Biological Conservation 228 (2018) 310–318

Contents lists available at ScienceDirect

Biological Conservation

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

Multi-scale effects of land cover and urbanization on the habitat suitability of an endangered toad

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ARTICLE INFO

Keywords:
Watersheds
Structural equation model
California
Arroyo toad
Anaxyrus californicus
Anthropogenic development
Riparian areas

ABSTRACT

Habitat degradation, entwined with land cover change, is a major driver of biodiversity loss. Effects of land cover change on species can be direct (when habitat is converted to alternative land cover types) or indirect (when land outside of the species habitat is altered). Hydrologic and ecological connections between terrestrial and aquatic systems are well understood, exemplifying how spatially disparate land cover conditions may influence aquatic habitats, but are rarely examined. We sought to quantify relative effects of land cover at two different but interacting scales on habitat suitability for the endangered arroyo toad (*Anaxyrus californicus*). Based on an existing distribution model for the arroyo toad and available land cover data, we estimated effects of land cover along streams and within entire watersheds on habitat suitability using structural equation modeling. Relationships between land cover and habitat suitability differed between scales, and broader, watershed-scale conditions influenced land cover along the embedded stream networks. We found anthropogenic development and forest cover at the watershed-scale negatively impacted habitat suitability, but development along stream networks was positively associated with suitability. The positive association between development along streams and habitat suitability may be attributable to increased spatial heterogeneity along urbanized streams, or related factors including policies designed to conserve riparian habitats amidst development. These findings show arroyo toad habitat is influenced by land cover across multiple scales, and can inform conservation of the species. Furthermore, our methodology can help elucidate similar dynamics with other taxa, particularly those reliant on both terrestrial and aquatic environments.

1. Introduction

Understanding and mitigating anthropogenic impacts on species and ecosystems is a perpetual challenge for conservation (Millennium Ecosystem Assessment, 2005; Lal, 2010). Habitat loss and degradation are widely acknowledged as major threats to various taxa (e.g., Millennium Ecosystem Assessment, 2005; Sodhi et al., 2008; Schipper et al., 2008; Böhm et al., 2013), and while conservation actions are frequently implemented at fine scales to immediately benefit species, broad-scale factors can ultimately drive biodiversity loss. Roads, for instance, can directly contribute to habitat loss and fragmentation, and influence the physical structure of sand dunes resulting in disassembly of lizard communities (Vega et al., 2000; Leavitt and Fitzgerald, 2013). Similarly, stream habitats can be influenced by broad-scale land cover conditions through changes to hydrologic regimes and sediment transport processes (Allan, 2004). Thus, effective conservation measures should be informed by knowledge of how anthropogenic activities at multiple scales influence species habitats and ecosystem functions (Poiani et al., 2000; Subalusky et al., 2009).

The watershed is perhaps the most appropriate scale at which to manage freshwater and coastal ecosystems because the system boundaries determined by topography and physical processes that structure species' habitats are tightly linked (Beechie et al., 2010). Higher levels of urbanization in a watershed, for instance, are commonly tied to reduced taxonomic richness, species abundance, and water quality of freshwater and marine systems (King et al., 2005, 2011; Riley et al., 2005; Klein et al., 2012). Such findings can help guide restoration of aquatic ecosystems and inform strategies for mitigating threats to water

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https://doi.org/10.1016/j.biocon.2018.10.032
Received 23 June 2018; Received in revised form 20 October 2018; Accepted 29 October 2018

quality (Leach and Pelkey, 2001; Pires, 2004), such as targeted planning of future development across watersheds, or changes in management practices.

Management at smaller scales is also important for conservation of aquatic ecosystems. Land cover immediately surrounding aquatic habitats can influence water quality, and vegetation buffers are often used along streams and ponds to counter negative effects of development (Peterjohn and Correll, 1984; Clinton, 2011). Furthermore, riparian areas provide considerable nutrient resources (Polis et al., 1997; Lowe et al., 2006) and habitat for amphibians, turtles, and other taxa that rely on aquatic and terrestrial habitats during various life stages (Gibbons, 2003; Subalusky et al., 2009).

However, a limited number of studies have examined relative influences of land cover conditions at multiple scales on specific taxa and communities. For example, Lowe and Bolger (2002) analyzed effects of landscape-scale timber harvest history and local stream conditions on *Gyrinophilus porphyriticus*. This study, however, focused only on small stream sections in two watersheds. Ficetola et al. (2011) analyzed effects of land cover characteristics within 400 m and 100 m of sampling points, and local water conditions on *Salamandra salamandra* and the larger amphibian communities. These authors did not examine possible effects of broader watershed-scale land cover conditions on habitat suitability or species assembly. Canessa and Parris (2013) alluded to potential effects of watershed-scale conditions on focal amphibian communities, but primarily documented effects of land cover within a 500 m radius of sampling points. In contrast to the aforementioned studies, Barrett et al. (2010) documented linkages between watershed-scale conditions, stream conditions, and abundance of *Eurycea cirrigera* in the southeastern United States. Also in the southeastern United States, Cecala et al. (2018) found of catchment-scale variables have greater effects on occupancy of two salamander species compared to reach-scale variables, and Jachowski and Hopkins (2018) found riparian cover type across catchments to be a strong driver of demographic structure in *Cryptobranchus alleganiensis*, possibly through effects on downstream conditions. While these studies suggest habitats used by aquatic species are structured by both fine-scale stream properties and land cover at the meso-scale, influences of watershed-scale land cover conditions, and multi-scale land cover interactions on aquatic species' habitats remains under-studied. Understanding these effects can link broader patterns of land cover to site-specific habitat conditions, ultimately informing improved recommendations for biodiversity conservation.

To gain insight into effects of land cover on habitat conditions, we examined the relationships between land cover characteristics at two different scales and habitat suitability for the arroyo toad (*Anaxyrus californicus*). The arroyo toad is endemic to southern California, USA, and northern Baja California, Mexico, and listed as endangered by the IUCN and the U.S. Endangered Species Act (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 requires adjacent terrestrial environments for post-metamorphosis life stages (Sweet and Sullivan, 2005). Declines of the species have been attributed to habitat loss and degradation associated with altered hydrology and invasive species (U.S. Fish and Wildlife Service, 1999; Sweet and Sullivan, 2005). Given arroyo toads' requirements for aquatic and terrestrial habitats, sensitivity of populations to surface water availability (Fisher et al., 2018), its conservation status, and known linkages between watershed-scale land cover and riparian conditions (Allan, 2004), we identified it as a model organism for examining relative influences of conditions across multiple scales on habitat suitability. We based this work on a conceptual model of how land cover at multiple scales may influence habitat, informed by previous literature (Fig. 1, derived from Ficetola et al. (2011)).

To identify how land cover at multiple scales influences habitat suitability in this system, we used an existing model of habitat suitability based on recent presence/absence data, supplemented by pseudoabsence data, and a suite of environmental variables (Treglia, 2014; Treglia et al., 2015), and applied structural equation modeling to examine four main research questions: (1) how is habitat suitability for arroyo toads within watersheds affected by land cover characteristics in entire watersheds?; (2) how is habitat suitability affected by land cover within stream networks?; (3) is habitat suitability affected by watershed-scale land cover indirectly, through effects on land cover of contained associated stream networks?; and (4) is habitat suitability influenced by the spatial clumpiness of land cover types, measured as landscape contagion? Answering these questions allows us to identify and interpret how land cover at multiple scales affects habitat suitability and species' presence in a riparian landscape.

2. Methods

2.1. Study area and units of analysis

We focused this study in southern California, in an area for which Treglia et al. (2015) developed a distribution model for the arroyo toad. We 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 approximately 4000–16,000 ha, 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), which can feed back into land management practices, and the scale is relevant to conditions of contained aquatic systems (e.g., Strager et al., 2009; Tomer et al., 2013). We examined all HUC-12 basins contained within the range of the toad south of the Santa Ana River watershed to the Mexican Border (the study region of Treglia et al., 2015; $n = 110$).

2.2. Data sources and preparation

Using variables from both the watershed and stream network scales to develop a new distribution model is fraught with statistical challenges. For example, without sampling to confirm presence/absence across all focal watersheds, a model could only be based on a data from a small subset of our study region. Furthermore, for watersheds in which there are both documented presences and absences, there is no clear way to handle the mixture of data points, particularly given incomplete sampling; using all presence and absence data within a watershed would pose the issue of pseudoreplication, with multiple points being in the same measurement unit and violating any assumptions of independence. Given these limitations we used the average probability of presence modeled for arroyo toads within each HUC-12 watershed as our dependent variable (hereafter, Habitat Suitability; example shown in Fig. 2-A; see Figs. 2–4 in Treglia et al., 2015). The distribution model was developed using recent (2005–2013) presence/absence data for arroyo toads (supplemented with pseudoabsence data), for streams and streamside habitats represented by 200 m pixels (Treglia et al., 2015, the distribution model is available online through the KNB Data Repository (Treglia et al., 2017)). Predictor variables used in the distribution model included recent remotely sensed data derived from 2010 Landsat imagery as well as long-term climate characteristics, topography, geomorphology, and soil characteristics. The remotely sensed variables were used as continuous measures associated with temporally relevant habitat features.

We derived independent variables from the 2006 National Land Cover Database (NLCD), which was classified from Landsat imagery with a pixel size of 30 × 30 m (Fry et al., 2011). We used data on the percent of impervious cover per pixel, and Level I land cover classes composed of: Open Water; Development; 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 our knowledge it was the most accurate,

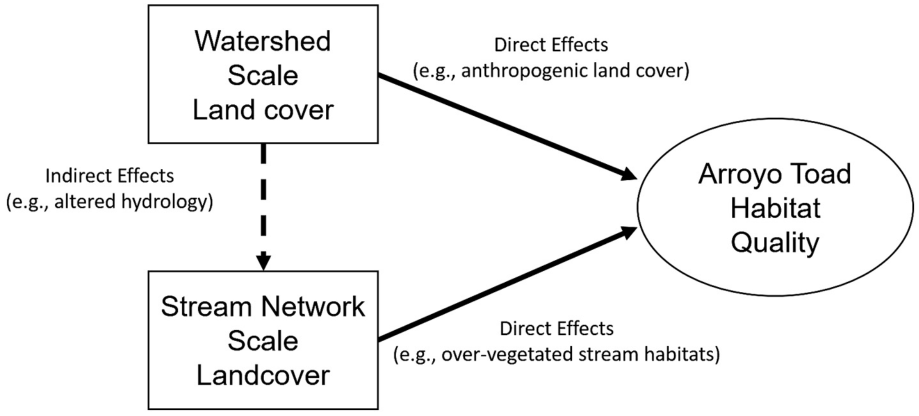


Fig. 1. Conceptual model of linkages between land cover at the scale of entire watersheds, land cover along stream networks, and habitat quality for arroyo toads. Solid arrows represent potential direct effects of land cover variables on arroyo toad habitat suitability; the dashed-arrow represents potential effects of watershed conditions on land cover conditions within stream networks, yielding an indirect effect of watershed-scale conditions on habitat suitability.

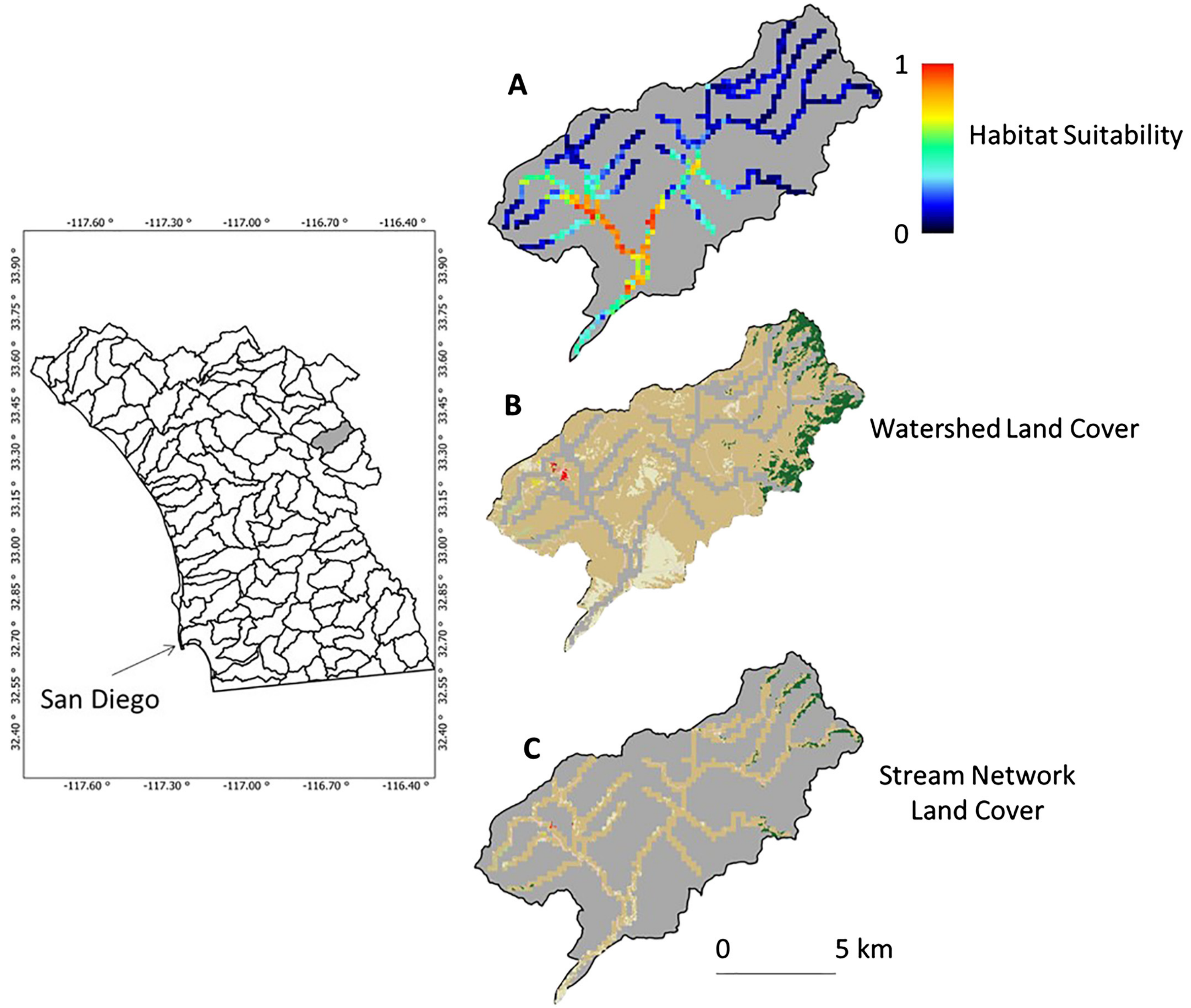
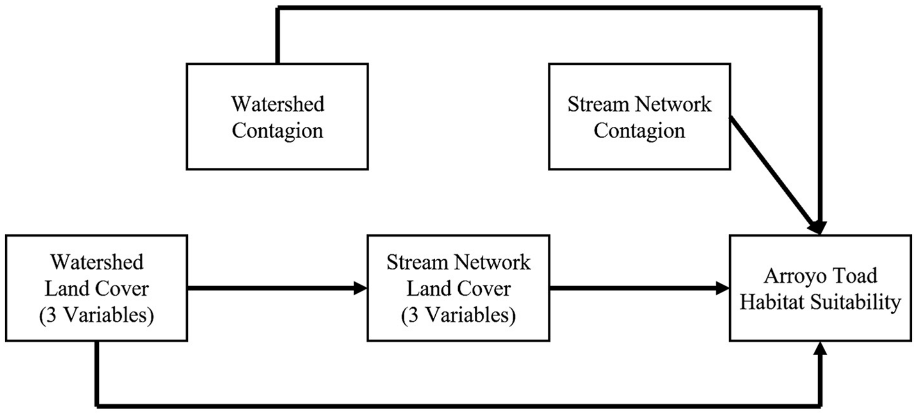
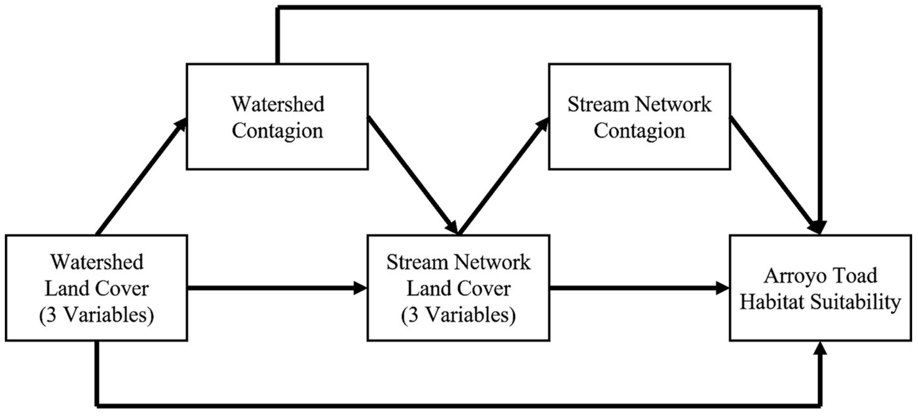


Fig. 2. Example map illustrating the 110 HUCs of original data used to calculate the variables for structural equation models, including Habitat Suitability (A), Land Cover for the Watershed scale (B), and Land Cover for the Stream Network scale (C). These datasets are highlighted for a single watershed 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 at http://www.mrlc.gov/nlcd06_leg.php (Fry et al., 2011).



A. Contagion Direct Model



B. Contagion Mediated Model

Fig. 3. Schematics of the structural equation models used to explore possible effects of land cover characteristics on arroyo toad habitat suitability within watersheds. All direct linkages in the Contagion Mediated Model are presented in Table 2 and total effects are presented in Table 3; the Contagion Direct Model was a poor fit to the data, thus we do not present specific results for the contained paths.

high-resolution land cover dataset available for the study area at the time of analysis.

For independent variables representing the scale of entire watersheds, we calculated the mean, median, and variance of percent impervious cover, and the percentage of each land cover class per basin (e.g., Fig. 2-B). We also calculated total contagion (a measure of clumpiness of landscape attributes) 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, we calculated the same metrics as for watersheds, but only for areas contained by all the 200 m pixels for which arroyo toad habitat was modeled within each watershed (e.g., Fig. 2-C). In calculating watershed-scale variables, we masked out stream network areas, ensuring that one would not be a subset of the other. We calculated impervious cover measures using SAGA GIS version 2.1.1 (Böhner, 2013), and percentages of each land cover type and contagion using Fragstats version 4.2 (McGarigal et al., 2012).

We used separate principal component analyses (PCAs) to reduce the dimensionality of the independent variable set for the two focal scales; this reduced the number of parameters estimated, allowing the structural equation model to be identified given our sample size. We 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). We retained three PCs for each scale, which had similar variable loadings across scales (Appendix S1). 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). We maintained contagion as separate variables at each scale because it is a measure of pattern and configuration of different land cover types. Hereafter, we denote the corresponding scale before variable names as Watershed or Stream (e.g., Watershed Development or Stream Development).

2.3. *Analysis*

We used structural equation modeling to test the influence of land cover characteristics on arroyo toad habitat suitability at the two focal scales. Structural equation modeling (SEM) is a multivariate analytical technique capable of testing direct and indirect relationships among multiple independent and dependent variables simultaneously (Kline, 2011). More specifically, SEM allows the analyst to test the relationship between "…a dataset, empirical covariance matrix, and an estimated

Table 1
Baseline and comparative fit measures for structural equation models.

	AIC[a]	BIC[b]	CFI[c]	NNFI[d]	SRMR[e]	χ^{2f}	*df*	*p*
Contagion Mediated Model	2113.813	2251.538	0.998	0.932	0.01	2.434	1	0.119
Contagion Direct Model	2278.565	2383.884	0.760	0.161	0.198	191.186	10	< 0.001

[a] Akaike's Information Criterion.
[b] Bayes' Information Criterion.
[c] Comparative Fit Index.
[d] Non-normed Fit Index.
[e] Standardized Root Mean Square Error.
[f] Bollen-Stine χ^2.

population covariance matrix that is produced as a function of the model parameter estimates" (Ullman and Bentler, 2013, p. 663). Therefore, when using SEM, the analyst can ask questions about causal inference and test their plausibility given associations observed within the obtained data. When a given model is revealed to be an acceptable fit, the analyst is able to reject the series of null hypotheses being tested in the hypothesized model and conclude that the hypothesized model is a feasible explanation of the observed phenomena with the understanding that other competing explanations may also be viable. The ability to test a hypothesized model against observed data is a key distinction between SEM and alternative multi-model inference frameworks.

Model development for SEM is guided by theory and knowledge of the system of interest (Grace, 2006). The specific relationships that we hypothesized are based on the results of existing research and our conceptual understanding of arroyo toad habitat. Following Ficetola et al. (2011), we hypothesized that watershed-scale land cover and stream-network scale land cover types would exert direct effects on habitat suitability for the arroyo toad.

Additionally, we hypothesized that watershed-scale land cover types would be positively correlated with corresponding land cover types at the stream-network scale, as characteristics of the smaller scale may be driven by patterns of the larger scale. We also hypothesized that anthropogenic land cover types would predict natural ones (i.e., Development and Agriculture predict Forest, and Development predicts Agriculture). Furthermore, we hypothesized that Watershed Development and Watershed Agriculture would predict 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).

Finally, though past work provides a framework to conceptualize relationships between watershed and stream-scale land cover types and habitat suitability, other variables may be relevant in describing patterns of habitat suitability. Contagion of land cover types can influence suitability of sites for species (Roseberry and Sudkamp, 1998), and while it describes spatial patterns, can be influenced by anthropogenic land covers in various ways (Li et al., 2005; Wu et al., 2011). However, the role of contagion in influencing habitat suitability remains largely unknown. Thus, we tested two competing models where contagion has only direct effects on habitat suitability (Contagion Direct Model), and where it mediates relationships between land cover types at the watershed scale and stream-network scale, and land cover types and habitat suitability at both scales (Contagion Mediated Model, Fig. 3).

We evaluated model fit using the Bollen-Stine chi-squared statistic (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). Acceptable model fit was determined when a non-significant chi-squared statistic was observed ($p \geq 0.05$), values of CFI and NNFI exceeded 0.95, and SRMR was below 0.06 (Hu and Bentler, 1999). In addition to formal tests and indices common for evaluating fit of structural equation models, we 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). We set $\alpha = 0.05$ for bootstrapped z-tests to test significance of individual paths, mediating effects (i.e., indirect linkages between variables), and total effects.

We $\log_{10}$-transformed the Development variables at both scales to minimize effects of right-skew in the data. We estimated parameters using a bootstrapped maximum likelihood estimator using 1000 draws from the PCA-transformed dataset to account for small sample size and lack of multivariate normality (Cheung and Lau, 2008). We 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).

3. Results

Across all of the 110 HUCs included in the study, the Contagion Mediated Model fit the data better than the Contagion Direct Model based on all fit measures that we considered (Table 1). In fact, the Contagion Direct Model did not adequately fit the data (Bollen-Stine $\chi^2 = 191.186$, $df = 10$, $p < 0.001$; $n = 110$). Thus, we only present results for the Contagion Mediated Model. The final model, which contains nine more estimated parameters than the Contagion Direct Model, demonstrated an acceptable fit (Bollen-Stine $\chi^2 = 2.434$, $df = 1$, $p = 0.119$; $n = 110$). The R^2 for arroyo toad habitat suitability in this model was 0.344.

Parameter estimates reported for structural equation models can be interpreted in a manner similar to other linear regressions. Parameters, in this study, are reported in the standardized functional form. For instance, a positive relationship suggests that for every one standard deviation increase in variable x, there is a "β" standard deviation increase in variable y.

3.1. 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 ($\beta = -0.704$; $z = -2.21$, $p = 0.027$), but Stream Development had a positive direct effect ($\beta = 0.682$, $z = 2.10$, $p = 0.036$). Thus, our hypothesis that watershed-scale and stream-network land cover characteristics would influence habitat suitability was confirmed, but only for Development. Full results for tests of direct effects are presented in Table 2.

3.2. Indirect paths and total effects on arroyo toad habitat suitability

We identified two significant indirect effects of watershed-scale characteristics on Habitat Suitability. Watershed Forest had a net negative effect on Habitat Suitability ($\beta = -0.428$, $z = -3.84$, $p < 0.001$) mediated by stream-network land cover characteristics and contagion. Watershed Development had a positive indirect effect on Habitat Suitability ($\beta = 0.679$, $z = 2.16$, $p = 0.031$) mediated by watershed contagion, stream network land cover and contagion, but given

Table 2
Bootstrapped maximum likelihood estimates of direct effects in the Contagion Mediated Model for Habitat Suitability across the 110 HUCs.

Dependent variable	Direct effect	Standardized path coefficient	Bootstrap SE	*z*	*p*
Habitat Suitability for Arroyo Toads	Stream Development	0.682	0.3252	2.10	0.036
$R^2 = 0.344$	Stream Forest	0.033	0.2307	0.14	0.888
	Stream Contagion	−0.389	0.2103	−1.85	0.064
	Stream Agriculture	−0.038	0.1355	0.28	0.780
	Watershed Development	−0.704	0.3190	−2.21	0.027
	Watershed Contagion	0.162	0.1949	0.83	0.405
	Watershed Agriculture	−0.103	0.1493	−0.69	0.490
	Watershed Forest	−0.342	0.2373	−1.44	0.149
Watershed Contagion	Watershed Development	0.168	0.0876	1.92	0.055
$R^2 = 0.428$	Watershed Agriculture	0.362	0.0703	5.14	< 0.001
	Watershed Forest	0.573	0.0952	6.01	< 0.001
Watershed Agriculture	Watershed Development	−0.115	0.0759	−1.52	0.129
$R^2 = 0.013$					
Watershed Forest	Watershed Development	−0.239	0.1100	−2.17	0.030
$R^2 = 0.056$	Watershed Agriculture	−0.028	0.1037	−0.27	0.791
Stream Development	Watershed Development	0.899	0.0543	16.57	< 0.001
$R^2 = 0.848$	Watershed Contagion	0.120	0.0562	2.14	0.032
	Watershed Forest	−0.057	0.0685	−0.83	0.406
	Watershed Agriculture	−0.040	0.0372	−1.08	0.280
Stream Forest	Watershed Forest	0.682	0.0982	6.95	< 0.001
$R^2 = 0.738$	Watershed Contagion	0.217	0.0843	2.57	0.010
	Watershed Development	0.498	0.2236	2.23	0.026
	Stream Development	−0.604	0.2233	−2.70	0.007
	Watershed Agriculture	0.089	0.1168	0.77	0.444
	Stream Agriculture	−0.051	0.1059	−0.48	0.629
Stream Agriculture	Watershed Contagion	−0.007	0.0574	−0.13	0.898
$R^2 = 0.730$	Watershed Agriculture	0.851	0.0976	8.72	< 0.001
	Watershed Development	−0.213	0.1418	−1.50	0.113
	Stream Development	0.340	0.1428	2.38	0.017
Stream Contagion	Watershed Contagion	0.724	0.0562	12.87	< 0.001
$R^2 = 0.793$	Stream Development	−0.290	0.1656	−1.75	0.080
	Stream Forest	0.384	0.1498	2.57	0.010
	Stream Agriculture	−0.004	0.1410	−0.02	0.980
	Watershed Development	0.400	0.1644	2.43	0.015
	Watershed Agriculture	0.038	0.1687	0.22	0.823
	Watershed Forest	−0.170	0.1432	−1.18	0.236

the negative direct effect of Watershed Development and the positive indirect effect, the total effect was not significant ($\beta = -0.025$, $z = -0.250$, $p = 0.804$).

No stream network landcover variables had significant indirect effects on arroyo toad habitat, though Stream Development had a significant net effect on Habitat Suitability ($\beta = 0.880$, $z = 2.59$, $p = 0.010$; Table 3). Full results for tests of total effects are presented in Table 3 and results for tests of indirect effects are presented in Supporting Information (Appendix S2).

4. Discussion

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

The first two key questions we posed for this study were centered on how habitat suitability for arroyo toads is influenced by land cover characteristics at distinct scales of stream networks and watersheds. In general, we found Development was the primary land cover category influencing arroyo toad habitat suitability, but its effects differed across our focal scales; Watershed Development had a negative direct effect, but Stream Development had a positive effect. Arroyo toads are unlikely to perceive conditions outside 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 that factors we were not able to include due to data limitations were in play, such as fine-scale hydrology. We anticipated potential perennialization of streams in watersheds with higher levels of development would cause increased values in the Stream Forest path (White and Greer, 2006), but the measured increase was not statistically significant. The large swath of the stream network-scale for these analyses (200 m pixels), while relevant to areas arroyo toads may use, may have been too large to allow detection of such an effect if there was one, given wetted portions of streams can vary from only a few meters to approximately 30 m in width. Furthermore, vegetation change does not occur instantaneously, and multi-temporal data may better elucidate effects of Watershed Development, with a time-lag.

The positive relationship between Stream Development and habitat suitability for arroyo toads was contrary to what we anticipated, and we interpret this result with caution. 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 this apparent contradiction across scales is that the NLCD Level I category of Development, which loaded high on the “Development” principle components, includes finer categories of “Development Open Space” and “Development 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. There was also a strong positive influence of Stream Development on Habitat Suitability via negative (albeit non-significant) direct effects on Stream Contagion ($\beta = -0.389$, $z = -1.85$, $p = 0.064$; Table 2), which helps explain how Stream Development

Table 3

Bootstrapped maximum likelihood estimates of total effects in the Contagion Mediated Model for Habitat Suitability across the 110 HUCs.

Dependent variable	Total effect	Standardized path coefficient	Bootstrap SE	z	p
Habitat Suitability for Arroyo Toads	Stream Development	0.880	0.3399	2.59	0.010
$R^2 = 0.344$	Stream Forest	−0.117	0.2518	−0.46	0.643
	Stream Contagion	−0.389	0.2103	−1.85	0.064
	Stream Agriculture	0.045	0.1526	0.30	0.767
	Watershed Development	−0.025	0.1021	−0.25	0.804
	Watershed Contagion	−0.039	0.1278	−0.30	0.761
	Watershed Agriculture	−0.127	0.1062	−1.20	0.231
	Watershed Forest	−0.428	0.1189	−3.60	< 0.001
Watershed Contagion	Watershed Development	−0.008	0.1106	−0.08	0.938
$R^2 = 0.428$	Watershed Agriculture	0.346	0.0890	3.88	< 0.001
	Watershed Forest	0.573	0.0952	6.01	< 0.001
Watershed Agriculture	Watershed Development	−0.115	0.0759	−1.52	0.129
$R^2 = 0.013$					
Watershed Forest	Watershed Development	−0.236	0.1037	−2.16	0.031
$R^2 = 0.056$	Watershed Agriculture	−0.028	0.1038	−0.27	0.791
Stream Development	Watershed Development	0.916	0.0580	15.79	< 0.001
$R^2 = 0.848$	Watershed Contagion	0.120	0.0562	2.14	0.032
	Watershed Forest	0.012	0.0481	0.25	0.804
	Watershed Agriculture	0.003	0.0333	0.09	0.929
Stream Forest	Watershed Forest	0.800	0.0751	10.57	< 0.001
$R^2 = 0.738$	Watershed Contagion	0.142	0.0756	1.89	0.058
	Watershed Development	−0.228	0.1045	−2.18	0.029
	Stream Development	−0.621	0.2116	−2.94	0.003
	Watershed Agriculture	0.100	0.0984	1.02	0.308
	Stream Agriculture	−0.051	0.1059	−0.48	0.629
Stream Agriculture	Watershed Contagion	0.034	0.0607	0.55	0.581
$R^2 = 0.730$	Watershed Agriculture	0.849	0.0910	9.33	< 0.001
	Watershed Development	0.000	0.0736	0.00	0.996
	Stream Development	0.340	0.1428	2.38	0.017
Stream Contagion	Watershed Contagion	0.743	0.0626	11.87	< 0.001
$R^2 = 0.793$	Stream Development	−0.530	0.2034	−2.60	0.009
	Stream Forest	0.384	0.1498	2.57	0.010
	Stream Agriculture	−0.023	0.1302	−0.18	0.859
	Watershed Development	0.077	0.1105	0.69	0.489
	Watershed Agriculture	0.327	0.0828	3.96	< 0.001
	Watershed Forest	0.548	0.7254	7.56	< 0.001

could be positively associated with stream-scale habitat suitability. Aspects of urbanization patterns at this scale may help disaggregate land cover types, yielding spatially heterogeneous conditions. Fire, flood, and drought events, which arroyo toads are largely adapted to, can help maintain habitat 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 environmental disturbance. Other benefits of development may be associated with increased sediment load or decreased riparian vegetation. However, it is important to investigate these relationships further, while continuing to allow fine-scale management to be guided by knowledge of the species' ecology and natural history. In other words, urbanization may have some positive implications for arroyo toad habitat suitability at the stream scale if it disrupts the negative influences of other anthropogenic drivers of change, like fire-suppression.

With regard to the third key question of our study, focused on whether watershed-scale land cover influences habitat suitability through effects on stream network scale land cover, we found indirect effects of watershed-scale land cover on habitat suitability. In particular, our results indicate that watershed-scale land cover has relatively little influence on arroyo toad habitat when accounting for land cover along stream networks, with the positive effect of Stream Development. This finding was surprising, given 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 we used in this study, stream networks, was represented by 200 m pixels, studies that found negative impacts of large-scale development focused on finer-scale stream characteristics such as hydrologic flow metrics and water chemistry. We 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 our 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.

With regard to the fourth key question of our study, focused on whether clumpiness of land cover types, measured as contagion, influences habitat for arroyo toads, we found no strong evidence that it does. We considered contagion because the configuration of land cover types across landscapes may influence biophysical processes, and have been linked to habitat quality for species (Roseberry and Sudkamp, 1998). Furthermore, contagion can be driven in part by development patterns (Li et al., 2005; Wu et al., 2011), and is ultimately a tangible landscape feature that can be intentionally planned out with ongoing pressures of urbanization. We did find, however, that contagion substantially improved the fit of our statistical model, indicating it couples dynamics across our focal scales. In sum, the results provide partial support for our main hypotheses, namely that 1) arroyo toad habitat suitability is a function of watershed-scale land cover, 2) stream-network scale land cover, and 3) the interactive effects of land cover at multiple scales. Additionally, we found support for the proposition that watershed-scale anthropogenic land cover types (development and agriculture) influence finer-scale anthropogenic land cover types (White and Greer, 2006; Hawley and Bledsoe, 2013).

Our approach bears lessons for integrative projections of how future land cover change is most likely to affect amount and distribution of habitats for biodiversity dependent on riparian systems. Structural equation modeling has been used 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 of ecological change in aquatic ecosystems. Our results show relationships between land cover across watersheds, stream networks, and habitat for the arroyo toad are complex, but indicate the need for long-term watershed-scale management. For example, planning and policy to minimize or assess placement of future development across watersheds is one potential strategy for improving conservation of the species, while local-scale efforts may be more nuanced and on shorter time scales. Our general approach, that is, combining species' distribution information, habitat requirements, land cover variables, and structural equation modeling, could be applied to predict multi-scale effects of land cover change in habitat for stream fishes, stream invertebrates, or riparian forest wildlife. Though we 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 species' 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.

Studies that elucidate underlying watershed or landscape processes driving species' declines are needed to inform on-the-ground, long-term conservation actions. With knowledge of underlying processes affecting species and ecosystems at multiple scales, integrative approaches that combine knowledge of species' distributions and natural history with analyses of land cover change may yield critical information to guide the most practical and effective long-term solutions.

Acknowledgements

MLT and ACL were supported by NSF-IGERT Traineeships in the Applied Biodiversity Science Program at Texas A&M University (NSF DGE 0654377). MLT was also funded by a Tom Slick Doctoral Fellowship from Texas A&M University, an E.E. Williams Research Grant from the Herpetologists League, and the Sylvia Scholarship from the Mensa Foundation. We also thank the Fitzgerald Lab at Texas A&M for support and input throughout this project. The use of trade names does not imply U.S. Government endorsement. This paper is contribution number 647 of the U.S. Geological Survey's Amphibian Research and Monitoring Initiative, and publication number 1581 of the Biodiversity Research and Teaching Collections at Texas A&M University.

Appendix A. Supplementary materials

Results of principal component analyses (Appendix S1), and complete results for tests of indirect effects in the Contagion Mediated Model (Appendix S2) are available online. Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.10.032.

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