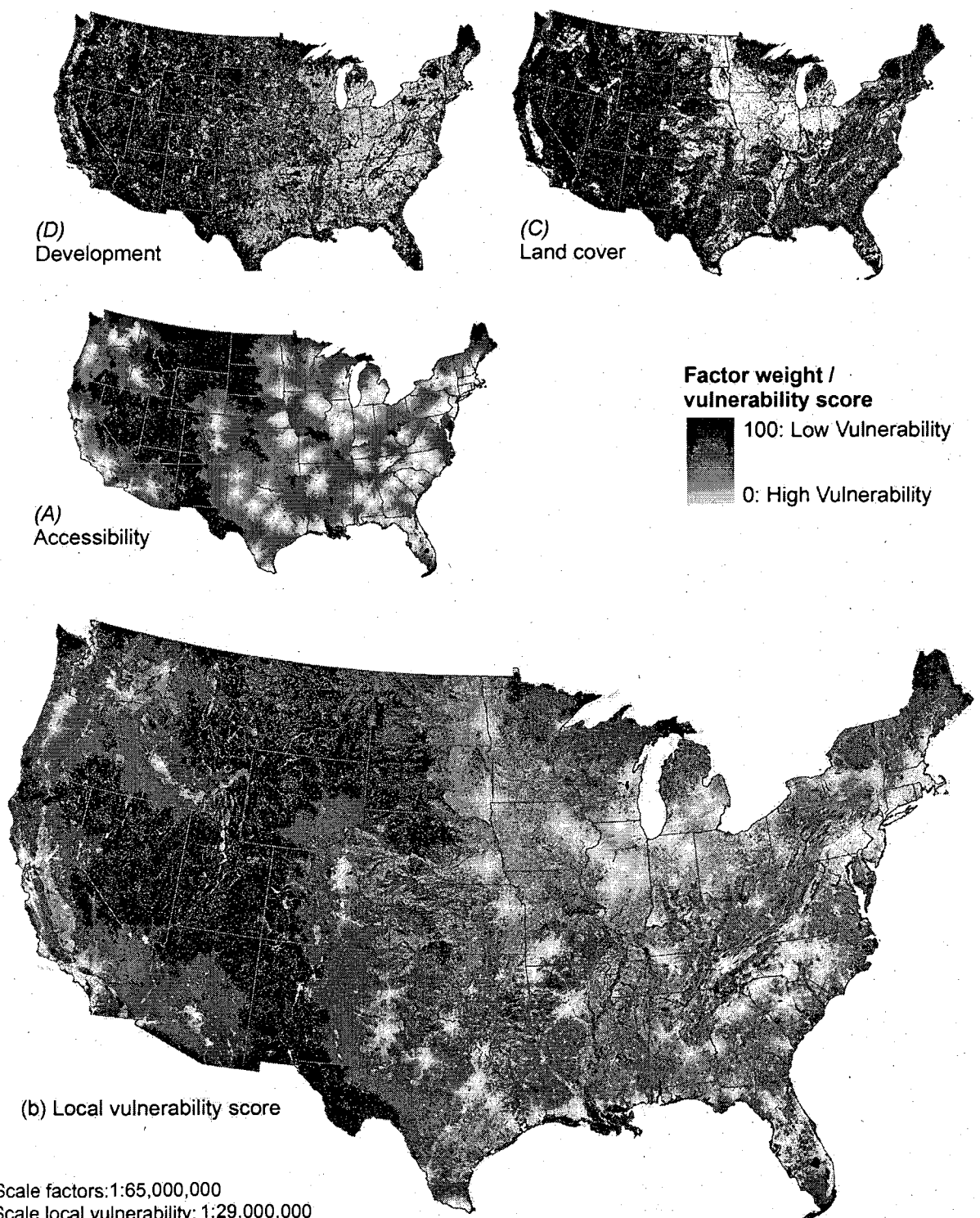


Fig. 2.1. Schematic of the vulnerability matrix for comparing local (Y axis) and context (X axis) threat vulnerability to assess integrated vulnerability (a). Our methods provide continuous values for local and context threat vulnerability scores, but we show four primary vulnerability categories here for simplicity and use categories in our results to assist in mapping and discussion. The vulnerability matrix suggests conservation actions (arrows) to shift lands within the matrix for improved conservation. Considering protection status (Z axis) suggests conservation actions to either withdraw existing protected areas from the conservation network, or formalize protection for currently unprotected areas, depending on local factors and goals. (b) We used the deciles from our calculated local and context threat vulnerability scores as thresholds to bin lands in the U.S. into the four vulnerability categories based on combinations of relatively extreme values. We also added a fifth category of “buffer” for lands that had moderate values but may be important in buffering conservation lands from adjacent threats.



Scale factors: 1:65,000,000

Scale local vulnerability: 1:29,000,000

Fig. 2.2. Map of threat factors, and their assigned threat values: (D) development, (C) land cover, and (A) accessibility. The fourth threat factor, (E) extraction, was not visible at this scale and is not shown. Threat values ranged from a maximum of 100 (darker areas, lowest vulnerability) to a minimum of 0 (lighter areas, highest vulnerability). (b) The local vulnerability score was calculated as the geometric mean of the four threat factor values.

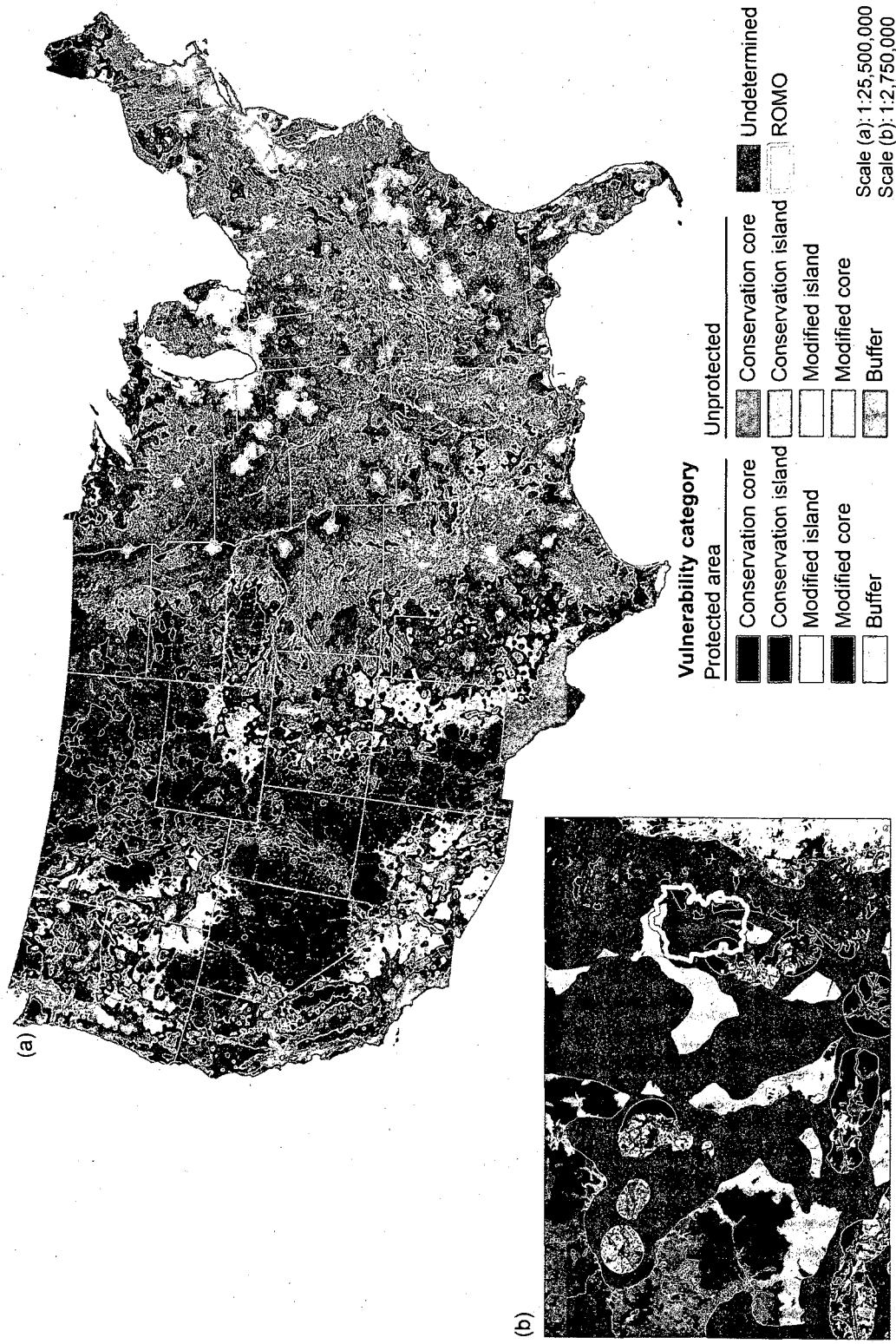


Fig. 2.3. Map of vulnerability categories for all protected and unprotected lands (a) in the conterminous U.S. and (b) detail of area around Rocky Mountain National Park, CO (ROMO).

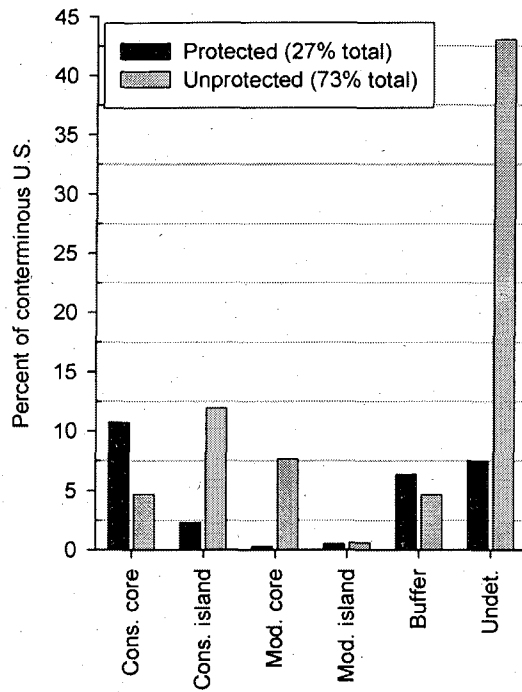


Fig. 2.4. Vulnerability category summary for the entire U.S. comparing protected vs. unprotected lands.

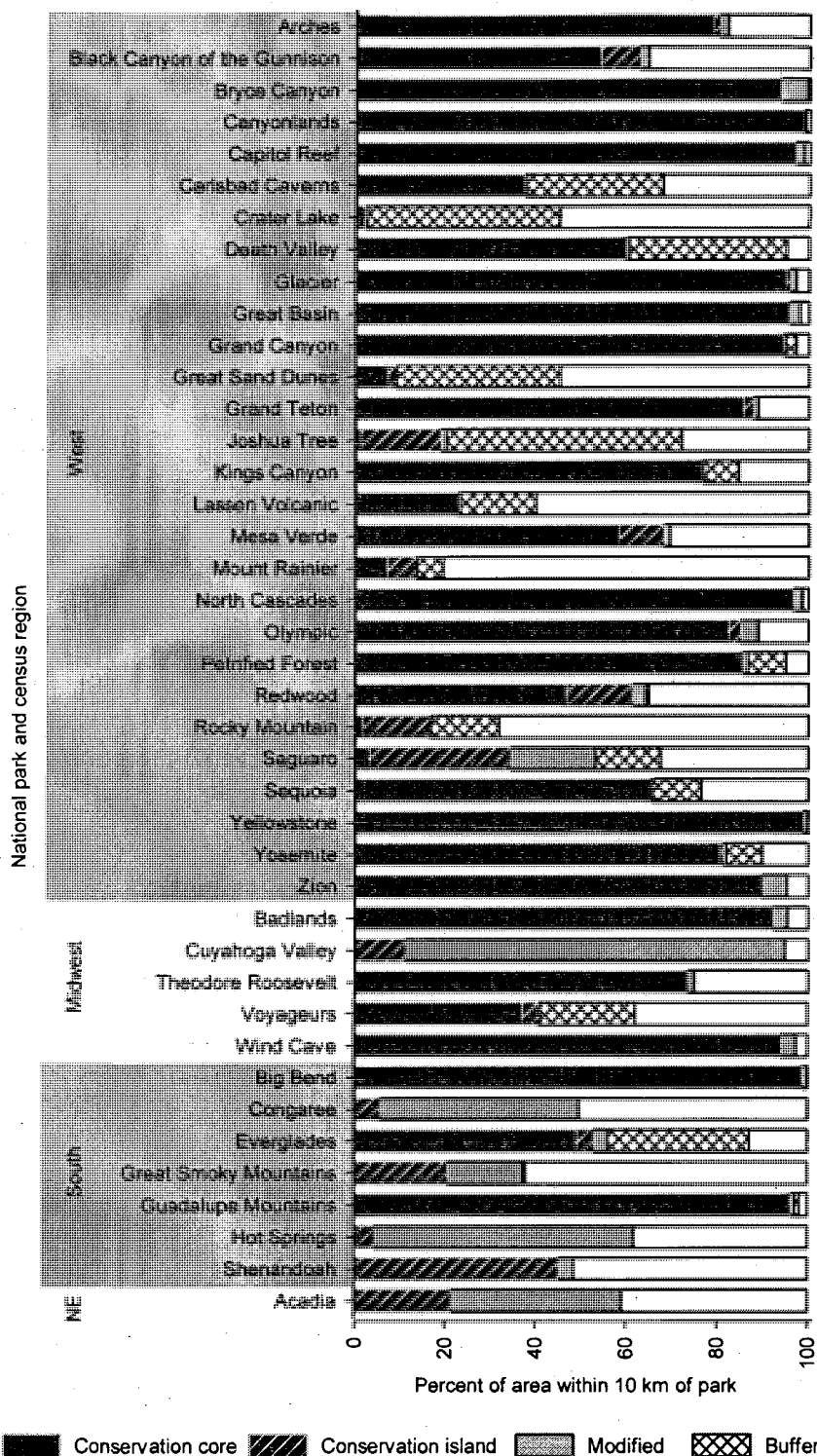


Fig. 2.5. Vulnerability category summary for percent of area within 10 km of a national park. For summary, the modified core and island categories have been combined, and the percent area for which we did not calculate a vulnerability category (undetermined) are shown in white. Parks are ordered alphabetically within the four U.S. Census regions: West; Midwest; South; Northeast (NE).

CHAPTER 3. RESIDENTIAL DEVELOPMENT ENCROACHMENT ON U.S. PROTECTED AREAS³

Abstract

Conservation of ecological processes and biodiversity may require the development of a conservation system consisting of protected “cores” surrounded by “buffer zones” that effectively expand and connect the cores. However, residential development near protected areas may threaten any de facto, and hinder the development of an official, conservation system in the United States. We identified potential conservation cores based on existing protected areas, and using a spatially explicit model of housing densities, we quantified how residential development has altered the structural context around cores nationally from 1970 through 2000, and forecast changes for years 2000 through 2030. We found that residential housing development has likely occurred preferentially near some cores, and if encroachment near cores continues at projected rates, the amount of buffer zone will have been reduced by a total of 12% by 2030, with much of this change occurring directly at core edges. Furthermore, we found that development will have reduced the average connectedness (valence) of cores by 6% from 1970 to 2030. Although patterns of encroachment roughly increased west to east, our results painted a more complex picture of the difficulties that would be faced if

³ This chapter is a manuscript, co-authored with David M. Theobald, in press at Conservation Biology.

establishment of an official conservation system was ever attempted. At a minimum, prioritizing future conservation action must consider adjacent land uses, and a key conservation strategy will be to work cooperatively across land ownership boundaries, particularly for smaller protected areas, which will tend to dominate future conservation activities.

3.1 Introduction

An ideal conservation system may consist of protected conservation “cores” surrounded by “buffer zones” of relatively unaltered land-use types that protect the cores from external threats, effectively expanding and providing connections between them (MAB 1974; Noss & Harris 1986; Sarkar 2003). Despite a long-standing call for action (e.g., Shelford 1933), no such formalized conservation system yet exists in the United States. Although many existing protected areas in the United States were established for reasons other than biodiversity conservation, protected areas provide a foundation for realizing this idealized conservation system. However, residential development near protected areas may threaten any de facto, and hinder the development of an official, conservation system.

Expansion of residential development is a key driver of species endangerment (Wilcove et al. 1998) and is a primary threat to protected-area resources (GAO 1994; Wittemyer et al. 2008). Development at exurban densities (>1 unit/ 16 ha) is occurring particularly rapidly (Theobald 2001). Recent assessments of the threats to protected areas from residential development focus either on case studies with targeted geographic or ecological scope (e.g., Hansen & Rotella 2002; Parks & Harcourt 2002; Gude et al. 2007) or on more intensely developed lands (e.g., Scott et al. 2004; Leu et al. 2008; McDonald

et al. 2008). We are unaware of any national, spatially detailed examination of when and where residential development, including exurban densities, has encroached on protected areas and how that translates into structural changes to an idealized conservation system in the United States.

Potential ecological consequences of residential encroachment and increased human proximity adjacent to protected areas include intensification of edge effects, direct reduction of the effective size of protected areas, and reduction in linkages between protected areas and resulting disruption of ecological flows (Hansen & DeFries 2007). As natural and agricultural lands are converted to residential uses, the likelihood of negative edge effects increases (Parks & Harcourt 2002) and the effective area for dynamic processes is reduced (Noss & Harris 1986). Most protected areas are too small to meet the minimum area required to support viable populations for many species (Newmark 1985) or to allow natural disturbance dynamics (Noss 1983). Developed areas surrounding protected lands also reduce connectedness between protected areas, resulting in habitat fragmentation and a reduction in ecological flows of energy, genetic information, and biological matter, threatening species survival (Crooks & Sanjayan 2006). Roads associated with development particularly affect connectedness between protected areas (Schonewald-Cox & Buechner 1992). Disruption of landscape connectedness may be particularly detrimental under climate change, reducing opportunities for movement to more suitable climactic conditions (Heller & Zavaleta 2009).

We conducted a national, spatially explicit, quantitative assessment of how residential development has altered the structural context for conservation areas in the

conterminous United States relative to an idealized core-in-buffer-zone conservation system as articulated by Noss and Harris (1986) and others. We illustrate the potential ecological consequences from residential encroachment by quantifying loss of buffer at core edge as a proxy for increased edge effects; loss of area in the buffer zone around cores as a proxy for reduction in the effective area for dynamic ecological processes; and changes in the connectedness between cores as a proxy for disruption of ecological flows. We examined changes from 1970 through 2000, forecast changes for years 2000 to 2030, and summarized our findings nationally and by state.

3.2 Methods

3.2.1 Core, potential buffer, and developed lands

To represent the existing expression of an idealized conservation system, we classified within a geographic information system (GIS) all land in the conterminous United States into three categories: core, potential buffer, and developed (Table 3.1). We defined conservation cores as lands identified as either GAP (U.S. Geological Survey's Gap Analysis Program) stewardship level 1 or 2 that, when grouped, covered at least 1000 ha. These lands are assumed to be protected in perpetuity from residential development and to be managed primarily for conservation purposes (Jennings 2000). We defined potential buffer as any GAP stewardship 1 and 2 lands too small to be considered a core; GAP stewardship level-3 lands (protected in perpetuity, but not necessarily managed for conservation; Jennings 2000); and privately owned lands developed at rural or lower housing densities (< 1 unit/ 16 ha; not protected in perpetuity and not necessarily managed for conservation). We considered land not categorized as core or buffer to be developed land. We defined developed lands as those with exurban or

higher housing densities (> 1 unit/ 16 ha) or those that were commercially developed or underlying major highways.

Housing densities for 1970 and 2000 were estimated from Census 2000 block-level data (USCB 2000a). We used the spatially explicit regional growth model (SERGoM) and county-level population projections to forecast population densities for the year 2030. (See Table 3.1 and Theobald [2005] for details on methods we used to calculate housing densities for the three study years).

3.2.2 Development encroachment on cores

Prior to assessing how residential development had altered an idealized conservation system, we determined whether our historical and projected data supported the findings of other studies (e.g., Frenzt et al. 2004; McDonald et al. 2007) that encroachment occurs preferentially near protected areas. We considered lands where housing density intensified from 1970 through 2000. We considered density intensified if the housing density category increased along a scale of undeveloped, rural, exurban, suburban, and urban (Table 3.1).

To better control for factors that could confound our findings, we considered only the proportion of land with intensification on developable lands (i.e., privately owned lands not already intensely developed and with gentle [$<25\%$] slopes). We compared the proportion of developable area that intensified in development density within all core edge (defined here as within 10 km of a core boundary) with all areas outside core edge. Because development patterns are often driven by road access, we also stratified results by travel time to the nearest urban area. We approximated travel time (minutes) from small and large urban areas (population of 10,000-50,000 and $> 50,000$, respectively;

urban boundaries and population from Census 2000 (USCB 2000b) based on anticipated travel speeds for specific road types (StreetMap data set [ESRI 2005]). Assumed travel speeds (km/hr) by road type were as follows: interstate highway, 112; federal highway, 88; secondary state and county road, 64; local road, 48; four wheel drive road, 17. Off-road travel speeds were assumed to follow Tobler's (1993) equation of walking speeds adjusted by slope ($6^{-3.5*|slope+0.05|}$). To combine distances from small and large urban areas, we weighted travel times based on the median population for each urban size category.

3.2.3 *Changes in buffer zones*

We defined buffer zones as any potential buffer area contiguous with a core (Table 3.1). We recognize that all potential buffer lands do not provide equal conservation value. Many of the lands included as buffer zones are undoubtedly overgrazed, weed infested, or otherwise do little to support biodiversity. However, our goal was to provide a national summary of structural changes in a conceptual conservation system, not to spatially identify lands with maximum capacity for biodiversity conservation. When charting changes in buffer area, we stratified all results by buffer land type (GAP stewardship 1, 2, or 3; undeveloped; and rural), including the additional category of crop lands to provide a coarse distinction in buffer-zone quality.

As a proxy for protection from edge effects, we calculated and charted the proportion of buffer within core edge for each of the 3 study years (1970, 2000, 2030). We defined core edge as the area within 10 km of a core boundary. We chose a distance of 10 km because it includes direct and indirect effects of development on neighboring systems. To illustrate the magnitude of change, we also charted the total buffer area lost from within core edges between study years.

To estimate changes in the amount of area for dynamic processes occurring within cores, we charted total area of buffer zone for each study year, and normalized each year's total to the area in 1970. To assess the magnitude of impacts to buffer zones over time, we also charted the total amount of buffer zone lost to development between study years.

To explicitly illustrate where future development may have the greatest effect on buffer zones, we used clusters of cores as a mapping unit because they show change over time and are relevant to an idealized conservation system. Noss and Harris (1986) refer to such a unit as a "network," but we avoided this term because of its specific ecological meaning in more recent studies. We defined clusters as contiguous areas of cores and buffer zones (Table 3.1). Two or more cores connected by uninterrupted buffer zone formed a cluster, although here, for mapping change in buffer area, we also allowed a single core and its surrounding buffer zone to be mapped as a cluster. Specifically, our mapping unit was the cluster as identified in the year 2000, and we mapped the percent reduction in buffer zone area from 2000 through 2030.

3.2.4 Changes in connectedness

Because we were concerned with general changes in landscape structure, and not with specific species impacts, we used proxy measures to assess changes in structural connectedness rather than functional connectivity. Functional connectivity is an emergent property of the interaction between the landscape and a particular species (Taylor et al. 2006) and requires a species-based approach (Hansen & Urban 1992). Structural connectedness relates only to the spatial arrangement of landscape features (Lindenmayer & Fisher 2006). We used two measures to assess structural connectedness: a metric that

summarized the width and length of a passageway through the buffer zone that connected any two cores and the mean valence for all cores. We defined a passageway as a contiguous path through the buffer zone that connects any two cores. We avoided using the term corridor because of its specific ecological meaning related to functional connectivity (e.g., Hilty et al. 2006). By definition, passageways only exist between cores within a cluster.

As development occurred in the buffer zone, a passageway could become narrower (constrict in width) or elongate because a more circuitous route between cores was required. Thus, we first used a metric that would account for both of these changes in a single value. We measured the width of each passageway at the half-way point between two cores. In GIS terms, the width of a passageway is actually the number of side-by-side pixels defining Thiessen polygons expanding out through the buffer around each core. For each pixel along the width of a given passageway, we calculated the inverse of the distance between cores connected by that passageway. We then calculated the sum of inverse distances of all of these pixels for all passageways and charted that value for all years, relative to the value in 1970.

We calculated valence as a second connectedness metric to provide an estimate of the number of connections between cores. In graph theory, valence (or degree) is the number of edges between nodes. In our application, passageways are edges and cores are nodes. We calculated and charted the average valence for the entire conterminous United States for each year, again normalizing each year's value to the value in 1970.

To estimate spatially where connectedness would be most affected, we mapped the percent reduction in the sum of inverse distances along passageways for each cluster

from 2000 through 2030. Again, our mapping unit was clusters in the year 2000, although here, we only mapped true clusters that had two or more cores.

3.2.5 Sensitivity analyses

We assessed how sensitive our results were to two parameters. First, we considered how minimum core size affected our results. We defined core as at least 1000 contiguous ha in GAP stewardship level 1 or 2 because we believe 1000 ha represents a middle ground between the importance of large reserves for the protection of species with large home ranges and dispersal areas (e.g., Schonewald-Cox 1983) and the importance of smaller areas for protecting smaller species, ecosystem remnants, and stepping-stone corridors (Shafer 1995). Furthermore, the 1000-ha minimum size has been used by others (e.g., Savings 1998). However, to examine the sensitivity of our findings to the minimum threshold of core size, we compared results for 100 ha and 10,000 ha minimum core sizes.

Second, the distance from a core boundary used to define “edge” might influence results when assessing encroachment of development on cores. Thus, in addition to our main encroachment analysis, where we used a 10-km definition of edge, we also considered edge distances of 5, 20, 50, and 100 km from a core boundary.

3.3 Results

3.3.6 Core, potential buffer, and developed lands

Six percent of the area in the conterminous United States was protected area core, and for the 2547 unique cores identified, the median size was 5300 ha. Western states had significantly more core relative to land area and significantly larger cores (Fig. 3.1a).

States in the northeast had the second highest proportion of core and the second greatest

median core size. To provide context for the sensitivity analysis results, discussed below, when we changed the minimum size threshold used to define cores from 1000 ha to 100 ha or 10,000 ha, we identified 8356 and 619 unique cores with median sizes of 500 and 36,940 ha, respectively.

Potential buffer was 87%, 80%, and 76% of the total area for years 1970, 2000, and 2030, respectively. Developed lands covered 7%, 14%, and 18% for the same years. Exurban housing densities made up the majority of developed lands. Seventy percent, 80%, and 82% of developed lands were developed at exurban densities for the 3 study years, respectively, with the remaining percentage developed at suburban or urban densities.

3.3.7 Development encroachment on cores

Cores in the Northeast had the greatest proportion of developed land at their edges, and cores in the West had the least development at their edges (Fig. 3.1b). However, we projected that cores in western states will undergo the greatest increase in surrounding development, on average, from 2000 to 2030 (Fig. 3.1c).

A greater proportion of the developable area within core edges experienced development intensification compared with the area beyond the core edge from 1970 to 2000 (Fig. 3.2). This remained true across all categories of travel time to urban areas, and the greater the distance from an urban area, the greater the difference in development within a core edge compared with outside of an edge. This trend was not sensitive to altering our minimum threshold of core size.

Our findings of relatively higher development intensification within core edge were insensitive to our definition of edge, out to a distance of 50 km. The farther the

distance used to define edge, the greater the absolute difference between proportion of development intensification within and outside of core edge. However, the ratio of the difference between the proportion of intensified lands inside and outside of edge remained constant. At an edge defined as 100 km from cores' boundaries, the trend remained, but the ratio of difference between intensification within and outside of edges was higher (even greater intensification within an edge compared with outside).

To better parse out state and regional differences in encroachment and provided an initial assessment of whether the encroachment was occurring preferentially or as a result of the location of cores, for each state, we plotted the ratio of the proportion of area that intensified in housing density within a core edge to the proportion of intensified area in the entire state (years 1970-2000) against the ratio of the median travel time to an urban area within a core edge to median travel time to an urban area for the entire state (Fig. 3.3). Dividing the plot into four quadrants based on the 1:1 ratio for each axis, states fell into one of the quadrants depending on whether cores in that state had surrounding development intensification that was greater or less than the average development within the entire state, and depending on whether the distance of travel time from core edge was greater or less than the average travel time to urban area in the rest of the state: (1) states with cores that had relatively high rates of surrounding development intensification and that were relatively close to urban areas; (2) states with cores that were both far from urban centers and that had experienced relatively high rates of surrounding development, (3) states with cores that were relatively close to urban areas, but had less surrounding development than expected, and (4) states with cores that had lower relative rates of surrounding development and were relatively isolated from urban areas. Most

Midwestern and western states were in quadrant 1. Northeastern and southern states were most often in quadrant 4. Quadrants 1 and 4 had the most states, and there were almost equal numbers of states in each, whereas there were the fewest states in quadrant 3. Of the states in quadrant 2, the Midwest, South, and West were equally represented.

3.3.8 Changes in buffer zones

Nearly 6% (over 10 million ha) of the area within core edge changed from buffer to developed from 1970 through 2000 (Fig. 3.4a). The greatest losses came from open land conversion to developed, followed by rural land-use conversion. Although the pace of development was expected to slow, our projections indicated that almost an additional 5% (over 5 million ha) of the buffer within core edge would be developed by 2030.

The total buffer-zone area decreased more than buffer within core edge from 1970 through 2000 (decrease of 8%, total loss of 36 million ha) (Fig. 3.4b). We projected an additional 4% (or 19 million ha) to be lost for years 2000 to 2030. Again, losses of buffer land were most prominent on open lands, followed by rural and crop lands. The majority (97%) of buffer-zone loss from 1970 through 2030 was due to transition to exurban, rather than suburban or urban, housing density. Maps of total loss of buffer zone for years 2000 to 2030 (Fig. 3.5a) showed clusters in the Midwest, East, and Northeast projected to be most affected, although numerous clusters along the Pacific coast and along the Front Range in Colorado were also projected to lose over 5% of their buffer zone. On average, cores in northeastern states were predicted to have the greatest decrease in total buffer zone, although some states in the Midwest were predicted to have the largest percent declines (Fig. 3.1d).

These trends were robust to our sensitivity analysis of the minimum size used to define a core. The larger the minimum core size we used, the greater the buffer area in 1970 and the greater the loss over time. From 1970 through 2030, for both edge and total buffer zone analyses, changing the minimum core size from 100 to 1000 ha increased the loss of buffer by half the amount compared with changing minimum core size from 1000 to 10,000 ha; a perfect logarithmic trend.

3.3.9 Connectedness

Residential development reduced connectedness between protected area cores. The sum of inverse distance to connection measured along passageway midpoints fell 6% from 1970 through 2000, and we projected an additional decline of 3% by 2030 (Fig. 3.4c). These changes resulted in an average loss of valence between cores of 3% for each of the study periods. Mapping changes in connectedness illustrated smaller hotspots of disconnection distributed throughout the United States, with particularly large clusters or groups of clusters with high rates of disconnection observed in Colorado, Minnesota, Texas, and the Northeast (Fig. 3.5b). By state, cores in Ohio, Massachusetts, and Alabama were expected to have the highest total percent decline in cluster connectedness (Fig. 3.1e).

The sensitivity analysis showed that the larger the minimum core size used in the analysis, the less the loss of connectedness over time. Again, changing the minimum core size from 100 to 1000 ha increased the loss of connectedness by about half the amount compared with changing minimum core size from 1000 to 10,000 ha, providing a nearly perfect logarithmic trend.

3.4 Discussion

Our results demonstrate that residential housing development has substantially changed the land use context around cores, defined here based on existing protected areas, potentially reducing their effectiveness and limiting options for future conservation action. Our findings support land managers' concerns over development encroachment, and we found that encroachment had occurred and would continue to occur near cores.

In keeping with other studies (e.g., Frentz et al. 2004; McDonald et al. 2007), our results suggest that "preferential" encroachment had occurred near some cores. The national summary comparison of lands within versus those beyond a core edge averaged out the complexities in the spatial relationship between cores and development (Fig. 3.2). Here, our results partially arose because of the sheer amount of (developable) undeveloped land outside of core edge that was far from urban areas swamped the amount within core edge. This also explained our sensitivity analysis results that an edge distance of 100 km increased the differential between development intensification within and external to core edge. Our comparison at the state level shed more light on the complexities of development and proximity to cores and urban areas (Fig. 3.3). The cores in states that fell in quadrant 2 have characteristics that suggest preferential development near cores because, despite being relatively far from an urban area, people have chosen to develop their homes within the core edge. Very few states had cores with characteristics of quadrant 3 (less development intensification than expected for a given distance to an urban area), and states with core edge development likely driven by cores' proximity to urban areas (quadrants 2 and 4) were approximately a wash. Thus, it appears that our finding of greater development at core edge was predominantly driven by locations where

preferential encroachment occurred; cores in states such as Iowa, Washington, Oklahoma, Ohio, and Texas (Fig. 3.3). There are likely other potential confounding factors, and the question of why preferential encroachment may be occurring in some states and not in others remains.

Results indicated that development encroachment will have reduced the amount of buffer at core edge by 11% from 1970 through 2030 and that the total area of buffer zone will have been reduced by 22% over the same time period (Fig. 3.4a, b). A greater proportion of total buffer zone, compared with buffer at core edge, was developed from 1970 through 2030. However, a slightly greater proportion of area was projected to be developed at core edge than within the entire buffer zone from 2000 through 2030, which suggests our development model predicted increased core encroachment. Whether development occurs more rapidly at core edge or within the broader buffer zone, taken individually, these values likely underestimate the cumulative impact to ecological processes within cores because penetration of edge effects from housing development compounds the loss of total area for dynamic processes (Wilcove & May 1986; Revilla et al. 2001). Similarly, these results do not quantify how impacts will be aggravated by development primarily occurring at exurban densities, which may have more intense impacts than otherwise suggested by their relatively low densities (Odell & Knight 2001; Parks & Harcourt 2002; Hansen et al. 2005). Dispersed growth patterns are likely associated with increased traffic volume and a larger footprint of human modification per housing unit.

We reiterate that our goal in assessing connectedness was to create an overall measure for comparison across years, not to conduct a core-by-core assessment of

functional connectivity. Relatively low exurban housing densities may not negatively affect connectivity for some species, and our definition of buffer may not allow functional connectivity for others. Furthermore, it is unclear whether connectedness is as important as core size (Simberloff et al. 1992; Beier & Noss 1998; Haddad et al. 2000; Falcy & Estades 2007). However, few would disagree that an ideal conservation system should include maximized core sizes with redundant connections through optimal habitat. Our results suggest there will be a 9% decrease from 1970 through 2030 in the sum of inverse distance along passageways (Fig. 3.4c). Change in the sum of inverse distance measure occurred both as a result of lengthening connections and constriction of passageways. Connections at the shortest distances are most likely to be suitable across multiple scales of species dispersal and movement, and losses to these connections may have the greatest impact on regional conservation. However, connectedness at all scales may be critical as climate change alters habitat distributions and locations (Moritz et al. 2008), and our measure of valence showed an overall reduction in landscape connectedness.

Although general trends were robust across a 100-fold increase in minimum core size and differences were almost linear when plotted on a logarithmic scale, analyses conducted with a smaller minimum core size consistently showed a greater magnitude of impact to the idealized core-in-buffer-zone conservation system. Therefore, our results are likely conservative because using the 1000-ha minimum size ignored 70% of the cores identified based on a minimum size-threshold of 100 ha. Our results may also have been conservative given the limitations of data used in the modeling of housing densities. Our results reflect an expected slow down in development expansion from 2000 to 2030.

This forecasted slowdown primarily resulted from limitations of data for the road network. That is, growth usually includes expansion of the transportation network and other infrastructure, which are difficult to forecast. Yet, development location was modeled in part based on road accessibility. As a result, the forecast patterns of housing development tended to be less concentrated, resulting in fewer areas identified as exceeding the density threshold to be considered “developed.”

The informal conservation system in the United States is primarily made up of small cores, and smaller cores are particularly reliant on surrounding buffer lands to meet minimum area requirements for suitable habitat and ecological processes. However, smaller cores are likely to be situated in highly developed areas and are therefore most likely to suffer the double jeopardy of loss of area for dynamic processes from surrounding development and from more intense edge effects (Parks & Harcourt 2002). We found a clear trend of more development surrounding smaller cores in the East (Fig. 3.1a, b). Our mapping of loss of buffer zones illustrated this general trend, with more clusters predicted to have greater percent loss of buffer area in the East (Figs. 3.1d, 3.5a) than in any other area. We expected this, given that the larger cores in the West were also predicted to have larger buffer areas; thus, it took more development to have an equivalent percent reduction in a large buffer zone. However, a simple west-to-east summary of impacts would over simplify our findings. Numerous small cores in the West and some larger cores in California and Washington were predicted to have a relatively high percent reduction in buffer zone area by 2030.

Our map of projected change in connectedness illustrated disconnections were not easily predictable along a west-to-east gradient; areas of high disconnection were either

cluster (Fig. 3.5b) or state specific (Fig. 3.1e). Finally, preferential encroachment did not appear to be regionally driven (Fig. 3.3). Our results painted a more complex picture of the difficulties that would be faced if establishment of an official conservation system was ever attempted. Overlaying the maps of buffer zones and connectedness (Fig. 3.5a, b) showed that many clusters will have suffered either a high percent loss of buffer zone area or connectedness, or both, by the year 2030. Even in the West, where most large conservation schemes are imagined, the relatively high increase of development at core edge (Fig. 3.1c) would eventually limit options beyond the limitations identified here.

At a minimum, prioritizing future conservation action must at least consider adjacent land uses and the threats and benefits they may confer to a conservation system (Groves et al. 2002; Wilson et al. 2005). The buffer zones we identified relied more heavily on private than public lands, and despite the numerous difficulties in engaging the private sector in land conservation (Schonewald-Cox et al. 1992), a key conservation strategy will be to work cooperatively across land ownership boundaries (e.g., USDA 2007) and to engage and educate private landowners in conservation strategies (Shafer 1999). Our results illustrate that this is particularly critical for smaller protected areas, which will tend to dominate future conservation activities given the increasingly competitive trade-off between conservation and development.

Acknowledgments

Helpful comments and discussions were provided on earlier drafts by R. I. McDonald, two anonymous reviewers, N. Piekeliak, P. Barry, D. Kashian, and A. Hansen. This research was supported in part by the U.S. Department of Agriculture (USDA)

under National Needs Fellowship Grant 2002-38420-11713, the Environmental Protection Agency under the Science to Achieve Results (STAR) Fellowship Program, and the National Science Foundation under Integrative Graduate Education and Research Traineeship grant DGE-0221595 (to A.A.W.) and by USDA National Research Initiative Award 2003-35401-13801 and National Aeronautics and Space Administration Decision Support System award (to D.M.T.). None of the supporting agencies have officially endorsed this publication.

Tables

Table 3.1. Method details for defining core, core edge, potential buffer, buffer zones, developed lands, clusters, and passageways in a study of residential development encroachment on protected areas in the United States.

Term	Land-use type	Units/ha	Data sources	Details ^a
Core	GAP stewardship 1 or 2: lands with permanent protection and managed predominantly for the protection of natural processes (Jennings 2000) (e.g., national parks, wilderness areas, and some national forests)	0	GAP stewardship level: Protected Area Database (CBI 2006) improved with updated data where available	core: contiguous ^b area of stewardship level 1 and 2 lands with a minimum size of 1000 ha core edge: area within 10 km of a core boundary
Potential buffer	small GAP stewardship 1 and 2 and all GAP stewardship 3: lands permanently protected but subject to extractive uses such as logging or mining (Jennings 2000) (e.g., Bureau of Land Management, forest, and privately protected lands [where data available])	0		buffer zone: potential buffer land contiguous ^b to core cluster: contiguous ^b area of core and buffer zone passageway: contiguous ^b path through the buffer zone connecting any two cores
Developed	undeveloped (private)	< 0.001	housing densities ^c (USCB 2000a)	cropland: NLCD category 82, separated out from other undeveloped land
	Rural	0.001 - 0.062	National Land Cover Dataset (NLCD)	commercial area: NLCD categories 23 and 24 and major highways considered developed because of their critical effects on habitat quality and connectedness (Hilly et al. 2006)
	Exurban	0.062 - 1.45	(Vogelmann et al. 2001)	
	Suburban	1.45 - 4.12	major highways (BTS 2005)	
	Urban	> 4.12		

Notes for Table 3.1

^aAll GIS analyses had a grid-cell mapping unit of minimum 1 ha in Albers equal area projection.

^bContiguous defined based on the eight-neighbor rule in GIS.

^c1970 housing densities computed from "year housing built" data in the SF3 form; 2000 housing units from the block-level data from SF1 form with final density computed after removing portions of blocks that were undevelopable (e.g., protected, public, water, etc.) and units were allocated within a partial block based on land cover, groundwater well density, and road accessibility; 2030 densities were modeled using a spatially explicit regional growth model (SERGoM) that used county population projections to drive new housing units that were allocated based on distance to urban areas along the transportation network. See Theobald (2005). Density categories are consistent with U.S. Census Bureau definitions and other studies pertaining to exurbanization (e.g., Odell & Knight 2001; Hansen et al. 2005).

Figures

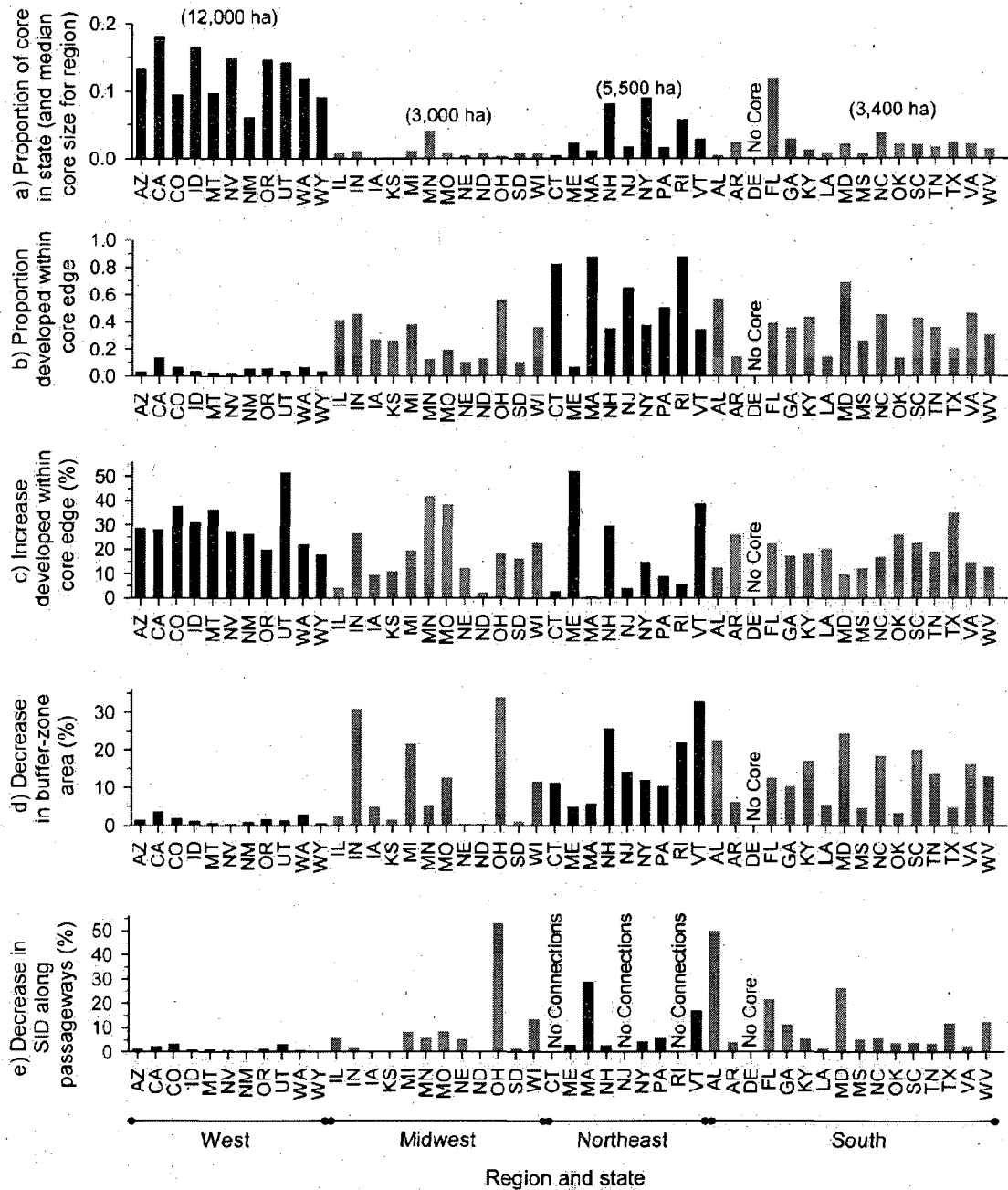


Fig. 3.1. Comparison of core, buffer area, and connectedness metrics for the 48 conterminous states, with states arranged alphabetically within census region: (a) proportion of core in state (with median core size for region listed in parentheses [ha]), (b) proportion of area at core edge developed at exurban or higher housing densities in 2000, (c) increase in development within core edge from 2000 through 2030, (d) decrease in buffer zone area from 2000 through 2030, and (e) decrease in sum of inverse distance (SID) measured along midpoint of passageways connecting cores from 2000 through 2030.

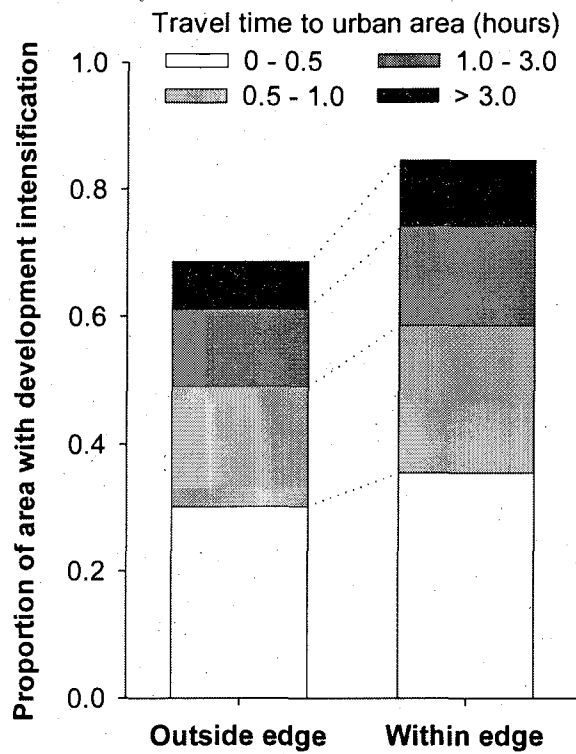


Fig. 3.2. Comparison of proportion of developable area between areas outside and within core edge that experienced development intensification (increase in housing-density category) from 1970 through 2000. Proportion of area with intensification is categorized by (population weighted) travel time to nearest urban area.

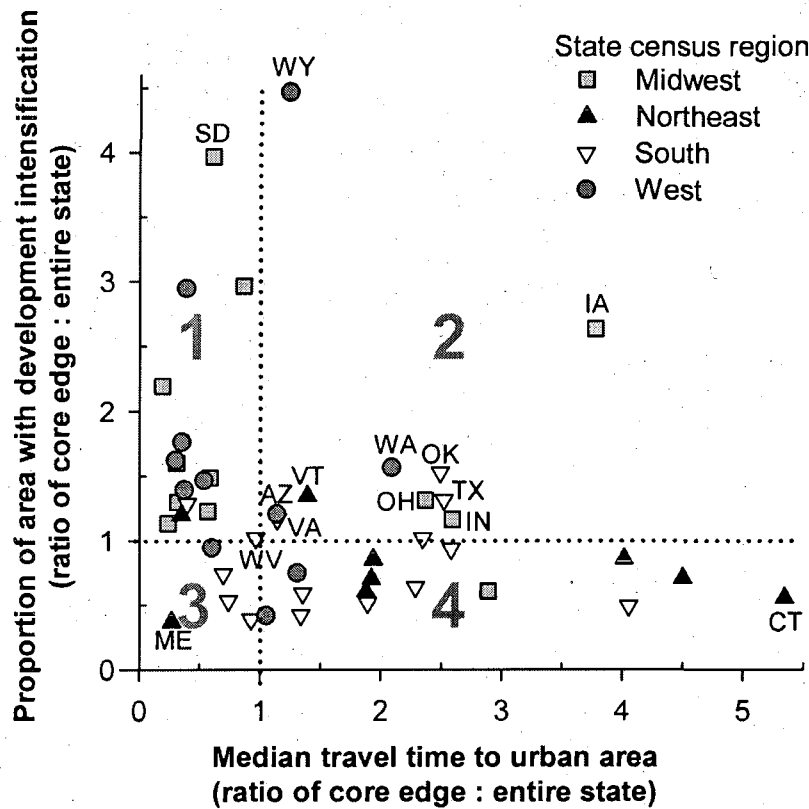


Fig. 3.3. *Quadrants of encroachment.* The ratio of the proportion of area that intensified in housing density within core edge within a state to the proportion of intensified area in the entire state (1970-2000) plotted against the ratio of the median travel time to an urban area within core edge within a state to median travel time to an urban area for the entire state. Dotted lines represent the 1:1 ratio for each axis. States fell into one of the quadrants depending on whether cores in that state had surrounding development intensification that was greater or less than the average development within the entire state, and depending on whether the distance of travel time from core edge was greater or less than the average travel time to urban area in the rest of the state. Selected states have been labeled with their postal code abbreviation.

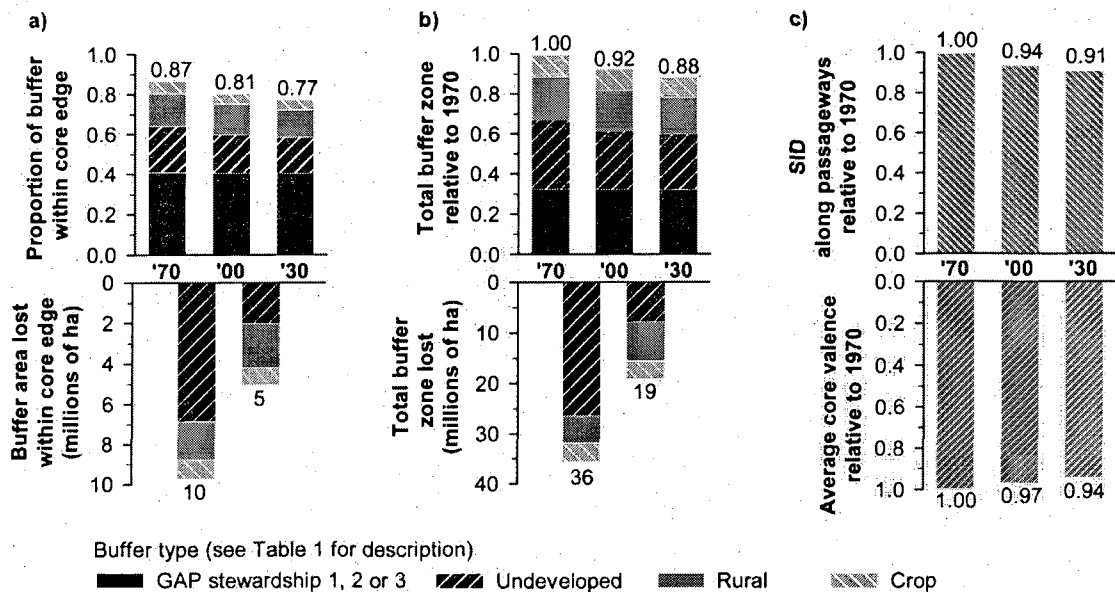
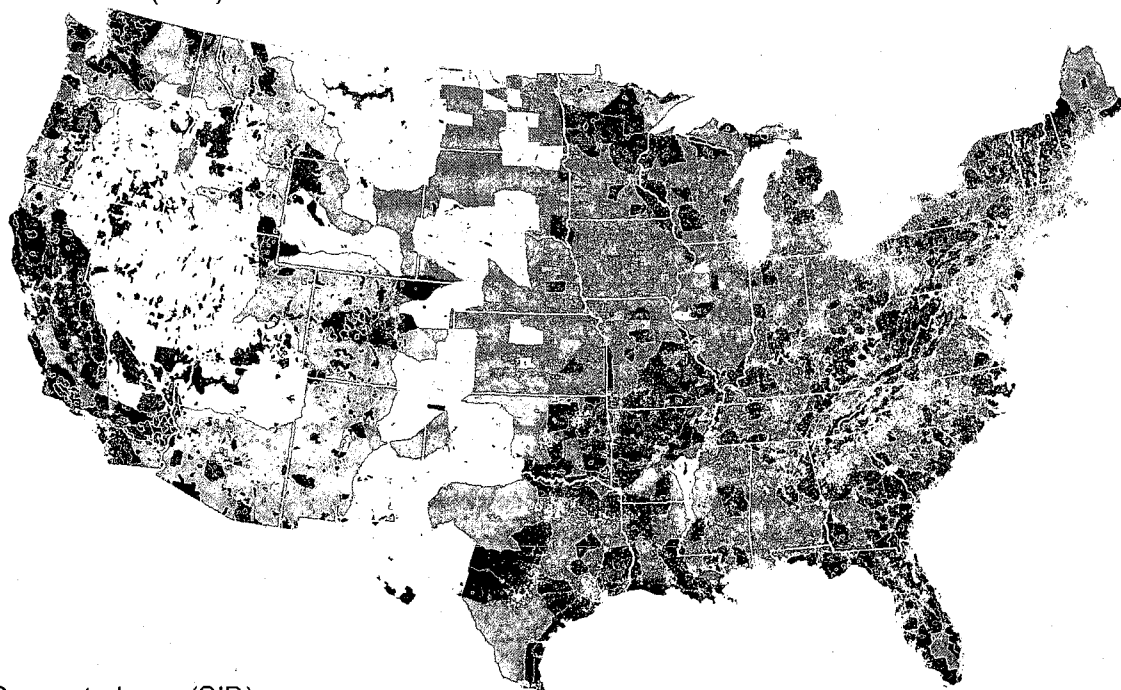
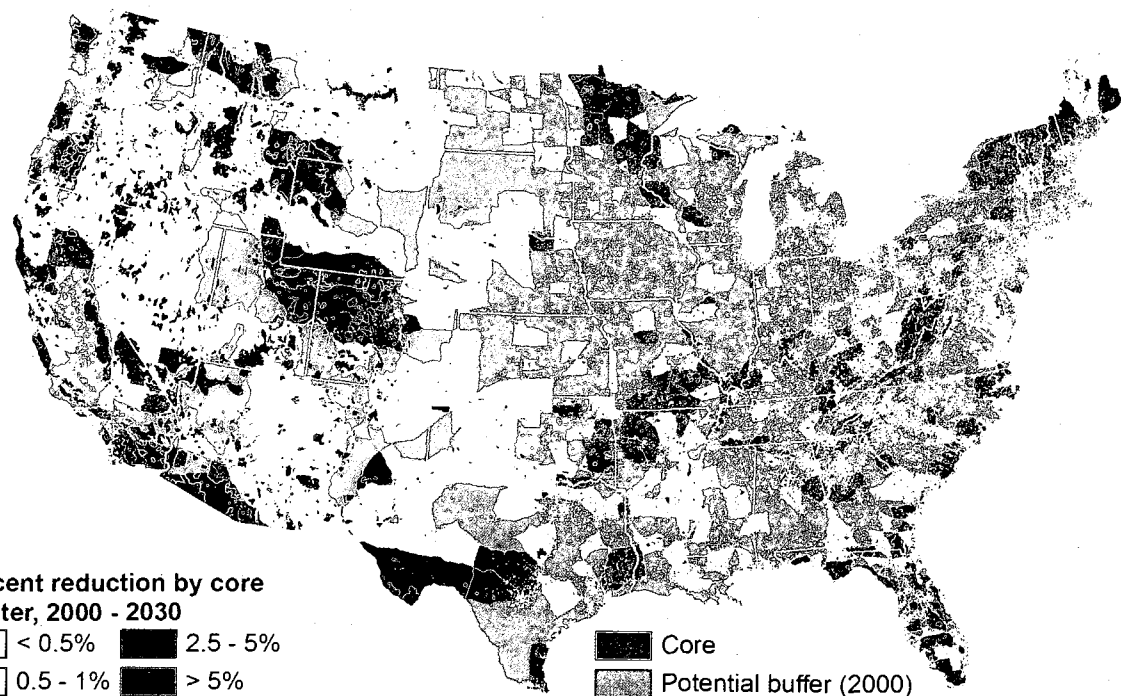


Fig. 3.4. Summary of change across or between study years 1970, 2000, and 2030 in (a) buffer within edge, (b) total buffer zone (top, normalized to 1970 amounts; bottom, loss between study years for all cores), and (c) connectedness (top, sum of inverse distance [SID] to connection measured along half-way point of all passageways connecting two cores, normalized to SID for 1970; bottom, average core valence [total no. cores/total no. passageways] for entire conterminous U.S. for each study year, normalized to 1970 amounts).

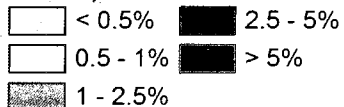
a) Buffer zones (area)



b) Connectedness (SID)



Percent reduction by core cluster, 2000 - 2030



 Core
 Potential buffer (2000)

Scale: 1:27,000,000

Fig. 3.5. Core clusters mapped for year 2000 categorized by (a) percent reduction in area of buffer zone within cluster from 2000 through 2030 and (b) percent reduction in sum of inverse distance (SID), measured within each cluster, from 2000 through 2030.

CHAPTER 4. HOW DO HIERARCHAL SCALES OF UPSLOPE LAND COVER INTERACT TO INFLUENCE AQUATIC INTEGRITY? ⁴

Abstract

The hierarchical spatial nature of ecological processes has been well documented but often is not captured in statistical models. This paper illustrates how basic theoretical concepts of spatial interactions in aquatic ecology can be included in linear regression analysis to provide more ecologically-relevant inference from model results. We used a simple conceptual model of how land cover at different upslope scales influences aquatic integrity to guide our statistical approach and frame our inference. We began with single-scale regressions, then applied multi-scale regressions, and finished with a hierarchical multiple regression model. We trace how altering our statistical approach based on the conceptual model led to alternate inference. We found that comparing analyses conducted at a single spatial scale suggested the predominant influence of urban land cover at the catchment scale, but that analyses based on our conceptual model of interacting spatial scales suggested that finer-scales played a more substantial role in explaining variance in aquatic integrity. Our results also suggested that our conceptual model was a reasonable representation of the system. We present this study as a cautionary tale to watershed managers. Appropriate watershed management relies on practitioners understanding the

⁴ This chapter will be submitted as a manuscript, co-authored with Jennifer A. Hoeting.

implications of the model underlying the science that drives management decisions. This does not require significantly more complex modeling approaches, only that the research questions drive the modeling process, not visa versa.

4.1 Introduction

Land cover and land use change may be one of the most critical factors affecting aquatic ecological integrity (Naiman & Turner 2000; Allan 2004) because land cover in the watershed directly influences downstream aquatic systems (Hynes 1975). River networks are systems of nested hierarchical spatial scales, in which coarser-scale ecological processes influence and interact with finer-scale processes to influence stream biology (Frissell et al. 1986; Poff 1997; Montgomery 1999; Fausch et al. 2002; Benda et al. 2004). These spatial relationships between land cover modification and aquatic ecological integrity have important implications for watershed management and restoration (Fausch et al. 2002).

Accordingly, previous studies have sought to identify the ecological scale that drives the relationship between anthropogenic land cover and measures of ecological integrity. The statistical approach of many previous studies has been to calculate the proportion of land cover type at various upslope extents (scales) that contribute to downstream flow, and then to correlate or regress those land cover scales against an indicator of aquatic integrity – a chemical, physical, or biotic measure representing a stream's ability to self-repair or maintain an adaptive community of native organisms (Karr et al. 1986). The scale that has the strongest predictive relationship with some indicator is then identified as the primary determinant of aquatic integrity (e.g., Roth et al.

1996; Lammert & Allan 1999; Fitzpatrick et al. 2001; Sponseller et al. 2001; Wang et al. 2001; Morley & Karr 2002; Snyder et al. 2003; Strayer et al. 2003).

Studies that focus on the single scale that explains the most variance in an indicator overlook the principle of ecological hierarchies (Allen & Starr 1982) and may not accurately reflect the ecological processes interacting across scales in aquatic systems (Downes et al. 2002). This may lead to ambivalent direction for management. Previous study results have been ambiguous in regard to which scale drives the relationship between land cover and aquatic integrity (Allan 2004). For example, some studies recommend restoration efforts focus on riparian buffers (e.g., Sponseller et al. 2001), while other studies find that land cover at the riparian scale has little influence on aquatic integrity (e.g., Snyder et al. 2003).

Assessing the relationship between ecological processes within a conceptual model grounded in ecological theory maximizes ecological insight (Barber 1994; Noon et al. 1999) and allows for targeted conservation planning (Lehman 1986; Noon 2003). This is particularly true in aquatic systems, where the exact spatial processes governing aquatic integrity are unknown. Thus, here, we illustrate how theoretical concepts of spatial interactions in aquatic ecology might be used to guide applied statistical analysis. We use a simple conceptual model of how land cover at different scales influences aquatic integrity, and we trace how altering our focus from maximizing predictive power to partitioning influence between scales as suggested by our conceptual model leads to different inferences from results. We use a case study of Maryland streams surrounded by varying degrees of urban and natural land cover to illustrate the differences in approaches

and discuss the implications for modeling aquatic integrity and ecological processes in general.

In our analysis of upslope land cover influences on aquatic integrity, we focus primarily on urban (residential and commercial) development because the impacts of urban areas on aquatic systems are well studied (Booth & Reinelt 1993; Allan 2004; Walsh et al. 2005). The associated increase in impervious surfaces is one of the best understood threats from anthropogenic land cover (see Schueler 1994; Brabec et al. 2002 for reviews) and stormwater runoff arising from imperviousness is a predominant driver of urban impacts to streams (Walsh et al. 2005). Increased chemical pollutant loads are widespread in urban streams (Walsh et al. 2005) and can be observed at relatively low levels of catchment urban land cover (Hatt et al. 2004). These changes to the physical properties of aquatic systems result in dominance by more tolerant species and shifts in species composition and structure (Wente 2000; Snyder et al. 2003; Strayer et al. 2003; Gray 2004; Meyer et al. 2005). Here we represent aquatic integrity using the Benthic Index of Biotic Integrity (BIBI). Indices of biotic integrity (Karr 1981) are multimetric indices that have become widespread in watershed assessments and studies. BIBI combines metrics on benthic species richness, composition, trophic structure, and abundance into a single index. Multimetric indices of river biota integrate processes that affect aquatic systems across an entire watershed (Karr 1999; Adams 2002) and are frequently used to assess river degradation (Norris & Hawkins 2000).

4.2 Methods

4.2.1 Study area, benthic index of biotic integrity, land cover, and scales of analysis

Our study area consisted of the Gunpowder Hydrologic Unit (Code 0206003; Maryland, USA; Fig. 4.1). We chose this hydrologic unit because of the availability of aquatic integrity data and the diversity of land cover in the area. The unit included the Bush, Gunpowder, and Patapsco River basins, covering approximately 4,000 ha.

BIBI data were collected by the Maryland Biological Stream Survey (MBSS) (MDNR 1997) between 1995 and 1997. BIBI scores were determined by comparing the mean of several benthic metrics at each randomly chosen sample site to those found at reference sites with relatively minimal human impact. A separate BIBI was developed for each of the Eastern Piedmont and Coastal Plain geographic regions (Stribling et al. 1998).

We mapped urban and natural land cover types (Fig. 4.1) based on the 1992 National Land Cover Dataset (NLCD) (USGS 1992). These data were obtained from classifying 30-meter resolution Landsat satellite imagery from early- to mid-1990 into 21 land cover types. The NLCD data are one of the most widely available and used means for identifying human land covers in stream impact research (e.g., Richards et al. 1996; Allan et al. 1997; Johnson et al. 1997; Griffith et al. 2002; Snyder et al. 2003; Strayer et al. 2003; McBride & Booth 2005). To represent areas that were developed, we grouped together all land cover types associated with urban development (NLCD codes 21, 22, 23, 85). We defined natural land cover as forest and wetland land cover types (NLCD codes 41, 42, 43, 91, and 92). There were five other NLCD codes in our study area. We did not include open water, quarries/mines, or transitional land cover types (NLCD codes 11, 32, and 33, respectively) because they were not clearly urban or natural. We also did not

include agricultural cover types (NLCD codes 81 and 82) in the analysis. Although agricultural land use has been shown to affect downstream integrity, we did not include it here because the proportion of agriculture is inversely related to the amount of urban land cover in the watershed. We focused instead on urban because we were more interested in the effects of urban land use and because there may be a stronger relationship between urban land use and biotic integrity than between agricultural land use and biotic integrity (Snyder et al. 2003; Roy et al. 2007). Within the Gunpowder Hydrologic Unit, urban and natural land cover accounted for 45% of the total area.

We used three scales of upslope contributing area extent that were similar to previous studies: local, riparian, and catchment (e.g., Lammert & Allan 1999; Wang et al. 2001; McBride & Booth 2005) (Fig. 4.1). Using a GIS, we created each of the three scales upslope of each MBSS sampling location. All GIS analyses were conducted in Maryland State Plan NAD83 projection. To create the three scales of upslope extent, we first “snapped” the sampling location points to the stream network (as defined by the National Hydrography Dataset, medium-resolution) (USGS 2007), forcing all sampling location points to lie directly on a stream. Seven of the original 194 MBSS point locations with complete BIBI data did not snap correctly, and we removed these from the analysis (they were farther from a stream shown in the National Hydrography Dataset than a 150 m maximum snapping threshold). Based on an underlying 30-m model of elevation (USGS 1999), we used ArcHydro Tools (Maidment 2002) to identify the entire upslope catchment that contributed flow to the MBSS point. This was the catchment scale. We removed an additional three MBSS points from our analysis at this stage because of incorrect catchment delineation (because of low topography, the ArcHydro Tool was not

able to identify the upstream catchment correctly), leaving us with a total dataset of 184 MBSS points. We defined the riparian scale as the area within 100 m on each side of a stream up to a maximum distance of 2 km upslope from the MBSS point. We defined the local scale as the area within 100 m upslope of any MBSS sample point. We then calculated the proportion of area, for each scale and for each MBSS point, that was either urban or natural land cover.

4.2.2 Conceptual model

Our data analysis process was rooted in a conceptual model of the influence of spatial hierarchies of upslope land cover on BIBI (Fig. 4.2). The amount of urbanization in the entire upslope catchment accumulates and concentrates runoff from the largest area, and we thus expected that the catchment scale would have the greatest single-scale ability to predict BIBI. However, when combining scales, we hypothesized that the more proximal urban land cover was to a stream, the more likely it would have a direct ecological effect on aquatic integrity. This would largely be because intervening natural land cover should mediate the impact of urban land cover at more distant, coarser scales. The ability of natural areas to mitigate urban influences should relate to both the proximity of the natural area to the stream as well as the amount of stream buffered by natural land cover. Thus, we expected natural land cover within the riparian buffer to provide the most effective filter from upslope urban areas as observed in previous studies (Osborne & Kovacic 1993; Vought et al. 1995). We hypothesized that the importance of natural land cover in the entire catchment would depend on spatial arrangement; natural cover at the catchment scale would be important if it was located between urban cover and the stream.

4.2.3 Single-scale linear regression models

4.2.3.1 Comparison of adjusted R^2 values

Following the methods of many previous studies, we first considered the relationship between land cover and aquatic integrity within each, single scale and compared results based on the adjusted R^2 value (e.g., Roth et al. 1996; Sponseller et al. 2001; Strayer et al. 2003). We applied a simple or multiple linear regression model regressing land cover covariates against BIBI within each individual scale. The full model for each scale included both the proportion of natural and urban land cover within that scale, and the reduced models included only natural or urban land cover. We calculated the adjusted R^2 (hereafter referred to as R^2_{adj}) for the full model and the reduced models (i.e., just the urban or just the natural land cover covariate) for each scale to determine which scale had the strongest relationship with aquatic integrity. The R^2_{adj} is a modification of the standard coefficient of determination, imposing a penalty for the number of explanatory terms in the model.

4.2.3.2 Comparison of Akaike weights

Our first enhancement to the commonly applied methods of previous studies was the use of Akaike weights to compare and rank “best” single-scale models (see for example Roy et al. 2007 for another use of Akaike weights). Although R^2_{adj} values provide useful information on the amount of variation explained in a model, they are not optimal for model selection (McQuarrie & Tsai 1998). A preferred model selection approach is the use of Akaike’s Information Criterion (AIC) (Burnam & Anderson 2002). AIC uses a maximum log likelihood method to compare models, penalizing for the

addition of variables, with the lowest AIC indicating the best-supported model from within a set of considered models. AIC is calculated upon an information-theoretic approach, and is particularly appropriate for use in comparing ecologically derived a priori models. AIC values can then be used to calculate Akaike weights (w_i), computed as $w_i = \exp(-1/2\Delta_i) / \sum_n \exp(-1/2\Delta_i)$, where Δ_i equals the difference in AIC for the i^{th} model in the set of models $n=1 \dots I$, compared to the model with the lowest AIC in the set. Akaike weights can be interpreted as the support in the data for each model given a suite of nested models, and the weights can be used to rank-order nested models. We calculated Akaike weights to compare, both within and between scales, how much support there was in the data for urban or natural land cover as the primary driver of downstream aquatic integrity. These single-scale statistical approaches were not guided by our conceptual model, but we use the conceptual model to frame our inference from results from the single-scale analyses.

4.2.4 Single scale linear regression models; non-overlapping scales

To begin to parse out the different influences between scales, we again conducted single-scale analyses, but used non-overlapping, mutually-exclusive scales. We used GIS to create areas exclusive to a single scale by clipping out the extent of the finer scale(s) (see for example Wang et al. 2001 for a similar approach). For example, the non-overlapping catchment scale included the catchment area that did not coincide with the riparian or local scales (in set theory, this would be the complement of the riparian plus local scales). Using these non-overlapping, exclusive-area scales, we recalculated the proportion of urban and natural cover within each of the catchment and riparian scales

(there was no exclusive local scale; there was no finer-scale to remove from its area), and reran the regression single-scale regression analyses. We recalculated the R^2_{adj} and Akaike weights for the single-scale catchment and riparian regressions so as to compare model weighting and ordering against the model ordering of the complete, shared-area scale analyses.

4.2.5 Cross-scale linear regression models; non-overlapping scales

To begin to assess multi-scale spatial interactions, we regressed BIBI on the full cross-scale model, including all six possible covariates (natural and urban, at each of the three [clipped] scales). We also used a regression tree to check for interactions between covariates in the full cross-scale model. We calculated the Akaike weights for all (63) reduced permutations of the full model (and the full model itself) and used the weights to rank-order all model permutations. We also calculated R^2_{adj} for all of the permutations. We used the non-overlapping scales for this analysis.

4.2.6 Cross-scale hierarchical multiple regression; non-overlapping scales

In our final analysis, we explicitly included the hierarchical nature of scales of land cover influence from our conceptual model into our statistical approach. We conducted hierarchical multiple regression, whereby we sequentially added covariates to the model based on our assumptions about how the aquatic system would be hierarchically influenced by various land covers at different scales. Hierarchical multiple regression differs from standard multiple regression in that it allows for the ordered partitioning of variance between each of the successive additions of covariates (or blocks thereof). In hierarchical multiple regression, one begins with the simplest reduced model,

and at each successive stage, one additional covariate (or block of covariates) is added until the full model is built. We first added the local scale effects, followed by the riparian, followed by the catchment scale influences. Within a scale, we added the natural land cover proportion first, followed by the urban. We chose this ordering because our conceptual model suggested that the more proximal buffer would mitigate the more distal urban influences, and this is the appropriate sequencing of covariates in hierarchical multiple regression (Cohen & Cohen 1975). However, because we do not know that this is the best model order, we also considered other sequential ordering of variables for comparison. We tested the significance of the sequential addition (Type I Sums of Squares) of each covariate using a partial F-test, based on the extra sum of squares concept, and we only included those covariates found to be sequentially significant. Thus, at each stage, the R^2_{adj} increased, resulting in an ordered cumulative R^2_{adj} series (Cohen & Cohen 1975). We then used the extra sums of squares to partition the variance accounted for by each covariate (or block of covariates), which, at each stage, represented the partial increase in variance accounted for beyond what had been accounted for at the previous stage. We used the non-overlapping scales for this analysis.

4.2.7 Checking regression assumptions

For all statistical analyses, we checked residual plots to ensure assumptions of normality for regression analyses were met. Residual plots indicated curvature in the relationship between urban land cover and BIBI, and at each single scale, AIC comparisons selected for the inclusion of a second degree polynomial term for the urban land cover and its inclusion normalized residual plots. When combining scales, AIC comparisons only selected for the inclusion of the squared term for the urban land cover

proportion at the coarsest scale in the model, and this again normalized residual plots (e.g., in a model including both riparian and catchment urban covariates, only the catchment urban squared term was necessary). Thus, for all non-hierarchical regression analyses, we only included a squared term for the coarsest scaled urban covariate in a model. However, the hierarchical multiple regression analysis required that reduced models be fully nested within the full model (Cohen & Cohen 1975). At the local scale, the reduced model required a local urban squared term to ensure normality of errors. Thus, to keep models nested, we had to carry that squared term through the building up to the full model. This was true for the riparian urban and catchment urban squared terms as well. Thus, the final level of the model (the full model) included squared terms for all urban covariates.

Covariate data were also scaled and centered to reduce multicollinearity. Multicollinearity is a measure of correlation between two covariates within a multiple regression. We first used a Pearson's correlation matrix to test correlation between all first-order covariates in the model combining both urban and natural land cover covariates at all three scales. The covariate riparian urban was highly correlated with catchment urbanization ($r = .94$), and combining the two covariates in a multiple regression against BIBI changed the sign of their associated coefficients. Although multicollinearity between covariates must be avoided when analyses rely on the interpretation of regression coefficients (Kutner et al. 2004), here, our analysis does not consider regression coefficients. Thus, we chose to include the riparian urban term because of our a priori belief that it was important. We explicitly discuss when multicollinearity may have influenced results.

Lastly, we computed empirical variograms using robust estimators (Cressie & Hawkins 1980) to assess the amount of spatial autocorrelation in the data. Variography based on spatial coordinates (latitude and longitude) of the sample points indicated no autocorrelation once the trend for catchment urban land cover was removed. Thus, we did not further account for autocorrelation in our analyses. We acknowledge that Euclidean proximity may not relate to hydrologic, in-stream distance. However, previous research suggests that Euclidean distance is the most suitable distance measure for regional statistics modeling of spatial data (Peterson et al. 2006). All statistical analyses were performed using the R statistical package (R Development Core Team 2008).

4.3 Results

4.3.8 Single-scale linear regression models

Using linear regression models, we found significant relationships between aquatic integrity regressed on each of the full and reduced models of land cover type at each of the three individual scales (Table 4.1). The proportion of urban land cover explained a greater amount of the variance in BIBI than did the proportion of natural land cover for all scales, and coarser scales explained more of the variance than finer scales based on comparisons of R^2_{adj} . The proportion of natural land cover in the riparian scale explained the most variance in aquatic integrity (followed by natural land cover at the local scale, with the amount of natural land cover at the catchment scale explaining the least amount of variance).

At all scales, the reduced model including only the natural land cover covariate had no support in the data (i.e., had a Akaike weight of 0%; Table 4.1). However, using the non-overlapping scales slightly reduced the support in the data for including natural

land cover as a second covariate at the coarser scales. For example, excluding the local scale area from the riparian scale, the Akaike weight for the riparian scale model that included both urban and natural land cover fell by 2%. At the catchment scale, clipping out the riparian and local scales resulted in Akaike weights slightly favoring the reduced model including only urban land cover, as compared to the slightly higher ranking for the full model in the overlapping-scale analysis.

4.3.9 Cross-scales linear regression models

A multiple linear regression of BIBI against the full cross-scales (non-overlapping) model demonstrated that the influence of urbanization at the catchment scale swamped other influences, and only the catchment urban term (and the intercept and second degree polynomial term for catchment urban) was significant (t-test at $\alpha = .05$) within the full model. We found no significant interaction terms between the covariates in the full model, although the regression tree suggested the potential importance of riparian natural land cover buffers at low levels of catchment urbanization.

When we compared Akaike weights, the full cross-scales model (with all 6 covariates) was the lowest ranked model of the 63 possible permutations with any support in the data ($w_i = 0.4\%$; Table 4.2). The top ranked model, with 17% of the support in the data, included the riparian natural and catchment urban covariates. The percent support in the remaining models was often similar, tending to be grouped based on number of covariates in the model. R^2_{adj} values were nearly identical for most models.

Applying a hierarchical multiple regression, partial F-test results from the full cross-scales (non-overlapping) model indicated that once natural land cover at finer scales was accounted for, the inclusion of the catchment natural term was not significant.

Thus, we ran an hierarchical multiple regression including the sequentially entered terms: local natural, local urban, riparian natural, riparian urban, and catchment urban. Partial F-tests from this hierarchical multiple regression indicated that sequentially adding each variable based on the order suggested by our conceptual model significantly increased the explanatory power of the model (Table 4.3). Partitioning the variance between each stage of the hierarchical model based on extra sums of squares, we attributed 14% of the variance explained to natural land cover at the local scale. Seventy-one percent of the variance explained was attributed to the full local scale model. Once local scale land cover was partitioned out, the hierarchical model attributed approximately 5% of the remaining variance explained to riparian buffers, and another 13% to riparian urban land cover. The remaining 11% of the explained variance was attributed to urban land cover at the catchment scale.

For comparison, we also ran two additional hierarchical multiple regressions, each only including catchment urban and riparian natural. When riparian natural land cover was entered first, followed by catchment urban, partial F-tests indicated both were significant at $\alpha = 0.0001$, and we attributed sequentially partialled variance of 22% and 78%, respectively. When we reversed that order (entering catchment urban first, followed by riparian natural), riparian natural was only significant at $\alpha = 0.1$, and sequentially partialled variances were 98% and 2%, respectively.

4.4 Discussion

Our single-scale model results were as we expected; catchment urban land cover had the strongest predictive relationship with BIBI (Table 4.1). Further, in the multiple regression on the full cross-scale model, only the catchment urban covariate was

significant. We note that this result was likely influenced by multicollinearity, a limitation of the multiple linear regression approach. Multiple linear regression can not alone parse out the relative influence of covariates that share explanatory power. The predictive power of urbanization that is accumulated across the entire watershed swamps the influence of natural land cover and land cover effects at other scales. Yet, theory in aquatic ecology (Frissell et al. 1986; Poff 1997; Montgomery 1999) and previous empirical studies (e.g., Steedman 1988; Hunsaker & Levine 1995; Lammert & Allan 1999; Sponseller et al. 2001) demonstrate the importance of other scales and the hierarchical interactions between them. Ecological inference based on a single organizational level may misrepresent the ecological processes that reflect system dynamics (Wiens 1989).

Our single-scale analysis results showed that all land covers at all scales had some influence on aquatic integrity, despite them having lower predictive power compared to catchment-wide urban land cover (Table 4.1). Additionally, clipping out the finer-scale to create non-overlapping scales consistently reduced the support in the data (Akaike weights) for the inclusion of natural land cover in the coarser-scale model. These results suggest that natural land cover at finer scales mediates the effect of urbanization at coarser scales, as per our conceptual model. These ecologically relevant insights would be overlooked if comparing only the R^2_{adj} for each individual scale, ascertaining only the best predictive relationship.

The comparison of Akaike weights between all permutations of the full, multiple regression model provided some additional insight. The inclusion of the riparian urban covariate in the 3rd ranked model (Table 4.2) suggested that was the covariate of next

import following catchment urban and riparian natural. However, although 83% of the support in the data remained to be distributed amongst other models after the top model was identified, Akaike weights were not able to clearly differentiate between most of the other considered models, and it was unclear whether local natural, local urban, or catchment natural was the next most important covariate. Relying only on AIC model ranking, we would identify the importance of the riparian buffers as they mediate catchment urbanization. But the importance of other land cover types and other scales would be inseparable, and the statistical model chosen would not reflect what we learned from comparing the non-overlapping and overlapping scale analyses.

The hierarchical multiple regression allowed us to directly incorporate our conceptual model of the system into our statistical model. We were first able to identify that catchment natural land cover was not influential in our particular study area. Our approach did not allow us to test whether this was because of the spatial arrangement between catchment urban and natural land cover, but this remains a rational explanation. Once the catchment natural land cover covariate was removed, the addition of all other covariates, ordered as suggested by our conceptual model, significantly increased the explanatory power of the model. Although our hypothesis about riparian buffers – that natural land cover at the riparian scale was the most important – was supported when we compared the R^2_{adj} values for natural land cover at various scales, sequential variance partitioning from our hierarchical multiple regression suggested that only 5% of the variance explained by the full model could be attributed to riparian buffers once local scale land cover was removed. Further, although all previous analyses focused on predictive power suggested that catchment urban land cover drove aquatic integrity

response, once finer scales were accounted for, sequential partitioning of variance attributed only 11% of the explained variance in BIBI to urban cover at the catchment scale.

In aquatic ecology, linking empirical data and conservation of streams demands a more integrative approach than focusing on a single scale of influence (Fausch et al. 2002). Given the known multi-scale processes in watersheds (Allan 2004), we argue that the statistical methods should not be designed to answer “at which scale does land cover most strongly influence aquatic integrity”, but instead aim to answer the question “how do the hierarchical scales of land cover interact to influence aquatic integrity?” In applied ecology, there is growing support for the idea that models serve as hypotheses themselves (Hobbs & Hilborn 2006). Thus, the statistical models employed should be grounded in conceptual models based on accepted ecological theory (e.g., Cushman & McGarigal 2002; Olden et al. 2006; Lookingbill et al. 2007).

Our partitioning of variance from the hierarchical multiple regression does not definitively answer the question of how scales interact. It only answers the question relative to our conceptual model. However, conceptual models that provide a structured expression of the a priori hypotheses about system allow for formal testing about how components and processes are related (Manley et al. 2004). We tested all other possible orderings of the covariates in our full cross-scale hierarchical regression model, and we found that the partial F-tests were not sequentially significant. Thus, the ordering of our conceptual model was the only sequential ordering that supported inclusion of all covariates (except catchment natural land cover). That each land cover type at each scale had a significant relationship with BIBI supports the concept that all scales should be

included in the model. Including all covariates is not the most parsimonious model that explains the system. But, it ensures that the model we use to represent the system incorporates the full range of spatial interactions that we determined to be operating in the system.

Even when we included only the covariates in the “top” model as selected by Akaike weights, changing the order in the hierarchical multiple regression substantially altered the amount of variance partitioned between either catchment urban or riparian natural land cover. If catchment urban was entered first, riparian natural only accounted for 2% of the sequentially explained variance, but if the order was reversed, riparian natural accounted for 22% of the sequentially explained variance. Using the more standard Type II sums of squares for a components of variance analysis would be useful in an experimental design that ensured independence of the covariates. However, in real-world analyses of ecological systems, the covariates are often correlated, and the sequential partitioning of variance based on a pre-specified sequence of covariates is a means to avoid this problem.

More detailed models (both conceptual and statistical) would be needed to more authoritatively elucidate and test the interactions between anthropogenic land cover, spatial hierarchies, and aquatic integrity. For example, we do not consider the effects of agricultural land cover, legacy land uses, nonlinear responses, intermediate processes that link the initial stressor to the biological indicators, or rare or unique features that are all critical influences on the spatial interactions (Fausch et al. 2002; Allan 2004; Benda et al. 2004; King et al. 2005).

Several other studies have begun to empirically confront more complex conceptual models combined with advanced statistical approaches to address the implications for spatial hierarchies in ecological systems (e.g., Olden et al. 2006; Burcher et al. 2007; Novotny et al. 2009). We do not advance our partitioning method as the best approach; the partitioning of influence from other, more detailed models and approaches are likely more accurate. Instead, we present this work as a cautionary tale to watershed managers about the importance of carefully choosing any modeling approach. Even if more detailed conceptual models are used, the inference will only be as good as the model. Conceptual models provide a method of testing alternative hypotheses and placing boundaries on results. However, in studies of ecological interactions, it is almost impossible to know if the model is “true”. Any model is merely a reflection of reality. The goal is not to replicate ecological reality in all its complexity, but to apply a model that best represents our understanding of the system and then to explicitly acknowledge the assumptions embedded in the model – and ultimately, the modeled outcomes.

Our study shows that different statistical analyses, while equally valid, can substantially alter inference. For example, our final results indicated that managing land cover directly adjacent to the stream was of primary importance. This was a reversal from our initial findings of the catchment scale driving impacts, and it was also not supportive of our hypothesis that riparian natural areas might be of foremost importance. When we looked only at catchment urban and riparian natural, altering the order that they were placed in the hierarchical regression model, results suggested that either riparian buffers were unimportant or that they accounted for almost 25% of the variance. Depending on

the modeling approach taken, a watershed manager might significantly alter management actions.

We urge watershed managers and conservation planners, and the scientists that conduct the studies that guide their decisions, to consider the implications of the statistical model that underlies the inference that is then translated to management action. While more detailed conceptual models and advanced multilevel and multivariate statistical approaches may further improve ecological insight, they are not requisite. We suggest that management professionals without the resources for more detailed approaches, or perhaps looking for a low-commitment first-pass assessment, would be better served if they applied and tested any simple conceptual model that includes the hierarchical nature of the system. These models can then be refined, expanded, and further tested as information emerges. But even if the conceptual map of the system remains simplistic, our results indicated that managers must be wary of the models they choose. Statistical tools should not drive the research question, instead research questions should drive the analysis.

Tables

Table 4.1. Adjusted R^2 (R^2_{adj}) and Akaike weights (w_i) for single-scale regressions of aquatic integrity on proportion of urban and natural land cover within each of the three scales compared between models using overlapping and non-overlapping scales (extents of finer scales clipped from coarser scales).

Scale	Model Covariates	Overlapping		Non-overlapping	
		$R^2_{adj}^*$	w_i	$R^2_{adj}^*$	w_i
Local	Natural	0.06	0%		
	Urban	0.34	73%		
	Natural, Urban	0.33	27%		
Riparian	Natural	0.11	0%	0.10	0%
	Urban	0.41	37%	0.41	39%
	Natural, Urban	0.42	63%	0.41	61%
Catchment	Natural	0.05	0%	0.04	0%
	Urban	0.46	43%	0.46	54%
	Natural, Urban	0.46	57%	0.46	46%

*All regressions significant at $\alpha=.005$, using an overall F-test for the model.

Table 4.2. Models, of 63 possible full cross-model permutations, ranked by Akaike weights (w_i). All models with greater than 0.1% support in the data shown.

Rank	Model Covariates	R^2_{adj}	w_i
1	riparian natural, catchment urban	0.47	17.4%
2	catchment urban	0.46	7.1%
3	riparian natural, riparian urban, catchment urban	0.46	7.0%
4	local natural, riparian natural, catchment urban	0.46	6.5%
5	riparian natural, catchment natural, catchment urban	0.46	6.5%
6	local urban, riparian natural, catchment urban	0.46	6.4%
7	catchment natural, catchment urban	0.46	6.0%
8	local natural, catchment urban	0.46	3.8%
9	riparian urban, catchment urban	0.46	3.5%
10	riparian urban, catchment natural, catchment urban	0.46	3.0%
11	local urban, riparian natural, riparian urban, catchment urban	0.46	2.6%
12	riparian natural, riparian urban, catchment natural, catchment urban	0.46	2.6%
13	local natural, riparian urban, riparian natural, catchment urban	0.46	2.6%
14	local natural, catchment natural, catchment urban	0.46	2.5%
15	local natural, riparian natural, catchment natural, catchment urban	0.46	2.4%
16	local natural, local urban, riparian natural, catchment urban	0.46	2.4%
17	local urban, riparian natural, catchment natural, catchment urban	0.46	2.4%
18	local urban, catchment natural, catchment urban	0.46	2.2%
19	local natural, riparian urban, catchment urban	0.45	1.7%
20	local natural, local urban, catchment urban	0.45	1.4%
21	local urban, riparian urban, catchment urban	0.45	1.3%
22	local natural, riparian urban, catchment natural, catchment urban	0.45	1.2%
23	local urban, riparian urban, catchment natural, catchment urban	0.45	1.1%
24	local urban, riparian natural, riparian urban, catchment natural, catchment urban	0.46	1.0%
25	local natural, riparian natural, riparian urban, catchment natural, catchment urban	0.46	1.0%
26	local natural, local urban, riparian natural, riparian urban, catchment urban	0.46	1.0%
27	local natural, local urban, catchment natural, catchment urban	0.45	0.9%
28	local natural, local urban, riparian natural, catchment natural, catchment urban	0.46	0.9%
29	local natural, local urban, riparian urban, catchment urban	0.45	0.7%
30	local natural, local urban, riparian urban, catchment natural, catchment urban	0.45	0.5%
31	local natural, local urban, riparian natural, riparian urban, catchment natural, catchment	0.45	0.4%

*All regression models significant at $\alpha=.0001$, using an overall F-test for the model.

Table 4.3. Model summary and analysis of variance for hierarchical multiple regression

Model Stage	R^2_{adj}	Pr(> t)	Residual df (N=184)	Regression SS (Type I)	Pr(>F)	Partitioned variance
Stage 1: local natural	0.06	<0.0001	182	11.19	n/a	13.8%
Stage 2: local natural, local urban	0.33	<0.0001	180	46.76	<0.0001	57.5%
Stage 3: local natural, local urban, riparian natural	0.35	<0.0001	179	3.70	0.007	4.6%
Stage 4: local natural, local urban, riparian natural, riparian urban	0.41	<0.0001	177	10.63	<0.0001	13.1%
Stage 5: local natural, local urban, riparian natural, riparian urban, catchment urban	0.46	<0.0001	175	8.97	0.0002	11.0%
Residual SS				88.22		
Total SS				169.47		

Figures

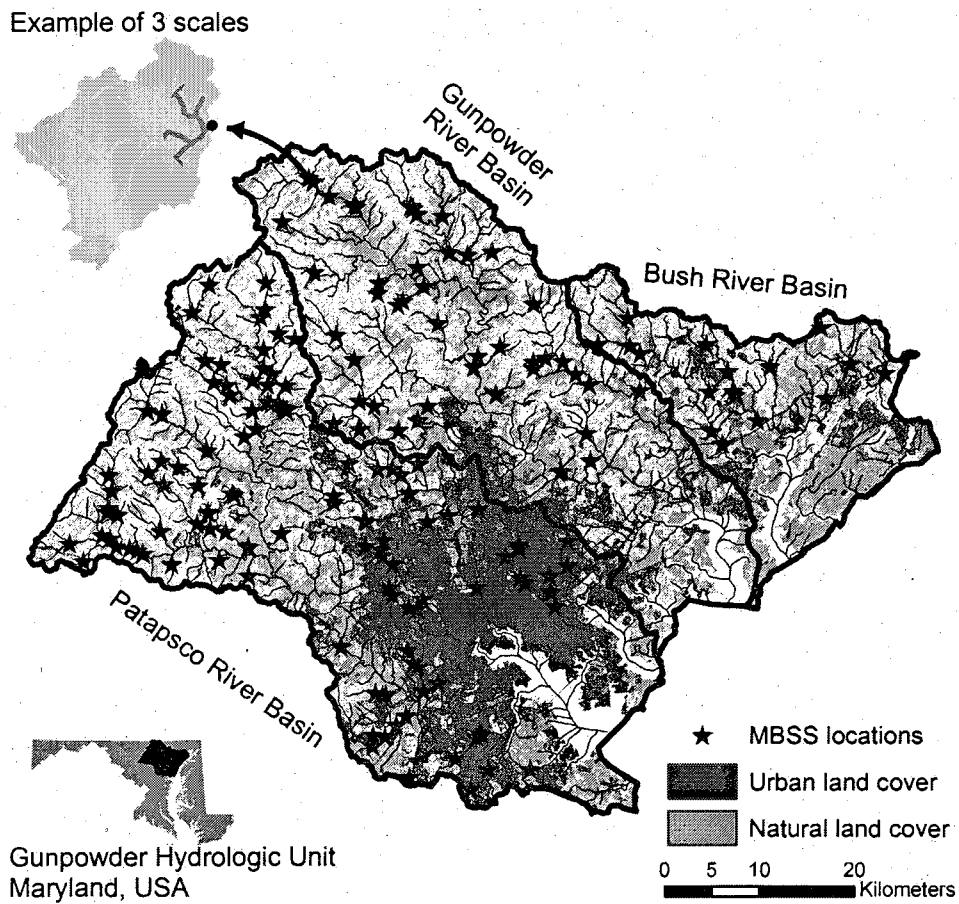


Fig. 4.1. Gunpowder Hydrologic Unit, located in Maryland, USA. Maryland Biological Stream Survey (MBSS) sampling locations are indicated with stars. An example of the 3 upslope scales (inset, top left) is shown for one MBSS sampling location in the Gunpowder River Basin. Scales include local (black), riparian (dark grey), and catchment (light grey).

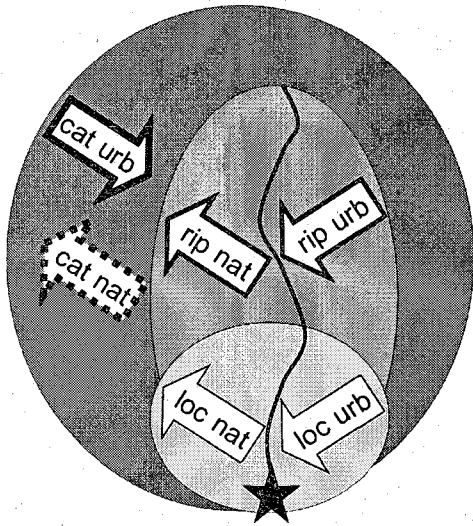


Fig. 4.2. Conceptual model of the interaction of urban (urb) and natural (nat) land cover at the catchment (cat), riparian (rip), and local (loc) scales of flow accumulation. Urban land cover at the catchment scale likely has the greatest magnitude of impact on aquatic integrity (as measured at the sampling location marked with a star) because of the greater area of accumulation, but urbanization at the more proximal riparian and local scales should also have a direct effect. Intervening natural land cover should mitigate the effects of upslope urban land cover, particularly at the riparian scale.

CHAPTER 5. CONCLUSIONS

5.1 Summary of research and conservation implications

The influences of land-use modification on biodiversity and ecological conservation are well documented for both terrestrial (Baker 1992; Blair 1996; Czech et al. 2000; Theobald 2000; McKinney 2002; Maestas et al. 2003; Hansen et al. 2005; Hawbaker et al. 2005; McDonald et al. 2008) and aquatic systems (Bledsoe & Watson 2001; Sonoda et al. 2001; Allan 2004; Meyer et al. 2005; Morgan & Cushman 2005; Chadwick et al. 2006; Alberti et al. 2007). My research builds on this past work while suggesting new specific approaches and tools for conservation planners.

I found that protected areas are vulnerable to threats from adjacent human activities, and these threats limit conservation options. Indeed, my results show that areas specifically dedicated to conservation may be most threatened by adjacent human land cover. By incorporating both adjacent and in-situ threats into a protected area vulnerability assessment, I identified numerous existing protected areas that were likely threatened, particularly smaller protected areas in the southern and northeastern U.S. I also found many areas with relatively low vulnerability to human related threats, presenting potential opportunities for conservation action. However, any future development of an official conservation system, or the management of the existing de facto conservation network, must struggle with the implications of continued land cover modification, which I forecast will continue to both reduce the amount of buffer that

mitigates threats to conservation lands and reduce the amount of structural landscape connectedness between conservation areas.

All results herewith point to the importance of adjacent land uses. Thus, one critical take-home message is that a key conservation strategy will be to work cooperatively across land ownership boundaries. If human land-use modification is occurring most rapidly adjacent to the most critical ecological systems (i.e., aquatic systems and conservation areas; Theobald et al. 1996; McDonald et al. 2007), then conservation planners must act to protect neighboring lands from future development (e.g., Gordona et al. 2009) while land managers must educate existing adjacent private-land owners (Shafer 1999). Although many privately held lands are already well stewarded, concerns over rapid declines in important habitat and biodiversity hotspots on private lands remain (Bean & Wilcove 1997; Noss et al. 1997; Dale et al. 2000).

Schonewald-Cox et al. (1992) review strategies to engage private landowners in conservation, including forming advisory groups, constituency building, and cooperative agreements to meet shared goals (such as pest control), but they also list numerous constraints and obstacles to cross-boundary management, including too many stakeholders for effective communication or a lack of sufficient data on biological resources and consensus on how to manage them across diverse parties. Despite these difficulties, as human land uses continue to encroach on relatively natural ecological systems, managers will be forced to educate and work cooperatively with a growing cadre of stakeholders and land owners. Conservation planning and management should encourage public-private partnerships and provide incentives for private land owners' participation to ensure biodiversity protection (Theobald & Hobbs 2002; Maestas et al.

2003; Higgins et al. 2007). Success will require consideration of the biodiversity goals and the biophysical and socioeconomic setting that allows balancing of human land use needs and ecological function (DeFries et al. 2007).

A second take-home message is that a priori, ecologically determined conceptual models may be useful for framing ecological analyses. Using a conceptual model of the interactions within a system to guide analysis may alter inference, and ultimately, alter management actions. Framing research with conceptual models does not necessarily require a complex model that incorporates all aspects of the system nor significantly more complex analysis methods. The use of conceptual models can be incorporated into tools with which managers are already comfortable to better illustrate and test possible conservation options. Conceptual models can serve as testable hypotheses themselves or as bounds for our inference, providing a reality check of results that do not come from directly testable research questions. Because many ecosystem management hypotheses can not be directly tested, land managers and conservation planners may find conceptual models useful to fill in gaps of missing data or testable interactions. The critical point is that managers and planners must acknowledge that the conceptual model and the statistical model they choose may affect their results and, ultimately, their management decisions.

5.2 Future research directions

One primary direction for improving and expanding my research would be to incorporate biodiversity data directly into the integrated vulnerability assessment presented in Chapter Two. Similarly, a more accurate depiction of habitat quality would greatly improve the assessment of changes to potential buffer lands surrounding

conservation areas as presented in Chapter Three. Both of these improvements suggest the need to test the models and methods presented here with finer-scale applications to provide conservation managers and planners with more immediately practical tools. Finer-scaled, richer land cover data, such as the use of the spatially explicit housing density data (Theobald 2005) used in Chapters Two and Three, would also benefit the research on hierarchical scales of land use and land cover influence on aquatic systems presented in Chapter Four. Combined with a distributed watershed flow model, more spatially explicit data on urban land uses would better account for the importance of spatial arrangement of land cover in the watershed (e.g., Strayer et al. 2003; King et al. 2005).

Synthesizing concepts from this dissertation into a local study using finer-scaled data would allow for two important and critical improvements for future work: (1) applying more detailed conceptual models of the spatial pathways linking anthropogenic stressors to neighboring ecological systems to guide analysis and (2) consideration of the paramount implications of climate change in conservation planning.

Several recent studies in aquatic ecology have begun to confront detailed conceptual models of the transport processes linking anthropogenic stressors to aquatic integrity with spatial data. Combined with powerful statistical methods, these studies are shedding light on the ecological processes and pathways by which humans modify their environment (e.g., King et al. 2005; Novotny et al. 2005; Johnson et al. 2007). Perhaps the most exciting of these studies is by Burcher et al. (2007), wherein a path analysis statistical approach (Shipley 2000) is combined with a conceptual model of the cascading mechanisms of influence linking land cover to biotic aquatic endpoints.

These studies suggest the a new direction in ecology whereby conceptual models detail explicit ecological pathways – some transmitting medium that propagates anthropogenic stressors to an ultimate ecological consequence (Reiners & Driese 2004). Applying the models of ecological pathways as hypotheses about the system, future work empirically testing the strength of the pathways would both provide new insights in spatial ecology and inform decisions concerning ecosystem management.

A potential synthesis of my dissertation work would be in developing a more ambitious and detailed model of multiple pathways that transport and translate land use-associated stressors with indicators of aquatic integrity (Fig. 5.1). Such a model would incorporate the mechanisms of influence [the general processes that link cause and effect through space are the mechanisms of influence (after Reiners & Driese 2004)], as well as including both the proximal stressor mechanism that directly threatens aquatic integrity and the spatial transport mechanism that the original stressors follow. The transport mechanism could be represented by both a transporting vector (e.g., water, human, and wind transport, which include both an identifiable direction and a magnitude) and vector modifiers, such as landscape characteristics that may attenuate, amplify, or transform the stresses as they travel. Additionally, the model should include confounding factors, stressor entities in the study area that arise from sources not directly linked to urbanization but that require consideration to avoid spurious results.

The conceptual model would then provide a priori hypotheses about the links between urbanization and a specific indicator of aquatic integrity which could be tested empirically. Several statistical methods lend themselves to this type of structured hypothesis testing (Johnson & Gage 1997), such as artificial neural networks (e.g., Olden

et al. 2006; Novotny et al. 2009), and structured equation modeling and path analysis (e.g., Burcher et al. 2007), both of which have become easier to implement with off-the-shelf software programs. Another potential approach is the use of multilevel models, which account for different process interactions at different spatial scales (Wikle 2003). If an ecological process is occurring at different rates over different scales, it can be very difficult to specify the model at each scale. Hierarchical models attempt to reduce this complexity by decomposing the problem into a series of conditional models; for example, conditioning the behavior of the process at one spatial extent on the process at the larger spatial extent in which it is nested. Hierarchical models can be implemented using frequentist maximum likelihood methods, but a Bayesian framework provides advantages and reduced complexity (Wikle 2003). Further, Bayesian hierarchical methods can be used to account for problems specific to spatial, coarse-scale models including heterogeneity of sampling methods, spatial misalignment (e.g., fine-scale ecological data being compared to coarse-scale landscape measures), categorization uncertainty, particularly arising from the use of remotely sensed data, and spatially based latent processes (Mugglin et al. 2000; Hooten et al. 2003; Penttinen et al. 2003)

A second extension of this research would be incorporate the implications of climate change. The research presented in Chapter Three looks at changes to the landscape structure surrounding protected areas resulting from increased urbanization. Although the research includes forecasts of future land use change, other landscape aspects are assumed to be temporally static. This is unlikely given current climate change projections (Hannah 2008). As discussed in Chapter Three, maintaining landscape connectivity is a critical tool for protecting biodiversity as landscapes become more

fragmented (Hilty et al. 2006). However, climate change will likely impact flora and fauna across a range of ecosystems, organizational hierarchies, and scales (Walther et al. 2002), and it is estimated that some 15-37% of species are at risk of extinction from climate change (Thomas et al. 2004). Climate change and landscape connectivity are inextricably linked as species viability will depend on connectivity to allow for species range shifts and dispersal along changing climate gradients (Honnay et al. 2002). Given that land use conversion for residential development and associated impacts (e.g., roads and agricultural conversion) is another primary threat to species endangerment in the U.S. (Czech et al. 2000), the cumulative impact of climate change and development on connectivity is critically under-unexplored. The compounding threats could be simultaneously considered in a spatiotemporal approach to ensure that development does not close the door on conservation linkages necessary under a changing climate.

One approach to combining effects from urbanization and climate change would be to identify contiguous “dispersal chains” between existing and future habitat across “time slices”, $T_0, T_1, \dots, T_n$ (Williams et al. 2005; Phillips et al. 2008). While this approach has been used to model seed dispersal in a binary system of suitable or unsuitable habitat, for application in terrestrial vertebrates, the variable habitat quality of the intervening matrix would also need to be considered (Taylor et al. 2006). Therefore, combining habitat suitability indexes based on dynamic vegetation models (which project biome extents under novel climates) with forecasts of increased housing density could be combined to identify the corridors for terrestrial species movement that would need to be maintained across both space and time. Forecasts of increased housing density could also incorporate influences of climate change based on the recently created EPA set of

national land use scenarios that are consistent with Intergovernmental Panel on Climate Change global change story lines (EPA 2008).

Figures

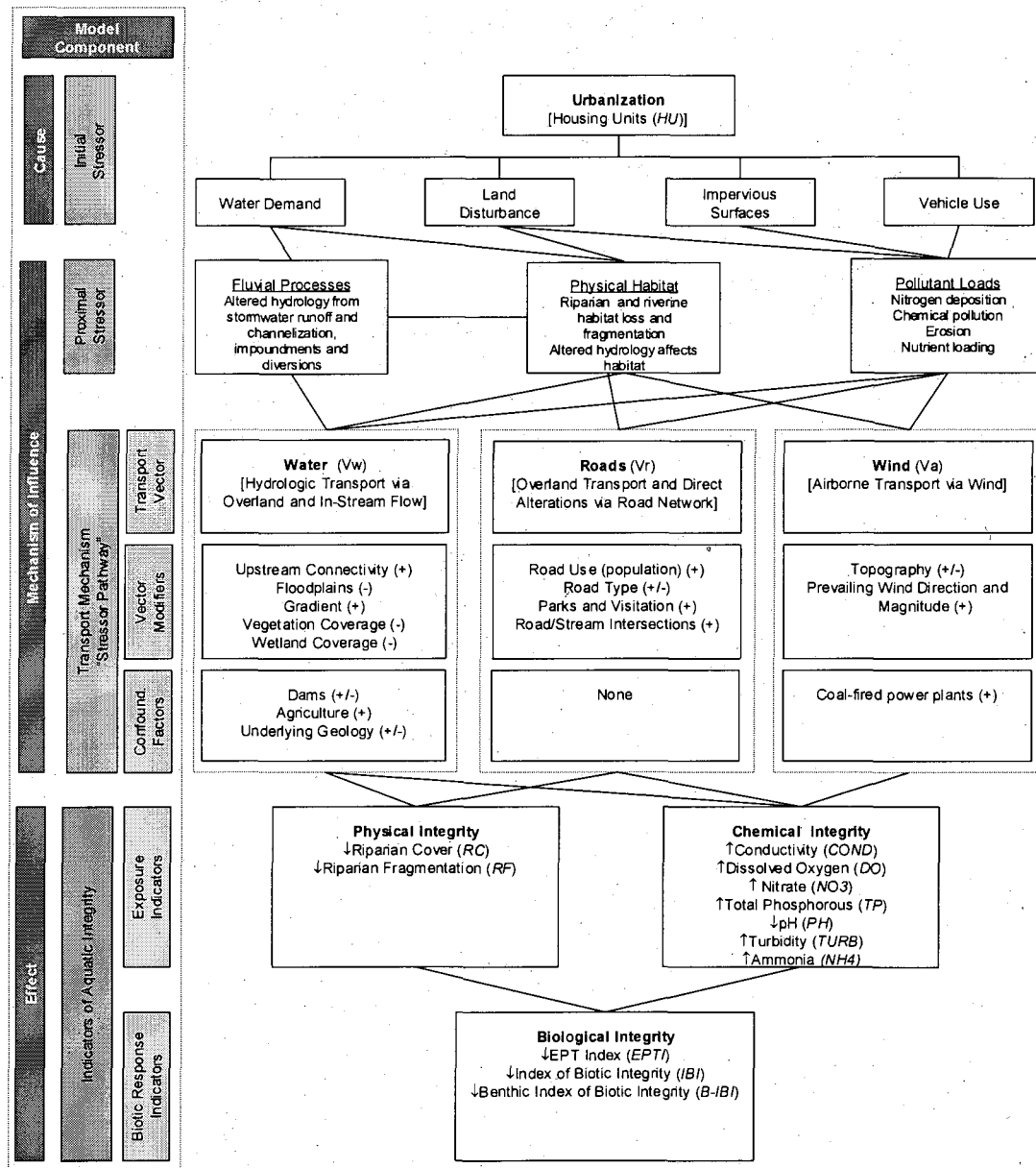


Fig. 5.1. An example of a detailed conceptual model of the ecological mechanisms that transport and translate stressors associated with urbanization and influences to aquatic systems.

CHAPTER 6. REFLECTIONS ON MY PHD EXPERIENCE

It is difficult to summarize my last six years as a doctoral student as merely an “experience.” However, during my graduate education at Colorado State University, there have been a number of experiences, both positive and negative, that have shaped who I am as a scientist, and as a person.

First, pursuing this PhD has allowed me to even consider myself a scientist. With a background in policy and management, it was my dissertation research that first introduced me to the scientific method. Although my research interests remain at the intersection of conservation science and applied conservation planning, my doctoral studies have greatly expanded my comfort with the scientific and quantitative methods. Several courses have provided invaluable guidance on identifying research questions and designing methods to address them, notably a landscape ecology course (taught by D.M. Theobald and B.R. Noon) and a course in ecosystem ecology (taught by B. Lauenroth and I. Burke). My interest in learning more about quantitative methods was largely thanks to a course in systems ecology (taught by N.T. Hobbs), which also led to my involvement with the Program for Interdisciplinary Mathematics, Ecology, and Statistics (PRIMES). Although adding at least a year to my graduate studies, the opportunity to have been involved with PRIMES was well worth it.

Although one regret is not having taken additional quantitative courses, it was my research outside the classroom that provided the greatest opportunity for expanding my

knowledge of science and applicable methods; specifically, my failures in research taught me the most. I spent over two years refining my proposed research approach, only to find it was largely untenable. This experience showed me the importance of limiting the scope of one's research question, although this is an issue with which I will undoubtedly continue to grapple. I spent over a year wrestling with and learning Bayesian hierarchical modeling methods, only to recognize that it was not the appropriate method for the question. This experience reminded me to have the science drive the method, not visa versa. However, of the new tools I've learned, I have the best grasp of the Bayesian modeling despite it not appearing within the pages of this dissertation. I also feel fortunate to have had my first submitted manuscript rejected by a very esteemed journal. The comments I received from the reviewers were both technically insightful and provided valuable insight into the importance of how one should frame a research question.

A highlight of my graduate school experience was the forging of new relationships, both personal and professional. Perhaps the greatest benefit from PRIMES was developing a cohort of ecologists, mathematicians, and statisticians that I can turn to with research questions. Working on a multi-disciplinary project for PRIMES revealed both the benefits and challenges of working with a cohort of scientists from other fields. I was forced to delve into the inner-workings of modeling software I had previously taken at face-value, providing me with both a new skill and a new sense of confidence. I discovered that when working in a large group representing many interests and much expertise, the smallest detail could expand to an entire research project itself. I learned to communicate more carefully, not assuming that others implicitly understood ecology,

GIS, or spatial statistics terms. Overall, I found the process of interdisciplinary research stimulating because it afforded the group the capacity to expand research into new directions that no one person had the skills to tackle. A regret of my PhD experience is that I did not find more opportunities for collaborative work.

One negative was that I found my doctoral studies to be relatively isolating. Although I work in a field that is considered interdisciplinary, I often worked alone. This is undoubtedly related to having been a non-traditional student and having moved away two years prior to completion of my PhD. But I also believe there is a fundamental need for my college to provide a better foundation for active intellectual community that includes graduate students. During my tenure in Fort Collins, I worked with other students to change this; I hope this effort continues.

There were numerous technical difficulties in my research. My computer crashed a lot. I constantly ran out of data storage space. My taus never converged. I could not obtain the necessary data. Yet, by far my greatest challenges were personal in nature. I discovered that my tendency for very broad-scale thinking was great for policy, but potentially hindered my ability to ask tractable research questions. I learned my passion for conservation and teaching also make me sensitive to rejection. I learned I need to exercise and take vacations to maintain my intensity. Most importantly, I learned that if I can teach a new course, read for my upcoming post-doc, and raise a toddler with my co-parent working insanely as a new faculty member – if I can do that AND put in a final push to complete my dissertation – I can do anything. I just need to embrace humor, frozen food, and a dirty house. Thank you to everyone who supported me in this “experience.”

LITERATURE CITED

- Abbitt, R. J. F., J. M. Scott, and D. S. Wilcove. 2000. The geography of vulnerability: incorporating species geography and human development patterns into conservation planning. *Biological Conservation* **96**:169-175.
- Adams, S. M. 2002. Biological Indicators of Aquatic Ecosystem Stress: Introduction and Overview. Pages 1-11 in S. M. Adams, editor. *Biological Indicators of Aquatic Ecosystem Stress*. American Fisheries Society, Bethesda.
- Alberti, M., D. Booth, K. Hill, B. Coburn, C. Avolio, S. Coe, and D. Spirandelli. 2007. The impact of urban patterns on aquatic ecosystems: An empirical analysis in Puget lowland sub-basins. *Landscape and Urban Planning* **80**:345-361.
- Allan, J. D. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology Evolution and Systematics* **35**:257-284.
- Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology* **37**:149-161.
- Allen, T. F. H., and T. B. Starr 1982. *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago, IL.
- Aplet, G., J. Thompson, and M. Wilbert. 2000. Indicators of wilderness: Using attributes of the land to assess the context of wilderness in D. N. Cole, and S. F. McCool, editors. *Wilderness Science in a Time of Change*. USDA, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Aspinall, R., and D. Pearson. 2000. Integrated geographical assessment of environmental condition in water catchments: Linking landscape ecology, environmental modelling and GIS. *Journal of Environmental Management* **59**:299-319.
- Baker, W. L. 1992. Effects of Settlement and Fire Suppression on Landscape Structure. *Ecology* **73**:1879-1887.
- Barber, M. C., ed. 1994. Environmental monitoring and assessment program indicator development strategy. Page 74. Environmental Protection Agency, Office of Research and Development, Environmental Research Laboratory, Athens, GA.
- Baron, J. S., D. R. Beeson, S. A. Zary, P. M. Walthall, W. L. Lindsay, and D. M. Swift. 1985. Long-term research into the effects of atmospheric deposition in Rocky

- Mountain National Park; summary report 1980-1984. Page 43. U.S. National Park Service.
- Bean, M. J., and D. S. Wilcove. 1997. The private-land problem. *Conservation Biology* **11**:1-2.
- Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* **12**:1241-1252.
- Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: How channel networks structure riverine habitats. *BioScience* **54**:413-427.
- Bennett, A. F. 1999. Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation. Page 254. International Union for the Conservation of Nature, Gland, Switzerland.
- Berger, J. 2004. The last mile: How to sustain long-distance migration in mammals. *Conservation Biology* **18**:320-331.
- Berry, J. 1993. *Beyond Mapping: Concepts, Algorithms, and Issues in GIS*. John Wiley & Sons, Hoboken, N.J.
- Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. *Ecological Applications* **6**:506-519.
- Bledsoe, B. P., and C. C. Watson. 2001. Effects of urbanization on channel instability. *Journal of the American Water Resources Association* **37**:255-270.
- Booth, D. B., and L. E. Reinelt. 1993. Consequences of urbanization on aquatic systems - Measured effects, degradation thresholds, and corrective strategies. Watershed '93: A National Conference on Watershed Management, Alexandria, VA.
- Boulton, A. J. 1999. An overview of river health assessment: philosophies, practice, problems, and prognosis. *Freshwater Biology* **41**:469-479.
- Brabec, E., S. Schulte, and P. L. Richards. 2002. Impervious surfaces and water quality: a review of current literature and its implications for watershed planning. *Journal of Planning Literature* **16**:499-514.
- BTS (Bureau of Transportation Statistics). 2005. National Highway Planning Network. Federal Highway Administration, Washington, D.C.
- Bunn, S. E., P. M. Davies, and T. D. Mosisch. 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. *Freshwater Biology* **41**:333-345.

- Burcher, C. L., H. M. Valett, and E. F. Benfield. 2007. The land-cover cascade: Relationships coupling land and water. *Ecology* **88**:228-242.
- Burke, I. C. 2000. Landscape and regional biogeochemistry: approaches in O. Sala, and H. A. Mooney, editors. *Methods in Ecosystem Science*. Springer-Verlag, New York.
- Burnam, K. P., and D. R. Anderson 2002. *Model Selection and Multi-model Inference: A practical information-theoretical approach*. Springer, New York.
- Busch, D. E., and J. C. Trexler, editors. 2003. *Monitoring Ecosystems- Interdisciplinary Approaches for Evaluating Ecoregional Initiatives*. Island Press, Washington, D.C.
- California Resources Agency Legacy Project. 2004. Public and Conservation Trust Lands. Data developed under contract by VESTRA Resources, Inc.; Data updated by The Nature Conservancy 2005 and 2006.
- Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* **8**:559-568.
- CBI (Conservation Biology Institute). 2006. Protected Areas Database, v.4. Conservation Biology Institute. See DellaSala and others (2001), Corvallis, OR.
- Center for Watershed Protection. 1997. Technical note #116. Housing density and urban land use as indicators of stream quality. Pages 735-739. *Watershed Protection Techniques*.
- Chadwick, M. A., D. R. Dobberfuhl, A. C. Benke, A. D. Huryn, K. Suberkropp, and J. E. Thiele. 2006. Urbanization affects stream ecosystem function by altering hydrology, chemistry, and biotic richness. *Ecological Applications* **16**:1796-1807.
- Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge, M. Pascual, R. Pielke, W. Pizer, C. Pringle, W. V. Reid, K. A. Rose, O. Sala, W. H. Schlesinger, D. H. Wall, and D. Wear. 2001. Ecological forecasts: An emerging imperative. *Science* **293**:657-660.
- Cohen, J., and P. Cohen 1975. *Applied Multiple Regression/ Correlation Analysis for the Behavioral Sciences*. Lawrence Erlbaum Associates, Inc., Hillsdale, New Jersey.
- Cole, D. N., and P. B. Landres. 1996. Threats to wilderness ecosystems: Impacts and research needs. *Ecological Applications* **6**:168-184.
- Cowling, R. M., and R. L. Pressey. 2003. Introduction to systematic conservation planning in the Cape Floristic Region. *Biological Conservation* **112**:1-13.

- Cressie, N., and D. H. Hawkins. 1980. Robust estimation of the variogram: I. *Mathematical Geology* **12**:115-125.
- Crooks, K. R., and M. A. Sanjayan. 2006. Connectivity conservation: maintaining connections for nature. Pages 1-19 in K. R. Crooks, and M. A. Sanjayan, editors. *Connectivity conservation*. Cambridge University Press, New York.
- Cushman, S. A., and K. McGarigal. 2002. Hierarchical, multi-scale decomposition of species-environment relationships. *Landscape Ecology* **17**:637-646.
- Czech, B., and P. R. Krausman. 1997. Distribution and causation of species endangerment in the United States. *Science* **277**:1116-1117.
- Czech, B., P. R. Krausman, and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. *BioScience* **50**:593-601.
- Dale, V. H., S. Brown, R. A. Haeuber, N. T. Hobbs, N. Huntly, R. J. Naiman, W. E. Riebsame, M. G. Turner, and T. J. Valone. 2000. Ecological principles and guidelines for managing the use of land. *Ecological Applications* **10**:639-670.
- Davis, F. W., C. Costello, and D. Stoms. 2006. Efficient conservation in a utility-maximization framework. *Ecology and Society* **11**.
- Davis, N. M., V. Weaver, K. Parks, and M. J. Lydy. 2003. An assessment of water quality, physical habitat, and biological integrity of an urban stream in Wichita, Kansas, prior to restoration improvements (Phase I). *Environmental Contamination and Toxicology* **44**:351-359.
- DeFries, R., A. Hansen, B. L. Turner, R. Reid, and J. G. Liu. 2007. Land use change around protected areas: Management to balance human needs and ecological function. *Ecological Applications* **17**:1031-1038.
- Dillaha, T. A., R. B. Reneau, S. Mostaghimi, and D. Lee. 1989. Vegetative Filter Strips for Agricultural Nonpoint Source Pollution-Control. *Transactions of the Asae* **32**:513-519.
- Downes, B. J., L. A. Barmuta, P. G. Fairweather, D. P. Faith, M. J. Keough, P. S. Lake, B. D. Mapstone, and G. P. Quinn. 2002. *Monitoring Ecological Impacts: concepts and practice in flowing water*. Cambridge University Press, New York, New York.
- Ervin, J. 2003. Protected area assessments in perspective. *BioScience* **53**:819-822.
- ESRI. 2005. *Geographic Data Technology StreetMap Dataset [CD-ROM]*. ESRI, Redlands, CA.

- Falcuy, M. R., and C. F. Estades. 2007. Effectiveness of corridors relative to enlargement of habitat patches. *Conservation Biology* **21**:1341-1346.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *Bioscience* **52**:483-498.
- Fitzpatrick, F. A., B. C. Scudder, B. N. Lenz, and D. J. Sullivan. 2001. Effects of multi-scale environmental characteristics on agricultural stream biota in eastern Wisconsin. *Journal of the American Water Resources Association* **37**:1489-1507.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29**:207-+.
- Frentz, I. C., F. L. Farmer, J. M. Guldin, and K. G. Smith. 2004. Public lands and population growth. *Society & Natural Resources* **17**:57-68.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A Hierarchical Framework for Stream Habitat Classification - Viewing Streams in a Watershed Context. *Environmental Management* **10**:199-214.
- GAO (US General Accounting Office). 1994. National Park Service: activities outside park borders have caused damage to resources and will likely cause more. USGAO, Washington, D.C.
- Gaston, K. J., R. L. Pressey, and C. R. Margules. 2002. Persistence and vulnerability: retaining biodiversity in the landscape and in protected areas. *Journal of Biosciences* **27**:361-384.
- Goodwin, B. J. 2003. Is landscape connectivity a dependent or independent variable? *Landscape Ecology* **18**:687-699.
- Gordona, A., D. Simondson, M. White, A. Moilanen, and S. A. Bekessy. 2009. Integrating conservation planning and land use planning in urban landscapes. *Landscape Ecology* **91**:183-194.
- Gray, L. 2004. Changes in water quality and macroinvertebrate communities resulting from urban stormflows in the Provo River, Utah, USA. *Hydrobiologia* **518**:33-46.
- Griffith, J. A., E. A. Martinko, J. L. Whistler, and K. P. Price. 2002. Interrelationships among landscapes, NDVI, and stream water quality in the U.S. Central Plains. *Ecological Applications* **12**:1702-1718.
- Groves, C. R., D. B. Jensen, L. L. Valutis, K. H. Redford, M. L. Shaffer, J. M. Scott, J. V. Baumgartner, J. V. Higgins, M. W. Beck, and M. G. Anderson. 2002. Planning

for biodiversity conservation: putting conservation science into practice. *BioScience* **52**:499-512.

Gude, P. H., A. J. Hansen, and D. A. Jones. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. *Ecological Applications* **17**:1004-1018.

Haddad, N. M., D. K. Rosenberg, and B. R. Noon. 2000. On experimentation and the study of corridors: response to Beier and Noss. *Conservation Biology* **14**:1543-1545.

Hannah, L. 2008. Protected areas and climate change. Pages 201-212. *Year in Ecology and Conservation Biology* 2008.

Hannah, L., G. Midgley, S. Andelman, M. Araujo, G. Hughes, E. Martinez-Meyer, R. Pearson, and P. Williams. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* **5**:131-138.

Hansen, A. J., and R. DeFries. 2007. Ecological mechanisms linking protected areas to surrounding lands. *Ecological Applications* **17**:974-988.

Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. H. Gude, and A. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecological Applications* **15**:1893-1905.

Hansen, A. J., R. Rasker, B. Maxwell, J. R. Rotella, J. D. Johnson, A. W. Parmenter, L. Langner, W. B. Cohen, R. L. Lawrence, and M. P. V. Kraska. 2002. Ecological causes and consequences of demographic change in the new west. *BioScience* **52**:151-162.

Hansen, A. J., and J. J. Rotella. 2002. Biophysical factors, land use, and species viability in and around nature reserves. *Conservation Biology* **16**:1112-1122.

Hansen, A. J., and D. L. Urban. 1992. Avian response to landscape pattern: the role of species life histories. *Landscape Ecology* **7**:163-180.

Harris, L., and G. Silva-Lopez. 1992. Forest fragmentation and the conservation of biological diversity. Pages 196-237 in P. Fiedler, and S. Jain, editors. *Conservation Biology: The Theory and Practice of Nature Conservation, Preservation, and Management*. Chapman and Hall, New York.

Hatt, B. E., T. D. Fletcher, C. J. Walsh, and S. L. Taylor. 2004. The influence of urban density and drainage infrastructure on the concentrations and loads of pollutants in small streams. *Environmental Management* **34**:112-124.

- Hawbaker, T. J., V. C. Radeloff, R. B. Hammer, and M. K. Clayton. 2005. Road density and landscape pattern in relation to housing density, land ownership, land cover, and soils. *Landscape Ecology* **20**:609-625.
- Heit, M., C. Klusek, and J. Baron. 1984. Evidence of Deposition of Anthropogenic Pollutants in Remote Rocky-Mountain Lakes. *Water Air and Soil Pollution* **22**:403-416.
- Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation* **142**:14-32.
- Herlihy, A. T., J. L. Stoddard, and C. B. Johnson. 1998. The relationship between stream chemistry and watershed land cover data in the mid-Atlantic region, US. *Water Air and Soil Pollution* **105**:377-386.
- Higgins, A., K. Serbesoff-King, M. King, and K. O'Reilly-Doyle. 2007. The power of partnerships: Landscape scale conservation through public/private collaboration. *Natural Areas Journal* **27**:236-250.
- Hilty, J. A., W. Z. Lidicker, and A. M. Merenlender 2006. *Corridor ecology: the science and practice of linking landscapes for biodiversity conservation*. Island Press, Washington, D.C.
- Hobbs, N. T., and R. Hilborn. 2006. Alternatives to statistical hypothesis testing in ecology: a guide to self teaching. *Ecological Applications* **16**:5-19.
- Hobbs, N. T., and D. M. Theobald. 2001. Effects of land-use change on wildlife habitat: Applying ecological principles and guidelines in the western United States. Pages 37-53 in V. H. Dale, and R. A. Haeuber, editors. *Applying Ecological Principles to Land Management*. Springer-Verlag, New York.
- Hockings, M. 2003. Systems for assessing the effectiveness of management in protected areas. *BioScience* **53**:823-832.
- Honnay, O., K. Verheyen, J. Butaye, H. Jacquemyn, B. Bossuyt, and M. Hermy. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters* **5**:525-530.
- Hooten, M. B., D. R. Larsen, and C. K. Wikle. 2003. Predicting the spatial distribution of ground flora on large domains using a hierarchical Bayesian model. *Landscape Ecology* **18**:487-502.
- Howe, J., E. McMahon, and L. Propst 1997. *Balancing nature and commerce in gateway communities*. Island Press, Washington, D.C.

- Hunsaker, C. T., and D. A. Levine. 1995. Hierarchical Approaches to the Study of Water-Quality in Rivers. *BioScience* **45**:193-203.
- Hynes, H. B. N. 1975. The stream and its valley. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* **19**:1-15.
- Innis, S. A., R. J. Naiman, and S. R. Elliott. 2000. Indicators and assessment methods for measuring the ecological integrity of semi-aquatic terrestrial environments. *Hydrobiologia* **422**:111-131.
- International Union for Conservation of Nature and The Conservation Measures Partnership (IUCN-CMP). 2006. Unified Classification of Direct Threats, Version 1.0.
- Jackson, L. J., A. S. Trebitz, and K. L. Cottingham. 2000. An introduction to the practice of ecological modeling. *Bioscience* **50**:694-706.
- Janzen, D. H. 1983. No park is an island: Increase in interference from outside as park size decreases. *Oikos* **41**:402-410.
- Jennings, M. D. 2000. Gap analysis: concepts, methods, and recent results. *Landscape Ecology* **15**:5-20.
- Johnson, L. B., and S. H. Gage. 1997. Landscape approaches to the analysis of aquatic ecosystems. *Freshwater Biology* **37**:113-132.
- Johnson, L. B., C. Richards, G. E. Host, and J. W. Arthur. 1997. Landscape influences on water chemistry in Midwestern stream ecosystems. *Freshwater Biology* **37**:193-208.
- Johnson, T. E., J. N. McNair, P. Srivastava, and D. D. Hart. 2007. Stream ecosystem responses to spatially variable land cover: an empirically based model for developing riparian restoration strategies. *Freshwater Biology* **52**:680-695.
- Karr, J. R. 1981. Assessment of Biotic Integrity Using Fish Communities. *Fisheries* **6**:21-27.
- Karr, J. R. 1987. Biological Monitoring and Environmental Assessment - a Conceptual-Framework. *Environmental Management* **11**:249-256.
- Karr, J. R. 1993. Defining and Assessing Ecological Integrity: Beyond Water-Quality. *Environmental Toxicology and Chemistry* **12**:1521-1531.
- Karr, J. R. 1999. Defining and measuring river health. *Freshwater Biology* **41**:221-234.

- Karr, J. R., K. D. Fausch, P. L. Angermeier, P. R. Yant, and I. J. Schlosser 1986. Assessing Biological Integrity in Running Waters: A Method and its Rationale. Special Publication 5, Illinois Natural History Survey, Champaign, IL.
- King, R. S., M. E. Baker, D. F. Whigham, D. E. Weller, T. E. Jordan, P. F. Kazyak, and M. K. Hurd. 2005. Spatial considerations for linking watershed land cover to ecological indicators in streams. *Ecological Applications* **15**:137-153.
- Kuehne, R. A. 1962. A classification of streams, illustrated by fish distribution in an eastern Kentucky creek. *Ecology* **43**:608-614.
- Kutner, M. H., C. J. Nachtsheim, and J. Neter 2004. *Applied Linear Regression Models*. McGraw-Hill/Irwin, New York.
- Lammert, M., and J. D. Allan. 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.
- Lande, R. 1998. Anthropogenic, ecological, and genetic factors in extinction in G. M. Mace, A. Balmford, and J. R. Ginsberg, editors. *Conservation in a Changing World*. Cambridge University Press, Cambridge (United Kingdom).
- Lathrop, R. G., and J. A. Bognar. 1998. Applying GIS and landscape ecological principles to evaluate land conservation alternatives. *Landscape and Urban Planning* **41**:27-41.
- Lehman, J. T. 1986. The Goal of Understanding in Limnology. *Limnology and Oceanography* **31**:1160-1166.
- Lenat, D. R., and J. K. Crawford. 1994. Effects of Land-Use on Water-Quality and Aquatic Biota of 3 North-Carolina Piedmont Streams. *Hydrobiologia* **294**:185-199.
- Lesslie, R., and M. Malsen 1995. *National Wilderness Inventory Handbook of Procedures, Content, and Usage*. Australian Government Publishing Service, Canberra, Australia.
- Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications* **18**:1119-1139.
- Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology. *Ecology* **73**:1943-1967.
- Lindenmayer, D. B., and J. Fisher 2006. *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis*. Island Press, Covelo, CA.

- Locke, H., and P. Dearden. 2005. Rethinking protected area categories and the new paradigm. *Environmental Conservation* **32**:1-10.
- Lookingbill, T. R., R. H. Gardner, P. A. Townsend, and S. L. Carter. 2007. Conceptual models as hypotheses in monitoring urban landscapes. *Environmental Management* **40**:171-182.
- Lorenz, C. M., G. M. Van Dijk, A. G. M. Van Hattum, and W. P. Cofino. 1997. Concepts in river ecology: Implications for indicator development. *Regulated Rivers-Research & Management* **13**:501-516.
- Luck, G. W. 2007. A review of the relationships between human population density and biodiversity. *Biological Reviews* **82**:607-645.
- MAB (Man and the Biosphere Task Force). 1974. Criteria and guidelines for the choice and establishment of biosphere reserves. Page 61. UNESCO, Paris.
- Maestas, J. D., R. L. Knight, and W. C. Gilgert. 2003. Biodiversity across a rural land-use gradient. *Conservation Biology* **17**:1425-1434.
- Maidment, D. 2002. Arc Hydro: GIS for water resources. Page 220. ESRI, Redlands, CA.
- Manley, P. N., W. J. Zielinski, M. D. Schlesinger, and S. R. Mori. 2004. Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. *Ecological Applications* **14**:296-310.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* **405**:243-253.
- Marzluff, J. M., and K. Ewing. 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology* **9**:280-292.
- May, C. W., R. R. Horner, J. R. Karr, B. W. Mar, and E. B. Welch. 1997. Effects of urbanization on small streams in the Puget Sound lowland ecoregion. *Watershed Protection Techniques* **2**:483-494.
- McBride, M., and D. B. Booth. 2005. Urban impacts on physical stream condition: Effects of spatial scale, connectivity, and longitudinal trends. *Journal of the American Water Resources Association* **41**:565-580.
- McDonald, R. I., P. Kareiva, and R. T. Forman. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation* **141**:1695-1703.

- McDonald, R. I., C. Yuan-Farrell, C. Fievet, M. Moeller, P. Kareiva, D. Foster, T. Gragson, A. Kinzig, L. Kuby, and C. Redman. 2007. Estimating the effect of protected lands on the development and conservation of their surroundings. *Conservation Biology* **21**:1526-1536.
- McGranahan, D. A. 1999. Natural Amenities Drive Population Change. Food and Rural Economics Division, Economic Research Service, US Department of Agriculture, Washington, D.C.
- McKee, J. K., P. W. Sciulli, C. D. Fooce, and T. A. Waite. 2004. Forecasting global biodiversity threats associated with human population growth. *Biological Conservation* **115**:161-164.
- McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. *Bioscience* **52**:883-890.
- McQuarrie, A. D. R., and C.-L. Tsai 1998. Regression and time series model selection. World Scientific Publishing Company, Singapore.
- MDNR (Maryland Department of of Natural Resources). 1997. Maryland Biological Stream Survey (MBSS).
- Meyer, J. L., M. J. Paul, and W. K. Taulbee. 2005. Stream ecosystem function in urbanizing landscapes. *Journal of the North American Benthological Society* **24**:602-612.
- Meyer, W. B., and B. L. Turner 1994. Changes in Land Use and Land Cover: a Global Perspective. Cambridge University Press, Cambridge, U.K.
- Michener, W. K., T. J. Baerwald, P. Firth, M. A. Palmer, J. L. Rosenberger, E. A. Sandlin, and H. Zimmerman. 2001. Defining and unraveling biocomplexity. *Bioscience* **51**:1018-1023.
- Millennium Ecosystem Assessment 2003. Ecosystems and human well-being: a framework for assessment. Island Press, Washington, D.C.
- Montgomery, D. R. 1999. Process domains and the river continuum. *Journal of the American Water Resources Association* **35**:397-410.
- Morgan, R. P., and S. E. Cushman. 2005. Urbanization effects on stream fish assemblages in Maryland, USA. *Journal of the North American Benthological Society* **24**:643-655.
- Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322**:261-264.

- Morley, S. A., and J. R. Karr. 2002. Assessing and restoring the health of urban streams in the Puget Sound basin. *Conservation Biology* **16**:1498-1509.
- Mugglin, A. S., B. P. Carlin, and A. E. Gelfand. 2000. Fully model-based approaches for spatially misaligned data. *Journal of the American Statistical Association* **95**:877-887.
- Murdoch, W., S. Polasky, K. A. Wilson, H. P. Possingham, P. Kareiva, and R. Shaw. 2007. Maximizing return on investment in conservation. *Biological Conservation* **139**:375-388.
- Naiman, R. J., and H. Decamps, editors. 1990. *The Ecology and Management of Aquatic-Terrestrial Ecotones*. UNESCO-Parthenon Publishing Group, Carnforth, U.K.
- Naiman, R. J., and M. G. Turner. 2000. A future perspective on North America's freshwater ecosystems. *Ecological Applications* **10**:958-970.
- Newmark, W. D. 1985. Legal and biotic boundaries of western North American national parks: a problem of congruence. *Biological Conservation* **33**:197-208.
- Noon, B. R. 2003. Conceptual issues in monitoring ecological resources. Pages 27-71 in D. E. Busch, and J. C. Trexler, editors. *Monitoring Ecosystems: Interdisciplinary Approaches for Evaluating Ecoregional Initiatives*. Island Press, Washington, D.C.
- Noon, B. R., T. A. Spies, and M. G. Raphael. 1999. Chapter 2: Conceptual Basis for Designing an Effectiveness Monitoring Program. Page 138 in B. S. Mulder, B. R. Noon, T. A. Spies, M. G. Raphael, C. J. Palmer, A. R. Olsen, G. H. Reeves, and H. H. Welsh, editors. *The Strategy and Design of the Effectiveness Monitoring Program for the Northwest Forest Plan*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- Norris, R. H., and C. P. Hawkins. 2000. Monitoring river health. *Hydrobiologia* **435**:5-17.
- Norris, R. H., and M. C. Thoms. 1999. What is river health? *Freshwater Biology* **41**:197-209.
- Noss, R., M. A. O'Connell, and D. D. Murphy 1997. *The Science of Conservation Planning*. Island Press, Washington, D.C.
- Noss, R. F. 1983. A regional landscape approach to maintain diversity. *BioScience* **33**:700-706.
- Noss, R. F. 1987. Protecting natural areas in fragmented landscapes. *Natural Areas Journal* **7**:1-13.

- Noss, R. F., and L. D. Harris. 1986. Nodes, networks, and MUMs: preserving diversity at all scales. *Environmental Management* **10**:299-309.
- Novotny, V., A. Bartosova, N. O'Reilly, and T. Ehlinger. 2005. Unlocking the relationship of biotic integrity of impaired waters to anthropogenic stresses. *Water Research* **39**:184-198.
- Novotny, V., D. Bedoya, H. Virani, and E. Manolakos. 2009. Linking indices of biotic integrity to environmental and land use variables: multimetric clustering and predictive models. *Water Science and Technology* **59**:1-8.
- NRC. 1995. Review of EPA's environmental monitoring and assessment program: Overall evaluation in N. R. Council, editor. National Academy Press, Washington, D.C.
- O'Neill, R. V., J. R. Krumme, R. H. Gardner, G. Sugihara, B. Jackson, D. L. DeAngelis, B. T. Milne, M. G. Turner, B. Zygmunt, S. W. Christensen, V. H. Dale, and R. L. Graham. 1988. Indices of landscape pattern. *Landscape Ecology* **1**:153-162.
- Odell, E. A., and R. L. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. *Conservation Biology* **15**:1143-1150.
- Odum, E. P. 1953. *Fundamentals of Ecology*. Saunders, Philadelphia, PA.
- Olden, J. D., N. L. Poff, and B. P. Bledsoe. 2006. Incorporating ecological knowledge into ecoinformatics: An example of modeling hierarchically structured aquatic communities with neural networks. *Ecological Informatics* **1**:33-42.
- Osborne, L. L., and D. A. Kovacic. 1993. Riparian Vegetated Buffer Strips in Water-Quality Restoration and Stream Management. *Freshwater Biology* **29**:243-258.
- Osborne, L. L., and M. J. Wiley. 1988. Empirical Relationships between Land-Use Cover and Stream Water-Quality in an Agricultural Watershed. *Journal of Environmental Management* **26**:9-27.
- Parks, S. A., and A. H. Harcourt. 2002. Reserve size, local human density, and mammalian extinctions in US protected areas. *Conservation Biology* **16**:800-808.
- Parrish, J. D., D. P. Braun, and R. S. Unnasch. 2003. Are we conserving what we say we are? Measuring ecological integrity within protected areas. *BioScience* **53**:851-860.
- Pejchar, L., P. M. Morgan, M. R. Caldwell, C. Palmer, and G. C. Daily. 2007. Evaluating the Potential for Conservation Development: Biophysical, Economic, and Institutional Perspectives. *Conservation Biology* **21**:69-78.

- Penttinen, A., F. Divino, and A. Riiali. 2003. Spatial hierarchical Bayesian models in ecological applications. Pages 271-299 in P. J. P. J. Green, N. L. Hjort, and S. S. Richardson, editors. Highly structured stochastic systems. Oxford University Press, New York.
- Peterson, E. E., A. A. Merton, D. M. Theobald, and N. S. Urquhart. 2006. Patterns of spatial autocorrelation in stream water chemistry. *Environmental Monitoring and Assessment* **121**:571-596.
- Phillips, S. J., P. Williams, G. Midgley, and A. Archer. 2008. Optimizing dispersal corridors for the Cape Proteaceae using network flow. *Ecological Applications* **18**:1200-1211.
- Pickett, S. T. A. 2000. Land use as an ecological variable. USGS.
- Pierce, S. M., R. M. Cowling, A. T. Knight, A. T. Lombard, M. Rouget, and T. Wolf. 2005. Systematic conservation planning products for land-use planning: Interpretation for implementation. *Biological Conservation* **125**:441-458.
- Poff, N. L. 1997. Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16**:391-409.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**:289-316.
- Postel, S., and B. Richter 2003. *Rivers for life : managing water for people and nature*. Island Press, Washington, D.C.
- Pressey, R. L., and M. C. Bottrill. 2008. Opportunism, Threats, and the Evolution of Systematic Conservation Planning. *Conservation Biology* **22**:1340-1345.
- Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling, and K. A. Wilson. 2007. Conservation planning in a changing world. *Trends in Ecology & Evolution* **22**:583-592.
- Pressey, R. L., S. Ferrier, T. C. Hager, C. A. Woods, S. L. Tully, and K. M. Weinman. 1996. How well protected are the forests of north-eastern New South Wales? Analyses of forest environments in relation to formal protection measures, land tenure, and vulnerability to clearing. *Forest Ecology and Management* **85**:311-333.
- Pringle, C. M. 2000. Threats to US public lands from cumulative hydrologic alterations outside of their boundaries. *Ecological Applications* **10**:971-989.

- Pusey, B. J., and A. H. Arthington. 2003. Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research* **54**:1-16.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, Vienna, Austria.
- Randa, L. A., and J. A. Yunger. 2006. Carnivore occurrence along an urban-rural gradient: A landscape-level analysis. *Journal of Mammalogy* **87**:1154-1164.
- Rasker, R., and A. J. Hansen. 2000. Natural amenities and population growth in the Greater Yellowstone region. *Research in Human Ecology* **7**:30-40.
- Reiners, W. A., and K. L. Driese 2004. Transport processes in nature: propagation of ecological influences through environmental space. Cambridge University Press, New York, NY.
- Reuter, D. J. 1998. Developing indicators for monitoring catchment health: the challenges. *Australian Journal of Experimental Agriculture* **38**:637-648.
- Revilla, E., F. Palomares, and M. Delibes. 2001. Edge-core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Donana National Park. *Conservation Biology* **15**:148-158.
- Reyers, B. 2004. Incorporating anthropogenic threats into evaluations of regional biodiversity and prioritisation of conservation areas in the Limpopo Province, South Africa. *Biological Conservation* **118**:521-531.
- Richards, C., L. B. Johnson, and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. *Canadian Journal of Fisheries and Aquatic Science* **53**:295-311.
- Ricketts, T., and M. Imhoff. 2003. Biodiversity, urban areas, and agriculture: Locating priority ecoregions for conservation. *Conservation Ecology* **8**.
- Riitters, K., and J. D. Wickham. 2003. How far to the nearest road? *Frontiers in Ecology and the Environment* **1**:125-129.
- Rogers, C. E., D. J. Brabander, M. T. Barbour, and H. F. Hemond. 2002. Use of physical, chemical, and biological indices to assess impacts of contaminants and physical habitat alteration in urban streams. *Environmental Toxicology and Chemistry* **21**:1156-1167.
- Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology* **11**:141-156.

- Roy, A. H., B. J. Freeman, and M. C. Freeman. 2007. Riparian influences on stream fish assemblage structure in urbanizing streams. *Landscape Ecology* **22**:385-402.
- Salafsky, N., D. Salzer, A. J. Stattersfield, C. Hilton-Taylor, R. Neugarten, S. H. M. Butchart, B. Collen, N. Cox, L. L. Master, S. O'Connor, and D. Wilkie. 2008. A standard lexicon for biodiversity conservation: Unified classifications of threats and actions. *Conservation Biology* **22**:897-911.
- Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. *BioScience* **52**:891-904.
- Sarkar, S. 1999. Wilderness preservation and biodiversity conservation - keeping divergent goals distinct. *BioScience* **49**:405-412.
- Sarkar, S. 2003. Conservation area networks. *Conservation and Society* **1**:v-vii.
- Sarkar, S., R. L. Pressey, D. P. Faith, C. R. Margules, T. Fuller, D. M. Stoms, A. Moffett, K. A. Wilson, K. J. Williams, P. H. Williams, and S. Andelman. 2006. Biodiversity conservation planning tools: Present status and challenges for the future. *Annual Review of Environment and Resources* **31**:123-159.
- Savings, S. 1998. Core.aml fragmentation assessment program. California Department of Forestry and Fire Protection, Sacramento, CA.
- Schindler, D. W. 1995. Linking species and communities to ecosystem management: a perspective from the experimental lakes experience in C. G. Jones, and J. H. Lawton, editors. *Linking Species and Ecosystems*. Chapman and Hall, New York.
- Schonewald-Cox, C. M. 1983. Conclusions: guidelines to management: a beginning attempt. Pages 414-445 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas, editors. *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Benjamin/Cummings, Menlo Park, CA.
- Schonewald-Cox, C. M., and M. Buechner. 1992. Park protection and public roads. Pages 373-395 in P. Fiedler, and S. Jain, editors. *Conservation Biology: The Theory and Practice of Nature Conservation, Preservation, and Management*. Chapman and Hall, New York.
- Schonewald-Cox, C. M., M. Buechner, R. Sauvajot, and B. A. Wilcox. 1992. Cross-boundary management between national parks and surrounding lands: a review and discussion. *Environmental Management* **16**:273-282.
- Schueler, T. R. 1994. The importance of imperviousness. *Watershed Protection Techniques* **1**:100-111.

- Scott, J. M., F. W. Davis, R. G. McGhie, R. G. Wright, C. Groves, and J. Estes. 2001. Nature reserves: Do they capture the full range of America's biological diversity? *Ecological Applications* **11**:999-1007.
- Scott, J. M., T. R. Loveland, K. Gergely, J. R. Strittholt, and N. L. Staus. 2004. National wildlife refuge system: ecological context and integrity. *Natural Resources Journal* **44**:1041-1066.
- Shafer, C. L. 1995. Values and shortcomings of small reserves. *BioScience* **45**:80-88.
- Shafer, C. L. 1999. National park and reserve planning to protect biological diversity: some basic elements. *Landscape and Urban Planning* **44**:123-153.
- Shelford, V. E. 1933. The preservation of natural biotic communities. *Ecology* **14**:240-245.
- Simberloff, D., J. A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments. *Conservation Biology* **6**:493-504.
- Snyder, C. D., J. A. Young, R. Vilella, and D. P. Lemarie. 2003. Influences of upland and riparian land use patterns on stream biotic integrity. *Landscape Ecology* **18**:647-664.
- Sonoda, K., J. A. Yeakley, and C. E. Walker. 2001. Near-stream landuse effects on streamwater nutrient distribution in an urbanizing watershed. *Journal of the American Water Resources Association* **37**:1517-1532.
- Soule, M. E., D. T. Bolger, A. C. Alberts, R. Sauvajot, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* **2**:75-92.
- South Dakota Gap Analysis Project. 2002. Land stewardship map. South Dakota Fish and Wildlife Research Unit, Brookings, SD.
- Sovern, D. T., and P. M. Washington. 1997. Effects of urban growth on stream habitat. Pages 163-177 in L. A. Roesner, editor. *Effects of Watershed Development and Management on Aquatic Ecosystems*. American Society of Civil Engineers, New York, NY.
- Sponseller, R. A., E. F. Benfield, and H. M. Valett. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology* **46**:1409-1424.

- Steedman, R. J. 1988. Modification and Assessment of an Index of Biotic Integrity to Quantify Stream Quality in Southern Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* **45**:492-501.
- Stoms, D. M. 2000. GAP management status and regional indicators of threats to biodiversity. *Landscape Ecology* **15**:21-33.
- Strayer, D. L., R. E. Beighley, L. C. Thompson, S. Brooks, C. Nilsson, G. Pinay, and R. J. Naiman. 2003. Effects of land cover on stream ecosystems: Roles of empirical models and scaling issues. *Ecosystems* **6**:407-423.
- Stribling, J. B., B. K. Jessup, J. S. White, D. Boward, and M. Hurd. 1998. Development of a Benthic Index of Biotic Integrity for Maryland streams. Maryland Department of Natural Resources, Monitoring and Non-Tidal Assessment Program.
- Taylor, P. D., L. Fahrig, and K. A. With. 2006. Landscape connectivity: a return to the basics. Pages 29-43 in K. R. Crooks, and M. A. Sanjayan, editors. *Connectivity conservation*. Cambridge University Press, New York.
- Terborgh, J. W. 1999. *Requiem for Nature*. Island Press, Washington (DC).
- The Nature Conservancy (TNC). 2006. Managed areas 1/1/2006 for New England. The Nature Conservancy, Boston, MA.
- Theobald, D. M. 2000. Fragmentation by inholdings and exurban development. Pages 155-174 in R. L. Knight, F. W. Smith, B. S.W., W. H. Romme, and W. L. Baker, editors. *Forest Fragmentation in the Central Rocky Mountains*. University Press of Colorado, Boulder.
- Theobald, D. M. 2001. Land-use dynamics beyond the American urban fringe. *Geographical Review* **91**:544-564.
- Theobald, D. M. 2005. Landscape patterns of exurban growth in the USA from 1980 to 2020. *Ecology and Society*.
- Theobald, D. M. 2006. Exploring the functional connectivity of landscapes using landscape networks. Pages 416-443 in K. R. Crooks, and M. A. Sanjayan, editors. *Connectivity Conservation*. Cambridge University Press, New York.
- Theobald, D. M., H. Gosnell, and W. E. Riebsame. 1996. Land use and landscape change in the Colorado Mountains 2. A case study of the East River Valley. *Mountain Research and Development* **16**:407-418.

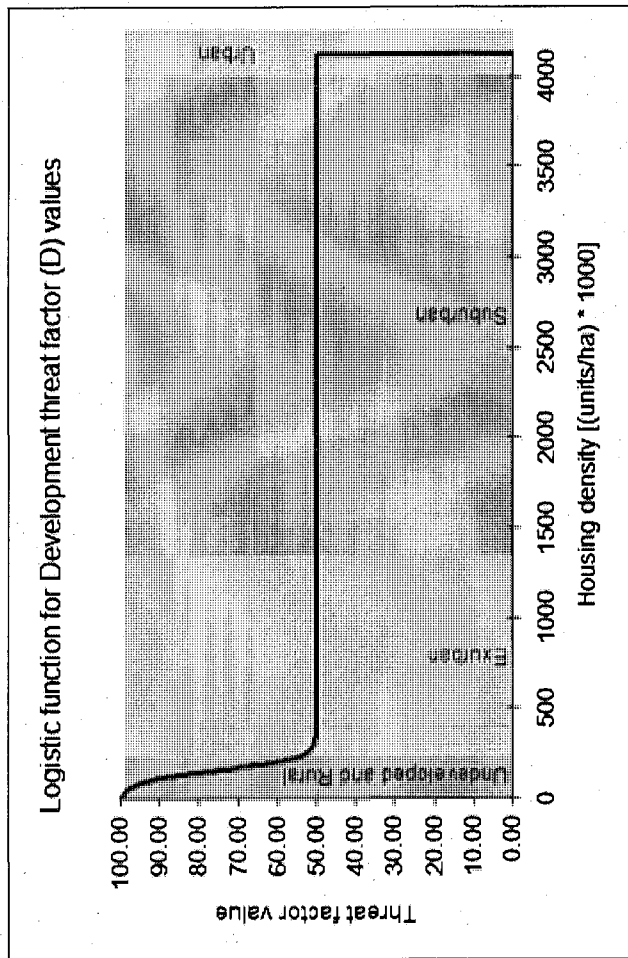
- Theobald, D. M., and N. T. Hobbs. 1998. Forecasting rural land use change: A comparison of regression- and spatial transition-based models. *Geographical and Environmental Modelling* **2**:57-74.
- Theobald, D. M., and N. T. Hobbs. 2002. A framework for evaluating land use planning alternatives: Protecting biodiversity on private land. *Conservation Ecology*.
- Theobald, D. M., N. T. Hobbs, T. Bearly, J. A. Zack, T. Shenk, and W. E. Riebsame. 2000. Incorporating biological information in local land-use decision making: Designing a system for conservation planning. *Landscape Ecology* **15**:35-45.
- Theobald, D. M., G. Wilcox, and J. Whisman. 2007. Report to Great Outdoors Colorado: Inventory of open space in Colorado: Status and trends of protected lands in 2007. Natural Resources Ecology Lab, Colorado State University, Fort Collins, CO.
- Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* **427**:145-148.
- Tobler, W. 1993. Three presentations on geographical analysis and modeling. Pages http://www.ncgia.ucsb.edu/Publications/Tech_Reports/93/93-91.PDF. National Center for Geographic Information and Analysis, University of California, Santa Barbara.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* **14**:18-30.
- UNEP (United Nations Environment Programme). 2003. Status and Trends of, and Threats to, Protected Areas. Page 19 in T. Subsidiary Body on Scientific, and Technological Advice, editor. Convention on Biological Diversity. UNEP, Montreal.
- US Environmental Protection Agency (EPA). 2008. DRAFT: The development of integrated climate and land use scenarios. Page 98. US Environmental Protection Agency, Global Change Research Program, NCEA, Washington, D.C.
- USCB (US Census Bureau). 2000a. Gateway to Census 2000.
- USCB (US Census Bureau). 2000b. Geographic Areas Reference Manual. US Census Bureau.
- USDA (US Department of Agriculture). 2007. Forest Service open space conservation strategy. US Forest Service, Washington, D.C.

- USGAO (US General Accounting Office). 1994. National Park Service: activities outside park borders have caused damage to resources and will likely cause more. USGAO, Washington, D.C.
- USGS (US Geological Survey). 1992. National Land Cover Dataset.
- USGS (US Geological Survey). 1995. National Oil and Gas Assessment. USGS.
- USGS (US Geological Survey). 1999. National Elevation Dataset (NED) digital elevation model.
- USGS (US Geological Survey). 2003. Active Mines and Mineral Processing Plants in the US. USGS.
- USGS (US Geological Survey). 2007. National Hydrography Dataset.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:130-137.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494-499.
- Vogelmann, J. E., S. M. Howard, L. M. Yang, C. R. Larson, B. K. Wylie, and N. Van Driel. 2001. National Land Cover Database (NLCD). U.S. Geological Survey, EROS Data Center, MRLC Project, Sioux Falls, South Dakota, USA.
- Vought, L. B. M., G. Pinay, A. Fuglsang, and C. Ruffinoni. 1995. Structure and Function of Buffer Strips from a Water-Quality Perspective in Agricultural Landscapes. *Landscape and Urban Planning* **31**:323-331.
- Wallace, J. B., J. W. Grubaugh, and M. R. Whiles. 1996. Biotic indices and stream ecosystem processes: results from an experimental study. *Ecological Applications* **6**:140-151.
- Walsh, C. J., A. H. Roy, J. W. Feminella, P. D. Cottingham, P. M. Groffman, and R. P. Morgan. 2005. The urban stream syndrome: current knowledge and the search for a cure. *Journal of the North American Benthological Society* **24**:706-723.
- Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* **416**:389-395.
- Wang, L. Z., J. Lyons, and P. Kanehl. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environmental Management* **28**:255-266.

- Watts, R. D., R. W. Compton, J. H. McCammon, C. L. Rich, S. M. Wright, T. Owens, and D. S. Ouren. 2007. Roadless space of the conterminous United States. *Science* **316**:736-738.
- Weber, A., N. Fohrer, and D. Moller. 2001. Long-term land use changes in a mesoscale watershed due to socio-economic factors - effects on landscape structures and functions. *Ecological Modelling* **140**:125-140.
- Weller, C., J. Thomson, P. Morton, and G. Aplet. 2002. Fragmenting our lands: the ecological footprint from oil and gas development. The Wilderness Society, Washington, D.C.
- Wente, S. P. 2000. Proximity-based measures of land use impacts to aquatic ecosystem integrity. *Environmental Toxicology and Chemistry* **19**:1148-1152.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385-397.
- Wiens, J. A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology* **47**:501-515.
- Wiens, J. A., B. Van Horne, and B. R. Noon. 2002. Integrating landscape structure and scale into natural resource management. Page 485 in J. G. Liu, and W. W. Taylor, editors. *Integrating Landscape Ecology into Natural Resource Management*. Cambridge University Press, Cambridge (UK).
- Wikle, C. K. 2003. Hierarchical models in environmental science. *International Statistical Review* **71**:181-199.
- Wilcove, D. S., and R. M. May. 1986. Biological conservation: national park boundaries and ecological realities. *Nature* **324**:206-207.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* **48**:607-615.
- Wiley, M. J., S. L. Kohler, and P. W. Seelbach. 1997. Reconciling landscape and local views of aquatic communities: Lessons from Michigan trout streams. *Freshwater Biology* **37**:133-&.
- Williams, P., L. Hannah, S. Andelman, G. Midgley, M. Araujo, G. Hughes, L. Manne, E. Martinez-Meyer, and R. Pearson. 2005. Planning for climate change: Identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology* **19**:1063-1074.
- Wilson, K., R. L. Pressey, A. Newton, M. Burgman, H. Possingham, and C. Weston. 2005. Measuring and incorporating vulnerability into conservation planning. *Environmental Management* **35**:527-543.

- Wilson, K. A., M. F. McBride, M. Bode, and H. P. Possingham. 2006. Prioritizing global conservation efforts. *Nature* **440**:337-340.
- Wilson, K. A., E. C. Underwood, S. A. Morrison, K. R. Klausmeyer, W. W. Murdoch, B. Reyers, G. Wardell-Johnson, P. A. Marquet, P. W. Rundel, M. F. McBride, R. L. Pressey, M. Bode, J. M. Hoekstra, S. Andelman, M. Looker, C. Rondinini, P. Kareiva, M. R. Shaw, and H. P. Possingham. 2007. Conserving biodiversity efficiently: What to do, where, and when. *Plos Biology* **5**:1850-1861.
- Wittemyer, G., P. Elsen, W. T. Bean, A. C. O. Burton, and J. S. Brashares. 2008. Accelerated human population growth at protected area edges. *Science* **321**:123-126.
- Woolmer, G., S. C. Trombulak, J. C. Ray, P. J. Doran, M. G. Anderson, R. F. Baldwin, A. Morgan, and E. W. Sanderson. 2008. Rescaling the Human Footprint: A tool for conservation planning at an ecoregional scale. *Landscape and Urban Planning* **87**:42-53.
- Wu, J. G., and R. Hobbs. 2002. Key issues and research priorities in landscape ecology: An idiosyncratic synthesis. *Landscape Ecology* **17**:355-365.

**APPENDIX A. LOGISTIC FUNCTION FOR DEVELOPMENT THREAT
FACTOR**



APPENDIX B. GIS ANALYSIS DATA AND FLOWCHARTS

Publicly available GIS data locations

Chapter 2

California Resource Agency's Legacy Project (2004; obtained from The Nature Conservancy)

Census 2000 population data <http://www.census.gov/main/www/cen2000.html>

Census 2000 urban areas <http://www.census.gov/geo/www/garm.html>

CoMap <http://www.nrel.colostate.edu/projects/comap/>

South Dakota GAP Analysis Program (2002; obtained from South Dakota Fish and Wildlife Research Unit)

ESRI StreetMap Dataset (CD-ROM; see ESRI 2005)

Mines data <http://mrdata.usgs.gov>

National Land Cover Dataset 2001 <http://www.mrlc.gov/>

Oil and Gas Wells data <http://energy.cr.usgs.gov/oilgas/noga/>

Protected Area Database <http://www.consbio.org/what-we-do/protected-areas-database-pad-version-4>

The Nature Conservancy, Managed areas for New England (2006; obtained from The Nature Conservancy)

Chapter 3

Same as Chapter 2

Chapter 4

Digital Elevation Model <http://seamless.usgs.gov/index.php>

Maryland Biological Stream Survey data

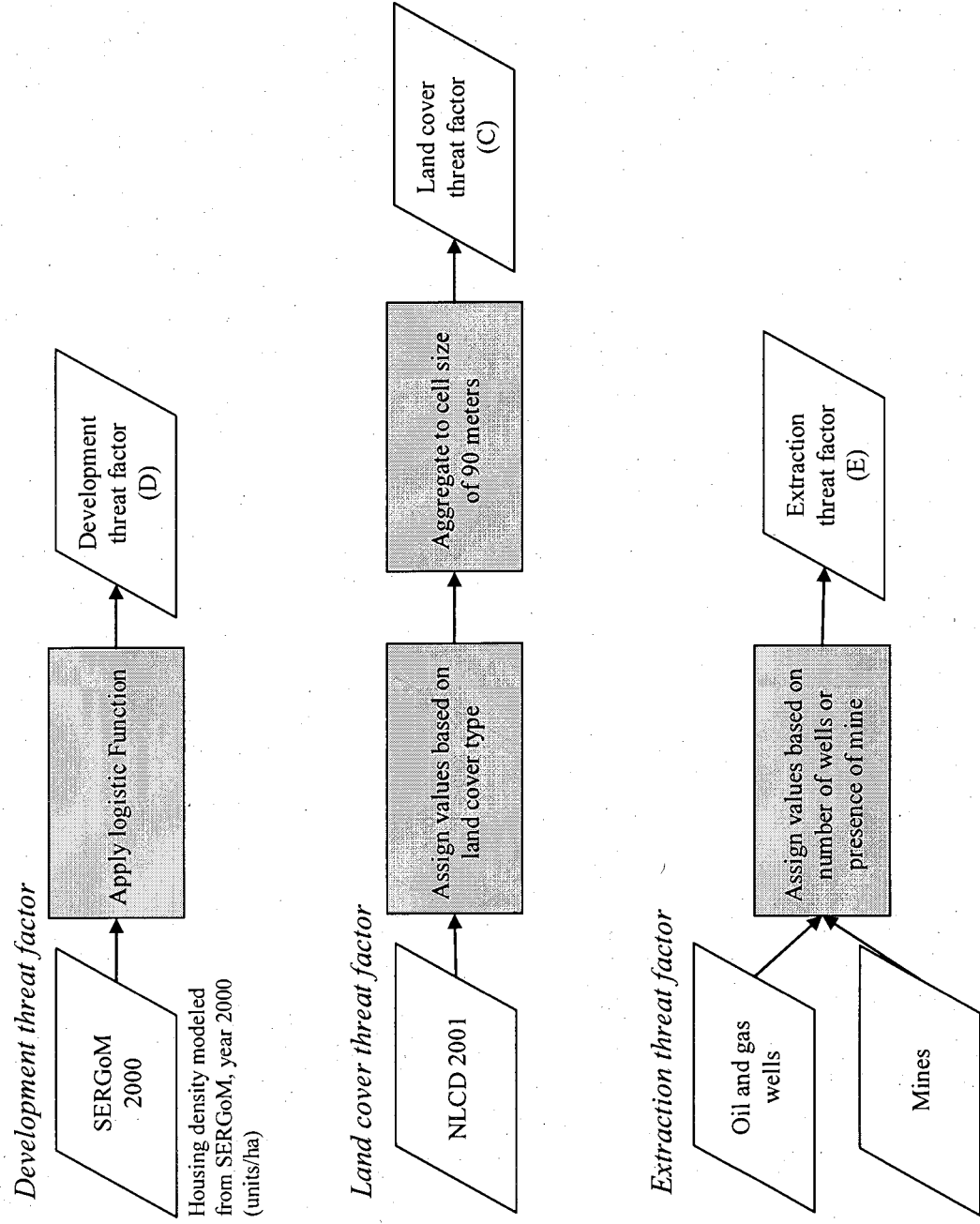
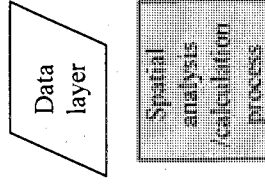
<http://mddnr.chesapeakebay.net/mbss/search.cfm>

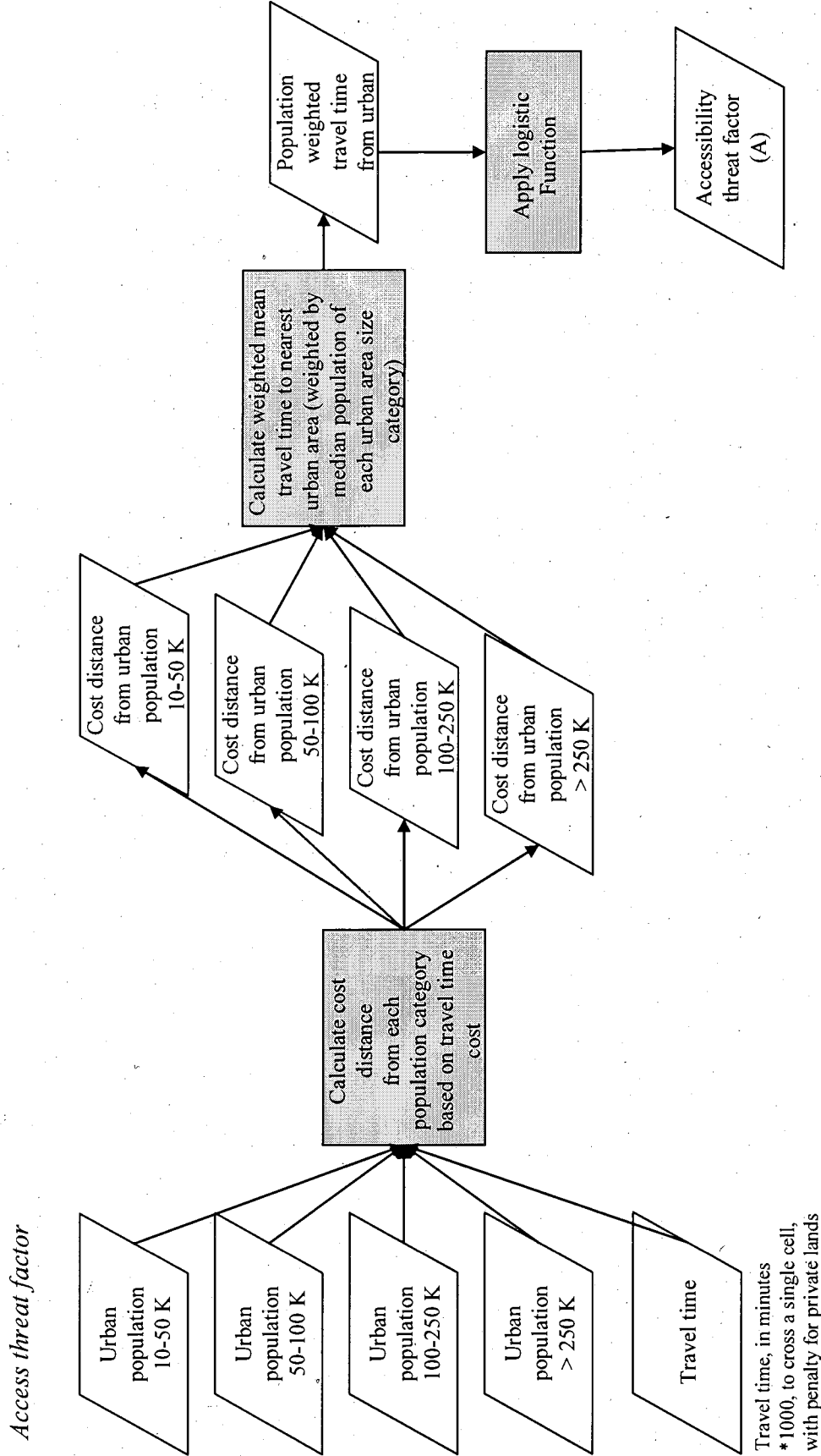
National Hydrography Dataset <http://nhd.usgs.gov/index.html>

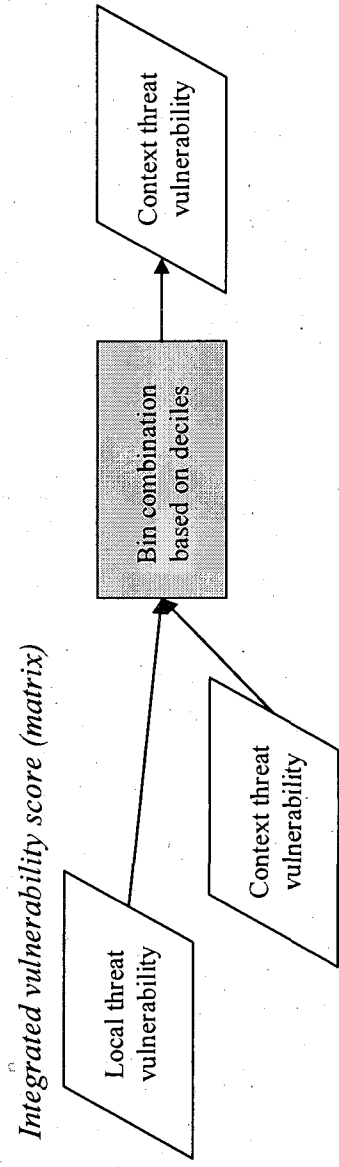
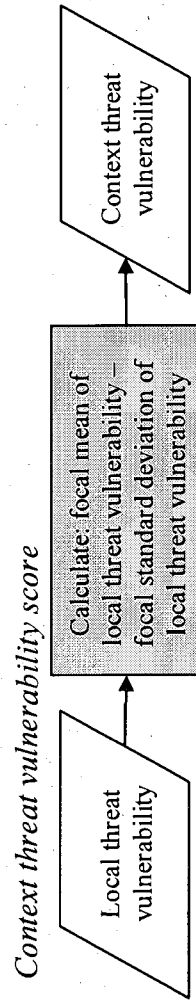
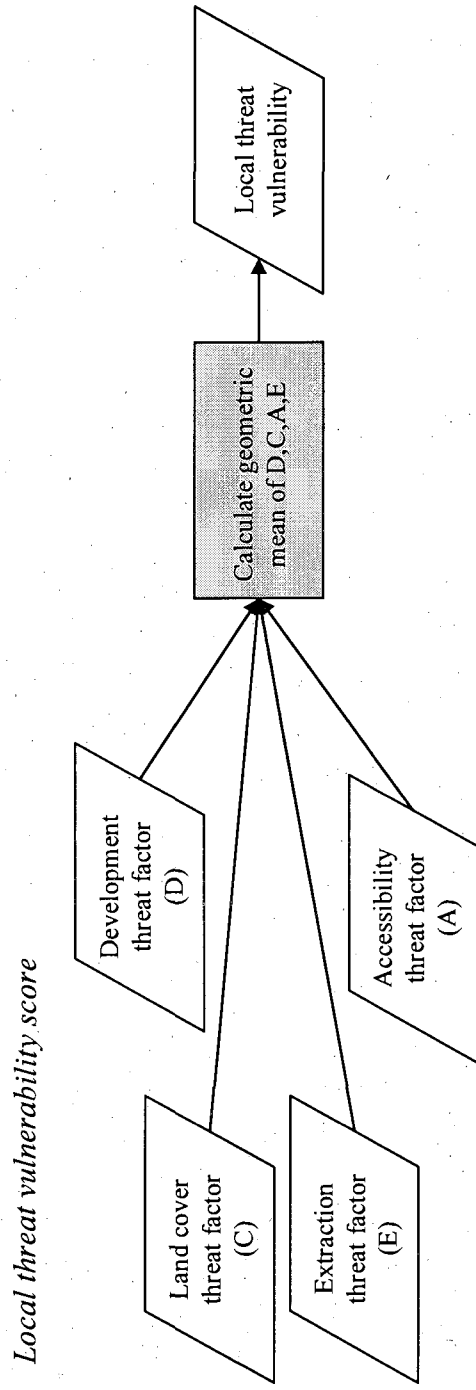
National Land Cover Dataset 1992 <http://www.mrlc.gov/>

GIS Analyses for Chapter Two

Legend

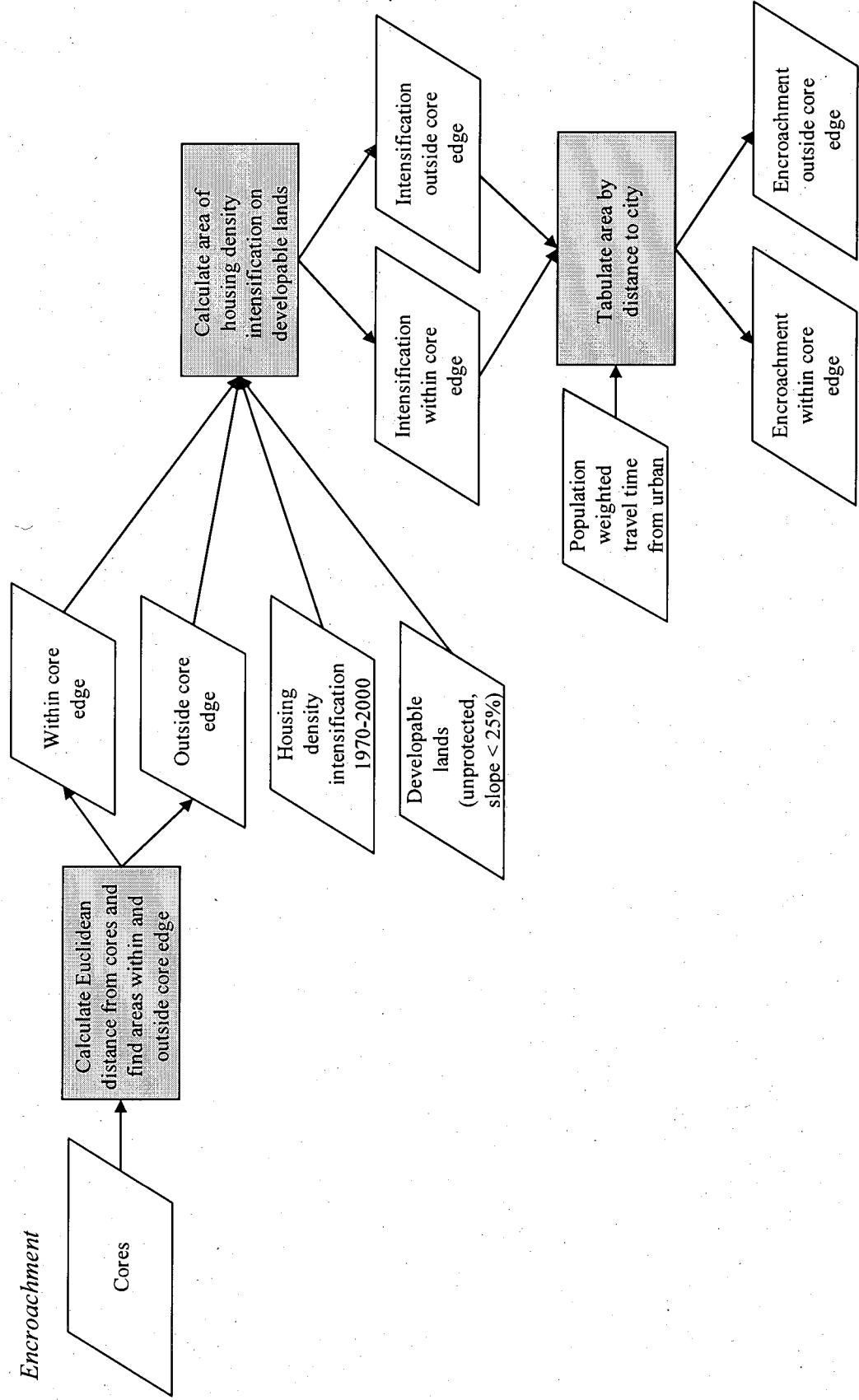




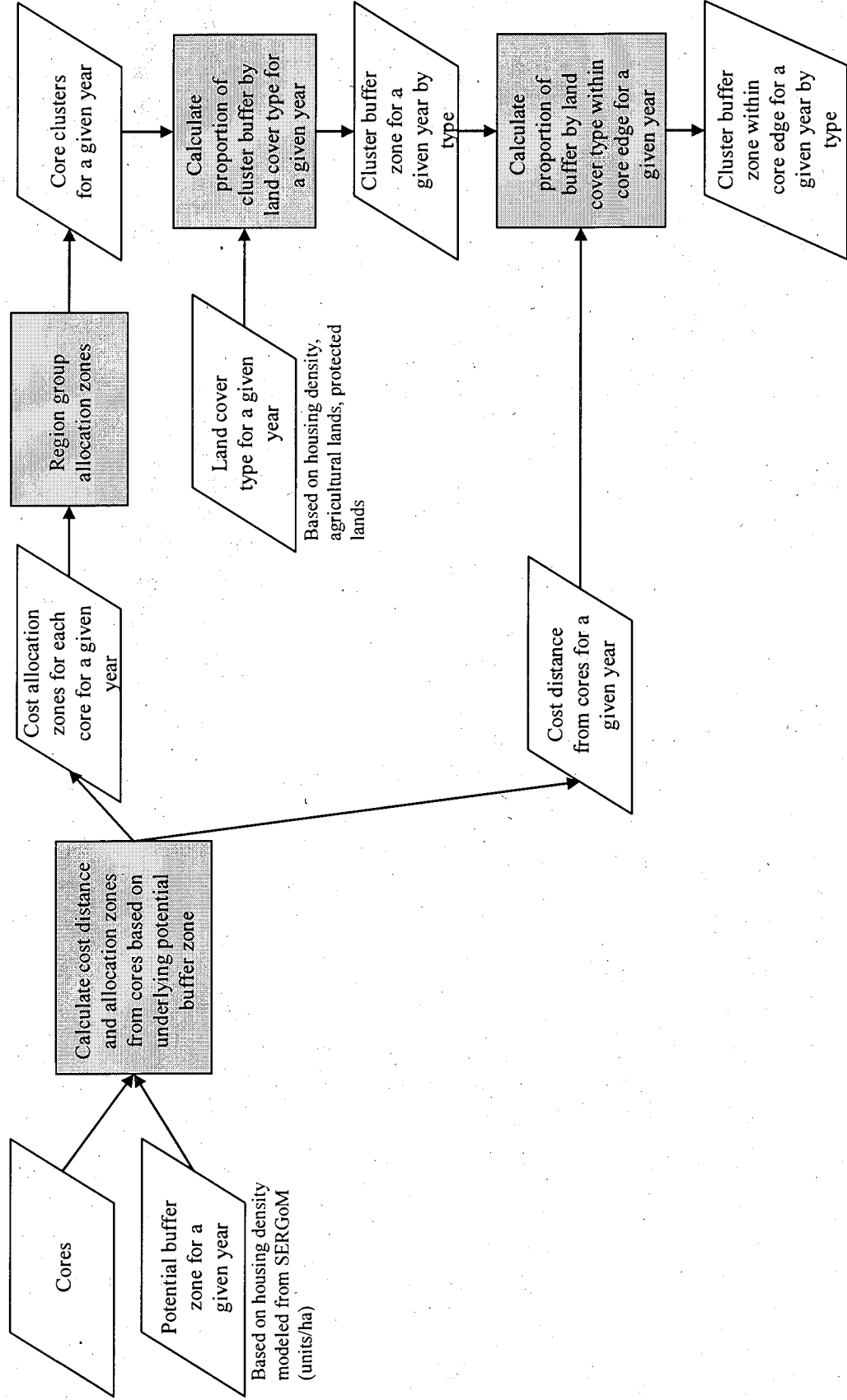


GIS Analyses for Chapter Three

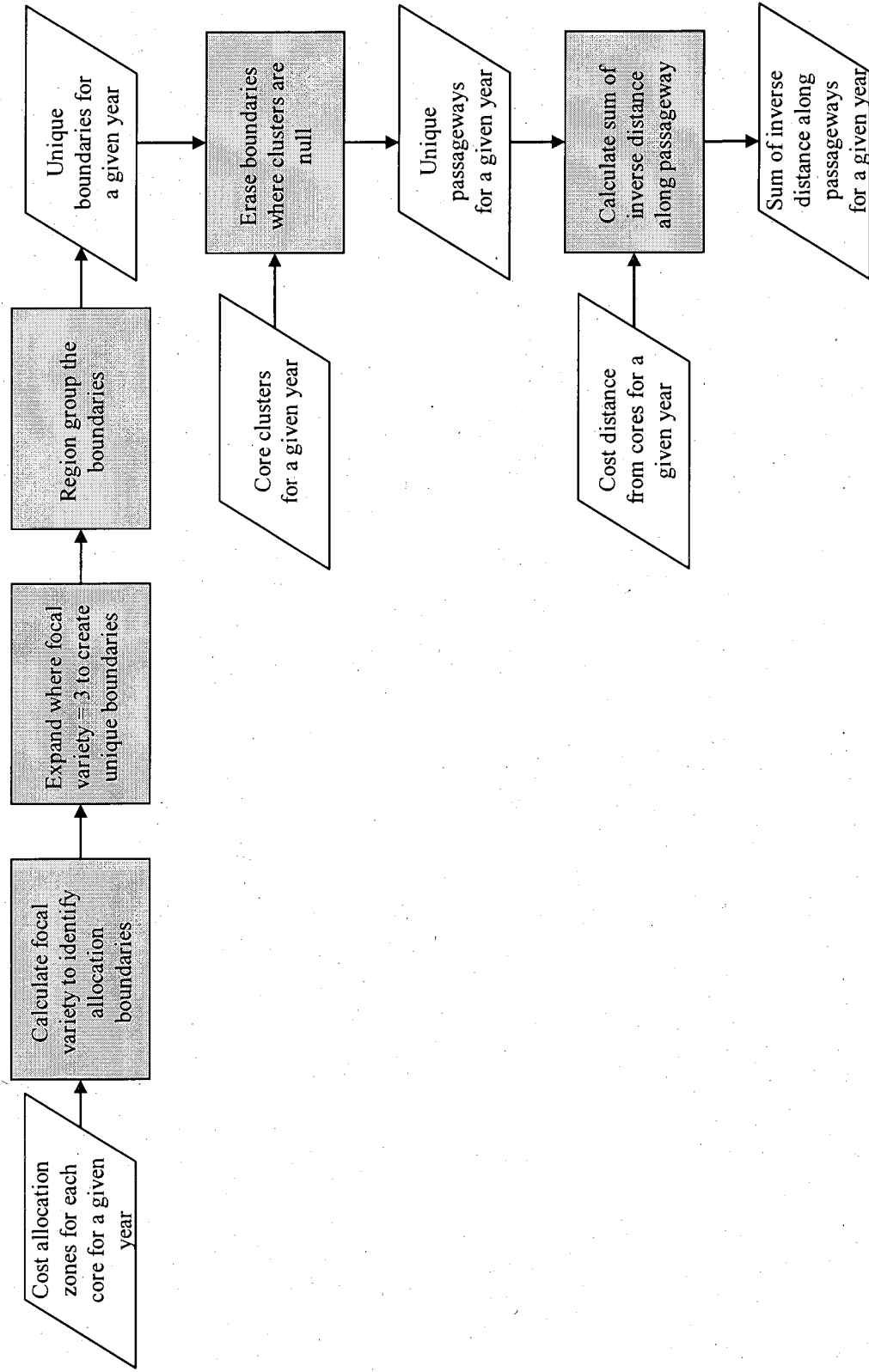
Encroachment



Buffer



Connectedness



GIS Analyses for Chapter Four

