BIODIVERSITY RESEARCH

Effects of roads and land use on frog distributions across spatial scales and regions in the Eastern and Central United States

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ABSTRACT

Aim Understanding the scales over which land use affects animal populations is critical for conservation planning, and it can provide information about the mechanisms that underlie correlations between species distributions and land use. We used a citizen science database of anuran surveys to examine the relationship between road density, land use and the distribution of frogs and toads across spatial scales and regions of the United States.

Location Eastern and Central United States.

Methods We compiled data on anuran occupancy collected from 1999 to 2013 across 13 states in the North American Amphibian Monitoring Program, a citizen science survey of calling frogs. These data were indexed to measures of land use within buffers ranging from 300 m to 10 km.

Results The negative effects of road density and development on anuran richness were strongest at the smallest scales (300–1000 m), and this pattern was consistent across regions. In contrast, the relationships of anuran richness to agriculture and forest cover were similar across local scales but varied among regions. Richness had a negative relationship with agriculture/forest loss in the Midwest but a positive relationship with agriculture in the Northeast. Anuran richness was more closely related to primary/secondary road density than to rural road density, and the negative effects of larger roads increased at smaller scales. Individual species differed in the scales over which roads and development affected their distributions, but these differences were not closely related to either body size or movement ability.

Main conclusions This study further refines our understanding of the relationship between roads and amphibian populations and highlights the need for research into the specific mechanisms by which roads affect amphibians. Additionally, we find that relationships between land use and species richness can differ substantially across regions, demonstrating that one should use caution in generalizing from one region to another, even when species composition is similar.

INTRODUCTION

Land use change is a major driver of amphibian declines world-wide (Stuart et al., 2004; Hamer & McDonnell, 2008). Increased urbanization can alter the hydrology of aquatic habitats and increase concentrations of sediment and pollutants (Riley et al., 2005; Brand et al., 2010). Roads create additional problems for amphibians, including direct mortality from traffic, barriers to movement and habitat degradation along the road corridor (Hels & Buchwald, 2001; Karraker et al., 2008; Langen et al., 2009, 2015). Large-scale agriculture may also negatively affect amphibians; for example, increased eutrophication of aquatic habitats may increase the frequency of parasitic diseases (Johnson et al., 2007). In addition, unfavourable land uses can fragment amphibian habitats at larger spatial scales, reducing long-term population viability (Sjögren-Gulve & Ray, 1996; Hels & Nachman, 2002). However, development can sometimes provide new breeding habitats for amphibians (Birx-Raybuck et al., 2010; Brand & Snodgrass, 2010; Valdez et al., 2015), and many of the species common in areas long-inhabited by humans (e.g. Europe and Eastern North America) are likely tolerant to changes in landscape composition (Hartel et al., 2010). The relative strengths of the various factors influencing amphibians in changing landscapes is usually not known and can be particularly difficult to discern from small-scale studies confined to one specific study area.

One critical aspect of relating amphibian distributions to land use is spatial scale. Even when the land uses affecting amphibians are known, the strength of effects will usually depend on scale (e.g. Willson & Dorcas, 2003; Houlahan & Findlay, 2004). For example, roads may influence amphibians locally through direct mortality or runoff but may also affect amphibians at larger scales through the isolation of subpopulations connected by infrequent dispersal (i.e. metapopulations). Similarly, forest loss may reduce the availability of terrestrial habitats at a local scale and also eliminate or fragment dispersal corridors at a larger scale (Cushman, 2006). Thus, effective conservation planning requires knowledge of the scales over which changes in land use affect animal populations, both to predict the effects of land use changes on populations of conservation interest and to identify areas that are critical for conservation at a landscape scale (Pellet et al., 2004). In addition, knowing the scales over which land uses affect populations can provide indirect evidence about the underlying mechanisms involved. Localized effects of land uses tend to be associated with direct effects on individual survival, whereas effects at larger scales imply more diffuse effects on populations via habitat fragmentation and reduction in metapopulation connectivity (e.g. Cushman & McGarigal, 2004).

In a previous study (Cosentino et al., 2014), we combined citizen science data on frog and toad distributions (North American Amphibian Monitoring Program, 'NAAMP'; Weir & Mossman, 2005) with geospatial data on land cover within 1000 m of survey sites. We then analysed the relationship between land use and amphibian distributions across the Eastern and Central United States. We found that the effects of roads, from both road density and traffic volume, exerted a consistent negative influence on anuran species richness. In contrast, effects of development (i.e. proportion of the landscape developed) were weakly positive with respect to anuran richness, and effects of forest and agriculture were generally neutral with respect to species richness. Although the 1000-m scale that we used is similar to that employed in other studies of amphibian landscape ecology (e.g. Knutson et al., 1999; Guerry & Hunter, 2002), it did not allow us to determine the spatial scales over which each of these factors influence anuran distributions. Similarly, our previous analyses combined data across the entire study area; we did not determine whether effects differed across regions (e.g. Northeast versus Southeast).

In the current study, we expanded upon our previous analyses by examining the effects of land cover on anuran distributions across a range of spatial scales and across distinct regions of the United States with a new set of randomly selected NAAMP survey sites. In particular, we sought to determine whether relationships between land use and anuran distributions vary across spatial scales, and if so, whether this variation can provide insight on the mechanisms by which land use affects anurans. In addition, we asked whether relationships between land use and anuran distributions vary across regions of the United States, and which kinds of land use variables tend to be more consistent in their effects on anurans.

Furthermore, we addressed several additional questions raised by our previous analysis. First, we asked whether the negative relationships observed between road density and anurans are associated more with larger roads such as highways, or with the narrow, rural roads that are abundant in most areas. Second, we asked whether a more restrictive classification of 'developed land' would alter the positive effect of development on anuran richness that we observed in our previous study (Cosentino et al., 2014). Previously, we had estimated development by combining all 'developed' categories from the National Land Cover Database (NLCD; Fry et al., 2011), including 'developed open space' such as urban parkland. Third, we asked whether focusing specifically on row crop agriculture would change the neutral relationship between agriculture and anuran richness that we reported previously (Cosentino et al., 2014). Taking these questions as

a framework for analysis, we analysed relationships between anuran richness, individual species occupancy and land use variables at five distinct spatial scales from 300 m to 10 km across three regions (Northeast, Southeast and Midwest) of the United States.

METHODS

We compiled data on anuran distributions from NAAMP, a citizen science initiative coordinated by the United States Geological Survey (USGS; Weir & Mossman, 2005). NAAMP is based on 16-km road-based routes that are selected at random within each state and then assigned to volunteer monitors. Monitors perform an initial daytime survey of their route and establish 10 stops at least 0.8 km apart at roadside sites having water bodies within 200 m. They then survey these sites three nights each year during preselected time windows that overlap with anuran breeding periods. At each stop, monitors get out of their vehicle, note the time, temperature and weather conditions, and then record all frog species heard for a 5-min period. Following the survey, monitors' data are checked by a state NAAMP coordinator and then uploaded to the USGS. Because we were analysing land cover in comparatively large areas around each NAAMP stop (10 km), we randomly subsampled one stop from within each route to avoid spatial overlap in land cover buffers. The resulting dataset consisted of 567 NAAMP stops, more than 70% of which were not analysed in our previous study (Cosentino *et al.*, 2014).

With amphibian call survey data, both false positives and false negatives are potential sources of bias. To reduce false positives, we used county-based distribution maps for frogs from the National Amphibian Atlas (USGS, 2013) to remove records of species from outside their known range. To reduce false negatives, we excluded stops that had data from fewer than nine surveys (i.e. 3 years of data), leaving 399 total stops. We then took the number of unique species detected at each stop as our metric of species richness. In this dataset, the mean stop had 21.5 surveys (range 9–84)

taken over 6.4 years. Few stops had surveys that encompassed the entire period 1999–2013, and 86% of the stops included 10 or fewer years of data. After the exclusion of stops having fewer than nine surveys, the remaining correlation between estimated richness and the number of surveys was < 0.10. In addition, variance in observed richness was also only weakly affected by survey number; stops having 9–14 surveys had a variance in richness of 7.53 vs. 6.25 for stops with at least 15 surveys.

Land cover variables were chosen to represent factors known to be important from prior studies of anurans in North America (Table 1). These included the proportion of area surrounding a survey site covered by row crop agriculture, forest, wetlands or development. Development here included NLCD categories 22–24 (Developed, Low Intensity through Developed, High Intensity) but not category 21 (Developed Open Space). Wetland data were taken from the 2013 National Wetlands Inventory (U.S. Department of the Interior, 2013), whereas the other land cover variables were taken from the 2006 NLCD (Fry *et al.*, 2011). We also measured road density around each NAAMP stop from the 2013 TIGER road database (U.S. Census Bureau, 2013), which classifies primary roads (S1100) as divided highways, secondary roads (S1200) as other state and county highways and rural roads (S1400) as other paved and unpaved numbered or named roads. Because NAAMP stops are adjacent to roads, it was not possible to determine distance to nearest road. Instead, we defined the variable 'total roads' to represent the density of primary, secondary and rural roads, as well as other road classes such as private driveways, exit ramps and alleyways within each buffer zone. We then subdivided 'total roads' into a variable for primary and secondary road density ('P/S roads') and a variable for rural roads ('rural roads'). Finally, we measured impervious surface cover (from NLCD), which combines road cover with other types of higher-intensity development within each buffer. In practice, impervious surface and development were closely correlated.

Each of the land cover variables (Table 1) were measured in buffers around NAAMP survey stops at five scales: 300 m,

Table 1 Land cover variables included in analyses of anuran species richness and sources of data for each. Hypothesized effects based on prior research (shown in 'CITATIONS' column) are for species richness overall – effects on individual species might differ depending on tolerance of disturbance and on habitat use. NLCD indicates the National Land Cover Database (Fry *et al.*, 2011) and TIGER represents Topologically Integrated Geographic Encoding and Referencing (United States Census Bureau, 2013).

Variable	Data source	Hypothesized effect	Citations
Row crop agriculture	NLCD, class 82	Negative	(Joly *et al.*, 2001; Beja & Alcazar, 2003)
Forest cover	NLCD, classes 41–43	Positive	(Findlay & Houlahan, 1997; Guerry & Hunter, 2002)
Wetland area	National Wetlands Inventory, all classes	Positive	(Findlay & Houlahan, 1997; Knutson *et al.*, 1999)
Development	NLCD, classes 22–24	Negative	(Knutson *et al.*, 1999; Pellet *et al.*, 2004)
Impervious surface cover	NLCD	Negative	(Simon *et al.*, 2009; Sutherland *et al.*, 2010)
Total road density	TIGER Roads, all classes	Negative	(Fahrig *et al.*, 1995; Findlay & Houlahan, 1997)
Primary/secondary road density	TIGER Roads, classes S1100, S1200	Negative	(Fahrig *et al.*, 1995; Findlay & Houlahan, 1997)
Rural road density	TIGER Roads, class S1400	Negative	(Fahrig *et al.*, 1995; Findlay & Houlahan, 1997)

600 m, 1000 m, 5 km and 10 km. The smallest scale corresponds to a typical migration distance for an individual anuran, whereas the largest distance is similar to the maximum dispersal distance observed for any anuran (Smith & Green, 2005). The largest buffers occasionally (< 5%) overlapped with one another (i.e. across different NAAMP routes), but any overlap was typically a small proportion of the total area. Data layers were assembled and land use indices were calculated using QGIS version 1.8 (qGIS Development Team, 2013).

Land cover data for NAAMP sites were compiled on a state-by-state basis by undergraduate classes participating in the larger project (Cosentino *et al.*, 2014). As a quality control check, two students were independently assigned to compile the data for each survey stop. If, upon data submission, both datasets matched, then these values were entered into the full database. If the data did not match, students recalculated the values together until they reached consensus. To promote consistency, data from across states were collated at a conference including instructors and students from each participating institution. This process included additional quality control checks; unusually high and low values were manually checked for accuracy, searches were performed for duplicated data, and stops with land cover variables totalling more than 100% were removed.

Data analysis

Species richness

We examined the relationship between each of the land use variables and species richness using generalized linear models. Species richness was modelled as Poisson, and based on residual deviance values, these models provided a good fit to the data (i.e. no overdispersion). Because different areas varied considerably in anuran richness (e.g. Northern Minnesota with four species versus Coastal South Carolina with up to 16 species), we included net primary productivity (NPP, FAO GeoNetwork, http://www.fao.org/geonetwork) as a covariate in all models for species richness. Net primary productivity has been shown to strongly predict amphibian species richness over large geographic scales (Buckley & Jetz, 2007; Pyron & Wiens, 2013), and after correcting for NPP, residual species richness was similar across regions. Similarly, to account for bias due to sampling effort, we included the number of total surveys as a covariate in all models; survey number typically reduced AIC by 10–20 units. Land use variables were standardized to allow direct comparison of the strength of their relationships with species richness. To determine the scales over which each land use variable affected species richness, we regressed species richness residuals on each land use variable across the range of scales from 300 m to 10 km. Poisson regression coefficients (β's) were then used to compare the strength of each relationship across scales, and 95% confidence intervals on these parameters were used to delineate positive or negative relationships among variables.

Generalized linear models were fit for the entire dataset but also separately for three regions: the Northeast (126 routes from Vermont, New Hampshire, Massachusetts, New York, Pennsylvania, Maryland and Virginia), the Southeast (89 routes from North Carolina, South Carolina, Georgia and Florida) and Midwest (184 routes from Missouri and Minnesota). In the United States, the Northeast region is characterized by low anuran species richness, with most species being widespread. The landscape is a mix of large urban areas, farmland and forest with relatively high road densities

Table 2 Comparison of anuran species richness and land cover indices within 1000-m buffers across the Northeast, Southeast and Midwest regions of the United States. Residual richness refers to the species richness after accounting for net primary productivity (i.e. climate) and the number of surveys of each site. For estimated parameters, values show means across all stops with ≥ nine surveys, with standard deviations and ranges in parentheses. Land cover variables are given as proportions of the total buffer area, whereas road density variables reflect linear metres of road within the buffer. 'P/S road density' refers to the combined density of primary and secondary roads.

Variable	Northeast Mean (SD; range)	Southeast Mean (SD; range)	Midwest Mean (SD; range)
Years	1999–2013	2002–2013	1999–2013
Stops	126	89	184
Richness	5.9 (2.6; 0–15)	8.0 (3.1; 1–16)	5.4 (1.8; 0–9)
Residual richness	−0.44 (0.97)	0.16 (1.1)	0.08 (0.8)
Row crop cover	0.10 (0.26; 0–0.83)	0.06 (0.15; 0–0.92)	0.26 (0.32, 0–0.96)
Forest cover	0.49 (0.25; 0–0.98)	0.46 (0.25; 0–0.97)	0.28 (0.25; 0–0.92)
Wetland cover	0.09 (0.18; 0–0.90)	0.13 (0.18; 0–0.93)	0.16 (0.19; 0–0.99)
Development	0.04 (0.08; 0–0.69)	0.02 (0.05; 0–0.97)	0.02 (0.06; 0–0.59)
Impervious Surface	0.03 (0.04; 0–0.37)	0.01 (0.02; 0–0.13)	0.01 (0.03; 0–0.29)
Total Road Density (km)	10.0 (5.0; 0.2–39.1)	7.4 (4.6; 0.2–24.5)	6.2 (4.1; 1.9–31.1)
P/S road density (km)	1.7 (1.6; 0–5.9)	0.8 (1.3; 0–5.0)	0.4 (1.0; 0–4.9)
Rural road density (km)	8.0 (4.4; 0–33.7)	6.6 (4.4; 1.3–24.0)	5.8 (3.6; 1.8–27.1)

(Table 2). The Southeast has very high anuran richness with many species that are distinct to the region and some that have highly restricted distributions. This region generally has lower human population densities than the Northeast, and the landscape is a mix of farmland, plantation forestry and lowlands with high wetland densities (Table 2). In the Midwest, anuran species richness is similar to the Northeast (with overlapping species composition). However, human population densities are much lower than in the other regions, and the landscape includes large-scale industrial farming of corn and soya beans (Table 2).

Relationships between anuran species richness and land cover variables were compared across regions both graphically and with estimates for region-by-factor interaction terms. For these analyses, models that included a region-by-factor interaction were compared to models that excluded an interaction using a likelihood ratio test. For simplicity, these comparisons were carried out at the 1000-m scale, although results were similar for smaller or larger scales.

Generalized linear models were also used to compare the relative effects of different road types (primary/secondary versus rural roads) on species richness and to examine the scales over which these different road types were most influential. To compare the effects of different road types, we examined four models for species richness residuals: one that included total road density, one that included only the density of primary/secondary roads, one that included only the density of rural roads and a null model not incorporating road density. For our initial comparison, we used model selection with AIC (Burnham & Anderson, 2002) to compare the relative fit of each of these models within a 1000-m buffer. We then used regression to compare the strength of effect (i.e. magnitude of β) for primary/secondary versus rural roads across the range of spatial scales. As detection of frogs can be reduced near roads, we repeated these analyses including the frequency of surveys for which external noise was documented ('noise frequency') as a covariate.

Because NAAMP surveys cover a relatively long period of time (1999–2013 in this study) and because land cover variables were estimated at different time points (e.g. 2006 for NLCD versus 2013 for TIGER road data), our results could be influenced by landscape change over the survey period. To test this possibility, we used NLCD imagery from 2001 to 2011 to identify all NAAMP stops that showed > 10% land cover change over this period. We then dropped these sites ($n = 92$) and reran the analyses described above including only the sites that had limited land cover change (i.e. < 10%) during the survey period.

Individual species analysis

Individual anuran species use aquatic and terrestrial habitats in distinct ways and disperse over different scales, producing species-specific responses to roads and development. To examine species-specific responses, we performed a series of analyses relating a species' occurrence to road density and

development variables across the range of measured scales. We selected a subset of species that were detected at between approximately 20% and 80% of all stops within their range and that had at least 60 stops where the species had been detected (as in Cosentino *et al.*, 2014). This subset included the following eight species: *Anaxyrus americanus* (314 detections, 71% occupancy), *Hyla cinerea* (98 detections, 55% occupancy), *Hyla chrysoscelis/versicolor* (374 detections, 73% occupancy), *Lithobates catesbeianus* (181 detections, 43% occupancy), *Lithobates clamitans* (242 detections, 51% occupancy), *Lithobates palustris* (66 detections, 19% occupancy), *Lithobates sphenocephalus* (157 detections, 58% occupancy) and *Lithobates sylvaticus* (155 detections, 52% occupancy). The diploid gray treefrog (*H. chrysoscelis*) was combined with the tetraploid species (*H. versicolor*) because their calls can be difficult for volunteers to differentiate in the field (Genet & Sargent, 2003).

For each species, we used occupancy modelling in presence (MacKenzie *et al.*, 2006) to estimate the number of surveys required to achieve a 0.90 probability of detecting a species that is present at a site (see Cosentino *et al.*, 2014 for details). We then subsampled stops from the full dataset including only stops with sufficient surveys to reach this goal for a species. In principle, dynamic occupancy modelling would be suitable for the overall analysis of species-specific responses (MacKenzie *et al.*, 2003; Jones & Tupper, 2015). However, because NAAMP data spanned different years in different states and such missing blocks of data were not independent of variation in land cover variables, these models rarely achieved convergence in parameter estimates. Therefore, we used logistic regression to model presence/absence as a static, binary variable based on stops with sufficient surveys to achieve 90% detectability.

Logistic regressions relating occupancy to road density variables and impervious surface were carried out for each of the eight species at each of the five relevant spatial scales. The explanatory value of the variables across scales was compared using logistic regression coefficients (β's). The scale of maximal effect for each species was then related to two species traits: a species average size (snout–vent length; Olalla-Tárraga & Rodríguez, 2007) and its maximum known movement distance (Smith & Green, 2005). In addition, for each species we used AIC to compare the overall explanatory value of the different road types (i.e. total road density versus primary/secondary road density versus rural road density) and a null model within the 1000-m buffer. All analyses were carried out using R version 3.12 (R Core Team, 2014), and raw data are available through the Dryad digital repository (http://datadryad.org).

RESULTS

Species richness and land cover

After quality control screens, we obtained data from 567 NAAMP stops across 13 states in the Eastern and Central United States. For species richness analysis, these data were

reduced to 399 stops that had each been surveyed at least nine times. Among land cover variables, row crop agriculture was most highly correlated across spatial scales (Appendix S1, Table S1); most correlations were > 0.90 and even the correlation between agricultural cover within 300 m and agricultural cover within 10 km was > 0.80. Forest cover, impervious surface, development and wetland area were all moderately to highly correlated across scales, whereas road density variables showed lower correlations across scales (Appendix S1, Table S1). Given these correlations, agricultural cover was expected to show minimal differences in correlations with species richness across spatial scales, and forest cover, impervious surface, development and wetland area were expected to show only small to moderate differences in correlations with species richness across spatial scales. Because road density variables were much less correlated across scales, these variables allowed for greater resolution in their relationships with species richness and individual species distributions.

For the pooled data from all regions, anuran species richness was negatively related to row crop agriculture at all spatial scales (Fig. 1), although 95% confidence intervals on beta coefficients overlapped zero at scales ≤ 600 m. Richness was not related to forest cover, whereas richness was positively related to wetland cover across scales (Fig. 1). Anuran richness was negatively related to both development and impervious surface; these relationships tended to be strongest at the smallest scales. Anuran richness was negatively related to total road density, and this relationship was similar across spatial scales (Fig. 1). These results did not appear to be influenced by landscape change over the survey period. When we dropped sites with > 10% land cover change

between 2001 and 2011 (n = 92), results were largely similar (Appendix S1, Fig. S1). The one apparent difference was that the effect of forest cover on richness became more positive (Appendix S1, Fig. S1); this occurred because the majority of the excluded sites were in the Southeast where richness is highest in coastal lowlands with limited forest cover.

Across different regions, relationships between species richness and landscape variables were consistent for roads, development and wetlands, but varied for agriculture and forest (Fig. 2). In the Midwest, species richness showed a strong negative relationship with agriculture at all scales and a strong positive relationship with forest cover. In the Northeast and Southeast, relationships between species richness and agriculture were positive to neutral, and relationships between richness and forest were neutral (Northeast) to negative (Southeast). These differences in landscape–richness relationships were apparent as statistical interactions between region and agriculture (χ^2 = 19.02, d.f. = 2, P < 0.0001) and between region and forest (χ^2 = 19.8, d.f. = 2, P < 0.0001). Because agricultural cover and forest cover had a high negative correlation, particularly in the Midwest (r = −0.61 to −0.79), these differences should be regarded as a single response to landscape change.

Road type, development and impervious surface

At the 1000-m scale, species richness showed a stronger negative relationship with the density of primary/secondary roads than with total road density or rural road density (Table 3). However, the effects of road types varied among spatial scales. Richness was negatively related to the density
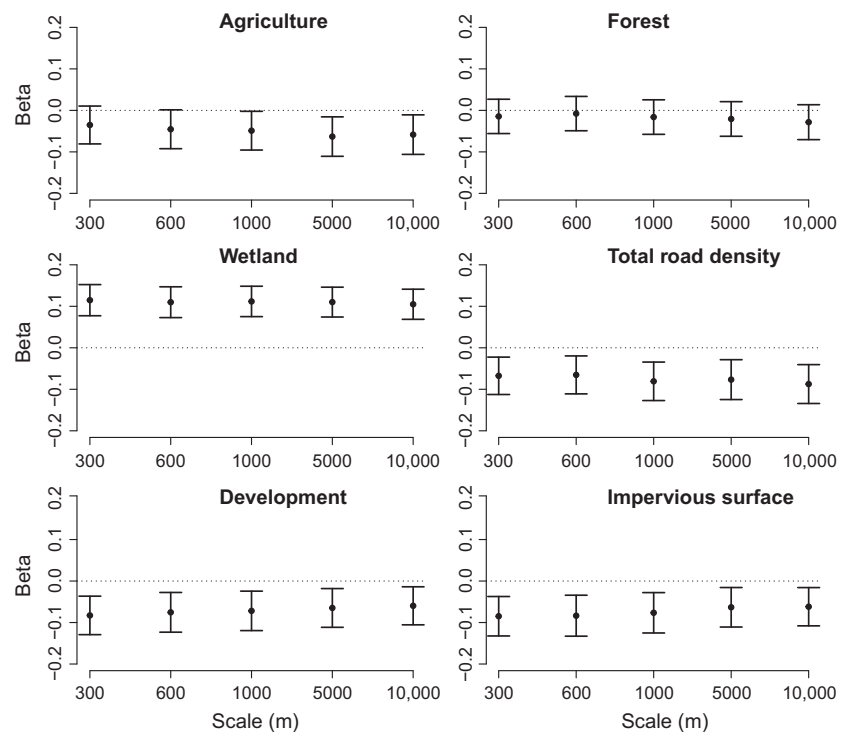

Figure 1 Beta coefficients from regression between land cover variables and species richness for all regions combined. Agriculture, forest, wetland, development, and impervious surface refer to proportion of land area assigned to each variable within the buffer. Road density refers to the total length of roads within the buffer. Error bars represent 95% confidence intervals.
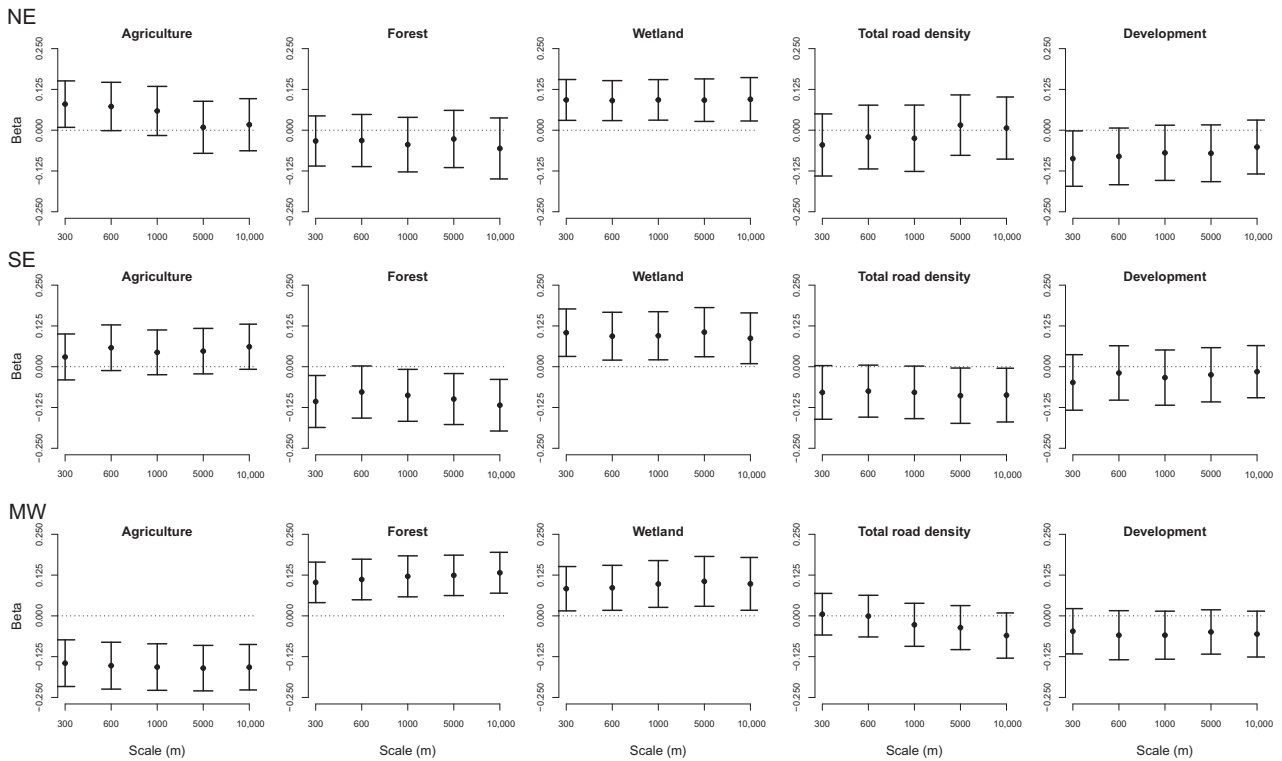
Figure 2 Relationships between land cover variables and species richness for each individual region. Northeast (NE) includes the states of Virginia, Maryland, Pennsylvania, New York, Massachusetts, Vermont and New Hampshire. Southeast (SE) includes North Carolina, South Carolina, Georgia and Florida, and Midwest (MW) includes Missouri and Minnesota. Error bars represent 95% confidence intervals.

Table 3 Comparison of models relating anuran species richness to road density for different classes of roads. Models compared are as follows: (1) density of primary/secondary roads within 1000 m, (2) total road density within 1000 m, (3) rural/other road density within 1000 m and (4) a null model with no coefficient for road density. ΔAIC refers to the difference in Akaike information criteria values between each model and the best model in the set. ω is the model weight, the probability that a model is the best model in the set given the data. LL is the log likelihood of the data given the model, K is the number of parameters in the model, and R^2 is the proportion of variation in species richness explained by each variable. Beta refers to the regression coefficient for each variable with 95% confidence intervals.

Model	ΔAIC	ω	LL	K	R^2	Beta (95% CI)
Primary/secondary	0.00	0.98	−880.37	4	0.25	−0.10 (−0.14 to −0.05)
Total	7.66	0.02	−884.19	4	0.23	−0.08 (−0.12 to −0.03)
Rural	16.28	0.00	−888.51	4	0.21	−0.04 (−0.08 to 0.00)
Null	18.52	0.00	−890.63	3	NA	NA

of primary/secondary roads across scales, but the strength of this relationship declined with buffer size (Fig. 3a). In contrast, richness was unrelated to the density of rural roads at small scales (300–1000 m) but was negatively related to rural road density at large scales (≥ 5 km; Fig. 3a). These relationships were unchanged when we included the frequency of recorded noise as a covariate in these analyses (Fig. 3b). There were also no detectable interactions between total road density and region ($\chi^2 = 1.08$, d.f. = 2, $P = 0.58$), indicating relatively consistent effects of roads across regions.

The negative relationship between species richness and both impervious surface cover and development was strongest at 300 m. At this distance, a comparison between a model including development ($K = 4$) and a model including impervious surface cover ($K = 4$) yielded similar fits to the species richness data (Δ log likelihood = −0.3, Δ AIC = 0.6). The pattern of change across scales was also similar between the two variables, with correlations between richness and each development index declining substantially at scales larger than 1000 m. The negative relationships between development/impervious surface and species
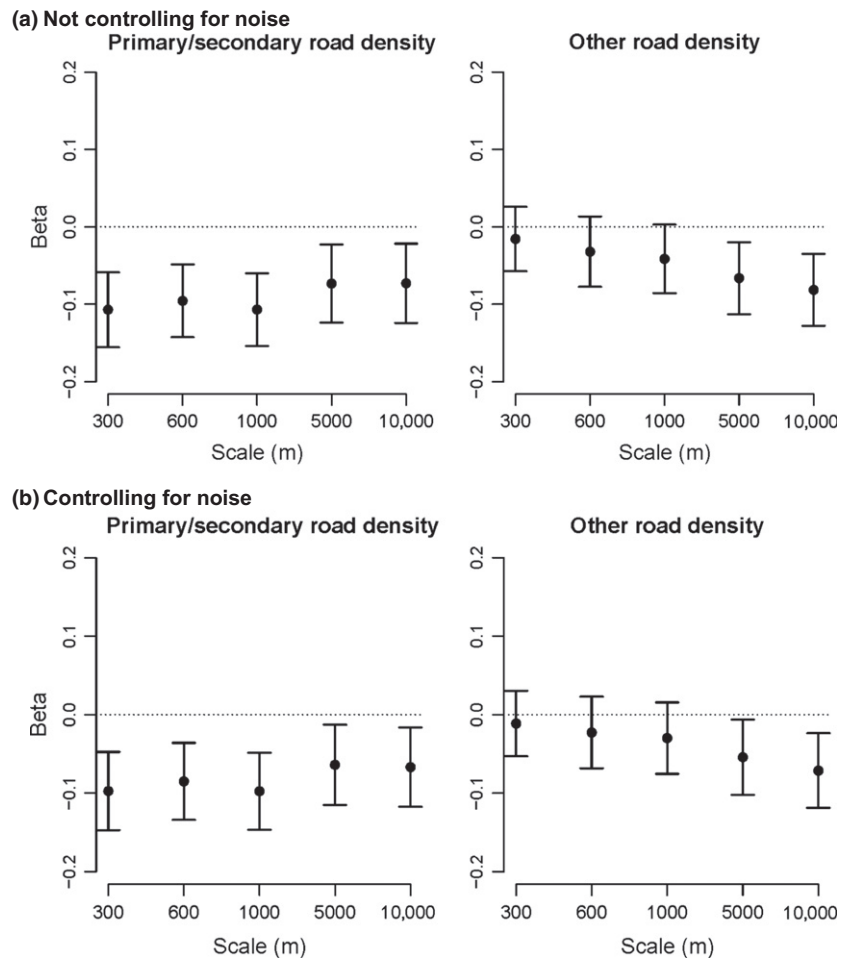
Figure 3 Relationships between road density and anuran species richness across scales for different road types with road noise excluded from the model (a) and included as a covariate in the model (b). Primary/secondary roads refer to divided two-lane or four-lane roads. Other roads refer to all other roads, primarily undivided rural roads. Error bars represent 95% confidence intervals.

richness were also consistent across regions ($\chi^2 = 0.14$, d.f. = 2, $P = 0.93$).

Individual species distributions

Individual species varied in the scales at which roads and impervious surface affected their distributions (see Appendix S2 in Supporting Information). *A. americanus*, *H. chrysoscelis/versicolor* and *L. catesbeianus* all showed negative relationships with road density variables at smaller scales (Table 4). *Hyla cinerea* had a negative relationship with primary/secondary road density only at 5 km, and *L. sylvaticus* distributions were negatively related to road density at all scales. *L. sphenocephalus* had no relationship with road density, and the relationships between *L. clamitans* and *L. palustris* distributions and road density were positive at larger scales (> 5 km).

For impervious surface, *A. americanus* and *L. catesbeianus* had negative relationships only at smaller spatial scales, and *L. sphenocephalus* were negatively related to impervious surface at all scales. Five taxa – *L. clamitans*, *L. palustris*, *L. sylvaticus*, *H. cinerea* and *H. chrysoscelis/versicolor* had no significant relationship with impervious surface cover, although some marginal negative relationships were apparent (Appendix S2).

Although individual species varied widely in the scale of their responses to roads and impervious surface (Appendix S2; Table 4), we found no clear relationship between the scale of their response and either adult size or maximum movement ability. With respect to size, the largest frog (*L. catesbeianus*) showed effects predominantly at small spatial scales, as did the smallest frog in the sample (*H. chrysoscelis/versicolor*). In contrast, *H. cinerea*, which is similar in size to *H. chrysoscelis/versicolor*, showed effects that peaked strongly at the second-largest scale (5 km). With respect to maximum movement distance, the highly mobile *L. clamitans* was affected by roads and development at larger spatial scales. But *A. americanus*, which is also highly mobile, mainly showed effects at small spatial scales. *L. sylvaticus*, which have limited movement ability, were affected by roads across a range of spatial scales. Thus, it appears that variation in the scale of road impacts was not closely related to adult size or movement ability.

DISCUSSION

Understanding the spatial scales over which land use affects animal populations is critical for effective conservation planning. Because many frogs and toads need to move between terrestrial and aquatic habitats, they may be sensitive to

Table 4 Summary of relationships between roads/impervious surface and the occupancy of individual species across spatial scales from 300 m to 10 km.

Variable	Total roads	Primary/secondary roads	Other roads	Impervious surface	SVL (max mm)	Movement (max m)
Richness	(−) ALL	(−) ALL	(−) ≥ 5000 m	(−) ALL	NA	NA
ANAM	(−) ≤ 1000 m	(−) ALL except 5000 m	No effect	(−) ≤ 1000 m	111	6437
HYCI	No Effect	(−) 5000 m	No effect	No effect	64	no data
HYCV	No effect	(−) ALL except 5000 m	No effect	No effect	60	125
LICA	(−) ≤ 1000 m	No effect	No effect	(−) ≤ 600 m	203	1600
LICL	(+) 10,000 m	(+) 10,000 m	(+) 10,000 m	No effect	102	4800
LIPA	(+) 5000 m	(+) 5000 m	No effect	No effect	87	no data
LISP	No effect	No effect	No effect	(−) ALL	127	no data
LISY	(−) ALL	(−) ALL except 5000 m	(−) 10,000 m	No effect	83	60

(+) indicates a positive relationship between variables (i.e. 95% confidence intervals on the parameter did not overlap zero) and (−) indicates a negative relationship between variables. 'ALL' indicates that the relationship was seen at all scales tested. Data on snout–vent Length (SVL) are from Olalla-Tárraga & Rodríguez (2007) and movement data are from Smith & Green (2005). ANAM, *Anaxyrus americanus*; HYCI, *Hyla cinerea*; HYCV, *Hyla chrysoscelis/versicolor*; LICA, *Lithobates catesbeianus*; LICL, *Lithobates clamitans*; LIPA, *Lithobates palustris*; LISP, *Lithobates sphenocephalus*; LISY, *Lithobates sylvaticus*.

changes in land use affecting either habitat type over a range of scales (Vos & Stumpel, 1995; Pope *et al.*, 2000). That said, whether land use effects differ across scales in real landscapes depends on the structure of the landscape and the scales over which land uses actually vary. We found that for land use buffers of 300 m–10 km, forest and row crop cover were each highly correlated across scales and thus had consistent relationships with anuran species richness. However, among regions (e.g. Northeast versus Midwest), these relationships often differed substantially. In contrast, for primary and secondary road density and development/impervious surface cover, relationships with anuran species richness were consistently negative in all three studied regions but tended to be stronger at the smallest scales (300–1000 m).

Variation in the scales over which land use affects animal populations can also provide insight into mechanisms underlying these effects. For example, negative relationships between road density and amphibian richness could be caused by habitat alteration, mortality or dispersal barriers acting at local scales or by habitat fragmentation acting at larger scales (Forman & Alexander, 1998; Marsh & Jaeger, 2015). We found that the negative relationship between species richness and road density was stronger for primary/secondary road density than for total roads or rural roads. Stronger negative effects of larger or more heavily trafficked roads on amphibians have been reported in several previous studies (Fahrig *et al.*, 1995; Hels & Buchwald, 2001; Gibbs & Shriver, 2005). Interestingly though, the effects of primary/secondary roads appeared strongest at smaller scales (300–1000 m), whereas the effects of rural roads were negligible at smaller scales but were significantly negative at larger scales (5 and 10 km). This result suggests that the major effects of roads on anurans are caused by larger roads acting locally on populations through decreased habitat quality or increased road mortality (e.g. Hels & Buchwald, 2001). Nevertheless, smaller roads may exert some additional influence on anurans via habitat fragmentation or disruption of

metapopulation connectivity at larger scales (e.g. Hels & Nachman, 2002).

Whereas the effects of roads on anuran richness were relatively consistent across regions, the effects of forest and row crop cover differed considerably between the Midwest and the Northeast and Southeast United States. In the Midwest, forest cover had a consistent positive relationship with anuran richness (see also, Knutson *et al.*, 1999), whereas row crop agriculture was negatively related to richness. In contrast, in the Northeast and Southeast, the relationship between anuran richness and forest was neutral to negative, and the relationship between row crop agriculture and richness was neutral to positive. One difference between these regions is that farms in the Midwest tend to be large monocultures in rotation between corn and soya beans (Meehan *et al.*, 2011). In contrast, agricultural land uses in the Southeast and Northeast are more varied, and many agricultural operations are smaller scale. Larger agricultural operations are likely to use pesticides and fertilizers more intensively than smaller farms, and habitat diversity is likely to be lower in these areas. Previously, Knutson *et al.* (1999) reported an analogous difference in the effects of agriculture between frogs in Wisconsin and frogs in Iowa. In Wisconsin, where agricultural intensity is comparatively low, associations between frogs and agriculture were mostly positive whereas in Iowa, where agricultural intensity is much higher, associations between frogs and agriculture were neutral to negative. Similarly, results from studies carried out in a single region have varied in terms of whether associations between amphibians and agriculture have been neutral (Pellet *et al.*, 2004), positive (Knutson *et al.*, 1999) or negative (Joly *et al.*, 2001; Beja & Alcazar, 2003)

Individual species differed in terms of the scales over which roads and development affected their distributions. Three species (*A. americanus*, *H. chrysoscelis/versicolor* and *L. catesbeianus*) were most sensitive to road effects at small scales, and these species were largely responsible for the overall

patterns in species richness. In contrast, two species (*L. clamitans* and *L. palustris*) showed positive relationships with road density at larger scales. These differences among species were not obviously related to either anuran size or movement ability, two characteristics that have been shown to explain variation in landscape responses for other taxa (Gehring & Swihart, 2003; Reinhardt *et al.*, 2005). Instead, variation among species could reflect differential use of habitats that are associated with roads or development (e.g. roadside ditches or retention ponds); different behavioural responses to traffic, roadways and roadside verges (Carr & Fahrig, 2001; Karraker & Gibbs, 2011; Langen *et al.*, 2015); differences in sensitivity to the conditions of roadside habitats (Jackson *et al.*, 2015a,b); or some unmeasured aspect of these species' life histories. Differences among amphibian species in land use associations have been observed in a number of previous studies (Knutson *et al.*, 1999; Hazell *et al.*, 2001; Gagné & Fahrig, 2007) and highlight the need for caution in generalizing about groups of amphibians or about the effects of specific land uses (Koumaris & Fahrig, 2016). For example, all of the species we analysed are widespread (which was necessary for us to have sufficient distributional data) and therefore are unlikely to be highly sensitive to disturbance. Anuran species with narrower distributions, or more poorly dispersing salamanders, could show very different relationships with roads across this range of spatial scales.

Given that NAAMP surveys were conducted along roadsides with traffic noise, it was necessary to separate effects of roads on actual occupancy from effects of roads on the detection of frogs. In particular, traffic noise may prevent observers from hearing frog calls, or road noise may reduce calling rates even when they are present (Lengagne, 2008; but see Kaiser & Hammers, 2009). To ensure high detection rates, we only analysed data for sites that had sufficient surveys to achieve 90% detection probabilities for each species (as in Cosentino *et al.*, 2014). In addition, we analysed road density/richness relationships including a covariate for the proportion of surveys where traffic noise was noted. Given that that our results were largely unchanged when including noise as a covariate, we believe our findings with respect to roads reflect patterns of actual occupancy rather than biases in detection rates. However, difficulty in distinguishing effects on occupancy from effects on detention remains an inherent problem with roadside surveys.

An additional limitation of our study is that data were compiled over a period a decade or more. Some changes in land use and species assemblages almost certainly occurred within this extended survey period. Although results were similar when we analysed only stops with < 10% landscape change from 2001 to 2011 (Appendix S1, Fig. S1), it is possible more subtle effects of land use change or effects with lag times would have been missed. In addition, by compiling richness over an extended period, our study would have missed local extinctions and recolonization, processes that can be important within amphibian assemblages (Marsh & Trenham, 2001; Walls *et al.*, 2011). Unfortunately, data on

any single species were usually too sparse to permit analysis of year-by-year changes across the study region.

One important difference from our previous work is how we treated 'development' in the context of land cover. In the current study, we excluded 'developed open space' and only included NLCD categories for suburban development and more intense development. The resulting metric closely corresponded with impervious surface coverage, which has been used in other studies of urbanization and amphibians (Simon *et al.*, 2009; Sutherland *et al.*, 2010). This difference in categorization likely accounts for the fact that development in the current study was negatively related to species richness, whereas the effects of development in the previous study were weakly positive. This implies that that low-intensity development (e.g. developed open space) may be positively related to anuran species richness, but that higher-intensity development may have negative effects on anuran richness. This suggestion is consistent with results from other regions where urban development has tended to be negatively related to amphibian species richness (Gagné & Fahrig, 2007; Eskew *et al.*, 2012; Kruger *et al.*, 2015).

Our results have several implications for landscape ecology and amphibian conservation. First, we demonstrate that the effects of localized landscape features such as roads and development are scale dependent. However, when land use encompasses very large areas (e.g. forest, agriculture), relationships between land use and occupancy or abundance will tend to be similar across scales. Interestingly, agriculture and forest, which did not vary in their effects across scales from 300 m to 10 km, had very different relationships with anuran richness across regions of the United States. In particular, the relationship between agriculture and richness was positive in the Northeast region but strongly negative in the Midwest region. Second, our results show that the effects of road density on amphibian richness, well documented in previous studies (Findlay *et al.*, 2001; Pellet *et al.*, 2004; Johnson *et al.*, 2013), are primarily associated with small-scale effects of larger roads, and secondarily associated with larger-scale effects of smaller roads. Although these relationships were variable among species, they suggest that negative effects of roads are more likely to be due to local effects (e.g. road mortality, degraded roadside habitat), than to large-scale fragmentation effects. This is potentially useful for conservation planning and mitigation in that mitigation for local effects of roads (reviewed in Jackson *et al.*, 2015a,b) is typically more straightforward and cost-efficient than is large-scale landscape planning. That said, the precise mechanisms by which larger roads affect amphibians (e.g. vehicle impacts versus pollution of adjacent habitats) still need to be better understood before the negative consequences of roads can be properly mitigated.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Coefficients from regression between land cover variables and species richness including only sites with minimal (< 10%) land cover change.

Figure S2. Effects of roads and impervious surface on *Anaxyrus americanus*.

Figure S3. Effects of roads and impervious surface on *Hyla chrysoscelis/versicolor*.

Figure S4. Effects of roads and impervious surface on *Hyla cinerea*.

Figure S5. Effects of roads and impervious surface on *Lithobates catesbeianus*.

Figure S6. Effects of roads and impervious surface on *Lithobates clamitans*.

Figure S7. Effects of roads and impervious surface on *Lithobates palustris*.

Figure S8. Effects of roads and impervious surface on *Lithobates sphenocephalus*.

Figure S9. Effects of roads and impervious surface on *Lithobates sylvaticus*.

Table S1. Correlations across spatial scales for landscape variables.

Table S2. Comparison of road types for individual anuran species.

Appendix S1. Ancillary species richness analyses.

Appendix S2. Detailed analyses for individual frog and toad species.

BIOSKETCH

David Marsh is a professor of biology at Washington and Lee University. His current research focuses on the effects of land use and climate change on salamanders and frogs.

Author contributions: D.M. designed the project and led the writing of the manuscript, with contributions from B.C. and K.B. B.C., D.M. and K.J. compiled and analysed the final dataset. D.M., B.C., J.J.A., K.H.B., J.M.B., C.B., D.C., J.F.C., A.D., E.A.F., M.F., J.G., K.S.G., M.H., K.R.H., S.A.H., F.I., N.E.K., E.S.K., T.A.L., J.L., K.L., A.M., J.N., S.P., A.P., C.S., N.S., N.S., M.T., J.M.T. and J.R.V. carried out the data compilation and analysis within their individual states.

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