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

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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 response to changes in the spatial pattern of exurban development. 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. 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 landscape extent. In contrast, the spatial configuration of exurban development was an important predictor of occurrence and abundance for only a few species at the local extent. The positive response of forest birds to compactness at the landscape extent could represent a systematic trajectory of decline and could be highly detrimental to bird diversity if exurban growth continues and becomes more compacted development.

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15 **ABSTRACT**

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17 growing forms of land-use change in the United States. Exurban development's attraction to
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27 buffer). Our results show that most forest birds and some forest-edge species were positively
28 associated with high levels of compactness at the landscape extent. In contrast, the spatial
29 configuration of exurban development was an important predictor of occurrence and abundance
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31 the landscape extent could represent a systematic trajectory of decline and could be highly
32 detrimental to bird diversity if exurban growth continues and becomes more compacted
33 development.

34

35 **Keywords** Exurban growth, infilling; low-density residential; urban fringe; ecological effect
36 zone

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; 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 further 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 United States, 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).

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). In addition, the loss of vegetation cover and structural complexity around houses in exurban areas may have negative impacts on wildlife communities (Casey et al. 2009; Odell & Knight 2001) by fragmenting and 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 house/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 U.S., 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 U.S., 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). However, 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 response to changes in the spatial pattern of exurban development. 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 U.S. 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 pattern at the local (400-m radius buffer) and landscape scale (1-km radius buffer). We hypothesized that exurban development would be 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.

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). 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.

105 2012a), stimulated at least in part by the close proximity of natural amenities (Suarez-Rubio et
106 al. 2012b).

107 **Breeding bird survey**

108 Using the North America Breeding Bird Survey (BBS) (Peterjohn & Sauer 1994; Sauer et al.
109 2003), a large-scale annual roadside survey to monitor the status and trend of breeding bird
110 populations in the United States and southern Canada, we selected two groups of species that
111 represent contrasting habitat preferences (forest vs. edge). Forest species ─Ovenbird (*Seiurus*
112 *aurocapilla*), Red-eyed Vireo (*Vireo olivaceus*), American Redstart (*Setophaga ruticilla*), Wood
113 Thrush (*Hylocichla mustelina*), Scarlet Tanager (*Piranga olivacea*), and Eastern Wood-Pewee
114 (*Contopus virens*) (Poole 2005)─ were defined as birds that utilize a wide variety of deciduous
115 and mixed deciduous-coniferous forests and that might favor interior forested habitats
116 (Mikusiñski et al. 2001). Forest-edge species ─Eastern Towhee (*Pipilo erythrophthalmus*),
117 Eastern Phoebe (*Sayornis phoebe*), Gray Catbird (*Dumetella carolinensis*), Northern Cardinal
118 (*Cardinalis cardinalis*), and Indigo Bunting (*Passerina cyanea*) (Poole 2005)─ are those species
119 that are strongly associated with forest edges and open habitats (Mikusiñski et al. 2001). These
120 11 species were also selected because they were detected on at least 5% of surveys during the
121 1986-2009 interval. In addition, many of the species are reported to have experienced population
122 declines or reduced fecundity in their distribution range due to habitat loss or fragmentation
123 (Donovan & Flather 2002; Hagan 1993; Sherry & Holmes 1997; U.S. NABCI Committee 2009).
124 From each BBS route located in the study area, we uniformly selected a maximum of 10
125 survey stops (every fifth stop along the route) to reduce overlap between adjacent areas around
126 survey stops and decrease the likelihood of spatial autocorrelation. We only considered survey
127 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. The full model was then:

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

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

150 convergence, we derived estimates of the count at each stop and in each year which were then
151 used for the threshold analysis.

152 **Defining exurban development**

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

165 For pixels belonging to branches of the decision trees that could not discriminate between
166 exurban and urban areas based on spectral characteristics alone, we used morphological spatial
167 pattern analysis (MSPA) to classify the imagery (Soille 2003; Vogt et al. 2007). The analysis
168 evaluates map geometry by applying mathematical morphological operators to allocate each
169 pixel to one of a mutually exclusive set of classes. We used an 8-neighbor rule as our structural
170 element (i.e., both cardinal directions and diagonal neighbors are considered) and edge width of
171 one. Pixels that fell into the MSPA-Islet (representative of isolated housing units), Bridge,
172 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.

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 the Islet class (i.e. isolated pixels) 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 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 species adjusted counts 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 to test for nonlinear threshold response was used.

We estimated potential species thresholds 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 taxa along an environmental gradient. It distinguishes responses of individual taxa with low occurrence frequencies or highly variable abundances and does not assume linear response along all or part of an environmental gradient. TITAN uses normalized indicator species taxa scores (z) to establish a change-point location that separates the data into two groups and maximizes association of each taxon with one side of the partition. Z scores measure the association of taxon abundance weighted by their occurrence and is normalized to facilitate cross-taxa comparison. Thus, TITAN distinguishes negative (z-) and positive (z+) indicator response taxa.

To measure quality of the indicator 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 nonlinear response in taxon abundance whereas broad quantile intervals are characteristic of taxa with linear or more gradual response. Diagnostic indices of the quality of the indicator 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 for the 11 selected bird species and compactness index in R 3.0.1 (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).

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 scatter 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 exurban development (Pearson's correlation coefficient for 400-m buffer: 0.38, and 1-km buffer: 0.46) and not correlated with forest at neither extent (Pearson's correlation coefficient for 400-m buffer: -0.15, 1-km buffer: 0.04).

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 adjusted counts of selected bird species (see examples in 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 was significant and reliable indicator taxa. Scarlet Tanager responded negatively to the compactness of exurban development. 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 were positive indicator taxa of compactness, with reliability values and change points similar to those exhibited by forest species.

In general, reliability information was redundant with purity (i.e., taxa with ≥ 0.95 purity were usually also reliable) (Table 2). Rarely did the direction of the response change with extent of analysis. For example, Ovenbird 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 marginally significant ($p = 0.052$) and poorly reliable at this extent (reliability = 0.38). In general, 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, which occurred only at the 400-m radius buffer.

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 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 the relatively intact forests adjacent to the study area (e.g., protected areas). 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, response of forest birds may follow a systematic temporal trajectory (Pidgeon et al. 2014). In a first stage of development, bird species richness has either a stable or positive association with residential development because of resources introduced by people (e.g., feeders) and subsequently, as the number of houses increases over time, the association becomes negative (Pidgeon et al. 2014). Therefore, the

283 positive response of forest birds to compactness may suggest that the study area is in a first stage
284 of development when the housing density is still low, but if compactness or exurban growth
285 continues, it would inevitably lead to the second phase which could represent species losses.
286 Surprisingly, Indigo Bunting and Gray Catbird (i.e., forest-edge species) also responded
287 positively to compactness of exurban development at the landscape extent with change points
288 similar to those exhibited by forest birds (Table 2, Fig. 4B). Although Indigo Bunting is known
289 for its strong preference for edges, and surely human habitat modification (e.g., clearing of
290 woods) increases suitable habitat for buntings (Payne 2006), bunting numbers have declined in
291 eastern North America since the last quarter of the twentieth century (Sauer et al. 2014). These
292 declines have been associated with increasing levels of brood parasitism and predation that occur
293 in fragmented habitats (Donovan & Flather 2002; Robinson et al. 1995). Gray Catbird also
294 prefers early successional habitats, and shrubs around houses have probably increased the
295 availability of breeding habitat for this species (Smith et al. 2011b). Compact exurban
296 development perhaps minimize the disturbance associated with domestic predators introduced in
297 exurban areas that usually prey directly on nests (Balogh et al. 2011; Lepczyk et al. 2003;
298 Lumpkin et al. 2012).
299 At the local extent (i.e., 400-m radius buffer), Scarlet Tanager responded negatively,
300 whereas Gray Catbird responded positively to compactness of exurban development, with both
301 exhibiting gradual responses (Fig. 4A). Scarlet Tanager is an interior forest species that is very
302 sensitive to forest fragmentation (Rosenberg et al. 1999). In a previous study, this species was
303 found to have a negative response to the amount of exurban development at very low levels
304 (Suarez-Rubio et al. 2013). Thus, Scarlet Tanager appears to be negatively affected by exurban
305 development regardless of its spatial configuration. The positive response of Gray Catbird to

306 compactness of exurban development perhaps indicate that predation pressure by introduced
307 domestic predators in exurban areas (Lepczyk et al. 2003; Lumpkin et al. 2012) affects catbirds
308 at the local extent. Exurban areas have large numbers of non-native plant species (Gavier-Pizarro
309 et al. 2010; Lenth et al. 2006; Maestas et al. 2003), and there is some evidence that nests in
310 exotic shrubs are twice as likely to be depredated and suffer higher rates of nest failure than nests
311 in native shrubs (Borgmann & Rodewald 2004), although this is not always the case (Meyer et
312 al. 2015).

313 Interestingly, most forest birds did not exhibit threshold responses to compactness of
314 exurban development at the local extent. This difference in response at the local and landscape
315 extent suggests that the effects of compactness of exurban development are scale dependent.
316 Smith et al. (2011a) demonstrated that effects of fragmentation change with the extent of
317 analysis because ecological processes (e.g. predation) act at different spatial scales. Thus, the
318 effects of compactness of exurban development might be associated with the size of the
319 disturbance zone. Other studies have found an ecological effect zone of up to 200 m from
320 exurban homes in which avian densities were altered (Glennon & Kretser 2013; Odell & Knight
321 2001).

322 Our results reveal that the responses of forest birds varied, but extended well beyond a
323 200-m radius. When considering a 400-m zone of influence, most forest birds did not respond
324 significantly to the spatial pattern of exurban development. However, the spatial compactness of
325 development was associated with a positive response at the 1-km zone for nearly all forest bird
326 species. Previous studies have shown that forest birds are very sensitive to the amount of exurban
327 development (e.g., Pidgeon et al. 2007; Suarez-Rubio et al. 2013). Our results show that forest
328 birds are also sensitive to its spatial configuration at large extents. In general, if exurban

329 development occurs in the landscape, it affects the entire 400-m radius buffer regardless of its
330 arrangement, but by aggregating exurban development within the 1-km radius buffer, safe zones
331 were retained that could support forest birds.

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

341 A critical unknown of exurban growth is the possible cumulative impacts on wildlife.
342 Evaluating potential cumulative impacts requires an enhanced understanding of both the density
343 and patterns of residential development and of the distinct effects of these two components of
344 landscape change (Pidgeon et al. 2014; Theobald et al. 1997). We have taken a first step by
345 identifying the extent at which forest and forest-edge species respond to the spatial patterning of
346 exurban development and highlight that the positive response of forest birds to compactness at
347 the larger extent should be taken cautiously because this could represent a systematic trajectory
348 of decline (Pidgeon et al. 2014) and if exurban growth continues to increase, as trends suggest,
349 this will lead towards more contagious development which could be highly detrimental to bird
350 diversity.

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Figure 1(on next page)

Study area (shaded region).

Circles represent 125 North American Breeding Bird Survey (BBS) routes that were uniformly selected from routes.

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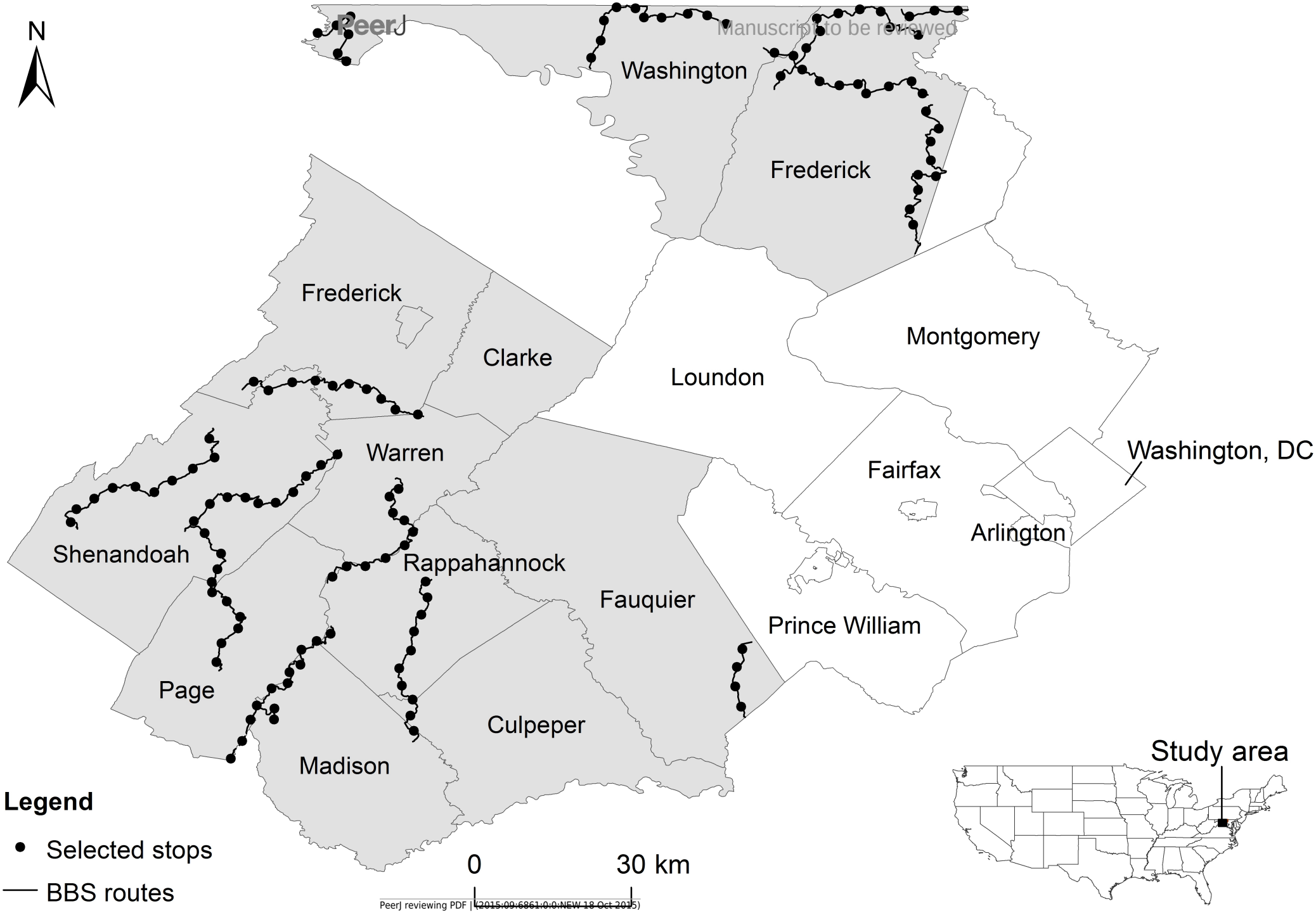

Figure 2(on next page)

Example of morphological spatial pattern analysis (MSPA) output used to derive level of compactness of exurban development around surrounding areas of selected BBS stops.

The illustration shows compactness around 1-km radius buffer of three different BBS stops in 2009 with similar amount of exurban development (20.0 ± 1.3%) among the three landscapes.

Compactness: 12 %
52 %
83 %
Legend
MSPA - Islet
MSPA - All other classes

Figure 3(on next page)

Example relationships between compactness of exurban development and adjusted counts of selected bird species around BBS stops.

A, C represent forest-edge and B, D forest birds for 400-m (upper panels) and 1-km radius buffer (bottom panels).

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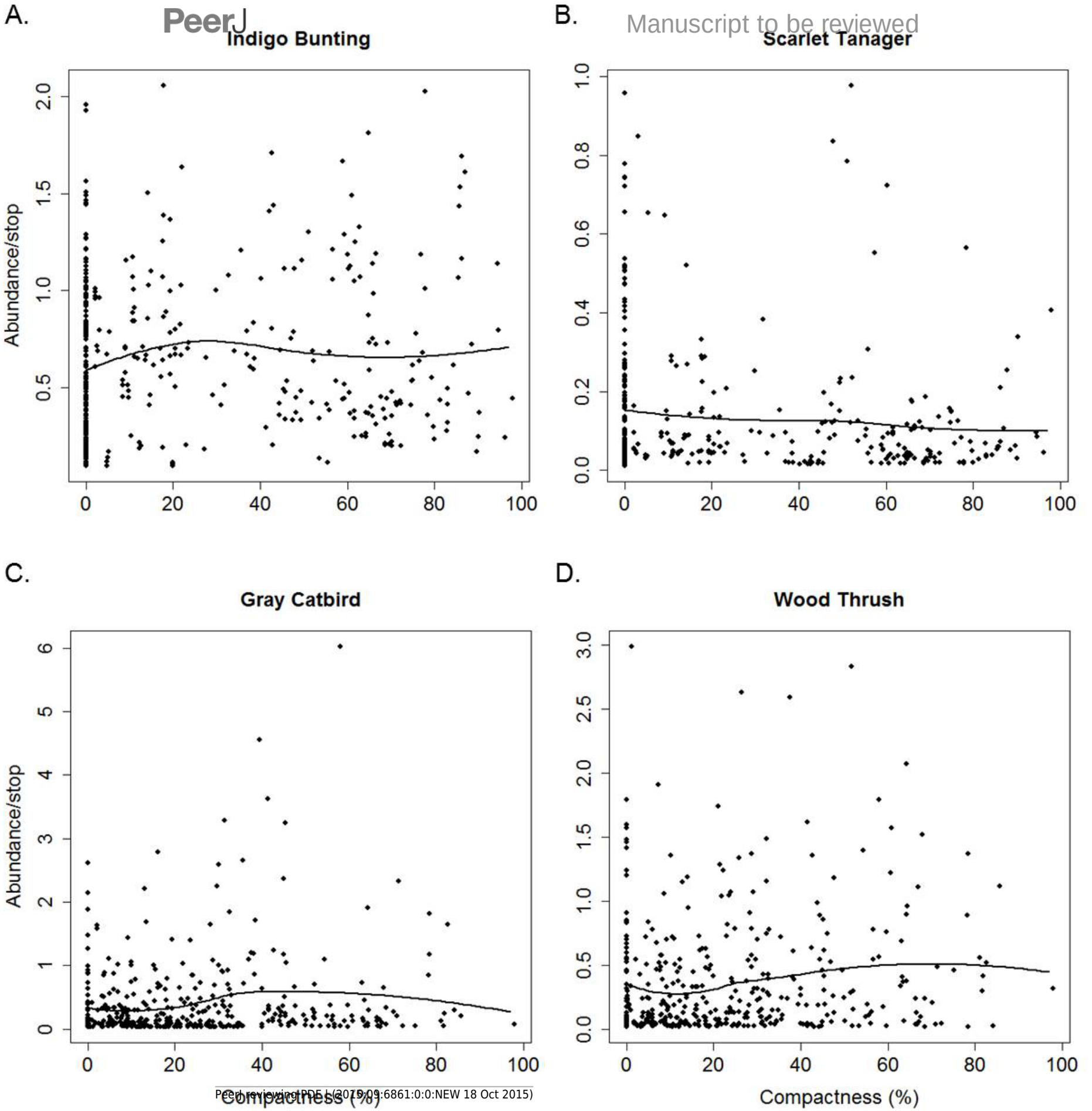
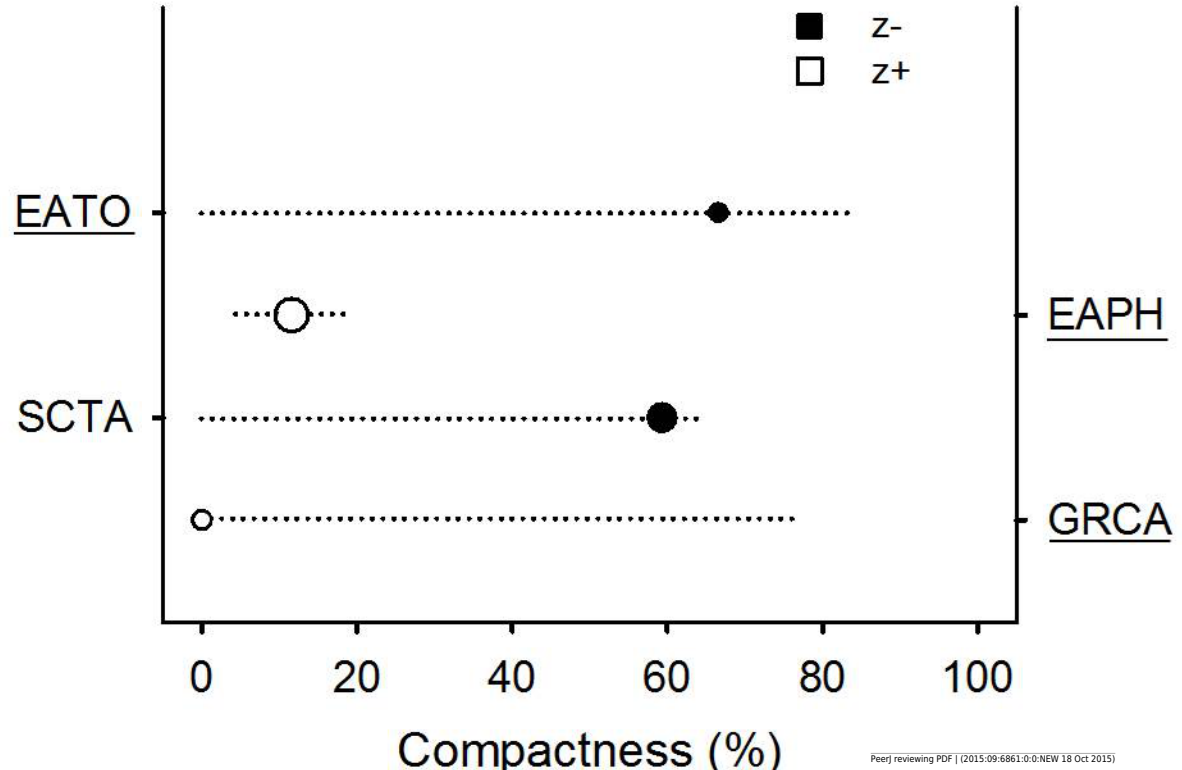


Figure 4(on next page)

Change points of significant ($p < 0.05$) and reliable (purity ≥ 0.90 and reliability ≥ 0.90) indicator bird species of compactness of exurban development for (A) 400-m and (B) 1-km radius buffer around selected BBS stops.

Indicator taxa are plotted in increasing order with respect to their observed change point. Solid circles represent negative (z-) indicator taxa (with corresponding species on the left axes) and open circle correspond to positive (z+) indicator taxa (with corresponding species on the right axes). Circles are sized based on z scores, and lines represent the 5 and 95% percentiles among 250 bootstrap replicates. Short lines indicate nonlinear response in taxon abundance, whereas long lines represent linear or more gradual response. Taxa IDs correspond to the American Ornithologist Union alpha codes for English common names. Underlined codes denote forest-edge species.Change points of significant ($p < 0.05$) and reliable (purity ≥ 0.90 and reliability ≥ 0.90) indicator bird species of compactness of exurban development for (A) 400-m and (B) 1-km radius buffer around selected BBS stops. Indicator taxa are plotted in increasing order with respect to their observed change point. Solid circles represent negative (z-) indicator taxa (with corresponding species on the left axes) and open circle correspond to positive (z+) indicator taxa (with corresponding species on the right axes). Circles are sized based on z scores, and lines represent the 5 and 95% percentiles among 250 bootstrap replicates. Short lines indicate nonlinear response in taxon abundance, whereas long lines represent linear or more gradual response. Taxa IDs correspond to the American Ornithologist Union alpha codes for English common names. Underlined codes denote forest-edge species.


A.
z-
z+
EATO
SCTA
EAPH
GRCA
0
20
40
60
80
100
Compactness (%)

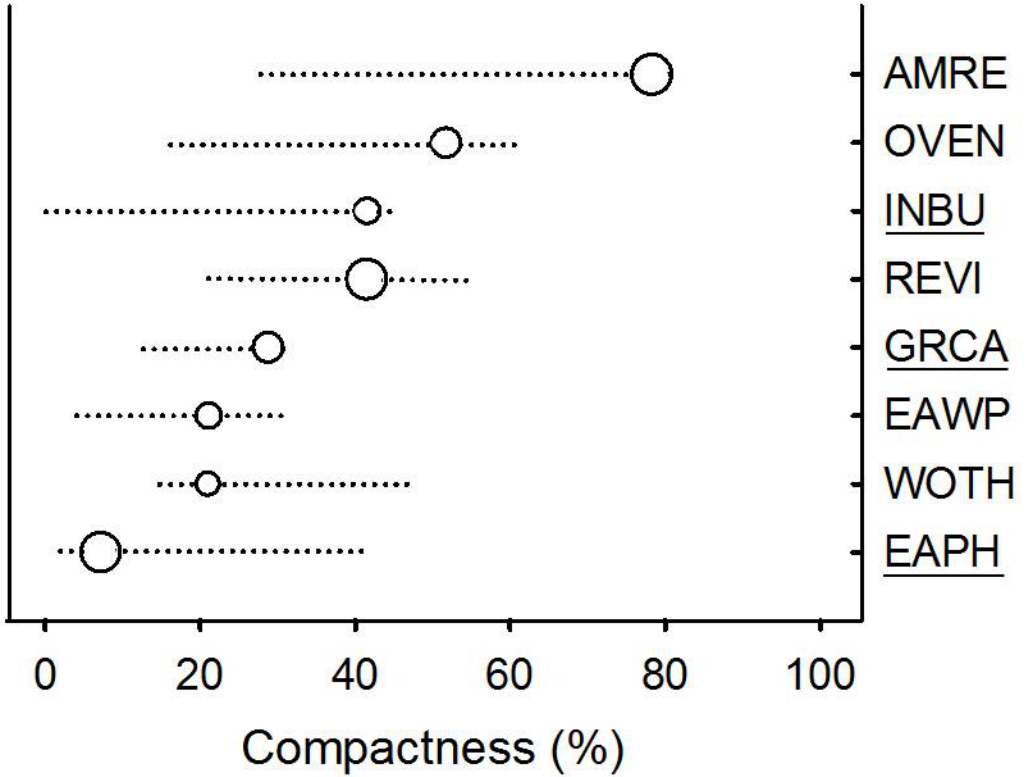

B.
AMRE
OVEN
INBU
REVI
GRCA
EAWP
WOTH
EAPH
0
20
40
60
80
100
Compactness (%)

Table 1(on next page)

Landscape composition and compactness of exurban development (mean ± s.d.) at 400-m and 1-km radius buffer around selected Breeding Bird Survey stops from 1986 to 2009.

1 **Table 1:** Landscape composition and compactness of exurban development (mean ± s.d.) at 400-
2 m and 1-km radius buffer around selected Breeding Bird Survey stops from 1986 to 2009
3

Variables	1986	1993	2000	2009
All survey stops				
400-m radius buffer (n = 97)				
Forest (%)	35.2 ± 32.8	33.6 ± 32.0	31.4 ± 30.9	25.7 ± 28.1
Exurban development (%)	11.3 ± 6.5	12.1 ± 6.6	13.4 ± 7.0	17.4 ± 9.5
Compactness (%)	17.5 ± 26.3	18.1 ± 25.8	25.1 ± 28.8	38.9 ± 34.4
1-km radius buffer (n = 105)				
Forest (%)	41.2 ± 30.9	40.1 ± 30.5	38.5 ± 30.3	32.4 ± 28.6
Exurban development (%)	10.0 ± 4.6	10.9 ± 4.8	12.1 ± 5.3	16.1 ± 7.4
Compactness (%)	11.2 ± 12.6	13.6 ± 13.3	23.2 ± 18.0	43.9 ± 23.5
Survey stops in protected area (n = 26)				
400-m radius buffer				
Forest (%)	100.0 ± 0.0	100.0 ± 0.0	99.9 ± 0.4	99.9 ± 0.4
Exurban development (%)	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.3
1-km radius buffer				
Forest (%)	98.7 ± 3.5	98.7 ± 3.7	98.6 ± 3.8	98.1 ± 4.5
Exurban development (%)	0.3 ± 1.0	0.3 ± 1.0	0.4 ± 1.1	0.7 ± 1.8

4
5

Table 2(on next page)

Threshold Indicator Taxa ANalysis (TITAN) results at the 400-m and 1-km radius buffer.

Significant ($p < 0.05$) and reliable (purity ≥ 0.90 and reliability ≥ 0.90) indicator species are shown in bold

Table 2: Threshold Indicator Taxa ANalysis (TITAN) results at the 400-m and 1-km radius buffer. Significant ($p < 0.05$) and reliable (purity ≥ 0.90 and reliability ≥ 0.90) indicator species are shown in bold

Species	Indicator	z	Change point			Purity	Reliability	*p*
			Obs.	5%	95%			
400-m radius buffer								
Forest birds								
AMRE	z-	0.94	0.00	0.00	84.92	0.54	0.31	0.180
EAWP	z-	1.28	89.19	0.00	89.58	0.54	0.47	0.116
OVEN	z-	1.84	0.00	0.00	87.40	0.59	0.38	0.052
REVI	z-	1.52	0.00	0.00	86.16	0.56	0.40	0.072
SCTA	z-	4.85	59.33	0.00	64.09	1.00	0.99	0.004
WOTH	z-	3.00	18.81	0.00	77.75	0.81	0.80	0.012
Forest-edge species								
EAPH	z+	5.81	11.57	4.40	19.30	0.98	0.98	0.004
EATO	z-	3.06	66.60	0.00	82.98	0.93	0.91	0.004
GRCA	z+	3.26	0.00	0.00	78.92	0.96	0.94	0.008
INBU	z+	3.41	9.05	0.00	85.84	0.90	0.89	0.008
NOCA	z+	1.95	74.91	0.00	89.19	0.80	0.71	0.056
1-km radius buffer								
Forest birds								
AMRE	z+	7.03	78.26	27.58	80.66	1.00	1.00	0.004
EAWP	z+	4.45	21.11	4.00	31.27	0.99	0.98	0.004
OVEN	z+	5.16	51.70	16.07	61.89	0.99	0.99	0.004
REVI	z+	6.99	41.47	20.98	55.16	1.00	1.00	0.004
SCTA	z+	3.92	53.86	0.00	60.16	0.89	0.89	0.008
WOTH	z+	4.06	20.98	14.98	47.12	0.97	0.96	0.004
Forest-edge species								
EAPH	z+	6.86	7.15	1.85	41.76	1.00	1.00	0.004
EATO	z+	2.73	78.26	0.00	81.38	0.86	0.84	0.016
GRCA	z+	5.25	28.74	12.46	31.33	1.00	0.99	0.004
INBU	z+	4.48	41.54	0.00	45.00	0.99	0.98	0.004
NOCA	z+	4.13	28.54	0.00	81.74	0.82	0.82	0.004