A dark morph of a male Fowler's Toad (*Anaxyrus fowleri*) in a cranberry (*Vaccinium macrocarpon*) bog. The toad was vocalizing just before this picture was taken. The uninflated and darkly pigmented vocal sac is partially visible. *Photo by Brad Timm.*

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Fowler's Toad (*Anaxyrus fowleri*) occupancy in the southern mid-Atlantic, USA

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***Abstract.*—We assessed the effects of landscape structure on *Anaxyrus fowleri* (Fowler's Toad) site occupancy using 14 years of call survey data collected from 250 sites in Virginia and Maryland, and landscape variables derived from the National Wetlands Inventory, U.S. Census Bureau, National Land Cover Databases, and U.S. Department of Agriculture. We also conducted a time series analysis on *A. fowleri* occupancy rates using call survey data collected throughout Virginia and Maryland. We found *A. fowleri* site occupancy to be negatively affected by deciduous forest, hay crops, development and agricultural pesticides, and we identified a negative interannual trend in occupancy rates between 1999 and 2012.**

Key words. Fowler's toad, amphibian declines, calling anuran surveys, North American Amphibian Monitoring Program, landscape ecology, species-habitat modeling, anurans

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Introduction

Amphibian populations are declining globally, with anthropogenic degradation of landscapes near wetlands having a major impact on many species of pond-breeding amphibians (Findlay and Houlahan 1997; Blaustein and Kiesecker 2002). Upland habitats surrounding wetlands are vital for successful dispersal, foraging, and non-breeding activities, making upland habitat quality critical to the life history of pond-breeding amphibians (Windmiller 1996; Semlitsch 2000; Gibbons 2003; Bartlet et al. 2004). The negative effects of landscape degradation on many amphibian species, including hydroperiod alteration, pollution of wetlands from roadway runoff and agricultural chemicals, and mechanical disturbance of foraging, retreat and burrowing sites (Luo et al. 1999; Turtle 2001; Gray et al. 2004b) are fairly well understood. These anthropogenic disturbances can ultimately impact mobility and survival of larval, juvenile, and adult amphibians, and can lead to population declines and extirpations (Blaustein and Kiesecker 2002; Gray et al. 2004a). Thus, understanding how natural and anthropogenic landscape-level processes effect amphibian populations is critical to amphibian conservation.

The Fowler's Toad, *Anaxyrus* (*Bufo*) *fowleri*, is widely but irregularly distributed throughout the eastern United States, occurring from southern New England to the Florida Panhandle and as far west as Missouri, Arkansas, and Louisiana (Netting and Goin 1945; Green 1992; Klemens 1993; Conant and Collins 1998). Though typically associated with coastal dune systems and scrub-pine forests, *A. fowleri* also occurs in rocky and sparsely vegetated areas in dry, sandy, deciduous woodlands, and in agricultural and developed areas (Schlaugh 1976, 1978; Klemens 1993; Zampella and Bunnell 2000; Rubbo and Kiesecker 2005; Gooch et al. 2006). Some biologists and naturalists have thus described *A. fowleri* as being tolerant of urbanization, and scarification in agricultural areas (Ferguson 1960; Martof et al. 1980; Klemens 1993; Rubbo and Kiesecker 2005; Gooch et al. 2006). However, other studies suggest that *A. fowleri* are habitat specialists sensitive to environmental perturbations (Breden 1988; Green 2005; Tupper and Cook 2008).

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In Canada, *A. fowleri* are federally protected (Oldham 2003), but they are not considered a species of concern in the United States. *Anaxyrus fowleri* populations are believed to be relatively stable and abundant in the eastern United States (Conant and Collins 1998). However, *A. fowleri* extirpations have been documented in the northeastern and southeastern United States (Breden 1988; Klemens 1993; Mierzwa et al. 1998; Tupper and Cook 2008; Walls et al., 2011; Milko 2012). These extirpations were largely attributed to anthropogenic disturbances, such as habitat degradation, pesticide application, road mortality (National Park Service, unpubl. data), hydroperiod alteration, competition from invasive species, and probable increased predation pressures from urban tolerant predators such as skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) (Schaff and Garton 1970; Lazell 1976; Groves 1980; Klemens 1993; Tupper and Cook 2008; Milko 2012).

In the southern mid-Atlantic region, *A. fowleri* occur throughout Virginia and Maryland, but are less common outside of the Coastal Plain (Mitchell and Reay 1999). Coastal regions are thought to contain more favorable upland habitats for this species (see Martof et al. 1980; Mitchell and Reay 1999; Cook et al. In prep), but much of the Coastal Plain in Virginia and Maryland is more densely populated and intensely developed than western regions. For instance, the mid-Atlantic Coastal Plain has the highest population density and second-highest growth rate of all ecoregions in Virginia (VGDIF 2005). If *A. fowleri* are sensitive to landscape perturbations, human population growth and development may lead to *A. fowleri* population declines in the southern mid-Atlantic.

To the best of our knowledge, quantitative data describing the effects of landscape-level variables on *A. fowleri* are non-existent for the mid-Atlantic and are limited elsewhere (see Gooch et al. 2006; Tupper and Cook 2008; Birx-Raybuck 2010; Eskew et al. 2011). Occupancy trend analyses of *A. fowleri* populations indicate that they are stable in most mid-Atlantic states (except Maryland; see Weir et al. 2014), but these analyses are temporally limited (Weir et al. 2009). Thus, critical thresholds in landscape-level variables essential to *A. fowleri* occupancy are unknown and it is unclear if southern mid-Atlantic populations are stable over the long term. Therefore our objectives were to identify and describe landscape-level variables that influence *A. fowleri* site occupancy and to complete a more comprehensive time-series analysis for this species in the southern mid-Atlantic.

Materials and Methods

Site selection and data collection

We randomly selected 250 sites in Virginia and Maryland for landscape-level analyses (Fig. 1). Selected sites were North American Amphibian Monitoring Program (NAAMP) calling anuran survey points (adjacent to wetlands) that were surveyed with anuran call counts between 1999 and 2012 (Weir and Mossman 2005). Movement data for *A. fowleri* are limited, but available studies indicate that a 1 km buffer surrounding breeding wetlands is a biologically meaningful distance for analyzing the effects of landscape features on anuran (including *Anaxyrus* spp.) occurrence (Clarke 1974; Miaud et al. 2000; Muths 2003; Bartlet et al. 2004; Smith and Green 2005; Forester et al. 2006). Therefore, our landscape variables were derived from 1 km buffers surrounding calling survey points. Any calling survey points found to have overlapping buffers were removed from analysis. Anuran call data (ranked ordinal values based on chorus intensity [0–3]) and sampling covariates (ambient temperatures, sky and wind conditions, and noise disturbance levels) were collected in accordance with NAAMP guidelines by trained NAAMP volunteers (Weir and Mossman, 2005).

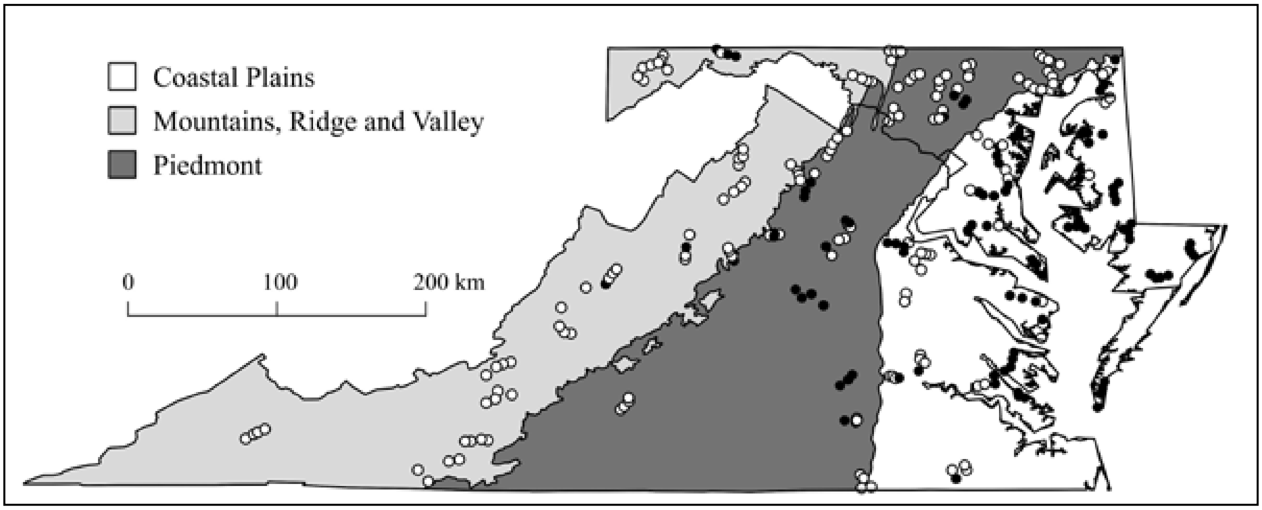

Fig. 1. Map of calling anuran surveys conducted in Maryland and Virginia. Closed circles indicate sites occupied by *A. fowleri* and open circles indicate unoccupied sites.

Calculation of landscape variables

We quantified landscape variables using data from four publicly available sources: (1) the National Wetlands Inventory (NWI) from the U.S. Fish and Wildlife Service; (2) 2012 TIGER/Line road data from the U.S. Census Bureau; (3) the National Land Cover Database (NLCD2006) from the Multi-Resolution Land Characteristics Consortium; and (4) the National Pesticide Use Database from the U.S. Department of Agriculture. Initial data manipulation was done in QuantumGIS (QGIS; QGIS Development Team 2011). For NWI data, we extracted distance from calling survey sites to nearest wetland and determined the number and types of wetlands within a 1 km buffer zone of calling survey sites. Using TIGER/Line road files, we calculated road length and type within 1 km buffers. We prepared land cover data by clipping NLCD2006 data for each buffer into an individual raster file. These files were then imported into R (R Core Team 2013) and analyzed using the SDMTools package (VanDerWal 2013). Total pesticide application rate (kg/km^2) at each site was determined by calculating the sum of application levels within each buffer for all pesticides listed in the National Pesticide Use Database.

Data Analyses

We used the R package Unmarked (Fiske and Chandler 2011) to identify landscape-level variables associated with *A. fowleri* occupancy. Landscape level habitat data were only available for a single year, so we used MacKenzie et al.'s (2002) occupancy model to account for imperfect detectability, particularly false-negative detections, when evaluating habitat variables. False-positive detections can also result in high site occupancy biases, but false-positive detection rates vary between species, and previous tests of NAAMP volunteers resulted in no false-positive detections of *A. fowleri*, even amongst inexperienced volunteers (Genet and Sargent 2003; Royle and Link 2006; McClintock et al. 2010). Therefore, false-positive detections of *A. fowleri* were unlikely to be at levels high enough to bias site occupancy and were not considered in the modeling process.

We assessed models using a multimodel inference approach (see Burnham et al. 2011). We used 19 non-correlated site covariates (Table 1) considered to be biologically meaningful in anuran breeding site selection when creating a priori models (Cushman 2006). Julian date (date) and temperature (temp) were found to affect detection probability; therefore these two sampling covariates were used in all models. We ranked competing models with Akaike Information Criterion (for data sets with high independent to dependent variable ratio [AICc]) by calculating differences between candidate models and the lowest AICc (Δ_i AICc) model. We used Akaike weight (w_i) for each model to guide selection.

To determine change in occupancy between years, we fit a colonization-extinction model (MacKenzie et al. 2003) using date and temp as covariates to account for differences in repeated sampling periods. We then used a smoothed trajectory to determine mean occupancy for each year (Weir et al. 2009). Serial autocorrelation in

Table 1. Landscape variables used in analyses of *A. fowleri* calling anuran survey data for in Virginia and Maryland.

Variable	Description
Crops	Proportion of area used for annual crops or perennial woody crops
Dec	Proportion of forest with >75% canopy cover of deciduous trees
Dev	Proportion of area that has been developed, including suburban and urban areas
Ever	Proportion of forest with >75% or more evergreen trees
For	Proportion of all forest habitats (Dec + Ever + Mix)
Grass	Proportion of area with graminoids or herbaceous vegetation covering over 80% of land which might be grazed but not tilled
H	Habitat Diversity, calculated as Shannon's diversity index using habitat proportions
Hay	Proportion of area planted with grass/legume mixtures used for grazing or hay crops
Mix	Proportion of mixed forest with neither deciduous nor evergreen dominant
Patch	Number of terrestrial habitat patches divided by total number of possible habitat patches (i.e., if each raster square represented a different type of habitat)
Pesticides	Total kg/km^2 of agricultural pesticides applied within 1 km radius of buffer from CSS
Road	Total length of all roads in a 1 km radius buffer from CSS
Shrub	Proportion of area with canopy less than 5 m tall (e.g., shrubs and early successional forest)
Wavg	Average size of wetlands in a 1 km radius buffer from CSS ± in m^2
Wdis	Distance (m) of nearest wetland from Calling Survey Site (CSS)
Wet	Proportion of total buffer area covered by wetlands
Wnear	Size (ha) of the wetland nearest to the CSS
Wnum	Number of wetlands in a 1 km radius buffer from CSS
Wtype	Number of different types of wetlands in a 1 km radius buffer from CSS

the residuals violated assumptions of a parametric linear regression analysis; therefore we used a non-seasonal Autoregressive Integrated Moving Average (ARIMA) analysis to better understand changes in *A. fowleri* occupancy rates over time. We determined significance of parameters using a conditional least squares estimation. We assessed model fit with a Ljung-Box Q-test whereby a high *P*-value indicates that autocorrelation functions are not significantly different than white noise (Ljung and Box 1978).

We used an empirical Bayesian approach to determine conditional distribution of occurrence from the colonization-extinction model and then extrapolated best unbiased predictions of occupancy probability at each site. All sites with an occupancy probability ≥ 0.75 were considered occupied. To determine distributions of specific variables at occupied and unoccupied sites, we created site occupancy accumulation curves for each habitat variable. Habitat recommendations are based on maximum values found at 90% of occupied sites.

Trend analysis was completed in Minitab v.16 (Minitab Inc., Pennsylvania, USA) and all other analyses were completed in R v.3.0.2. Maps and figures were created using QGIS 2.0 and Excel 2010 (Microsoft Corp., Washington, USA).

Results

Landscape analyses

Two hundred fifty sites were sampled between 1999 and 2012 throughout Maryland and Virginia, 108 (42.8%) of which had at least one detection of *A. fowleri*. Approximately eight-percent (300/3841) of sampling events resulted in detections. Not all sites were sampled every year (ranging from 1–14 years, $\bar{x}$ = 6.22; ± 0.197), but most sites were surveyed > 10 times ($\bar{x}$ = 23.1; ± 1.09).

Table 2. Top five models and full model from unmarked analysis of *A. fowleri* occupancy in Virginia and Maryland. Models are ranked from lowest to highest with AICc values. Julian date and temperature were used as sampling covariates in all models. The full model was constructed using the maximum number of site covariates which would create a model that converged: Wnum + Wavg + Road + Ever + Dec + Mix + Crops + Hay + Dev + Wet + Core + Patch + Pesticides.

Model	AICc	Δ_i AICc	w_i
Dec + Hay + Dev + Pesticides	1768.65	0	0.62
Dec + Hay + Dev	1769.55	0.91	0.38
Dec + Hay + Pesticides	1780.54	11.90	0.00
Dec + Dev + Pesticides	1791.16	22.52	0.00
Pesticides	1964.45	195.80	0.00
Full model	2958.68	1190.03	0.00

Table 3. Transformed and untransformed beta coefficients from top occupancy models.

Variable	Untransformed	Transformed	Estimated SE
(Intercept)	3.887	0.980	0.017
Dec	-6.148	0.002	0.002
Hay	-5.373	0.005	0.005
Dev	-4.814	0.008	0.009
Pesticides	-0.005	0.499	0.013

Bayesian analysis indicated that only two sites where no detections occurred had an occupancy probability ≥ 0.75.

We found strong support for a model indicating that deciduous forest, hay, development and pesticides negatively influenced *A. fowleri* occupancy (AICc = 1768.65, w_i = 0.62; Tables 2 and 3). The buffers ranged from 0–97% deciduous forest ($\bar{x}$ = 0.32; ± 0.015), 0–74% hay ($\bar{x}$ = 0.18; ± 0.011), 0–83% development ($\bar{x}$ = 0.12; ± 0.009), and 0–535 kg pesticides applied ($\bar{x}$ = 55.7; ± 5.231). Ninety-percent of occupied sites were covered by less than 25% development, 35% hay, and 50% decidu-

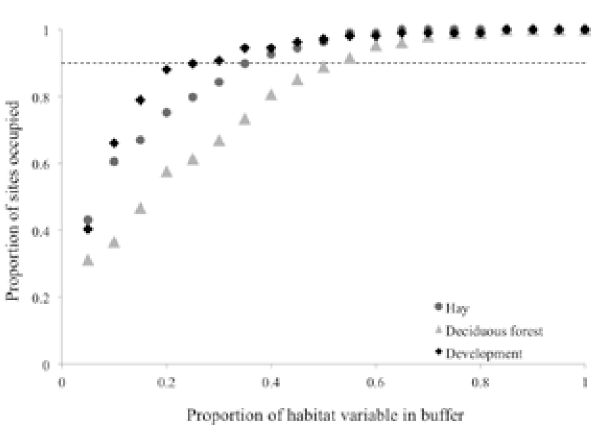

Fig. 2. Accumulation curve showing the maximum proportions of habitat variables found at each occupied site. Ninety-percent of occupied sites were covered by less than 0.25 development, 0.35 hay, and 0.50 deciduous forest cover.

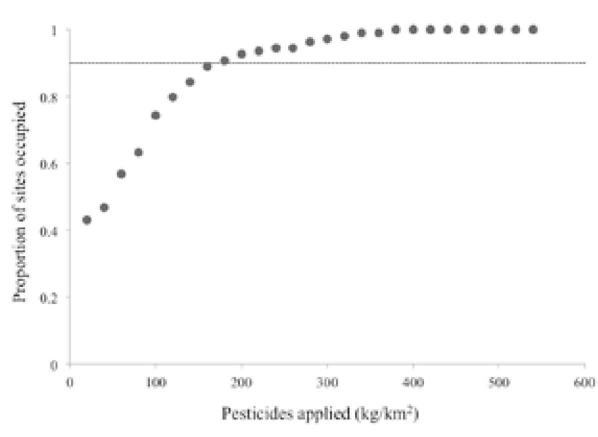

Fig. 3. Accumulation curve showing the maximum agricultural pesticide application rates at occupied sites. The maximum amount of pesticides applied at 90% of occupied sites was 165 kg/km^2.

ous forest (Fig. 2). The maximum amount of pesticides applied at 90% of occupied sites was 165 kg/km^2 (Fig. 3).

Time-series analyses

Using ARIMA analysis, we found that a single autoregressive term was contributing to interannual changes in *A. fowleri* occupancy rates ($t = 4.32$, $P < 0.001$). We confirmed that the model was valid, with uncorrelated residuals ($Q = 13.2$, df = 9, $P = 0.152$). Trend analysis indicated a downward trend in occupancy rates over time, with occupancy decreasing from 55.3% in 1999 to 29.5% in 2012 (Fig. 4).

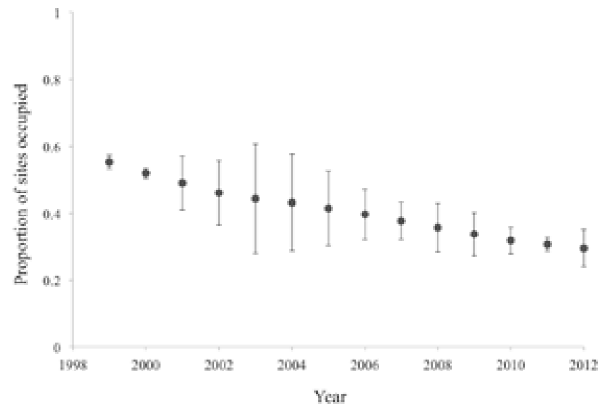

Fig. 4. Mean site occupancy and confidence intervals of *A. fowleri* in Virginia and Maryland from 1999–2012. Time series analysis indicates a 53% decrease in site occupancy, from 55.3% in 1999 to 29.5% in 2012.

Discussion

Forest cover

Many contemporary landscape-level studies indicate a positive relationship between amphibian species and forested habitat within buffers of varying sizes around breeding ponds (see Cushman 2006). We were able to distinguish between forest types on a fairly large scale and identified a negative relationship between *A. fowleri* occupancy and deciduous forest. Although both species can be sympatric, *A. fowleri* is largely replaced by American Toads (*Anaxyrus americanus*) in later successional forests that are dominated by moister, more nutrient rich soils, and hardwood trees (Wright and Wright 1967; Lazell 1976; Klemens 1993). Our results confirm long-standing observations made across *A. fowleri*’s range that suggest they are more common in early successional habitats that are either relatively open or dominated by mixed or coniferous forest (Hubbs 1918; Hoopes 1930; Netting and Goin 1945; Littleford 1946; Cory and Manion 1955; Wright and Wright 1967; Clarke 1974; Green 1989; Lazell 1976; Klemens 1993; Zampella and Bunnell 2000; Tupper and Cook 2008).

Hay

The proportion of area covered by grass/legume mixtures used for grazing or hay crops within the 1 km buffer was

The Provincelands of Cape Cod National Seashore, Barnstable County, Massachusetts, USA. The reddish vegetation in the center of the photo is a cranberry (*Vaccinium macrocarpon*) bog, a wetland used for breeding by the Fowler’s toad. The surrounding landscape is ideal for the Fowler’s toad and supports one of the largest populations of this species in the United States. The landscape contains a patchwork of sand, pitch pine (*Pinus rigida*), scrub oak (*Quercus ilicifolia*), and dune grass (*Ammophila breviligulata*). *Photo by Rebecca Flaherty.*

found to have a significantly negative impact on *A. fowleri* occurrence. Agricultural development can negatively affect anuran dispersal abilities, and soil compaction associated with agricultural landscape alterations may prohibit anuran burrowing (Whalley et al. 1995; Jansen et al. 2001; Gray et al. 2004b). Wetlands within agricultural landscapes may be altered physically and biologically such that postmetamorphic anurans emerge smaller and presumably less fit (Beja and Alcazar 2003; Gray et al. 2004a,b).

Development

We found development to be another significant variable negatively affecting *A. fowleri* occurrence. Development contributes to reduced genetic diversity in pond breeding amphibians, increased pollution of upland and wetland habitats, increased road mortality, and microclimate alteration of remaining habitat patches (Soulé 1987; Reh and Seitz 1989; Fahrig 1995; deMayndier and Hunter 1998; deMaynadier and Hunter 2000; Turtle 2001; Timm and McGarigal 2014). Various studies indicate that development and fragmentation is detrimental to amphibian persistence (see review in Cushman 2006), including *A. fowleri* and congener *A. americanus* (Schlauch 1976, 1978; Gibbs et al. 2005; Walls et al. 2011). However, studies conducted throughout the United States (e.g. New Jersey [Zampella and Bunnell 2000], Pennsylvania [Rubbo and Kiesecker 2005], North Carolina [Gooch et al. 2006], and Louisiana [Milko 2012]) suggest that *A. fowleri* are urban tolerant. While these studies have shown that *A. fowleri* can occur in developed habitats, they do not include pre-development population sizes, are temporally and spatially limited, and are likely referring to suburbanization rather than large-scale urbanization (see Schlauch 1978).

Pesticides

While the differences in AICc values between the top two models were small, four out of the top five models included agricultural pesticide application levels as a negative covariate, indicating that pesticide exposure may play an important role in *A. fowleri* site occupancy. Data suggest that chemical pesticides associated with agriculture have wide-ranging direct effects on amphibians, including endocrine disruption, immunosuppression, developmental delays, and increased mortality (Mann et al. 2009). Exposure to insecticides was found to be highly toxic to larval *A. fowleri* in laboratory studies (see review in Green 2005) and had sub-lethal effects its congener, *A. americanus*, causing eye and limb deformities, increased time to metamorphosis, and reduced post-metamorphic body size (Harris et al. 2000; Boone and James 2003; Howe et al. 2004). Agricultural runoff containing pesticides may be contaminating certain wetlands in this study, thus potentially accounting for reduced *A. fowleri* occupancy rates in agricultural landscapes.

Trends

By pooling data from Maryland and Virginia, we estimate that *A. fowleri* occupancy has decreased by approximately 53% over the last 14 years. Weir et al. (2009) found a significant, but negligible, negative occupancy trend for *A. fowleri* in Delaware, and indicated unchanging occupancy rates in Virginia, Maryland, West Virginia, and New Jersey between 2001 and 2007. However, a more recent study (conducted as the same time as ours, with a similar data set, see Weir et al. 2014) also indicated *A. fowleri* declines in Maryland. Differences in trend estimates between our study and Weir et al. (2009, 2014) may be due to differing sample sizes. Since we nearly doubled the scope of analysis of Weir et al. (2009) and have three more years than Weir et al. (2014), we believe our results more accurately describe trends in *A. fowleri* occupancy in Maryland and Virginia. Although a more comprehensive analysis is needed to identify the proximate causes of decline in *A. fowleri* in Maryland and Virginia, we suspect that its declines are in part due to the recent loss of subclimax communities. Virginia has lost 51.6% of its softwood forest since 1940 (VDOF 2014) and early successional habitats have been steadily juxtaposing to later successional seres throughout Maryland: As of 2008 less than 10% of existing Maryland forests were occupied by early successional regimes (Lister 2011).

Anaxyrus fowleri may be able to persist longer in moderately developed coastal environments (Schlauch 1978) than other pond-breeding amphibians due to their high fecundity rates, salt tolerance, desiccation resistance, and ability to breed in wetlands with varying hydroperiod regimes (Wright and Wright 1967; Claussen 1974; Markow 1997; Tupper and Cook 2008; Birx-Raybuck 2010; Eskew et al. 2012). The ability of *A. fowleri* to occupy these types of habitats is advantageous because they harbor fewer interspecific amphibian competitors (see Martof et al. 1980; Klemens 1993; Mitchell and Reay 1999). If early successional habitats continue to become less widespread in the mid-Atlantic, coastal regions may become more important to the long-term persistence of *A. fowleri*. However, much of the southern mid-Atlantic coastal plain is densely populated (VGDIF 2005) and intensely developed. Thus, successional changes occurring further inland coupled with increased urbanization of the southern mid-Atlantic coastal plain could potentially exacerbate declines.

Conclusions

Amphibian populations are more vulnerable to habitat loss and fragmentation when located on the margins of their geographic range (Swihart et al. 2003). Our data indicate that even in the middle of their range, *A. fowleri* occupancy rates are declining. Landscapes most appropriate for this species appear to contain only moderate amounts of deciduous forest (≤ 50%), few hay crops (≤ 35%), relatively little development (≤ 25%), and low pesticide application rates.

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