More than just a roof under their feet: How spatial and structural features of a coastal city predict nest site selection in the urban-nesting Glaucous-winged Gull (*Larus glaucescens*)

Edward Kroc, Louise K. Blight & Min Hai Cao

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More than just a roof under their feet: How spatial and structural features of a coastal city predict nest site selection in the urban-nesting Glaucous-winged Gull (*Larus glaucescens*)

Edward Kroc [a,*], Louise K. Blight [b,c], Min Hai Cao [a]

[a] Measurement, Evaluation, and Research Methodology, University of British Columbia, 2125 Main Mall, Vancouver, V6T 1Z4, BC, Canada
[b] Procellaria Research and Consulting, Sunset Drive, Salt Spring Island, V8K 1G2, BC, Canada
[c] School of Environmental Studies, University of Victoria, David Turpin Building, B243, Victoria, V8W 2Y2, BC, Canada

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ABSTRACT

How birds use and interact with an urban environment has been of interest for a variety of species across the globe. This has particularly been the case for gulls (Laridae) as species in this family nest and otherwise occupy habitat in urban areas on six continents, often coming into conflict with humans as they do so. In this study, we combine survey data of urban-nesting Glaucous-winged Gulls *Larus glaucescens* in Vancouver, Canada with detailed information on architectural and spatial features of the structures on which they nest to build an explanatory and predictive statistical model for nest-site selection in our study city. We find that building height is by far the most important explanatory variable in this selection process and that rooftops of higher structures are generally more attractive to nesters, but only up to a certain point. Flat rooftops in non-residential areas that are near water are also highly valued. However, complex relationships exist between these and other variables that offer detailed insights into urban nesting patterns. We use our modelling approach to predict that roughly 1,800 pairs of Glaucous-winged Gulls nested in the city in 2017 and over 2,000 pairs nested in the city in 2023. Combining this with high exact nest and rooftop recurrence rates derived from additional survey data taken between 2015 and 2019, and with historical population data, we argue that this urban population is likely to continue to expand in the near future at roughly 4% per annum. As this species has suffered declines in its natural breeding colonies across the region, this suggests its future in the region may be increasingly urban-centric.

1. Introduction

As human activity and development transform natural landscapes and remove habitat, many species are displaced; indeed, habitat loss from urbanization and other causes is one of the leading causes of species' declines worldwide (Díaz et al., 2019). With the increasing urbanization of human society has come an increase in biological studies of various aspects of urban ecology, especially those related to birds, and including investigations of why certain species thrive in urban areas (Marzluff, 2016). Gulls (Laridae) are one taxonomic group that has been particularly well-studied in this context, given their highly visible nature and behaviours that not infrequently bring them into conflict with humans (De Faria et al., 2022).

For example, many recent studies have examined various aspects of the biology of rooftop-nesting urban gulls, including their reproductive ecology (Perlut et al., 2016; Kroc, 2018b; Zelenskaya, 2019; Lopes et al., 2020; Bellout et al., 2022; De Faria et al., 2023), foraging strategies and food choice (Sontillo González, 2020; Zelenskaya, 2021; Shlepr et al., 2021; Gutowsky et al., 2021; Langley et al., 2022), and population dynamics (Morris et al., 2011; Beasley, 2017; Blight et al., 2019; Zelenskaya, 2019). This interest spans the globe and a large subset of the Laridae family, including the Slaty-backed Gull (*Larus schistisagus*) of the northeast Asian coast (Zelenskaya, 2019, 2021), the Silver Gull (*Chroicocephalus novaehollandiae*) of Australia (Auman et al., 2011), the Herring (*L. argentatus*) and Lesser Black-backed (*L. fuscus*) gulls of the British Isles (Feist et al., 2023; Langley et al., 2022), the Glaucous-winged Gull (*L. glaucescens*) of the northwest coast of North America (Kroc, 2018b; Blight et al., 2019), and others (De Faria et al., 2022).

Understanding the size of urban-nesting bird populations and the characteristics of their nesting locations is important from both general ecological and wildlife management perspectives. This is particularly so

* Corresponding author.
E-mail addresses: ed.kroc@ubc.ca (E. Kroc), lkblight@interchange.ubc.ca (L.K. Blight), wilson.cao97@gmail.com (M.H. Cao).

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for gulls since they exhibit strong inter-annual and inter-generational fidelity to successful nesting sites (Southern and Southern, 1982; Reid, 1988; Nisbet et al., 2017; Zelenskaya, 2019). Some studies have reported detailed information about the types of city structures on which gulls have chosen to nest (Hooper, 1988; Zelenskaya, 2019; Blight et al., 2019), including information about whether rooftops were flat or pitched, or if they were open or contained various mechanical features and other obstructions. However, to our knowledge, no study has yet tried to statistically model various structural characteristics of the built environment to explain where gulls choose to nest and then predict where they might be most likely to be found nesting. Such an approach could be particularly attractive within the context of urban ecology, as complete censuses in an urban environment are often unfeasible due to sheer size, inaccessibility of many locations, and the fact that urban nesters tend to be dispersed, unlike in natural seabird colonies (Kroc, 2018b; De Faria et al., 2022, 2023).

This is the approach we take in this paper for the Glaucous-winged Gull in the City of Vancouver, Canada. With over 662,000 people in the city proper and 2.46 million in the greater metropolitan area, Vancouver is the third largest urban area in the nation (Statistics Canada, 2021). It is situated on the Salish Sea, a large body of water on the Pacific coast of North America straddling the Canada–US border and including the Strait of Georgia, the Strait of Juan de Fuca, and Puget Sound (Fig. 1). Glaucous-winged Gulls have likely nested on the numerous rocky islets of the Salish Sea since time immemorial (Hayward and Verbeek, 2020) and began to colonize its various urban centres in the 1940s (Oldaker, 1963; Eddy, 1982). Recently, studies have appeared documenting this gull's reproductive ecology and colonization patterns in these urban areas (Kroc, 2018b,a; Blight et al., 2019). However, this gull has experienced an estimated 30%–50% decline in its breeding population from the mid-1980s to 2010 across its traditional Salish Sea range (Blight et al., 2015; Rodway et al., 2024), as well as apparent declines in hatching success, nesting success, clutch size, and egg mass (Blight et al., 2022). At the same time, urban colonies appear to be growing (Blight et al., 2019; Rodway et al., 2024); it is thus all the more imperative to improve our understanding of how the species is using the cities in this region.

This study's two main goals were as follows: (1) To build a statistical model using various structural and spatial features of the City of Vancouver's urban environment to explain nest site selection among urban-nesting Glaucous-winged Gulls there; and (2) To use this information to predict the size and scope of the urban-nesting population across the entire city. We also had the secondary aims of quantifying exact nesting site and rooftop nesting site recurrence rates across consecutive breeding seasons, quantifying temporal variability, and developing a general approach that can be applied in other urban areas. To our knowledge, this is the first study of its kind to consider using structural and spatial variables about an urban landscape to model the incidence of urban-nesting and to predict the size of an urban-breeding population of bird.

To accomplish the two main tasks of our study, we surveyed subsets of 4980 structures across the City of Vancouver in the summers of 2015–19 and 2023 for active gull nests and collected or constructed structural information on all buildings in the city from open access city documentation and maps. For the secondary task of quantifying nesting recurrence rates, we surveyed a smaller subset of city structures from the 2015–19 breeding seasons and constructed point estimates. These were then combined with analyses on the larger data sets from 2017 and 2023 to derive reasonable estimates of temporal change. This workflow is summarized in Fig. 2.

2. Materials and methods

2.1. Study area

Our study location was the City of Vancouver, British Columbia (BC), Canada, a large urban centre on the Pacific coast of North America, located within the year-round (breeding and wintering) range of the Glaucous-winged Gull (Hayward and Verbeek, 2020). As of the 2021 Canadian federal census (Statistics Canada, 2021), the city was home to 662,248 people with an average population growth rate of about 1% annually. The city occupies about 116 km^2 of urbanized land (this excludes the uninhabited forested areas of Stanley Park and Pacific Spirit Regional Park), making for a population density of 5750 people per square kilometre, the densest city in Canada (Statistics Canada, 2021).

Fig. 1. [colour] Map of the Salish Sea on the northwest Pacific coast of North America. The City of Vancouver is situated at the approximate geographic middle of this region. Map attribution: Reference Map for the Salish Sea Bioregion, Aquila Flower, 2020; downloaded from https://wp.wwu.edu/salishseaatlas. Image is licensed under a Creative Commons Attribution, Non-Commercial, No Derivatives 4.0 International License.

The City of Vancouver is the major urban centre of Greater Vancouver which comprises the city itself and many neighbouring cities, the largest of which are Surrey, Burnaby, and Richmond (see Fig. 3). Many of these cities lie along at least one body of water, share a similar urban geography with the City of Vancouver, and are connected to each other by many automobile, train, bike, and pedestrian bridges. The Greater Vancouver area extends south to the US/Canada border, east to the farming and more suburban centres of the Fraser River Valley, north to the North Shore Mountains, and west to the Strait of Georgia.

2.2. Variables of interest

As urban gulls use rooftops of various city structures to nest in all but a few exceptional cases (see Results), *rooftops* comprised our main unit of analysis. We define rooftop as per the 'building-footprints-2009' open GIS data set from the City of Vancouver (City of Vancouver, 2020). This data set reflects the fact that a single building may contain or be composed of many structures that have their own rooftops of different areas, slopes, and heights from the ground. Thus, a single

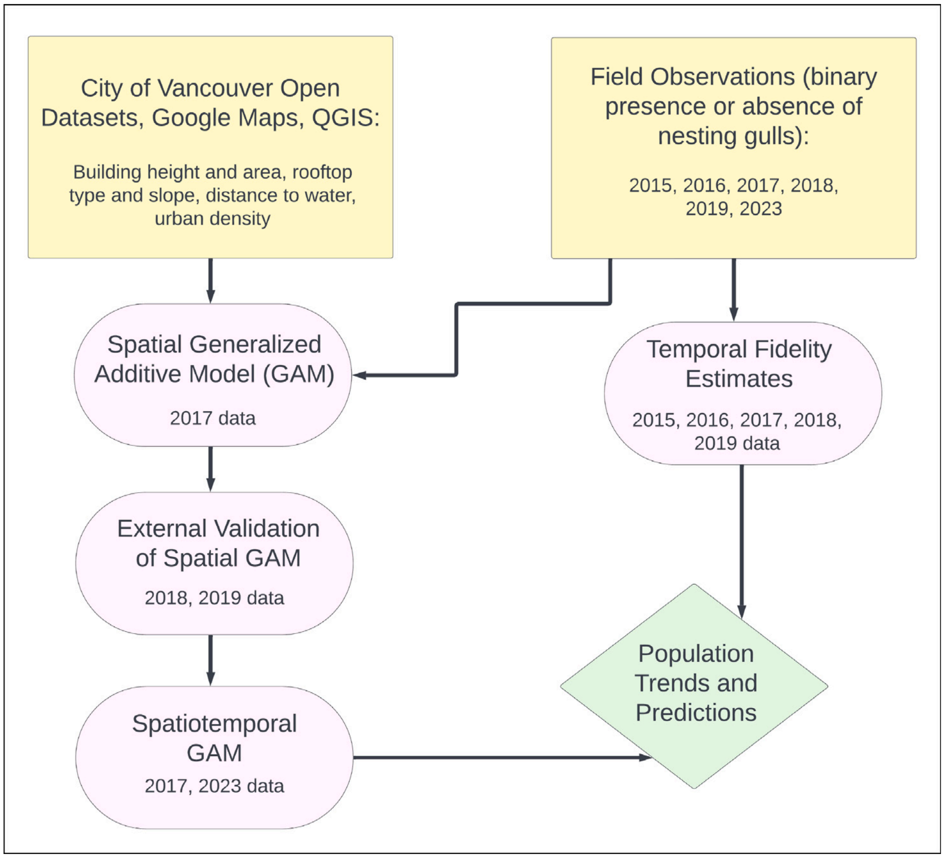

Fig. 2. [colour] Conceptual diagram of this paper's methodology. Data sources (yellow) map to statistical models and estimates (pink) which were then used to predict population patterns and trends (green) in the City of Vancouver.

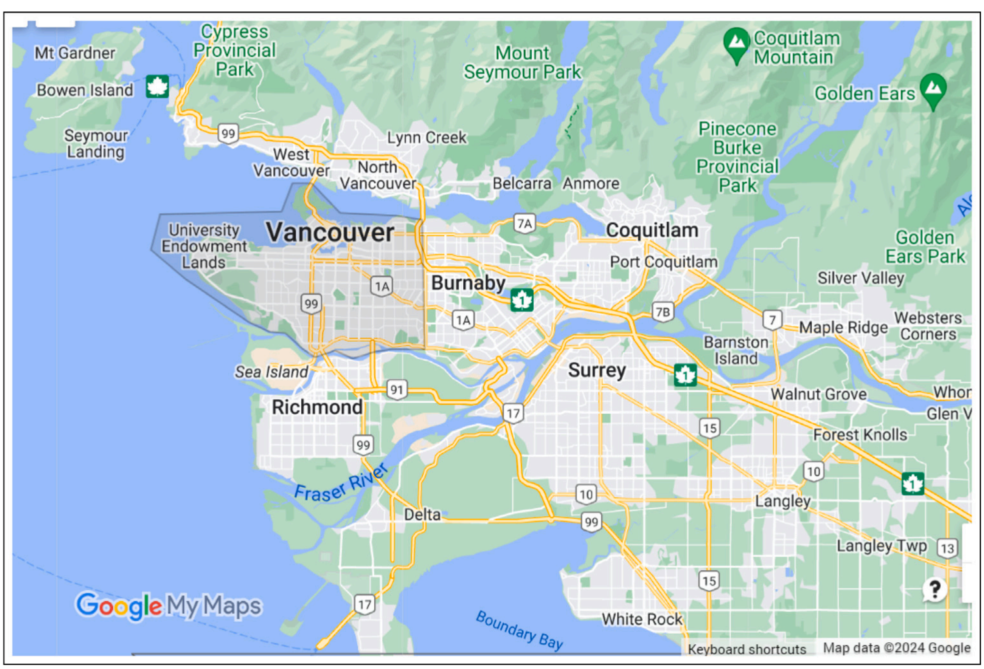

Fig. 3. [colour] Map of Greater Vancouver with the City of Vancouver outlined in grey. Map attribution: Google 2024.

building may contain multiple *structures*, each with their own *rooftop*. We will maintain this terminological distinction between *building*, *structure*, and *rooftop* throughout. Our data set contained 124,072 rooftops with complete information on all predictor variables (see following paragraphs), comprising the entirety of the legal boundaries of the City of Vancouver, minus Stanley Park.

A variety of features are attached to each structure/rooftop in the City of Vancouver data set, and we chose to work with features that characterize the physical aspects of a structure/rooftop. Structure area, $Area$, is taken as a proxy for rooftop area, and structure height, Hgt, is taken as a proxy for rooftop height. Across the entire data set, structure areas ranged from 5 m^2 to 39,011 m^2, with 95% of structure areas ranging between 42 m^2 and 783 m^2. We chose 100 square metres as our unit of measure for $Area$. To put that into context, a typical City of Vancouver city block measures 100 m × 175 m = 17,500 m^2 (175 units of area), and a typical Vancouver single-family house is built on 70% of a 33 by 122 ft lot, or on an area of about 258 m^2 (2.6 units of area). Structure height was measured in metres, ranging from 0 m to 198 m. To aid interpretation, we converted structure height to units of typical building storey, which in the City of Vancouver measures 3.2 m; thus, structure height ranged from 0 to 62 storeys in the dataset. More than 95% of structure heights in the city range between 3.2 m and 20.0 m, or 1 and 6 storeys, though this range depends heavily on zoning (see below), with 95% of structures categorized as "comprehensive development" ranging between 3.4 m and 83.2 m, or 1 and 26 storeys. We hypothesized a more complex relationship between structure area and height and nesting activity, as rooftops that are either too large or too small, or too tall or too short, could be considered unattractive for a variety of different reasons such as predator access or lack of suitable nest substrate.

The median slope of the rooftop, $MedSlope$, and whether or not the rooftop is flat or complex, $RoofType$, are also considered relevant as gulls can have great difficulty building nests or incubating eggs atop a steep gradient or on a rooftop with features that are too complicated. Median slope is measured in degrees from the horizontal and ranged from 0 to 55, with 95% of rooftop complexes having a median slope measure between 0 and 37 degrees. We hypothesized that flatter rooftops would make for more attractive nesting sites.

Finally, we considered including a variable indicating the elevation above sea-level of each city rooftop; however, this variable was ultimately discarded as it correlated highly with the more informative $DistToWater$ variable (defined below) and displayed no extra predictive power. This is likely a reflection of the natural geography of the coastal City of Vancouver, where virtually all of the lowest lying regions are adjacent to water with a generally upwards topographical gradient moving perpendicular from the shorelines. The city is surrounded by water on three sides (see Fig. 4) meaning that there is little geographical opportunity for these trends to be disrupted.

As one cannot expect gulls to select a rooftop for a nesting site independently of the surrounding structures, we constructed an *urban density* variable, $UrbDen$, as a log-average of a random subsample of surrounding structure heights, appropriately standardized to facilitate comparisons between more and less densely urbanized parts of the city. Complete details on this process are recorded in Appendix A. The urban density variable has contrived units and its theoretical values range from 0 to 5, with 99% of values between 1.79 and 3.91. We also constructed a distance to water variable, $DistToWater$, by calculating the Euclidean distance between the centroid of a structure and the nearest body of substantial water (fresh or not); i.e., either the Burrard Inlet, English Bay, False Creek, Georgia Strait, or Fraser River (see Fig. 4). Distance to water is measured in kilometres and ranges from 0 km to 4.5 km. Calculations for both these variables were carried out in QGIS (2023).

In addition to considering basic physical features of buildings, we wanted to examine how human use of those buildings might predict gull nesting activity. To this end, we combined City of Vancouver 'Zoning District' and 'Tax' open GIS data sets (City of Vancouver, 2021, 2023) to assign a simplified zoning feature to each structure. There are 12 different zoning categories that the City of Vancouver can assign to a structure or lot; however, 5 of these categories are quite rare (each assigned to less than 1% of structures), while others were not expected to capture meaningful distinctions in human usage for our research context (e.g. one-family dwelling vs. two-family dwelling). Consequently, we collapsed these 12 categories into 4 simplified *Zones*: commercial, comprehensive development, industrial, and residential. Complete details of and rationale for this process are documented in Appendix A.

2.3. Sampling scheme

Structures were chosen for measurement according to a hybrid convenience-stratified-targeted sampling scheme. Because of the passive observation design, sites needed to be sampled where measurements could actually be conducted for all structures within the sampled polygon, without the need to secure access to any particular sample rooftop within the sampled polygon. Simple random sampling was thus not feasible and an element of convenience sampling became necessary. Moreover, in order to study suspected interactions between predictor variables, we needed to ensure that we recorded enough data across the population domains of these variables and their interactions; e.g., we needed to sample residential areas of the city both close to and far from water, with varying levels of urban density. This too would have made simple random sampling very inefficient by requiring massive oversampling of certain predictor values to ensure reasonable statistical power uniformly, and so a stratified scheme was employed instead (see Appendix C for details). Finally, because gulls do not choose nest sites independently of each other, some amount of spatial autocorrelation is to be expected in the response process of interest. Thus, in order to avoid visibility bias and not artificially remove spatial dependence between nesting sites, sample polygons had to be chosen so that all structures within a sampled polygon could be assessed for the presence or absence of a nest.

In total, 20 diverse regions of the city were sampled in 2017 (see Fig. 4) according to these criteria. The sizes of these sampled polygons varied between 0.04 and 1.93 square kilometres and all structures within each sampled polygon were assessed for the presence or absence of a nest. Table B.5 of Appendix B contains more detailed information on the 20 sample polygons. These sample polygons totalled 11.67 km^2, or about 10% of the total urbanized area of the City of Vancouver.

An additional 10 polygonal regions of the city were sampled in 2018 and 2019 (see Fig. 4) for external validation purposes. These sites were small, ranging in size from 0.034 km^2 to 0.655 km^2, and were chosen for their variation over key predictor variables and their isolation from the 2017 sampled polygons. A subset of all 30 sample polygons were sampled in 2023; using the nomenclature of Fig. 4, polygons 4, 6, 7, 9, 11, 16, 17, 19, f, g, and j were sampled in 2023, as well as subsets of polygons 8, 12, and 20.

2.4. Measurement scheme

A total of 7515 measurements on 4980 rooftops were conducted across the City of Vancouver in the summers of 2015 through 2019 and 2023. Of this total, 3923 rooftop measurements were collected in 2017 (approximately 3% of all City of Vancouver rooftops) and 1907 rooftop measurements were collected in 2023. These data were used for our main descriptive and predictive modelling purposes (see Sections 2.5 and 2.7). In 2018–19, 1051 rooftop measurements were collected and these data were used to externally validate spatial model predictions. An additional 634 rooftop measurements were collected in 2015–16 and these data, along with subsets of the 2017 and 2018–19 data, were used to construct temporal estimates of nest site fidelity (see Section 2.6). Data from all years were used to examine temporal trends and variability.

Observations were limited to the breeding season, from late May to mid-August. A rooftop was recorded as containing a nest, $Nest = 1$, if visual confirmation of either eggs or chicks was possible at some point during these months (prior to individual chicks fledging), and we also recorded if multiple nests occurred on a single rooftop. In low density areas of the city, it was also possible to detect nesting sites by sound when chicks could be definitively heard and their source rooftop identified. A few exceptional nests appeared inside structures instead of atop them (e.g. bridges, pillars for elevated train tracks); see Results for more information.

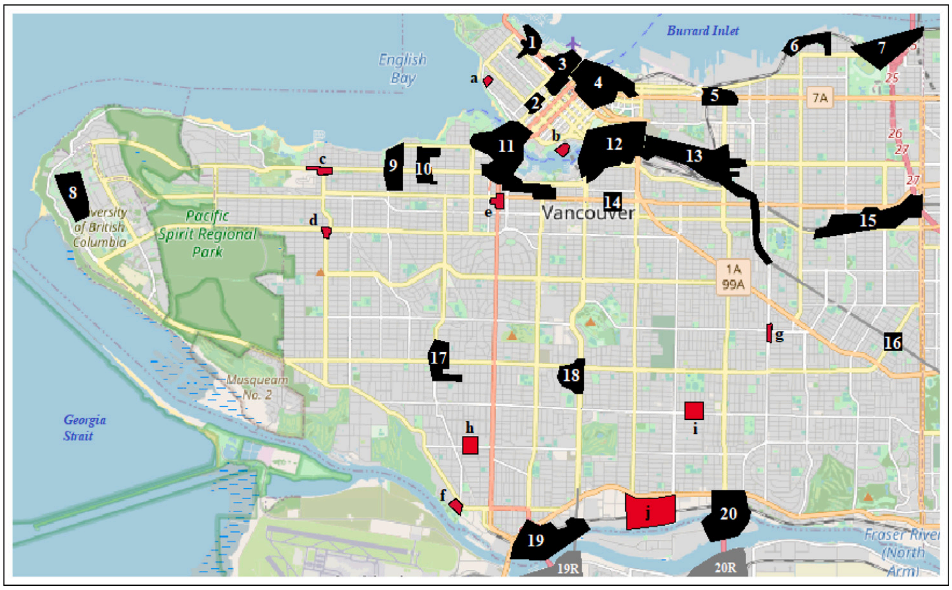

Fig. 4. [colour] City of Vancouver with sampled polygons highlighted in black and red. All black highlighted polygons were sampled in 2017; subsets of these polygons were sampled in 2015, 2016, 2018, and 2019. Red polygons were sampled in 2018 or 2019 for external validation purposes only. A subset of the black and red polygons were sampled in 2023. Grey polygons 19R and 20R lie in the City of Richmond and were sampled in several years, though not included in our formal analysis. Note: False Creek is the small body of water east of English Bay and immediately south of downtown (polygons 1 through 4); the Fraser River forms the southern boundary of the City of Vancouver. Map attribution: Google 2020.

All observations were conducted from a distance and were made at dozens of vantage points throughout the city, usually from a variety of elevated locations, both publicly accessible and via private access (with appropriate permissions). Observations were passive as they did not involve interaction with any gulls, neither adults or their eggs or young. This was partly purposeful (to not disturb nesting or young birds) and partly practical, as there would be no way to secure building and rooftop access to all study sites (nearly 5000 unique structures). All observations were made with either a Canon Powershot SX50 HS camera with 50x optical zoom and 200x combined zoom, a Nikon D7100 with Tamron SP 150–600 mm telescopic lens, or Bushnell 10 × 25 and Nikon 8 × 42 binoculars.

2.5. Statistical analysis and spatial model building

All statistical analyses were conducted using R (R Core Team, 2022). We fit semiparametric generalized additive models (GAMs) using a quasibinomial likelihood and penalized least squares to construct our predictive model for the probability of nest presence or absence in 2017:

$$g(\mu_i) = \sum_{j=1}^{m} \beta_j X_{i,j} + s(Lon_i, Lat_i), \quad (1)$$

where μ_i is the probability of a nest being present at structure i (conditional on all predictors), $g(\cdot)$ is the logit function, j indexes the predictors (except for latitude and longitude) in the parametric part of the model, and s is a thin plate regression spline over the two dimensional study domain indexed by latitude and longitude (see Wood (2003) for details on this object). This nonparametric term was added to account for possible site effects that could not be captured by the combination of predictor variables of interest (see Appendix B for more details). Models were fit using the 'gam()' function of the 'mgcv' package (Wood, 2003). Prediction intervals for final count predictions were calculated by empirical bootstrap on 10,000 iterations.

We had good a priori reason to believe that all predictor variables should enter into our predictive model in some way. However, finding the best functional form for these predictors required a standard recipe of exploration and model diagnostics (see Appendix D for complete details on this process).

Our final model contained the following first order predictors in its parametric portion: $UrbDen$, $DistToWater$, $Area$, Hgt, $MedSlope$, $RoofType$, and $Zone$. A quadratic effect for both $Area$ and Hgt, as well as a cubic effect for Hgt were also included to capture important curvature in the relationship between these variables and the probability of observing a nest on a rooftop. The model also included the following interaction terms: $UrbDen \times Zone$, $UrbDen \times DistToWater$, $MedSlope \times RoofType$, $Area \times MedSlope$, $Area \times DistToWater$, and $Area \times Hgt$. The thin plate smoother was tuned to a basis of approximately 16 effective degrees of freedom, roughly one for each sampled polygon.

The final GAM was selected due to its best behaved residuals and minimal AIC and residual deviance. The final model also performed best among candidate models according to a leave-one-out cross validation comparison of prediction errors. Further, external validation using data from subsequent years and regions of the city different from those used to construct the model leant further credibility to its viability (see Section 3.4).

2.6. Temporal fidelity estimates

Exact nest site recurrence rates were calculated as the proportion of nests in breeding season t that were reused in breeding season $t+1$, with "reused" in this context meaning a nest rebuilt on the same location the following season. Raw rooftop recurrence rates were calculated as the proportion of rooftops with nests in breeding season t that were reused in breeding season $t+1$. Adjusted rooftop recurrence rates were calculated as the proportion of rooftops with nests in breeding season t that were accessible to nesters in breeding season $t+1$ and were reused in breeding season $t+1$; we needed to develop an adjusted recurrence rate as some study buildings were demolished or otherwise unavailable to gulls in subsequent years. Adjusted rooftop recurrence can thus be thought of as a quantification of how often gulls reuse a rooftop in a subsequent breeding season *when that rooftop has not been made inaccessible* by human intervention.

Nominal rooftop colonization rates were calculated as the proportion of nests appearing on rooftops in breeding season $t+1$ that were not used for nesting in breeding season t. Finally, actual rooftop colonization rates were calculated as the difference between 100% and the sum of that year's raw rooftop recurrence and nominal rooftop colonization rates:

$$\Delta ARC(t,t+1) = \left(\frac{\#RN(t,t+1)}{\#RN(t)} + \frac{\#RN(\sim t,t+1)}{\#RN(t)} \right) - 1,$$

where $\Delta ARC(t, t+1)$ is the observed actual rooftop colonization rate from year t to t+1, $\#RN(t)$ is the observed number of rooftops with nests in year t, $\#RN(t,t+1)$ is the observed number of rooftops with nests in both years t and $t+1$, and $\#RN(\sim t, t+1)$ is the observed number of rooftops with nests in year t+1 but not in year t. Since some nesters have no choice but to relocate from one year to the next due to construction, building demolition, or netting of a previous year's nesting location (all somewhat rare but regular events that we observed between breeding seasons), these nesters may plausibly choose to colonize new but nearby rooftops. If the overall nesting population was not growing in size, then the sum of these raw rooftop recurrence and nominal rooftop colonization rates would equal 100% on average. Anything in excess or less would be consistent with a growth or decline, respectively, in the overall nesting population; hence, our definition of the actual rooftop colonization rate.

2.7. Spatiotemporal modelling

Using the 2023 data, we augmented model (1) to a spatiotemporal GAM:

$$g(\mu_{i(t)}) = \sum_{j=1}^{m'} \beta_j X_{i(t),j} + s_1(Lon_{i(t)}, Lat_{i(t)}) + s_2(Structure_{i(t)}), \quad (2)$$

where $\mu_{i(t)}$ is the probability of a nest being present at structure i in year t (conditional on all other predictors), $g(\cdot)$ is the logit function, j indexes the predictors in the parametric part of the model, s_1 is a thin plate regression spline over latitude and longitude, and s_2 is an independent and identically distributed (i.i.d.) Gaussian random effect for structure. That is, a random intercept for each structure is generated, with all intercepts modelled as i.i.d. normal, in order to account for temporal autocorrelation in the response process. As before, this model is fit using a quasibinomial likelihood and penalized least squares. It is well known that this penalized regression approach to generalized additive models can be viewed as a generalization of fully parametric generalized linear mixed effects modelling (Wood, 2017).

To find the best functional form of the parametric portion of model (2), we started with the final model derived from model (1) on the 2017 data and validated on the 2018–19 data, and considered adding additional parametric terms that depended on time; i.e., sample $Year$. Using the same recipe of exploration and model diagnostics as for model (1), we found that only a simple first-order $Year$ effect was necessary to be added for model (2). In particular, no interactions of $Year$ with any of the other structural fixed effects improved model validity or fit.

3. Results

3.1. Basic geospatial and urban features of observed nests

In 2017, 316 active nests were observed on 278 rooftops of distinct structures over all 3923 sampled structures across the City of Vancouver, a raw rooftop colonization rate of slightly more than 7%. Most gulls (255 pairs) chose to nest solitarily on rooftops, while 14 rooftops contained two nests, 6 contained three nests, 2 contained four nests, and 1 contained seven nests (the helipad of the Canada Post building in downtown Vancouver; see Kroc 2018a for more details). While most nests occurred on building rooftops, several nests occurred on bridges, either atop a concrete tower (Burrard Bridge; see Fig. 5), at the base of the bridge's piers (Burrard Bridge), or within the bridge's steel trusses (Iron Worker's Memorial Bridge). One nest was actually observed beneath the city's elevated Skytrain tracks, atop a support pillar; see Fig. 5. These tracks carry constant and extremely loud commuter trains daily from approximately 5 AM to 1 AM at roughly 6 min intervals.

Typical nesting sites occur on flat rooftops, with or without green cover, and are usually big enough to house only a single gull pair's territory (Fig. 6). However, certain rooftops were extremely small and/or abnormally shaped (see Fig. 6) and larger rooftops may attract multiple pairs as long as the space is ample enough.

Nest structure varied substantially with individual pair: some were robust and large, while others were minimalist scrapes (see Fig. 7). Nearby nuisance structures or effigies of predatory birds such as owls did not seem to deter nesting probability, nor did nearby construction or other sources of extreme noise disturbance, although such effects were not formally quantified.

The vast majority of nests occurred in areas zoned for comprehensive development (77%), followed by commercial and industrial (9% each), and then residential (5%), although it should be noted that most nests (73%) were observed at one of the downtown polygons (sites 1, 2, 3, 4, 11, or 12 of Fig. 4) where structures are almost exclusively zoned for comprehensive development. Most rooftops where nests occurred were categorized as flat (74%), with 75% having a median slope below 16 degrees from the horizontal. Only 18% of nests occurred on structures below 3 storeys in height, while the interquartile range of structure heights where nests occurred was 3.6 to 10.2 storeys (median = 6.2 storeys). Median structure area was 474 m^2, with an interquartile range of 197 m^2 to 889 m^2. The distribution of urban density of structures with nests was wider and greater on average than the distribution of urban density of structures without nests; however, these differences mostly vanished after stratifying by zoning classification. Slightly more than 93% of nests were observed within 1 km of water, although this result is driven heavily by the number of nests recorded downtown and the geographic structure of that part of the city (see Fig. 4). See Fig. 8 for more detailed information on the distributions of predictor variables over structures with recorded nests.

3.2. Modelling nest site selection via geospatial and urban features

The (mostly) marginal distributions of predictor variables described in the previous section hide many important aspects that explain how Glaucous-winged Gulls seem to select sites to nest in the City of Vancouver. To better understand the joint explanatory and predictive structure of these variables on nest site selection, we constructed the best fitting GAM described in Table 1 according to model (1) and the statistical principles outlined in Section 2.5 and Appendix D.

Our model clearly indicates that there are a variety of complex relationships at play that best explain nest site selection of City of Vancouver gulls. The clearest findings are that buildings zoned for purely residential use are much less attractive nesting sites, while other zoning categories are largely interchangeable in their attractiveness, and that higher structures make for more attractive nesting sites, but only up to a point. In particular, the cubic dependency on height suggests that the predictive effect of structure height on probability of nest occurrence is positive when structure storeys range between 0 and 12 (and is greatest for shorter structures), moderately negative when structure storeys range between 18 and 40, and approximately zero when structure storeys range between 12 and 18 or between 40 and 45 (see Fig. 9). The interaction between structure height and area does little to change this general trend. Compared to all other predictor variables, the predictive value of structure height was by far the largest and most robust to alternative model specifications, and significantly cubic. Heights between 12 and 18 storeys are associated with the highest (marginal) probability of nest occurrence, while rooftops near ground-level and above about 40 storeys are associated with the lowest (marginal) probability of nest occurrence (see Fig. 9). As rooftop area increases, all these probabilities of nest occurrence decrease, with the fastest decreases in probability for the tallest structures.

Fig. 5. [colour] Top: A nest atop the Burrard Bridge, identified by the white box. Bottom: A nest underneath the rapid transit Skytrain tracks of the Canada Line. The white box identifies the nest, approximately 2 m below the operational tracks. A chick can be seen in the zoomed-in frame to the lower right.

Table 1
Estimated coefficients (on the logit scale) and standard errors for best fitting quasibinomial GAM, with a null deviance of 1992.1 (df = 3923) and residual deviance of 1500.9 (df = 3886). The estimated thin plate smoother over latitude and longitude has 16.15 effective degrees of freedom. $UrbDen$ has a contrived scale ranging between 0 and 5, $DistToWater$ is measured in km, $Area$ is measured in 100 square metres, Hgt is measured in typical building storeys (i.e., 1 storey = 3.2 m), and $MedSlope$ is measured in degrees from the horizontal (see Section 2.2 for more information).

Predictor	Estimated coefficient	Standard error	Standardized estimated coefficient	p-value
(Intercept)	−8.543	2.161	−3.953	<0.001
UrbDen	0.834	0.780	1.069	0.285
DistToWater**	−3.273	1.044	−3.136	0.002
Area***	0.063	0.017	3.633	<0.001
Area^{2} **	−0.0005	0.0002	−3.216	0.001
Hgt***	0.613	0.075	8.208	≪0.001
Hgt^{2} ***	−0.028	0.005	−5.751	≪0.001
Hgt^{3} ***	0.0003	0.0001	3.767	< 0.001
RoofType(Flat)*	0.890	0.449	1.981	0.048
Zone(Com vs. Res)**	7.012	2.682	2.614	0.009
Zone(CD vs. Res)***	6.973	2.135	3.266	0.001
Zone(Ind vs. Res)**	8.562	2.865	2.988	0.003
UrbDen × Zone(Com vs. Res)*	−2.332	1.063	−2.195	0.029
UrbDen × Zone(CD vs. Res)**	−2.244	0.780	−2.878	0.004
UrbDen × Zone(Ind vs. Res)*	−3.099	1.182	−2.621	0.009
UrbDen × DistToWater***	1.301	0.352	3.698	< 0.001
MedSlope × RoofType(Complex)	−0.020	0.014	−1.413	0.158
MedSlope × RoofType(Flat)**	−0.064	0.022	−2.906	0.004
Area × MedSlope*	0.003	0.001	2.276	0.023
Area × DistToWater*	0.018	0.008	2.225	0.026
Area × Hgt*	−0.005	0.002	−2.176	0.030

Flatter rooftops are more likely to house nests, although this effect is mitigated by the median slope of the rooftop and disappears once the median slope is greater than about 15 degrees from the horizontal (note that 98% of flat rooftops have median slope no greater than 15 degrees; see Appendix C). This mitigating relationship is slightly tempered by structure area, with larger aread structures losing nesting attractiveness more slowly with increasing median slope of rooftop. Structure area has a consistently positive predictive effect on the probability of nest occurrence, and this effect increases slightly with distance to water (the tempering effects of median slope of rooftop and structure height are practically negligible).

Fig. 6. [colour] Top row: Typical rooftop nest sites. Middle row: Precarious nests: first, a nest atop a rooftop ledge more than 20 storeys above the ground; second, a nest atop the ledge of a church steeple; third, zoomed in. Bottom row: A large rooftop housing three active nests identified by the white boxes.

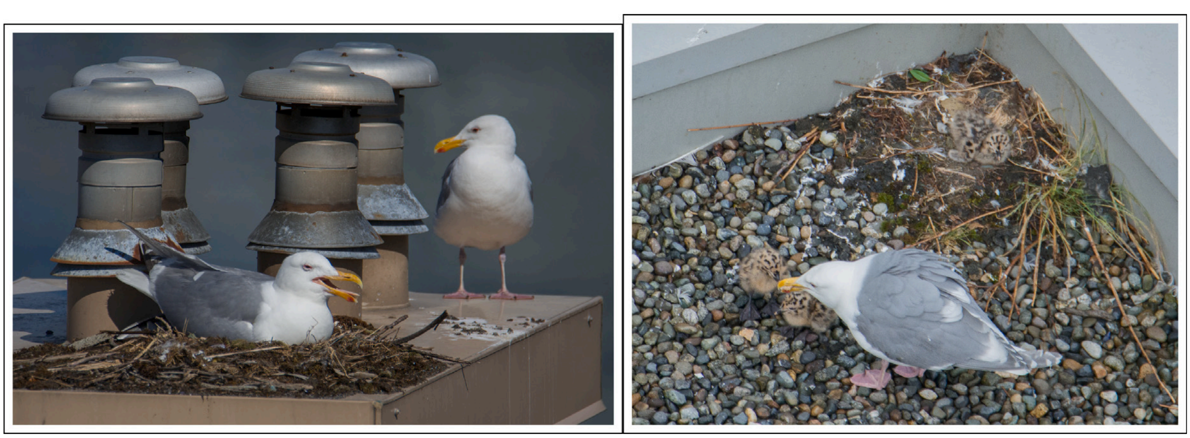

Fig. 7. [colour] A robustly built nest atop a small platform (left) and a sparsely built nest (albeit retaining some nest structure from a previous year) with hatchlings atop a 1.5 m by 4 m rooftop (right).

There appears to be a complex joint predictive relationship between urban density, distance to water, and zoning category. Urban density does not have any predictive power on its own, due largely to the fact that it is highly correlated with structure height (sample Pearson correlation of 0.59). However, denser regions that are not zoned as residential appear to be more attractive nesting sites when these regions are about 1 km or more from water, and density has essentially no detectable effect (positive or negative) for regions closer to water. However, structures further from water are also less attractive nesting sites, though this effect is tempered by larger structure area. It appears then that we see a positive effect of urban density only if that density is great enough and only if the structure is far enough from water, in

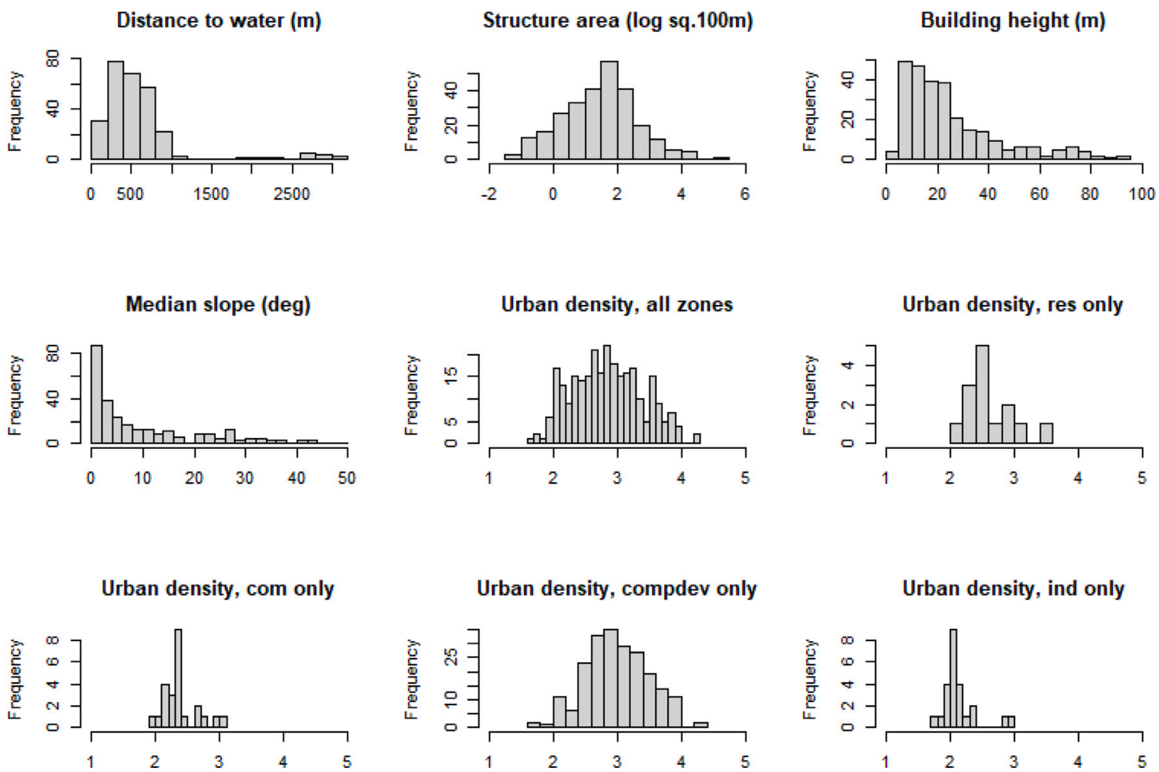

Fig. 8. [b&w] Distributions of predictor variables over rooftops where nests were observed. Note that structure area is displayed on a logarithmic scale.

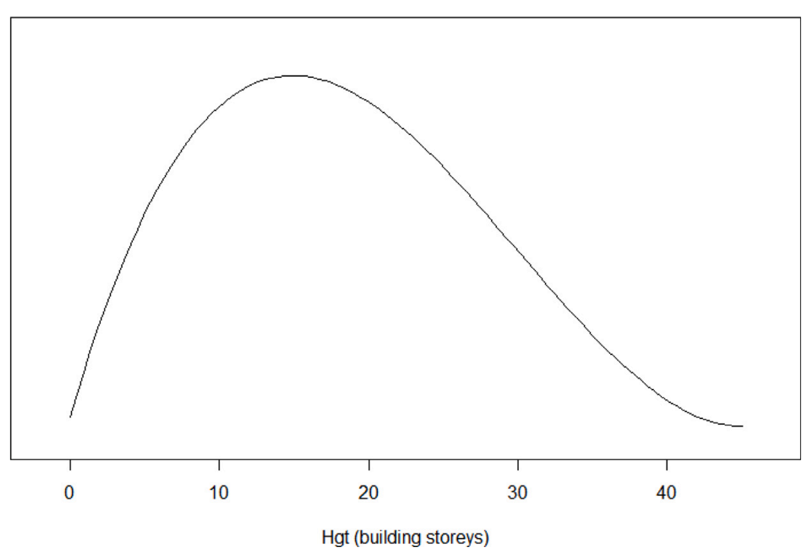

Fig. 9. [b&w] The fitted marginal relationship between structure height and likelihood of nest occurrence at median rooftop area. Vertical axis units have been suppressed since the scale is arbitrary.

non-residential zones. Increased urban density in residential zones is estimated to always be more attractive, regardless of distance to water.

3.3. Spatial model-based predictions

We can use our best fitting GAM described in the previous subsection to make predictions about where we are likely to find gulls nesting in the City of Vancouver, and to make predictions about the total size of the city's breeding population in 2017. Fig. 10 displays our model's predicted probabilities of nest occurrence for each structure in the City of Vancouver. Each dot corresponds to a structure, and dots are coloured in 1 of 5 shades of blue, with lighter shades indicating smaller predicted probabilities of nest occurrence and darker shades indicating larger probabilities. The partition used to form this discretized gradient along the interval [0,1] is as follows: lightest = [0, 0.001), [0.001, 0.01), [0.01, 0.1), [0.1, 0.2), [0.2, 1] = darkest.

Unsurprisingly, the regions of lowest predicted probability typically correspond to areas of the city that are zoned as purely residential, containing almost exclusively single-family homes. One can also clearly see that nests are generally predicted to occur closer to water, although not uniformly so, as the negative effect of residential zoning is still apparent. Downtown Vancouver (Fig. 10, panel c) has the highest concentration of large predicted probabilities. Other regions with high predicted activity include the University of British Columbia (far western edge of the city), the region south of False Creek (including Fig. 10,

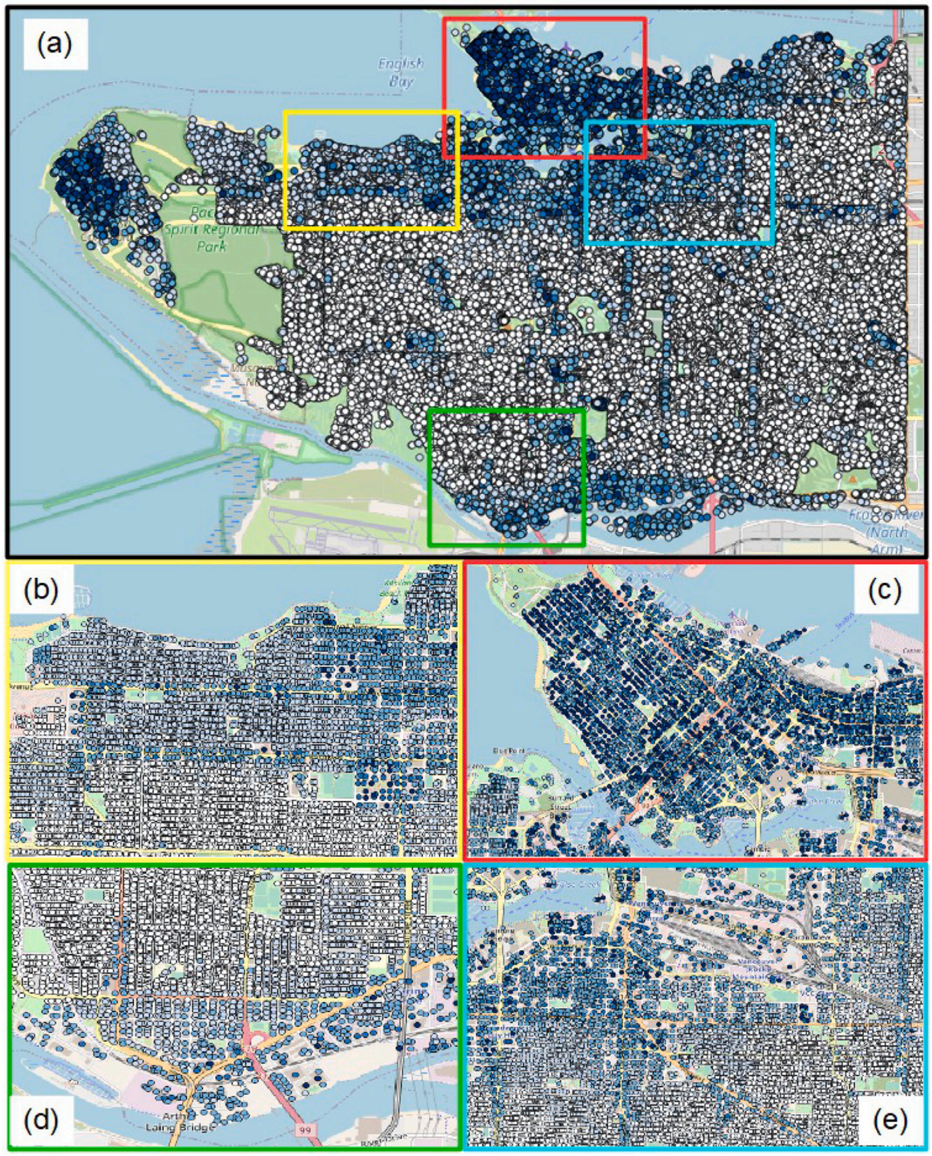

Fig. 10. [colour] (a) Model-based predictions of probability of nest occurrence by structure across the City of Vancouver. Each dot corresponds to one city structure. Darker dots indicate higher probabilities of nest occurrence, while lighter dots indicate lower probabilities. Close-ups of predictions for the Vancouver neighbourhoods of Kitsilano (b), Downtown (c), Marpole (d), and Mount Pleasant/Railtown (e) are also shown.

panel e), and the industrial regions of the city along the Fraser River to the south (Fig. 10, panel d) and along the Burrard Inlet to the north. There is also a tendency to predict higher probabilities of nest occurrence along busy and large streets that form commercial corridors. This is readily visible in Fig. 10, panel b, where probabilities are higher along 4th Ave. and Broadway, two major commercial corridors of the Kitsilano neighbourhood. The commercial corridor effect is apparent in many other regions of the city as well, including Fraser St. and Victoria Dr. both running substantially inland.

Aggregating our city-wide estimates, our model predicts that there were approximately 1482 structures with active nest sites in 2017, with a corresponding 95% prediction interval of [1287, 1852]. If we use the observed, naive point estimate of 316/278 = 1.137 nests per site predicted to contain at least one nest, then we can use our model to predict that the breeding population in the City of Vancouver totalled approximately 1685 (95% PI: 1463, 2106) gull pairs in 2017. Combining this estimate with observations at sample polygons 19R and 20R in the adjacent City of Richmond (see Fig. 4), the approximate City of Vancouver and adjacent breeding population would total more than 1900 pairs. This increase is partly due to the existence of a large single rooftop colony contained in Richmond's sample polygon 19R, which routinely houses approximately 150 active nests (Rodway et al., 2024). Furthermore, the City of Richmond on the south side of the Fraser River is known to house many more active nest sites beyond those observed in these two small sample polygons (Kroc, pers. obs.).

3.4. External validation

By mathematical necessity, our model-based predictions align very well with the observed nesting patterns at our sampled polygons, but we wanted to test the accuracy of our model against totally new observations. Consequently, we collected data at 10 new sample polygons in 2018 and 2019 (see Fig. 4) to assess the external validity of our predictive model. These sites were small, ranging in size from 0.034 km^2 to 0.655 km^2, and were chosen for their variation over key predictor variables and their isolation from the 2017 sampled polygons used to construct the GAM in model (1).

Table 2 contains relevant information on values of key predictors over the 10 sample polygons used for external validation, along with

Table 2
Descriptive breakdown of 2018 and 2019 sampled polygons for external validation of best-fitting GAM.

Sampled polygon	City region	Area, km^2	No. of structures	Avg. urban density	Distance to water of centroid, m	Zoning distribution cd/com/res/ind	Predicted number of structures with nests	Observed number of structures with nests
a	West End	0.034	34	3.193	125	24/0/76/0	7.99	5
b	Yaletown	0.051	40	3.349	112	100/0/0/0	1.93	2
c	Point Grey, Alma	0.035	69	2.209	516	0/67/33/0	2.99	2
d	Point Grey, Dunbar	0.042	38	2.189	1710	0/74/26/0	0.51	1
e	Granville and Broadway	0.052	74	2.640	626	1/92/7/0	4.50	4
f	Marine Drive, West	0.069	59	1.999	219	83/0/17/0	0.22	0
g	Victoria Drive	0.086	90	1.952	3381	8/81/11/0	0.51	2
h	57th Ave.	0.125	232	1.941	1172	0/2/98/0	0.07	0
i	49th Ave.	0.107	313	1.874	2017	0/0/100/0	0.10	0
j	Marine Drive, Fraser	0.655	102	2.124	260	0/1/2/97	5.45	7

Notes: Zoning abbreviations are cd = comprehensive development, com = commercial, res = residential, ind = industrial.

Table 3
Estimated annual exact nest site recurrence, raw and adjusted rooftop recurrence, nominal colonization, and actual colonization rates.

Years	2015–16	2016–17	2017–18	2018–19	Aggregate, 95% CIs
Nest recur	84.21% (16/19)	78.26% (18/23)	77.27% (17/22)	76.92% (10/13)	79.22% [68.46%, 87.63%]
Rooftop recur raw	87.63% (85/97)	76.47% (78/102)	90.91% (100/110)	89.47% (17/19)	85.37% [81.07%, 89.01%]
Rooftop recur adjusted	93.41% (85/91)	86.67% (78/90)	91.74% (100/109)	94.44% (17/18)	90.91% [87.13%, 93.87%]
Nominal colonization rate	16.67% (17/102)	29.09% (32/110)	11.50% (13/113)	5.56% (1/18)	18.37%
Actual colonization rate	4.30%	5.56%	2.41%	−4.97%	3.73%

the predicted number of structures with nests at each polygon according to our best fitting GAM and the actual observed number of structures with nests at each polygon recorded in either 2018 or 2019.

In general, our predictions aligned well with future observations, though less so at two sites (West End and Victoria Drive; see the Discussion). Overall, the GAM seems to accurately predict that nests will not occur when they in fact do not occur, and also usually accurately estimates how many nests will occur when they in fact do occur. Over all 10 sites, the GAM predicted approximately 24 nests to occur, while actual observations indicated that 23 nests were present.

3.5. Nest site fidelity through time

Measurements were made at the sampled polygons numbered 1 and 4 and at subsets of the sampled polygons numbered 11 and 12 in the five consecutive breeding seasons of 2015 through 2019 (see Fig. 4). This resulted in temporal data for 110 of the 158 total rooftops with observed nests at these sites in 2017. Moreover, observation vantage points at these polygons enabled recording of exact locations of nests on rooftops for 23 of these 110 nests. We were thus able to estimate both rooftop nesting recurrence rates and exact nesting location recurrence rates over the four return breeding seasons; estimates and 95% confidence intervals are recorded in Table 3.

Raw rooftop nesting fidelity ranged between 76.47% and 90.91% across the four return breeding seasons, yielding an aggregated estimate of annual rooftop return fidelity of 85.37% (95% CI: 81.07%, 89.01%). Exact nesting location return rates ranged between 76.92% and 84.21% across the four return breeding seasons, yielding an aggregated estimate of annual exact nest site fidelity of 79.22% (95% CI: 68.46%, 87.67%). Note that we were not able to determine whether re-nesting birds were the same pairs or individuals from previous years.

Between subsequent breeding seasons, some rooftops were made inaccessible to nesting gulls either by installation of deterrence nets or due to construction or building demolition. Consequently, gulls had no choice but to not re-nest on these rooftops. Excluding these structures from rooftop recurrence observations leads to the adjusted rooftop recurrence rates (Table 3). Adjusted rooftop nesting fidelity ranged between 86.67% and 94.44% across the four breeding seasons, yielding an aggregated estimate of annual adjusted rooftop return fidelity of 90.91% (95% CI: 87.13%, 93.87%).

Row 4 of Table 3 records the percentage of nests that occurred on new rooftops between subsequent breeding seasons, the nominal colonization rate. The sample size weighted aggregate estimate of these nominal colonization rates was 18.37%. Adding these numbers to the raw rooftop recurrence rates of row 2, Table 3 and subtracting by 100% gives an estimate of the actual growth of the rooftop nesting population across the sampled polygons over subsequent breeding seasons (row 5, Table 3). The sample size weighted aggregate actual colonization rate for new nests was 3.73%.

3.6. Spatiotemporal model-based predictions

Data were collected in 2023 from 14 of the sampling polygons pictured in Fig. 4 (see Section 2.3 for details). In total, 170 active nests were observed on 138 rooftops of distinct structures over 1907 sampled structures across the City of Vancouver, a raw rooftop colonization rate of slightly more than 7%. Most gulls (121 pairs) chose to nest solitarily on rooftops, while 9 rooftops contained two nests, 5 contained three nests, and 1 each contained four, five, and seven nests. Nest sites and structures were similar to those observed in 2017.

Using these data, we extended the best-fitting GAM of model (1) summarized in Table 1 to include a temporal component. The subsequent best-fitting spatiotemporal GAM, model (2), augmented the previous model by including a first-order fixed effect for *Year* and an additional smoother for *Structure* to account for autocorrelation of observations through time (see Section 2.7 for details). All model estimates were consistent with those from the previous spatial model using only 2017 data; in particular, the strong cubic relationship between structure height and probability of nest occurrence was clearly recovered by the spatiotemporal fit. There was a significant positive effect of *Year* on probability of nest occurrence and no temporal interactions with spatial fixed effects. See Appendix D for further details about this model and complete information on model parameterization, estimates, and consistency checks with the 2017 model.

Using the fitted spatiotemporal model, we predict that there were approximately 1708 structures with nest sites in 2017 (95% PI: 1496, 2258) and approximately 2194 structure with nest sites in 2023 (95% PI: 1827, 3011). The 170 nests observed atop 138 distinct structures in 2023 yields a naive point estimate of 1.232 nests per site predicted to contain at least one nest. Combining this number with the 1.137 naive point estimate obtained from the 2017 observations, we constructed a sample size weighted average estimate of 1.168 nests per site predicted to contain at least one nest. Applying this conversion factor to the predicted number of nests from our spatiotemporal model, we predict that the breeding population in the City of Vancouver totalled approximately 1995 (95% PI: 1747, 2637) gull pairs in 2017 and 2563 (95% PI: 2134, 3517) gull pairs in 2023. Using these two point predictions, and assuming a constant annual growth rate, the estimated annual colonization rate for new nests was 4.26%.

Finally, we have no principled or methodological reason to prefer the population estimates for 2017 derived from either the spatial GAM of model (1) or the spatiotemporal GAM of model (2). Discrepancies of point estimates are most parsimoniously attributed to sampling error due to the fact that model (2) was built on a larger dataset (containing observations from 2023) than was model (1). Consequently, a single "best" estimate for the breeding population in 2017 could reasonably be given by the simple average of these two model predictions: approximately 1840 (95% PI: 1605, 2371) pairs.

4. Discussion

Glaucous-winged Gulls nesting in the City of Vancouver make use of a massive variety of different structures, including rooftops, chimneys, ledges, and bridge structures. Nevertheless, our analyses suggest some general trends of this breeding population and how it interacts with the urban environment. Our observations and predictive models show a strong predilection to choose nest sites in the most crowded parts of the city, most clearly reflected in the high number of observed nests in the downtown core and in the highly significant effect of structure height on probability of nest occurrence. This phenomenon could be at least partially due to a legacy effect, with gulls initially nesting in and around downtown (Vermeer et al., 1988) because of its close proximity to the Port of Vancouver and the convergence of the Strait of Georgia with the Burrard Inlet and False Creek (see Fig. 4). Historically, this may have made the area particularly abundant in marine sources of food (e.g., fish from commercial vessels). However, commercial fishery operations in the City of Vancouver's waters are now minimal. In addition, availability of forage fish has declined in the Salish Sea over recent decades (Therriault et al., 2009) meaning that urban-nesters may now have to frequently travel greater distances to secure high quality food for their young. Glaucous-winged Gulls in the region have indeed been observed to routinely travel long distances (10s of kms) for food (J. Elliott, unpubl. data), and urban gulls in the City of Vancouver and Victoria have been observed feeding forage fish to their young (rather than urban food waste; Kroc, pers. obs.; Blight, pers. obs.). There is also evidence that this non-local foraging is common behaviour among other gull species nesting in traditional island habitats (Shlepr et al., 2021) or urban centres (Spelt, 2020).

4.1. "Islands in the sky"

The third order (marginal) relationship observed between structure height and probability of nest occurrence (see Fig. 9) is not totally surprising, although both the strength and robustness of this effect may be. We propose that this relationship can be understood as an "islands in the sky" effect, where the geography of the urban environment can in many ways mimic the geography of the traditional breeding habitat of the Glaucous-winged Gull. As illustrated in Fig. 11, isolated rooftop nesting sites in an urban environment can superficially mimic the structure of a small islet in a natural (i.e., non-urban) coastal environment. In particular, both habitats provide near-total protection from terrestrial predators via separation from surrounding landmasses. In the traditional habitat, this is accomplished via a water barrier while structure height can occupy the same function in the urban environment. We note that no predation by terrestrial mammals was observed throughout data collection for this study, nor were such events observed by Kroc (2018b) when studying reproductive success of rooftop-nesting gulls in the City of Vancouver.

However, structure height will only act as a barrier from terrestrial predators, which in this case includes humans liable to disturb a nesting pair, when a structure's height is sufficiently high above the ground, with higher structures naturally providing greater protection. Eventually though, structure height may become so high that its rooftop loses its nesting appeal. More than 99.5% of structures in the City of Vancouver have heights less than 20 storeys, meaning structures that exceed this height will be more vertically isolated, making them simultaneously more visible to avian predators, such as Bald Eagles (*Haliaeetus leucocephalus*), and more susceptible to elemental exposures like lack of shade and extreme heat. Indeed, occasional predation by nearby nesting Bald Eagles was observed during our surveys and others (Blight pers. obs., Kroc pers. obs.). These site attractants and deterrents seem to be captured by the curvilinear marginal relationship between structure height and probability of nest occurrence. The third order nature of this relationship suggests that, on a relative scale, a unit increase in building height is a much greater attractant for shorter structures (less than about 10 storeys) than it is a deterrent for already very high structures (greater than about 20 storeys).

Glaucous-winged Gulls seem to choose to nest on rooftops in residential zones at a notably lower rate than other areas of the City of Vancouver. Only 5% of nests were observed on residentially zoned buildings and our model (1) predicts that just 25.8% of nests across the city as a whole occurred there in 2017, despite the fact that 85.5% of buildings in the City of Vancouver are zoned residential. This effect is consonant with the strong effect of structure height on nesting probability, as more than 95% of residential structures in the city have heights below 3 storeys, where the joint effect of structure height and structure zone is substantially negative: about −7.5 on the logit scale, compared to only about −1 when a structure with the same height falls in a non-residential zone, using the 2017 GAM of model (1). Moreover, residential zones tend to be further away from water (median of 2 km, compared to medians of 1.3 km, 0.7 km, and 0.6 km for commercial, comprehensive development, and industrial zones, respectively) with substantially smaller urban densities (median of 1.95, compared to medians of 2.18, 2.48, and 2.12 for commercial, comprehensive development, and industrial zones, respectively; also, see Fig. 8), all combining to have a negative joint effect on nesting probability (see Table 1). Also, rooftops of many single family-homes in the city are peaked and Glaucous-winged Gulls seem to prefer flat rooftops (see the next subsection), a phenomenon also observed in the nearby city of Victoria (Hooper, 1987; Blight et al., 2019).

It is interesting to note that urban density does seem to have a significantly positive effect on probability of nest occurrence when the structure's distance from water is large enough, particularly for non-residential zones (this effect is present in both the 2017 GAM and the temporal GAM). This can help explain why nesting probabilities are predicted to be so much higher along commercial corridors, like Victoria Dr. or Fraser St., in the interior of the city domain (see Fig. 10).

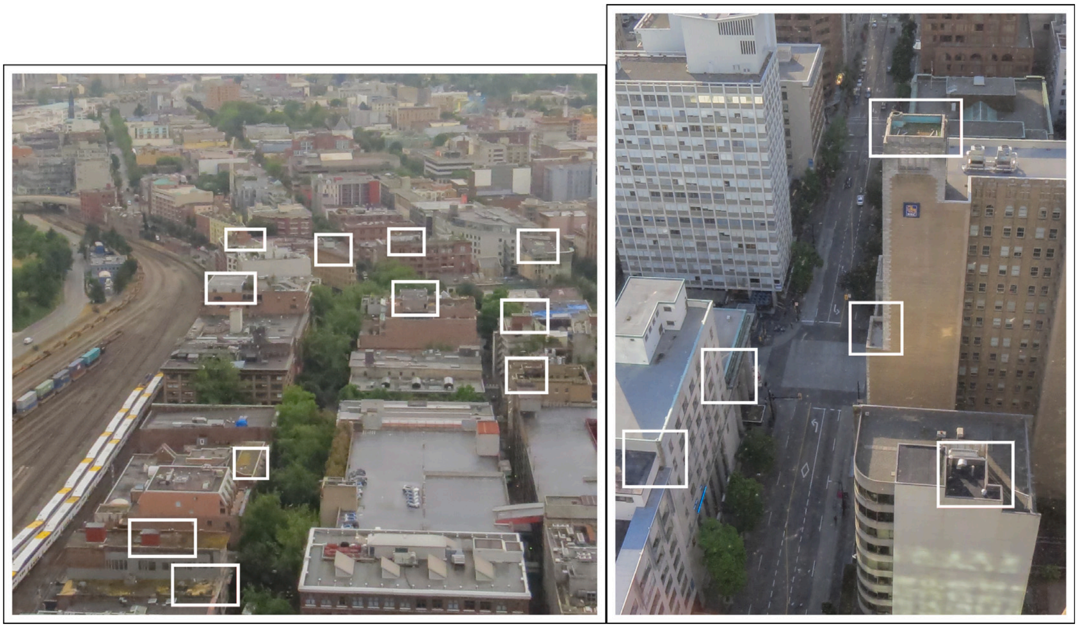

Fig. 11. [colour] Two examples of the "islands in the sky" type nesting pattern in downtown Vancouver. White boxes identify single nests on isolated rooftops.

Table 4
Summary statistics of key spatial and structural variables for rooftops with nesting gulls for this study (years 2017 and 2023), Vermeer et al. (1988), and Hooper (1988).

Variable	This study 2017	This study 2023	Vermeer et al. 1988	Hooper 1988
Avg. height (SD), m	25.9 (19.8)	21.5 (19.1)	7.8 (3.1)	13.3 (4.9)[a]
Avg. area (SD), m^2	708 (981)	601 (728)	1265 (1043)	–
Avg. dist. to water (SD), m	603 (569)	539 (528)	212 (85)	0–500[b]
Peaked vs. Flat	27%/73%	23%/77%	24%/76%	25%/75%
Zoning (res/com/cd/ind)	5%/9%/77%/9%	7%/9%/65%/19%	–	18%/62%/20%[c]

Notes:
[a] These estimates are based on a sample size of 33.
[b] Hooper (1988) only reports an approximate range of distance to water.
[c] Hooper (1988) reports 62% of nests on "business or commercial buildings", so we cannot partition this number into official commercial vs. comprehensive development zoning counts.

4.2. Comparisons to previous urban gull work in the Salish Sea

Two previous studies reported some similar building characteristics to ours for rooftop nesting Glaucous-winged Gulls in urban centres of the Salish Sea: Vermeer et al. (1988) reported aggregate information on building height, area, distance to water and rooftop type for a sample of 34 buildings in the City of Vancouver in 1986, while Hooper (1988) reported aggregate information on building height, distance to water, rooftop type, and zoning for a sample of 99 rooftop nests in nearby Victoria, BC in 1986. Table 4 gives these summary statistics alongside the analogous ones for the two primary study years of this paper. Building heights and distance to water are larger on average and in variability from our study compared to Vermeer et al.'s and Hooper's. Rooftop areas are smaller on average between our study and Vermeer et al.'s. Proportions of peaked vs. flat rooftops housing nests are very similar across all samples, whereas zoning distributions show some disproportionality between residential and industrial zoning categories across samples.

The most obvious reason for the observed differences in these statistics is the very different sampling methodologies employed between the three studies. We employed a hybrid convenience-stratified sampling approach specifically engineered to achieve comparable statistical power to estimate probability of nesting occurrence across the City of Vancouver, while neither Vermeer et al. nor Hooper reported sampling rooftops in any structured way. Vermeer et al.'s sample was derived from two shoreline locations in the City of Vancouver, roughly corresponding to our site 12 (False Creek) and our sites 1, 3, 4, 6, and 7 (Burrard Inlet; see Fig. 4). Hooper only reported collecting data in and around Victoria that was "on any man-made structure considered to be part of an urban environment". Moreover, it is unknown how well either Vermeer et al.'s or Hooper's definitions of peaked vs. flat roof align with the official City of Vancouver's designations (City of Vancouver, 2020). Therefore, we caution the reader against taking these comparisons at face-value.

Nevertheless, it is interesting that the proportion of rooftops that are either peaked or flat housing nests remains so stable across the three studies. Vermeer et al. found no significant difference between the presence of nesting gulls on flat or peaked rooftops using a sample of 126 rooftops, whereas we found only a marginally significant preference for flat rooftops (p-value = 0.048, see Table 1) based on a sample of 3923 rooftops; this discrepancy is easily attributable to differences in statistical power. It remains numerically true, however, that about 75% of nests appear on flat rooftops across all studies and years. The fact that this effect in our models is only marginally significant is not unexpected though because $RoofType$ correlates with other more predictive variables, notably $MedSlope$ ($r = 0.77$) and $Area$ ($r = 0.25$). The effect of $RoofType$ then is best understood as marginal only after accounting for these more predictive structural variables.

The differences between studies in average building height, area, and distance to water are almost surely attributable to differences in sampling methodology. However, since building heights have continued to increase, both in the extreme and on average, across urban centres of North America in the past 40 years (Kontokosta, 2013; Jedwab et al., 2022), this also seems likely to have contributed to the differences in average building height across studies as well. Finally, there are some apparent fluctuations in residential and industrial zoning proportions across both of this paper's study years and Hooper's; however, we remind the reader that our formal analysis of Section 3.6 detected no temporal interactions of probability of nest occurrence with any of the spatial or structural variables under investigation here. It certainly remains possible that certain temporal trends exist, but our analysis provides some assurance that these effects must be rather small.

4.3. Implications for colonization and population trends

Regarding the external validity of our spatial model, predictions aligned well with future observations except possibly at two sites: West End and Victoria Drive (see Fig. 4 and Table 2). The former site housed a cluster of six tall residential towers interspersed with mixed-use midrange structures that the GAM predicted to be of high attractive value for nesting. While this appeared to be generally corroborated by observation of actual nests (albeit at lower numbers than predicted), it appears that the GAM may not be sufficiently taking into account the spatial dynamics between neighbouring nesters, and in particular, the repulsive effect of pairs nesting in too close a proximity to each other when other, less crowded options are available. This is in contrast to how gulls behave at "natural" colonies, where they are generally – although not always – highly colonial (Vermeer and Devito, 1989). The Victoria Drive site sits far from the nearest body of water and occupies a demographic cross-section that was rather sparsely populated by our data used for fitting the GAM. This points to a need to collect more data at city sites further from water, where we already suspect interesting, secondary dynamics are at play as evidenced by the commercial corridor effect previously described.

Nevertheless, the observed number of structures with nests fell comfortably within the bounds of the respective 95% prediction intervals for each polygon sampled for external validation. This, paired with the fact that the aggregate number of predicted structures with nests over all 10 sites was very close to the observed value (24 vs. 23, respectively), lends confidence to our predictions of the total size of the urban-nesting population in the City of Vancouver, which we predicted was roughly 1800 pairs in 2017.

The results of our spatiotemporal model using both data from 2017 and from 2023 are consistent with those of the original spatial model that was built from only the 2017 data. Model estimates and corresponding uncertainties were in good agreement between the two models (see Figs. D.16 and D.17 in Appendix D). A significant effect of time was detected though we were unable to detect any temporal interactions with spatial variables (see Table D.7 in Appendix D). While we cannot say that such interactions do not exist, it seems likely that their effects would be very small on a per annum basis, making our power to detect them quite low over the 6 year span considered by our dataset.

Vermeer et al. (1988) surveyed portions of the City of Vancouver and North Vancouver (see Fig. 3) in 1986 for rooftop nesting activity. The City of Vancouver sites corresponded roughly to the region composed of this study's sample polygons 1, 3, 4, 6, 7, and 12 (see Fig. 4). Vermeer et al. extrapolated to estimate the total size of the nesting population in Burrard Inlet and False Creek to be roughly 500 pairs (with 150 of those observed in North Vancouver). Given the lack of observations in the City of Vancouver's south and west sides, we can consider their North Vancouver counts as a rough substitute for these regions. Then, taking the estimate of 500 pairs at face value, our results suggest a three- to four-fold increase in rooftop nesting activity since the mid-1980s, or over almost 40 years. It is interesting to note that a similar growth figure was suggested for the nearby City of Victoria over the same timeframe (Blight et al., 2019; note that the City is the core municipality in the Greater Victoria area).

While data do not exist to definitively determine if this growth was linear over that time, our temporal estimates of actual rooftop colonization rates are consonant with a linear growth rate of roughly 3.73% per annum. Specifically, if one starts with Vermeer et al.'s estimate of 500 pairs in 1986 and assumes a constant annual growth rate of 3.73% over the 31 years between 1986 and 2017, the predicted 2017 nesting population would total roughly 1556 pairs. This is close to our 2017 model-based estimate of 1685 pairs using the 2017 estimated conversion factor of 1.137 nests per site predicted to contain at least one nest. If one instead uses our spatiotemporal model and sample size weighted conversion factor of 1.168 nests per site predicted to contain at least one nest, one would predict a 2017 nesting population of 1995 pairs. However, if one starts again with Vermeer et al.'s estimate of 500 pairs in 1986 and assumes a constant annual growth rate of 4.26% over the 31 years between 1986 and 2017 (derived from our spatiotemporal model), then the predicted 2017 nesting population would total roughly 1822 pairs.

One can make similar comparisons of predictions from our models/observations and extrapolations of Vermeer et al.'s observations for 2023 as well. Extrapolating Vermeer et al.'s counts assuming a constant annual growth rate of 3.73% or 4.26% yields a predicted 2023 nesting population of 1938 or 2341 pairs, respectively. This latter figure is close to the 2563 pairs predicted from our spatiotemporal model and sample size weighted conversion factor of 1.168 nests per site predicted to contain at least one nest. These comparisons are summarized in Fig. 12. Although a per annum growth of roughly 4% for this breeding population seems high, the figure is consistent with both the various analyses of this study and the extrapolations from Vermeer et al.'s 1986 observations.

In light of these facts, and given the preponderance of currently unused but ostensibly attractive rooftop nesting locations in the City of Vancouver, it seems likely that further growth of this urban population can be expected, assuming that population growth is not limited by food availability or some other extrinsic or intrinsic limiting factor. We currently lack data to determine the degree to which this population growth is intrinsic to our urban population vs. immigration from natural colonies. However, there is evidence to suggest that the reproductive success of urban gulls is superior to that of birds nesting in their traditional habitat (Kroc, 2018b), and population numbers and reproductive output have declined at these natural colonies over recent decades (Blight et al., 2015, 2022).

Moreover, although urban colonization seems to continue to increase in the Salish Sea (Blight et al., 2019), the fact that our spatial model performed well for data collected in subsequent years suggests that the dynamics of the colonization process may be somewhat stable, assuming that Glaucous-winged Gulls continue to nest at current densities. That is, we may be able to use this model to reasonably predict where any new colonization is most likely to occur. This could increase the efficiency of future monitoring efforts, and also has potentially important implications for city planners who wish to design and construct new buildings that have the least chance of inviting negative human–gull interactions. Such an approach to conflict mitigation would be particularly desirable since urban gulls will sometimes circumvent netting or other ad hoc deterrents and nest anyway (Kroc, 2018b; Buskin, pers. obs.; Chin & Chin, pers. obs.). Gulls are sometimes even harmed or killed as a result of interacting with such deterrents: the first author has witnessed this in two instances in the City of Vancouver and the second author has noted one gull killed by wire deterrents placed atop the cruise ship terminal in Victoria, BC (*cf*. Rodway et al., 2024).

The high point estimates we derived for both exact nest site recurrence (≈80%) and rooftop recurrence (≈90%) of nesters also suggest a robust stability of this urban population through time. Gulls are well known to be highly faithful to successful breeding sites across seasons and across generations (Southern and Southern, 1982; Reid, 1988; Nisbet et al., 2017), and although we did not identify individual birds in this portion of our study – i.e., we could not rule out renesting being carried out by conspecifics rather than by the same individuals or pairs as in previous years – our results corroborate this phenomenon for the urban environment. Some evidence even suggests that certain pairs will take up year-round residence at their urban breeding sites (Kroc, 2018a;

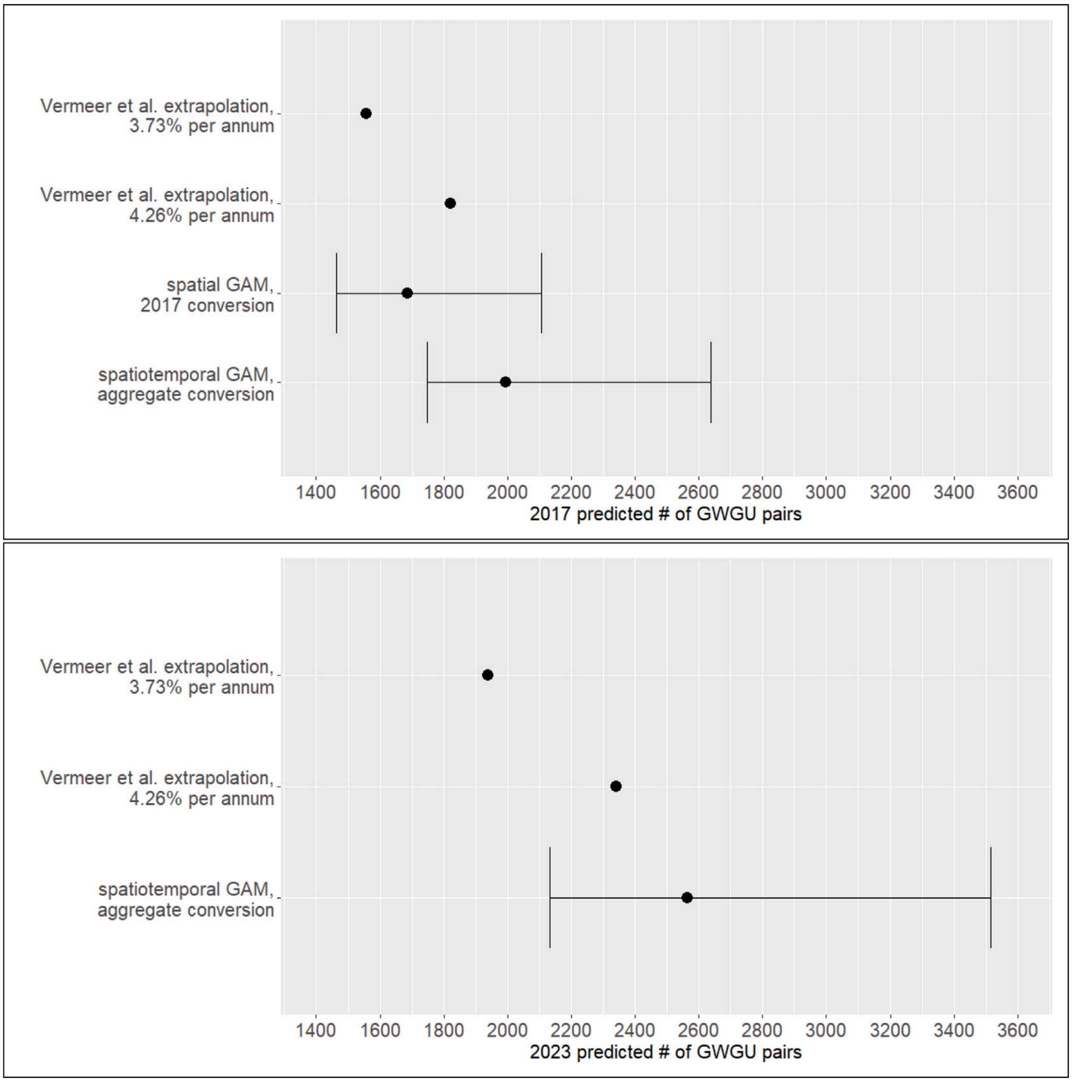

Fig. 12. [b&w] Different predictions of numbers of pairs of nesting gulls in the City of Vancouver in 2017 (above) and 2023 (below). Predictions from this study's models are flanked by 95% prediction intervals.

Blight, pers. obs.). This is in stark contrast with what has been observed in most gull species in general, where at least some amount of seasonal migration is expected (Spear, 1988; Hatch et al., 2011), but is consistent with the less migratory nature of the Glaucous-winged Gull of the Salish Sea (Butler et al., 1980).

Recent estimates in Rodway et al. (2024) suggest a total BC Salish Sea breeding population of roughly 11,000 Glaucous-winged Gull pairs which, based on our study's estimates, implies that the current City of Vancouver breeding population comprises about 20% of this total. Figures in Rodway et al. also suggest that about 500 pairs nest in other urban centres of Greater Vancouver outside the City of Vancouver itself, while perhaps another 1000 pairs nest in other urban centres of the BC Salish Sea, notably in Victoria (see Fig. 1). This means that urban breeders now likely comprise approximately one-third of the BC Salish Sea breeding population. These numbers further underscore the need to more deeply understand urban breeding dynamics and how they relate to or diverge from their traditional, non-urban counterparts.

4.4. Generalizability

It would be interesting to see if future studies could reproduce similar effects of structural and spatial features of the urban environment on nest site selection patterns in other cities and for other species of gull. For instance, do urban-nesting Glaucous-winged Gulls exhibit similar preferences for rooftop selection in Victoria, Canada and Seattle, USA, the two nearest urban centres to Vancouver in the Salish Sea (see Fig. 1)? Could the results of this study generalize to other species of urban-nesting gull as well? Future work by the authors and other collaborators aims to address these questions. Preliminary data and analyses suggest that our predictive model may be useful for other urban centres of the Salish Sea, primarily due to the facts that these cities have similar built environments to the City of Vancouver and that their resident gulls share a similar population ecology (Blight et al., 2019). However, whether urban-nesting Glaucous-winged Gulls exhibit similar preferences for rooftop selection in other cities in the area is still to be determined.

It seems quite plausible that this study's results could be generalized to other cities in Greater Vancouver, particularly to the geographically adjacent and structurally similar cities of Richmond and North Vancouver (see Fig. 3). However, as noted in the Results, Richmond is home to a large single rooftop colony that regularly contains roughly 150 active nests (Rodway et al., 2024). The City of Vancouver is not known to house an analogous site, suggesting that at least some important differences in converting our binary model predictions (i.e., is a rooftop likely to contain at least one nest or not?) into reasonable estimates of a city-wide breeding population.

Outside the Salish Sea, the generalizability of our model is more suspect, though we do think that the general methodological and model-building approach could yield equally useful results. Anecdotal evidence suggests that urban-nesting Western Gulls (*Larus occidentalis*) of California, USA do not select rooftop nesting sites in exactly the same way as their Glaucous-winged counterparts (E. Kroc, unpubl. data). In particular, building height seems to be less of an important factor, and distance to water seems to be much more so. Western Gulls have also been noted to exhibit much stronger colonial tendencies in an urban environment, and solitary nests on isolated rooftops do not appear to be as common as for gulls of the Salish Sea (E. Kroc, unpubl. data).

However, it is important to realize that these apparent differences could be attributable at least in part to differences in how various cities are built, and how urban areas developed over the decades as gulls became urban nesters. The built landscape of the City of Vancouver does not necessarily look very similar to the built landscape of many California cities, where architectural and urban design norms are different. It seems unlikely that all the attractive effects quantified in this study could be replicated for gull species outside of North America, especially in Europe and Asia where many cities are centuries older. This is pure conjecture, however; further studies are needed to test these speculations.

4.5. Limitations

There are a few noteworthy limitations of this work. First, it is unclear if many future studies seeking to generalize what we have done here to other cities and/or species would be feasible. One would need access to similar types of datasets on structural parameters of the local built environment. Failing this, one would need to create the dataset from scratch which would likely require a massive amount of work fraught with frequent potential for error. Absent open city data, measurements for some variables could be automatically scraped from Google Maps or a similar geographical information source, particularly building area. Other variables, including the most important one for this study, building height, might prove more challenging to generate without a definitive source. Still, it would be worthwhile to see what datasets already exist that could aid in this task for other cities of interest.

A related important limitation of note is that the City of Vancouver open datasets that were used in this paper represent the urban landscape of the city as of 2009, but our models fit response data that were collected in 2017 and 2023. These city data are still the most up-to-date comprehensive records of city structure features available for Vancouver. For example, the more recent 'building-footprint-2015' open dataset (City of Vancouver, 2022) does not contain all relevant information about structures, notably lacking building height information. Nevertheless, the city landscape is constantly changing, and certainly the city as of 2009 did not look identical to the city as of 2017 or 2023. We attempted to at least partially account for this reality by making manual adjustments to the dataset for major construction sites and new buildings in sampled polygons that were not captured by the original dataset, but this was not done for the entire city (i.e., in unsampled regions).

Another limitation is that we used a naive point multiplier to convert our model-based predictions of how many structures contained nests in the city to predictions of how many gull pairs nest in the city. The model is based on a binary response (i.e., Is a nest present or not?), while this population figure is based on a count response (i.e., How many nests are present or not?). From a theoretical point of view, it would certainly be most desirable to build a statistical model for this count response process directly to avoid having to make that final naive conversion. This was actually our original intention. However, it quickly became apparent that such an approach would not be feasible due to the sparsity of non-zero or -one response data. Over 90% of structures where nests were observed contained only a single nest (255 out of 278); over 95% contained only one or two nests. Thus, there was not enough observed variability in the count response process to reliably explain with the structural and spatial features that were of greatest interest. However, this limitation may not present itself for other cities and/or species. For example, shared rooftop nesting seems to be more common for the Slaty-backed Gull of Magadan, Russia (Zelenskaya, 2019).

5. Concluding remarks

This study used semiparametric generalized additive models to quantify the complex relationships between where Glaucous-winged Gulls choose to nest in the City of Vancouver, Canada, and a host of structural and spatial features that characterize the city's urban landscape. Using these models, we predicted that roughly 1800 gull pairs nested in the city in 2017 and more than 2000 pairs nested in the city in 2023. Combined with our estimates for exact nest site, rooftop recurrence, and actual rooftop colonization rates, we argue that this urban population is quite stable, and likely growing at roughly 4% per annum. Given that the Glaucous-winged Gull has suffered declines in its population and reproductive output across its natural colonies in the Salish Sea over recent decades, the importance of this urban population to the overall health and viability of the species in this region is significant.

CRediT authorship contribution statement

Edward Kroc: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Louise K. Blight:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Min Hai Cao:** Writing – review & editing, Writing – original draft, Software, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Further details on predictor variable creation

The *urban density* variable, $UrbDen$, is a log-average of a random subsample of the surrounding structure heights, standardized to facilitate comparisons between more and less densely urbanized parts of the city. Specifically, we used QGIS to create Voronoi polygons over a (uniform) random subsample of 10% of all city structures (approximately 12,000 rooftops). Each structure was then assigned the mean height of all structures (less the one structure in question) that fell within its intersecting polygon. This index was then log-transformed to make its artificial range tighter and more normally distributed. The exact variable specification is as follows:

$$UrbDen_{i,j} = \log\left(\frac{\#Str_j \times AvgHgt_j - Hgt_{i,j}}{\max(\#Str_j - 1, 1) + 1}\right),$$

where $\#Str_j$ denotes the number of structures in polygon j, $AvgHgt_j$ denotes the average height of all structures in polygon j, and $Hgt_{i,j}$ denotes the height of structure i within polygon j.

The zoning variable, $Zone$ was created by collapsing the 12 City of Vancouver zoning districts into 4 simplifed zoning categories as follows:

- **Commercial (3.5%)** ⟸ Commercial (3.5%)
- **Comprehensive Development (8.3%)** ⟸ Comprehensive Development (7.2%) + Historical Area (0.4%) + UBC (0.7%)
- **Industrial (2.7%)** ⟸ Industrial (1.1%) + Light Industrial (1.6%)
- **Residential (85.5%)** ⟸ Residential (0.6%) + One-Family Dwelling (66.1%) + Two-Family Dwelling (11.2%) + Multi-Family Dwelling (6.7%) + Limited Agriculture (0.4%) + Other (0.6%)

Notice that each of the 5 zoning districts Historical Area, UBC, Residential, Limited Agriculture, and Other each comprise less than 1% of structures. The district of Limited Agriculture is composed of mostly residential structures, some with small private farms, on the southwest boundary of the City of Vancouver, between Marine Drive and the Fraser River, west of Granville and east of the University Endowment Lands. The district of Other was composed of mostly scattered structures used primarily for residential purposes. The simplified zoning category of Comprehensive Development broadly captures a heavy mixture of concurrent residential and commercial use.

Appendix B. Features of the study sites

Sample polygons 19 and 20 extended into the adjacent city of Richmond where additional structures were surveyed for nesting activity; these polygons are labelled as 19R and 20R in Fig. 4. These nests and structures have been excluded from our formal analyses due to a lack of access to reliable data for predictors on sample structures. Table B.5 contains detailed information on urban and geographic features of the 20 sample polygons used for our formal analyses for model (1).

Table B.5
Descriptive breakdown of 2017 sampled polygons.

Sampled polygon	City region	Area, km^2	No. of structures	Avg. urban density	Distance to water of centroid, m	Zoning distribution cd/com/res/ind
1	Coal Harbour	0.283	109	3.234	254	85/4/11/0
2	Downtown Burrard South	0.157	84	2.811	820	69/26/5/0
3	Downtown Burrard North	0.562	303	3.642	432	100/0/0/0
4	Downtown Lookout Tower	1.176	601	3.238	394	100/0/0/0
5	Clark & Hastings	0.345	77	2.065	592	8/0/6/86
6	East Vancouver	0.395	110	2.089	223	11/0/89/0
7	Second Narrows Bridge	0.832	40	2.747	146	69/0/3/28
8	UBC	0.650	103	2.617	787	100/0/0/0
9	Kitsilano West	0.487	430	2.215	427	0/7/93/0
10	Kitsilano East	0.385	204	2.388	462	0/15/85/0
11	False Creek West	1.791	579	2.489	302	47/19/30/4
12	False Creek East	1.629	209	2.947	18	79/16/0/5
13	Skytrain West Corridor	1.925	295	2.193	1880	6/20/33/40
14	Broadway	0.068	28	2.176	959	0/61/14/25
15	Skytrain East Corridor	1.260	185	2.052	3102	52/8/11/29
16	Joyce Station	0.035	17	2.475	3512	41/59/0/0
17	Kerrisdale	0.501	167	2.264	2261	4/44/52/0
18	Oakridge	0.423	96	2.308	2799	76/15/9/0
19	Oak St. Bridge	1.258	149	2.085	201	4/0/5/91
20	Knight St. Bridge	1.129	143	1.983	39	0/1/31/68

Appendix C. Sampling efficiently to improve statistical power

We designed our study to have reasonable statistical power to detect not just main effects of interest, but also interactions of those effects. Consequently, we required sufficient sample sizes on all possible cross-sections arising from potential interactions of interest (the strata of our sampling scheme). Note that, unlike global simple random sampling, this means that we would not expect the observed sample distributions of our main effects to match with their population (i.e., City of Vancouver) distributions. Indeed, such matching would be highly inefficient as it would entail massive oversampling from certain strata (to achieve comparable statistical power) or massive undersampling from other strata (to the detriment of statistical power). See Lohr (1999) for technical details on the benefits of stratified sampling, including unbiasedness of sample estimators.

Table C.6
Population vs. observed sample distributions for $Zone$ and $RoofType$ variables.

Zone	Pop.%	Sample%	RoofType	Pop.%	Sample%
Commercial	3.5%	10.7%	Flat	21.1%	48.5%
Comp. Dev.	8.3%	41.2%	Complex/Pitched	78.9%	51.5%
Industrial	2.7%	26.5%			
Residential	85.5%	21.5%			

The largest deviations in observed sample distribution from population distribution came from the $Zone$ and $RoofType$ variables (see Table C.6). The vast majority of the City of Vancouver is zoned residential (85.5%), with less than 7% zoned as either commercial or industrial. Our stratified sampling approach therefore required us to target non-residential zones at a much higher rate than what would be observed under simple random sampling. A similar adjustment can be observed for the $RoofType$ variable. It is important to note that 71.5% of all complex/pitched rooftops in the City of Vancouver are zoned residential; thus, balancing sample sizes over these two variables simultaneously was largely accomplished by balancing over $Zone$ only.

Observed sample distributions displayed acceptable balance across all categories with the exceptions of commercial and comprehensive development zoning categories. Comprehensive development received a larger share of the overall sample size because 70.8% of buildings over 6 storeys in height, and 86.8% of buildings over 15 storeys in height, fall into this zoning category. Thus, we needed to prioritize comprehensive development over other zoning categories in order to ensure sufficient statistical power to estimate the predictive effects of building height on probability of nest occurrence. Buildings zoned for commercial use proved more difficult to sample in any one contiguous polygon due to the fact that most of these buildings are strung out along long commercial roads that often stretch the entire length of the city. To ensure that we avoided visibility bias and did not artificially remove spatial autocorrelation in our observed responses by sampling within unreasonably long and narrow polygons, we thus had to settle on sampling relatively fewer commercially zoned buildings (perhaps hurting our power to as accurately estimate commercial-zoning-specific effects).

Figs. C.13, C.14, and C.15 display the observed sample distributions versus population distributions of the continuous predictors of interest crossed by $Zone$. Again, observing these strata interacted with $Zone$

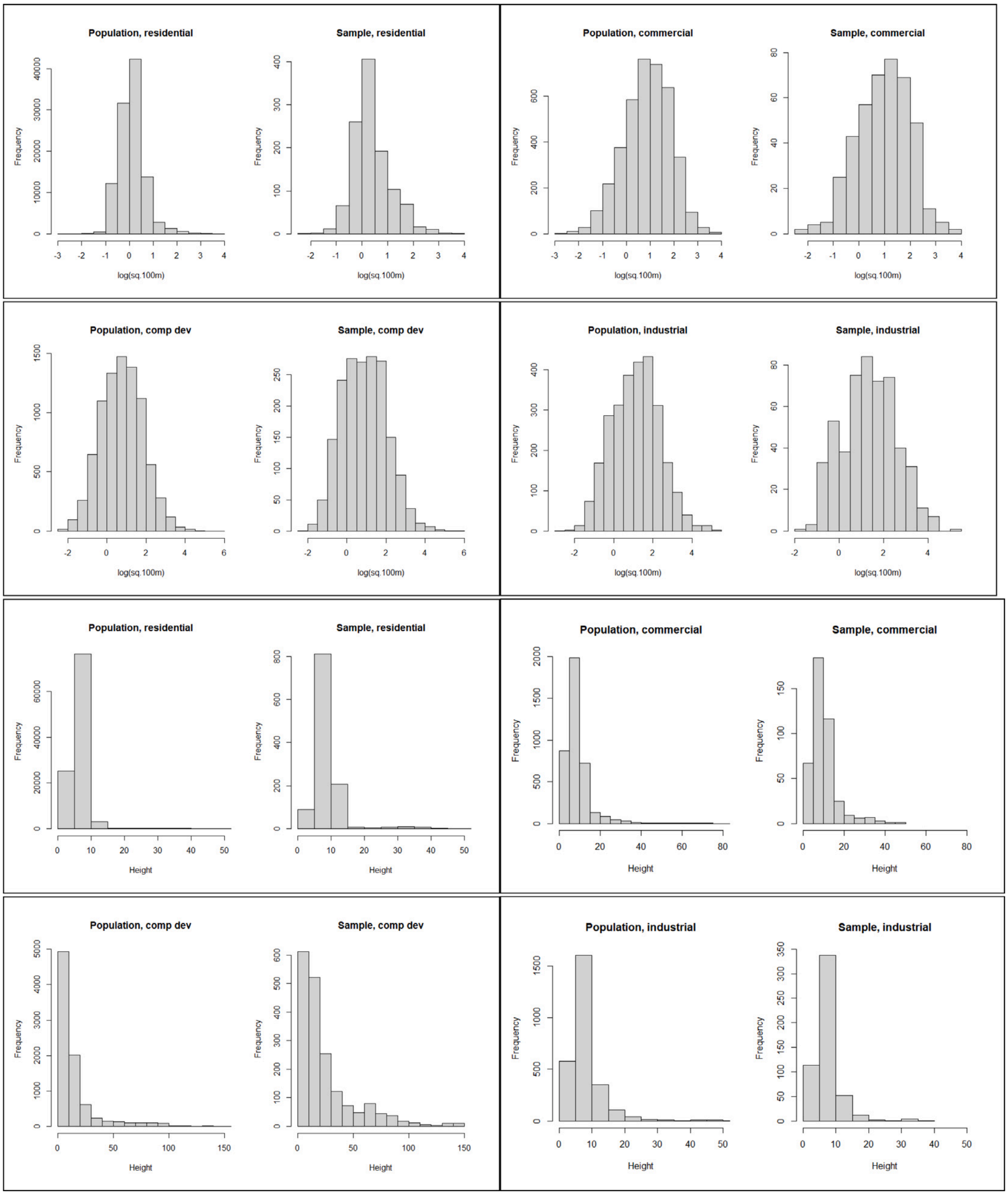

Fig. C.13. [b&w] Population vs. observed sample distributions of $Area$ by $Zone$ (top two rows) and Hgt by $Zone$ (bottom two rows).

was important because of how different these distributions are across zoning type. Overall, observed sample and population distributions match well across strata with the possible exception of those for the $DistToWater$ predictor (Fig. C.15). It is apparent that we sampled relatively more buildings closer to water than in the population as a whole. Again, this decision was made to balance out competing power considerations: Only 0.5% of buildings more than 1 km from water are above 6 storeys in height, and only 0.03% are above 15 storeys in height.

Appendix D. Model-building details

As mentioned in Sections 2.5 and 2.7, to find the best functional form for the predictors in our predictive GAMs required a standard recipe of exploration and model diagnostics. We describe this process in detail here.

We first looked for evidence of second-order predictor phenomena (i.e., interactions between predictors and quadratic curvature within predictors) by examining visual interactions of the variables with the binary response and by fitting simplified generalized linear models (GLMs) between the nest presence/absence response process and the appropriate pairs of predictors. Substantial improvements in explanatory power over first-order only models led us to include the corresponding second-order predictor in our candidate predictive model. Improvements in model fit were quantified by improved behaviour of the model residuals and substantial reduction in residual deviance, AIC, and BIC. Information criteria were all calculated from an ordinary likelihood fit of the models; only after arriving at a final model for analysis did we switch to quasilikelihood to correct standard errors. This analysis gave clear and strong evidence for the inclusion of $UrbDen \times DistToWater$, $UrbDen \times Hgt$, $DistToWater \times Area$, $DistToWater \times Hgt$, and $Area \times MedSlope$ as possible informative interactions, and $Area^2$, and Hgt^2 as possible informative marginal curvature terms, with

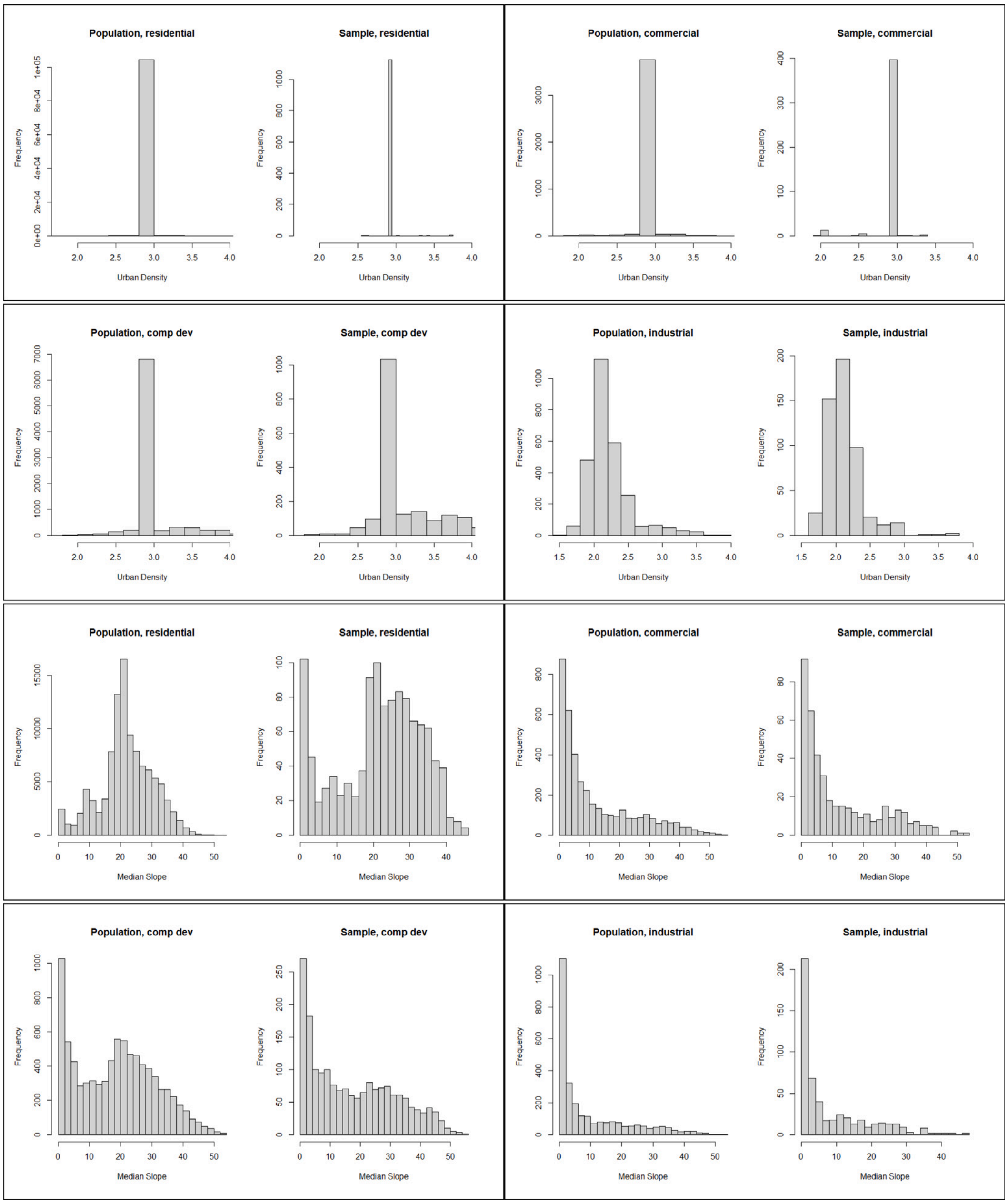

Fig. C.14. [b&w] Population vs. observed sample distributions of $UrbDen$ by $Zone$ (top two rows) and $MedSlope$ by $Zone$ (bottom two rows).

weak evidence for the inclusion of possible $RoofType \times MedSlope$, $RoofType{\times}Zone$, and $Hgt{\times}Zone$ interactions, and for quadratic curvature in $DistToWater$. Evidence for third-order phenomena proceeded in the same manner, but here we found strong evidence only for possible cubic curvature in the Hgt variable, and only weak evidence for a possible $UrbDen \times DistToWater \times Area$ three-way interaction.

A variety of GLMs that satisfied the above criteria were subsequently analysed for appropriate fit and optimality properties among candidate models. Predictably, expanding the model to a GAM framework that included the nonparametric thin plate regression term $s(Lat, Long)$ in order to account for spatial effects of latitude and longitude substantially improved model fit according to residual deviance, AIC, and BIC. Inclusion of this spatial effect also lead to mild reductions in spatial residual patterns across the fitted domain. The smoother was tuned to a basis of approximately 16 effective degrees of freedom, driven substantially by the number of unique sampled strata that comprised our data set. Our final model was selected due to its best behaved residuals and effectively minimal AIC and residual deviance. The final model also performed best among candidate models according to a leave-one-out cross validation comparison of prediction errors. Further, external validation using data from subsequent years and regions of the city different from those used to construct the model lended further credibility to its viability (see Section 3.4).

To construct the spatiotemporal GAM, we started with the optimal fixed effects structure that the above model-building process produced and added a simple first-order effect of study $Year$ and a Gaussian random effect for $Structure$ to account for possible temporal autocorrelation. This approach was taken rather than constructing a fixed

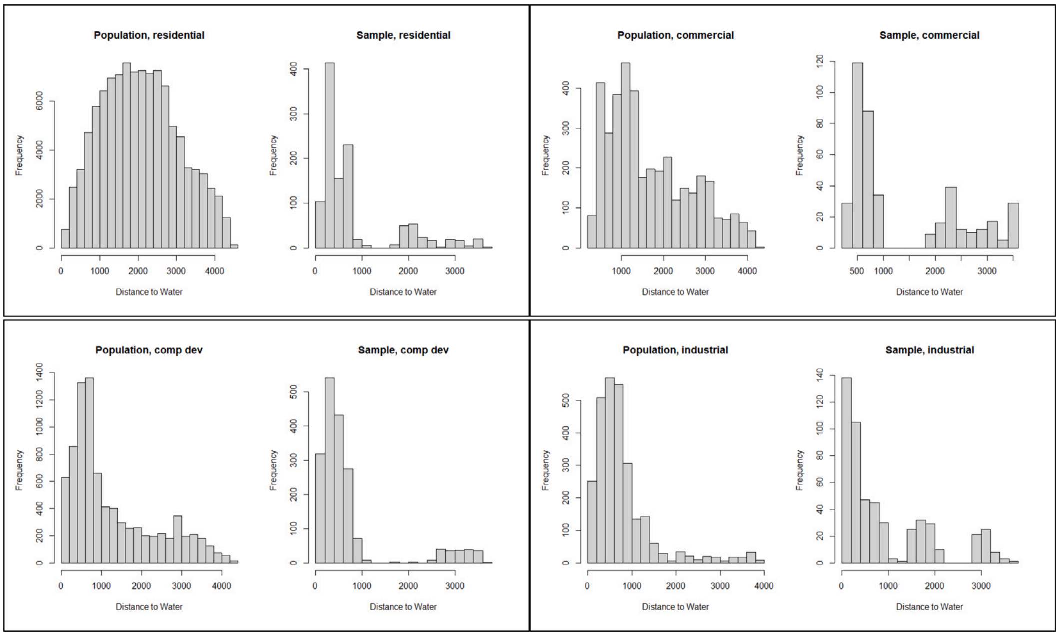

Fig. C.15. [b&w] Population vs. observed sample distributions of $DistToWater$ by $Zone$.

Table D.7
Estimated coefficients (on the logit scale) and standard errors for best fitting quasibinomial GAM, model (2), with a null deviance of 2982.7 (df = 5829) and residual deviance of 2246.1 (df = 5789). The estimated thin plate smoother over latitude and longitude has 17.72 effective degrees of freedom (p-value $\ll 0.001$). The random effect for temporal autocorrelation at structure site has 0.95 effective degrees of freedom (p-value = 0.009). Spatial variables are encoded on the same scale as before. *Year* equals either 2017 or 2023 for this model fit.

Predictor	Estimated coefficient	Standard error	Standardized estimated coefficient	p-value
(Intercept)	−111.6	46.42	−2.404	0.016
Year*	0.052	0.023	2.258	0.024
UrbDen	0.141	0.612	0.231	0.817
DistToWater*	−2.116	0.893	−2.370	0.018
Area***	0.064	0.013	4.735	<0.001
Area^{2} **	−0.0003	0.0001	−3.127	0.002
Hgt***	0.582	0.061	9.595	$\ll 0.001$
Hgt^{2} ***	−0.027	0.004	−6.938	$\ll 0.001$
Hgt^{3} ***	0.0003	0.0001	4.877	<0.001
RoofType(Flat)	0.630	0.367	1.716	0.086
Zone(Com vs. Res)*	4.418	2.043	2.162	0.031
Zone(CD vs. Res)**	4.566	1.591	2.869	0.004
Zone(Ind vs. Res)	3.720	1.985	1.875	0.061
UrbDen × Zone(Com vs. Res)	−1.364	0.841	−1.621	0.105
UrbDen × Zone(CD vs. Res)*	−1.354	0.609	−2.226	0.026
UrbDen × Zone(Ind vs. Res)	−1.163	0.832	−1.397	0.162
UrbDen × DistToWater***	1.029	0.299	3.439	< 0.001
MedSlope × RoofType(Complex)*	−0.028	0.012	−2.378	0.017
MedSlope × RoofType(Flat)**	−0.047	0.018	−2.703	0.007
Area × MedSlope**	0.003	0.001	2.872	0.004
Area × DistToWater	0.006	0.005	1.320	0.187
Area × Hgt**	−0.005	0.002	−3.048	0.002

effects structure from scratch because the data used to construct the first model were specifically sampled to optimize discriminatory power and predictive performance (see Section 2.3), and because the first model was externally validated to an acceptable degree with new data from subsequent years. Standard residual diagnostics indicated that the resulting spatiotemporal model was comparably valid to the original spatial GAM. We then considered adding further temporal fixed effects, interacting $Year$ with other spatial fixed effects. No such alternative model yielded noticeably different residual structure nor was model fit improved according to any criteria. Consequently, the spatiotemporal GAM differed from the spatial GAM only by inclusion of the first-order $Year$ effect and the random $Structure$ effect. The results of this modelling procedure are displayed in Table D.7.

The estimated coefficients of model (2) align quite well with those estimated from model (1); Figs. D.16 and D.17 facilitate this comparison. The thin plate spline was tuned to a basis of approximately 18 degrees of freedom, a slight increase from model (2) which was not surprising given that the 2023 data included 3 new sample polygons that were not part of the 2017 sampling frame (see Section 2.3). The random $Structure$ effect was significant, indicating temporal autocorrelation in the naive residuals.

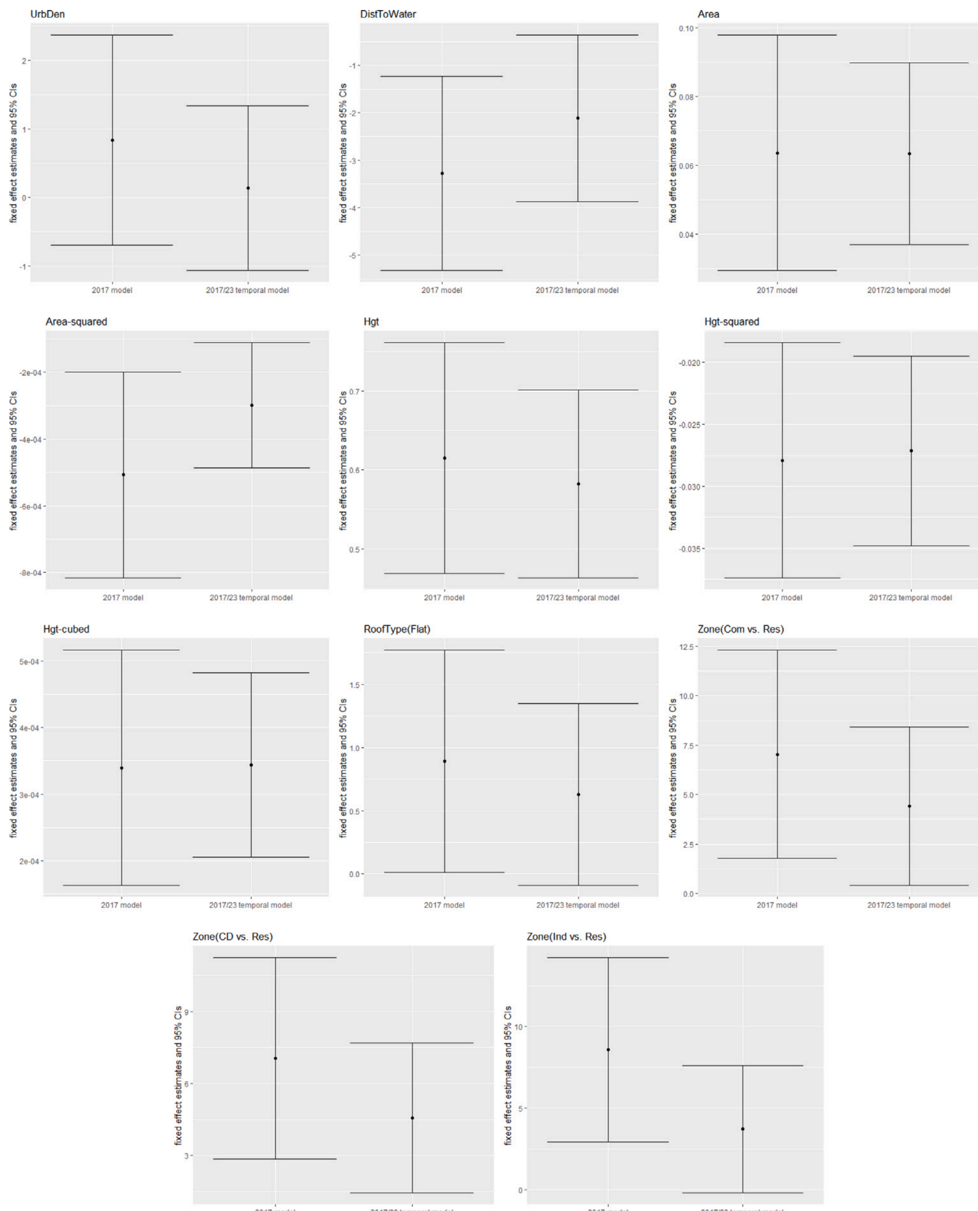

Fig. D.16. [b&w] Point estimates and 95% confidence intervals of marginal effects compared between the spatial model built using only the 2017 data, model (1), and the spatiotemporal model built using data from both 2017 and 2023, model (2).

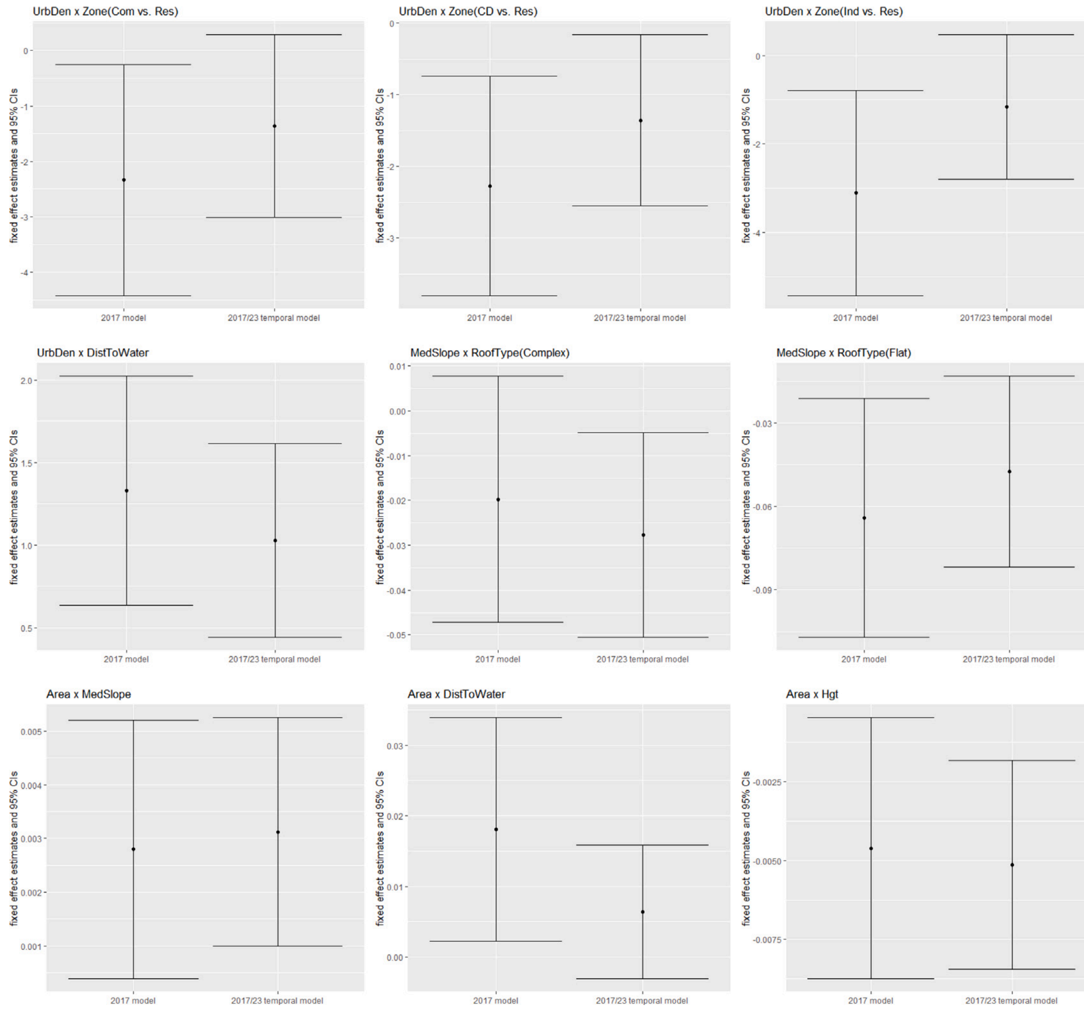

Fig. D.17. [b&w] Point estimates and 95% confidence intervals of interactions compared between the spatial model built using only the 2017 data, model (1), and the spatiotemporal model built using data from both 2017 and 2023, model (2).

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