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The trade-off between housing density and sprawl area: Minimising impacts to forest breeding birds

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Abstract

Increasing housing density is generally assumed to confer negative effects on forest breeding birds. This implies we should build at low density over the landscape to conserve these species. However, for a given human population, low-density development must cover a large area, resulting in sprawl. A pertinent question is then: at what housing density are the impacts of a given human population on forest biodiversity minimised? For a given human population, it is unclear whether the impacts on forest biodiversity are less where housing density is high and sprawl area is small or where housing density is low and sprawl area is large. We addressed this question using the abundance, species richness and evenness of forest birds in Ottawa, Ontario and Gatineau, Quebec, Canada. First, we counted breeding birds at 22 sites representing a range of housing densities. We then used these empirical measurements to estimate forest bird abundance, species richness and evenness in four hypothetical development scenarios representing the trade-off between housing density and sprawl area. With the exception of the Undeveloped scenario (i.e., continuous forest), forest birds and forest interior birds were most abundant in the Compact scenario and most speciose in the Semi-compact scenario, whereas forest edge birds were most abundant and speciose in the Dispersed scenario. All three bird groups were most even in the Compact scenario. We conclude that compact housing development (building at high density over a small area) minimises the impacts of a given human population on forest breeding birds.

Zusammenfassung

Im Allgemeinen wird angenommen, dass zunehmende Besiedlungsdichte negative Auswirkungen auf im Wald brütende Vögel hat. Dies bedeutet, dass wir mit geringer Dichte über die Landschaft hinweg siedeln sollten, um diese Arten zu erhalten. Für eine gegebene menschliche Bevölkerung bedeutet dies jedoch, dass die Bebauung bei geringer Dichte eine große Fläche einnimmt und zur Zersiedelung führt. Eine bleibende Frage ist deshalb: Bei welchen Siedlungsdichten sind die Auswirkungen einer gegebenen menschlichen Population auf die Biodiversität im Wald minimiert? Für eine gegebene menschliche Population

Keywords: Avian conservation; Conservation subdivisions; Ecological disturbance; Edge effects; Forest fragmentation; Rural residential development; Urban planning; Urban ecology

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ist bisher ungeklärt, ob die Auswirkungen auf die Waldbiodiversität geringer sind, wenn die Siedlungsdichte hoch und das besiedelte Gebiet klein ist, oder wenn die Dichte gering und das besiedelte Gebiet groß ist. Wir wendeten uns dieser Frage zu und verwendeten dafür die Häufigkeit, den Artenreichtum und die Evenness von Waldvögeln in Ottawa, Ontario und Gatinenau, Quebec, Kanada.

Zuerst zählten wir die brütenden Vögel auf 22 Probeflächen, die eine Bandbreite von Bebauungsdichten repräsentierten. Dann nutzten wir diese empirischen Ergebnisse um die Häufigkeit, den Artenreichtum und die Evenness in vier hypothetischen Entwicklungsszenarien einzuschätzen, die einen 'trade-off' zwischen Siedlungsdichte und Siedlungsfläche darstellten. Mit der Ausnahme des unbebauten Szenarios (d. h. eines durchgehenden Waldes) waren die Waldvögel und die Vögel des Waldinneren am häufigsten in dem kompakten Szenario und am artenreichsten in dem semikompakten Szenario, während die Vögel des Waldrandes am häufigsten und artenreichsten im zerstreuten Szenario waren. Alle drei Vogelgruppen zeigten im kompakten Szenario die höchste Evenness. Wir schließen daraus, dass eine kompakte Siedlungsentwicklung (Bebauung bei hoher Dichte über geringe Flächen) die Auswirkungen einer gegebenen menschlichen Population auf im Wald brütende Vögel minimiert.

Introduction

Urban populations in both the United States and Canada have increased by more than 130% since 1950 and are projected to increase by a further 50% by 2050 (United Nations 2008). A recent trend has been increased exurban development, or low-density housing typically occurring in rural areas on the outskirts of large metropolitan centres. For example, of the land area converted to housing in the United States between 1994 and 1997, 80% occurred outside large metropolitan areas and 57% of this was at very low densities (one house on 10 or more acres) (Heimlich & Anderson 2001). Brown, Johnson, Loveland, and Theobald (2005) estimated that nearly a quarter of the land surface of the conterminous United States is now covered by exurban development.

Land cover change at such scales has prompted much research on the patterns of response of populations and communities to urbanization, with a particular emphasis on birds (McDonnell & Hahs 2008). In particular, forest bird abundance and species richness have been found to decline with increasing housing density (Friesen, Eagles, & MacKay 1995; Pidgeon et al. 2007).

The openings created by houses in a forested matrix appear to result in changes to the forest bird community dissimilar to those caused by natural disturbances such as windthrow and fire. For instance, in forests of northeastern Minnesota, disturbances such as stand-replacing fire and severe windstorms result in increased avian species richness and territory density up to 30 years following perturbation (Haney, Apfelbaum, & Burris 2008; Lain, Haney, Burris, & Burton 2008). In contrast, forests that undergo suburban development exhibit dramatically reduced forest bird species richness and territory density for at least 37 years (Aldrich & Coffin 1980). These different responses are due to the fundamentally different nature of the openings created by natural disturbances and residential development. The latter result from the permanent removal of the original native vegetation and its replacement by impervious surfaces, lawns and ornamental herb and shrub species, whereas the former are characterised by a temporary reduction in vegetative cover that is reversed as regeneration and succession take place. The loss of vegetative cover and structural complexity in openings created by houses results in the loss of nesting and foraging habitat for many forest bird species (Beissinger & Osborne 1982). In addition, increased predation (Engels & Sexton 1994) and brood parasitism (Rodewald & Shustack 2008), disturbance from humans (Miller, Wiens, Hobbs, & Theobald 2003) and competition from species better adapted to the dramatically altered conditions surrounding houses (Marzluff 2001) may all contribute to long-term reductions in forest bird populations following residential development.

Declines in forest bird abundance and species richness with increasing housing density could be interpreted to suggest that, to conserve forest biodiversity, we should build at low density over the landscape. However, to accommodate a given human population, low-density development must cover a large area, resulting in sprawl and significant negative impacts to native plant and animal communities (reviewed in Hansen et al. 2005). A pertinent question is then: at what housing density are the impacts of a given human population on forest biodiversity minimised? For a given human population, it is unclear whether the impacts on forest biodiversity are less where housing density is high and sprawl area is small or where housing density is low and sprawl area is large.

We evaluated this trade-off using the abundance, species richness and evenness of forest breeding birds in Ottawa, Ontario and Gatineau, Quebec, Canada. Our methodology can be described in two parts. First, we counted breeding birds in sites of the same size representing a range of housing densities. Second, we used these empirical data to estimate the abundance, species richness and evenness of forest breeding birds in four hypothetical development scenarios representing the trade-off between housing density and sprawl area. Development scenarios were hypothetical forested landscapes of the same size that accommodated a given human population at different housing densities, resulting in dispersed, semi-compact and compact development patterns. We identified the housing density that minimised the impacts of a given human population on forest breeding birds by comparing abundance, species richness and evenness estimates among scenarios.

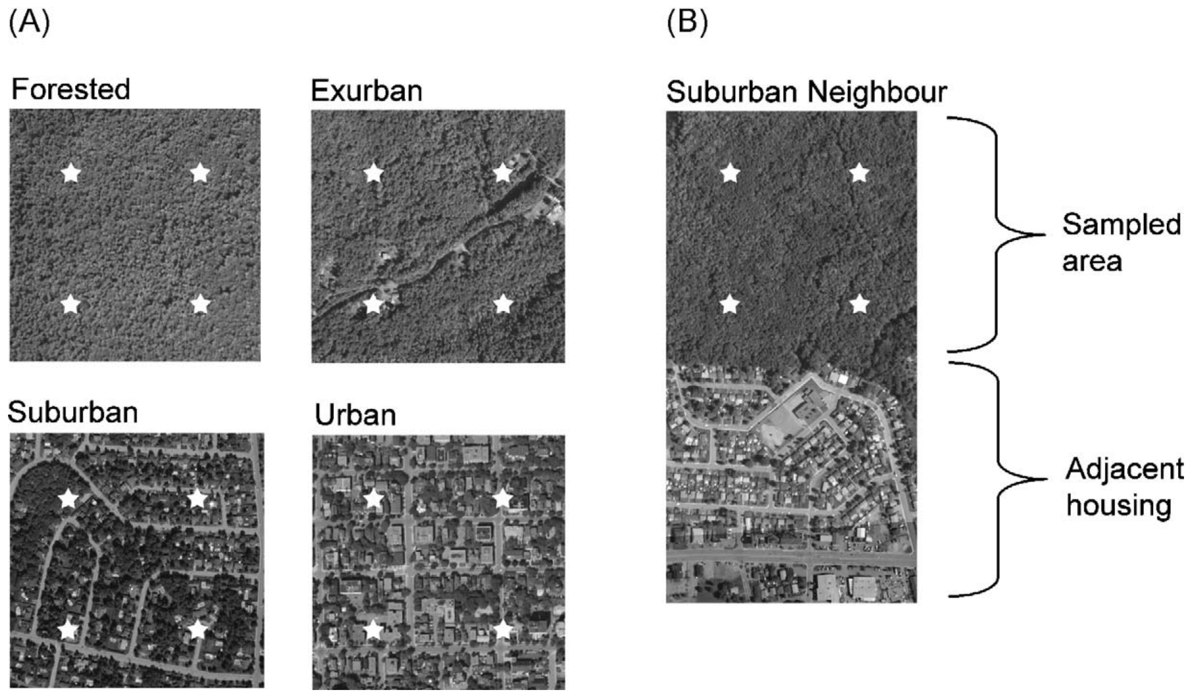

Fig. 1. Typical sites (500 m × 500 m) in which breeding birds were surveyed. Point count stations are shown as white stars.

Methods

Bird abundance data collection

Study area

We sampled breeding bird populations at 22 sites in and around Ottawa, Ontario and Gatineau, Quebec, Canada (see Appendix A: Fig. S1). The study area encompassed approximately 4040 km^2 on both sides of the Ottawa River. The northern half of the study area forms part of the Southern Laurentians ecoregion and the southern half is encompassed by the St. Lawrence Lowlands ecoregion. All housing categories (see below) were approximately equally represented in both ecoregions to account for possible differences in forest composition (see Appendix A: Fig. S1). In addition, we tested *a posteriori* for differences in tree community composition between ecoregions using a redundancy analysis. The single constrained eigenvalue was not significant (100 permutations, $F_{1,2} = 2.37$, $p = 0.29$).

Site selection

We selected four sites in each of four housing density categories: Forested (0 dwellings/km^2), Exurban (<56 dwellings/km^2, mean = 31 ± 9 (SE) dwellings/km^2), Suburban (140–712 dwellings/km^2, mean = 555 ± 101 (SE) dwellings/km^2) and Urban (>1244 dwellings/km^2, mean = 3754 ± 492 (SE) dwellings/km^2) (Fig. 1A). Each site comprised the area within a 500 m × 500 m square (0.25 km^2). Housing density categories did not represent a continuous gradient of housing types. Exurban and Suburban sites were dominated by single-family structures, exclusively detached in Exurban sites and a mix of detached and attached in Suburban sites, whereas Urban sites were composed of single-family structures and a variety of multi-family complexes (e.g., low-rise and high-rise apartment buildings). We focused on housing density (number of dwellings) irrespective of housing type due to the availability of suitable sites in the study area considering the other criteria used for site selection (see below). In addition to these 16 sites, we selected six forested sites, equal in size to those described above, adjacent to developments of Suburban and Urban housing densities (three sites each) (Fig. 1B). In contrast to the Forested sites which were embedded in a larger forested area, these Neighbour sites were chosen to incorporate the possible effects of adjacent urban development on breeding bird populations in forest habitat.

We searched for sites using a combination of historical topographic maps (~1/50 000, Centre for Topographic Information, Natural Resources Canada) and the most recent aerial photographs available (2002, 1/15 000, City of Ottawa). Using topographic maps, we located areas that were forested prior to development. We then checked the present housing density of these areas on aerial photographs to determine whether they could be placed into our pre-defined categories. In this way, we selected sites that were not subjected to agricultural use for at least as many years as topographic maps have been produced (approximately 80 years). We minimised edge effects by choosing only sites that were surrounded by >100 m of development of a similar housing density or forest cover, depending on the housing category. Finally, we ground-truthed all sites to ensure they met our criteria. The number of dwellings at each site and in 500 m × 500 m devel-

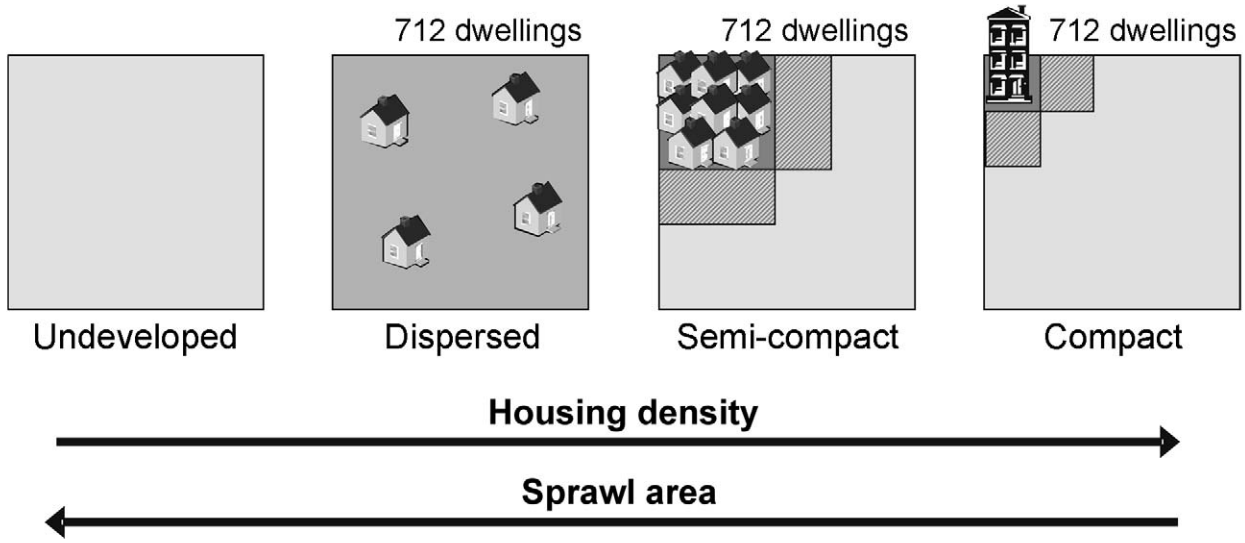

Fig. 2. Hypothetical development scenarios representing a gradient of increasing housing density and decreasing sprawl area. For a given forested area (the Undeveloped scenario), the same number of dwellings is depicted at three housing densities, Exurban, Suburban and Urban, resulting in dispersed, semi-compact and compact development patterns, respectively. Hatched areas in the Semi-compact and Compact scenarios represent forest habitat adjacent to development, typical of Suburban Neighbour and Urban Neighbour survey sites, respectively. Drawings, including proportions of each cover type in each scenario, are not to scale.

oped areas adjacent to Neighbour sites were counted on the ground in August 2006.

Breeding bird surveys

We counted breeding birds at four stations in each site using the Ontario Forest Bird Monitoring Program protocol (Cadman, Dewar, & Welsh 1998). At each site, we centred a station in each quarter; stations were thus 250 m apart (Fig. 1). We conducted two point count surveys at each station in 2006, the first between May 24 and June 6 and the second between June 13 and June 28. During each period, we surveyed two sites per day. Each day, we chose sites from different categories and as far as possible from one another. The order of sites surveyed per day was reversed between the two surveys to minimise any bias in the data due to individual species preferentially vocalising at a particular time of day. This also ensured that each site was surveyed once at a time of day when traffic volume was very low, thus minimising the effect of traffic noise on our ability to detect bird vocalisations. We visited stations within sites in the same order during both surveys.

During each survey, we conducted a 10-min point count at each station between a half-hour before sunrise and 5 h after sunrise. We only performed point counts when the wind was <3 on the Beaufort scale and it was not raining. If these conditions were not met, we cancelled the count(s) and resumed the next possible day. We counted all adult birds seen or heard during the 10-min period at an unlimited distance from the station. We did not include birds passing high overhead.

Comparison of development scenarios

Hypothetical development scenarios

We used the data described above to estimate forest bird abundance, species richness and evenness along a gradient of increasing housing density and decreasing sprawl area. We represented this gradient with hypothetical development scenarios (Fig. 2). Development scenarios can be envisioned as forested landscapes of the same size, into which the same number of dwellings were placed, but in contrasting patterns. One end of the gradient, where housing density is low and sprawl area is large, was represented by the Dispersed scenario, which was completely covered by Exurban-density development. The other end of the gradient, where housing density is high and sprawl area is small, was represented by the Compact scenario. The Compact scenario was home to the same number of dwellings as the Dispersed scenario but the dwellings were clustered at an Urban density and the remainder of the Compact scenario was undeveloped forest. We also estimated forest bird abundance, species richness and evenness for an intermediate development scenario, the Semi-compact scenario. The same number of dwellings as in the other two development scenarios was represented at a Suburban density, with the remainder of the Semi-compact scenario in undeveloped forest. Finally, for comparison, we estimated forest bird abundance, species richness and evenness for an Undeveloped scenario, i.e., the same area as for the developed scenarios but covered entirely in forest.

We defined a development scenario as a 22.96 km^2 square area, or an area equivalent to 91.83 units of the 500 m × 500 m

($0.25\,km^2$) bird survey sites. We arrived at this development scenario size by calculating the area required to accommodate a given number of dwellings (the mean number of dwellings at our Urban and Urban Neighbour bird survey sites (712 dwellings)) at the lowest housing density (the Exurban density, mean = 31 dwellings/km^2). In this way, we created the Dispersed scenario, covered entirely by 712 dwellings at the Exurban housing density or, equivalently, 91.83 Exurban bird survey sites. In a similar fashion, we determined the size of the developed area (measured in km^2 or in the number of Suburban or Urban bird survey sites) within the Semi-compact and Compact scenarios. For these, we created square developed areas positioned in one corner of each development scenario to represent the area needed to contain 712 dwellings at the mean Urban or Suburban densities ($0.25\,km^2$ and $1.42\,km^2$, respectively). For the Semi-compact and Compact scenarios, we assumed that the forest cover adjacent to the developed area had forest bird abundances, species richnesses and evenness typical of our Neighbour bird survey sites adjacent to Suburban- and Urban-density development, respectively. We calculated the area of this adjacent forest cover as the number of Neighbour bird survey sites required to line both edges of the developed area. Finally, we assumed that the remaining area in the Semi-compact and Compact scenarios was typical of our Forested bird survey sites. We assumed the Undeveloped scenario was covered entirely in forest cover typical of our Forested bird survey sites.

Theoretical forest bird species abundances

We estimated the abundance of each forest bird species observed during our breeding bird surveys for each development scenario. First, we calculated the abundance of a species at each bird survey site by summing the counts of the species at all four stations in the site during each survey period and selecting the maximum survey count as the abundance of the species at the site. Recall that we measured the area of each development scenario in terms of the numbers of bird survey sites of each housing category making up the development scenario (see above). To estimate the total abundance of a species for a development scenario, we moved through the scenario, one site area at a time, and randomly selected an abundance value for the species from one of the three or four bird survey sites in that housing category (Fig. 3). For areas in the development scenario making up proportions of bird survey sites, we multiplied the randomly selected abundance value by that proportion. We summed these 91.83 abundance values to yield the estimated abundance of a species in the whole development scenario. We repeated this estimation procedure 1000 times, resulting in an abundance distribution for each species in each development scenario. In the same manner, we also estimated the total abundance of all forest birds in each development scenario and the total abundance of birds belonging to species classified as ‘forest interior’ and ‘forest edge’ in each development scenario (see Appendix A: Table S1).

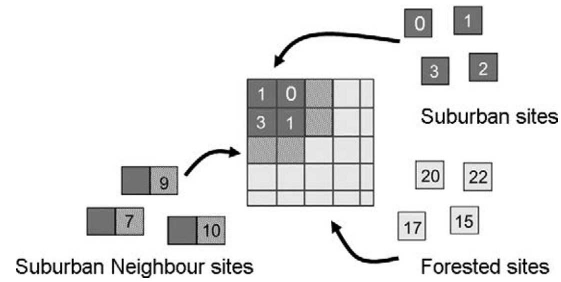

Fig. 3. Illustration of the method for estimating the abundance of a typical forest bird species in a development scenario. Shown is the Semi-compact scenario. Numbers represent the abundance of the species in each bird survey site. Three types of bird survey sites make up the Semi-compact scenario: Suburban, Suburban Neighbour and Forested. For each site area in the scenario, an abundance value was randomly chosen from the replicate bird survey sites in the appropriate housing category. To illustrate this, the developed portion of the scenario has been filled in with randomly chosen abundance values from the Suburban bird survey sites. For areas in the development scenario that are smaller than site areas, the abundance value was multiplied by the proportion of a site area represented. Finally, the randomly selected values for the entire Semi-compact scenario were summed to yield an estimate of the abundance of the forest bird species in the whole development scenario.

Theoretical forest bird species richnesses and evenness

We estimated the species richness of all forest birds, forest interior birds and forest edge birds in each development scenario. Using species accumulation curves constructed for each housing category and for each bird group (Colwell & Coddington 1994), we estimated that during our point counts we observed >90% of species predicted to be present in each type of site. We also estimated the predicted species richness of each bird group in each housing category using Chao’s (1984) estimator, which has been shown to exhibit the least bias compared to other non-parametric asymptotic species richness estimators when sample size is small (Colwell & Coddington 1994). Using Chao’s (1984) estimator, we calculated that we counted an average of 83% of species estimated to be in each housing category (minimum: 64% of forest edge bird species in Suburban survey sites; maximum: 100% of forest bird species in Urban survey sites and 100% of forest interior bird species in Urban Neighbour survey sites). In particular, using Chao’s (1984) estimator, we calculated that we observed 87% of forest bird species predicted to be present in Forested survey sites. Therefore, for the purposes of the present analysis, we assumed that we recorded the entire community of birds present in each housing category. Using this information, we estimated the species richness of each bird group in each development scenario with a procedure similar to that described for abundance. For each site area in a development scenario, we randomly selected an actual sampled site from the appropriate housing category and applied the species observed there to the site area in the development scenario. We repeated this procedure for every site area in the

Table 1. Forest bird abundance, species richness and evenness (mean ± SE) at 500 m × 500 m bird survey sites in six housing categories. Individual-based rarefied richness was estimated over all survey sites in each housing category, using the number of individuals from the housing category with the fewest birds as the sample size. The Simpson evenness index (the reciprocal of Simpson's index of diversity divided by the number of species) was used to estimate evenness.

	Forested	Exurban	Suburban	Urban	Suburban neighbour	Urban neighbour
n	4	4	4	4	3	3
Housing density (mean ± SE dwellings/km^2)	0	31.00 ± 9.30	555.00 ± 101.10	3754.00 ± 491.92	434.68 ± 159.53	1637.32 ± 281.98
All forest birds						
Abundance	66.50 ± 5.14	59.25 ± 5.59	24.75 ± 4.64	3.50 ± 1.19	23.33 ± 4.37	21.33 ± 5.84
Species richness	19.75 ± 1.11	18.75 ± 2.06	7.00 ± 1.08	1.50 ± 0.29	15.00 ± 3.46	14.67 ± 0.33
Rarefied richness	10.03 ± 1.41	9.53 ± 1.40	5.84 ± 1.25	3.00 ± 0.00	8.84 ± 1.39	8.00 ± 1.40
Evenness	0.58 ± 0.02	0.56 ± 0.04	0.50 ± 0.06	0.93 ± 0.07	0.58 ± 0.04	0.54 ± 0.04
Forest interior birds						
Abundance	31.00 ± 2.88	18.75 ± 3.96	3.75 ± 2.06	0	17.33 ± 7.97	18.33 ± 0.88
Species richness	8.75 ± 0.75	6.75 ± 1.11	1.25 ± 0.63	0	5.33 ± 1.85	5.67 ± 0.88
Rarefied richness	7.68 ± 1.34	6.24 ± 1.13	4.00 ± 0.00	0	5.83 ± 1.06	5.48 ± 1.09
Evenness	0.59 ± 0.03	0.60 ± 0.06	0.98 ± 0.02	0	0.61 ± 0.00	0.50 ± 0.05
Forest edge birds						
Abundance	35.50 ± 4.05	40.50 ± 2.06	21.00 ± 3.14	3.50 ± 1.19	33.67 ± 3.84	38.33 ± 1.33
Species richness	11.00 ± 1.47	12.00 ± 1.08	5.75 ± 0.48	1.50 ± 0.29	9.67 ± 1.85	9.00 ± 0.58
Rarefied richness	8.37 ± 1.30	8.18 ± 1.32	4.83 ± 1.14	3.00 ± 0.00	7.22 ± 1.30	6.49 ± 1.23
Evenness	0.62 ± 0.05	0.59 ± 0.04	0.50 ± 0.07	0.93 ± 0.07	0.60 ± 0.04	0.60 ± 0.03

development scenario, successively adding any new species to the development scenario's species list. For areas in the development scenario making up fractions of bird survey site areas, we randomly selected without replacement the observations from one, two or three of the sampling stations within a randomly selected bird survey site, depending on the size of the fraction of the site area. The development scenario's final species list once every site area had been 'filled' with species was the species richness of that whole development scenario.

Initially, the total number of bird survey sites available for selection differed among development scenarios (four each in the Undeveloped and Dispersed scenarios and 11 each in the Semi-compact and Compact scenarios). This represented a difference in sample size among the development scenarios, which could bias the results such that the estimated richnesses in the Undeveloped and Dispersed scenarios would be lower than they should be, relative to the richnesses in the Semi-compact and Compact scenarios. We corrected for this by randomly selecting two Forested bird survey sites, one Suburban or Urban site and one Suburban Neighbour or Urban Neighbour site prior to estimating the species richness of each bird group in the Semi-compact and Compact scenarios, respectively. Finally, we estimated the species richness of each bird group in each development scenario 1000 times to yield distributions of possible species richness values for each scenario.

We estimated the evenness of each bird group in each development scenario using the Simpson evenness index (Magurran 2004). This index is calculated by dividing the reciprocal form of Simpson's index of diversity by the number of species in a community. Communities of differing numbers of species can be compared with the Simpson evenness index because it is insensitive to species richness (Magurran 2004). For each bird group in a development scenario, we calculated the Simpson evenness index using species richness taken from the scenario's final generated species list (see above). Although not used in the estimation of species richness, each species in a scenario's final species list was associated with an estimated abundance in the scenario. Thus, for each bird group, each scenario was characterised by an estimated community of species with their associated abundances. We used this information to calculate the Simpson evenness index. We calculated the index for each iteration of the species richness estimation procedure (i.e., 1000 times). All analyses were carried out in R version 2.6.0 (R Development Core Team 2007).

Results

Bird abundance, species richness and evenness in the survey sites

We observed 39 native forest bird species during our surveys, 16 of which we classified as forest interior species and 23 as forest edge species (see Appendix A: Table S1). Species varied in abundance from one individual (Blue-headed Vireo *Vireo solitarius*, Canada Warbler *Wilsonia canadensis*, Golden-crowned Kinglet *Regulus satrapa*, Swainson's Thrush *Catharus ustulatus*) to 168 individuals (Black-capped Chickadee *Poecile atricapilla*) across all survey sites. Seven species were detected at only one bird survey site (the four species above plus Mourning Warbler *Oporornis philadelphia*, Ruffed Grouse *Bonasa umbellus*, and Warbling Vireo *V. gilvus*) and the most widespread species, Black-capped Chickadee, was detected at 21 of the 22 bird survey sites.

In the bird survey sites, the abundance and species richness of all forest birds and forest interior birds declined as housing density increased from the Forested to the Urban housing categories (Table 1). Neighbour bird survey sites had intermediate values of forest bird and forest interior bird abundance and species richness. Forest edge birds were most abundant and speciose in Exurban survey sites, followed closely by Forested and Neighbour sites (Table 1). In addition to comparing raw counts of species (i.e., species richnesses) among housing categories, we calculated the individual-based rarefied richness of each bird group in each housing category. For each bird group and each housing category, we estimated rarefied richness across all survey sites using the number of individuals from the housing category with the fewest birds as the sample size (14 individuals in the Urban category for forest birds and forest edge birds and 15 individuals in the Suburban category for forest interior birds) (Magurran 2004). Patterns of rarefied richness among housing categories were very similar to those of uncorrected species richness (Table 1). Finally, the Simpson evenness index for all three bird groups varied among housing categories, with the Suburban and Urban categories having higher index values (indicating greater evenness) than the other housing categories (Table 1).

Effects of housing density vs. sprawl area in the hypothetical development scenarios

Of the developed scenarios, over half of the 39 forest bird species observed during our surveys were estimated to be most abundant in the Compact scenario (22 species, 56%) (see Appendix A: Table S1). Approximately one-third of the forest species were estimated to be most abundant in the Dispersed scenario (13 species, 33%) and only four species (10%) were estimated to be most abundant in the Semi-compact scenario.

With the exception of the Undeveloped scenario, the estimated abundance of all forest birds and of forest interior birds was highest in the Compact scenario (Fig. 4A and B). In contrast, the estimated abundance of forest edge birds was highest in the Dispersed scenario (Fig. 4C). The Undeveloped scenario had the highest estimated species richness for all three bird groups (Fig. 4D, E and F). Considering only the developed scenarios, the estimated species richness of all forest

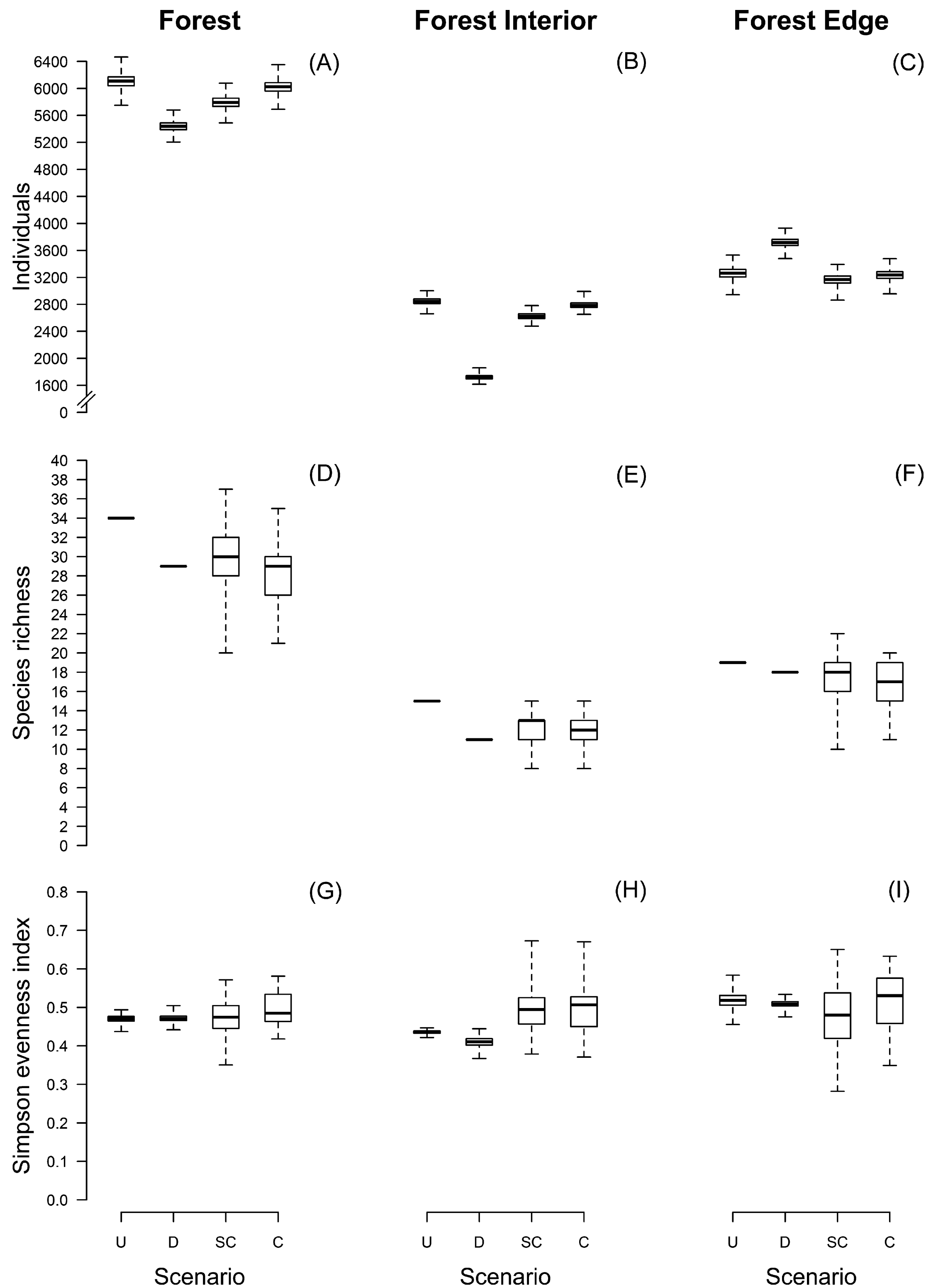

Fig. 4. Estimates of the abundance, species richness and evenness of three bird groups in four hypothetical development scenarios: U, Undeveloped; D, Dispersed; SC, Semi-compact; C, Compact. The lower edge of each box is the first quartile, the bold centre line is the median and the upper edge is the third quartile of the distribution. Whiskers extend to the minimum and maximum values. Species richness estimates for the Undeveloped and Dispersed scenarios had zero variance. This is because all bird species counted in the four Forested survey sites (for the Undeveloped scenario) and the four Exurban survey sites (for the Dispersed scenario) were always estimated to be in at least one of the large number (91.83) of replicate site areas in these scenarios.

birds and of forest interior birds was highest in the Semi-compact scenario (Fig. 4D and E) whereas the estimated species richness of forest edge birds was highest in the Dispersed scenario (Fig. 4F). The estimated species richness of forest edge birds was also high in the Semi-compact scenario, but exhibited greater variance than in the Dispersed scenario (Fig. 4F, see legend for explanation). All three bird groups were estimated to exhibit the greatest degree of evenness in the Compact scenario (Fig. 4G, H, and I).

Discussion

Our results suggest that clustering housing development at a Suburban or Urban density minimises the impacts of a given human population on forest breeding birds (Fig. 4). To our knowledge, only one other study to date has compared animal community structure in clustered and dispersed housing developments. Lenth, Knight, and Gilgert (2006) compared bird, mammal and plant communities among dispersed developments, clustered developments, and undeveloped areas in Colorado. They reported no significant differences between development types, but found that both types had significantly more non-native and human-commensal species and significantly fewer native and human-sensitive species than undeveloped areas. Several reasons could account for the disparity between Lenth et al.'s (2006) results and our own. Lenth et al. (2006) performed their study at a relatively small scale (their largest housing development was 2.92 km^2). In this study, we estimated forest bird abundance and species richness in hypothetical landscapes of 22.96 km^2. As well, the sites used by Lenth et al. (2006) were subjected to grazing pressure in addition to being developed, whereas we assumed that the only other land use in our hypothetical landscapes was recreation. Finally, Lenth et al. (2006) did not control for site size among their treatments. To our knowledge, our work is the first to compare abundance, species richness and evenness estimates of any taxon among development patterns in landscapes of the same size.

The dearth of studies investigating the consequences for biodiversity of building dispersed vs. compact developments veils the importance of the question. Sutherland et al. (2009) recently listed the question addressed here as one of the 100 questions that, if answered and acted upon, would have the greatest impact on the conservation of biological diversity worldwide. The likely reason for the lack of attention to the issue of dispersed vs. compact developments is the enormous difficulty and expense involved in collecting community data at large spatial scales. We certainly encountered this difficulty and our sample size, 3–4 sites in each housing category, reflects this. However, we collected high-quality information at each of these sites, which captured the patterns of response of forest bird communities to housing density (Table 1). These patterns are indicative of the response of breeding bird communities during a single breeding season and do not account for inter-annual variation in breeding bird abundance and species richness, which may be large. However, it appears that the effects of urbanization are strong enough to elicit similar responses in bird communities sampled in 1 year (e.g., Germaine, Rosenstock, Schweinsburg, & Richardson 1998) or many (Pidgeon et al. 2007). Thus, we would expect the overall patterns evident in our data to be generally consistent from year to year. It should also be noted that housing density is the ultimate cause of the changes in forest bird community structure that we report. Residential development results in dramatic changes to vegetative cover and structural complexity, among other factors (see Introduction), that are the proximate causes of alterations to forest bird community structure with increasing housing density. Finally, the method employed here, of using empirical data to construct hypothetical scenarios, is very versatile. Our method could easily be transplanted to other cities with differing regional contexts, be applied to other taxa in other biomes, and incorporate related questions (see below).

In creating our development scenarios, we assumed that development occurred in a corner of the Semi-compact and Compact scenarios. This assumption may have underestimated the edge effects of the development on the surrounding forest habitat and biased our estimates of forest bird abundance, species richness and evenness in these scenarios. To determine if this was the case, we repeated our analysis using scenarios with housing developments in the centre of each landscape. This resulted in very similar results overall, with slightly altered results for three species: Pine Warbler *Dendroica pinus* abundance was highest in the Compact rather than the Semi-compact scenario, Purple Finch *Carpodacus purpureus* abundance was highest in the Dispersed rather than the Semi-compact scenario, and Yellow-throated Vireo *V. flavifrons* abundance was highest in the Semi-compact rather than the Compact scenario. Despite the overall similarity in forest bird abundance, species richness and evenness estimates between these two development scenario configurations, it is still possible that edge effects extend beyond the 500 m of our Neighbour sites, and that this distance may be different for Suburban- and Urban-density development. To our knowledge, however, empirical evidence to support an edge effect distance greater than 500 m is lacking in the literature and, given the large differences we estimated among our scenarios, an increase in edge effect distance is not likely to change our overall results. Nevertheless, this issue warrants further research as does the related question of how large the undeveloped portion of a developed landscape needs to be to maintain populations of sensitive species.

The estimated patterns of bird abundance in development scenarios were in part likely driven by a gradient in forest cover in the scenarios. For example, the estimated abundance of forest birds was highest in the Undeveloped scenario, followed by the Compact, Semi-compact and Dispersed scenarios (Fig. 4A), a pattern that mirrors the proportion of forest cover typical of Forested survey sites in the scenarios (100% in the Undeveloped scenario, 97% in the Compact scenario, 89% in the Semi-compact scenario, and 0% in the Dispersed scenario). Thus, patterns of estimated abundance could be different than those reported here if the proportion of Forested survey site areas in scenarios (and the proportions of Neighbour survey site areas and developed areas) were different. To investigate the possible range of the proportions of cover types making up a scenario, we varied scenario size using extreme values of the number of dwellings in Urban and Urban Neighbour housing categories and the housing density of Exurban survey sites (rather than the average values used in the present analysis). We illustrate these calculations with the Compact scenario. To accommodate the maximum number of dwellings in Urban and Urban Neighbour survey sites (1167 dwellings) at the minimum Exurban housing density (12 dwellings/km^2), scenario size would have to be 97.25 km^2. Urban survey site areas would cover 0.3%, Urban Neighbour survey site areas would cover 0.5% and Forested survey site areas would cover 99.2% of the scenario. To accommodate the minimum number of dwellings in Urban and Urban Neighbour survey sites (311 dwellings) at the maximum Exurban housing density (56 dwellings/km^2), scenario size would shrink to 5.55 km^2, of which 4.5% would be covered by Urban survey site areas, 9.0% would be covered by Urban Neighbour survey site areas and 86.5% would be covered by Forested survey site areas. Thus, using the housing density values typical of Ottawa, Ontario and Gatineau, Quebec, the Compact scenario remains largely composed of Forested survey site areas and estimated patterns of bird abundance in development scenarios would remain relatively unchanged. However, it is unclear how the use of housing density values outside of the range typical in our study area would impact scenario structure and this represents an important avenue of further research.

The application of the housing density/sprawl area model we developed here to cities larger than Ottawa, Ontario and Gatineau, Quebec would also enable a more continuous approach to the characterisation of housing density compared to the four representative categories used in the present analysis. A greater number of developed scenarios than the three presented in this paper could be constructed to investigate the range of development patterns that support a diverse and abundant forest bird community. In addition, a more continuous approach would enable investigations into the existence of thresholds along the housing density/sprawl area gradient. For example, it would be very interesting to determine if a threshold exists along the gradient where the abundance of introduced species abruptly changes.

In conclusion, we present evidence that compact as opposed to dispersed housing developments minimise the impacts of a given human population on forest breeding birds. The bundling of roads (Jaeger, Fahrig, & Ewald 2005) has also been shown to minimise impacts on biodiversity given a set of economic constraints. Taken together, this and other studies suggest we must explicitly account for human use of the landscape in order to effectively conserve biodiversity and that an often ignored solution may be to minimise the habitat lost to this use.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2010.09.001.

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