Forest birds respond to the spatial pattern of exurban development in the Mid-Atlantic region, USA

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ABSTRACT

Housing development beyond the urban fringe (i.e. exurban development) is one of the fastest growing forms of land-use change in the United States. Exurban development's attraction to natural and recreational amenities has raised concerns for conservation and represents a potential threat to wildlife. Although forest-dependent species have been found particularly sensitive to low housing densities, it is unclear how the spatial distribution of houses affects forest birds. The aim of this study was to assess forest bird responses to changes in the spatial pattern of exurban development and also to examine species responses when forest loss and fragmentation were considered. We evaluated landscape composition around North American Breeding Bird Survey stops between 1986 and 2009 by developing a compactness index to assess changes in the spatial pattern of exurban development over time. Compactness was defined as the degree of clumpiness of exurban development surrounding each survey stop at each time period considered. We used Threshold Indicator Taxa Analysis to detect the response of forest and forest-edge species in terms of occurrence and relative abundance along the compactness gradient at two spatial extents (400-m and 1-km radius buffer). Our results show that most forest birds and some forest-edge species were positively associated with high levels of compactness at the larger spatial scale although the proportion of forest in the surrounding landscape had also a significant effect when forest loss and fragmentation were accounted for. In contrast, the spatial configuration of exurban development was an important predictor of occurrence and abundance for only a few species at the smaller spatial scale. The positive response of forest birds to compactness at the larger scale could represent a systematic trajectory of decline and could be highly detrimental to bird diversity if exurban growth continues and creates more compacted development.

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INTRODUCTION

As the world's human population has grown over the last century and residential housing has continued to sprawl even in areas where human population is declining (Pendall 2003; Seto et al. 2012), the rapid increase of housing development has expanded not only at the edge of cities but also beyond the urban fringe to increasingly more rural areas (e.g., Davis & Hansen 2011; Hansen et al. 2005; Marzluff 2001; McKenzie et al. 2011; Suarez-Rubio et al. 2012a). Housing development beyond the urban fringe (i.e. exurban development) is characterized by low-density, scattered housing units farther away than the suburbs but within commuting distance to an urban center (Berube et al. 2006; Daniels 1999; Lamb 1983; Nelson 1992; Theobald 2001). In the conterminous USA, low-density development has been prominent since the 1950s (Brown et al. 2005) and growing at a rate of about 10% to 15% per year (Theobald 2001). By 2000, 25% of the nation was already considered exurbia (Brown et al. 2005) and forecasts have indicated that this pattern of land use will continue into the future (Brown et al. 2014; Kirk et al. 2012).

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The attraction of exurban development to areas with high quality natural and recreational amenities (Gonzalez-Abraham et al. 2007; Hammer et al. 2004) has raised environmental and ecological concerns (Gude et al. 2006; Hansen et al. 2005; Leu et al. 2008; Sampson & DeCoster 2000). Exurban development can alter disturbance regimes such as wildfires (NIFC 2013; Radeloff et al. 2005) and biogeochemical cycles by changing greenhouse gas fluxes (Dale et al. 2005; Huang et al. 2014). By converting natural habitats into exurban development habitat is lost and fragmented which reduces habitat quality for many native species and increases habitat quality for many early successional and non-native species (Donnelly & Marzluff 2006). In addition to the loss of vegetation cover, changes in structural complexity around houses in exurban areas may have negative impacts on natural communities (Casey et al. 2009; Odell &

Knight 2001) by degrading habitats and natural resources (Friesen et al. 1995; Suarez-Rubio et al. 2013; Theobald et al. 1997). As a consequence, exurban development has been linked to reduced survival and reproduction of some wildlife species (Riley et al. 2003; Tewksbury et al. 1998) and changes in the behavior and habitat use of other species, for example by interrupting bird migration and movement (Lepczyk et al. 2004; Miller et al. 1998).

Forest birds have been found particularly sensitive to new housing (Pidgeon et al. 2007) even at densities as low as 0.095 houses/ha (Friesen et al. 1995; Merenlender et al. 2009; Suarez-Rubio et al. 2011). Area-sensitive, some cavity-nesting, and bark-foraging birds are relatively more susceptible to the effects of exurban development than granivores, omnivores, and ground foragers (Fraterrigo & Wiens 2005; Glennon & Kretser 2013; Kluza et al. 2000; Merenlender et al. 2009). Although the mechanisms are not well understood, changes in bird communities have been associated with increased predation (Engels & Sexton 1994; Lumpkin et al. 2012), brood parasitism (Chace et al. 2003), free-roaming pets (Dauphiné & Cooper 2009), and activities of landowners (Lepczyk et al. 2004).

The effects of exurban development extend beyond immediate house surroundings. In the Rocky Mountain region of the western USA, an impact zone of up to 180 m from houses has been observed for bird and small-mammal communities (Odell & Knight 2001). Similarly, in the northeastern USA, an ecological effect zone of up to 200 m has been documented for breeding birds (Glennon & Kretser 2013). It is likely that the size of the zone of influence of exurban development is dependent upon the spatial distribution of houses (Hansen et al. 2005). If houses are clustered, the ecological effects of each house overlap, reducing the overall negative impacts. Thus, clustered development is thought to minimize impacts on wildlife habitat relative to highly dispersed low-density housing (Gagné & Fahrig 2010; Glennon & Kretser 2013; Odell et al. 2003; Theobald et al. 1997). Although the relative importance of habitat quantity over habitat

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pattern has been shown especially for birds in fragmented systems (Alberti & Marzluff 2004; Donnelly & Marzluff 2006; Fahrig 1997; Lichstein et al. 2002), little is known about how the spatial pattern of exurban areas changes as this form of development progresses and whether forest birds respond to changes in exurban spatial pattern.

The aim of this study was to assess forest bird responses to changes in the spatial pattern of exurban development and also to examine species responses when forest loss and fragmentation was considered. We developed a compactness index to quantify the spatial configuration of exurban development around North American Breeding Bird Survey stops in the Mid-Atlantic region of the USA between 1986 and 2009 and assessed the response of selected bird species (i.e., forest and forest-edge species) along this compactness gradient. In addition, we determined whether species responded differently to exurban patterns at the local (400-m radius buffer) and landscape scale (1-km radius buffer). We hypothesized that exurban development would become more compact overtime and thus forest birds would exhibit a decrease in occurrence and relative abundance, whereas forest-edge species would respond positively to compactness of exurban development. To our knowledge, this is the first time that a continuous gradient approach has been used to quantify compactness as exurban development progresses and to identify threshold responses along this gradient.

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MATERIALS AND METHODS

Study area

Our study area encompassed approximately 4300 km^2 and included nine counties in north-central Virginia (Clarke, Culpeper, Fauquier, Frederick, Madison, Page, Rappahannock, Shenandoah, and Warren) and two in western Maryland (Washington and most of Frederick; Fig. 1), USA. The region has experienced high population growth rates, ranging from 4% (Page County) to

36% (Culpeper County) in the past decade (U.S. Census Bureau 2013). The region has also experienced an increase in exurban settlements over the same time period (Suarez-Rubio et al. 2012a), stimulated at least in part by the close proximity of natural amenities (Suarez-Rubio et al. 2012b).

Breeding bird survey

Using the North America Breeding Bird Survey (BBS) (Peterjohn & Sauer 1994; Sauer et al. 2003), a large-scale annual roadside survey to monitor the status and trend of breeding bird populations in the USA and southern Canada, we selected two groups of species that represent contrasting habitat preferences (forest vs. edge). Forest species — Ovenbird (*Seiurus aurocapilla*), Red-eyed Vireo (*Vireo olivaceus*), American Redstart (*Setophaga ruticilla*), Wood Thrush (*Hylocichla mustelina*), Scarlet Tanager (*Piranga olivacea*), and Eastern Wood-Pewee (*Contopus virens*) (Poole 2005) — were defined as birds that use a wide variety of deciduous and mixed deciduous-coniferous forests and that might favor interior forested habitats (Mikusiñski et al. 2001). Forest-edge species — Eastern Towhee (*Pipilo erythrophthalmus*), Eastern Phoebe (*Sayornis phoebe*), Gray Catbird (*Dumetella carolinensis*), Northern Cardinal (*Cardinalis cardinalis*), and Indigo Bunting (*Passerina cyanea*) (Poole 2005) — are those species that are strongly associated with forest edges and open habitats (Mikusiñski et al. 2001). These 11 species were also selected because they were detected on at least 5% of surveys during the 1986-2009 interval. In addition, many of the species are reported to have experienced population declines or reduced fecundity due to habitat loss or fragmentation (Donovan & Flather 2002; Hagan 1993; Sherry & Holmes 1997; U.S. NABCI Committee 2009).

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BBS routes involve 24.5 mile-long road transects, with 3-minute point count surveys conducted at stops every 0.5 miles. From each BBS route located in the study area, we selected

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every fifth stop along the route to reduce overlap between adjacent areas around survey stops and decrease the likelihood of spatial autocorrelation (Moran's I = 0.108, p = 0.182). We only considered survey stops that had detailed direction descriptions (i.e., geocoding information and characterization of site-specific features) and fell within the study region (125 survey points in total) (Fig. 1). We focused our analysis on survey stops instead of the entire route because of our interest in local variability of breeding habitats.

To characterize local characteristics of breeding habitats, we established potential zones of influence (Glennon & Kretser 2013) of 400-m and 1-km radius around the selected BBS stops. These areas represented both breeding bird territories (Bowman 2003; Mazerolle & Hobson 2004), which were assumed to be in the immediate surroundings of survey stops, and areas feasibly visited during bird daily movements (Krementz & Powell 2000; Lang et al. 2002). Within these areas, we quantified the proportion of forest and exurban development and the spatial pattern of exurban development from 1986 to 2009.

We used a hierarchical Bayesian model to adjust BBS counts (Suarez-Rubio et al. 2013) and account for BBS sources of variability such as observer differences (Sauer et al., 1994), first-year observers' skills (Erskine 1978; Kendall et al. 1996), environmental conditions (Robbins et al. 1986), and habitat features (Sauer et al. 1995). We modeled count data as hierarchical over-dispersed Poisson and fit models using Markov Chain Monte Carlo (MCMC) methods in WinBUGS 1.4.3 (Lunn et al. 2000). We specified C_{it} as the count for each species on stop i and time t where i =1,..., N; t = 1,…, T; and N and T were the number of stops and the number of years species were observed, respectively. C_{it} was assumed to be Poisson distributed with mean μ_{it}

$$C_{it} \sim Pois(\mu_{it})$$

and the full model was:

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$$\log(\mu_{it}) = \beta_{0stop} + \beta_{1stop} \times Year_t + \beta_2 \times FirstYear_{it} + Route_{it} + Observer_{it} + Noise_{it}$$

where each stop was assumed to have a separate intercept (β_0) and time trend (β_1). We used two Markov chains for each model and examined model convergence and performance through Gelman-Rubin diagnostics (Gelman et al. 2004; Link & Barker 2010). Once the model reached convergence, we derived estimates of the count at each stop and in each year which were then used for the threshold analysis.

Defining exurban development

To characterize the land cover in the areas around survey stops, we classified Landsat 5 TM images (pixel size: 30 m) for 1986, 1993, 2000, and 2009. We performed standard pre-processing procedures (atmospheric and topographic correction) prior to image classification and conducted a supervised classification of areas of exurban development using a training dataset generated from aerial photos. Exurban development was defined as areas with housing densities between 1 unit per 0.4 ha and 1 unit per 16.3 ha (e.g., 6 - 250 houses per km^2) (Brown et al. 2005). We identified exurban development using both spectral and structural characteristics following the methods outlined in Suarez-Rubio (2012a). We derived spectral characteristics from spectral mixture analysis (Adams et al. 1986) of the corrected Landsat images to estimate the fractional cover of vegetation, substrate, non-photosynthetic vegetation, and shade within each image. Based on spectral mixture analysis outputs, we built decision trees to classify exurban development for each of the four image dates.

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To further analyze pixels belonging to branches of the decision trees that could not discriminate between exurban and urban areas based on spectral characteristics alone, we used morphological spatial pattern analysis (MSPA) (Soille 2003; Vogt et al. 2007). The analysis evaluates map geometry by applying mathematical morphological operators to allocate each pixel to one of a mutually exclusive set of classes. We used an 8-neighbor rule as our structural element (i.e., both cardinal directions and diagonal neighbors are considered) and edge width of one. Pixels that fell into the MSPA-Islet (representative of isolated housing units), Bridge, Branch, and Loop classes (representative of associated roads) were considered exurban development. All other MSPA classes were considered urban development. Lastly, all cells originally designated as exurban development in the decision tree were then added back to attain the final exurban development maps. Overall classification accuracy for the final exurban development maps ranged from 93 to 98% (kappa: 0.87 to 0.96) (Suarez-Rubio et al. 2012a).

Analyzing the spatial pattern of exurban development

To examine the spatial pattern of exurban development, we used the final exurban development maps as foreground and analyzed them using MSPA. Here, we focused specifically on the Islet class which represented scattered, isolated housing units. Using the MSPA classification output, we developed a compactness index to describe the degree of compactness of exurban development surrounding each survey stop at each time period considered. The index is a measure of the proportion of exurban development within any MSPA classes other than the Islet class (i.e., 1 – (Exurban Development islets / Exurban Development all classes)) and ranged from 0% (all Islets) to 100% (no Islets). Survey stops lacking exurban development within the potential zone of influence were excluded from the analysis (28 and 20 survey stops for the 400-m and 1-km radius buffers, respectively were excluded). Hence, dispersed exurban development was represented by 0% and maximally clumped exurban development by 100% compactness (see example in Fig. 2).

Identifying species response to compactness of exurban development

To examine the relationship between compactness of exurban development and bird species at the survey stops, we fitted a non-parametric locally weighted polynomial regression (loess) (Cleveland & Devlin 1988). When the loess regression highlighted nonlinearity in the relationship, then a change-point analysis was used to test for a nonlinear threshold response.

We estimated potential species threshold responses to compactness of exurban development using Threshold Indicator Taxa ANalysis (TITAN) (Baker & King 2010). TITAN allows the identification of change points in both occurrence frequency and relative abundance of individual species along an environmental gradient. It distinguishes responses of individual species with low occurrence frequencies or highly variable abundances and does not assume a linear response along all or part of an environmental gradient. TITAN uses normalized species scores (z) to establish a change-point location that separates the data into two groups and maximizes association of each species with one side of the partition. Z scores measure the association of a species' abundance weighted by their occurrence and are normalized to facilitate cross-species comparison. Thus, TITAN distinguishes if a species responds to an environmental stressor (in this case compactness of exurban development) and whether the response is negative (z-) or positive (z+).

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To measure quality of the response and assess uncertainty around change-point locations, TITAN bootstraps the original dataset and recalculates change points with each simulation. Uncertainty is expressed as quantiles of the change-point distribution. Narrow intervals between upper and lower change-point quantiles (i.e., 5 and 95%) indicate a nonlinear response in species abundance whereas broad quantile intervals are characteristic of species with a linear or more gradual response. Diagnostic indices of the quality of the response are purity and reliability.

Purity is the proportion of bootstrap replicates that agree with the direction of the change-point for the observed response. Pure indicators (purity ≥ 0.95) are those that consistently assign the same response direction during the resampling procedure. Reliability is the proportion of change-point individual value scores (IndVal) among the bootstrap replicates that consistently have p-values below defined probability levels (0.05). Reliable indicators (reliability ≥ 0.95) are those with consistently large IndVal.

We ran TITAN (R package: TITAN2) (Baker & King 2010) for the 11 selected bird species and compactness index in R 3.1.1 (R Development Core Team 2013). We used the minimum number of observations on each side of the threshold split that is required by TITAN (n = 5) and specified 250 permutations to compute z scores and diagnostic indices as suggested by Baker and King (2010).

Evaluating species responses to forest loss and fragmentation in relation to compactness of exurban development

To evaluate the effects of compactness of exurban development in relation to other factors known to affect birds (i.e., forest loss and fragmentation), we used generalized additive models (GAMs) (Hastie & Tibshirani 1990). GAMs were used to better account for potential non-linear trends between the response and predictor variables (e.g., Guisan et al. 2002; Zuur et al. 2009). GAMs require fewer assumptions of data distributions and error structures, assuming only that functions are additive and components can be smoothed by local fitting to subsets of the data.

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The models used adjusted counts for each bird species as dependent variables and compactness of exurban development, proportion of exurban development, proportion of forest, number of forest patches greater than 0.45 ha, and length of forest edge as predictor variables. The later variables were estimated following Suarez-Rubio et al. (2013). Gaussian errors and an

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identity link were used and smoothing parameters were automatically selected based on the effective degrees of freedom and a generalized cross validation criterion in R package mgcv (Wood 2001; Wood 2006). Models were evaluated based on graphical diagnostic plots and the explanatory power of the model was assessed by examining the amount of the explained deviance. Predictors with high significance levels ($p < 0.01$) were identified as key factors that have strong effects on bird species.

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RESULTS

Landscape composition and compactness of exurban development around survey stops

Landscape composition around survey stops changed through time during the time period studied, except for the 21% of stops that were inside protected areas (Table 1). The inclusion here of MSPA classes that represented associated roads (i.e., Bridge, Branch, and Loop) in addition to scattered isolated pixels (i.e., Islets) in the definition of exurban development differed from other operational definitions of exurban development used in previous work; as a result, the total amount of development that was classified as exurban was higher for our study than was reported for more restrictive definitions (e.g., Suarez-Rubio et al. 2012a). For both the 400-m and 1-km radius buffers, there was a 6% increase in exurban development from 1986 to 2009 (Table 1).

Compactness of exurban development also increased over time (Table 1). For the 400-m radius buffer, compactness increased from 18% in 1986 to 39% in 2009. For the 1-km radius buffer, compactness increased even more, from 11% in 1986 to 44% in 2009. For both extents, the increase was higher between 2000 and 2009 than for any other time period. Compactness was slightly correlated with the amount of exurban development (Pearson’s correlation coefficient for 400-m buffer: 0.38, and 1-km buffer: 0.46) and not correlated with forest at either extent (Pearson’s correlation coefficient for 400-m buffer: -0.15, 1-km buffer: 0.04).

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Response of bird species to compactness of exurban development

Non-parametric locally weighted polynomial regression (loess) models indicated a non-linear relationship between the compactness index and abundance of selected bird species (Fig. 3). Forest species differed in their threshold response to compactness of exurban development (Fig. 4). For the 400-m radius buffer, only one of the six forest species (i.e. Scarlet Tanager) showed a significant and reliable threshold response to compactness. Although Wood Thrush also responded negatively, the quality of the indicator was less reliable (0.80) (Table 2). In contrast, for the 1-km radius buffer, almost all forest species responded positively and reliably to the compactness of exurban development (Table 2).

Forest-edge species also had significant though less consistent threshold responses to compactness of exurban development at both extents (Fig. 4). For the 400-m radius buffer, Eastern Phoebe and Gray Catbird had a significant positive response to the compactness metric, while Eastern Towhee responded negatively to compactness. For the 1-km radius buffer, Eastern Phoebe, Gray Catbird, and Indigo Bunting responded positively to compactness, with reliability values and change points similar to those exhibited by forest species (e.g., Red-eyed Vireo, Eastern Wood-Pewee; Fig. 4).

In general, reliability information was redundant with purity (i.e., species with ≥ 0.95 purity were usually also reliable) (Table 2). In some instances, the direction of the response changed with extent of analysis. Wood Thrush responded positively to compactness of exurban development for the 1-km radius buffer. Although the direction of the response changed for the 400-m radius buffer, the indicator was not reliable at this extent (reliability = 0.80). For the other species (i.e. Scarlet Tanager and Eastern Towhee), wide confidence bands and reduced z scores when compared to the reliable extent, highlighted uncertainty when the abundance distributions did not show a clear response. Therefore, where there were differences in the reliability and direction of response at different extents, the 1-km relationships were more reliable.

Most species (both forest and forest-edge) had relatively broad bootstrapped change-point distributions indicating a more gradual response to the level of compactness of exurban development (Fig. 4). In addition, the width of the bootstrapped change-point distributions varied between the two buffer distances for only a few species. For example, Eastern Phoebe was one of the few species with a sharp response to compactness, but this occurred only at the 400-m radius buffer.

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Response of bird species to forest loss and fragmentation in relation to compactness of exurban development

When forest loss and fragmentation were included as predictor variables in addition to the exurban development measures (i.e., proportion and compactness), forest had a highly significant effect on all forest species modeled and most forest-edge species at the 1-km radius buffer (Table 3). Number of forest patches had a significant influence on Red-eyed Vireo and Scarlet Tanager and forest edge did not affect any of the forest species. The effect of exurban development varied among forest species. Only Red-eyed Vireo was significantly influenced by both proportion of exurban development and compactness of exurban development. Eastern Wood-Pewee and Wood Thrush were influenced by compactness of exurban development, whereas Scarlet Tanager was only influenced by proportion of exurban development.

None of the forest-edge species were influenced by compactness of exurban development at the 1-km radius buffer, although Eastern Phoebe, Eastern Towhee and Indigo Bunting were affected by its proportion. Regarding forest fragmentation, only Indigo Bunting was influenced by number of forest patches, whereas Eastern Phoebe and Eastern Towhee were affected by forest edge. Neither Gray Catbird nor Northern Cardinal was influenced by forest loss, forest fragmentation, proportion of exurban development and compactness of exurban development. Models at the 400-m buffer and for American Redstart and Ovenbird at the 1-km buffer did not converge.

DISCUSSION

Our results suggest that both forest birds and some forest-edge species responded to spatial patterns of exurban development at the landscape extent (1-km radius buffer) (Fig. 4B). Contrary to our prediction, forest birds exhibited a positive response to compactness of exurban development with change points between 21% and 78% (Table 2). These results indicate that frequency and abundance of forest birds increase as compactness increases. There are a few reasons that could explain this pattern. First, although compactness of exurban development increased over time, these bird species were also increasing in abundance generally in the region (Suarez-Rubio et al. 2013) partly due to forest regrowth (Bowen et al. 2007) and protected areas adjacent to the study area. Second, forest disturbance associated with exurban development may benefit forest birds, especially forest birds such as American Redstart and Red-eyed Vireo that seem to occur more frequently in early and mid-successional forests and even start to decline as forests mature (Holmes & Sherry 2001; Hunt 1998). Lastly, even though forest decreased around survey stops, forest cover was nonetheless above the minimum amount of habitat necessary for the persistence of forest birds (> 30%; Andrén 1994; Betts et al. 2007; Radford et al. 2005; Suarez-Rubio et al. 2013; Zuckerberg & Porter 2010).

When the effects of compactness of exurban development were assessed in relation to forest loss and fragmentation, proportion of forest had a highly significant effect compared to compactness in most cases (Table 3). This indicates that for forest birds, proportion of forest at the landscape extent may be more important than exurban development. However, proportion of exurban development and compactness also had a significant effect which suggests that if proportion of exurban development or compactness continues this would inevitably lead to the loss of forest species.

Surprisingly, Indigo Bunting and Gray Catbird (i.e., forest-edge species) also responded positively to compactness of exurban development at the landscape extent with change points similar to those exhibited by forest birds (Table 2, Fig. 4B). Although Indigo Bunting is known for its strong preference for edges, and surely human habitat modification (e.g., clearing of woods) increases suitable habitat for buntings (Payne 2006), bunting numbers have declined in eastern North America since the last quarter of the twentieth century (Sauer et al. 2014). These declines have been associated with increasing levels of brood parasitism and predation that occur in fragmented habitats (Donovan & Flather 2002; Robinson et al. 1995) but also to forest regrowth which has reduced shrubby habitats that they tend to use (DeGraaf & Yamasaki 2003). It is important to note that when forest loss and fragmentation were also considered, the effect of compactness was reduced and proportion of forest and exurban development had a greater influence. This suggests that buntings may be more sensitive to habitat quantity than the spatial pattern of exurban development.

Gray Catbird is frequently associated with suburbia and also prefers early successional habitats, and shrubs around houses have probably increased the availability of breeding habitat for this species (Smith et al. 2011b). Although compact exurban development may minimize the disturbance associated with domestic predators introduced in exurban areas that usually prey directly on nests (Balogh et al. 2011; Lepczyk et al. 2003; Lumpkin et al. 2012), the effects of compactness diminished when forest loss and fragmentation were also taken into account at the landscape extent.

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At the local extent (i.e., 400-m radius buffer), Scarlet Tanager responded negatively, whereas Gray Catbird responded positively to compactness of exurban development, with both exhibiting gradual responses (Fig. 4A). Scarlet Tanager is an interior forest species that is very sensitive to forest fragmentation (Rosenberg et al. 1999). In a previous study, this species was found to have a negative response to the amount of exurban development at very low levels (Suarez-Rubio et al. 2013). Thus, Scarlet Tanager appears to be negatively affected by exurban development regardless of its spatial configuration which was also the case for the landscape extent. The positive response of Gray Catbird to compactness of exurban development perhaps indicates that predation pressure by introduced domestic predators in exurban areas (Lepczyk et al. 2003; Lumpkin et al. 2012) affects catbirds at the local extent. Exurban areas have large numbers of non-native plant species (Gavier-Pizarro et al. 2010; Lenth et al. 2006; Maestas et al. 2003), and there is some evidence that nests in exotic shrubs are twice as likely to be depredated and suffer higher rates of nest failure than nests in native shrubs (Borgmann & Rodewald 2004), although this is not always the case (Meyer et al. 2015).

Interestingly, most forest birds did not exhibit threshold responses to compactness of exurban development at the local extent. This difference in response at the local and landscape extent suggests that the effects of compactness of exurban development are scale dependent. Smith et al. (2011a) demonstrated that effects of fragmentation change with the extent of analysis because ecological processes (e.g. predation) act at different spatial scales. Thus, the effects of compactness of exurban development might be associated with the size of the disturbance zone. Other studies have found an ecological effect zone of up to 200 m from exurban homes in which avian densities were altered (Glennon & Kretser 2013; Odell & Knight 2001).

Our results reveal that the responses of forest birds varied, but extended well beyond a 200-m radius. When considering a 400-m zone of influence, most forest birds did not respond significantly to the spatial pattern of exurban development. However, the spatial compactness of development was associated with a positive response at the 1-km zone for nearly all forest bird species. Previous studies have shown that forest birds are very sensitive to the proportion of exurban development (e.g., Pidgeon et al. 2007; Suarez-Rubio et al. 2013). Our results show that forest birds are also sensitive to its spatial configuration at large extents. In general, if exurban development occurs in the landscape, it affects the entire 400-m radius buffer regardless of its arrangement, but by aggregating exurban development within the 1-km radius buffer, safe zones were retained that could support forest birds and the effects of compactness of exurban development were reduced.

By assessing the spatial pattern of exurban development for the multiple images, we were able to capture the dynamics of landscape change over time (Table 1) as was also done previously for the conterminous United States (e.g., Mockrin et al. 2012; Pidgeon et al. 2014). As exurban areas grew, scattered, isolated exurban development became more contiguous and clumped. Thus, our results demonstrate the effects of the spatial pattern of exurban development within the larger context of forest habitat loss. At the level of individual survey stops, the positive but weak correlation between exurban development and compactness indicates that there is variance in spatial configuration that is independent from the overall amount of exurban development.

Although the total amount of exurban development around survey stops increased compared to previous operational definitions (Suarez-Rubio et al. 2013), forest loss and fragmentation did not vary when definitions were compared (Appendix 1). Thus, by including both isolated and scattered housing units and associated roads into our definition, we were able to reflect the substantial expansion of exurban development that has occurred in the region (e.g., Suarez-Rubio et al. 2012a). In addition, by considering the effects of the spatial pattern of exurban development besides forest loss and fragmentation, we identified the importance of compactness in light of other factors that are known to affect forest birds.

Nonetheless, some caveats arise. The use of bird counts along BBS routes may not fully reflect occurrence and abundance of more sensitive species such as Kentucky Warbler. Although counts along roadsides have been shown to be representative of changes occurring over much broader areas (Keller & Scallan 1999), our findings cannot be generalized beyond the range of housing density included in this study (e.g., to wilder or more urbanized areas). In addition, the compactness index was developed to assess the clumpiness of exurban housing and assumed presence of housing units thus it is not suitable for comparison to areas without development.

A critical unknown of exurban growth is the possible cumulative impacts on wildlife. Evaluating potential cumulative impacts requires an enhanced understanding of both the density and patterns of residential development and of the distinct effects of these two components of landscape change (Pidgeon et al. 2014; Theobald et al. 1997). We have taken a first step by identifying the extent at which forest and forest-edge species respond to the spatial patterning of exurban development and highlight that the positive response of forest birds to compactness at the larger extent should be taken cautiously because this could represent a systematic trajectory of decline (Pidgeon et al. 2014) and if exurban growth continues to increase, as trends suggest, this will lead towards more contagious development which could be highly detrimental to bird diversity. Thus, management efforts should try to concentrate development away from ecological sensitive areas, create or maintain safe zones, and minimize forest loss or fragmentation (i.e., increase compactness) to support forest birds.

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REFERENCES

Adams JB, Smith MO, and Johnson PE. 1986. Spectral mixture modeling: a new analysis of rock and soil types at the Viking Lander 1 site. *Journal of Geophysical Research* 91:8098-8112. DOI 10.1029/JB091iB08p08098

Alberti M, and Marzluff JM. 2004. Ecological resilience in urban ecosystems: linking urban patterns to human and ecological functions. *Urban Ecosystems* 7:241-265. DOI 10.1023/B:UECO.0000044038.90173.c6

Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *OIKOS* 71:355-366.

Baker ME, and King RS. 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution* 1:25-37. DOI 10.1111/j.2041-210X.2009.00007.x

Balogh AL, Ryder TB, and Marra PP. 2011. Population demography of Gray Catbirds in the suburban matrix: sources, sinks and domestic cats. *Journal of Ornithology* 152:717-726. DOI 10.1007/s10336-011-0648-7

Berube A, Singer A, Wilson JH, and Frey WH. 2006. Finding exurbia: America's fast-growing communities at the metropolitan fringe. *The Brookings Institution, Living Cities Census Series*:1-47.

Betts MG, Forbes GJ, and Diamond AW. 2007. Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology* 21:1046-1058. DOI: 10.1111/j.1523-1739.2007.00723.x

Borgmann KL, and Rodewald AD. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. *Ecological Applications* 14:1757-1765. DOI 10.1890/03-5129

Bowen ME, McAlpine CA, House APN, and Smith GC. 2007. Regrowth forests on abandoned agricultural land: a review of their habitat values for recovering forest fauna. *Biological Conservation* 140:273-296. DOI: 10.1016/j.biocon.2007.08.012

Bowman J. 2003. Is dispersal distance of birds proportional to territory size? *Canadian Journal of Zoology* 81:195-202. DOI 10.1139/z02-237

Brown DG, Johnson KM, Oveland TR, and Theobald DM. 2005. Rural land-use trends in the conterminous United States, 1950-2000. *Ecological Applications* 15:1851–1863. DOI 10.1890/03-5220

Brown ML, Donovan TM, Schwenk WS, and Theobald DM. 2014. Predicting impacts of future human population growth and development on occupancy rates of forest-dependent birds. *Biological Conservation* 170:311-320. DOI 10.1016/j.biocon.2013.07.039

Casey JM, Wilson ME, Hollingshead N, and Haskell DG. 2009. The effects of exurbanization on bird and macroinvertebrate communities in deciduous forests on the Cumberland Plateau, Tennessee. *International Journal of Ecology* 2009:10 pages. DOI 10.1155/2009/539417

Chace JFWJJ, Cruz A, Prather JW, and Swanson HM. 2003. Spatial and temporal activity patterns of the brood parasitic brown-headed cowbird at an urban/wildland interface. *Landscape and Urban Planning* 64:173-190. DOI 10.1016/S0169-2046(02)00220-7

Cleveland WS, and Devlin SJ. 1988. Locally-weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association* 83:596–610. DOI 10.1080/01621459.1988.10478639

Dale V, Archer S, Chang M, and Ojima D. 2005. Ecological impacts and mitigation strategies for rural land management. *Ecological Applications* 15:1879-1892. DOI 10.1890/03-5330

Daniels T. 1999. *When city and country collide: managing growth in the metropolitan fringe*. Washington, D.C., USA: Island Press.

Dauphiné N, and Cooper RJ. 2009. Impacts of free-ranging domestic cats (*Felis catus*) on birds in the United States: a review of recent research with conservation and management recommendations In: Rich TD, Arizmendi C, Demarest DW, and Thompson C, editors. Proceedings of the Fourth International Partners in Flight Conference. p 205–219.

Davis CR, and Hansen AJ. 2011. Trajectories in land use change around U.S. National Parks and challenges and opportunities for management. *Ecological Applications* 21:3299-3316. DOI 10.1890/10-2404.1

DeGraaf RM, and Yamasaki M. 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *Forest Ecology and Management* 185:179-191. DOI 10.1016/S0378-1127(03)00254-8

Donnelly R, and Marzluff JM. 2006. Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments. *Urban Ecosystems* 9:99-117. DOI 10.1007/s11252-006-7904-2

Donovan TM, and Flather CH. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications* 12:364-374. DOI 10.1890/1051-0761(2002)012[0364:RANAST]2.0.CO;2

Engels TM, and Sexton CW. 1994. Negative correlation of Blue jays and Golden-cheeked Warblers near an urbanizing area. *Conservation Biology* 8:286-290. DOI 10.1046/j.1523-1739.1994.08010286.x

Erskine AJ. 1978. The first ten years of the cooperative breeding bird survey in Canada. *Canadian Wildlife Service Report Series* 42:1-61.

Fahrig L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management* 61:603-610.

Fraterrigo JM, and Wiens JA. 2005. Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. *Landscape and Urban Planning* 71:263-275. DOI 10.1016/j.landurbplan.2004.03.008

Friesen LE, Eagles PFJ, and Mackay RJ. 1995. Effects of residential development on forest-dwelling Neotropical migrant songbirds. *Conservation Biology* 9:1408-1414. DOI 10.1046/j.1523-1739.1995.09061408.x

Gagné SA, and Fahrig L. 2010. The trade-off between housing density and sprawl area: minimising impacts to forest breeding birds. *Basic and Applied Ecology* 11:723-733. DOI 10.1016/j.baae.2010.09.001

Gavier-Pizarro GI, Radeloff VC, Stewart SI, Huebner CD, and Keuler NS. 2010. Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecological Applications* 20:1913-1925. DOI 10.1890/09-2168.1

Gelman A, Carlin JB, Stern HS, and Rubin DB. 2004. *Bayesian data analysis*. Boca Raton, Florida, USA: Chapman and Hall/CRC.

Glennon MJ, and Kretser HE. 2013. Size of the ecological effect zone associated with exurban development in the Adirondack Park, NY. *Landscape and Urban Planning* 112:10-17. DOI 10.1016/j.landurbplan.2012.12.008

Gonzalez-Abraham CE, Radeloff VC, Hammer RB, Hawbaker TJ, Stewart SI, and Clayton MK. 2007. Building patterns and landscape fragmentation in northern Wisconsin, USA. *Landscape Ecology* 22:217-230. DOI 10.1007/s10980-006-9016-z

Gude PH, Hansen AJ, Rasker R, and Maxwell B. 2006. Rates and drivers of rural residential development in the Greater Yellowstone. *Landscape and Urban Planning* 77:131-151. DOI 10.1016/j.landurbplan.2005.02.004

Guisan A, Edwards TC, Jr., and Hastie T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157:89-100.

Hagan JM, III. 1993. Decline of the Rufous-sided Towhee in the Eastern United States. *The Auk* 110:863-874.

Hammer RB, Stewart SI, Winkler RL, Radeloff VC, and Voss PR. 2004. Characterizing dynamic spatial and temporal residential density patterns from 1940 to 1990 across the North Central United States. *Landscape and Urban Planning* 69:183-199. DOI 10.1016/j.landurbplan.2003.08.011

Hansen AJ, Knight RL, Marzluff JM, Powell S, Brown K, Gude PH, and Jones K. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecological Applications* 15:1893–1905. DOI 10.1890/05-5221

Hastie TJ, and Tibshirani RJ. 1990. *Generalized Additive Models.* 1st ed. London, UK: Chapman & Hall.

Holmes RT, and Sherry TW. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *The Auk* 118:589-609. DOI 10.2307/4089923

Huang Q, Robinson D, and Parker D. 2014. Quantifying spatial–temporal change in land-cover and carbon storage among exurban residential parcels. *Landscape Ecology* 29:275-291. DOI 10.1007/s10980-013-9963-0

Hunt PD. 1998. Evidence from a landscape population model of the importance of early successional habitat to the American Redstart. *Conservation Biology* 12:1377-1389.

Keller CME, and Scallan JT. 1999. Potential roadside biases due to habitat changes along breeding bird survey routes. *Condor* 101:50-57. DOI 10.2307/1370445

Kendall WL, Peterjohn BG, and Sauer JR. 1996. First time observer effects in the North American Breeding Bird Survey. *The Auk* 113:823-829. DOI 10.2307/4088860

Kirk RW, Bolstad PV, and Manson SM. 2012. Spatio-temporal trend analysis of long-term development patterns (1900–2030) in a Southern Appalachian County. *Landscape and Urban Planning* 104:47-58. DOI 10.1016/j.landurbplan.2011.09.008

Kluza DA, Griffin CR, and Degraaf RM. 2000. Housing developments in rural New England: effects on forest birds. *Animal Conservation* 3:15-26. DOI 10.1111/j.1469-1795.2000.tb00083.x

Krementz DG, and Powell LA. 2000. Breeding season demography and movements of Eastern Towhees at the Savanna River site, South Carolina. *Wilson Bulletin* 112:243-248. DOI 10.1676/0043-5643(2000)112[0243:BSDAMO]2.0.CO;2

Lamb RF. 1983. The extent and form of exurban sprawl. *Growth and Change* 14:40-47. DOI 10.1111/j.1468-2257.1983.tb00395.x

Lang JD, Powell LA, Krementz DG, and Conroy MJ. 2002. Wood Thrush movements and habitat use: effects of forest management for Red-cockaded Woodpeckers. *The Auk* 119:109-124. DOI 10.1676/09-105.1

Lenth BA, Knight RL, and Gilgert WC. 2006. Conservation value of clustered housing developments. *Conservation Biology* 20:1445-1456. DOI 10.1111/j.1523-1739.2006.00491.x

Lepczyk CA, Mertig, A. G., and Liu aJG. 2003. Landowners and cat predation across rural-to-urban landscapes. *Biological Conservation* 115:191-201. DOI dx.doi.org/10.1016/S0006-3207(03)00107-1

Lepczyk CA, Mertig AG, and Liu JG. 2004. Assessing landowner activities related to birds across rural-to-urban landscapes. *Environmental Management* 33:110-125. DOI 10.1007/s00267-003-0036-z

Leu M, Hanser SE, and Knick ST. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications* 18:1119-1139. DOI 10.1890/07-0480.1

Lichstein JW, Simons TR, and Franzreb KE. 2002. Landscape effects on breeding songbird abundance in managed forests. *Ecological Applications* 12:836-857. DOI 10.1890/1051-0761(2002)012[0836:leobsa]2.0.co;2

Link WA, and Barker RJ. 2010. *Bayesian inference with ecological applications*. London, UK: Academic Press.

Lumpkin HA, Pearson SM, and Turner MG. 2012. Effects of climate and exurban development on nest predation and predator presence in the southern Appalachian Mountains (U.S.A.). *Conservation Biology* 26:679-688. DOI 10.1111/j.1523-1739.2012.01851.x

Lunn DJ, Thomas A, Best N, and Spiegelhalter D. 2000. WinBUGS a Bayesian modeling framework: concepts, structure and extensibility. *Statistics and Computing* 10:325-337. DOI 10.1023/A:1008929526011

Maestas JD, Knight RL, and Gilgert WC. 2003. Biodiversity across a rural land-use gradient. *Conservation Biology* 17:1425–1434. DOI 10.1046/j.1523-1739.2003.02371.x

Marzluff JM. 2001. Worldwide urbanization and its effects on birds. In: Marzluff JM, Bowman R, and Donnelly R, eds. *Avian ecology and conservation in an urbanizing world*. Boston, USA: Kluwer Academic Publishers, 19-47.

Mazerolle DF, and Hobson KA. 2004. Territory size and overlap in male Ovenbirds: contrasting a fragmented and contiguous boreal forest. *Canadian Journal of Zoology* 82:1774-1781. DOI 10.1139/z04-175

McKenzie P, Cooper A, McCann T, and Rogers D. 2011. The ecological impact of rural building on habitats in an agricultural landscape. *Landscape and Urban Planning* 101:262-268. DOI 10.1016/j.landurbplan.2011.02.031

Merenlender AM, Reed SE, and Heise KL. 2009. Exurban development influences woodland bird composition. *Landscape and Urban Planning* 92:255-263. DOI 10.1016/j.landurbplan.2009.05.004

Meyer LM, Schmidt KA, and Robertson BA. 2015. Evaluating exotic plants as evolutionary traps for nesting Veeries. *The Condor* 117:320-327. DOI 10.1650/CONDOR-14-101.1

Mikusiñski G, Gromadzki M, and Chylarecki P. 2001. Woodpeckers as indicators of forest bird diversity. *Conservation Biology* 15:208-217. DOI 10.1111/j.1523-1739.2001.99236.x

Miller SG, Knight RL, and Miller CK. 1998. Influence of recreational trails on breeding bird communities. *Ecological Applications* 8:162–169. DOI 10.1890/1051-0761(1998)008[0162:IORTOB]2.0.CO;2

Mockrin MH, Stewart SI, Radeloff VC, Hammer RB, and Johnson KM. 2012. Spatial and temporal residential density patterns from 1940 to 2000 in and around the Northern Forest of the Northeastern United States. *Population and Environment* 34:400-419. DOI 10.1007/s11111-012-0165-5

Nelson AC. 1992. Characterizing exurbia. *Journal of Planning Literature* 6:350-368. DOI 10.1177/088541229200600402

NIFC (National Interagency Fire Center). 2013. Wildland fire statistics. *Available at www.nifc.gov* (accessed 5 March 2014).

Odell EA, and Knight RL. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. *Conservation Biology* 15:1143-1150. DOI 10.1046/j.1523-1739.2001.0150041143.x

Odell EA, Theobald DM, and Knight RL. 2003. Incorporating ecology into land use planning: the songbirds' case for clustered development. *Journal of the American Planning Association* 69:72–82. DOI 10.1080/01944360308976294

Payne RB. 2006. Indigo Bunting (*Passerina cyanea*) The Birds of North America Online. Cornell Lab of Ornithology *Available at http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/004* (accessed 28 April 2014).

Pendall R. 2003. Sprawl without Growth: the Upstate Paradox. *The Brookings Institution, Center on Urban and Metropolitan Policy Survey Series, 11 pp*.

Peterjohn BG, and Sauer JR. 1994. Population trends of woodland birds from the North American Breeding Bird Survey. *Wildlife Society Bulletin* 22:155-164.

Pidgeon AM, Flather CH, Radeloff VC, Lepczyk CA, Keuler NS, Wood EM, Stewart SI, and Hammer RB. 2014. Systematic temporal patterns in the relationship between housing development and forest bird biodiversity. *Conservation Biology* 28:1291-1301. DOI 10.1111/cobi.12291

Pidgeon AM, Radeloff VC, Flather CH, Lepczyk CA, Clayton MK, Hawbaker TJ, and Hammer RB. 2007. Associations of forest bird species richness with housing and landscape patterns across the USA. *Ecological Applications* 17:1989-2010. DOI dx.doi.org/10.1890/06-1489.1

Poole AE. 2005. The Birds of North America Online Cornell Laboratory of Ornithology *Available at http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/BNA/* (accessed 10 July 2012).

R Development Core Team. 2013. R: a language and environment for statistical computing http://www.R-project.org. v 3.0.1 ed. R Foundation for Statistical Computing, Vienna, Austria.

Radeloff VC, Hammer RB, Stewart SI, Fried JS, Holcomb SS, and McKeefry JF. 2005. The wildland-urban interface in the United States. *Ecological Applications* 15:799-805. DOI dx.doi.org/10.1890/04-1413

Riley SPD, Sauvajot RM, Fuller TK, York EC, Kamradt DA, Bromley C, and Wayne RK. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology* 17:566-576. DOI 10.1046/j.1523-1739.2003.01458.x

Robbins CS, Bystrak D, and Geissler PH. 1986. The Breeding Bird Survey: its first fifteen years, 1965-1979. Resource Publication 157. Washington, D.C, USA: U.S. Fish and Wildlife Service.

Robinson SK, Thompson III FR, Donovan TM, Whitehead DR, and Faaborg J. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987-1990.

Rosenberg KV, Lowe JD, and Dhondt AA. 1999. Effects of forest fragmentation on breeding tanagers: a continental perspective. *Conservation Biology* 13:568–583. DOI 10.1046/j.1523-1739.1999.98020.x

Sampson N, and DeCoster L. 2000. Forest fragmentation: implications for sustainable private forests. *Journal of Forestry* 98:4-8.

Sauer JR, Fallon JE, and Johnson R. 2003. Use of North American Breeding Bird Survey data to estimate population change for bird conservation regions. *The Journal of Wildlife Management* 67:372-389.

Sauer JR, Hines JE, Fallon JE, Pardieck KL, Ziolkowski DJJ, and Link WA. 2014. The North American Breeding Bird Survey, Results and Analysis 1966 - 2012. Version 02.19.2014 *Available at http://www.mbr-pwrc.usgs.gov/bbs/bbs.html* (accessed 28 April 2014).

Sauer JR, Pendleton GW, and Orsillo S. 1995. Mapping of bird distributions from point count surveys. In: Ralph CJ, Sauer JR, and Droege S, editors. General Technical Report PSW-GTR-149. Pacific Southwest Research Station: USDA Forest Service. p 151- 160.

Seto KC, Güneralp B, and Hutyra LR. 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences* 109:16083-16088. DOI 10.1073/pnas.1211658109

Sherry TW, and Holmes RT. 1997. American Redstart (*Setophaga ruticilla*) The Birds of North America Online. Cornell Lab of Ornithology. *Available at http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/277* (accessed 10 July 2012).

Smith AC, Fahrig L, and Francis CM. 2011a. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography* 34:103-113. DOI 10.1111/j.1600-0587.2010.06201.x

Smith RJ, Hatch MI, Cimprich DA, and Moore FR. 2011b. Gray Catbird (*Dumetella carolinensis*).The Birds of North America Online. Cornell Lab of Ornithology. *Available at http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/167* (accessed 29 April 2014).

Soille P. 2003. *Morphological image analysis: principles and applications*. Berlin, Germany: Springer-Verlag.

Suarez-Rubio M, Lookingbill TR, and Elmore AJ. 2012a. Exurban development from 1986 to 2009 surrounding the District of Columbia, USA. *Remote Sensing of Environment* 124:360-370. DOI 10.1016/j.rse.2012.03.029

Suarez-Rubio M, Lookingbill TR, and Wainger LA. 2012b. Modeling exurban development near Washington, DC, USA: comparison of a pattern-based model and a spatially-explicit econometric model. *Landscape Ecology* 27:1047-1061. DOI 10.1007/s10980-012-9760-1

Suarez-Rubio M, Renner SC, and Leimgruber P. 2011. Influence of exurban development on bird species richness and diversity. *Journal of Ornithology* 152:461-471. DOI 10.1007/s10336-010-0605-x

Suarez-Rubio M, Wilson S, Leimgruber P, and Lookingbill T. 2013. Threshold responses of forest birds to landscape changes around exurban development. *PLoS One* 8:e67593. DOI 10.1371/journal.pone.0067593

Tewksbury JJ, Hejl SJ, and Martin TE. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890-2903. DOI 10.1890/0012-9658(1998)079[2890:BPDNDW]2.0.CO;2

Theobald DM. 2001. Land use dynamics beyond the American urban fringe. *Geographical Review* 91:544–564. DOI 10.1111/j.1931-0846.2001.tb00240.x

Theobald DM, Miller JR, and Hobbs NT. 1997. Estimating the cumulative effects of development on wildlife habitat. *Landscape and Urban Planning* 39:25-36. DOI 10.1016/S0169-2046(97)00041-8

U.S. Census Bureau. 2013. State and County quick facts. *Available at http://quickfacts.census.gov* (accessed 2 January 2014).

U.S. NABCI Committee. 2009. The State of the Birds, United States of America, 2009. Washington, D.C.: U.S. Department of the Interior.

Vogt P, Riitters K, Estreguil C, Kozak J, Wade T, and Wickham J. 2007. Mapping spatial patterns with morphological image processing. *Landscape Ecology* 22:171-177. DOI 10.1007/s10980-006-9013-2

Wood SN. 2001. mgcv: GAMs and Generalized Ridge Regression for R. *R News* 1:20-25.

Wood SN. 2006. *Generalized Additive Models: an introduction with R.* London, UK: Chapman and Hall/CRC.

Zuckerberg B, and Porter WF. 2010. Thresholds in the long-term responses of breeding birds to forest cover and fragmentation. *Biological Conservation* 143:952-962. DOI 10.1016/j.biocon.2010.01.004

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, and Smith GM. 2009. *Mixed effects models and extensions in ecology with R.* New York, USA: Springer.