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Research Paper

Do species distribution models predict species richness in urban and natural green spaces? A case study using amphibians

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HIGHLIGHTS

- Amphibian species richness maps significantly over-predicted species richness.
- Over-prediction may have partially been a result of undersampling during surveys.
- Over-prediction was likely due to poor model performance and undersampling.
- Despite over-prediction, models did project relative species richness well.

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ABSTRACT

Urban green spaces are potentially important to biodiversity conservation because they could provide patches of high quality habitat or connectivity to nearby habitat. Presence-only species distribution models (SDMs) represent a potential tool for assessing the biodiversity value of urban green space; however, there is limited research to validate SDM results with field surveys to see if the predictions accurately represent observed species richness. We generated a range of SDMs using multiple suitability thresholds for 23 species of amphibians that occur in southwest, Ohio, USA. The distributions were overlaid to enumerate species richness. We surveyed 20 sites for amphibian species to evaluate model predictions. Our models over-predicted species richness relative to survey data. For example, we observed a mean pairwise difference of 14 species between models of species richness and observed values. Our results suggest either SDMs built with landscape variables we selected did not represent accurately amphibian richness, or the amphibian surveys did not detect all species present. Analyzing sites that had more than three sampling events suggests the explanation of inadequate sampling effort is only partially correct. Differences such as that between predicted and observed values of species richness is a challenge for land managers and conservation biologists that need a tool for modeling biodiversity. Species distribution models did project relative species richness well in urban and non-urban green space, which suggests this technique offers a spatially explicit way to identify more species rich areas and may help managers and conservation biologists manage systems with greater efficiency.

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1. Introduction

Much of global population growth is occurring in urban areas (United Nations, 2004; Wu, Jenerett, Buyantuyev, & Redman, 2011) and over one-half of the United States population resides in urban areas (MacKun & Wilson, 2011). Nevertheless, human land use patterns are dynamic and some locations within urban areas are experiencing declining populations. Such declines can result in land abandonment and provide an opportunity to replace developed habitat with green infrastructure. It is well established that urbanization changes the biotic and abiotic properties of an ecosystem and these impacts can reach far outside the urban area (Gaston, 2010). To reduce these effects, there has been a movement to implement green infrastructure or incorporate green space to urban areas. The benefits of green space in urban systems include increased psychological well-being, recreational opportunities, and human health benefits (e.g., Barton & Pretty, 2010; Breuste & Qureshi, 2011; Tzoulas et al., 2007; van den Berg, Hartig, & Staats, 2007). These benefits are often predicated by ecosystem services and functions such green space in urban ecosystems provide (e.g.,

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water filtration and quality; Bolund & Hunhammar, 1999; Faulkner, 2004; Gaston, Davies, & Edmondson, 2010). Whereas urban habitats may not act as smaller versions of undeveloped patches of land, they may still provide ecological and human-oriented benefits such as providing habitat connectivity, which helps to sustain regional biodiversity (Goddard, Dougill, & Benton, 2009; Irvine et al., 2010; Luck & Smallbone, 2010), or providing permeable surface for stormwater infiltration, or water purification (Boyer & Polasky, 2004). Monitoring and management for biodiversity has inherent value (Connery, 2009) and biodiversity conservation within urban areas can help minimize extinction risk of some species and increase the value of biota to humans as they more frequently encounter wildlife (Goddard et al., 2009). Toward this end, metrics are needed to measure the degree to which urban green spaces sustain biota and subsequent biodiversity.

An ideal metric would use taxa that serve as indicators of overall biodiversity, provide an ecosystem service, and are a critical link to the biotic community within the green space (i.e., provide ecosystem functions). Amphibians are often the most abundant, diverse group of vertebrate organisms in forested and wetland systems, they serve as important food resources for higher trophic levels, and in many systems are considered the top-predators (Burton & Likens, 1975; Davic & Welsh, 2004; Gibbons et al., 2006). Amphibians are also considered to be indicators of environmental stress (DeGarady & Halbrook, 2006; Southerland et al., 2004; Welsh & Droege, 2001; Welsh & Ollivier, 1998), but see Kerby, Richards-Hrdlicka, Storfer, and Skelly (2010), and are known to provide a number of ecosystem functions in natural ecosystems (Davic & Welsh, 2004; Regester, Lips, & Whiles, 2006; Regester & Whiles, 2006; Whiles et al., 2006). Moreover, amphibians in urban environments, like other biota, can enhance educational opportunities for human inhabitants (Pickett et al., 2001). Because of their importance to ecosystems, ability to indicate environmental stress, and education value, research involving amphibians in urban systems is warranted (Hamer & McDonnell, 2008; McDonnell & Hahs, 2008; Pickett et al., 2001; Smallbone, Luck, & Wassens, 2011). Due to time and financial constraints associated with conducting biotic surveys, modeling methods may provide assistance in understanding the value of urban green space to this taxon.

Presence-only species distribution models (SDMs) are models that correlate species distribution records to environmental data to predict areas of suitable habitat for taxa (see review in Elith et al., 2006; Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000). They are a group of approaches for identifying species distributions of undersampled species, predicting impacts of environmental change on distributions, and identifying areas of conservation importance (Elith & Leathwick, 2009). In recent years, validations of models in various forms have been increasing. For example, methods utilizing species occupancy or detection (Franklin, Wejnert, Hathaway, Rochester, & Fisher, 2009; Rota, Fletcher, Evans, & Hutto, 2011), independent and non-independent data validation (Araujo, Pearson, Thuiller, & Erhard, 2005), and the incorporation of field/survey data to inform or test model accuracy (Newbold et al., 2010; Pineda & Lobo, 2009; Trotta-Moreu & Lobo, 2010) have been examined. However, studies simply using field data to validate whether models are projecting species distribution correctly are rare.

Others have noted several limitations to SDMs including exclusion of biotic, geographical, or physiological constraints on species distributions, use of museum records that may be widely variable in both spatial and temporal quality, and issues relating to extrapolation of model predictions (see review in Elith & Leathwick, 2009). These limitations may be exacerbated when modeling within spatial extents that include urban environments, because species are sampled less in urban areas as ecologists tend to focus collections or research on natural areas (Gaston et al., 2010; Martin, Blossey, & Ellis, 2012). Furthermore, lack of uniform sampling across gradients of development presents a challenge to using SDMs in an urban landscape because SDMs assume that biases in locality data (e.g., false absences) are not correlated with environmental gradients used to build projected distributions (Bean, Stafford, & Brashares, 2012; Hijmans, 2012). In addition, error in the predictions of SDMs varies over large spatial scales (extent and resolution) due to increased spatial heterogeneity (Osborne, Foody, & Suarez-Seoane, 2007; Smulders, Nelson, Jelinski, Nielsen, & Stenhouse, 2010; Zhang & Zhang, 2007), such as variation of environmental, landscape, and habitat structure. This trend may be seen at smaller spatial scales (extent and resolution) when using fine-scale data to build models (e.g., 30 m resolution) such as in urban areas that have several classes of land use categories (e.g., habitat heterogeneity), as the increased heterogeneity in urban areas within a smaller spatial scale could pose similar prediction errors.

We tested whether species richness maps generated from SDMs can be used to prioritize areas of high biodiversity value in urban and non-urban green space. We asked if SDMs built using landscape variables associated with amphibian species richness could be used to project areas of suitable habitat. We addressed this question by comparing modeled species richness maps (based on accumulated individual SDMs) to field surveys across a number of urban and non-urban green spaces. In addition, we investigated the landscape-level predictors of observed amphibian species richness to determine what variables may be important to include or protect in the creation, management, or conservation of urban and non-urban green space.

2. Materials and methods

2.1. Species distribution modeling using maximum entropy

We developed species distribution models using Maxent version 3.3.3a (Phillips & Dudik, 2008) for 23 species of amphibians with current distributions within Hamilton County, Ohio, U.S.A. Maxent is a software program that employs a machine learning method that is based on the principle of maximum entropy to model species distributions using presence-only data coupled with environmental data. Entropy is characterized by Shannon (1948) as “a measure of how much ‘choice’ is involved in the selection of an event” and is utilized in the framework of maximum entropy to examine species geographic distributions (Phillips, Anderson, & Schapire, 2006). The approach estimates habitat suitability based on an input set of environmental variables encompassing the region where a species is known to occur based on locality records. The program maximizes the entropy in the probability distribution of suitability across all areas of the distribution where empirical observations are lacking. For each species identified as occurring in Hamilton County, OH, species presence data were obtained for the period of 1997–2001 from HerpNET (http://www.herpnet.org), Global Biodiversity Information Facility (Lane, 2003; GBIF; http://www.gbif.org), and personal collections of herpetologists (Appendix A). All locality points were cross-referenced to each other and duplicate points were removed. Furthermore, localities that fell outside the current species range (identified by county-level distribution maps found in Lannoo, 2005) were not utilized to develop models. To maximize model quality, each model was built using at least 20 point locations for each species (Wisz et al., 2008).

We modeled the suitable habitat of each species across the National Hydrography Dataset Plus (U.S. Geological Survey, 2005; NHDPlus; retrieved from http://www.horizon-systems.com/nhdplus/) Region 05 Unit B watershed delineation. This delineation was necessary to encompass the environmental variability of each species and provide predicted records from across a larger geographic region adjacent to our primary study area. Additionally, amphibian distributions can be restricted by geographic barriers (i.e., large rivers), and this region encompassed a large portion of each species range, as well as the primary area of our field surveys used to validate our models. This watershed delineation also encompasses a number of similar adjacent urban areas (e.g., Lexington, KY, Indianapolis, IN, and Huntington, WV; Appendix B) that could be examined in future studies.

We chose 11 initial environmental variables that others have shown to be important to amphibians (e.g., Herrmann, Babbitt, Baber, & Congalton, 2005; Weyrauch & Grubb, 2004) and had data available. Geographic data layers were at a resolution of 30 m and variables extracted from these included land cover, elevation, canopy cover, distance from stream, and slope/aspect. We created three layers using a moving window analysis to compute a ratio of cells classified as urban or water within moving windows of 150, 300, and 500 m. Lastly, we calculated the number of cells representing wetland habitat, as defined by the National Wetlands Inventory layer (U.S. Fish and Wildlife Service, 2011; retrieved from http://www.fws.gov/wetlands/), within 300 m and 2 km moving windows. We tested collinearity of the 11 layers by extracting environmental information from 1000 randomly selected points (selected using the Random Point Generation Tool within Hawth's Analysis Tool software for ArcGIS) within the watershed. A correlation matrix was generated and correlations with $r \geq 0.70$ were considered highly correlated. When pairs of variables exceeded this threshold ($r \geq 0.70$), we chose one variable from the pair that we considered the most biologically relevant. Eight variables (listed below with the data source) were chosen for inclusion in the final distribution model. Land cover (Homer et al., 2007; retrieved from http://www.mrlc.gov/) was reclassified into one of the seven classes as follows (original land cover classes given in parenthesis): 'forest' (41, 42, and 43), water/wetlands (11, 90, and 95), 'low intensity developed' (21 and 22), 'medium intensity developed' (23), 'high intensity developed' (24), 'natural non-forest' (31, 52, and 71), and 'agriculture' (81 and 82). Canopy cover values were taken from the National Land Cover Database (NLCD; Homer et al., 2007; retrieved from http://www.mrlc.gov/). Elevation data were derived from NHDPlus (National Hydrography Dataset; U.S. Geological Survey, 2005; retrieved from www.horizon-systems.com/nhdplus/). The distance from stream (DSL) was measured as distance (in meters) from the nearest drainage. Drainages were delineated from the flow accumulation layer (downloaded from NHDPlus; retrieved from www.horizon-systems.com/nhdplus/) as areas that drained 100 ha or more. The synthetic slope/aspect layer (TASL; which represents aspect ranging from −1 [NE] to 1 [SW] and is weighted based on the steepness of the slope) was derived from NHDPlus elevation data following Pierce, Lookingbill, and Urban (2005). Finally, we selected three layers from the moving window analysis: sum of urban, water and wetland cells within a 300-m buffer. Urban and water cells were designated from our reclassified NLCD database, whereas wetland cells were designated from the National Wetlands Inventory layer (U.S. Fish and Wildlife Service, 2011; retrieved from http://www.fws.gov/wetlands/). We chose the 300-m buffer because a 290-m buffer is recommended for maintaining wetland and riparian habitat, thus this distance has been suggested to be important for encompassing the core habitat requirement for many amphibian populations (Semlitsch & Bodie, 2003). Moving window, DSL, and TASL layer calculations were performed using ArcGIS (version 9.3; ESRI, Redlands, CA).

Maxent was run from the command line using the default settings with exception of background points. A total of 620 target-group background data points representing localities of amphibians in the designated watershed were used to develop an initial environmental envelope to represent the range of environmental conditions within the modeled region. This method is used to reduce the bias inherent in sample locality data (Phillips et al., 2009). The target-group background approach uses background data (known as pseudo-absences) to develop the models. The background points are chosen with the same biases as occurrence data and produce an unbiased estimate of the geographic distribution of each species. The resulting background data provide an equitable sample of the environmental conditions within the region modeled. Due to the use of background points, we disabled the "addsamplestobackground" function. Further, we disabled the "extrapolate," "Do MESS with analysis when projecting," and "Do clamping" functions. Following methods in Milanovich, Peterman, Nibbelink, and Maerz (2010), a multiple threshold approach was used to designate a location as environmentally suitable for a species. Because Maxent produces a continuous probability of suitable habitat for each species, it is logistically unfeasible to present each location as a probability of occupancy; therefore, we converted the continuous suitability surface [0–1 from Maxent to presence/absence (1/0)] using four model output thresholds applied by Maxent; fixed cumulative value 10 (FC10), minimum training presence (MTP), 10 percentile training presence (10% TP), and maximum training sensitivity plus specificity (MTSPS). Next, we generated four species richness maps based on the accumulated binary modeled distributions of each species using the four Maxent thresholds. This four-threshold approach makes our results comparable to other studies that provide predictions based on strict environmental distributions of species (i.e., thresholds that maximize the agreement between observed and predicted distributions; Cramer, 2003). This approach allows us to present model predictions that relax the assumption of strict environmental control on species' distributions, and provides a range of scenarios that could influence the predicted suitable habitat at the species-level and comprehensive species richness.

We used null models to test the significance of each species distribution model (Raes & ter Steege, 2007). We generated five null data sets, each with 1000 sets of sample points that were randomly drawn without replacement from the pool of 620 background points. We generated a null data set with the number of random points per distribution equal to 20, 45, 75, 150 and 250 data points, which represented a range of presence points available to model each species. Maxent was used to calculate the area under the curve (AUC) for the 1000 null data sets to create an AUC frequency distribution. The calculated AUC for each species model was compared to the 95th percentile AUC value of the null frequency distribution created from the representative number of sample points (20, 45, 75, 150, or 250). A species model performs better than random (e.g., null model) and is considered significant if the calculated AUC is greater than the corresponding 95th percentile AUC of the null-distribution (Raes & ter Steege, 2007).

2.2. Examining differences in amphibian species richness

2.2.1. Amphibian surveys

To evaluate the degree to which SDMs accurately predict amphibian richness, we conducted amphibian surveys at 20 sites across the Cincinnati, OH metropolitan area following methods proposed in Shaffer et al. (1994). Each site consisted of identified green space, spanned a range of sizes (3–1758 ha; Appendix C), and were spread across a gradient of urbanization (e.g., within and outside the designated Cincinnati, OH metropolitan area; Fig. 1; Appendix B). Surveys were conducted March–June 2011 and each site was sampled three times with a 3- to 5-week period between repeat samples. To standardize our search effort within each site, nine plots were selected and surveyed at each site. We attempted to place three plots in each of three habitat types associated with

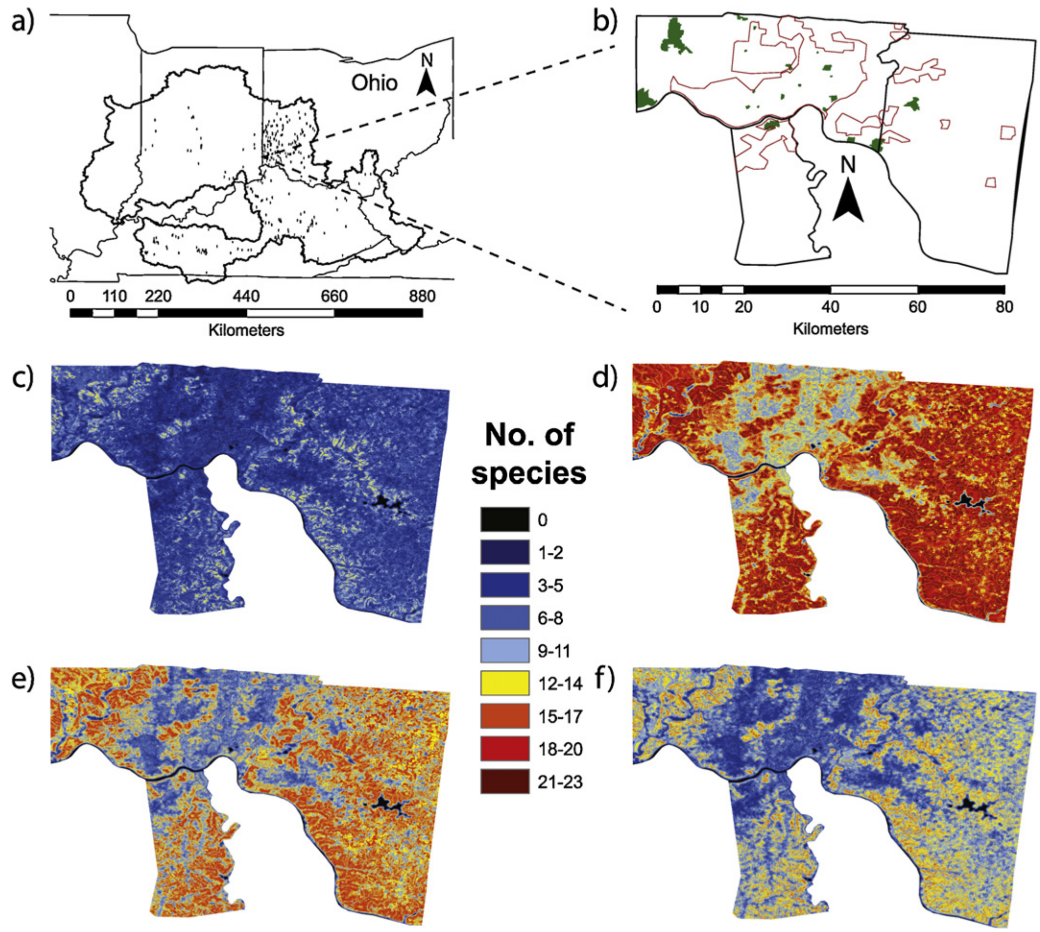

Fig. 1. (a) Distribution of locality points (black dots) used to model species suitable habitat within the watershed boundary. The boundary is located across several states with Ohio and Kentucky (the states where the surveys were conducted) located in the northeast and southern border of the map; and (b) the three counties where each green space (site) was surveyed; metropolitan areas are outlined with a red line and surveyed green spaces are represented by filled green polygons. Surveys were conducted throughout various locations within each site. The four lower panels represent the predicted amphibian species richness maps within the three counties surveyed as derived from the maximum training sensitivity plus specificity threshold (MTSPS) (c), minimum training presence threshold (MTP) (d), 10 percentile training presence threshold (10% TP) (e), and fixed cumulative value 10 threshold (FC10) (f).

amphibian richness: wetlands/ponds, streams, and terrestrial (forest or non-forest natural [e.g., grassland/prairie]) habitat. In the event that three each of wetlands/ponds or streams were not available, we increased the number of terrestrial plots to reach nine total plots for each site. If more than three of an aquatic habitat type were available (e.g., wetlands/ponds or streams) we sampled plots with the most suitable amphibian habitat (i.e., forested wetlands/ponds or streams). We employed three survey techniques at each site: area-sensitive dip-net surveys for pond and/or ephemeral wetland habitats, area sensitive terrestrial (searching cover objects) surveys, and leaf litter bags and dip-netting area-sensitive surveys for headwater streams following Chalmers and Droege (2002) and Waldron, Dodd, and Corser (2003). At each wetland/pond, we dip-netted several 1 m^2 areas adjacent to the bank using a 40.6 cm × 40.6 cm (3.2 mm mesh size) net. Plots were placed every 10 m until the entire perimeter of the body of water was sampled. For terrestrial plots, we surveyed five, 5 m^2 sub-plots at each site. Plots were chosen by placing a single 5 m^2 plot within the center of each habitat type occurring on the site (forest or non-forest natural [prairie or grassland habitats]) and an additional 5 m^2 plot in each cardinal direction 25 m from the center plot. Within each sub-plot, all cover objects and existing leaf litter were searched. Within each stream, five 1 m^2 plots were created every 10 m starting approximately 20 m from the confluence of a larger stream, road, or trail and continuing upstream. Within each plot, we placed one leaf litter bag (55 cm × 25 cm made with 1.3 cm^2 mesh) filled with deciduous leaf litter from the surrounding forest in a wetted portion of the stream channel with a large rock on top to prevent dislodging. We followed the methods of Nowakowski and Maerz (2009) and Peterman, Truslow, and Samuel (2008) to remove contents from each bag; we thoroughly dip-netted the 1 m^2 plot by dislodging substrate parallel to the stream bank across the width of the stream. In addition to our structured surveys, any animals encountered (seen or heard) while traveling between habitat types or plots within a site were noted. All animals captured or heard (frog calls) were identified to species.

2.2.2. Validation of amphibian surveys and richness comparisons

We examined how well predicted species richness matched observed species richness by comparing the maximum species richness value from each site between observed and predicted (from each Maxent threshold) values derived from our maps. We compared differences between species richness within “urban” and “non-urban” sites by categorizing a site as “urban” if ≥50% of the adjacent landscape within a 2-km buffer of the centroid of the site had urban cells (NLCD categories 21–24) based on our NLCD 2001 reclassified maps. To test for differences between predicted species richness from each model threshold, we used paired *t*-tests to compare observed and predicted (from each threshold) species richness values from each site surveyed.

To examine if we adequately sampled species richness, we estimated species richness using EstimateS version 8.2 (Colwell, 2009) for six sites that had been surveyed on at least 10 occasions. Additional survey data were derived from reports summarized in Davis, Krusling, and Ferner (1998). These reports summarized data from county-park-level surveys that took place between 1988 and 1995, surveyed a similar level of habitat heterogeneity and utilized similar survey methods to our study, and lasted approximately 1 year. We chose to make comparisons between species richness at this group of sites using the Chao 2 estimator because this algorithm produces species accumulation curves that approach maximum values with few samples (i.e., the estimator was the least sensitive to undersampling; Colwell & Coddington, 1994). The Chao 2 algorithm inflates the observed species richness by a factor derived from the number of species observed only once or twice within a total sample. The estimator is calculated as $S_{\text{Chao}\,2} = S_{\text{obs}} + {Q_1}^2/2Q_2$, where S_{obs} is the observed species richness and Q_1 and Q_2 are the number of species detected only once or twice per site, respectively. Thus, this estimator accounts for the fact that species differ in detectability and uses the relative frequencies of species that are rarely detected to estimate the number of taxa that are present but not detected (Chao, 1987; Colwell & Coddington, 1994). For each additional site we calculated coverage (number of species observed/number of species estimated × 100), exclusive species (percentage of species only observed in a given site or category), and completeness of a sample (species observed as a percentage of the total number of species expected in the site; Gardner et al., 2007). This approach estimated the amphibian species richness at sites visited ≥10 times and provided an estimate of the number of sampling periods needed to accurately capture the estimated richness value. These values were then compared to the observed amphibian species richness values derived from the current surveys and the surveys of Davis et al. (1998).

2.2.3. *Identifying factors that influence observed species richness*

We used a general linear model and an information theoretic approach to examine which environmental factors were most predictive of observed amphibian species richness. This model is specific to existing green spaces, unlike the species distribution models, which provide a more general estimate of species richness patterns. As a result, the environmental variables used in this analysis are similar to those in the distribution model; however, some differences do exist. Observed species richness was the dependent variable. Independent variables included the percent of urban land within a 2-km buffer of the centroid of each site (square root transformed), the number of wetlands within a 2-km buffer of the centroid of each site (log transformed), percent forest within each site (square root transformed), and percent non-forest natural habitat (agriculture and non-forested natural habitat) within each site (square root transformed) as continuous predictor variables. Using the same variables as above, we evaluated the importance of landscape variables on observed species richness using Akaike Information Criterion (Burnham & Anderson, 2002). These variables were derived from our reclassified NLCD 2001 land cover layer and a National Wetlands Inventory layer (U.S. Fish and Wildlife Service, 2011; http://www.fws.gov/wetlands/) and were chosen out of an initial set of 11 independent variables that we thought would have an influence on amphibian species richness (Table 3). We generated a correlation matrix of all 11 variables and chose four variables that were not correlated with each other ($r \leq 0.70$). Variables were transformed to meet normality assumptions (Sokal & Rohlf, 1995).

Lastly, to determine the relationship between our observed species richness values and the mean predicted species richness values across the urban gradient, we conducted an analysis of covariance. Maxent predictions (predicted species richness) and field observations (observed species richness) were factors in the analysis, percent urbanization within 2-km of each site (square root transformed) was our covariate, and observed species richness and mean predicted species richness values were used as our dependent variables. The significance of the interaction term was evaluated to determine if the relationship between observed and predicted species richness estimates differed across the urban treatments.

Table 1
Estimates of how much SDMs over-predicted species richness values in green spaces in and around Hamilton County, Ohio. Values in the table represent the percentage each threshold (MTP = minimum training presence threshold, MTSPS = maximum training sensitivity plus specificity threshold, 10% TP = 10 percentile training presence threshold, FC10 = fixed cumulative value 10 threshold) over-predicted species richness compared to surveyed values for all sites (overall), urban sites (sites with ≥50% urbanization within the 2-km buffer of centroid), non-urban sites (sites with ≤50% urbanization within 2-km buffer of centroid), and from eight sites where past species richness values (derived from county-park surveys) were added to our current species richness values derived from current surveys (labeled Additional).

Urbanization category	MTP	FC10	10% TP	MTSPS
Overall ($n = 20$)	558	467	373	253
Non-urban ($n = 6$)	619	572	468	343
Urban ($n = 14$)	532	422	333	215
Additional ($n = 8$)	98	81	50	14

3. Results

The mean AUC for amphibian distribution models based on landscape variables was 0.83 (range = 0.70–0.96; median = 0.83; Appendix A) and the AUC for each species was better than random (i.e., model AUC values exceeded the 95th percentile of the null AUC distributions). Observed and predicted species richness varied across each site (Appendix C). Mean observed species richness was triple in non-urban sites compared to the value in urban sites (mean species richness values; overall = 3.2, urban = 1.9, non-urban = 6.2). There were significant differences between observed and predicted species richness for each threshold (Table 1; all t-tests $P \leq 0.001$). Overall, mean differences between observed and predicted species richness within each threshold ranged from 253% to 558% (mean range = 8–18 species). These differences increased when “non-urban” sites were isolated from “urban” sites (mean range = 343–619%; mean range = 8–17 species) and decreased when sites sampled greater than 10 times were isolated from sites sampled three times (mean range = 14–98%; mean range = 2–11 species; see “Additional” column in Table 1).

The MTSPS threshold, our most conservative threshold, had the lowest levels of over-prediction between observed and predicted species richness in both urban and non-urban sites, whereas the MTP threshold had the greatest levels of over-prediction. The species accumulation curves (Fig. 2) for all green spaces sampled >3 times, except Farbach-Werner Nature Preserve, suggest these sites had been (more or less) exhaustively sampled (i.e., the species accumulation curve reaches a plateau). There was no site for which the final estimate of species richness from the species accumulation curves was achieved by the third sample (based on, e.g., Chao 2 richness estimator; Fig. 2 and Table 2).

Observed amphibian species richness varied depending on the number of wetlands and percent of urbanization within a 2-km buffer around the centroid of each site (Tables 3 and 4). Percent of forest or non-forest natural habitat within each site did not predict observed species richness (Table 3). The best model (based on lowest AICc and highest w_i) for observed species richness also includes number of wetlands and percent of urbanization within a 2-km buffer around the centroid of each site (Table 4). Percent of forest or non-forest natural habitat within each site did not predict observed species richness (Table 3). Despite the significant discrepancies in absolute richness values between the observed and predicted species richness values, there was a significant trend of decreasing

Table 2
Summary species richness data for amphibians at sites sampled ≥10 times in the Hamilton County, Ohio area.

Site	S_{obs}[a]	Chao 2 est. richness[b]	95% lower CI[b]	95% upper CI[b]	% Coverage[c]	% Exclusive species[d]	% Completeness[e]
Miami	12	12	12	12	100	10	60
Shawnee	10	10	10	11	100	0	50
Farbach-Werner	5	10	6	46	53	0	25
Triple Creek	9	9	9	10	100	0	45
Richardson	14	14	14	20	98	5	70
Withrow	9	9	9	10	100	15	45

[a] Number of species observed.
[b] Number of species estimated to be present (and associated 95% confidence intervals) based on the Chao 2 estimator.
[c] Number of species observed as a percentage of the average estimated species richness (Chao 2).
[d] Number of species not found elsewhere as a percentage of the landscape total.
[e] Number of species observed as a percentage of the landscape total.

Table 3
Results from a general linear model investigating the factors that influenced the observed amphibian species richness within each site and associated parameter estimates and 95% confidence intervals (CI). Percentage data were square root transformed and number of wetlands within 2-km buffer was log transformed. Excluded correlated variables not chosen for analysis were as follows: size; standard deviation of land cover within parks and 2-km buffer of centroid; percent forest, non-forest natural, and urban cells within 2-km buffer of centroid, and number of aquatic habitats surveyed within each site.

Source	*df*	MS	*F*	*P*	Parameter estimate	−95% CI	+95% CI
% Urbanization within 2-km buffer	1	11.717	5.465	0.034	−5.66	−10.82	−0.50
No. wetlands within 2-km buffer	1	15.118	7.052	0.018	0.97	0.19	1.75
% Forest within site	1	0.593	0.277	0.607	0.79	−2.40	3.98
% Non-forest natural within site	1	0.111	0.052	0.823	0.52	−4.35	5.39
Error	15	2.144	–	–	–	–	–

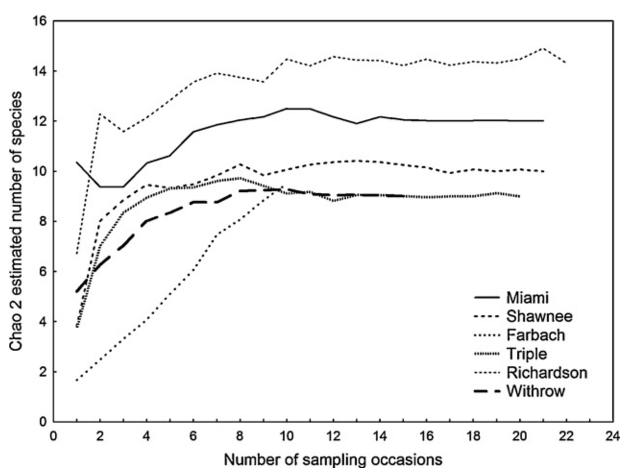

Fig. 2. Sample-based species accumulation curves for the six heavily sampled sites in the Hamilton County, Ohio metropolitan area.

richness with increasing urban habitat ($P < 0.001$ for both observed and mean predicted richness). Further, the slopes of these two trends did not differ ($P = 0.913$; Appendix D) between modeled and observed values and the relationships between observed and predicted species richness was significantly correlated to the level of adjacent urbanization (Appendix D).

Table 4
Best Akaike Information Criteria (AIC) models for observed species richness across all 20 green spaces. Shown are only the confidence set of candidate models (i.e., models with AIC w_i within 10% of highest model). Variables included were percent urbanization within 2-km buffer, number of wetlands within 2-km buffer, percent forest within site, and percent non-forest natural habitat within site.

Model	AICc	ΔAICc	w_i
No. wetlands + % urbanization	72.19	0.00	0.61
No. wetlands + % urbanization + % forest	75.35	3.16	0.13
No. wetlands + % urbanization + % non-forest	75.35	3.16	0.13
No. wetlands + % non-forest	76.26	4.07	0.08

4. Discussion and conclusions

The use of SDMs built with high-resolution landscape variables and real-time amphibian surveys allows us to assess whether this technique is a valid method to identify areas of higher and lower species richness across urban and non-urban green space. Our approach of modeling followed by field surveys revealed differences between observed and predicted species richness across urban and non-urban green space (Table 1). These differences can be interpreted as (1) sites were undersampled, thus our observed measure of species richness could be inaccurate or (2) the SDMs are over representing actual species distributions – which accumulate to unrealistic predictions of species richness across the landscape. Our results suggest the differences are likely due to both factors. First, species accumulation curves derived from the Chao 2 estimator based on six sites that were extensively surveyed (i.e., ≥10 sampling events over approximately 1 year), indicated three sampling periods was not a sufficient effort to capture species richness. In each of these six sites, species accumulation curves did not plateau until between six to 10 sampling periods (Fig. 2). We conducted an intensive single-season survey that reasonably mimics the effort many agencies would implement to understand factors driving species distributions of amphibians. We know from studies with a more intensive sampling effort that this is not sufficient to capture all species, because often species are unavailable for capture for entire breeding years (e.g., Barrett & Guyer, 2008).

However, undersampling alone did not explain all of the differences between observed and predicted species richness. Chao 2 species richness estimates showed SDMs still over-predicted species richness even in sites considered to be adequately sampled (Table 2). For that subset of sites, we have reasonable confidence (empirically demonstrated via richness estimator) that all differences between sampled and predicted species richness are not due to undersampling alone. This suggests the differences are at least partially a consequence of SDM predictions.

We propose the SDM influence on over-prediction is the result of the inherent nature of SDMs. By solely using environmental variables to construct predictions of a species' suitable habitat, SDMs fail to incorporate biological or geographic influence on species distributions (e.g., Guisan & Thuiller, 2005; Heikkinen et al., 2006;

Luoto, Pöyry, Heikkinen, & Saarinen, 2005), also referred to as realized versus fundamental niche (Rodda, Jarnevich, & Reed, 2011; Soberón & Peterson, 2005). This in turn can lead to an overestimation of species suitable habitat, as only areas of suitable habitat, not realized distribution, are projected. This overestimation may increase when adding multiple individual models to create species richness maps (Hortal & Lobo, 2006; Pineda & Lobo, 2009; Thullen, Sartoris, & Walton, 2002; Vasconcelos, Rodriguez, & Hawkins, 2011), as was the case in this study. Furthermore, although the use of target-group background data is suggested to reduce sampling bias (Phillips et al., 2009), use of this approach could be a possible source of overestimation. Models developed utilizing replicate samples and random background data could result in a greater or lesser over-estimation of species richness values. Further investigation into the influence of various modeling approaches to overestimation of species richness is warranted.

Using multiple thresholds to develop a range of scenario's of species predicted suitable habitat was a definite strength of this study (Fig. 1; Appendices B and C), and the differences between predicted species richness for different model thresholds should not be ignored. The importance of presenting a range of model thresholds has been supported in other studies (Liu, Berry, Dawson, & Pearson, 2005; Milanovich et al., 2010; Pineda & Lobo, 2009; Thullen et al., 2002). We suggest presenting a range of thresholds allowed the geographic range of suitable habitat for each species to be both larger and smaller than realized ranges. This may account for some of the geographic and biotic influences on species ranges; however, as our results indicate, threshold adjustment may be a necessary, but not entirely sufficient means for generating more precise SDMs.

Despite the over-prediction of our models and differences between model thresholds, we argue this technique is a useful tool for management of green space by identifying areas suitable for amphibians in urban ecosystems. Specifically, although the model richness estimate was high, there was no difference between the trend in observed richness and modeled richness across the urban treatments. Species distribution models are increasingly used to identify potential areas for conservation and management of biodiversity (Lawler, Wiersma, & Huettmann, 2011; Loiselle et al., 2003). In this study, SDMs identified areas of higher suitability, as green space with higher observed species richness generally had higher predicted species richness (Appendices B and C). For example, the Cincinnati Nature Center and Richardson Nature Preserve (the non-urban sites with the highest observed species richness) and Farbach-Werner Nature Preserve and Triple Creek Park (the urban sites with the highest observed species richness) each had some of the highest predicted species richness within each threshold (Appendix C). One commonality between these sites is each site had a high number of adjacent wetlands (within 2-km of the centroid), and therefore, a high number of aquatic habitats surveyed (Appendix C). With respect to management of existing or development of new urban green spaces, we found the number of wetlands adjacent to each site was a significant predictor of observed amphibian richness (Tables 3 and 4). Our predictive models support the importance of wetlands in urban green space to amphibian species richness, as the two urban sites with surveyed wetlands (Farbach-Werner N.P. and Triple Creek Park) had the highest predicted species richness of all urban sites. This highlights the importance of prioritizing the maintenance, restoration, or mitigation of wetlands in urban green space. Furthermore, this is a testament to the usefulness of SDMs for identifying areas of potential conservation importance, but emphasizes that models must be constructed with biologically relevant variables that facilitate the presence of a particular species or taxon (e.g., wetlands or forest for amphibians).

In conclusion, we tested whether species distribution models could be utilized to identify areas of higher amphibian species richness in urban ecosystems. If one's goal is to make rapid decisions concerning the management or creation of green space or infrastructure based on conserving areas of higher biodiversity, this method provides relative measures of richness. Our results indicate substantial effort is needed to sufficiently survey and identify areas of suitable habitat for amphibians in urban and non-urban green spaces. Field surveys often require expertise, time, energy, and funds, whereas SDMs can be developed using existing, readily available data (e.g., museum records) and can be conducted using a variety of freely available programs (Elith et al., 2006). We offer two suggestions on how to improve SDM use if one's goal is to identify areas important to high biodiversity. First, the development of species-specific models, particularly in cases where there may be a desire to increase the abundance of a particular species of concern, could enhance predictive ability. These models could utilize key (spatially explicit) variables important to the biology of a particular species. Second, we recommend using SDM approaches that incorporate an estimation of probability of occurrence and species detectability, where such data are available for species of interest. This method has been successfully utilized and detailed in more recent studies (e.g., Franklin et al., 2009; Newbold et al., 2010; Rota et al., 2011). Unfortunately, our data did not permit such analyses. We suggest incorporating one or both of these approaches to strengthen the accuracy of SDMs in predicting species richness.

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Appendix A. Area under curve (AUC) values.

Area under curve (AUC) values for each species modeled.

Species	AUC	Sample size
Northern Cricket Frog (*Acris crepitans*)	0.776	89
Streamside Salamander (*Ambystoma barbouri*)	0.816	31
Jefferson Salamander (*Ambystoma jeffersonianum*)	0.808	48
Spotted Salamander (*Ambystoma maculatum*)	0.827	54
Marbled Salamander (*Ambystoma opacum*)	0.957	28
Small-mouthed Salamander (*Ambystoma texanum*)	0.932	20
American Toad (*Bufo americanus*)	0.738	121
Fowler's Toad (*Bufo fowleri*)	0.782	23
Northern Dusky Salamander (*Desmognathus fuscus*)	0.831	20
Southern Two-lined Salamander (*Eurycea cirrigera*)	0.785	58
Long-tailed Salamander (*Eurycea longicauda*)	0.868	20
Cave Salamander (*Eurycea lucifuga*)	0.838	27
Spring Salamander (*Gyrinophilus porphyriticus*)	0.948	37
Cope's Grey Tree Frog (*Hyla chrysoscelis*)	0.799	65
American Bullfrog (*Rana catesbeiana*)	0.701	45
Green Frog (*Rana clamitans*)	0.736	114
Northern Leopard Frog (*Rana pipiens*)	0.798	40
Wood Frog (*Rana sylvatica*)	0.887	23
Eastern Red-backed Salamander (*Plethodon cinereus*)	0.828	37
Northern Ravine Salamander (*Plethodon electromorphus*)	0.919	20
Northern Slimy Salamander (*Plethodon glutinosus*)	0.901	21
Spring Peeper (*Pseudacris crucifer*)	0.778	99
Western Chorus Frog (*Pseudacris triseriata*)	0.883	24

Appendix B. Species richness maps.

See Fig. B1.

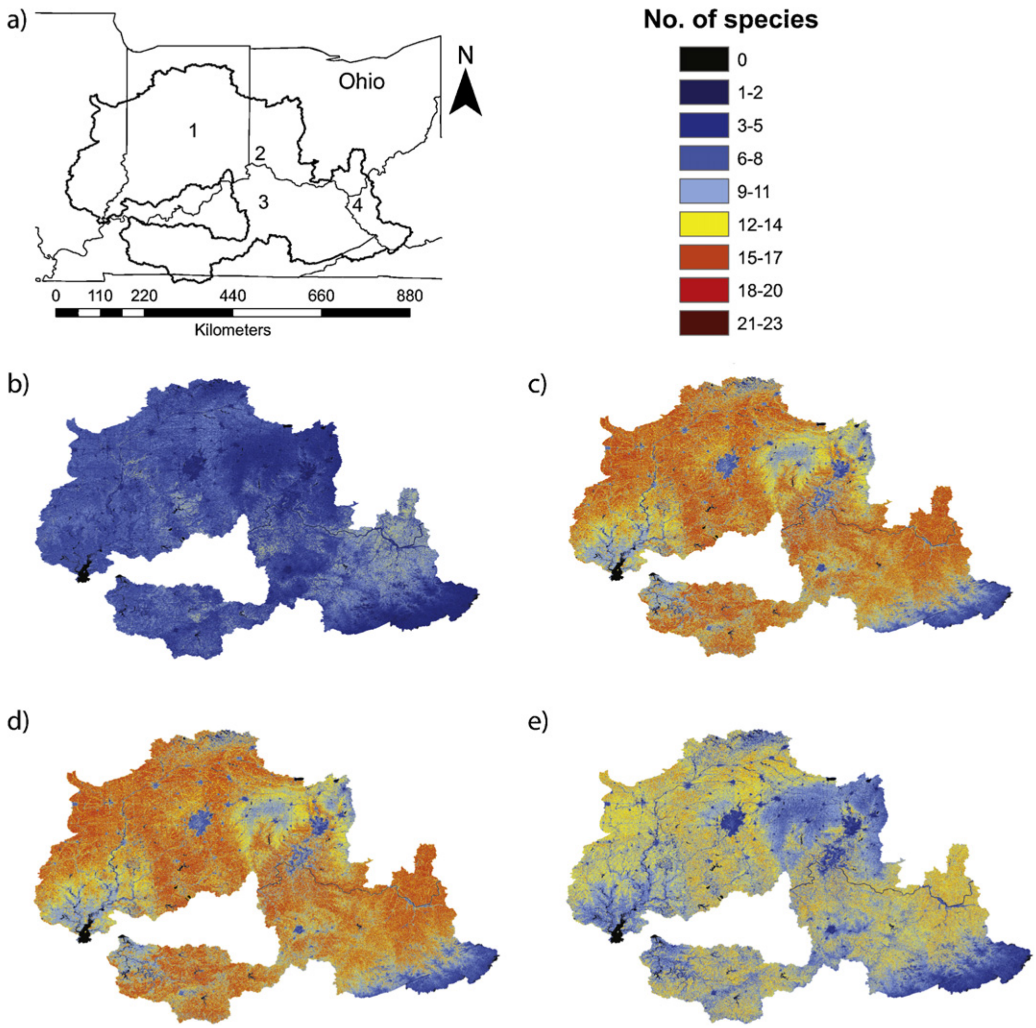

Fig. B1. Depictions of: (a) Cities of Indianapolis, Indiana (1), Cincinnati, Ohio (2) Lexington, Kentucky (3), and Huntington, West Virginia (4) located within the watershed boundary. Predicted amphibian species richness maps within the watershed boundary derived from the maximum training sensitivity plus specificity threshold (b), minimum training presence threshold (c), 10 percentile training presence threshold (d), and fixed cumulative value 10 threshold (e).

Appendix C. Summary data

Summary data including size (ha), species richness (SR; observed [Obs.] and predicted), and landscape variables (within 2-km buffer of the centroid of each site and within each site) for each site. MTP = minimum training presence threshold, MTSPS = maximum training sensitivity plus specificity threshold, 10% TP = 10 percentile training presence threshold, and FC10 = fixed cumulative value 10 threshold. FRS = forested area, NFRS = non-forested natural area, URB = urban area.

Site	Size (ha)	Obs. SR	SR threshold				% in 2-km buffer			% in site			No. wetlands within buffer	No. aquatic habitats surveyed
			FC10	MTP	MTSPS	10% TP	FRS	URB	NFRS	FRS	URB	NFRS		
Alms Park	38	1	17	21	13	17	26.7	64.5	6.6	81.4	16.2	2.4	6	0
Ault Park	89	2	20	23	14	20	23.4	57.9	7.6	76.4	21.4	2.3	6	2
Avon Woods	15	1	16	22	10	16	6.1	92.1	1.7	63.6	6.9	29.5	1	2
Bracken Woods	11	3	16	22	9	16	43.0	55.8	0.8	90.9	9.1	0.0	1	1
Burnet Woods	41	0	15	19	9	15	10.4	89.0	0.4	38.1	58.4	1.3	1	0
Cincinnati Nature Center	414	9	22	23	14	22	67.6	17.8	13.0	93.2	1.6	4.8	33	6
Devou Park	324	2	21	23	13	21	35.4	55.4	2.5	69.6	28.4	1.5	9	2
Farbach-Werner	9	5	14	17	7	14	16.0	83.6	0.3	72.7	27.3	0.0	24	3
French Park	115	2	20	23	13	20	25.6	72.8	1.4	83.3	15.7	0.8	6	2
Glenway Woods	8	2	18	21	10	18	26.2	73.1	0.1	98.7	1.3	0.0	2	0
Kennedy Park	3	1	11	16	7	11	19.3	79.4	1.4	34.4	65.6	0.0	2	1

Appendix C (*Continued*)

Site	Size (ha)	Obs. SR	SR threshold				% in 2-km buffer			% in site			No. wetlands within buffer	No. aquatic habitats surveyed
			FC10	MTP	MTSPS	10% TP	FRS	URB	NFRS	FRS	URB	NFRS		
Koeing Park	5	0	12	14	7	12	7.7	91.6	0.2	0.0	100	0.0	4	0
Miami Forest	1758	9	22	23	15	22	53.4	7.9	35.8	54.4	6.9	36.0	13	4
Rapid Run Park	22	1	16	20	8	16	16.1	83.4	0.5	50.6	46.9	4.9	1	1
Richardson	159	5	21	23	14	21	60.1	21.5	17.1	71.0	7.7	21.3	24	4
Seymour	83	2	22	23	13	22	29.5	65.0	4.4	87.0	6.1	6.9	5	2
Shawnee Forest	613	6	21	23	14	21	40.7	4.2	45.2	45.2	1.8	43.5	11	5
Triple Creek Park	72	5	16	19	8	16	30.1	66.5	2.8	16.8	72.1	4.5	21	2
Withrow	109	3	21	23	14	21	45.6	32.9	5.2	94.1	2.2	3.7	4	2
Woodland Mounds	431	5	22	23	14	22	68.3	13.4	7.0	80.4	9.2	10.4	19	3

Appendix D. Results from analysis of covariance.

Results of ANCOVA and regression analyses to determine if species richness observations/estimates differed across the urban gradient. Species richness was the dependent variable, which was estimated either through field-observations (observed SR) or Maxent-predictions (predicted SR). Square root transformed percent urbanization within 2 km of site was the covariate in the analysis. The non-significant interaction term indicates that the relationship between species richness estimates and urbanization was not different. Estimates for each method differed significantly, and urbanization had a significant, negative effect on richness estimates. Linear equations for observed and predicted species richness and percent urbanization within 2-km are as follows: observed species richness, $r^2 = 0.627$, $P \leq 0.001$, observed species richness = 9.597–0.896*% urbanization; predicted species richness, $r^2 = 0.491$, $P \leq 0.001$, predicted species richness = 23.765–0.925*% urbanization.

Source	*df*	MS	*F*	*P*
Predicted SR	1	1949.510	521.920	≤0.0001
% Urbanization within 2-km buffer	1	180.590	48.348	≤0.0001
Predicted SR × % urbanization within 2-km buffer	1	0.05	0.0121	0.913
% Forest within site	36	3.740	–	–

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