MULTI-SCALE CONSERVATION IN AN ALTERED LANDSCAPE: THE CASE OF THE ENDANGERED ARROYO TOAD IN SOUTHERN CALIFORNIA

A Dissertation

by

MICHAEL LOUIS TREGLIA

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Chair of Committee,	Lee A. Fitzgerald
Committee Members,	Robert N. Fisher
	Inci Güneralp
	Gerard T. Kyle
Head of Department,	Michael Masser

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ABSTRACT

Habitat loss and degradation are recognized as significant drivers of biodiversity loss in terrestrial and freshwater ecosystems. These issues are often associated with anthropogenic land cover changes, which can have direct and indirect impacts on species, and conservation strategies must take both into account for long-term success. I focused this dissertation on the endangered arroyo toad (*Anaxyrus califonicus*), endemic to southern California, USA and northern Baja California, Mexico. The species relies on open, sandy streams for breeding and larval development, and the adjacent terrestrial environments for post-metamorphosis life stages; primary threats include destruction and degradation of these habitats.

I conducted three studies to better understand threats to, and identify conservation opportunities for arroyo toads in southern California. First, I developed distribution models that enabled me to identify areas that could be used to create habitat for the species, which could then be colonized by nearby populations or populated via translocation efforts. Second, I used structural equation modeling to investigate relationships among land cover characteristics at multiple spatial scales and suitability of riparian areas for arroyo toads. This study yielded insight into how land cover of entire watersheds and along stream networks influence arroyo toad habitat. Lastly, I used a structural equation model in conjunction with a projection of development for my study area to forecast how future urbanization may influence suitability of habitats for arroyo toads in individual watersheds. I compared results for scenarios with high and low levels

of urbanization, and found conservation of natural land covers at the watershed scale can ultimately help maintain habitat in the long-term.

The results of these studies may guide both immediate and future conservation efforts for arroyo toads in my study area. My approaches can be applied to other systems for understanding conservation issues affecting other species. Furthermore, future work may build on this research to inform conservation in other parts of the arroyo toad’s range, and models can be iteratively improved as land cover changes occur and the species responds through time.

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CHAPTER I

INTRODUCTION

Conservation biologists face persistent challenges of mitigating anthropogenic impacts on individual species and entire ecosystems. Loss and degradation of natural habitats are widely acknowledged as significant threats to multiple taxa (e.g., Schipper et al. 2008, Sodhi et al. 2008, Böhm et al. 2013), and these problems are largely driven by anthropogenic development pressures, both directly and indirectly. Roads, for example, directly replace natural land covers with hard, impervious surfaces, effectively removing that natural habitat from existence, and indirectly they tend to decrease connectivity of animal populations (Andrews and Gibbons 2005, Clark et al. 2008, Holderegger and Di Giulio 2010). Furthermore, roads alter hydrology and sediment transport yielding impacts on aquatic habitats (Trombulak and Frissell 2000, Coffin 2007), and they interfere with physical processes that influence dune habitats, having effects on individual species and larger communities (Vega et al. 2000, Leavitt and Fitzgerald 2013).

Conservation actions frequently focus on the proximate causes of species declines (Pressey et al. 2007), and involve techniques such as direct improvement and restoration of habitat (Bond and Lake 2003) and translocation of organisms to expand their ranges (Griffith et al. 1989, Seddon 2010). Activities such as these undoubtedly yield immediate benefits to species, although they can be overwhelmed in the long-term by broad-scale processes that ultimately drive species declines (Pressey et al. 2007).

Long-term success of conservation projects may require repeated small-scale actions to effectively minimize local impacts of broad-scale drivers of decline. For example, site-specific removal of invasive species will require continuous investment of conservation resources into the future unless the problem species is completely eradicated from the region or excluded from the focal habitats into the future. Thus, it is important to consider multiple options for conservation and evaluate potential for long-term success (Wilson et al. 2007)

Aquatic habitats are prime examples of those that are impacted directly by local influences, and indirectly by spatially disparate factors (Allan 2004). For example, stream reaches can be drastically changed and even eliminated by local anthropogenic development, and watershed-scale land cover changes can alter conditions by changing hydrologic flow and sediment transport, among other processes. Supporting this, numerous studies have found clear impacts of watershed-scale urbanization on water quality metrics and aquatic ecological communities of (e.g., King et al. 2005a, Riley et al. 2005, Walsh et al. 2005, King et al. 2011). Given these results, watershed-scale management has been identified as a necessary strategy for conservation of freshwater ecosystems (e.g., Zedler 2003, Morton and Brown 2011), and has even been used to maintain quality of potable water for residents of New York City (Pires 2004).

I focused this dissertation on a species of stream-breeding amphibian, the arroyo toad (*Anaxyrus californicus*), which is endangered species endemic to southern California, USA and northern Baja California, Mexico. It is listed as endangered by the International Union for the Conservation of Nature (Hammerson and Santos-Barrera

2004), and has been protected by the in the United States under the Endangered Species Act since 1994 (U.S. Fish and Wildlife Service 1994). Arroyo toads are habitat specialists that rely on open, sandy streams for breeding and larval development, and the surrounding terrestrial environments for post-metamorphosis life stages (Griffin and Case 2001, Sweet and Sullivan 2005, Mitrovich et al. 2011). Declines of the species have been attributed to habitat loss, and habitat degradation associated with altered hydrologic regimes, encroachment of woody vegetation, and introduction of exotic predators (Sweet and Sullivan 2005). Most proximately, the species responds to the local environmental conditions, although the habitats are ultimately affected, in part, by broad-scale processes including hydrology and sediment transport. Given the species' requirements for terrestrial and aquatic habitats, its conservation status, and its potential responses to local- and broad-scale actions, I identified it as a model organism for which to examine opportunities for conservation at along streams and within entire watersheds.

In my first study (Chapter II), I identified riparian areas that may be suitable for arroyo toads based on intrinsic environmental characteristics including long-term climate, topography, and soil type which represented "potential habitat", and I identified "current habitat", or areas that may be currently suitable for the species based on the aforementioned features in conjunction with dynamic characteristics associated with vegetation and land cover. I employed distribution modeling techniques for this work, in which I used statistical relationships between the environmental data and known arroyo toad localities (Franklin 2009, Peterson et al. 2011) to identify areas as potential and current habitat. I compared the results of these analyses to determine where intrinsic conditions are likely suitable, but dynamic characteristics are not. I then identify these sites as areas that could be improved to create new habitat, which may then be colonized by nearby populations, or via translocation efforts.

In my second study second study (Chapter III) I estimated the relative influences of land cover conditions at multiple spatial scales on suitability of riparian habitats for arroyo toads. I used structural equation modeling (Grace 2006, Kline 2011) to test general hypotheses that: 1) average suitability of riparian areas for arroyo toads in individual watersheds is directly influenced by land cover conditions along the respective stream networks; 2) habitat suitability is directly influenced by land cover conditions of entire watersheds; and 3) watershed-scale land cover influences land cover along stream networks, yielding indirect effects of watershed-scale land cover on arroyo toad habitat. Importantly, results of this work can help identify what scales are most important for management, and I hope to provide managers with information that can guide effective, long-term conservation efforts.

In the third study of my dissertation (Chapter IV) I used structural equation modeling in conjunction with scenarios of future land cover in my study area, to forecast how continued urbanization may influence suitability of riparian areas for arroyo toads in individual watersheds. Though structural equation modeling been employed in other disciplines for forecasting (Outwater et al. 2003, Sohn and Moon 2003), to my knowledge this is the first application of this capability in a conservation biology or ecology context, and my approach can be used and further developed by others. I created two scenarios of future land cover based on a spatially-explicit development projection

(Landis and Reilly 2003), representing high and low levels of development in 2050. My forecasts of change in habitat suitability for arroyo toads allow me to represent possible effects of long-term anthropogenic development on the species, and comparison of results between the two scenarios is useful in identifying whether large-scale conservation can benefit riparian habitats that arroyo toads rely on

Overall, by studying how factors across multiple scales influence arroyo toad habitat, I hope to inform immediate habitat improvement efforts, as well as long-term, large-scale conservation planning. Future studies in this system can build on this research, using new data as it becomes available in conjunction with close tracking of land cover changes, to calibrate and improve the models that I present. Furthermore, the analytical approaches I use are broadly applicable, and can be employed to help identify conservation opportunities for myriad species in other systems.

CHAPTER II

MODELING POTENTIAL AND CURRENT HABITAT FOR AN ENDANGERED TOAD TO IDENTIFY CONSERVATION OPPORTUNITIES

Synopsis

Species distribution models (SDMs) are used for numerous purposes such as predicting changes in species’ occurrence patterns, forecasting distributions of invasive species, and identifying biodiversity hotspots. Although implications of SDMs for conservation are often implicit, few studies use SDMs explicitly to inform conservation efforts. Herein, I focused on the endangered arroyo toad (*Anaxyrus californicus*), which is a habitat specialist that relies on open, sandy streams and the surrounding floodplains in southern California, USA, and northern Baja California, Mexico. Declines of the species are largely attributed to habitat degradation associated with vegetation encroachment, establishment of invasive predators, and altered hydrologic regimes. I had three main goals: 1) develop a model of potential habitat for the arroyo toad, based on static, long-term environmental variables and all available locality data; 2) develop a model of the species’ current habitat by incorporating recent remotely-sensed variables and only using locality data since 2005; and 3) use the results of both models to identify sites that may be used for conservation of the arroyo toad. I used random forests with a combination of presence/absence and presence/pseudoabsence data to develop the models, focused on riparian zones in southern California. My models identified 14.37% and 10.50% of the study area as potential and current habitat for the arroyo toad, respectively. Generally, the inclusion of the remotely-sensed variables reduced the modeled suitability of sites, thus many areas modeled as potential habitat were not modeled as current habitat. I propose such sites could be made suitable for arroyo toads through active management, and populated via translocations or dispersal from nearby populations. If it is possible to improve conditions in all of these areas, current habitat could be increased by 67.02%. My general approach can be employed to guide conservation efforts of virtually any species with sufficient locality data, in regions with appropriate environmental datasets.

Introduction

Habitat loss and environmental degradation are major causes of biodiversity loss in terrestrial and freshwater ecosystems (Millenium Ecosystem Assessment 2005). Urbanization and agricultural expansion are among the most significant and pervasive forms of land conversion. Indirect effects also manifest in myriad ways: invasive vegetation can displace native species and alter physical habitat structure (Zedler and Kercher 2004); changes in hydrology can impact riparian conditions (Poff et al. 1997), and introduced animals can alter entire ecosystems through trophic interactions (Zavaleta et al. 2001). Site-specific actions can be used to improve habitats for individual species, though identifying the most appropriate locations is challenging (Clewell and Rieger 1997, Miller and Hobbs 2007).

Within the ever-expanding toolkit for conservation biologists, species distribution models (SDMs) have become commonly employed in recent years for various purposes (Franklin 2009, Peterson et al. 2011). Though species distribution modeling can have various connotations and meanings, herein, I follow Franklin's convention of using it to encompass the concept of habitat suitability models, environmental niche models, and others (Franklin 2009). The principle behind species distribution modeling is that species' locality data, and associated environmental variables can be used to make inferences of where else suitable environmental conditions exist (Peterson et al. 2011).

Common applications of SDMs include predicting how climate change may contribute to species extinctions and range shifts (e.g., Berry et al. 2002, Thomas et al. 2004, Loarie et al. 2008), identifying locations with undescribed species and new localities of known species (e.g., Raxworthy et al. 2003, Pearson et al. 2007), and projecting future distributions of invasive species in (e.g., Pyron et al. 2008, Rodda et al. 2009, Smolik et al. 2010). SDMs have also been used to estimate habitat loss for individual species (Barrows et al. 2008), and to predict future habitat loss given projected changes in variables likely to change substantially within a focal time period (Stanton et al. 2012). Although SDMs can also be employed to directly inform conservation, there are few published examples (Guisan et al. 2013).

I developed SDMs using static and dynamic environmental datasets (*sensu* Stanton et al. 2012) with an explicit objective of identifying opportunities for conservation of the endangered arroyo toad (*Anaxyrus californicus*) in southern California, USA. I had three main goals: 1) develop a model of potential habitat for arroyo toads, based on long-term, static environmental variables (hereafter, the "potential model"); 2) develop a model of the species' current habitat by incorporating time-sensitive remote sensing data and using only locality data since 2005 (hereafter, the "current model"); and 3) use the results of both models to identify sites that may be used for arroyo toad conservation.

The arroyo toad is endemic to southern California, USA and northern Baja California, Mexico (Hammerson and Santos-Barrera 2004, Sweet and Sullivan 2005). It is a habitat specialist, closely tied to ephemeral streams and surrounding floodplains (Griffin and Case 2001, Sweet and Sullivan 2005). The species is listed as endangered by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 1999, 2009a) and by the IUCN (Hammerson and Santos-Barrera 2004), facing threats of habitat destruction, habitat degradation, and invasive predators including American Bullfrogs (*Lithobates catesbeianus*), various fish species, and crayfish (*Procambarus clarkii*) (U.S. Fish and Wildlife Service 1999, Sweet and Sullivan 2005). Anthropogenic alterations to hydrologic regimes and wildfire frequency have contributed to these threats, though it is possible to improve habitat though site-specific actions. For example, decreases in American Bullfrogs can improve arroyo toad occupancy and abundance (Miller et al. 2012), and clearing of vegetation may benefit breeding habitat. SDMs exist for other amphibians in arid environments (Dayton and Fitzgerald 2006), and an early SDM was developed for arroyo toads in a portion of the study area (Barto 1999). My models cover a large spatial extent at high resolution, and help identify sites with potential for habitat improvement, translocation, and surveys for unknown populations. Furthermore, my methodology can be applied to other species in different systems as a guide for conservation efforts.

Methods

Study Area

I focused this study on five coastal watersheds of southern California (based on HUC-8 classification; U.S. Geological Survey 2012): the Aliso-San Onofre; the San Luis Rey-Escondido; the San Diego; and the U.S. portion of the Cottonwood-Tijuana watershed watersheds. This area has undergone significant anthropogenic land cover changes in recent decades (Biggs et al. 2010), and further development is projected into the future (Syphard et al. 2011). Twenty-two dams in the study region influence hydrologic flow regimes and sediment transport in streams (San Diego County Water Authority 2013), and anti-wildfire policies in conjunction with the spread of invasive plants have altered dynamics of terrestrial vegetation (Minnich 1983, Barbour et al. 2007). However, this region has active conservation policy and management tools (e.g., the Multiple Species Conservation Plan), with stakeholder groups working to restore native ecosystems (Regan et al. 2008), thus my results can be quickly and readily adopted to inform on-the-ground actions. Furthermore, range-wide genetic analyses by Lovich (2009) showed arroyo toad populations from these drainages were more closely related to each other than to populations in other areas, thus it may comprise a reasonable management unit for the species.

Units of Analysis

I focused on streams and stream-side areas, corresponding to primary habitats arroyo toads use throughout their lives (Griffin and Case 2001, Sweet and Sullivan 2005, Mitrovich et al. 2011). For the best spatial accuracy I used stream data from the 1:24,000 scale National Hydrography Dataset (NHD; http://nhd.usgs.gov, accessed on 28 May 2012). I excluded extremely small segments, known generally not to serve as habitat for arroyo toads, by eliminating sections that were not assigned an order in the 1:100,000 scale NHDPlus dataset (http://www.horizon-systems.com/nhdplus, accessed on 28 May 2012; 1:24,000 scale NHD data do contain stream order data). I accomplished this using used a spatial overlay with a 50m buffer of the stream data, to account for differences in spatial accuracy between these two datasets, using Manifold GIS version 2.0.28 (Manifold Software Limited).

I converted remaining NHD stream data to a raster dataset with 200m pixels, which allowed me to include metrics associated with streamside areas. Furthermore, while some small spatial inaccuracies exist in the stream data, these larger pixels allowed me to incorporate information from other layers that help to characterize streams but did not line up perfectly with the stream dataset. I removed pixels that had no calculable soil characteristics to effectively mask out large water bodies, also known not to serve as habitat or arroyo toads. This criterion was somewhat conservative, but an alternative of basing pixel removal on overlap with NHD water body boundaries was too liberal, eliminating sites with actual presence records.

Environmental Data

I derived the environmental data from freely available datasets. In both models I used static variables (*sensu* Stanton et al. 2012), including characteristics of climate, soil, topography, and geomorphology (Table 1). In the current model I also included dynamic variables (*sensu* Stanton et al. 2012) related to land cover, to add temporally-constrained information from the same period as the locality data for that model. I prepared the environmental data for analysis using SAGA GIS version 2.1.1 (Böhner 2013) and Manifold GIS version 8.0.28 (Manifold Software Limited).

As dynamic variables, I used indices of brightness, greenness and wetness (i.e., Tasseled Cap bands), derived from multi-season 2010 Landsat TM satellite imagery (NASA Landsat Program 2010). This year was fairly central in the study period (2005-2013) and climate conditions were nearly average (based on annual climate reports; http://www.ncdc.noaa.gov, accessed on 30 November 2012). I obtained cloud-free imagery for 27 March and 3 September, representing wet and dry seasons, respectively. For each image date I converted the raw data to top of atmosphere reflectances, atmospherically corrected them using dark object subtraction (Song et al. 2001), and derived the Tasseled Cap bands using the Tasseled Cap Transformation (Crist and Cicone 1984) in GRASS GIS version 6.4.4 (GRASS Development Team 2012). These variables have been shown to benefit habitat models, while maintaining interpretability (Paczkowski 2008). High brightness is generally associated with bare ground and total surface reflectance, greenness with vegetation, and wetness with surface water and water content of soil and plants (Crist and Cicone 1984, Seto et al. 2002).

Table 1. Description of environmental data layers used in models of arroyo toad habitat. Bracketed numbers following abbreviations denote corresponding months layers were from (1-12) or indicate that it is the annual average (13).

Name (Abbreviation)	Description	Value Used	Source and Citation
Climate Data			
Avg. Monthly. and Annual: -Precipitation (Ppt[01-13]) -Maximum Temperature (TMx [01-13]) - Minimum Temperature (TMn [01-13])	Data used were from 1981-2010; Pixels resolution was 800m; majority value for each analysis pixel was used.	Majority value per 200m pixel	Obtained directly from Prism Climate Group, Oregon State University; downloaded from http://www.prism.oregonstate.edu/ on 14 Jun 2013
Climate Data			
-% Clay (Clay) -% Sand (Sand) -% Silt (Silt) -Soil Water Storage Capacity (WaterSt)	Average values per soil type aggregated across all soil layers obtained from 1:100,000 scale soil data.	Average, weighted by area of each soil type per pixel	Derived from STATSGO2 Soil Data; (NRCS 2011), downloaded from http://websoilsurvey.sc.egov.usda.gov on 24 July 2012
Topography and Geomorphology			
- Elevation along Stream Segment (Elev)	Estimated as the lowest elevation value within analysis grid cells.	Calculated Value	Value from 10m National Elevation Dataset (Gesch 2007); downloaded from http://nationalmap.gov/ on 6 June 2011
-% Stream Slope (Slope)	Estimated, within each grid cell, as: [Max. Stream Elevation – Min. Stream Elevation]/Length of Stream.	Calculated value	Derived from 10m NED overlaid on 1:24,000 National Hydrography Dataset Flowlines; NHD Data downloaded from: http://nhd.usgs.gov/ on 28 May 2012

Table 1. Continued

Name (Abbreviation)	Description	Value Used	Source and Citation
Topography and Geomorphology (continued)			
-Multiresolution Index of Valley Bottom Flatness (MRVBF)	Measure of how flat and wide a valley is.	Maximum value per pixel	Derived from 10m NED, using methodology described by Gallant and Dowling (2003)
-Vector Ruggedness Measure (VRM03 and VRM18)	Measure of how rugged terrain is, based on, analysis windows of 3 and 18 pixels.	Minimum values per pixel	Derived from 10m NED, using methodology described by Sappington et al. (2007)
-Catchment Area (CatchArea)	Total area draining into a given pixel.	Maximum value per pixel	Derived from a sink-filled 10m NED using methodology described by Gruber and Peckham (2009)
Remotely Sensed Data			
-Brightness (Brt[03,09].Med; Brt[03,09].Var) -Greenness (Grn[03,09].Med; Grn[03,09].Var) -Wetness (Wet[03,09].Med; Wet[03,09].Var)	Indices of “brightness,” “greenness,” and “wetness” for 27 March and 9 Sept. 2010.	Median and Variance within pixel	Derived from Landsat TM imagery using the Tasseled Cap Transformation for Landsat data (Crist and Cicone 1984)

Arroyo Toad Locality Data

I obtained locality data for arroyo toads from multiple sources including the U.S. Fish and Wildlife Service (http://www.fws.gov/carlsbad/GIS/CFWOGIS.html, accessed on 13 September 2013) and the California Natural Diversity Database (http://www.dfg.ca.gov/biogeodata/cnddb, accessed on 13 September 2013). I also used museum records from the following institutions, accessed through the HerpNet data portal (http://herpnet.org/) on 13 September 2013: California Academy of Sciences; Natural History Museum of Los Angeles County; San Diego Natural History Museum; Smithsonian National Museum of Natural History; and University of California, Berkeley, Museum of Vertebrate Zoology. Additional data were provided by Cleveland National Forest (U.S. Forest Service), and I included locality information from USGS survey work (USGS San Diego Field Station, unpub. data). Given undocumented spatial accuracy for some sources, and my focus on stream habitats, I excluded data from outside a 50m buffer of the NHD stream data to help minimize potential error, and I removed data that had spatial accuracy documented as >160m in the USFWS dataset. The final locality data were indicated as presences in the 200m pixels for analysis. For the potential model I included all of these presences, among 1037 pixels, and for the current model I used presence records from 2005-2013, among 791 pixels.

I incorporated absence data into the current model, attained through standardized daytime and nighttime surveys designed to account for low detection probability (Atkinson et al. 2003, Miller et al. 2012). Based on the detectability of arroyo toads (Atkinson et al. 2003), I considered them absent from areas where they had not been detected in at least eight nighttime surveys or five daytime surveys since 2005. If data sources contrasted since 2005 (i.e., a source indicated presence in a grid cell site where surveys indicated absence) the presence record was given priority. Based on these criteria, I used 89 absence records in the current model.

To eliminate multicollinearity associated with the large number of predictor variables, and thus improve interpretability, I used principle component analyses (PCA) to derive reduced variable-sets (e.g., Loarie et al. 2008, Wang et al. 2013). For each model I conducted a PCA on the correlation matrix of predictor variables, and used principle components (PCs) with eigenvalues greater than one in place of the original data, following the Kaiser-Guttman criterion (Legendre and Legendre 2012). I inspected the loadings for each PC to discern underlying associations with individual variables; tables with the variable loadings and eigenvalues for each PC are presented in Appendix A. PCAs were conducted using the package 'vegan' (Oksanen et al. 2012) in R version 3.0.2 (R Core Team 2013).

Species Distribution Models

Model Development

I used random forests (Breiman 2001) to develop models of the potential and current habitat for arroyo toads in my study area. This is a machine-learning technique that merges classification and regression trees with a bootstrap resampling procedure to create an optimal model (Cutler et al. 2007). Random forests avoids problems of overfitting and does not rely on assumptions of parametric methods (Hastie et al. 2009, Evans et al. 2011). Because of its strengths, this technique has been implemented in a variety of ecological studies (e.g., Cutler et al. 2007, Evans and Cushman 2009, Oliveira et al. 2012).

Random forests is generally considered a presence/absence method (Franklin 2009), but has successfully been used with presence/pseudoabsence data (e.g., Hernandez et al. 2008, Senay et al. 2013). Pseudoabsences are used when true absence data are unavailable, and they are acquired by sampling locations from the study region that lack locality records (Peterson et al. 2011). In my models I used the aforementioned presence/absence data, and generated sufficient pseudoabsence data to balance the number of presences, to decrease model bias and improve model fit (Evans and Cushman 2009). To account for spatial biases in the data that could adversely affect model results, I selected pseudoabsences with the same biases as the actual data (Phillips et al. 2009, Elith et al. 2010, Fitzpatrick et al. 2013). I ran models 10 times with different pseudoabsence points and averaged the results (Barbet-Massin et al. 2012).

I used the implementation of random forests in the 'randomForest' package (Liaw and Wiener 2002) in R (R Core Team 2013). I set the number of bootstrapped trees (*k*) according to the point at which the error rate for withheld (out-of-bag [OOB]) samples stabilizes and ceases to improve. Given that variable interaction may stabilize at a slower rate than the OOB error (Evans et al. 2011), I used twice that number, setting *k*=10,001. In each tree, the OOB sample was 36.8%, and the number of variables permuted at each branching node was set to the square root of the number of variables. I used preliminary model comparisons to investigate whether removal of any PC-transformed variables would yield more parsimonious results based on the model improvement ratio (MIR; Evans and Cushman 2009, Murphy et al. 2010), though I found that inclusion of all variables yielded the best results. I used the final, averaged models to predict habitat in terms of "probability of occurrence" (Peterson et al. 2011) throughout my study area, and used the mean decrease in accuracy for randomized permutations of input variables as a measure of variable importance (Liaw and Wiener 2002).

Model Evaluation

I evaluated model performance by comparing probabilities of occurrence with the presence/pseudoabsence data (potential model) and true presence/absence data (current model). As a threshold-independent metric of model performance (Franklin 2009), I used the area under the receiver operating curve (AUC), which ranges 0.5-1.0. Models with AUC values of 0.7-0.9 are generally considered to have moderate performance and those with values >0.9 are considered to have high performance (Swets 1988, Manel et al. 2001). I note that AUC values based on presence-only data (without confirmed absences) can be biased low and should be interpreted cautiously (Peterson et al. 2008). As a measure of model significance, I also compared the models with 1000 models of randomized presence/absence data; calculating the p-value as the proportion of times that the OOB error in randomized models was less than that of my models (Evans and Cushman 2009, Murphy et al. 2010); I set α to 0.05.

I also used threshold dependent measures of model performance, in which probabilities of occurrence are converted to binary predictions of presence/absence and compared to the original data. I set the cutoff for binary predictions to the lowest probability of occurrence modeled for a pixel with confirmed presence of arroyo toads (Phillips et al. 2006, Pearson et al. 2007), as false positives were preferable to false negatives for this analysis. I present the True Skill Statistic for the models (TSS; Allouche et al. 2006), which ranges 0-1, with higher values indicating better performance.

Comparison of Potential Habitat and Current Habitat

To compare the amount of modeled potential and current habitat I created a transition map by subtracting binary predictions of presence/absence pixels of the current model from those of the potential model. The resulting map had three possible values for each pixel: 1 – predicted as habitat in the potential model but not the current model; 0 - no change in predictions; and -1 – predicted as habitat in the current model, but not the potential model. I anticipated values of -1 would be rare, but possible given that the current model may include interactions between dynamic variables and static data, not possible in the potential model. The transition map, along with individual models, enables me to identify places that are intrinsically suitable for arroyo toads, but are not optimal given current conditions.

Results

Model Evaluation and Summary

My models performed well based on all fit metrics (Table 2). All runs for the models were significant based on permutation tests ($p<0.001$), and AUC values were >0.950. For threshold dependent measures of fit, the cutoff values for binary predictions were 0.435 and 0.492 for potential and current models, respectively, resulting in and

TSS values of 0.809 and 1.000 (Table 2). Back-predictions to the presence/pseudoabsence and presence/absence data had 9.60% and 0.00% misclassification rates in the potential and current models, respectively. Maps illustrating the presence/absence predictions are presented in Figure 1.Distinct variables contributed the most to the potential and current models. In the potential model, PCs representing soil and topography were most influential, though in the current model the most important PCs represented aspects of climate, elevation, and wetness (Table 3). Given that machine learning techniques are optimized for predictive performance, and they can implicitly include complexities such as variable interactions, relationships among variables can be difficult to interpret (Cutler et al. 2007). Thus, I provide some interpretation of the model results (Table 3), but cannot present a statistical classification function.

Model Comparison and Potential Conservation Opportunities

With the aforementioned binary cutoff thresholds, my models predict potential habitat for arroyo toads habitat in 14.37%, and actual current habitat in only 10.50% of the 46,305 grid cells in my study area. Thus, I estimate a 26.93% net decrease in habitat on the landscape as a result of constraints associated with the dynamic variables. The transition map (Figure 2) yields more detailed insight into the potential changes in arroyo toad habitat. According to my models, 3,260 pixels are potential habitat, but not currently suitable. Conversely, 1,467 pixels are predicted as current habitat, but were not identified as habitat in the potential model. Cumulatively, 4,727 transitioned either direction and could potentially be used for conservation of the arroyo toad.

Table 2. Evaluation statistics for the potential and current distribution models of the arroyo toad.

Model	**Error Rate**	**AUC**	**True Skill Statistic**	**P-Value for Permutation Test**
Potential	9.60%	0.957	0.805	<0.001
Current	0.00%	1.000	1.000	<0.001

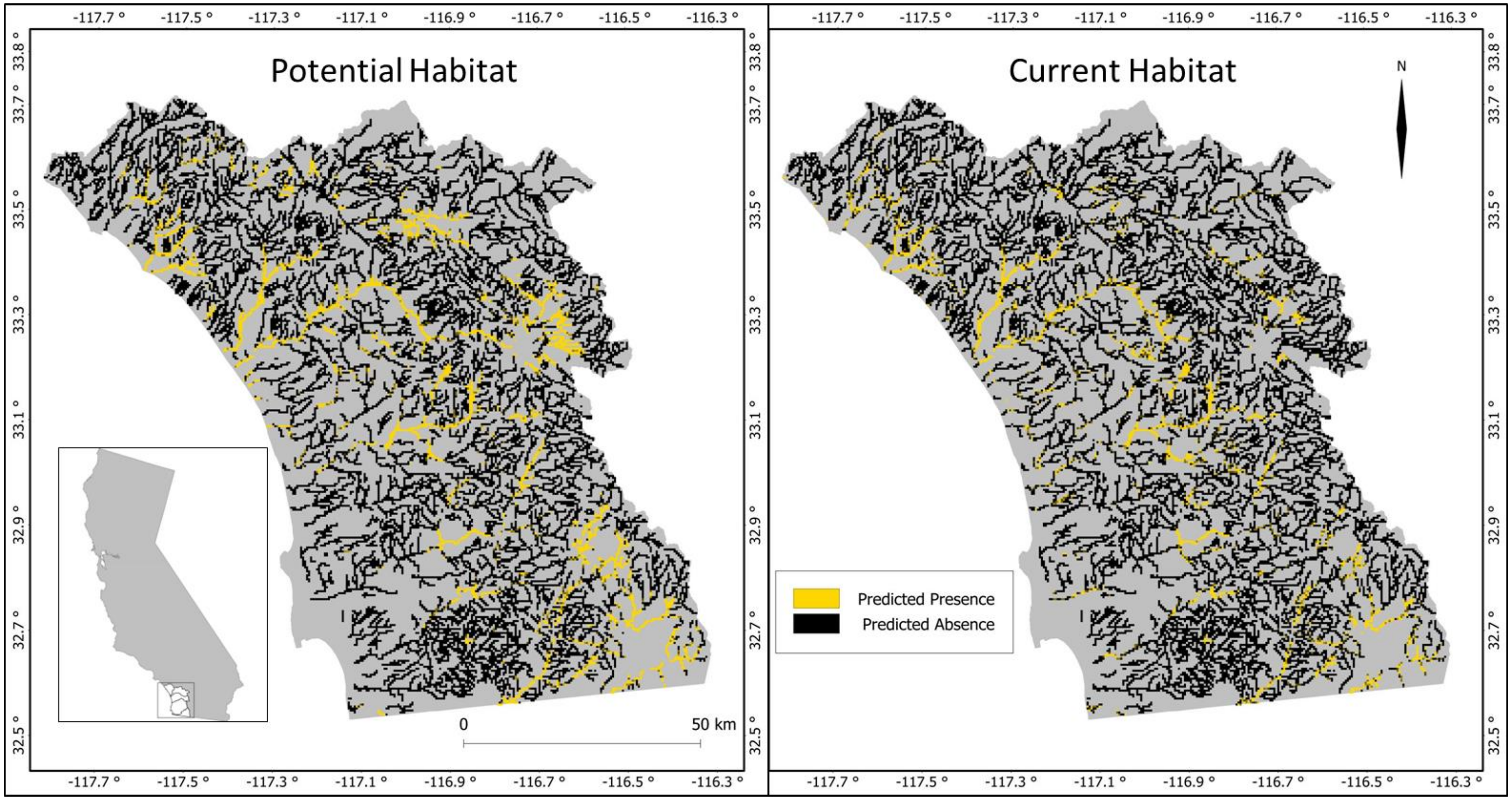

Figure 1. Predictions of potential and current habitat for the arroyo toad in the focal study area. The percentage of grid cells with predicted occurrence decreased by 26.93% from the potential to the historic model. The inset in the left panel shows the location of the study area, within the state of California.

Table 3. Importance of the PCA-transformed variables in the potential and current models of arroyo toad habitat. Principal components are listed with the highest loading environmental variables. Variables are listed in decreasing importance; relationships of variables with habitat predictions were discerned through inspection of model outputs.

Principal Component	Highest-Loading Environmental Variables (Positive and Negative)	Relationship w/ Habitat Predictions	Mean Decrease in Accuracy
Potential Model			
PC4	(+) MRVBF; WaterSt; Sand; CatchArea (-) VRM18; Slope; VRM03; Silt; Clay	+	0.107779
PC2	(+) TMx05; TMx09; TMx08; TMx06; TMx13 (-) TMn07; TMn08; Ppt06; TMn06; TMn09	+	0.07661
PC1	(+) Elev; Ppt09; Ppt08; Ppt07; Ppt13 (-) TMn04; TMn03; TMn05; TMn02; TMn10	-	0.0738
PC7	(+) Slope; Ppt06; Sand; TMn12; TMn01 (-) CatchArea; VRM03; WaterSt; VRM18; MRVBF	-	0.072659
PC3	(+) MRVBF; Ppt08; Ppt07; Sand; WaterSt (-) Ppt06; Ppt02; Ppt01; Ppt11; Ppt10	+	0.068875
PC6	(+) VRM03; Ppt06; TMx12; TMx01; TMx11 (-) TMn07; TMn08; TMx06; TMx07; TMn09	+	0.062834
PC5	(+) Silt; Clay; WaterSt; MRVBF; Ppt06 (-) Sand; VRM18; VRM03; Slope; CatchArea	-	0.057976

Table 3. Continued

Principle Component	Highest-Loading Environmental Variables (Positive and Negative)	Relationship w/ Habitat Predictions	Mean Decrease in Accuracy
Current Model			
PC1	(+) Elev; Ppt09; Ppt08; Ppt07; Ppt13 (-) TMn04; TMn03; TMn05; TMn02; TMn10	-	0.061128
PC2	(+) TMx05; TMx09; TMx06; TMx08; TMx13 (-) Wet09.Var; TMn07; TMn08; Ppt06; Wet03.Var	+	0.054001
PC7	(+) Silt; Clay; Grn03.Med; Wet03.Med; Grn09.Med (-) Sand; Ppt01; Brt09.Var; CatchArea; TMn07	-	0.045687
PC3	(+) Ppt06; TMx09; Ppt02; Ppt01; VRM18 (-) Brt09.Var; MRVBF; Brt03.Var; Ppt08; Ppt07	-	0.044683
PC10	(+) Grn03.Var; Wet09.Med; Grn09.Var; Brt09.Med; Slope (-) CatchArea; VRM03; WaterSt; VRM18; Brt09.Var	-	0.043204
PC4	(+) Wet09.Med; Wet03.Med; Brtr09.Med; Brt03.Med; Grn03.Med (-) Slope; VRM18; VRM03; Silt; Clay	+	0.030976
PC6	(+) Wet09.Var; Grn09.Var; Wet03.Var; Grn09.Med; Sand (-) Wet09.Var; Grn09.Var; Wet03.Var; Grn09.Med; Sand	+	0.028813
PC8	(+) Grn03.Var; VRM03; VRM18; Slope; Sand (-) MRVBF; TMn07; TMn08; Silt; TMx06	+	0.025513
PC9	(+) Brt09.Med; Brt03.Med; Wet09.Var; Ppt03; TMx11 (-) Brt03.Var; Grn09.Var; Grn03.Var; TMn07; TMn08	+	0.021633
PC5	(+) Brt03.Med; Brt09.Med; VRM18; Wet09.Var; Slope (-) Grn03.Var; Brt09.Var; Brt03.Var; MRVBF; WaterSt	-	0.010821

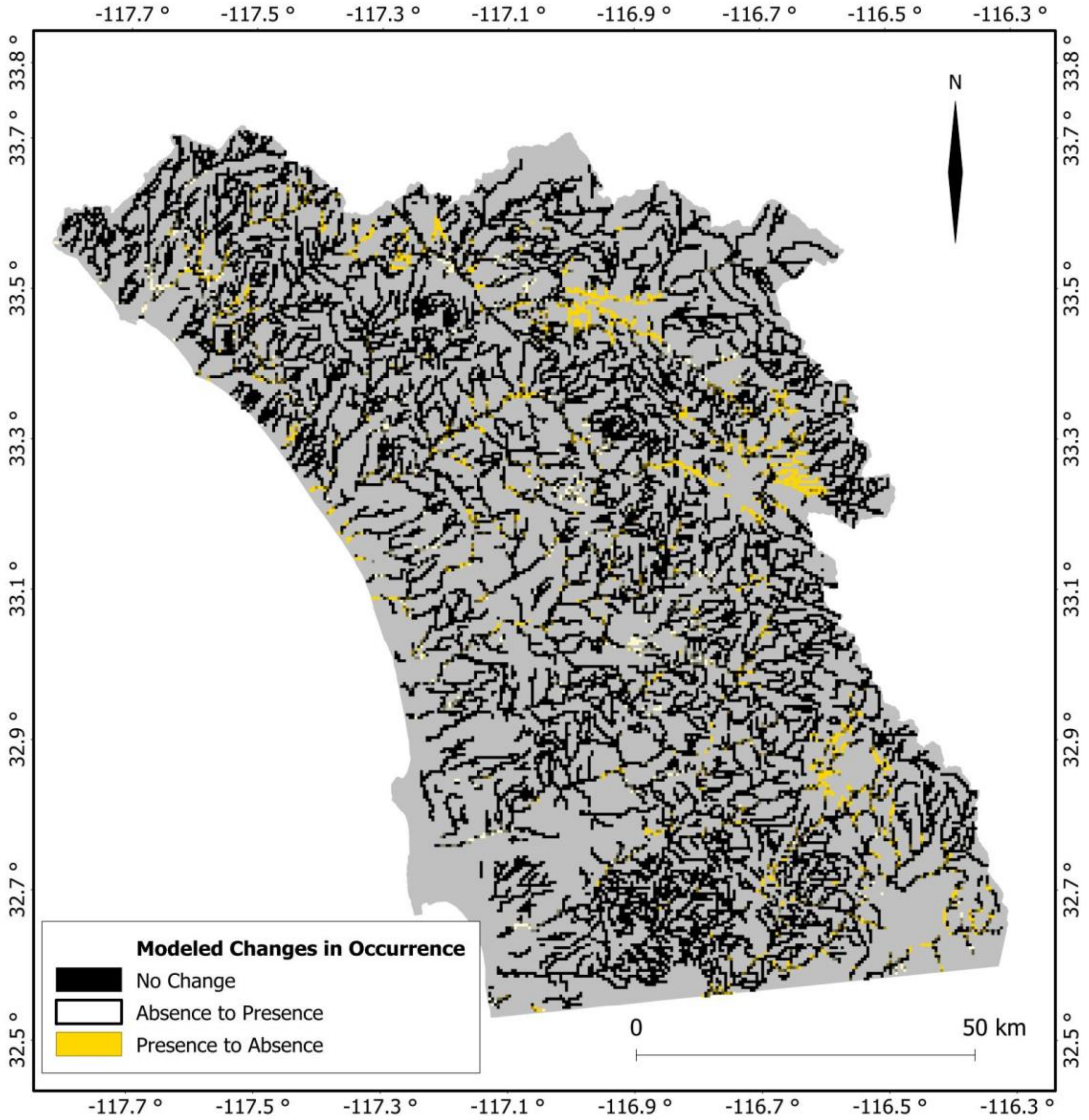

Figure 2. Map illustrating predicted transitions in occurrence based on the current and potential distributions models. Black, white, and yellow, correspond with calculated values of 0, -1, and 1, as described in the text.

Discussion

Together, these models of potential and current habitat for the arroyo toad identify sites that may be used for conservation of the species. My results suggest 10.50% of the pixels representing streams in the study area are currently suitable for arroyo toads, and an additional 7.04% have potential to become so based on static predictor variables. Subsequent steps necessary for conservation based on these results may involve site inspections and surveys to document unknown populations, habitat improvement actions such as removal of riparian vegetation and exotic predators, and translocation of the species to unoccupied sites. Naturally, the pace and extent of these efforts will depend on external factors such as funding, political will, and landowner cooperation. However, if all 3,620 pixels modeled as having potential habitat but not current habitat were transformed, current habitat in the study area could be increased dramatically, by 67.02%.

My general approach of modeling potential and current habitat to identify conservation opportunities can be broadly applied to virtually any taxa with sufficient locality information, in regions with relevant environmental datasets. I incorporated the concept of dynamic and static variables (Stanton et al. 2012) to develop my models, classifying variables as one or the other based on the focal time period and my objective of producing immediately applicable results. Future studies may incorporate additional variables in either category, or even reclassify data I used, if deemed appropriate. Specific modeling techniques employed in future studies can also be adjusted, though transition maps such as the one I developed will likely be useful for visualization of results and conveying information to stakeholders. Although I focused on an endangered species, my approach may also be applied to invasive species by helping identify identifying potential colonization sites.

In this study, general associations I identified between static variables and arroyo toad habitat (Table 3) are corroborated by results of Barto (1999), and other work summarized by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2009b). For example, those studies documented associations between arroyo toads and third and higher-order streams. I used several continuous geomorphological measures in place of stream order to more precisely represent conditions (Allan and Castillo 2007), but found comparable relationships, with habitat identified in areas with high MRVBF, low Slope, and low VRM. Similarly, my models and the earlier studies all document associations between arroyo toads and sandy soil types.

I found tasseled cap bands of wetness, greenness, and brightness from Landsat imagery served as effective dynamic variables, representing temporally-specific, continuous measures associated with land cover. Categorical land cover data may benefit interpretability of distribution models, though at the risk of decreased accuracy. For example, the most recent such dataset for the study area is the 2006 National Land Cover Dataset (NLCD; Fry et al. 2011), which has a documented accuracy of approximately 80% (Wickham et al. 2013); the 20% inaccuracy would contribute error in the current model. Additionally, broad land cover categories of classifications such as the NLCD cannot encompass fine-scale variability in land cover characteristics in the same detail as continuous variables (McGarigal and Cushman 2005, McGarigal et al. 2009). Visual inspection of the land cover data confirms this; complex features including sandy banks, and riparian vegetation, illustrated in Figure 3, are only depicted coarsely, if at all, in the NLCD.

Figure 3. Aerial image and photograph of a site with suitable habitat for the arroyo toad. The black star in the aerial image (left) indicates where the photograph was taken.

Of the 4,864 pixels identified as current habitat, only 791 have recent records of arroyo toads. Multiple factors may contribute to this. First, arroyo toads may be present in some of these sites where no surveys have been conducted to document them. Second, sites may currently be suitable, but historic conditions caused local extirpations. Lastly, some errors may exist, stemming in part from the fact that it is impossible to encompass all habitat variables relevant to the persistence of arroyo toads in such an analysis. For example, I could not incorporate variables reflective of fine-scale hydrology, which affect breeding success. Thus, existing information on natural history of the arroyo toad and fine-scale habitat use and occurrence patterns (e.g., Griffin and Case 2001, Sweet and Sullivan 2005, Mitrovich et al. 2011, Miller et al. 2012) should be coupled with my model results to guide specific actions at individual sites.

Though this study focuses on identifying site-specific opportunities for arroyo toad conservation, long-term strategies should also take large-scale processes that affect these habitats into account. Freshwater ecosystems are sensitive to environmental conditions across entire watersheds (King et al. 2005a, King et al. 2011), and in an area slightly north of mine, Riley et al (2005) showed negative relationships between watershed-scale urbanization and abundance of native amphibians. Complexities of multiple factors influencing habitat from multiple scales can create new challenges for conservation (Brown et al. 2013). However, integration of results from studies such as this with information on species' ecologies and causes of decline should yield the most effective strategies to protect and restore species across landscapes.

CHAPTER III

MULTI-SCALE EFFECTS OF LAND COVER CONDITIONS ON AN ENDANGERED TOAD

Synopsis

Habitat loss and degradation are widely recognized drivers of biodiversity loss, often stemming from anthropogenic land cover change. Effects of land cover change on individual species can be direct, in which fine scale habitat is converted to alternative land cover types, or indirect, in which land cover outside of current habitat areas is altered, influencing physical or biological processes that help maintain habitat and populations. Aquatic ecosystems are prime examples of how spatially disparate land cover conditions influence habitats and many studies have shown that urbanization within watersheds alters freshwater and coastal conditions. Areas immediately surrounding aquatic systems can also have strong influences on contained communities because they serve as terrestrial habitat for amphibious organisms, and associated vegetation can moderate effects of watershed-scale conditions. Despite our knowledge of how factors different scales influence aquatic systems, studies rarely consider the relative influences of conditions across scales on aquatic habitats. I focused this study on the endangered arroyo toad (*Anaxyrus californicus*), which is endemic to southern California, USA and Baja California, Mexico. The arroyo toad relies on open, sandy streams for breeding and adjacent terrestrial habitats for post-metamorphosis life stages. I used structural equation modeling to estimate the direct and indirect effects of land

cover characteristics within entire watersheds and along stream networks on habitat suitability for the species. My results showed relationships between land cover and habitat suitability for arroyo toads differed across scales, and that land cover along stream networks is influenced by watershed-scale conditions. I observed that anthropogenic development at the watershed-scale negatively impacts habitat suitability for arroyo toads, but development along stream networks was positively associated with habitat suitability. This positive association between development along streams and arroyo toad habitat may be attributable to higher levels of spatial heterogeneity along urbanized streams, or other aspects of development. These results can inform future conservation of arroyo toad habitat, although it will be critical to incorporate known ecological requirements of the species. My general methodology can also be employed more broadly to explore the relative effects of land cover change at different scales on various focal species.

Introduction

Understanding and mitigating anthropogenic impacts on species and ecosystems is a perpetual challenge for conservation (Millenium Ecosystem Assessment 2005, Lal 2010). Habitat loss and degradation are among the main threats to various taxa (e.g., Millenium Ecosystem Assessment 2005, Schipper et al. 2008, Sodhi et al. 2008, Böhm et al. 2013),and while conservation actions are frequently implemented at fine scales to provide immediate benefit to species, broad scale factors can ultimately drive declines. For example, though roads can directly contribute to habitat loss and fragmentation, their presence has been shown to influence physical structure of sand dunes, affecting associated lizard communities (Vega et al. 2000, Leavitt and Fitzgerald 2013). Similarly, aquatic habitats can be influenced by land cover conditions of the surrounding area through changes to water flow and sediment transport (Allan 2004). Thus, effective conservation measures should integrate an understanding of how factors at multiple scales influence species and ecosystems (Poiani et al. 2000).

The scale of watersheds has been identified as appropriate for managing freshwater and coastal ecosystems because the boundaries are physically defined by topography and they are inherently tied to processes such as of hydrologic flow and sediment transport (Beechie et al. 2010). In support of this, the amount of urbanization in watersheds has been shown to predict taxonomic richness, species abundance, and water quality of freshwater and marine systems (King et al. 2005b, Riley et al. 2005, King et al. 2011, Klein et al. 2012). Such findings have been used to guide restoration of aquatic ecosystems and to develop strategies for improvement of water quality (Leach and Pelkey 2001, Pires 2004).

Smaller scales of management are also important for conservation of aquatic ecosystems. Land cover immediately surrounding aquatic habitats has been shown to influence water quality, and vegetative buffers are often used along streams and ponds are to counter negative effects of large scale development (Peterjohn and Correll 1984, Clinton 2011). Furthermore, terrestrial areas adjacent to freshwater systems are important for amphibians, turtles, and other taxa that rely on aquatic and terrestrial habitats during various life stages (Gibbons 2003), and they contribute considerable nutrient resources (Polis et al. 1997, Lowe et al. 2006).

Some studies have examined the relative influences of conditions at multiple scales on specific taxa and larger communities, albeit to a limited extent. For example, Lowe and Bolger (2002) analyzed effects of landscape-scale timber harvest history and local stream conditions on *Gyrinophilus porphyriticus*, but they focused only on small stream sections in two watersheds. Ficetola et al. (2011) analyzed effects of land cover characteristics within 400m and 100m of specific sampling points, and local water conditions on *Salamandra salamandra* and the larger amphibian communities, but the authors did not examine possible effects of watershed-scale conditions. Canessa and Parris (2013) alluded to potential effects of watershed-scale conditions on their focal amphibian communities, but primarily documented effects of land cover within a 500m radius of sampling points. In contrast to the aforementioned studies, Barrett et al. (2010) documented linkages between watershed-scale conditions, stream conditions, and ultimately, abundance of *Eurycea cirrigera* in the southeastern United States.

In this study I examined how land cover characteristics at multiple scales influences habitat suitability for the arroyo toad (*Anaxyrus californicus*), which is listed as endangered by the IUCN and the U.S. Endangered Species Act, and is endemic to southern California, USA and northern Baja California, Mexico (U.S. Fish and Wildlife Service 1994, Hammerson and Santos-Barrera 2004). The species relies on open, sandy, stream habitats for breeding and larval development, and surrounding terrestrial environments for post-metamorphosis life stages (Sweet and Sullivan 2005). Declines of the species have been attributed to habitat loss, and habitat degradation associated with altered hydrology and invasive species (U.S. Fish and Wildlife Service 1999, Sweet and

Sullivan 2005). Given the arroyo toads' requirements for aquatic and adjacent terrestrial habitats, its' conservation status, and known linkages between watershed-scale land cover and riparian conditions (Allan 2004), I identified it as model organism for which to examine relative influences of conditions across multiple scales on habitat. I based this work on a conceptual model of how land cover at multiple scales may influence habitat, informed by previous literature (Figure 4, derived from Ficetola et al. (2011)).

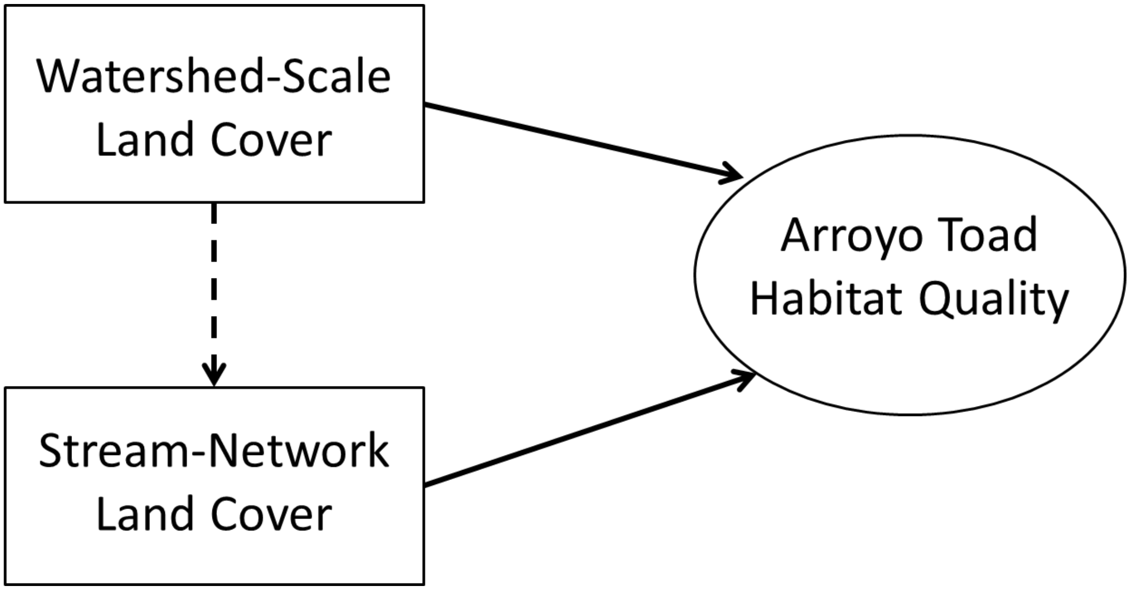

Figure 4. Conceptual model of linkages between land cover at the scale of entire watersheds, land cover along stream networks, and habitat quality for arroyo toads. Solid arrows represent potential direct effects of land cover variables on arroyo toad habitat suitability; the dashed-arrow represents potential effects of watershed conditions on land cover conditions within stream networks, yielding an indirect effect of watershed-scale conditions on habitat suitability.

Methods

Study Area and Units of Analysis

I focused this study in southern California, in an area for which I developed distribution model for the arroyo toad (Chapter II). I used watershed basins delineated at the HUC-12 scale in the National Hydrologic Dataset as units of analysis (Natural Resources Conservation Service 2010). HUC-12 basins typically range 10,000-40,000 acres, and have been identified as suitable management units because they are small enough that residents may have common ties to their communities, land, and water resources (Morton and Brown 2011), and the scale is relevant to conditions of contained aquatic systems (e.g., Strager et al. 2009, Tomer et al. 2013). I examined all HUC-12 units for which I developed a distribution model in Chapter II (n=110).

Data Sources and Preparation

My dependent variable was the average probability of presence modeled for arroyo toads within each HUC-12 watershed (hereafter, Habitat Suitability; example shown in Figure 5-A). The original distribution model was developed using presence/absence data for arroyo toads collected during 2005-2013, for streams and stream-side habitats represented by 200m pixels (Chapter II). Predictor variables included long-term climate characteristics, topography, geomorphology, soil, and remotely sensed data derived from 2010 Landsat imagery. The remotely sensed variables were used as continuous measures associated with dynamic habitat features and did not include discrete land cover classifications.

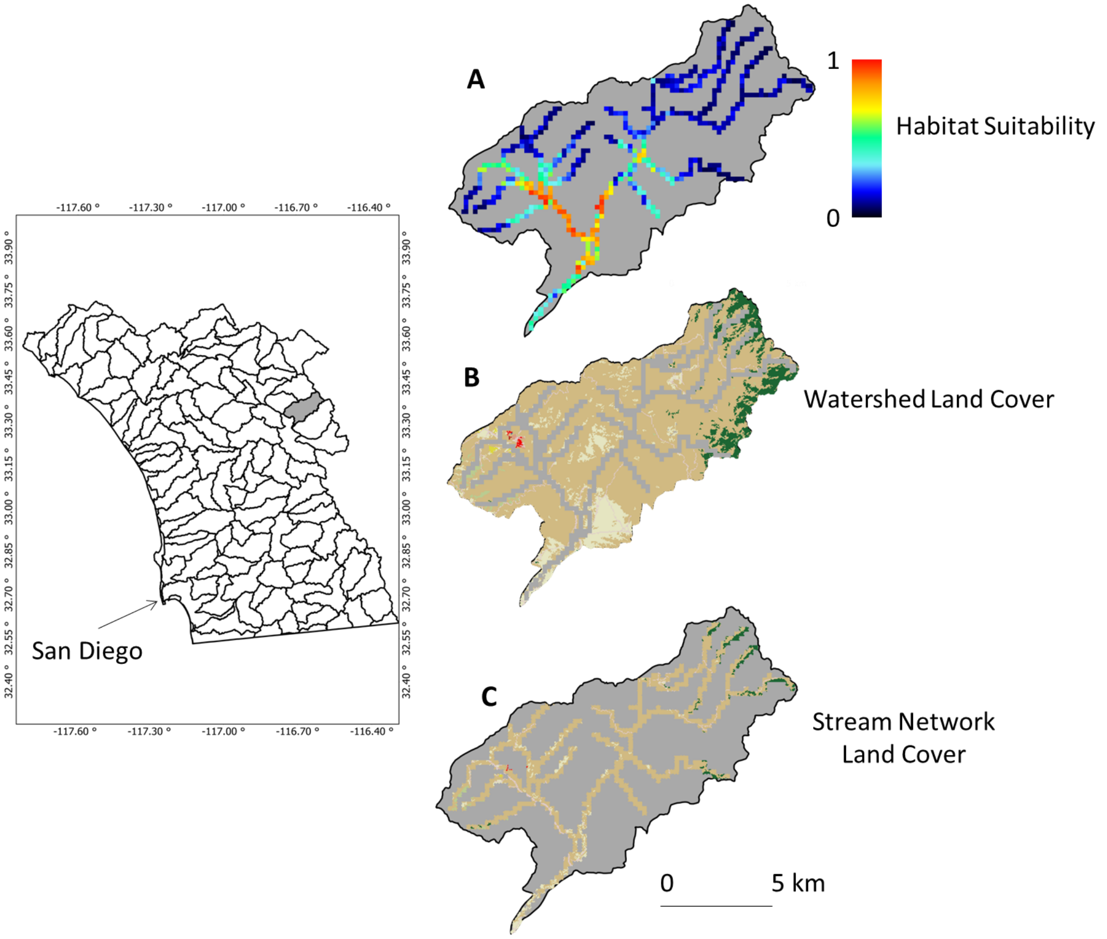

Figure 5. Maps illustrating examples of original data used to calculate the variables for structural equation models. These included Habitat Suitability (A), Land Cover for the Watershed scale (B), and Land Cover for the Stream Network scale (C). These datasets are highlighted for a single watershed in the study area, shaded gray in the inset, which also displays the entire study area. Unique colors in the land cover maps represent individual land cover classes explained in detail in the 2006 National Land Cover Dataset (Fry et al. 2011).

I derived independent variables from the 2006 National Land Cover Database (NLCD), which was classified from Landsat imagery with a pixel size of 30 x 30m (Fry et al. 2011). I used data on the percent of impervious cover per pixel, and Level I land cover classes comprised of: Open Water; Developed; Barren/Bare Ground; Forest; Shrubland; Herbaceous; Planted/Cultivated; and Wetlands. Wickham et al. (2013) reported this classification to be 87% accurate for the western United States, thus, to my knowledge it was the most accurate, high resolution land cover dataset available for the study area at the time of analysis.

For independent variables representing the scale of entire watersheds, I calculated the mean, median and variance of impervious cover, and the percentage of each land cover class per basin (e.g., Figure 5-B). I also calculated total contagion per watershed as a measure of land cover pattern and overall land cover class aggregation (Li and Reynolds 1993). To derive independent variables representing characteristics of the stream network in each watershed, I calculated the same metrics as for watersheds, but only for areas contained by the 200m pixels for which arroyo toad habitat was modeled (e.g., Figure 5-C). In calculating watershed-scale variables, I masked out stream network areas, ensuring that one would not be a subset of the other. I calculated impervious cover measures using SAGA GIS version 2.1.1 (Böhner 2013), and the percentages of each land cover type and contagion using Fragstats version 4.2 (McGarigal et al. 2012).

I used principal component analyses (PCAs) to reduce the dimensionality of the independent variable set, separately for the two focal scales. I conducted PCAs on the correlation matrices of the land cover variables using the ‘vegan’ package (Oksanen et al. 2012) in R version 3.0.2 (R Core Team 2013), and retained principle components (PCs) with eigenvalues greater than one in place of the original variables following the Kaiser-Guttman criterion (Legendre and Legendre 2012). I retained three PCs for each scale, which had similar variable loadings across scales (Appendix B). There were discernable gradients of land cover types along these PC axes, hereafter termed “Development” (PC1, representing urban and suburban areas vs. shrubland), “Forest” (PC2, representing forest vs. open habitat types), and “Agriculture” (PC3, representing agriculture vs. open water). I maintained contagion as separate variables at each scale because it is a measure of pattern and configuration of different land cover types. Hereafter, I denote the corresponding scale before variable names as Watershed or Stream (e.g., Watershed Development or Stream Development).

Structural Equation Modeling

To estimate the relative influence of land cover characteristics at the two focal scales on arroyo toad habitat I used structural equation modeling. This method allows for the simultaneous estimation of direct and indirect effects of predictor variables on dependent variables, while relying on theory and empirical knowledge of systems to guide model development (Grace 2006). Thus I tested models based on my conceptual framework (Figure 4). For the watershed-scale, I predicted paths from measures of more deterministic anthropogenic land cover types to more natural ones (Development and Agriculture on Forest, and Development on Agriculture). I predicted linkages between all watershed-scale variables on the corresponding stream network-scale variables, as characteristics of the smaller scale may be driven by patterns of the larger scale. I also predicted effects of Watershed Development and Watershed Agriculture on all stream-scale variables, as anthropogenic land covers have been shown to influence conditions along streams in this region (White and Greer 2006, Hawley and Bledsoe 2013).

Contagion of land cover types can influence suitability of sites for species (Roseberry and Sudkamp 1998), and while it describes spatial patterns, it has been shown to be influenced by anthropogenic land covers in various ways (Li et al. 2005, Wu et al. 2011). Thus, I explored models in which contagion could have only direct effects on habitat suitability (Contagion Direct Model, Figure 6), and in which it was could mediate effects of the land cover types (Contagion Mediated Model, Figure 6). I evaluated baseline fit of these two models using a Bollen-Stine chi-squared test (Bollen and Stine 1992), the comparative fit index (CFI), the non-normed fit index (NNFI), and the standardized root mean square error (SRMR; Hooper et al. 2008, Kline 2011). I also compared models using Akaike’s Information Criterion (AIC) and Bayes’ Information Criterion (BIC) to identify the best- model while considering parsimony, in which lower values indicate better fit (Raftery 1995, Burnham and Anderson 2002).

I considered three main hypotheses represented through paths in these models: 1) Habitat Suitability for arroyo toads within watersheds is directly affected by land cover characteristics in entire watersheds; 2) Habitat Suitability is directly affected by land cover within stream networks; and 3) Habitat Suitability is affected by watershed-scale land cover indirectly, through effects on land cover of contained associated stream networks. I set α = 0.05 for bootstrapped z-tests to test significance of individual paths, mediating effects (i.e., indirect linkages between variables), and net effects.

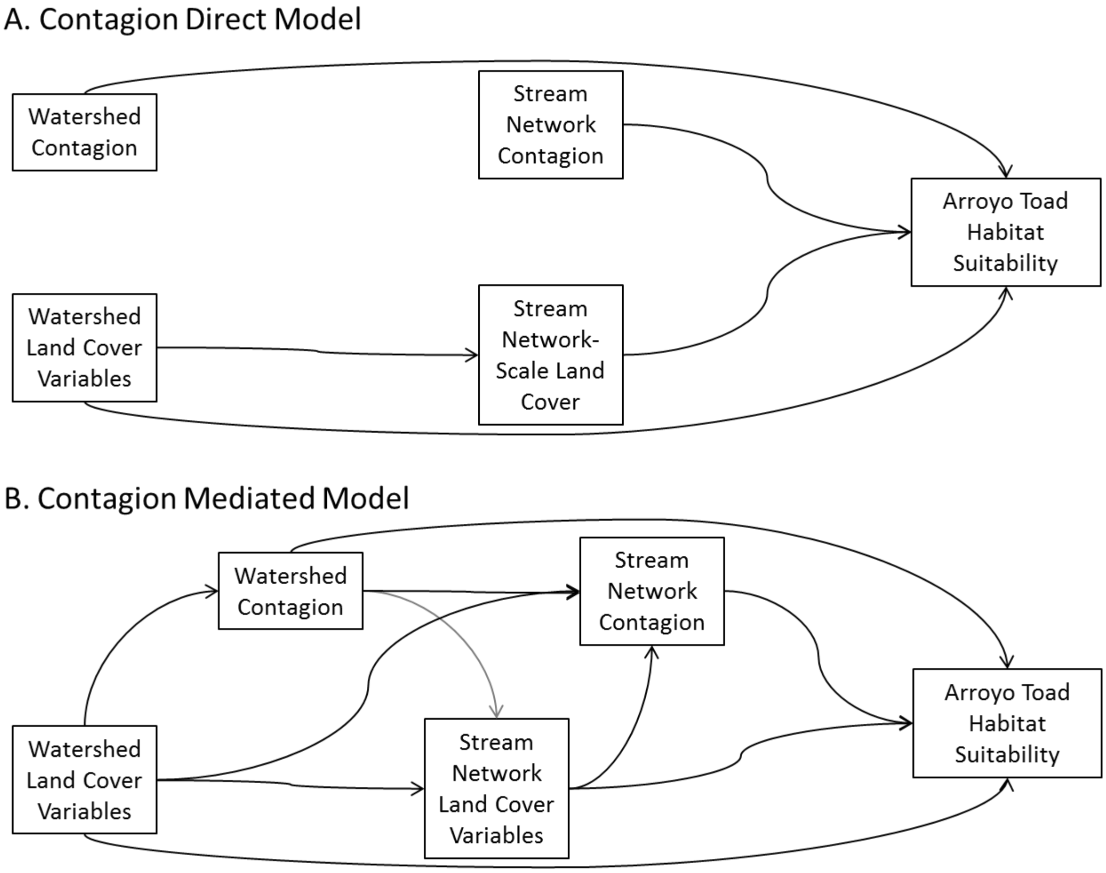

Figure 6. Schematics of the structural equation models used to explore effects of land cover characteristics on arroyo toad habitat suitability within watersheds. All individual linkages in the Contagion Mediated Model are presented in Table 5; the Contagion Direct Model was a poor fit to the data, thus I do not present specific results for the contained paths.

I $\log_{10}$-transformed the Development variables at both scales to minimize effects of right-skew in the data. I estimated parameters using a bootstrapped maximum likelihood estimator using with 1,000 draws from the PCA-transformed dataset to account for small sample size and lack of multivariate normality (Cheung and Lau 2008). I conducted these analyses using the 'lavaan' package (Rosseel 2012) in R version 3.0.2 (R Core Team 2013), and using Stata version 13.1 (StataCorp 2013).

Results

The Contagion Mediated Model was superior to the Contagion Direct Model based on all fit measures (Table 4). The model with contagion having only direct effects on arroyo toad habitat suitability did not adequately fit the data at all (Bollen-Stine χ^2= 120.488, *df*=11, p<0.001), thus, I only present results for the Contagion Mediated Model (Bollen-Stine χ^2= 2.434, *df*=1, p=0.248), for which I highlight the significant direct paths (Figure 7). The R^2 for suitability of arroyo toad habitat in this model was 0.344.

Table 4. Baseline and comparative fit measures for structural equation models. Baseline fit measures are: Bollen-Stine χ^2 statistics; Comparative Fit Index (CFI); and Standardized Root Mean Square Error (SRMR). I present Akaike's Information Criterion (AIC) and Bayes' Information Criterion (BIC) as comparative measures of model fit. Models are presented in order of best fit.

	AIC	**BIC**	**CFI**	**NNFI**	**SRMR**	χ^2	***df***	**p-value**
Contagion Mediated Model	238.388	376.113	0.998	0.932	0.01	2.434	1	0.248
Contagion Direct Model	322.443	414.259	0.825	0.475	0.182	120.488	11	<0.001

Direct Effects on Arroyo Toad Habitat

The only variables with significant, direct effects on Habitat Suitability were Watershed Development and Stream Development. Watershed Development had a negative effect on Habitat Suitability within the watersheds ($z=-2.297$, $p=0.022$, $\beta=-0.704$), but Stream Development had a positive effect ($z=2.165$, $p=0.030$, $\beta=0.682$; Table 5 and Figure 7).

Indirect Paths and Net Effects on Arroyo Toad Habitat Suitability

I identified two significant indirect effects of watershed-scale characteristics on Habitat Suitability. Watershed Contagion had a negative effect on Habitat Suitability ($z=-3.84$, $p<0.001$, $\beta=-0.002$) and Watershed Development had a positive effect ($z=2.16$, $p<0.031$, $\beta=0.099$). Given the negative direct effect of Watershed Development and the positive direct effect, the net effect was not significant ($z=-0.230$, $p<0.816$, $\beta=-0.004$).

At the stream-network scale I found that Stream Development had a positive effect ($z=2.730$, $p<0.006$, $\beta=0.033$) and Stream Forest had a negative effect ($z=-2.62$, $p<0.009$, $\beta=-0.129$). Stream Development was the only variable at this scale with a significant net effect on Habitat Suitability ($z=2.33$, $p<0.020$, $\beta=0.147$).

Table 5. Bootstrapped maximum likelihood estimates of direct effects in the Contagion Mediated Model. Significant paths ($p<0.05$) are highlighted in bold.

Dependent Variable	Direct Effect	Standardized Path Coefficient	Standard Error	z-value	p-value
Watershed Contagion	Watershed Urban	0.168	0.089	1.855	0.064
R^2=0.428	**Watershed Agriculture**	**0.362**	**0.067**	**5.104**	**<0.001**
	Watershed Forest	**0.573**	**0.099**	**5.874**	**<0.001**
Watershed Agriculture	Watershed Urban	-0.115	0.074	-1.539	0.124
R^2=0.013					
Watershed Forest	**Watershed Urban**	**-0.239**	**0.112**	**-2.097**	**0.036**
R^2=0.056	Watershed Agriculture	-0.028	0.103	-0.258	0.796
Stream Urban	**Watershed Urban**	**0.899**	**0.054**	**16.376**	**<0.0001**
R^2=0.848	**Watershed Contagion**	**0.120**	**0.056**	**2.307**	**0.021**
	Watershed Forest	-0.057	0.066	-0.862	0.389
	Watershed Agriculture	-0.040	0.036	-1.083	0.279
Stream Forest	**Watershed Forest**	**0.682**	**0.097**	**6.921**	**<0.001**
R^2=0.738	**Watershed Contagion**	**0.217**	**0.083**	**2.69**	**0.007**
	Watershed Urban	**0.498**	**0.213**	**2.33**	**0.02**
	Stream Urban	**-0.604**	**0.216**	**-2.83**	**0.005**
	Watershed Agriculture	0.089	0.110	0.777	0.437
	Stream Agriculture	0.051	0.100	-0.492	0.623
Stream Agriculture	Watershed Contagion	0.007	0.057	-0.129	0.898
R^2=0.730	**Watershed Agriculture**	**-0.851**	**0.096**	**8.583**	**<0.001**
	Watershed Urban	0.213	0.137	-1.548	0.122
	Stream Urban	**-0.34**	**0.141**	**2.482**	**0.013**

Table 5. Continued

Dependent Variable	Direct Effect	Standardized Path Coefficient	Standard Error	z-value	p-value
Stream Contagion R^2=0.793	**Watershed Contagion**	**0.724**	**0.058**	12.387	**<0.001**
	Stream Urban	-0.29	0.170	-1.830	0.067
	Stream Forest	**0.384**	**0.140**	**2.661**	**0.008**
	Stream Agriculture	0.004	0.137	-0.025	0.980
	Watershed Urban	**0.400**	**0.170**	**2.489**	**0.013**
	Watershed Agriculture	0.038	0.169	0.216	0.829
	Watershed Forest	-0.17	0.135	-1.189	0.235
Habitat Suitability for Arroyo Toads R^2=0.344	**Stream Urban**	**0.682**	**0.339**	**2.165**	**0.030**
	Stream Forest	0.033	0.223	0.142	0.887
	Stream Contagion	-0.389	0.206	-1.890	0.059
	Stream Agriculture	-0.038	0.135	0.274	0.784
	Watershed Urban	**-0.704**	**0.332**	**-2.297**	**0.022**
	Watershed Contagion	0.162	0.197	0.827	0.408
	Watershed Agriculture	-0.103	0.156	-0.678	0.498
	Watershed Forest	-0.342	0.231	-1.447	0.148

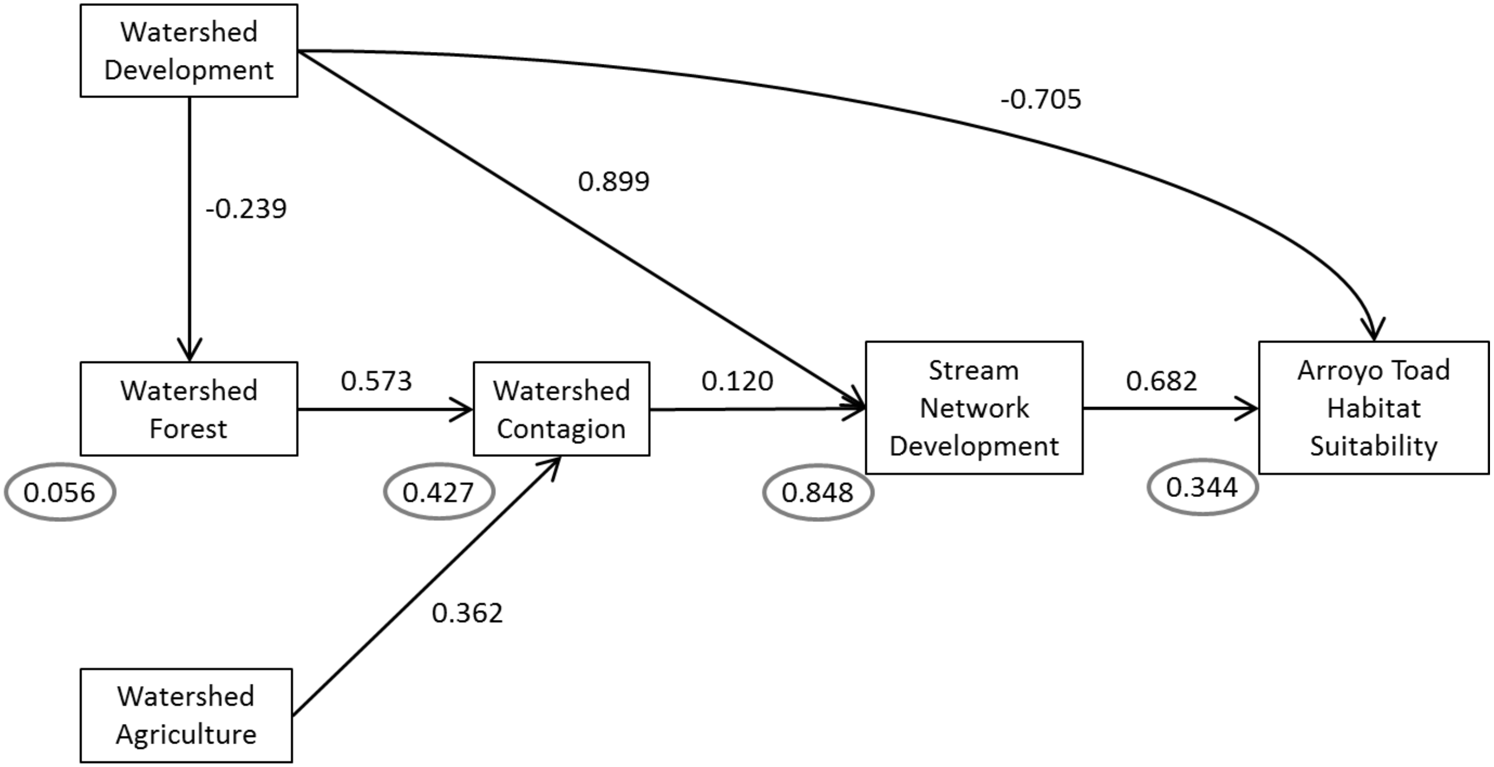

Figure 7. Schematic of the final structural equation model, illustrating the direct paths identified as significant in the Contagion Mediated Model. Standardized coefficients are presented along the corresponding paths and variable R^2 is presented in gray circles, to the lower-left of the respective variables.

Discussion

My results show that land cover characteristics of entire watersheds and along stream networks separately influence suitability of riparian areas for arroyo toads. To my knowledge, this is the most comprehensive study of its type, encompassing 110 HUC-12 watersheds, and it is one of few to estimate relative effects of factors at multiple spatial scales. The final model explains 34.44% of the variance in habitat suitability for arroyo toads across focal watersheds. This is substantial, particularly given that habitat is also known to be influenced at fine scales by static variables such as soil type and topography (Chapter II; Barto 1999, Sweet and Sullivan 2005).

I found Development had the largest effects on arroyo toad habitat suitability, and its effects differed across scales. Though Watershed Development had a negative direct effect, Stream Development had a positive effect. Arroyo toads are unlikely to experience conditions outside of what I analyzed as the stream network scale because the species is closely tied to riparian areas (Griffin and Case 2001, Mitrovich et al. 2011). However, the direct effects of Watershed Development may indicate presence of other mediating factors that I was not able to include, such as fine-scale hydrology. I anticipated that potential perennialization of streams in watersheds with higher levels of development cause increased Stream Forest (White and Greer 2006), but this path was not significant. The large swath of the stream network-scale for these analyses (200m pixels) may have been too large to allow me to detect such an effect if there was one. Furthermore, vegetation change does not occur instantaneously, and multi-temporal data may better elucidate such an effect if it is important.

The result of a positive relationship between Stream Development and habitat suitability for arroyo toads was contrary to what I expected, and I interpret this result cautiously. Arroyo toads are generally not associated with urban habitats, and urbanization has been cited as a cause of the species' decline (U.S. Fish and Wildlife Service 1999, Sweet and Sullivan 2005). A potential source of confusion is that the NLCD Level I category of Development, which loaded high on the "Development" principle components, includes finer categories of "Developed Open Space" and "Developed Low Intensity" that both contain <50% impervious surfaces. However, analysis of the original variables shows high correlation (r>0.90) between the percent of impervious cover and the percent of developed land cover at both scales, thus any confusion of this sort should have had minimal effects on the results.

Another potential driver of this result is a non-significant (p=0.059), albeit strong positive influence of Stream Development on Habitat Suitability through negative impacts on Stream Contagion (Table 5). Aspects of urbanization patterns at this scale may help disaggregate land cover types, yielding spatially heterogeneous conditions. Appropriately timed fire, flood, and drought events can help maintain habitat for arroyo toads by clearing vegetation, redistributing sediment, and removing predators (Madden-Smith et al. 2003, Mendelsohn et al. 2005, Miller et al. 2012). Thus urbanization and patch heterogeneity around riparian zones may effectively maintain some beneficial level of environmental disturbance. Other benefits of development may be associated with increased sediment load or decreased riparian vegetation. However, these relationships should be further investigated, and at this point fine-scale management is best guided by knowledge of the species' ecology and natural history.

My results indicate that watershed-scale land cover has little influence on arroyo toad habitat when accounting for land cover along stream networks. This is surprising, given that many studies have found negative influences of broad-scale urbanization on freshwater ecosystems (e.g., Riley et al. 2005, Barrett et al. 2010, Canessa and Parris 2013). While the mediating scale I used this study, stream networks, was represented by 200m pixels, studies that found negative impacts of large-scale development focused on finer-scale stream characteristics such as hydrologic flow metrics and water chemistry. Some fine-scale data are available for stream conditions in my study area (USGS San Diego Field Station, unpub. data), but the sampling has been spatially clustered in relatively few of my focal watersheds, and would not yield large enough sample sizes in the analyses I present here. Future sampling efforts may help distribute sampling of stream characteristics, allowing for further analyses. I did observe negative indirect effects of Stream Network Forest on arroyo toad habitat, and given that White and Greer (2006) documented increased riparian vegetation with increasing watershed urbanization, in Los Peñasquitos Creek of my study area, further investigation into these dynamics is warranted. Results of such studies may yield more insight into appropriate scales for managing stream habitats in southern California.

Future research may integrate my results with projections of future land cover to identify where habitat is most likely to be lost given direct and indirect effects of land cover change. Such work can inform anticipatory, proactive conservation efforts.

Additionally, though I used statistical inference to elucidate how land cover at multiple scales influences arroyo toad habitat, complementary strategies can further improve our understanding of the system. For example, agent based models that incorporate hydrologic flows and arroyo toad life history traits can be informative, and could be developed with various alternative landscape scenarios to identify ways to continue development with minimal impact on species of conservation concern.

Though conservation issues such as those facing the arroyo toad are undoubtedly complex, studies that elucidate underlying processes driving species' declines, may best inform on-the-ground, long-term actions. Structural equation modeling has been implemented in studies similar to ours (e.g., Barrett et al. 2010, Ficetola et al. 2011, Canessa and Parris 2013), and has proved effective for identifying drivers within models ecological change in aquatic ecosystems. I suggest that its use should be further expanded for studies of biodiversity conservation. With empirical knowledge of underlying processes affecting species and ecosystems at multiple scales, it may yield necessary information to guide the most practical and effective long-term solutions.

CHAPTER IV

FORECASTING IMPACTS OF URBANIZATION ON HABITAT FOR AN ENDANGERED TOAD USING STRUCTURAL EQUATION MODELING

Synopsis

Anthropogenic alterations to land cover can have direct and indirect impacts on biodiversity. Direct impacts are generally associated with immediate alterations of local conditions that affect organisms, while indirect impacts stem from broader influences on biological or physical processes that maintain populations and habitats. Structural equation models (SEMs) have been used in ecology to estimate the direct and indirect effects of ecosystem components on one another, and some studies have used it to identify paths through which anthropogenic disturbances influence ecological responses. SEMs are fundamentally similar to agent based dynamic systems models (ABMs) in that multiple variables can be simultaneously modeled to yield insight into the strength and significance direct and indirect pathways. Models developed in both techniques are based on empirical knowledge or theory about the focal system, though ABMs rely on bottom-up knowledge of how individual system components interact for parameterization while SEMs estimates parameters using statistical inference. While ABMs are often used to examine how systems will respond to alterations of individual components, SEMs are rarely used in such contexts despite their applicability for such work. I developed an SEM to estimate how land cover conditions of entire watersheds and along stream networks influence habitat for the endangered arroyo toad (*Anaxyrus* *californicus*), which is associated with streams and nearby terrestrial habitats. I then used urbanization projections to develop potential scenarios of future development in my study area, and used the SEM to forecast how habitat suitability for arroyo toads in my study region may change under those scenarios. For my focal area as a whole, projected urbanization is only predicted to have small, non-significant effects on habitat for arroyo toads. However, for individual watersheds the effects of future development can be severe, and maintaining more natural land covers can have clear benefits for arroyo toad habitat. This is the first ecological study to my knowledge to use structural equation modeling for forecasting effects of anthropogenic development ecosystems, and I suggest it can be more widely employed. Future work may focus on validation of forecasts, and integrating nonlinear dynamics into SEMs to more fully represent complex dynamics in forecasting changes to ecological systems.

Introduction

Habitat loss and degradation are primary drivers of biodiversity loss in terrestrial and freshwater ecosystems (Millenium Ecosystem Assessment 2005, Schipper et al. 2008, Sodhi et al. 2008, Böhm et al. 2013) and are largely caused by anthropogenic land cover changes (Kerley and Whitford 2000, McKinney 2002). Urban land cover represents only a small portion of Earth’s surface (Schneider et al. 2009), but it has wide-reaching effects on ecosystems (McKinney 2002). Directly, it replaces natural habitat at individual sites, though there are also indirect effects. For example, roads can serve as barriers to dispersal, decreasing connectivity of animal populations (Holderegger and Di Giulio 2010), and they can alter dynamic processes such as those that maintain dune habitats, ultimately influencing biotic communities (Vega et al. 2000, Leavitt and Fitzgerald 2013). Similarly, at the scale of entire watersheds, urbanization has been linked to degradation of associated stream ecosystems by altering the hydrology, sediment load, and pollution-load (Walsh et al. 2005, Coffin 2007).

The combination of direct and indirect effects of anthropogenic development on ecosystems poses considerable challenges in conservation biology. Not only must we use limited funds to prevent direct conversion of habitat to alternative states, but for long-term success, we must conserve large-scale processes that maintain habitats. The former can be done by using spatial overlays between current or projected future habitat for species and projections of land cover change (e.g., Theobald 2003). However, to deal with the latter we need to understand the processes through which habitat conditions can be affected by local and large-scale factors (Brown et al. 2013). Critically, such work can help identify when conservation actions at one scale may have unintended consequences elements of another scale.

In ecological studies, agent-based system dynamic models (ABMs) are frequently employed to better understand direct and indirect effects of variables on one another (Grimm 1999, Grimm et al. 2005). ABMs are developed from a conceptual understanding of relationships between individual variables or elements in a system, then parameterized with empirical measurements or estimates of these relationships, and iteratively improved to match reference conditions based on real data. Effects of changes to individual components in the system on other components can be examined through simulations with desired time-steps. Applications of ABMs in ecology and conservation have included modeling how animals perceive, learn, and adapt to environments (DeAngelis and Mooij 2005), and understanding of how environmental and social processes affect land use change (Matthews et al. 2007). Though they are invaluable in developing an understanding of complex systems making inference to effects of alternative conditions, they require a considerable bottom-up understanding of relationships between individual components of the system to estimate parameters that adequately reflect reality (Grimm 1999).

As with ABMs, structural equation models (SEMs) are powerful for understanding dynamics in complex systems, albeit from a top-down approach. SEMs are developed with a conceptual understanding of the focal system (Grace 2006); researchers hypothesize relationships among variables based on knowledge of the system, and they use observations of systems to test for significance of effects and estimate effect size, both in terms of direct and indirect effects. Direct effects represent the immediate relationships among individual variables, while indirect effects represent the effect of variables on one another through mediating variables (Kline 2011). Though structural equation modeling has largely been developed in biometry, econometrics, psychometrics, and sociometrics (Grace 2006), it has clear applications in ecology and conservation biology. In recent years it has been employed in studies of food web dynamics (e.g., Scherber et al. 2010), and for assessing causal relationships in threatened plant populations (e.g., Iriondo et al. 2003). Like ABMs, SEMs have the capability of being used to project effects of alternative states for individual variables on other elements of the system (e.g., Outwater et al. 2003, Sohn and Moon 2003), although to my knowledge this has not been done in ecological studies.

SEMs have particular utility in understanding influences of landscape characteristics on aquatic conditions and species, given physical processes that link large scales such as those of watersheds to these habitats. When precipitation falls, where the water goes and what it carries with it is largely dependent on what is on the ground there and in the larger watershed. Thus, Hecht-Leavitt (Hecht-Leavitt 2011) used SEMs to examine how land cover characteristics at multiple scales influence water quality and other attributes of habitat quality for inland lakes of Michigan. Similarly, other studies have employed SEMs to investigate how environmental characteristics at various scales affect stream habitats and the associated biodiversity (e.g., Barrett et al. 2010, Hermoso et al. 2010, Ficetola et al. 2011, Canessa and Parris 2013).

My objective was to develop forecast how future development may impact habitat for the endangered arroyo toad (*Anaxyrus californicus*) in southern California, USA using a structural equation model. I developed an SEM, informed by results of Chapter II, to associate land cover of individual watershed units with land cover along stream networks, and both of those with habitat suitability for the arroyo toad (modeled in Chapter I). I then used projections of future development for the region (Landis and Reilly 2003) to create alternative land cover scenarios, and used those with the SEM model habitat suitability per watershed under those conditions. Results of this work can guide landscape-scale conservation efforts to protect arroyo toads in my study system, and the general approach can also be applied to other systems.

Methods

Focal Species and Study Area

The arroyo toad is an endangered species, endemic to southern California, USA, and northern Baja California, Mexico (U.S. Fish and Wildlife Service 1994, Hammerson and Santos-Barrera 2004). The species relies on open, sandy streams for breeding and larval development, and adjacent terrestrial habitats for post-metamorphosis life stages (Griffin and Case 2001, Sweet and Sullivan 2005, Mitrovich et al. 2011). I conducted this research in southern California in an area for which I previously developed a fine-scale distribution model for arroyo toad (Chapter II) and I identified differential effects of land cover at multiple scales on average suitability of riparian habitats for the species (Chapter III). I found watershed-scale urbanization has negative influences on arroyo toad habitat, although urbanization along the associated stream networks had a positive relationship with habitat suitability. Building on these previous studies, I focused in the same region, and using watersheds delineated at the HUC-12 scale (Natural Resources Conservation Service 2010) as units of analysis.

Model Development

I developed an SEM model to estimate the relative influence of current land cover conditions along stream networks and within the larger watersheds based Chapter III. My dependent variable was the average suitability of riparian habitats for arroyo toads per HUC-12 watershed (Chapter II). I calculated independent variables for the two focal scale following the same methods employed in Chapter III (Figure 5), as percentages of Level I land cover classes in each watershed based on the 2006 National

Land Cover Dataset (Fry et al. 2011). Though similar studies have incorporated explicit measures of the percent of impervious pavement present (e.g., Canessa and Parris 2013; Chapter III) I excluded them because projections of future urbanization used in later analyses in the same model did not contain a comparable, continuous metric of development, only discrete classes (Landis and Reilly 2003). I processed spatial data layers using SAGA GIS version 2.1.1 (Böhner 2013) and calculated percentages of each land cover class per watershed using Fragstats version 4.2 (McGarigal et al. 2012).

I used principal components analyses to derive a reduced set of predictor variables at each scale (Hermoso et al. 2010, Ficetola et al. 2011), following same approach described in Chapter III. For each scale I retained three principal components (PCs) as new variables: "Development" (PC1, representing development vs. shrubland); "Forest" (PC2, representing forest vs. open habitat types); and "Agriculture" (PC3, representing agriculture vs. open water). Loadings of original variables on the principal components are presented in Appendix C. I carried out the principal component analyses using the 'vegan' package (Oksanen et al. 2012) in R version 3.0.2 (R Core Team 2013). To minimize effects of right-skew in principal components representing Development I $\log_{10}$-transformed them prior to analyses.

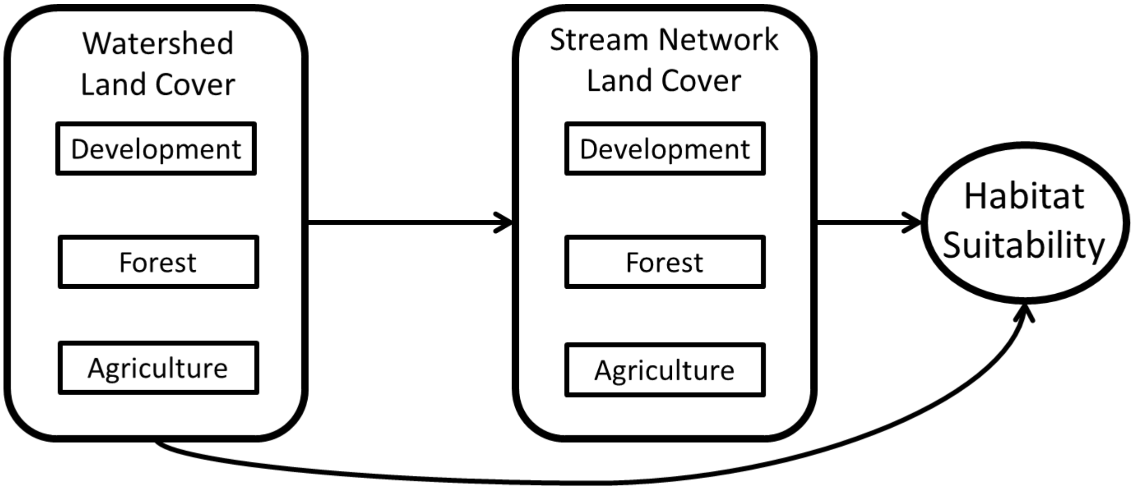

Figure 8. Schematic of all elements included in the structural equation model used in this study. Arrows indicate the general influence of the Watershed Land Cover on Stream Network Land Cover, and of both of those on Habitat suitability. All individual relationships examined in the model are presented in Table 6.

The model structure (Figure 8) was similar to that presented in Chapter III, with one main exception –the model in this study excluded contagion, a metric of land cover pattern that describes how contiguous land cover types are across a focal area (Li and Reynolds 1993), which can serve as a mediator between land cover variables and habitat suitability for arroyo toads. I excluded contagion because preliminary analyses indicated that it contributed to poor model fit. I attribute this to the only other difference between the models, which was exclusion of impervious cover in the original variable-set. For the watershed-scale, I included causal paths from measures of more deterministic anthropogenic land cover types to more natural ones (Development and Agriculture on Forest, and Development on Agriculture). I also included linkages between all watershed-scale variables on the corresponding stream network-scale variables, as characteristics of the smaller scale may be, in part, representative of patterns of the larger scale. I estimated parameters using 1,000 bootstrap replicates, and I evaluated model fit using a Bollen-Stine chi-squared test (Bollen and Stine 1992), the comparative fit index (CFI), and the standardized root mean square residual (Kline 2011). I tested for significance of individual paths, indirect effects, and total effects using bootstrapped z-tests, with $\alpha = 0.05$. I developed these models using Stata version 13.1 (StataCorp 2013), and used the ‘lavaan’ package (Rosseel 2012) in R version 3.0.2 (R Core Team 2013) to calculate the Bollen-Stine chi-squared metrics.

Future Land Cover Scenarios

I developed scenarios of potential future land cover based on the 2006 National Land Cover Dataset (NLCD; Fry et al. 2011) and a spatially explicit urbanization projection for California (Landis and Reilly 2003; available from Cal-Atlas (www.atlast.ca.gov)). For the first scenario (hereafter “high urbanization”), I overlaid the projected urbanization layer on the NLCD layer and reclassified any non-developed classes of the NLCD layer where the two overlapped to developed. For the second scenario (hereafter “low urbanization”), I used the same process, but excluded areas that are currently designated as conserved lands from transitioning to Developed. I acquired conserved lands layers from the U.S. Geological Survey, The Nature Conservancy, the California Department of Fish and Wildlife Natural Community Conservation Planning program, the Western Riverside County Regional Conservation Authority. Conserved lands are generally managed to for natural conditions in the long-term future. An assumption in both scenarios was that the only land cover changes would be from conversion of current non-developed classes to Developed. Maps of the 2006 NLCD data and both urbanization scenarios are presented in Figure 9.

Projections of Future Urbanization Effects on Arroyo Toad Habitat

I used the aforementioned SEM to forecast the effects of watershed-scale urbanization on habitat suitability for arroyo toads based on the high and low urbanization scenarios. For each scenario I calculated the percent of each land cover class for the watershed scale, then standardized all variables and transformed them into the same reduced variable-space as the land cover variables for the model of current conditions, using the loadings from the previous principal component analyses. Given the strong influence of watershed-scale conditions on stream-networks (Chapter III, Tables 4 and 5), and the relatively coarse scale of the projected urbanization layer (1 ha pixels), I only carried out these steps for the watershed-scale (excluding areas of the stream network). I then set values of watershed-scale conditions in the SEM according to the two scenarios and used the predictive relationships in the SEM to estimate future stream network conditions and ultimately average habitat suitability of riparian areas for arroyo toads per watershed.

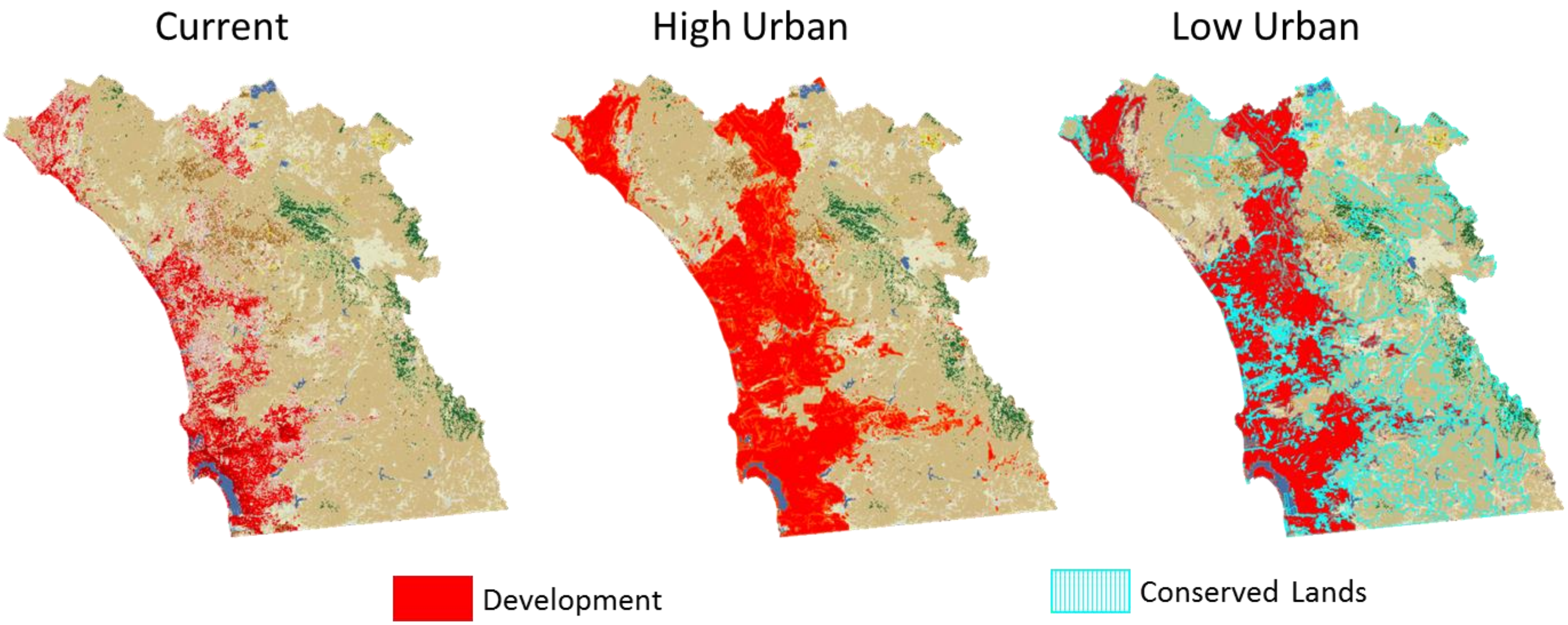

Figure 9. Maps of the study region illustrating developed land covers (in red) for the model of current conditions and High Urban and Low Urban Scenarios. The background map is the 2006 National Land Cover Dataset. On the map of the Low Urban Scenario cyan highlights conserved lands.

I used an analysis of variance to test for significant effects of projected urbanization on habitat suitability among all focal watersheds together. I also used post-hoc linear regressions to test whether the amount of projected urbanization in the two scenarios had significant effects on the modeled habitat suitability in individual watersheds. To accomplish this I calculated the projected increase in percent developed land cover per watershed from the 2006 land cover data to each future scenario, and regressed that measure against the difference in modeled habitat suitability in the respective watersheds for the respective scenarios.

Results

Structural Equation Model

The SEM adequately fit the data for current conditions well (Bollen-Stine χ^2=6.926, *df*=1, p=0.079; CFI=0.987; SRMR=0.028). Habitat suitability for arroyo toads was significantly influenced positively by Stream Development (z=2.56, p=0.008, β=0.509) and negatively by Watershed Development (z=-2.45, p=0.014, β=-0.105). Watershed Development and Watershed Forest also had positive indirect effects on habitat suitability (z=3.26, p=0.001, β=0.122 and z=2.56, p=0.008, β=0.509, respectively). The R^2 for Habitat Suitability was 0.288, and all Stream measures were strongly predicted within the model (R^2>0.65, Table 6).

Table 6. Bootstrapped maximum likelihood estimates of direct effects in the structural equation model used in this study. Significant paths ($p<0.05$) are highlighted in bold.

Dependent Variable	Direct Effect	Standardized Path Coefficient	Standard Error	z-value	p-value
Watershed Agriculture $R^2=0.007$	Watershed Urban	-.083	0.077	-1.09	0.278
Watershed Forest $R^2=0.046$	Watershed Urban	-0.216	0.114	-1.90	0.057
	Watershed Agriculture	-0.018	0.117	-0.15	0.877
Stream Urban $R^2=0.769$	**Watershed Urban**	**0.893**	**0.028**	**32.080**	**<0.0001**
	Watershed Forest	**0.181**	**0.059**	**3.090**	**0.002**
	Watershed Agriculture	-0.041	0.055	-0.750	0.456
Stream Forest $R^2=0.661$	**Watershed Forest**	**0.865**	**0.049**	**17.51**	**<0.001**
	Watershed Urban	**0.378**	**0.188**	**2.01**	**0.044**
	Stream Urban	-0.314	0.187	-1.67	0.095
	Watershed Agriculture	0.016	0.158	0.100	0.919
	Stream Agriculture	0.092	0.154	0.600	0.551
Stream Agriculture $R^2=0.744$	**Watershed Agriculture**	**0.863**	**0.055**	**15.83**	**<0.001**
	Watershed Urban	0.143	0.152	0.94	0.346
	Stream Urban	-0.223	0.169	-0.130	0.895
Habitat Suitability for Arroyo Toads $R^2=0.288$	**Stream Urban**	**0.593**	**0.224**	**2.650**	**0.008**
	Stream Forest	0.015	0.233	0.060	0.950
	Stream Agriculture	0.119	0.193	0.62	0.538
	Watershed Urban	**-0.565**	**0.216**	**-2.610**	**0.009**
	Watershed Agriculture	-0.237	0.186	-1.270	0.203
	Watershed Forest	**-0.548**	**0.232**	**-2.340**	**0.019**

Effects of Projected Urbanization on Habitat Suitability

There were only small, non-significant differences between region-wide predicted habitat suitability under current conditions and forecasted in the two future scenarios ($F_{2,327}$=2.88, p=0.0577). The average predicted habitat suitability for the current conditions across all watersheds was the highest among the current and projected future conditions (mean ± SD= 0.250 ± 0.452), followed by the low urbanization scenario (0.240 ± 0.035) and the high urbanization scenario (0.239 ± 0.035).

There were significant, negative relationships between projected development per watershed and habitat suitability. As the amount of projected development per watershed increased, average habitat suitability significantly decreased (high urbanization: $F_{1,108}$=74.26, p<0.001, R^2=0.402; low urbanization: $F_{1,108}$=63.11, p<0.001, R^2=0.363) (Figure 10). The negative effects of watershed-scale development are thus minimized in watersheds containing conserved lands in the low urbanization when compared to the high urbanization scenario, which did not incorporate any conserved lands (Figure 11).

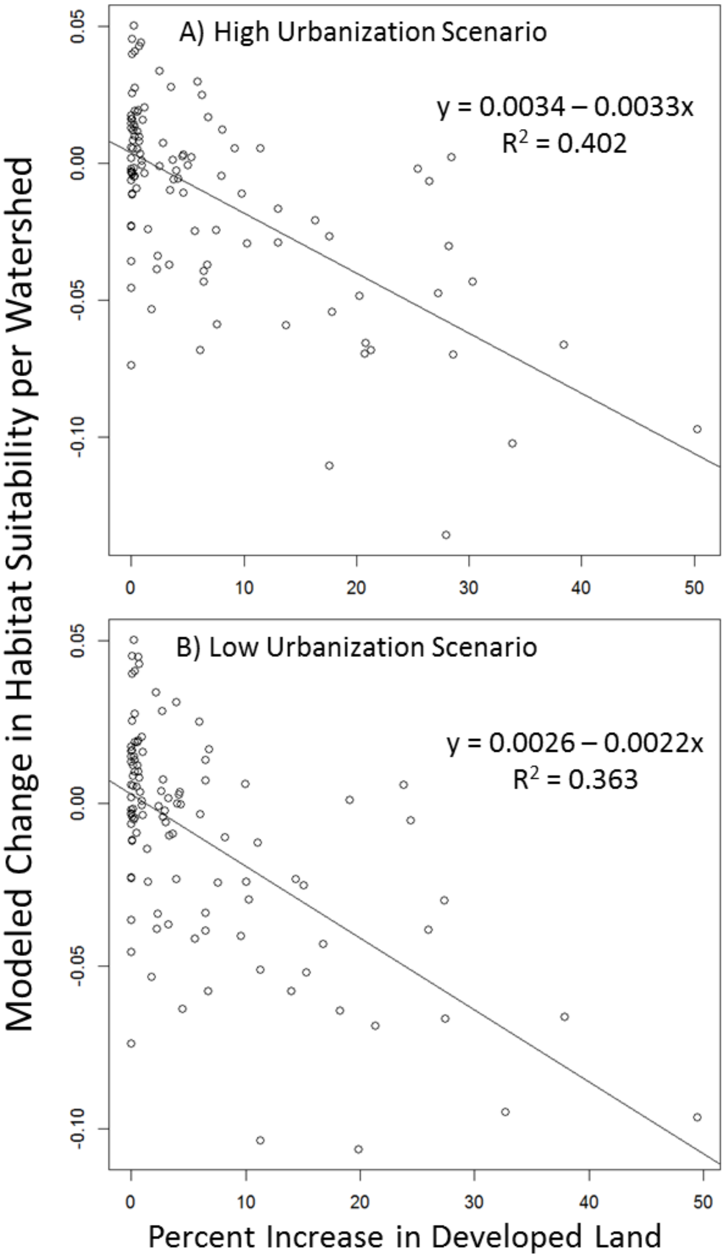

Figure 10. Linear regressions illustrating the change in modeled suitability of habitat for arroyo toads in focal watersheds of this study under High Urbanization (A) and Low Urbanization Scenarios (B). In both scenarios, higher levels of development per watershed are forecasted to cause decreases in suitability of riparian habitats for arroyo toads.

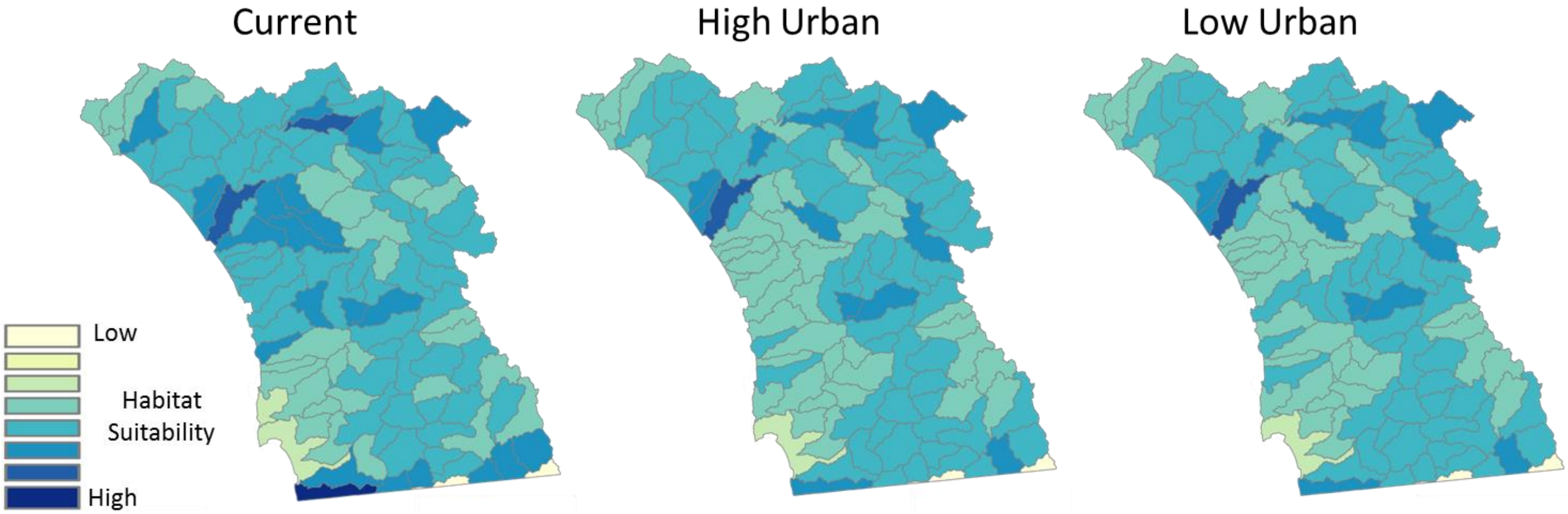

Figure 11. Maps of focal watersheds indicating modeled habitat suitability based on current land cover conditions, the High Urban Scenario, and the Low Urban Scenario.

Discussion

In this study I used structural equation modeling in conjunction with future land cover scenarios to forecast how future development may influence habitat suitability for arroyo toads in HUC-12 watersheds of southern California. The SEM showed that suitability of riparian habitats for arroyo toads is significantly influenced by land cover directly, both along stream networks and within entire watersheds. Furthermore, I found that land cover along stream networks is significantly influenced by watershed-scale characteristics, yielding indirect effects of watershed-scale land cover on arroyo toad habitat.

The forecasts of future habitat suitability under development scenarios showed that, given the relationships I found in the SEM, most watersheds with higher levels of projected development will likely exhibit the greatest decreases in habitat suitability (Figures 9 and 11). In the low urbanization scenarios, the benefit of conserved lands is evident, as some coastal watersheds with more areas precluded from development are forecasted to maintain higher habitat suitability for arroyo toads (Figures 9 and 11). The projected decrease in habitat suitability from current conditions to projected future scenarios across the region was not significant, though the regression analysis (Figure 10) showed that within individual watersheds, higher levels of future development will have significant, negative impacts on suitability of riparian habitats for arroyo toads.

The general results of this study are consistent with what has been shown in the literature for other stream systems. For example, Barrett et al. (2010), Ficetola et al. (2011), and Canessa and Parris (2013) all found that local stream conditions are influenced by broader-scale land cover conditions, and that both scales influence stream taxa. The linkages among scales are strongly supported by empirical knowledge of these systems, as watershed-scale processes including hydrology and sediment flow physically influence local conditions to which species directly respond (Allan 2004). My finding that suitability of arroyo toads is likely to decrease under future development scenarios is also expected, as urbanization has been noted as a considerable threat to the species (Sweet and Sullivan 2005), and at broad spatial scales is known to degrade stream conditions (Riley et al. 2005, Walsh et al. 2005).

Given that urbanization has been noted as a threat to arroyo toads, a surprising result of the SEM was that developed land cover along stream networks has a positive influence on habitat suitability for the species. There are numerous dams in the study area that affect stream hydrology and sediment flow (White and Greer 2006, San Diego County Water Authority 2013), thus it is possible that local urbanization has beneficial effects, such as preventing growth of riparian vegetation or increasing sediment load, which improve physical habitat structure for arroyo toads. White and Greer (2006) also found that for Los Peñasquitos Creek, in my study area, vegetation increased through time with watershed urbanization as a result of altered hydrology and channel geomorphology. Interestingly, I did not find similar patterns. It is possible the size of pixels I used to represent the stream network area (200m x 200m) was too large to detect such an effect, but the pixel size did permit consistent comparisons with earlier work on arroyo toad habitat modeling (Chapter II). I did find stream network Development was positively influenced by watershed Development, which may be attributable to anthropogenic development processes, rather than physical landscape processes for my focal scales.

Though SEM has been used to forecast effects of alternative conditions on larger systems in other fields (e.g., Outwater et al. 2003, Sohn and Moon 2003), this study is the first to my knowledge that does so in a conservation biology context. It is impossible to validate the forecast results based on currently available data, and future developments will likely differ to some extent from the scenarios I used (Oreskes et al. 1994). However, future studies may examine how land cover conditions and habitat suitability in the study area changed from an earlier time, to indicate whether my forecasts are consistent with historical patterns. Alternatively, a complementary, spatially explicit agent-based model could be developed to represent my focal system; effects of projected development on arroyo toad habitat could be simulated and compared to my forecasts. Such a complex model would require considerable data and would be computationally intense, and it can be difficult to develop equivalent models, but similar results across such independent techniques would provide support for my general conclusions (Hovmand 2003).

Though future studies should work to validate and improve the models presented here, my forecasts of alterations in habitat suitability for arroyo toads under future development scenarios are nonetheless informative, and consistent with the literature showing watershed-scale urbanization degrades stream and riparian habitats (e.g., King et al. 2005a, Riley et al. 2005, Walsh et al. 2005). The difference in my forecasts across the two development scenarios (Figure 11) indicates higher levels of conserved land at a watershed-scale are likely to benefit arroyo toads. Working towards that goal would also benefit other species on the landscape, simply by maintaining more habitat at a broad scale, regardless of the spatial configuration (Fahrig 2013). Currently, management of riparian areas to benefit arroyo toads focuses on predator removal (e.g., Brehme et al. 2008). However, if landscape conservation can help maintain natural disturbance regimes such as periodic drying of these systems, reduction in populations of predators that require permanent water bodies, such as bullfrogs and crayfish, may be achieved without repeated costs of active predator removal (Miller et al. 2012).

SEMs are becoming more commonly used in ecology, but their forecasting utility is virtually untapped. As illustrated here, SEMs can be used to understand how variables in a complex system are related using statistical inference, and then to make projections of system responses under alternative conditions. ABMs have great utility for such work, but rely on considerable data to parameterize all linkages from a bottom-up framework. Failure of ABMs to perform well and to be applied in real-world uses has been attributed, in part, to lack of data and computing resources (Matthews et al. 2007). SEMs often require relatively large sample sizes for parameter estimation (Grace 2006, Kline 2011), though depending on the study system this may be more reasonable to obtain than the data needed for ABMs. Currently, an advantage of ABMs is their ability to characterize nonlinear dynamics. The SEM I developed here only uses linear relationships, and it adequately fits the original data based on multiple fit metrics. However, capabilities of SEM are being further developed to take advantage of nonlinear and Bayesian frameworks (e.g., Jiang et al. 2010, Grace et al. 2012), which may better represent reality, and serve even greater utility in management applications.

CHAPTER V

CONCLUSIONS

In this dissertation I sought to identify opportunities for conservation of the endangered arroyo toad by examining factors that influence the species' occurrence across multiple scales. Like most amphibians, arroyo toads have a complex life history strategy in which they rely on streams for breeding and larval development, and surrounding terrestrial environments for post-metamorphosis life stages (Sweet and Sullivan 2005). Thus, direct alterations to either of these habitats can impact the species' long-term persistence. Furthermore, physical processes of hydrology and sediment flow can link watershed-scale patterns and processes to fine-scale habitat conditions (Allan 2004). Given these characteristics of arroyo toads and their habitats, it was important to examine effects of environmental characteristics along stream reaches, throughout stream networks, and within entire watersheds.

In my first study (Chapter II), I developed models of potential habitat for arroyo toads, based on long-term, relatively static environmental characteristics (e.g., climate, topography, soil type), and of current habitat, by incorporating dynamic, remotely-sensed environmental variables associated with vegetation and land cover. I focused these models on fine-scale stream areas represented by 200m pixels, which encompassed the stream itself, and the immediately surrounding terrestrial environments. This allowed me to incorporate areas required by all life stages of the species into these models. I identified 14.37% of the pixels in my study area as potential habitat, and 10.50% as current habitat. By comparing the two models, I identified sites where static environmental characteristics are likely suitable, but current conditions are not. Such sites may be improved through local management actions such as vegetation removal or redistribution of sediment, to create new habitat for arroyo toads. Following such activities, these areas could be colonized by arroyo toads naturally, if nearby populations exist, or via translocation efforts, to expand the species' range. Based my results, current habitat could be increased by as much as 67.02%.

In my second study (Chapter III) I used structural equation modeling to examine the how suitability of habitat for arroyo toads within individual watersheds may be influenced by land cover conditions along stream networks and within entire watersheds. I tested for direct effects of land cover conditions on arroyo toad habitat at these two scales, as well as indirect effects, in which variables at each scale could influence arroyo toad habitat through influences on other variables. Most strikingly, I found anthropogenic development along stream reaches has a positive effect on arroyo toad habitat. This is surprising given that urbanization has been identified as a threat to arroyo toads (U.S. Fish and Wildlife Service 1999, Sweet and Sullivan 2005), and in many studies anthropogenic development at various scales has been shown to degrade freshwater ecosystems (King et al. 2005a, Riley et al. 2005, Walsh et al. 2005). It is possible that development along streams helps maintain a moderate level of disturbance, increasing sediment load for example, which can improve the physical structure of riparian habitats for arroyo toads. However, I interpret this general result cautiously, and suggest that fine-scale habitat management is best guided by knowledge of the species' ecology, available in other studies (e.g., Griffin and Case 2001, Brehme et al. 2008, Turschak et al. 2008, Mitrovich et al. 2011). At the watershed scale, I found development has a negative impact on arroyo toad habitat, but it has positive influences on development along stream networks and the net effect is not significant. Although these results do not provide simple or direct prescriptions for management of arroyo toads, they illustrate the complexity of this system. Future investigations may build on this research by examining the effect of land cover patterns at multiple scales on finer-scale stream characteristics such as hydrology and channel geomorphology, to which arroyo toads may more directly respond.

In my third study (Chapter IV), I used a structural equation model of relationships between land cover within entire watersheds, land cover along stream networks, and suitability of riparian habitats for arroyo toads, in conjunction with scenarios of future development in my study region, to forecast how continued urbanization may influence arroyo toad habitat. I considered two land cover scenarios derived from a development projection by Landis and Reilly (2003) to represent high and low levels of urbanization. In both scenarios I found that suitability of habitats for arroyo toads within entire watersheds is likely to decrease, particularly in watersheds with higher levels of projected development. Comparison of results from the two scenarios indicates that mitigating watershed-scale development can benefit habitat for arroyo toads into the future. Thus, although the results presented Chapter III show net effects of watershed-scale development on arroyo toad habitat are not significant, my forecasts demonstrate that there may still be detectable, negative effects. Future work can further develop these models, and compare my work with results of other techniques such as agent based system dynamics models.

In summary, I conducted these three studies with a goal of obtaining results that managers can employ for conservation of arroyo toads in southern California. Most immediately, results of my distribution modeling study (Chapter II) can be used to identify sites appropriate for immediate habitat improvement, and potentially translocation efforts. Results of the structural equation modeling in Chapter III elucidate the complexities of how land cover characteristics of multiple spatial scales may affect arroyo toad habitat. Lastly, results of Chapter IV illustrate how future development may impact for habitat for arroyo toads, which can help managers prioritize watersheds for broad-scale conservation efforts. While I focused on a single species in one ecosystem, my approach of integrating techniques such as distribution modeling and structural equation modeling, with multi-scale datasets can be broadly applied to inform conservation actions of other taxa in various systems.

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APPENDIX A

RESULTS OF PRINCIPAL COMPONENT ANALYSES USED FOR VARIABLE REDUCTION IN CHAPTER II

Table A1. Eigenvalues, Percent of Variance Explained, and Variable Loadings for each Principal Component used in the Potential Model. Variable abbreviations are explained in Table 1 of the main text.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
Eigenvalue	24.8238	8.0977	5.0368	2.2044	1.7440	1.39586	1.0331
%Var Exp	50.66	16.53	10.25	4.50	3.56	2.85	2.11
Variable				**Variable Loadings**			
MRVBF	-0.0675	0.0511	0.2062	0.3949	0.1348	-0.1157	-0.1559
CatchArea	-0.0249	0.0091	0.0403	0.1639	-0.1274	0.0582	-0.6582
Elev	0.1909	-0.0190	0.0237	-0.0721	0.0118	-0.1906	0.0154
VRM03	0.0228	-0.0338	-0.1131	-0.3055	-0.1877	0.2082	-0.4926
VRM18	0.0251	-0.0630	-0.2044	-0.3853	-0.2031	0.1554	-0.2597
Ppt01	0.1361	-0.0844	-0.2463	0.1527	-0.0537	-0.1013	-0.0244
Ppt02	0.1373	-0.0733	-0.2492	0.1434	-0.0092	-0.0993	-0.0482
Ppt03	0.1563	-0.0358	-0.2011	0.1237	0.0648	0.1580	0.0171
Ppt04	0.1444	-0.0761	-0.2270	0.1574	0.0616	0.1008	-0.0133
Ppt05	0.1559	-0.0228	-0.2158	0.0859	0.0085	-0.1472	-0.0069
Ppt06	0.0087	-0.1193	-0.2917	0.0975	0.0826	0.1851	0.1215
Ppt07	0.1766	-0.0330	0.1158	-0.1015	0.0037	-0.2079	-0.0228
Ppt08	0.1771	-0.0326	0.1247	-0.0727	0.0174	-0.1169	-0.0205
Ppt09	0.1807	-0.0393	0.0478	-0.0564	0.0331	-0.0920	-0.0391
Ppt10	0.1482	-0.0624	-0.2323	0.1202	0.0324	0.0506	0.0128
Ppt11	0.1409	-0.0942	-0.2451	0.1592	0.0558	0.0506	-0.0095
Ppt12	0.1474	-0.0876	-0.2301	0.1327	0.0138	0.0094	-0.0302
Ppt13	0.1663	-0.0735	-0.2104	0.1239	0.0175	-0.0151	-0.0196
TMx01	-0.1845	0.0959	-0.0606	0.0697	0.0084	0.1735	0.0153
TMx02	-0.1840	0.1020	-0.0498	0.0668	0.0157	0.1717	0.0092
TMx03	-0.1657	0.1721	-0.0733	0.0500	0.0321	0.1268	0.0059
TMx04	-0.1400	0.2337	-0.0815	0.0039	0.0226	0.0192	-0.0086
TMx05	-0.0193	0.3330	-0.0855	-0.0484	0.0160	-0.1317	-0.0259

Table A1. Continued

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
TMx06	0.0746	0.2972	-0.0914	-0.0510	-0.0114	-0.2358	-0.0505
TMx07	0.0779	0.2867	-0.1301	-0.0465	-0.0133	-0.2323	-0.0325
TMx08	0.0612	0.2974	-0.1489	-0.0398	-0.0064	-0.2108	-0.0273
TMx09	0.0169	0.3168	-0.1680	-0.0304	0.0004	-0.1072	0.0030
TMx10	-0.1068	0.2677	-0.1426	0.0142	0.0057	0.0129	-0.0041
TMx11	-0.1706	0.1481	-0.0854	0.0627	0.0139	0.1719	0.0284
TMx12	-0.1836	0.0970	-0.0614	0.0725	0.0039	0.1819	0.0143
TMx13	-0.0922	0.2938	-0.1321	0.0113	0.0076	-0.0197	-0.0097
TMn01	-0.1778	-0.0980	-0.1294	0.0189	-0.0556	-0.0432	0.0530
TMn02	-0.1886	-0.0749	-0.0953	0.0330	-0.0456	-0.0062	0.0352
TMn03	-0.1923	-0.0757	-0.0656	0.0354	-0.0487	-0.0350	0.0037
TMn04	-0.1941	-0.0681	-0.0425	0.0350	-0.0398	-0.0238	-0.0097
TMn05	-0.1906	-0.0815	-0.0364	0.0347	-0.0499	-0.0730	-0.0323
TMn06	-0.1784	-0.1156	-0.0252	0.0160	-0.0710	-0.1690	-0.0483
TMn07	-0.1444	-0.1589	-0.0550	-0.0254	-0.1133	-0.3662	-0.0510
TMn08	-0.1567	-0.1374	-0.0716	-0.0259	-0.1096	-0.3187	-0.0285
TMn09	-0.1746	-0.1097	-0.1040	-0.0133	-0.0922	-0.2154	0.0067
TMn10	-0.1858	-0.0863	-0.1012	0.0079	-0.0667	-0.0956	0.0238
TMn11	-0.1752	-0.1075	-0.1328	0.0054	-0.0626	-0.0874	0.0480
TMn12	-0.1739	-0.1068	-0.1301	0.0077	-0.0614	-0.0664	0.0574
TMn13	-0.1854	-0.1004	-0.0875	0.0145	-0.0659	-0.1077	0.0100
Clay	-0.1144	-0.1008	-0.0637	-0.1687	0.4606	-0.0087	-0.0695
Silt	-0.0716	-0.0620	-0.1156	-0.2569	0.5097	-0.0885	-0.1059
Sand	0.1016	0.0771	0.0889	0.2038	-0.5087	0.0356	0.0786
WaterSt	-0.0526	-0.0205	0.0847	0.2660	0.1830	-0.1012	-0.3834
Slope	0.0559	-0.0442	-0.1549	-0.3645	-0.1778	0.0595	0.1297

Table A2. Eigenvalues, Percent of Variance Explained, and Variable Loadings for each Principal Component used in the Potential Model. Variable abbreviations are explained in Table 1 of the main text.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Eigenvalue	25.4482	8.5968	5.7111	3.2581	2.0800	2.0094	1.7587	1.5171	1.4546	1.0371
% Var Exp	41.72	14.09	9.36	5.34	3.41	3.29	2.88	2.49	2.39	1.70
Variable	**Variable Loadings**									
MRVBF	-0.0688	0.0722	-0.2019	0.1813	-0.2078	0.1477	-0.0318	-0.2297	0.1038	-0.1351
CatchArea	-0.0249	0.0105	-0.0377	0.0824	0.0213	0.1582	-0.1170	0.0010	0.0722	-0.5575
Elev	0.1889	-0.0153	-0.0284	-0.0284	0.0494	-0.0395	0.0228	-0.1265	-0.1216	0.0368
VRM03	0.0231	-0.0445	0.1035	-0.0858	0.2196	-0.0899	0.0432	0.3458	-0.1562	-0.4877
VRM18	0.0263	-0.0843	0.1931	-0.1314	0.2741	-0.1141	0.0337	0.3014	-0.1435	-0.2448
Ppt01	0.1349	-0.1005	0.1933	0.1586	-0.0462	-0.0155	-0.1245	-0.0903	-0.0401	-0.0431
Ppt02	0.1360	-0.0912	0.1994	0.1584	-0.0497	-0.0119	-0.0731	-0.1026	-0.0299	-0.0630
Ppt03	0.1544	-0.0515	0.1653	0.1221	-0.0973	-0.0269	0.0003	0.0705	0.1511	-0.0153
Ppt04	0.1424	-0.0913	0.1781	0.1554	-0.1197	-0.0351	-0.0180	0.0404	0.1095	-0.0379
Ppt05	0.1545	-0.0370	0.1743	0.1146	-0.0398	-0.0757	-0.0694	-0.1205	-0.0586	-0.0210
Ppt06	0.0093	-0.1324	0.2313	0.1082	-0.1601	-0.1799	-0.0631	0.1048	0.1228	0.0821
Ppt07	0.1744	-0.0207	-0.1116	-0.0610	0.0657	-0.0235	0.0412	-0.1202	-0.1524	0.0235
Ppt08	0.1746	-0.0203	-0.1189	-0.0505	0.0405	-0.0021	0.0531	-0.0643	-0.0854	0.0177
Ppt09	0.1782	-0.0351	-0.0499	-0.0114	0.0366	0.0041	0.0792	-0.0453	-0.0665	0.0111
Ppt10	0.1468	-0.0777	0.1857	0.1213	-0.0881	-0.0628	-0.0624	-0.0071	0.0766	-0.0299
Ppt11	0.1394	-0.1097	0.1917	0.1551	-0.1110	-0.0447	-0.0393	-0.0135	0.0857	-0.0364
Ppt12	0.1457	-0.1038	0.1815	0.1429	-0.0710	-0.0164	-0.0455	-0.0227	0.0358	-0.0562
Ppt13	0.1645	-0.0877	0.1649	0.1344	-0.0661	-0.0266	-0.0458	-0.0391	0.0252	-0.0363
TMx01	-0.1822	0.0863	0.0736	0.0301	-0.0524	0.0263	-0.0164	0.0991	0.1211	-0.0141
TMx02	-0.1818	0.0930	0.0651	0.0279	-0.0515	0.0304	-0.0047	0.0975	0.1205	-0.0179
TMx03	-0.1634	0.1580	0.0969	0.0241	-0.0378	0.0212	0.0111	0.0578	0.1019	-0.0246

Table A2. Continued

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
TMx04	-0.1378	0.2152	0.1171	0.0059	0.0046	0.0264	0.0302	-0.0004	0.0267	-0.0118
TMx05	-0.0182	0.3100	0.1344	-0.0115	0.0612	0.0179	0.0435	-0.0987	-0.0641	-0.0143
TMx06	0.0746	0.2762	0.1284	0.0005	0.0813	0.0036	0.0142	-0.1600	-0.1343	-0.0332
TMx07	0.0779	0.2631	0.1616	0.0095	0.0744	-0.0098	0.0025	-0.1587	-0.1330	-0.0171
TMx08	0.0615	0.2716	0.1808	0.0140	0.0663	-0.0116	0.0037	-0.1494	-0.1158	-0.0160
TMx09	0.0179	0.2879	0.2044	0.0140	0.0450	-0.0050	0.0099	-0.0790	-0.0545	0.0057
TMx10	-0.1047	0.2427	0.1768	0.0228	0.0039	0.0213	0.0067	-0.0032	0.0199	-0.0109
TMx11	-0.1683	0.1344	0.1043	0.0301	-0.0492	0.0201	-0.0121	0.0967	0.1239	-0.0034
TMx12	-0.1813	0.0874	0.0742	0.0324	-0.0541	0.0281	-0.0197	0.1088	0.1238	-0.0151
TMx13	-0.0902	0.2691	0.1692	0.0223	0.0136	0.0170	0.0061	-0.0290	0.0066	-0.0195
TMn01	-0.1748	-0.1042	0.1043	0.0264	0.0010	-0.0417	-0.0904	-0.0307	-0.0431	0.0461
TMn02	-0.1858	-0.0794	0.0772	0.0264	-0.0095	-0.0215	-0.0757	-0.0073	-0.0145	0.0268
TMn03	-0.1897	-0.0780	0.0500	0.0256	-0.0034	-0.0056	-0.0684	-0.0213	-0.0322	0.0043
TMn04	-0.1916	-0.0689	0.0309	0.0220	-0.0056	0.0043	-0.0523	-0.0123	-0.0247	-0.0057
TMn05	-0.1882	-0.0816	0.0227	0.0261	0.0054	0.0118	-0.0547	-0.0400	-0.0579	-0.0206
TMn06	-0.1762	-0.1132	0.0065	0.0207	0.0303	0.0069	-0.0651	-0.0919	-0.1271	-0.0213
TMn07	-0.1422	-0.1571	0.0247	0.0114	0.0899	-0.0240	-0.1058	-0.2193	-0.2485	-0.0129
TMn08	-0.1541	-0.1385	0.0455	0.0086	0.0864	-0.0207	-0.1021	-0.1909	-0.2140	0.0056
TMn09	-0.1716	-0.1140	0.0795	0.0138	0.0579	-0.0332	-0.1016	-0.1311	-0.1514	0.0231
TMn10	-0.1828	-0.0913	0.0816	0.0188	0.0215	-0.0248	-0.0831	-0.0563	-0.0772	0.0294
TMn11	-0.1722	-0.1137	0.1061	0.0217	0.0134	-0.0478	-0.0930	-0.0556	-0.0745	0.0467
TMn12	-0.1708	-0.1126	0.1036	0.0210	0.0097	-0.0489	-0.0949	-0.0442	-0.0614	0.0520
TMn13	-0.1826	-0.1035	0.0660	0.0218	0.0194	-0.0213	-0.0829	-0.0649	-0.0833	0.0171
Brt03.Med	-0.0186	0.0270	-0.1087	0.2964	0.3796	-0.2160	0.0184	0.0113	0.2003	0.0588
Brt03.Var	-0.0314	0.1305	-0.1802	0.1513	-0.2083	-0.2761	-0.0254	0.0873	-0.2787	-0.0642
Grn03.Med	-0.0614	0.0126	-0.1111	0.2922	-0.0298	0.0833	0.2392	0.1216	-0.2012	-0.0335

Table A2. Continued

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**
Grn03.Var	-0.0360	0.0038	0.0882	0.1074	-0.3145	0.0686	0.1975	0.3902	-0.2672	0.2404
Wet03.Med	-0.0092	0.0565	-0.1088	0.3339	0.1569	-0.1820	-0.0123	0.0357	-0.0792	0.0545
Wet03.Var	-0.0909	-0.1198	0.1191	0.0355	0.0291	0.2903	0.2337	0.1454	0.1192	0.0612
Brt09.Med	-0.0324	0.0189	-0.1064	0.3160	0.3373	-0.1809	0.0439	0.0265	0.2236	0.0969
Brt09.Var	-0.0371	0.0683	-0.2114	0.1025	-0.2182	-0.2567	-0.1220	0.1425	-0.1232	-0.1523
Grn09.Med	-0.0488	-0.0162	-0.0527	0.2880	0.0884	0.2498	0.2308	0.0014	-0.2110	-0.0588
Grn09.Var	0.0729	-0.0638	0.1275	0.1434	-0.0119	0.3309	0.2013	0.0094	-0.2777	0.1298
Wet09.Med	-0.0299	0.0458	-0.0486	0.3491	0.1659	-0.0303	0.0470	0.0346	-0.0035	0.1381
Wet09.Var	-0.0113	-0.1861	0.0514	0.0370	0.2470	0.3699	0.1262	-0.1085	0.1607	-0.1097
Clay	-0.1125	-0.1011	0.0472	-0.0717	-0.0858	-0.2267	0.3807	-0.1476	0.0865	-0.0818
Silt	-0.0699	-0.0670	0.1008	-0.0855	-0.0654	-0.2874	0.4575	-0.1772	-0.0123	-0.0641
Sand	0.0999	0.0827	-0.0771	0.0769	0.0447	0.2380	-0.4376	0.1935	-0.1243	0.0649
WaterSt	-0.0540	-0.0064	-0.1057	0.1769	-0.2008	0.0445	0.0914	-0.1263	-0.0502	-0.3919
Slope	0.0564	-0.0602	0.1462	-0.1354	0.2406	-0.1190	0.0232	0.2227	-0.1628	0.0956

APPENDIX B

RESULTS OF PRINCIPAL COMPONENT ANALYSES USED FOR VARIABLE REDUCTION IN CHAPTER III

Table B1. Principal Component loadings for watershed-scale variables used in the structural equation models for Chapter III. Names of variables as presented throughout the chapter are in parentheses.

	PC1 (Developed)	**PC2 (Forest)**	**PC3 (Agriculture)**
Eigenvalue	4.86920	1.55690	1.06668
% Var. Explained	44.26	14.15	9.72
Variable		**Variable Loadings**	
Average % Impervious Pavement	0.44385	0.09713	-0.01962
Variance % Impervious Pavement	0.42405	-0.06796	-0.01133
Median of % Impervious	0.38862	0.25985	0.05996
Percent Open Water	0.16650	0.03434	0.42931
Percent Developed	0.44138	0.04187	-0.08924
Percent Barren/Bare Ground	0.22038	-0.38334	0.06856
Percent Forest	-0.15403	0.35150	-0.06871
Percent Scrub/Shrub	-0.39832	0.09074	0.19682
Percent Grassland	-0.10887	-0.60594	0.19707
Percent Planted/Cultivated	-0.03529	-0.16848	-0.84591
Percent Wetland	0.07457	-0.49114	0.03254

Table B2. Principal Component loadings for stream network-scale variables used in the structural equation models for Chapter III. Names of variables as presented throughout the chapter are in parentheses.

	PC1 (Developed)	**PC2 (Forest)**	**PC3 (Agriculture)**
Eigenvalue	4.53640	1.66300	1.05745
% Var. Explained	41.24	15.12	9.61
Variable	**Variable Loadings**		
Average % Impervious Pavement	0.46135	0.09047	-0.01299
Variance % Impervious Pavement	0.44791	0.00306	0.00169
Median of % Impervious	0.38709	0.19729	-0.03675
Percent Open Water	0.13338	-0.05477	0.41348
Percent Developed	0.45880	-0.00059	-0.01427
Percent Barren/Bare Ground	0.07249	-0.42292	0.13421
Percent Forest	-0.17729	0.33735	-0.29288
Percent Scrub/Shrub	-0.37750	0.28233	0.17610
Percent Grassland	-0.16841	-0.49427	0.26439
Percent Planted/Cultivated	-0.02671	-0.29978	-0.78641
Percent Wetland	0.01238	-0.49329	0.06455

APPENDIX C

RESULTS OF PRINCIPAL COMPONENT ANALYSES USED FOR VARIABLE REDUCTION IN CHAPTER IV

Table C1. Principal Component loadings for watershed-scale variables used in the structural equation model for Chapter IV. Names of PC-transformed variables as presented throughout the chapter are in parentheses.

	PC1 (Developed)	**PC2 (Forest)**	**PC3 (Agriculture)**
Eigenvalue	2.2454	1.3724	1.0620
% Var. Explained	30.67	17.16	13.27
Variable		**Variable Loadings**	
Percent Open Water	0.25351	0.14369	0.43736
Percent Developed	0.57509	0.25218	-0.06586
Percent Barren/Bare Ground	0.42353	-0.20179	0.07942
Percent Forest	-0.27070	0.32826	-0.03435
Percent Scrub/Shrub	-0.56339	-0.13076	0.17713
Percent Grassland	-0.01967	-0.69636	0.14780
Percent Planted/Cultivated	0.01519	-0.12382	-0.86236
Percent Wetland	0.18524	-0.49994	-0.00074

Table C2. Principal Component loadings for stream network-scale variables used in the structural equation models for Chapter IV. Names of PC-transformed variables as presented throughout the chapter are in parentheses.

	PC1 (Developed)	**PC2 (Forest)**	**PC3 (Agriculture)**
Eigenvalue	2.2450	1.1498	1.0562
% Var. Explained	28.06	18.72	13.20
Variable	**Variable Loadings**		
Percent Open Water	0.29341	-0.20578	0.34005
Percent Developed	0.59424	-0.29238	-0.03196
Percent Barren/Bare Ground	0.23368	0.35826	0.15230
Percent Forest	-0.35057	-0.19468	-0.28813
Percent Scrub/Shrub	-0.57918	-0.04520	0.17938
Percent Grassland	-0.08223	0.64394	0.31340
Percent Planted/Cultivated	0.09491	0.26616	-0.80156
Percent Wetland	0.17905	0.46730	-0.06502