Cavity nesting birds along an urban-wildland gradient: is human facilitation structuring the bird community?

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Abstract Urbanization brings dramatic and sudden changes to ecological conditions affecting natural communities. Cavity-nesting birds, both primary and secondary (hereafter PCN and SCN, respectively), may be limited in this novel environment because of reduced abundance of nesting sites (e.g. snags and cavities) and competition for cavities with non-native species. But humans can also directly and indirectly provide nest sites (e.g., nest boxes, crevices on houses), especially for SCN species, potentially partially compensating for negative effects. We investigated whether and how PCNs and humans facilitated the cavity-nesting bird community along a gradient of urbanization. To do so, we estimated the abundance of cavity-nesting species between 1998 and 2010 at 135, 1-km^2 sites that differed in the degree of urbanization (0–100 % forest cover). Also, we found 367 nests on a subset of 31 sites. PCNs ($n = 67$ nests) nested mostly on snags (98.5 %), while native SCNs ($n = 141$) used both natural (71.63 %) and anthropogenic (28.37 %) cavities. Non-native SCNs ($n = 159$ nests) used mostly anthropogenic cavities (98.11 %). PCN abundance facilitated native SCN abundance on sites with more than 12 % forest cover at 1-km^2 scale, but not at less forested sites. There, native SCNs nested primarily (59 %) in anthropogenic cavities. Human facilitation allowed native SCNs to successfully use and reproduce where snags were scarce, changing the composition and structure of the cavity-nesting bird community within the most urbanized sites. Flexible nest site selection and human facilitation provide new opportunities for native cavity-nesting birds in a rapidly changing world.

Keywords Stress gradient hypothesis · Nest box · Cavity-nesting birds · Non-native species

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Introduction

For decades, the study of species interactions in community and population ecology has been mainly approached from the point of view of negative interactions, notably competition and predation (Butterfield 2009). However, recent considerations have shown that facilitation (i.e., any positive interaction between two species where at least one of them is benefited and neither is harmed, Hacker and Gaines 1997; Stachowicz 2001), can structure ecological communities and regulate population dynamics (Stachowicz 2001; Bruno et al. 2003; Brooker et al. 2008), especially under stressful conditions (Bertness and Callaway 1994).

The urban ecosystem is a stressful environment for native species that require native vegetation or undisturbed settings. As urbanization expands globally, novel ecosystems have emerged (Kowarik 2011) and native bird communities have been affected by habitat loss and degradation, but also by changes in the abundance of food, disease transmission, predation and other interactions with native and non-native species (Blair 1996; Marzluff 2001; Kowarik 2011; Aronson et al. 2014). As such, the influence of facilitation to animals within urban ecosystems may be investigated by considering the stress-gradient hypothesis (SGH, Bertness and Callaway 1994), which posits that the importance of facilitative interactions is greatest at high levels of stress and it is less relevant

when stress levels are lower and other biotic interactions, such as competition, are more important. This shift in the form of species interactions has been documented for plants with different life histories and origins (native or non-native) in a wide variety of ecosystems and climates (He et al. 2013), yet testing of this framework in animal ecology is still lacking (Barrio et al. 2013). In fact, it seems that the common conception among animal ecologists is that competition is higher in stressful than in less stressful conditions (Barrio et al. 2013).

Urbanization is a multidimensional stress as biotic and abiotic dimensions are affected at the same time, normally on a cline between urban cores and the surrounding natural areas (Blair 1996; Marzluff 2001). Under these circumstances, it has been shown that different species respond differently to these novel habitats (Marzluff et al. 2015). Urban cores usually support high levels of avian biomass concentrated in few native and non-native species (Beissinger and Osborne 1982; Blair 1996; Melles et al. 2003; Chace and Walsh 2006; Chapman and Reich 2007; Møller 2009; MacGregor-Fors et al. 2012; Aronson et al. 2014; Shanahan et al. 2014; Sol et al. 2014). Native species, on the other hand, may be more prevalent in middle to low levels of urbanization, where more vegetation (native and non-native) is available, reaching the highest richness at middle levels of urbanization (ca. 30–70 % forest in the landscape, Hansen et al. 2005; Marzluff 2005; Tratalos et al. 2007; Blair and Johnson 2008; Pennington and Blair 2012; Shanahan et al. 2014).

Although cities are stressful for many avian species, human supplements may facilitate the presence of others (Faeth et al. 2005). People benefit birds by providing habitat in their backyards using landscaping, bird feeders, nest boxes, and water features, among other practices (Davies et al. 2009; Clucas et al. 2011; Clucas and Marzluff 2011; Marzluff 2014), increasing bird richness (Robb et al. 2008; Clucas and Marzluff 2015) and population size (Fuller et al. 2008).

The main objective of our work was to understand facilitative interactions between humans and a particular group of birds (cavity-nesting species) on a gradient of habitat disturbance, and therefore stress, which we consider to be correlated with the degree of urbanization. Cavity-nesting birds may be particularly sensitive to urbanization because they are normally limited by the availability of dead trees for nesting (Newton 1998) and habitat (e.g. forest cover). These key resources are usually lost or significantly reduced in urban areas (Blewett and Marzluff 2005; Donnelly and Marzluff 2006; Davis et al. 2014; LaMontagne et al. 2015) affecting occurrence and abundance of cavity-nesting species and other species that may interact with them as part of the ecological community (e.g. nest web, Martin and Eadie 1999). We studied the response of cavity-nesting species richness, abundance, community structure, nesting patterns and nesting success along a gradient of urbanization, paying particular attention to direct and indirect

facilitation by humans. In accordance with the stress-gradient hypothesis, we expect that the effects of human facilitation (if any) on cavity nesting birds will be strongest in sites with medium to high levels of disturbance (urban cores and suburban areas) and that humans may play a role structuring the community by favoring some species over others.

Methods

Study sites and focal species

We studied 5 primary cavity nesting bird species (e.g. woodpeckers, hereafter PCN) and 7 secondary cavity nesting bird species (hereafter SCN) between 1998 and 2010 along an urban-wildland gradient in the greater Seattle area (Table 1). This area comprises a mosaic of urban, suburban and forested land cover from the Puget Sound to the Cascade Mountain foothills (Fig. 1). We used forest cover (%, at a 1 km^2 scale) estimated based on classified 30 m resolution land cover data based on 2007 Landsat TM and ETM satellite imagery to define our urban-wildland gradient (Alberti et al. 2006). This dataset included 14 land cover categories, two of which where "forest" (coniferous forest, >80 % coniferous trees, and deciduous and mixed forest, 10–80 % deciduous or mixed forest, see Hepinstall et al. 2008 for more details). We chose forest cover as our independent variable because most of the species we studied live in the forest (so it is a direct quantification of their habitat) and sites have less forest normally because they have been converted to some level of urban use in our study area (Hepinstall et al. 2008). We used imagery from 2007 because changes to forest cover after this point were minimal, including sites that were developed during the early years of our study. All bird species are native to this area, except for European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*), both SCNs. These 12 species represent the full assemblage of diurnal land bird cavity nesters and all the woodpecker species present in the area. We did not include cavity nesting waterfowl or owls for logistical reasons.

Cavity-nesting bird community characterization

We described the cavity-nesting bird community using species presence, richness, and relative abundance of all the species mentioned. To do so, we estimated these parameters at 135, 1 km^2 square plots in sites with different levels of urbanization (0–100 % forest). On each site, we counted all birds seen and heard within 4–8 50-m-fixed-radius points for 10 min (Ralph et al. 1993). We accounted for this variation in effort by having similar number of point counts for most sites (mean ± SE, 7.05 ± 0.18 points), but also by visiting the sites multiple times during the breeding season (once a month during the breeding season, i.e. April–August) and over multiple years, resulting

Table 1 Number of nests of cavity nesting species found on the urban-wildland gradient of the Greater Seattle area between 1998 and 2010

| Species	Type of substrate								Total nests
	Natural				Anthropogenic				
	Snag	Tree	Other	Total	House/ building	Nest box	Other	Total	
Primary Cavity Nesting Species (PCN)									
Downy woodpecker (*Picoides pubescens*)	5	0	0	5	0	0	0	0	5
Hairy woodpecker (*Picoides villosus*)	23	1	0	24	0	0	0	0	24
Pileated woodpecker (*Dryocopus pileatus*)	3	0	0	3	0	0	0	0	3
Red-breasted sapsucker (*Sphyrapicus ruber*)	10	7	0	17	0	0	0	0	17
Northern flicker (*Colaptes auratus*)	17	0	0	17	1	0	0	1	18
Total PCN	58	8	0	66	1	0	0	1	67
Secondary Cavity Nesting Species (SCN)									
Native species									
Black-capped chickadee (*Poecile atricapillus*)	36	6	0	42	0	6	0	6	48
Chestnut-backed chickadee (*Poecile rufescens*)	38	9	0	47	0	1	0	1	48
Bewick's wren (*Thryomanes bewickii*)	2	0	4	6	1	2	3	6	12
Red-breasted nuthatch (*Sitta canadensis*)	6	0	0	6	0	0	0	0	6
Violet-green swallow* (*Tachycineta thalassina*)	0	0	0	0	27	0	0	27	27
Total native SCN species	82	15	4	101	28	9	3	40	141
Exotic Species									
European starling (*Sturnus vulgaris*)	3	0	0	3	116	0	1	117	120
House sparrow (*Passer domesticus*)	0	0	0	0	30	9	0	39	39
Total exotic SCN species	3	0	0	3	146	9	1	156	159
Total SCN	85	15	4	104	174	18	4	196	300
Total nests	143	23	4	170	175	18	4	197	367

*Migratory species

on an average of 726.15 ± 147.14 point counts per year. The point-count stations at least 150 m apart to reduce the probability of double-counting individuals on two plots. We (and field assistants) counted birds between 05:00 and 12:00, avoiding days when weather conditions would interfere with the detectability of the birds (rain, heavy winds, etc.). All participants on this study where trained on a consistent manner on how to detect and record the species during point counts to reduce observers' bias. In sites with built and forested portions, we allocated more points to the built portion (up to 6 out of 8) to account for higher variability of habitat and the bird community (Donnelly and Marzluff 2004; Donnelly and Marzluff 2006). However, because not all sites have both forest and built portions, the total allocation of point-counts was closer to a 3:7 ratio (304 point counts in the forest vs. 726 on the built matrix). This allocation allowed us to more fully describe the diversity of birds found at each site. We then averaged the relative abundance, expressed as number of individuals per count, to the site level. We used the average relative abundance per year to account for differences in effort between sites.

We estimated relative ocurrence and relative abundance within areas of small and fixed radius because land cover within developments is not homogeneous and distance to aural detections (the majority of cases in our heavily forested and built landscapes) may be difficult to estimate accurately (Hutto 2016). Because we used naïve estimates, our determination of relative abundance in forests may be biased low relative to distance-corrected estimates. Marzluff et al. (2015) reported that the overall detectability was higher on the urban portion than the forested portion of our study sites. Therefore, we exercise caution in interpreting species responses where abundance is lowest in forest and highest in more developed sites. This situation is only expected for urban-associated species such as the European Starling and House Sparrow, however, bias in their detection is minimal because of the gregarious and conspicuous nature.

Nesting patterns and nesting success

Because cavity-nesting birds can be limited by the availability of nesting sites (Newton 1998), our first approach to study

Fig. 1 Study area in Seattle, WA. Land cover types grouped as urban/suburban (in different degrees of urbanization), forest (including coniferous, deciduous or mixed) and other. Dots do not represent size of the sites
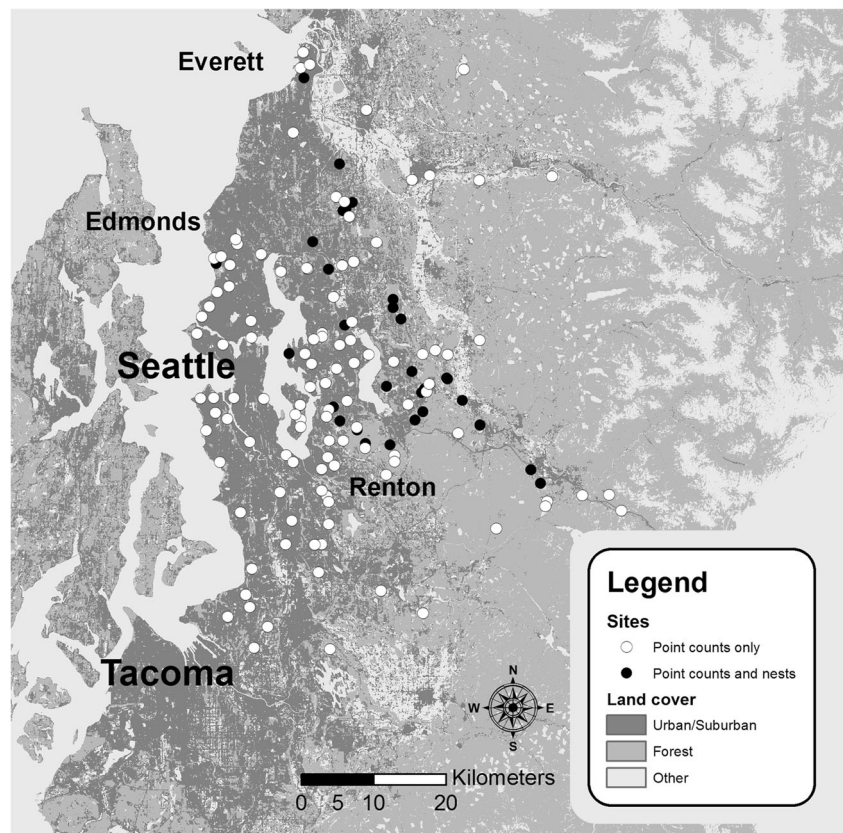
facilitation was to assess whether humans had any influence on this potentially limiting factor. We recorded nests in a subset of 31 sites that were subject to a more intensive monitoring scheme that included spot-mapping, mist-netting, and nest searching (Marzluff et al. 2015). We sampled these sites for different time spans, ranging from 1 to 10 years (mean ± SE, 6.06 ± 0.48 years). These sites represent a gradient of urbanization between urban cores and wild lands ranging from 0 to 99.8 % forest remaining (mean ± SE, 42.61 ± 4.93 %, Fig. 1). We used two nest-searching schemes: dedicated to cavity nesting birds (2000–2002, see Blewett and Marzluff 2005) and opportunistic (1998–1999, 2003–2010). The dedicated search scheme was more intensive and focused on both urban and forested portions of the study plots. The opportunistic search scheme was mostly focused on the forested portion of the study sites, but still recording nests in the urban portion where detections were easier as well. Field crews searched for nests approximately 2–3 h/site/week during the breeding season (April – August). They recorded all nests found, plus the date when they were found, the species they belonged to, and the substrate in which the nest was built. As for substrate, they recorded the species and type (e.g. tree, snag, stump, house, pole, etc.), and we later assigned its origin (natural or anthropogenic). We visited each nest found every three days to determine its fate. We considered a nest successful if at least one chick was able to fledge. If the nest attempt failed, the cause of

failure was recorded when possible. Because different sites were followed for different number of years, we used nests per year (average nests) as our dependent variable.

Our second approach to study facilitation was to assess the role of PCNs on the community. PCN species are providers of natural cavities that can be used as nesting sites by SCN species when PCNs abandon them (Martin and Eadie 1999), so we tested for relationships between the abundance of PCN and SCN species, as an indicator of facilitation where nesting sites may be the limiting factor.

Statistical analyses

We used logistic regression to determine the relationship between forest cover and the presence of each individual species. We also grouped species by guild (PCN, native SCN, non-native SCN, all SCN) and looked for changes in richness patterns related to forest cover using Poisson log-linear regression, linear regression, and non-linear regression. We related other continuous data (e.g. relative abundance) to forest cover with standard linear or non-linear regression as deemed appropriate based on visual inspection of the data and quantitative model selection using the Akaike Information Criterion (AIC; Akaike 1973, Wagenmakers and Farrell 2004). We calculated AIC values using package AICcmodavg (version 2.0–4, Mazerolle 2016) and we calculated Delta AIC and AIC weights using

package qpcR (version 1.4–0, Spiess 2014). We compared differences on means using paired t-test and we used Chi-squared tests to test for differences on proportions on nest success between different substrates or guilds (Zar 1999).

We looked for changes in trend or thresholds in nesting patterns related to the urban-wildland gradient using a segmented linear regression analysis (package segmented v0.2–9.4 for R, (Muggeo 2008) on the average number of nests (analyzing natural and anthropogenic nests separately) per guild. We compared this approach to other models, however our main objective was not to determine the best model of the full relationship, but rather to determine where any significant threshold in of resources occurred (e.g., nest substrate), which may provide evidence of anthropogenic facilitation by direct or indirect provision of nest sites. For this analysis, we considered each guild (PCN, native SCN, non-native SCN) individually. In the case of native SCN, we divided our dataset, analyzing Violet-green Swallow (*Tachycineta thalassina*) separately from the other species. We took this approach because this species has significantly different habitat requirements from the others, using open areas for foraging, and its gregarious nature results in a patchy distribution on the landscape (Brown et al. 2011). Whenever we found a significant change in trend using the segmented regression analysis (which yields a point estimate and a 95 % CI for the break point), we also ran a two-sided Davies' test (package segmented v0.2–9.4 for R, Muggeo 2008) to refine the estimate. We used the results of the Davies' test as a conservative approach to inform other analyses that built upon these results.

Based on the shift in use of nesting substrates at higher levels of urbanization that we found for native SCNs, we further divided our dataset into two groups (above and below the break point). We calculated relative abundance, relative occurrence and dominance of each species for each group. We then studied differences in community structure and the effect of urbanization on each group using a multivariate approach (McCune and Grace 2002).

As suggested for community structure data (McCune and Grace 2002), we checked for rare species. We did not need to delete rare species, however, as all of the species we included were present in more than 5 % of the sites. In order to equalize the contribution of each site regardless of their total abundance of birds, we used relativization by species maxima and by site total for the SCN community data (package vegan v 2.2–1 for R, Oksanen et al. 2013). This centers the focus on the structure of the community rather than on the abundance. We used Non-Metric Multidimensional Scaling (NMDS) to visualize the differences in community structure between sites (package vegan v 2.2–1 for R, Oksanen et al. 2013). NMDS is a useful ordination technique that makes no assumptions about the form of the relationships among variables. It also relieves the "zero-truncation" problem that other ordination techniques have and it can be constructed with any distance measure

(McCune and Grace 2002). In our case, we calculated differences in community structure with Bray-Curtis distance, which accounts for differences in abundance between species taking species identity into consideration (McCune and Grace 2002). We used the function metaMDS with the same parameters for all ordinations (autotransform = FALSE, distance = "Bray", tol = 1e-5, trymax =50). We tried uni-, bi- and tridimensional NMDS and selected the dimension that yielded the highest reduction in stress when comparing to the previous dimension.

We then tested for relationships between the SCN community and forest cover using PERMANOVA (McCune and Grace 2002) and the function adonis(), with Bray-Curtis distance and 1000 permutations for each run (package vegan for R). After determining significant relationships between forest cover and community structure, we plotted that relationships in ordination space with the function ordisurf() (available on package vegan). We calculated the residuals of this relationship by extracting the predicted forest cover from the generalized additive model (GAM) used by ordisurf() and the observed values for each site. We used these residuals to also interpret the potential role of human facilitation on different levels of urbanization, as we compared the predicted forest cover based on the community structure with the actual amount of forest cover of the site.

We also tested for differences in community structure above and below the threshold we found in nesting patterns by native SCN on anthropogenic substrates using Multi-response Permutational Procedure (MRPP, McCune and Grace 2002, available on package vegan). MRPP is a nonparametric technique used to test for differences among groups making no distributional assumptions about the data (such as multivariate normality and homogeneity of variances). We used Bray-Curtis distance (McCune and Grace 2002) with 1000 permutations.

We also looked for evidence of natural facilitation (i.e. by PCNs). To do so, we tested for a relationship between the abundance of PCN and SCN using Log-linear regression (Zar 1999). Our expectation was that PCN abundance should influence SCN abundance in places where nesting sites could be a limiting factor and PCNs are the main provider of such resource (Martin and Eadie 1999).

We conducted all analyses on R v3.1.0 ("Spring Dance") for Mac (R Core Team 2014) using RCommander v 2.1–7 (Fox 2005) and Rstudio v 0.98.1049 (RStudio Team 2014).

Results

Patterns of species presence and richness

Native and non-native cavity nesters responded to the gradient of urbanization in distinct ways. After evaluating different

models using AIC (Table 2), we found that PCNs richness was positively associated with forest cover, which was best described with a log-linear relationship (Poisson log-linear, $z = 4.77$, $df = 131$, $p < 0.0001$, Fig. 2a). All five species were present on sites ranging from 16 to 100 % cover, but their presence declined rapidly when forest cover was less than 16 %. As a group, richness of native SCNs peaked at 37 % forest and declined with more or less forest cover (Quadratic regression, $F_{2,130} = 3.71$, $p = 0.027$, Fig. 2b; Table 2 shows alternative models evaluated). Non-native SCNs' richness was negatively related to forest cover (Linear regression, Adj. $R^2 = 0.30$, $F_{1,131} = 58.71$, p < 0.0001, Fig. 2c; see Table 2 for alternative models contrasted). Most of the sites with less than 40 % forest cover contained native and non-native species, but non-native species were absent on sites with 90 % or more forest cover. The results for presence at the guild level held for nearly all the individual species (Table 3). Rather than presence of all species decreasing as forest cover increased, native species were typically positively associated forest cover and non-native species were negatively associated with it (Table 3). Exceptions included species known to exploit open areas, or edges between forest and developed lands, such as Black-capped Chickadee (*Poecile atricapillus*) and Northern Flicker (*Colaptes auratus*) that yielded no significant linear relationship with forest cover (Table 3).

Species relative abundance

Relative abundance of different cavity nesting groups showed different responses to the reduction in forest cover. As expected, the average relative abundance of PCN species was lower (mean $\pm$ SE, 0.17 ± 0.01 ind/count/year) than the abundance of SCN species (mean $\pm$ SE, 3.63 ± 0.17 ind/count/year) across all sites. PCN's relative abundance was not significantly correlated with the percentage remaining forest (Linear regression, Adj, $R^2 = -0.005$, $F_{1,126} = 0.40$, $p = 0.53$, Fig. 2d). However, some PCN species tended to be more abundant on either extreme of the urbanization gradient, while other species peaked at intermediate levels of urbanization. The most abundant PCN species was the Northern Flicker (mean $\pm$ SE, 0.11 ± 0.01 individuals/count/year), which was negatively related to forest cover (Table 3, Suppl1c). Hairy Woodpecker (*Picoides villosus*) abundance increased with increasing forest (Table 3, Suppl1b), while Downy (*Picoides pubescens,* Suppl1a) and Pileated Woodpecker (*Dryocopus pileatus,* Suppl1d) abundance peaked at sites with intermediate (ca. 40 %) forest cover.

Although the overall average relative abundance was not statistically different between native and non-native SCNs (1.82 vs. 1.81 ind/count/year, two-tailed paired t-test, $t_{127} = 0.06$, $p = 0.95$), their distributions along the gradient of urbanization were substantially different. Native SCN species showed a non-linear unimodal trend peaking in

Table 2 Alternative models relating richness, abundance and nesting pattern to % forest cover remaining. AIC are relevant to particular test presented. ΔAIC is relative to the best (first listed) model among the candidates

Model	ΔAIC	Relative Likelihood	w_i
Guild richness versus forest cover			
PCN			
Poisson Log-linear	0	1	0.9999
Linear	21.63	2.00E-05	2.00e-05
SCN			
Quadratic	0	1	0.923
Linear	4.97	8.32E-02	7.68E-02
Poisson Log-linear	88.33	6.59E-20	6.08E-20
Non-Native SCN			
Linear	0	1	1
Poisson Log-linear	91.62	1.27E-20	1.27E-20
Guild relative abundance versus forest cover			
SCN			
Quadratic	0	1	0.997
Linear	11.81	0.002	0.002
Average number of nests on anthropogenic substrates			
Native Secondary Cavity Nesting species (except Violet-green Swallow)			
Exponential decay	0	1	0.952
Segmented regression	5.97	5.04E-02	0.048
Multinomial regression (3rd degree)	34.47	3.27E-08	3.11E-08
Quadratic regression	52.71	3.58E-12	3.41E-12
Linear regression	67.64	2.05E-15	1.95E-15

Fig. 2 Species richness and average relative abundance (respectively) by guild along the gradient of urbanization (% forest cover) between 1999 and 2010: primary cavity-nesters (**a** and **d**), native secondary-cavity nesters (**b** and **e**), and non-native secondary-cavity nesters (**c** and **f**). Regression line and significance presented. See "Results" for more details
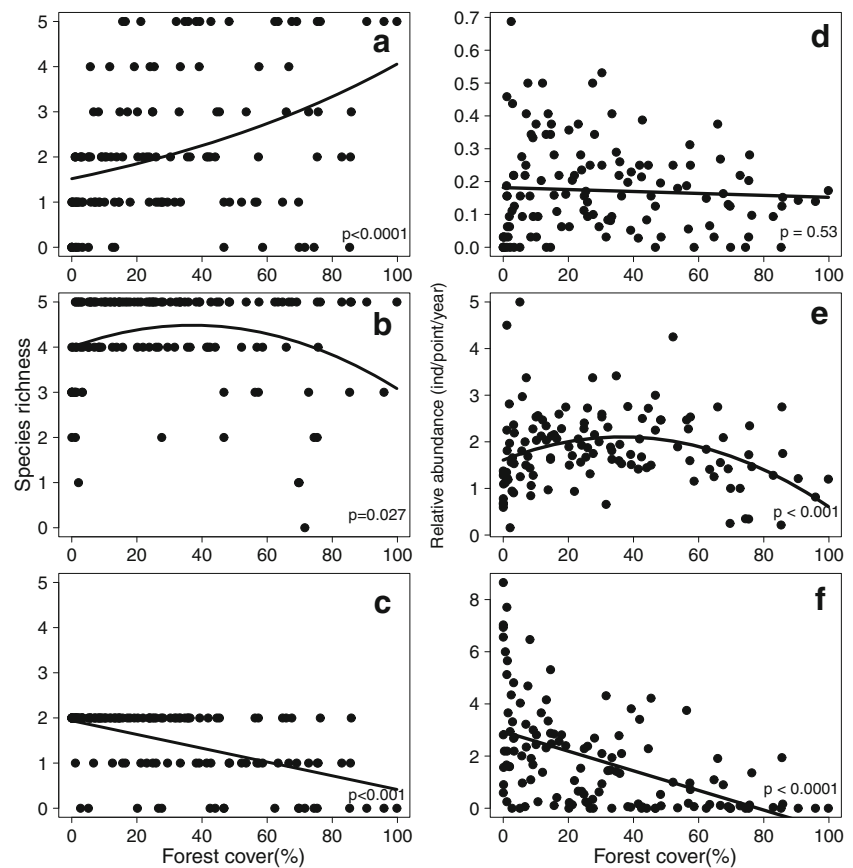
abundance at ca. 36 % forest cover (Quadratic regression, Adj, R^2 = 0.095, $F_{2, 125}$ = 7.68, p < 0.001, Fig. 2e, see Table 2 for alternative models). The abundance of Violet-green Swallows, which peaks at ca. 40 % forest cover, appeared to drive this pattern (Suppl 2e), but we found that the overall trend was robust even when excluding such species (Quadratic regression, Adj, R^2 = 0.044, $F_{2, 125}$ = 3.94, p = 0.022). On the other hand, non-native SCN decreased linearly as forest cover increased (Linear regression, Adj, R^2 = 0.27, $F_{1, 126}$ = 47.15, p < 0.0001, Fig. 2f). We also found variability in the relative abundance patterns among different SCN species (See Suppl2 and Suppl3). While some native species were more abundant as forest cover increased (e.g. Chestnut-backed Chickadee, *Poecile rufescens*, Table 3, Suppl2c); others decreased (e.g. Black-capped Chickadee, Table 3, Suppl2a). The abundance of both non-native species decreased with increase in forest cover (Table 3, Suppl3).

Nesting patterns

We found a total of 367 nests of both PCNs (n = 67 of 5 native species) and SCNs (n = 300; 141 of 5 native species, and 159 of 2 non-native species) in natural and anthropogenic substrates (Table 1). Most of the PCN nests were of Hairy Woodpeckers

(n = 24), Red-breasted Sapsuckers (*Sphyrapicus ruber*, n = 18) and Northern Flickers (n = 17). Most of the native SCN nests belonged to Chestnut-backed Chickadees (n = 49) and Black-capped Chickadees (n = 49), while non-native species' nests were mostly European Starling (n = 120).

PCN and SCN species differed in their use of natural and anthropogenic nest substrates. PCNs relied almost exclusively on natural substrates (98.51 %, Table 1), most of them snags (86.57 %, Table 1). The only PCN species that we documented using anthropogenic substrates was the Northern Flicker. We found no PCN nests on sites with less than 6 % forest remaining.

The proportionate use of natural and anthropogenic substrates was significantly different between native and non-native SCNs (X^2_{38} = 79.64, p < 0.001). Native SCNs used mostly natural substrates (71.63 %). Most natural nests occurred on snags (58.16 %) and occurred along the entire extent of the gradient of urbanization (Fig. 3a) suggesting little influence of forest cover (Linear regression, $F_{1, 28}$ = 0.21, p = 0.65). We did not find nests in natural substrates if the remaining forest cover was less than 9 % (Fig. 3a).

The number of nests on anthropogenic sites by native SCNs (except for Violet-green Swallow) decreased exponentially with increases of forest cover (Exponential decay model, residual std. error = 0.06, t_{28} = 9.336, p < 0.0001), and we

Table 3 Relationship between forest cover and presence and abundance of cavity-nesting bird species studied

Species	Presence vs. Forest cover				Abundance vs. Forest cover				
	Reg. model	Rel.	Z (df = 131)	P	Reg. model	Rel.	Adj. R^2	F or z (df = 127)	P
Primary Cavity Nesting Species (PCN)									
Downy woodpecker (*Picoides pubescens*)	Logit	+	2.411	0.0159	Linear	NS			
Hairy woodpecker (*Picoides villosus*)	Logit	+	5.048	<0.0001	Linear	+	0.22	36.65	<0.0001
Pileated woodpecker (*Dryocopus pileatus*)	Logit	+	3.068	0.0022	Linear	NS			
Red-breasted sapsucker (*Sphyrapicus ruber*)	Logit	+	3.29	<0.0001	Linear	(+)	0.02	3.837	0.0523
Northern flicker (*Colaptes auratus*)	Logit	NS			Linear	-	0.07	11	0.0012
Secondary Cavity Nesting Species (SCN)									
Native species									
Black-capped chickadee (*Poecile atricapillus*)	Logit	NS			Linear	-	0.11	16.61	<0.0001
Chestnut-backed chickadee (*Poecile rufescens*)	Logit	+	2.143	0.0321	Linear	+	0.09	13.88	<0.0003
Bewick's wren (*Thryomanes bewickii*)	Logit	-	3.864	<0.001	Linear	-	0.02	4.144	0.0446
Red-breasted nuthatch (*Sitta canadensis*)	Logit	+	2.605	0.0092	Linear	NS			
Violet-green swallow* (*Tachycineta thalassina*)	Logit	-	2.122	0.0338	Linear	NS			
Exotic Species									
European starling (*Sturnus vulgaris*)	Logit	-	4.075	<0.0001	Linear	-	0.22	37.39	<0.0001
House sparrow (*Passer domesticus*)	Logit	-	5.515	<0.0001	Poisson	-		5.883	<0.0001

found a strong break on the slope of this relationship (Segmented linear regression, Adj. R^2 = 0.92, $F_{3,26}$ = 112.5, p < 0.0001, Fig. 3b, see Table 2 for alternative models evaluated) at 9.45 % forest cover (95%CI: 2.87, 16.04, Fig. 3b). This is, when forest cover was less that 9.45 %, the average number of nests decreased much faster than when forest cover was great than 9.45 %. A more conservative estimate gauging the change in slope of the relationship between use of anthropogenic cavities and forest cover yielded a significant break point at 12.78 % forest cover (Two-sided Davies test, p < 0.0001), which we used for subsequent analyses. And although the exponential decay model was more parsimonious than the segmented regression as shown with the AIC analysis (Table 2), the segmented model helped us answer the question of whether there was a shift in trend on this relationship and objectively determine where that threshold was. This cannot be achieved with the exponential decay model given the gradual nature of the decay. We found no significant linear relationship between average number of Violet-green Swallow nests and forest cover (Linear regression, $F_{1, 28}$ = 0.96, p = 0.34). Most of the anthropogenic substrates where native SCNs (all species combined) nested were houses, buildings or other anthropogenic structures. Only 6.38 % of the nests of native SCN were placed in nest boxes. All native SCN species, except for Red-breasted Nuthatch (*Sitta canadensis*), used anthropogenic substrates when forest cover was less than 13 %.

Non-native SCNs placed almost all their nests on anthropogenic substrates (98.11 %, Table 1) with very little use of natural substrates (1.89 %, Table 1). Most (91.82 %) of the

nests were placed on houses and buildings (Table 1). Non-native SCNs nested along most of the gradient (3–75 % forest cover remaining) although we found 95 % of these nests on sites with 50 % forest remaining or less (Fig. 3c). We found a tendency for nests of this group to decline with increasing forest cover (Linear regression, $F_{1, 28}$ = 3.541, p = 0.07), however we found no significant break point for this relationship (Two-sided Davies test, p > 0.85).

Nesting success

We determined the fate of 58/67 (86.6 %) PCN nests and 296/300 (98.7 %) SCN nests. A large proportion of PCN nests were successful (n = 48, 71.64 %). The most common cause of failure in natural nests was eviction by European Starlings (n = 3), followed by abandonment (n = 2) and unknown (n = 2). Other causes of failure include predation (n = 1) and snag falling (n = 1). The only PCN nest we recorded in anthropogenic substrates failed also due to interference from European Starlings (Northern Flicker nest). When looking at SCNs, 266 of the nests were successful (39 native and 146 non-native nests in anthropogenic substrates and 80 native and 1 non-native nest in natural substrates, 88.67 %). In this case, nest success was significantly higher in anthropogenic structures than in natural substrates (94.4 % vs. 81 %, X_1^2 = 13.03, p = 0.0003), a trend that we also observed when looking at native SCNs in isolation (97.5 % vs. 79.2 %, X_1^2 = 5.6, p = 0.018). The most frequent cause of failure for SCN in natural nests was predation (n = 6),
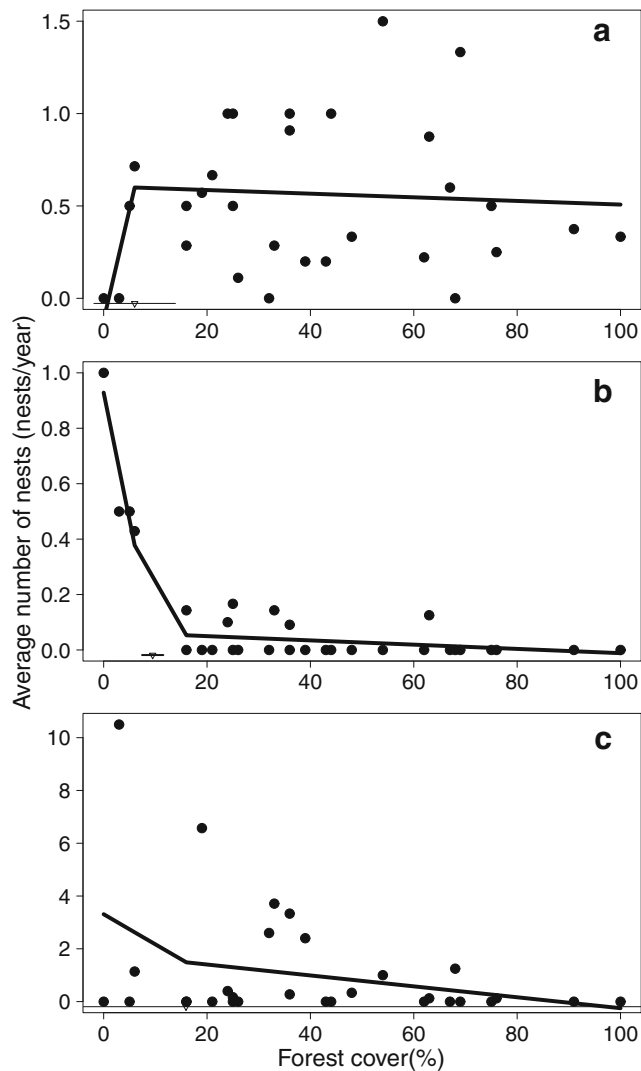
Fig. 3 Relationship (using segmented regression analysis) between average number of nests of cavity nesting birds per site and number of years surveyed and percentage of forest cover remaining along a gradient of urbanization between 1999 and 2010. **a** Native secondary cavity nesting species using natural substrates, (**b**) native secondary cavity nesting species using anthropogenic substrates, (**c**) non-native secondary cavity nesting species using anthropogenic substrates. Inverted triangle represents break point or threshold. See "Results" for more details

followed by unknown cause ($n = 5$) and abandonment ($n = 4$). The remaining 6 nests failed by causes that were observed only once (e.g. construction, logging, etc.). We could not determine the cause of failure for most failed nests in anthropogenic substrates ($n = 9$). When looking at nests in anthropogenic substrates, native SCN species had similar nest success as non-native species did (97.5 % vs. 93.6 %, $X^2_1 = 0.92$, p = 0.34).

Effects on SCN community structure

SCN community structure and composition were significantly related to forest cover (PERMANOVA, *pseudo-F$_{1, 126}$* = 29.11,

$p < 0.001$). Sites on the extremes of the gradient of forest cover were also represented at either end of the ordination space along the x-axis (NMDS, Fig. 4), which reflects their dissimilarities in the structure and composition of their SCN bird community. The nature of the relationship between the SCN community and forest cover changed above 40 %. Below 40 % forest cover there is a non-linear relationship between forest cover and community structure (Fig. 4), however above this threshold there is a clear linear relationship with forest cover as indicated by the parallel isoclines in Fig. 4. In fact, below 40 % forest cover there is wide variation in the composition and structure of the community, reflected by the wide dispersion of sites along the y-axis of ordination space (Fig. 4).

We found a significant difference in the SCN community structure and composition above and below the threshold where native SCNs significantly shift to nest predominantly in anthropogenic substrates (i.e. 12 % forest. MRPP, Within-group chance-corrected agreement A = 0.0677, $p = 0.00099$, Bray-Curtis distance). In fact, the relative importance of each species in the community changed between sites below and above this threshold (Fig. 5). For example, European Starlings dominated the community on sites below 12 % followed by House Sparrow and all the native species decreasing their dominance in a linear fashion, while sites above 12 % of forest remaining were dominated by Chestnut-backed Chickadees, Violet-green Swallows, European Starlings and Black-capped Chickadees to a similar degree. Examining the location of sites in ordination space and their relationship with forest cover, we found that 61.4 % of the sites below 12 % forest where predicted to have more than 12 % forest, which means that the structure and composition of these sites was more similar to sites with more forest than what they actually had. On the other hand, only 5.95 % of the sites above 12 % forest were predicted to have less forest than that, which suggests that the community of those sites have deteriorated to be similar to sites with less forest. In fact, those individual sites had higher abundance of non-native SCN than native SCNs (average ± SE native/non-native abundance ratio of those sites was 0.35 ± 0.068, while the rest of the sites above 12 % forest had an average native/exotic abundance ratio of 9.78 ± 2.302). Sites below 12 % had an average native/non-native ratio of 2.06 ± 0.871.

Finally, we found a significant positive relationship between the abundance of PCN species and the abundance of native SCN species on sites above 12 % forest (Log-linear regression, Adj. $R^2 = 0.1387$, $F_{1, 82} = 14.37$, $p < 0.0003$). However, this relationship did not hold for sites below 12 % forest (Log-linear regression, Adj. $R^2 = 0.042$, $F_{1, 42} = 2.88$, $p = 0.10$).

Discussion

Facilitation was prevalent in our system. As expected, woodpeckers (PCNs) facilitated native SCN species (Martin and

Fig. 4 Non-metric
multidimensional scaling
representation of the secondary
cavity-nesting bird community
along a gradient of urbanization
between 1999 and 2010. *Open
circles* represent sites that have
12 % forest cover or higher. *Black
circles* represent sites with less
than 12 % forest cover. Isoclines
represent relationship between
community structure and
composition and forest cover
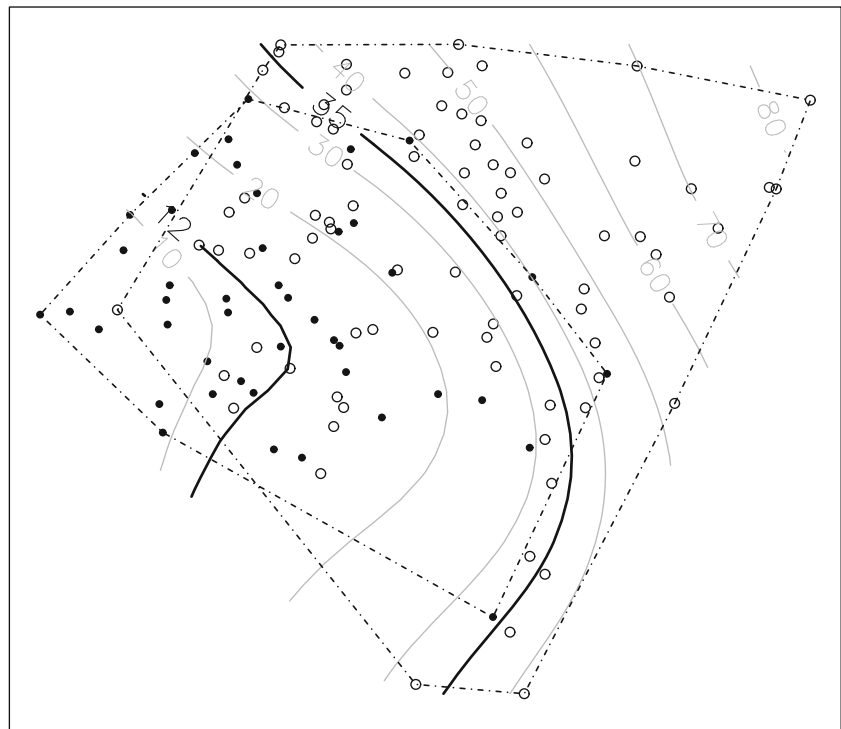
Eadie 1999) on sites with moderate to low levels of urbanization (specifically >12 % forest cover where snag abundance also increases; Blewett and Marzluff 2005), as suggested by the strong and positive correlation between the abundance of both groups. In addition, as urbanization increases (reducing forest cover to levels below 12 %), key nesting resources required by cavity nesting species are commonly lost (Blewett and Marzluff 2005; Harper et al. 2005; Davis et al. 2014; LaMontagne et al. 2015) and we found that in these more urban sites facilitation by humans enabled some native SCN species to overcome reductions in forest and natural cavities, by switching to nest on anthropogenic substrates. This anthropogenic facilitation reduced the dependence of SCNs on their natural facilitators in areas of moderate to extreme urbanization, as expected by the stress-gradient hypothesis (Bertness and Callaway 1994). This shift is especially important, as PCNs species started to disappear on sites with less than 16 % forest cover, which combined with the lack of snags could have jeopardized the persistence of native SCN species in urban settings. By taking advantage of the direct, and especially indirect, nesting opportunities provided by humans (Clucas et al. 2011), the composition and structure of the secondary cavity-nesting bird community changed and diversity was maintained in and beyond highly urbanized areas, as shown by richness, abundance, nesting and community structure data. The fact that ca. 60 % of the sites with less than 12 % forest had a SCN bird community that was typical of sites greater forest cover (as seen on Fig. 4) is a strong indication that native species were

present on sites where the may not have been without human facilitation.

Our finding that PCN and SCN diversity did not change in a linear fashion along a gradient of urbanization, contrasts with previous findings that cavity nesting bird species richness significantly increases with forest cover (DeGraaf and Wentworth 1986; Tilghman 1987; Pidgeon et al. 2007). It is important to note that these studies analyzed PCN and SCN species together, which may obscure the guild-specific trends we report, especially because we found that people rarely provide direct nesting opportunities for PCN species (in contrast with SCN species which can use nest boxes) and they were less likely to take advantage of indirect anthropogenic nesting opportunities than SCN species, with the exception of the Northern Flicker. This adaptable woodpecker was the most abundant PCN, especially in high levels of urbanization where parks were present. This is not surprising as flickers are known to exploit open areas for foraging on the ground (Moulton and Adams 1991; Elchuk and Wiebe 2003; Wiebe and Moore 2008), and while a completely urbanized site would be unsuitable, it is favored in areas were both trees and lawns are available (e.g. parks, Tilghman 1987; Morrison and Chapman 2005). Although this species seems to have many tools to deal with the changes in the habitat due to urbanization, it also faces other challenges, such as competition with European Starlings (Ingold 1994; Ingold 1996; Fisher and Wiebe 2006).

European Starlings dominated the SCN community on the most urban sites (less than 12 % forest remaining) and

Fig. 5 Relative dominance of secondary cavity-nesting birds on sites along a gradient of urbanization between 1999 and 2010. Species (on alphabetical order): BCCH: Black-capped Chickadee, BEWR: Bewick's Wren, CBCH: Chestnut-backed Chickadee, EUSP: European Starling, HOSP: House Sparrow, RBNU: Red-breasted Nuthatch, VGSW: Violet-green Swallow. Scientific names presented on text
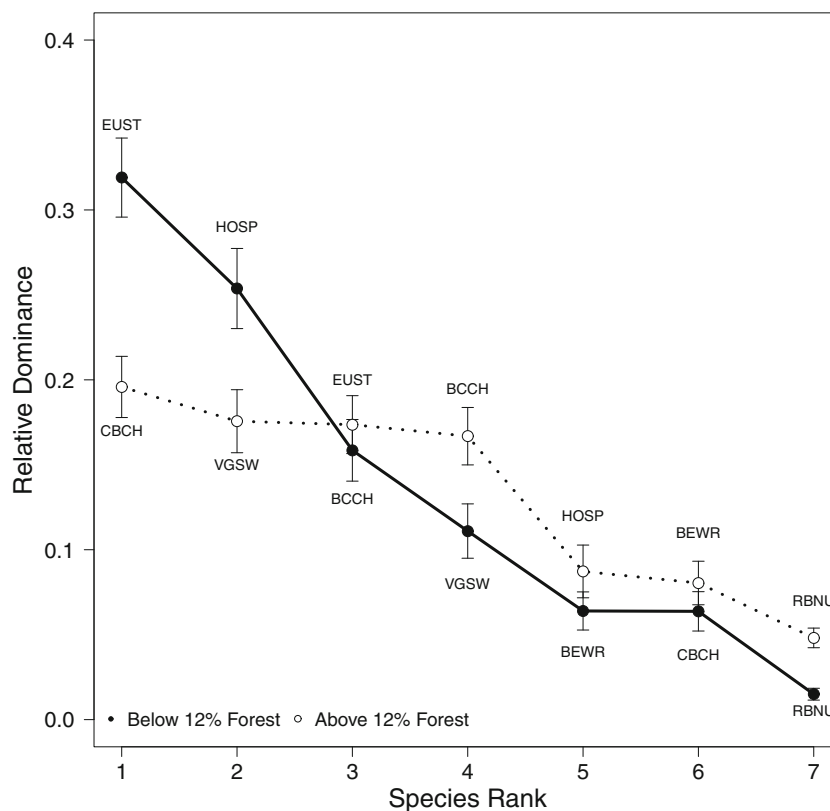
declined in abundance swiftly as forest cover increased. They caused nest failures among Northern Flickers (3 out of 8 failures) and Red-breasted Sapsuckers (2 out of 3 failures), but we found no evidence of competition with native SCN. Our sample size of nest failure is not large enough to make population-wide inference on the consequences of European Starlings on these species, but the pattern we found aligns with findings that Red-breasted Sapsuckers may be experiencing population reductions due to European Starlings, while the effects on Northern Flickers and SCNs are less pronounced country-wide (Koenig 2003). On the other hand, House Sparrows did not threaten nesting success among the species we studied. In fact, it seemed that both non-native SCN species were somehow constrained to areas with human presence, which is not unexpected (McKinney 2002; Blair 2004), but the fact that even when these non-native species ventured into forested settings they rarely nested in natural substrates, was surprising.

Native SCNs had higher nesting success in anthropogenic than in natural substrates suggesting lower predation and competition pressure when nesting on these novel substrates. It has been suggested that urban areas may have fewer native predators than natural areas (Adams 1994) potentially making them "safe zones" for nesting (Gering and Blair 1999). While it is often true that some natural predators are lost to urbanization (especially large species), other smaller generalist species like coyotes (*Canis latrans*), raccoons (*Procyon*

lotor) or raptors (e.g. Cooper's Hawk, *Accipiter cooperii* and Barred Owl, *Strix varia*) may thrive in urbanized areas (DeStefano and DeGraaf 2003; Chace and Walsh 2006; Rullman and Marzluff 2014), and even free-ranging domestic animals, like cats (*Felis catus*) may result in significantly high rates of predation (Loss et al. 2013). So, although this "safe nesting zone" hypothesis has not been supported for open-nesters (Jokimäki et al. 2005), which may suffer greater nest predation due to high densities of corvids and sciurids in urban areas (Marzluff et al. 2007), nests in cavities are known to be safer than open-cup nests against predation (Martin and Li 1992). And, while urban areas may harbor a wide assemblage of predators (Haskell et al. 2001; Rullman and Marzluff 2014), these hunters may not have developed a reliable search image for anthropogenic nests or those nests may be hard to access.

Cavity-nesting bird abundance (lumping PCN and SCN) has been documented to decrease from natural areas into urban areas (DeGraaf and Wentworth 1986; Tilghman 1987; Blair and Johnson 2008). We found that the abundance of PCN and SCN species responded differently along the gradient, and analyzed them accordingly. SCN abundance is typically reduced in urban areas compared to natural areas as some sensitive species are lost (Blair 1996; Blair and Johnson 2008) and/or key resources are reduced (e.g. snags, Blewett and Marzluff 2005; Harper et al. 2005; Blair and Johnson 2008; Davis et al. 2014; LaMontagne et al. 2015). In our case, we

did not observe a linear reduction in the abundance of native SCN, but rather a non-linear trend. This contrasted with the pattern we found for PCN, where the overall pattern was mostly driven by the abundance of Northern Flicker, the most abundant in the group; and for non-native SCN, where both species had similar abundances, but their responses to urbanization were the same. In the case of native SCN, most species had similar levels of abundance (except for the Red-breasted Nuthatch that had between half to a fifth of the average abundance of the other species), but had their peaks of abundance on different areas of the gradient. And thus, adding their abundances resulted on the hump-shaped pattern we observed.

The hump-shaped pattern of diversity along an urbanization gradient is not unexpected (Marzluff 2005). It could be the result of several factors (Graham and Duda 2011), which are not limited to: a) habitat heterogeneity found at medium levels of urbanization promotes the coexistence of synanthropic species along with early successional (e.g. Black-capped Chickadee and Bewick's Wren, (Marzluff 2005) and forest specialists species (e.g. Chestnut-backed Chickadee, Marzluff 2005), where factors such as development age, exotic shrub cover, urban land cover, and forest aggregation that affect different species in different degrees (Donnelly and Marzluff 2006) occur in different levels in close proximity; b) dynamic disturbances at intermediate levels of urbanization, which are characteristic of development (Marzluff et al. 2015), also promote the coexistence of competing species by changing habitat conditions and reducing the chance of competitive exclusion, as predicted by the Intermediate Disturbance Hypothesis (Connell 1978); c) overlap of human and PCN facilitation may augment the number of nesting sites or other resources, although we found no evidence of additive effects on the provision of nest sites where we found the peak of abundance, other forms of human facilitation (e.g. bird feeders) may have a direct contribution to the abundance of birds (Fuller et al. 2008; Robb et al. 2008) and may have a larger influence in suburban areas in Seattle (Clucas et al. 2011; Clucas and Marzluff 2012); and/or d) reduced predation pressure regulating the cavity nester population. The first three alternatives seem reasonable, but the last seems least likely as our study sites harbor a rich community of avian predators (Marzluff et al. 2007; Rullman and Marzluff 2014).

Conservation implications

In cities and their suburbs, the combination of natural resources and human subsidies may produce unexpected outcomes from the conservation perspective. In fact, urban and suburban areas are rarely conceived of as a place to practice species conservation despite their biological and social importance (Marzluff 2002; Miller and Hobbs 2002). Our data suggest that conservation can be successful in urban areas

because some native species that are sensitive to habitat degradation, such as cavity-nesting birds, can use resources provided by humans (directly or indirectly). Although we only quantified a partial aspect of this facilitation (provision of nesting sites), there is evidence that the presence and success of native SCNs may also influenced by other forms of human facilitation, such as provision of food (Clucas and Marzluff 2012).

The importance of positive interactions in ecological communities may profoundly affect our understanding of nature, even changing our approach to how ecological communities are structured, how species niches and important resources are defined, and where species conservation efforts should be focused (Bruno et al. 2003; Butterfield 2009). Our study adds to the increasing realization that humans not only destroy ecological function, they can also actively facilitate it (Marzluff 2014). Broadening our facilitory role may improve the conservation of biological diversity in an increasingly urban world.

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