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# Landscape associations and spatial redistribution of breeding heron and egret colonies under urban expansion in South Korea

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## Abstract

# Context.

Landscape composition shapes the distribution and abundance of breeding birds by determining the availability of nesting sites and foraging habitats. Colonial-breeding herons and egrets occupy diverse habitats and exhibit species-specific responses to landscape change including urbanization, providing opportunity to examine how landscape characteristics and urban expansion influence their colony distribution.

# Objectives.

We aimed to characterize changes in the spatial distribution and nest abundance of multi-species breeding colonies across South Korea and to identify the landscape characteristics associated with colony occurrence across multiple spatial scales. We further examined whether changes in colony distribution between survey periods were associated with urban expansion, with particular attention to directional shifts in breeding distributions among species.

# Methods.

We compiled colony locations, species composition, and nest abundance from nationwide surveys of six colonial-breeding heron and egret species across South Korea during the breeding seasons of 2011–2012 and 2018–2019. Then, we characterized surrounding landscape composition at multiple spatial scales and assessed changes in colony distribution, landscape associations, and urbanization between the two survey periods.

# Results.

Breeding colonies of Grey Heron and Great Egret occupied broader ranges than the other four smaller-sized species. Between the two survey periods, the numbers of colonies increased for Grey Heron and Great Egret but declined for the other four species, indicating contrasting population responses among species. Colony occurrence was positively associated with built-up areas, managed grasslands, and water-related land-cover types, whereas natural grasslands and forest cover were negatively associated with colony occurrence across spatial scales. The nest-weighted centroids of breeding distributions of the five out of six species shifted southward, while Grey Heron shifted northward. However, only the shift observed for Eastern Cattle Egret was significant. Changes in urbanization were associated with both greater centroid displacement and southward shifts in breeding distributions, suggesting that urban expansion may limit the persistence and spatial distribution of breeding colonies.

# Conclusions.

Our findings reveal species-specific changes in the spatial distribution of breeding Ardeidae and demonstrate that landscape composition and urban expansion are associated with the spatial dynamics of breeding colonies across South Korea. These results highlight the importance of incorporating landscape context and urbanization trajectories into the conservation planning of colonial-breeding herons and egrets.

## 1. Introduction

The spatial distribution and abundance of breeding bird populations is fundamentally shaped by landscape composition, which determines the availability and connectivity of habitats required for reproduction (Jones, 2001; Adler and Jedicke, 2022). Each species selects breeding sites within available habitats that maximize reproductive success and best satisfy its ecological requirements such as food, nest safety, and other niche-specific resources (Svärdson, 1949; Hildén, 1965). Accessible foraging patches with high proximity, connectivity, and habitat quality are critical because they minimize energy expenditure during reproduction and enhance breeding efficiency (Patenaude-Monette et al., 2014). In addition to selecting favorable habitats, breeding individuals may actively avoid habitat and landscape features that are associated with elevated predation risk, human disturbance, and other reproductive constraints (Fernández-Juricic, 2002; Thomson et al., 2006; van der Vliet et al., 2010).

Expansion of urban landscape is one of the most prominent phenomena of the anthropogenic world that involves direct landscape modification (Güneralp et al., 2020). As human activities increase, urbanization acts as a novel environmental filter that allows species with strong adaptation capability and tolerance to human, presenting both challenges and opportunities for many bird species (Chace and Walsh, 2006; Shanahan et al., 2014). Breeding birds are exposed to unique anthropogenic disturbances along the urban gradient including high human population density, frequent land conversion, and habitat loss and fragmentation (Grimm et al., 2008; Isaksson, 2018). Such disturbances can alter species distributions and community composition, often leading to the increased dominance of urban-adapted species. (Blair, 2004; Mckinney, 2006; Graciá et al., 2020). Urban adapters or synanthropic species are characterized by generalist traits such as large breeding ranges, omnivorous diet, and short flight initiation distances (Møller, 2009; Sol et al., 2020; Alba et al., 2025), and may benefit from supplementary resources, reduced predation from natural predators, stable microclimatic conditions, and milder winter of urban environment (Marzluff, 2001; Luniak, 2004; Cardilini et al., 2013). However, even urban adapters may still be negatively affected in densely urbanized environments where intensive human activities and habitat modification disrupt nesting and reproductive performances (Chamberlain et al., 2009; Strasser and Heath, 2013).

Colonial-breeding herons and egrets are model system for examining the ecological consequences of landscape change due to their abundance and widespread distribution. Their mixed-species breeding colonies integrate diverse habitat types for nesting and foraging (Kushlan and Hafner, 2000; Gibbs and Kinkel, 1997; Choi et al., 2007), while each species exhibit distinct ecological responses to surrounding environment and anthropogenic changes (Fujioka et al., 2010; Mashiko and Toquenaga, 2013; Kazantzidis et al., 2013; Ramo et al., 2013). Although many heron and egret species have successfully adapted to urban environments and frequently establish breeding colonies near human settlements (Chakraborty and Majumder, 2018; Zhang et al., 2018), these locations present both opportunities and constraints. Urban features such as building, road, impervious surface, suburban area, and human settlement are often related to the presence and new establishment of breeding colonies (Manikowska-Ślepowrońska et al., 2015; Carrasco et al., 2017). Breeding near human-modified urban environments may reduce natural predation pressure (Roshnath et al., 2019) and provide opportunities to exploit food from human-modified wetlands rice field, aquaculture, and artificial ponds (Fidorra et al., 2016). Conversely, several studies have reported that breeding colonies were more likely to occur in landscapes characterized by greater proximity to natural wetlands or lower levels of urban development (Carrasco et al., 2014; Frank et al., 2022). Continuous urban expansion may disturb nesting and foraging habitats and lower reproductive success (McKinney et al., 2010). The effects of urban habitats on breeding-colony occurrence remain inconsistent because species responses vary with regional environmental conditions and landscape contexts (Charutha et al., 2021). Taken together, these contrasting findings suggest that urbanization may produce complex changes in the distribution and nesting population of breeding colonies, highlighting the need to examine how landscape characteristics influence colony occurrence and long-term distributional patterns.

Previous studies have widely investigated habitat use by herons and egrets and the landscape characteristics related to breeding colony occurrence (Fasola et al., 1996; Tourenq et al., 2004; Kelly et al., 2008; Kirsch et al., 2008; Carrasco et al., 2014; Tian et al., 2025), yet further research is needed to evaluate how urbanization is associated with shifts in breeding colony distribution over time. First, long-term monitoring of breeding colonies as well as studies on urban habitat associations have each been conducted (Chakraborty and Majumder, 2018; Partridge et al., 2026), but relatively few studies have integrated these approaches to evaluate whether changes in colony distribution are associated with urban expansion or whether these responses differ among species with distinct ecological niches (Tuohetahong et al., 2024). Second, Colonial-breeding heron and egret species differ substantially in their abundance, ecological requirements, foraging strategies, and responses to anthropogenic environments (Choi et al., 2007; Kazantzidis et al., 2013), thus species-specific responses to urban expansion should be evaluated (Aouadi et al., 2021). Third, because landscape composition and the degree of urbanization vary substantially across geographically continuous regions, findings from local or regional studies cannot readily be generalized to nationwide distributional patterns. Together, these limitations highlight the need for nationwide assessments that evaluate changes in breeding colony distribution in relation to urban expansion, landscape characteristics, and species-specific ecological responses.

In this study, we investigated changes in distribution and nest abundance of herons and egrets in multi-species breeding colonies by integrating national-scale survey on breeding colony of herons and egrets. Specifically, we aimed to (1) characterize species-specific changes in the core distribution and abundance of breeding colonies between two survey periods; (2) identify the landscape characteristics associated with colony occurrence by estimating the effect of surrounding landscapes on the colonies compared to those of areas without them; and (3) evaluate shifts in spatial distribution patterns across South Korea and assess whether these patterns exhibit directional changes associated with urban expansion. We adapted multi-scale approach when measuring land-cover attributes to account for the spatial hierarchy of measurements as the spatial scales that most strongly affect breeding site selection may differ among habitat types (Wiens, 1989; Mayor et al., 2009; McGarigal et al., 2016).

## 2. Methods

# 2.1. Study species and breeding colony data

We compiled nationwide breeding colony data, including geographic coordinates, breeding species, and species-specific nest counts, for six heron and egret species that commonly breed in South Korea: Grey Heron (*Ardea cinerea*), Great Egret (*Ardea alba*), Intermediate Egret (*Ardea intermedia*), Little Egret (*Egretta garzetta*), Eastern Cattle Egret (*Ardea coromanda*), and Black-crowned Night Heron (*Nycticorax nycticorax*). Data were compliled for two survey periods, 2011–2012 and 2018–2019. For 2011–2012, we sued the information published by the National Institute of Environmental Research in Egrets and Herons in Korea (NIER, 2012). For 2018–2019, we used the colony records reported in this publication as a baseline and supplemented them with information obtained from research reports, published articles, expert consultations, and online sources. Based on this updated nationwide inventory, each colony site was visited at least twice to verify breeding activity and collect colony data. Field surveys during both periods were conducted from March to July. Geographic coordinates were recorded at the center of each colony using a handheld GPS, and species composition and species-specific nest counts were assessed through observations conducted within and around each colony.

## 2.2. Extraction of environmental variables

Fine-scale habitat composition surrounding colonies was quantified using the land-cover map from European Space Agency Climate Change Initiative (ESA CCI) Plant Functional Types (PFT) dataset (Harper et al., 2023; https://maps.elie.ucl.ac.be/CCI/viewer/, accessed 1 December 2025). The dataset represents land-cover fractions of 16 PFT classes at spatial resolution of 300m (Table 1). While extracting environmental variables, historical colonies surveyed in 2011–2012 were matched with the 2011 dataset, whereas colonies surveyed in 2018–2019 were matched with the 2018 dataset. All layers were reprojected to the Korea Transverse Mercator coordinate system (EPSG:5179). We extracted proportions of land-cover types within buffer radii of 500, 1,000, 3,000, 5,000, and 10,000 m around each colony to characterize the surrounding landscape context at multiple spatial scales (Carrasco et al., 2014; Lipsey et al., 2017; Tian et al., 2025). The exact values of the spatial scales were selected regarding the collective ecological features of the study species such as foraging distance and home range during breeding period (Wong et al., 1999; Manikowska-Ślepowrońska et al., 2025).

Table 1
Definitions of the ESA CCI Plant Functional Type (PFT) classes. Each PFT represents the fractional cover of a specific vegetation or surface functional category within a pixel, derived from the ESA Climate Change Initiative Land Cover product. The table summarizes the codes, long names, and concise descriptions for all PFT classes used in this study.

| Code | Long name | Description |
|---|---|---|
| **WATER** | Water | General water mask. Indicates the presence or proportion of all water surfaces, including both inland and oceanic water. |
| **WATER_INLAND** | Inland water | Proportion of inland water bodies such as lakes, rivers, and reservoirs within a pixel; excludes oceanic water. |
| **WATER_OCEAN** | Oceanic water | Proportion of marine or coastal ocean water within a pixel. |
| **LAND** | Land | Land–water mask used to distinguish terrestrial areas from aquatic surfaces; often used as a reference layer for PFT interpretation. |
| **BARE** | Bare | Proportion of non-vegetated bare surfaces such as rock, soil, gravel, sand, and deserts. |
| **BUILT** | Built | Proportion of artificial/urban surfaces, including buildings, roads, paved areas, and other human-made structures. |
| **GRASS_MAN** | Managed grasses | Proportion of managed herbaceous vegetation, including pasture, hayfields, and herbaceous croplands (e.g., cereals, rice, forage crops). |
| **GRASS_NAT** | Natural grasses | Proportion of natural herbaceous vegetation, including wild grasslands, natural meadows, and herbaceous wetland vegetation. |
| **SHRUBS_BD** | Broadleaved deciduous shrubs | Proportion of broadleaved deciduous shrubs, which shed leaves seasonally. |
| **SHRUBS_BE** | Broadleaved evergreen shrubs | Proportion of broadleaved evergreen shrubs, which retain leaves year-round. |
| **SHRUBS_ND** | Needleleaved deciduous shrubs | Proportion of needle-leaved deciduous shrubs, typically small larch-type shrubs that drop needles seasonally. |
| **SHRUBS_NE** | Needleleaved evergreen shrubs | Proportion of needle-leaved evergreen shrubs, low-stature coniferous shrubs that maintain needles year-round. |
| **TREES_BD** | Broadleaved deciduous trees | Proportion of broadleaved deciduous trees, typical of temperate deciduous forests (e.g., oaks, maples, birches). |
| **TREES_BE** | Broadleaved evergreen trees | Proportion of broadleaved evergreen trees, common in subtropical and warm-temperate evergreen forests (e.g., evergreen oaks, laurels). |
| **TREES_ND** | Needleleaved deciduous trees | Proportion of needle-leaved deciduous trees, such as larch (Larix spp.), which lose needles in winter. |
| **TREES_NE** | Needleleaved evergreen trees | Proportion of needle-leaved evergreen trees, including pines, firs, and spruces that retain needles throughout the year. |

## 2.3. Estimation of urbanization rate

Urbanization levels were estimated using the “BUILT” land-cover layer from PFT dataset, which provides continuous per-pixel values (0–1) that represent the proportion of impervious or artificial surfaces. We defined pixels with values > 0.5 as urban and calculated the proportion of urban pixels for each local-level administrative unit (si/gun/gu) (Schneider et al., 2012; Balk et al., 2018). Changes in urbanization level were defined as the percentage point difference of the proportions of urban pixels in each administrative unit between 2011 and 2018. The urbanization level of each administrative unit was assigned to the breeding colonies that spatially-intersect with the corresponding unit.

## 2.4. Statistical analyses

### 2.4.1. Weighted kernel density estimation

Spatial distribution patterns of breeding colonies were examined using weighted two-dimensional Gaussian kernel density estimation (KDE), with nest counts serving as weights. Spatial extent of the analyses was restricted to the mainland of South Korea as there was no breeding colonies found in Jeju Island at the time of both surveys. Bandwidths were estimated using a weighted adaptation of Scott’s rule (Terrell and Scott, 1992), and density surfaces were generated using a custom implementation that directly incorporated weights and bandwidth matrices. Density values were evaluated on a uniformly spaced grid covering the mainland, and values outside the mainland polygon were masked using GADM administrative boundaries (Database of Global Administrative Areas, version 4.1. Available online: https://gadm.org/,

accessed on 1 December 2025). Final density surfaces were visualized using the *viridis* continuous palette with administrative boundaries displayed as outlines.

## 2.4.2. Environmental drivers of colony site selection

To assess environmental factors associated with colony site selection, we fitted generalized linear models (GLMs) with a binomial error distribution and logit link function at each spatial scale. Proportional PFT composition was included as the predictor, and colony presence–absence within each buffer radius was used as the response variable. Because only colony presences were available, we generated pseudo-absence points by randomly sampling locations within the background area, following established approaches for presence-only data (Pearce and Boyce, 2006; Barbet-Massin et al., 2012). We used ten pseudo-absence points per observed presence to provide a relatively large pool of background locations for fitting the binomial GLMs. Odds ratios (OR) and 95% confidence intervals were derived, and only predictors with $p < 0.05$ and satisfactory diagnostic performance were considered significant (Guisan and Harrell, 2000). Significant effects were visualized across species and spatial scales using log-transformed point-range plots to compare effect sizes among land-cover variables.

## 2.4.3. Centroid estimation and permutation test

Nest-weighted centroids of the colony locations were calculated for each species and survey period (2011–2012 and 2018–2019) to quantify species-specific distributional shifts. To evaluate whether observed centroid shifts exceeded those expected under random relocation of nests, we performed permutation tests for each species (Lättman et al., 2009; Loehle, 2020). In each permutation, nest counts were randomly reassigned among colony coordinates within the same period while preserving the total number of colonies and the distribution of nest counts. Weighted centroids and corresponding shift distances were recalculated for 10,000 iterations. The resulting distribution of simulated shift distances were used as the null distribution of expected shift distances, and p-values were calculated as the proportion of permutations in which the simulated shifts exceeded the observed centroid shift.

## 2.4.4. Urbanization and directional changes in centroids

Geographic shift distances and directional changes in latitude and longitude were calculated for each species. Linear regression models were then used to assess whether changes in urbanization (%) were associated with centroid shift distance (km) or latitudinal change between the two survey periods.

## 2.4.5. Software

All analyses were conducted in R (version 4.5.1), using *sf* (Pebesma and Bivand, 2023) and *terra* (Hijmans et al., 2026) for spatial data processing, *geodata* (Hijmans, 2026a) for administrative-boundary integration, *geosphere* (Hijmans, 2026b) for distance calculations, and *ggplot2* (Wickham, 2016) for visualization (R core team, 2025).

# 3. Results

## 3.1. Distributional change of breeding colonies and weighted kernel density patterns

Colony distribution and nest counts across South Korea revealed that Grey Heron and Great Egret, both numerically dominant and large-bodied species, exhibited broadly distributed breeding sites in both survey periods, whereas smaller-bodied species were concentrated in the mid-western and southern regions of the country (Fig. 1). Between the two survey periods, the number of occupied colonies increased for Great Heron and Great Egret, while the number of colonies declined for all other species.

Incorporating nest numbers as weights in the kernel density estimation (KDE) provided a clearer depiction of core breeding areas and species-specific change of colony distributions (Fig. 2). The core breeding area with highest breeding densities were detected in either lowland and major estuaries along the west coast or extensive inland agricultural plains. Although Grey Heron and Great Egret both occupied wide geographic ranges, the core breeding area of Grey Heron have slightly shifted westward due to the increased colony density in the western plain, while the centralized distribution of Great Egrets around Sejong and Daejeon Metropolitan City in 2011–2012 dispersed throughout the country in later survey period. Species with smaller nest numbers displayed narrower distributional extents, developing distinct density centers near urbanized landscapes or intensively cultivated farmlands on the western plains. Among the latter species group, the core breeding area all shifted southwards, while distributional change of Eastern Cattle Egret was more conspicuous than other species.

## 3.2. Environmental correlates of colony occurrence across spatial scales

Logistic regression models fitted across multiple spatial scales (500 m to 10 km) demonstrated consistent associations between colony occurrence and surrounding land-cover variables (Fig. 3). Impervious and built-up surfaces (BUILT), managed grassland and agricultural fields (GRASS_MAN), and water-related land-cover types (WATER, WATER_INLAND) all increased the likelihood of colony presence. Built-up surfaces showed a constant positive effect across all spatial scales except at 10 km (OR = 1.014–1.016, $p < 0.01$). Interestingly, the positive association with built-up land disappeared at the 10-km scale. Managed grassland exhibited the strongest and most stable positive associations (OR = 1.005–1.017, mostly $p < 0.001$), while water-related variables contributed positively at finer scales (500 m; OR ≈ 1.008–1.014, $p < 0.05$). In contrast, natural grassland (GRASS_NAT) and forested land—both broadleaf (TREES_BD) and needleleaf (TREES_NE)—were consistently associated with reduced odds of colony occurrence across all spatial scales. Natural grassland showed significant negative association at finer scales (OR = 0.972–0.990, $p < 0.05$). Broadleaf forests demonstrated the strongest avoidance effect (OR = 0.949–0.989, all $p < 0.001$), with needleleaf forests also exerting a negative influence (OR = 0.966–0.991, $p < 0.05$). The direction and magnitude of these effects remained significantly stable from the 500 m to the 10 km spatial scale, highlighting robust habitat associations of colonial heronries.

## 3.3. Centroid shifts between periods and permutation-based evaluation

Comparison of weighted breeding centroids between 2011–2012 and 2018–2019 revealed that latitude shifts were more pronounced than longitude shifts (Table 2, Fig. 4). Five of the six species exhibited southward movement of breeding centroids, and Grey Heron was the only species that shifted northward. Observed centroid shift distances ranged from 14.14 to 62.41 km, with Grey Heron showing the smallest displacement and Eastern Cattle Egret the largest. Permutation tests revealed that only Eastern Cattle Egret exhibited significantly greater shift than that was expected under the null distribution ($p = 0.03$). Other species' observed shifts fell within the range of permutation-derived expectations, indicating no statistical evidence that they deviated from patterns expected under random colony redistribution.

Table 2
Spatiotemporal shifts in colony centroids, nest abundance, and breeding site numbers for six egret and heron species in Korea between 2011–2012 and 2018–2019. The table summarizes changes in central longitude and latitude, total number of nests, number of colony sites, and centroid shift metrics (distance, direction, and permutation test results) for Grey Heron, Great Egret, Intermediate Egret, Eastern Cattle Egret, Little Egret, and Black-crowned Night Heron. Shift distance and direction represent the movement of colony centroids between survey periods, and permutation tests evaluate whether observed shifts differ significantly from random expectations.

| Period | Grey Heron | | Great Egret | | Intermediate Egret | | Eastern Cattle Egret | | Little Egret | | Black-crowned Night Heron | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2011–2012 | 2018–2019 | 2011–2012 | 2018–2019 | 2011–2012 | 2018–2019 | 2011–2012 | 2018–2019 | 2011–2012 | 2018–2019 | 2011–2012 | 2018–2019 |
| Central longitude (°) | 127.77 | 127.72 | 127.77 | 127.79 | 127.11 | 127.06 | 127.23 | 127.41 | 127.44 | 127.52 | 127.15 | 127.33 |
| Central latitude (°) | 36.14 | 36.26 | 36.57 | 36.29 | 37.05 | 36.74 | 36.83 | 36.28 | 36.85 | 36.44 | 36.57 | 36.18 |
| No. of nests | 13,590 | 14,561 | 8,452 | 10,989 | 2,982 | 2,193 | 4,251 | 2,582 | 5,025 | 3,376 | 1,210 | 635 |
| No. of sites | 134 | 166 | 118 | 134 | 49 | 48 | 52 | 42 | 57 | 57 | 55 | 48 |
| Shift distance (km) | 14.14 | | 30.97 | | 34.73 | | 62.41 | | 45.75 | | 45.97 | |
| Shift direction | N | | S | | S | | S | | S | | S | |
| Permutation mean distance (km) | 17.75 ± 9.65 | | 19.63 ± 10.63 | | 44.11 ± 26.40 | | 29.86 ± 15.19 | | 31.19 ± 18.80 | | 39.17 ± 23.37 | |
| Permutation p value | 0.60 | | 0.13 | | 0.55 | | 0.03 | | 0.21 | | 0.34 | |

## 3.4. Relationships between centroid shifts and changes in urbanization

Linking centroid shifts to changes in urbanization between the two survey periods revealed significant associations in both direction and magnitude of movement. In the regression model assessing changes in latitude, urbanization change emerged as a significant negative predictor (Table 3; $\beta = -0.186$, $p < 0.05$), indicating that increases in urbanization were associated with southward movement of breeding centroids. Likewise, in the model using centroid shift distance (km) as the response variable, urbanization change showed a significant

positive effect ($\beta$ = 13.872, $p$ < 0.05), suggesting that greater increases in urbanization rate corresponded to a larger spatial displacements of breeding centers.

Table 3
Linear regression results examining the relationships between (a) latitude shift and response magnitude, and (b) centroid shift distance and response magnitude. The table reports model estimates, standard errors, t-values, and significance levels. In both models, the predictor variables (latitude shift and centroid shift distance) show significant positive or negative effects (p < 0.05), whereas intercept terms are not statistically significant.

| Model | Variables | Estimate | Std. Error | t value | Pr(>\|t\|) |
|---|---|---|---|---|---|
| (a) | (Intercept) | 0.301 | 0.193 | 1.556 | 0.195 |
| | Latitude shift | -0.186 | 0.057 | -3.243 | < 0.05 |
| (b) | (Intercept) | -5.851 | 13.040 | -0.449 | 0.677 |
| | Centroid shift distance (km) | 13.872 | 3.866 | 3.588 | < 0.05 |

## 4. Discussion

Our study has demonstrated nationwide density and distributional shifts of breeding colonies of 6 Ardeidae species between two survey periods and estimated the influence of surrounding land-cover types on the colony presence. Moreover, we found that the weighted centroids of the breeding colonies have shifted away from Seoul metropolitan area, as the pressure of urbanization is presumed to be the cause of the southward relocation of the core breeding areas of Eastern Cattle Egret on the domain of South Korea.

# 4.1. Distribution patterns of breeding colonies

The distribution of breeding areas exhibited relatively consistent patterns in all species and years, being concentrated in landscapes with high water availability and urbanized human settlements. Large-bodied and numerically dominant Grey Heron and Great Egret had more widespread breeding distribution throughout the peninsula, demonstrating their characteristics as habitat generalists (Recher, 1990; Tojo, 1996), whereas smaller-sized species such as Intermediate Egret, Little Egret, Eastern Cattle Egret, and Black-crowned Night Heron occupied more confined and limited areas predominantly on the western lowlands. The core breeding area of Eastern Cattle Egret in 2011–2012 as well as the breeding hotspots of Grey Heron, Intermediate Egret, Little Egret, and Black-crowned Night Heron in both survey periods were located on the southern and western peripheral of Seoul-Gyeonggi-Incheon metropolis. Estuaries and agricultural plains with abundant water bodies developed in these areas are suitable foraging habitat for herons and egrets (Fasola et al., 1996; Kushlan and Hanfer, 2000). These core areas support densely populated colonies with hundreds of nests, but also have been prone to high developmental pressure (Han et al., 2025), posing considerable threat to the existing colonies.

Changes in total nest counts and the number of occupied colonies differed markedly among species. Grey Heron and Great Egret were widely distributed and showed increases in both measures between the two survey periods. In contrast, the other four species had lower total nest counts, occupied more restricted geographic areas, and showed declines in both total nest counts and the number of occupied colonies, including the loss of several major colonies. The concentration of their nests and colonies within restricted areas may make these species particularly vulnerable to localized disturbance and the degradation of nesting or foraging habitats. Previous studies have shown that predation, climatic extremes, competition for nest sites, and changes in prey availability can affect colony persistence and reproductive performance in Ardeidae (Kim and Koo, 2009; Mashiko and Toquenaga, 2013; Galarza and Arizaga, 2014; Cardarelli, 2015; Uchida, 2017; Samraoui et al., 2025; Fasola et al., 2022). However, these mechanisms were not directly examined in our study and should therefore be regarded as possible explanations rather than demonstrated causes of the observed declines.

Similar contrasts between large and smaller heron and egret species have been reported in other regions. Expansions in breeding range and increases in abundance among large-bodied ardeids have been widely documented globally (Japan: Matsunaga et al., 2000; Fujioka et al., 2010; Europe and Africa: Ramo et al., 2013; Ławicki, 2014; Nagy et al., 2022; Warmer et al., 2025; North America: Zuckerberg et al., 2009; Shuford et al., 2020), but have been reported less frequently among smaller heron and egret species. Our findings are broadly consistent with patterns reported in neighboring Japan. Mashiko and Toquenaga (2013) found that breeding populations of Grey Heron and Intermediate Egret increased in Ibaraki, Japan, between 2002 and 2011, whereas those of Little Egret and Eastern Cattle Egret declined and those of Great Egret and Black-crowned Night Heron remained stable. A nationwide study in Japan similarly showed that the breeding ranges of Grey Heron and Great Egret more than doubled between 1978 and 1988, whereas those of other heron and egret species remained relatively stable (Fujioka et al., 2010). The expansion of widespread ardeid species may be facilitated by generalist resource use

and a high tolerance of urban environments (Davey et al., 2012; Le Louarn et al., 2018; Callaghan et al., 2019). However, responses among smaller species appear to vary geographically. For example, Naskar and Maheswaran (2025) described Little Egret as an urban-tolerant generalist in India, whereas Sadam et al. (2021) classified the same species as an urban avoider in Pakistan.

## 4.2. Environmental predictors of colony presence across spatial scales

Our findings on the multi-scale relationship between the breeding colony presence and surrounding land-cover support previous knowledge of colonial breeding herons and egrets' habitat use (Lee et al., 2026). The positive or negative impact of the environmental factors gradually varied throughout the spatial scales. Proportions of built-up surfaces had consistently demonstrated positive effect on both local and regional extents. Colonial-breeding Ardeidae species had historically developed human tolerance and participated in foraging and breeding activities in close proximity of residential area (Hwang et al., 2020). In modern urbanized landscape, low-intensity urban environment is positively associated with colony presence and breeding success of herons and egrets (Kelly et al., 2008). Their high urban-tolerance is presumed to be a predator avoidance strategy where safe nesting places such as islands or water-logged forests are insufficient (Parkes et al., 2012) as well as low density of natural predators (Roshnath et al., 2019). However, direct anthropogenic disturbance near colony site such as logging, land conversion, and human intrusion is detrimental to the breeding activities (Carney and Sydeman, 1999; Lee et al. 2014). Rather than the proximity to artificial structures itself, frequent trespassing of humans may induce stress and suspend incubation or food-provisioning activities, resulting in high breeding failure (Jakubas and Manikowska-Slepowronska, 2013). In conclusion, the presence of urbanized habitats around breeding colonies may be advantageous, but these positive effects may be diminished by the intensity and type of urbanization, as well as by direct human disturbance.

Proportions of managed grassland, which are primarily consist of agricultural lands, presented stronger effect on the local scales than the regional scales, implying its benefit on breeding colony presence at closer proximity. In South Korea, 44% of the agricultural land type is rice field (MCEE, 2025), which is an important foraging ground for herons and egrets, especially during their breeding season (Choi et al., 2004). In May-June, irrigated rice paddy provides shallow wetland environment filled with aquatic prey, along with the adjacent microhabitats such as grass-covered rice bank preferred by Eastern Cattle Egret and nearby reservoirs preferred by Grey Heron and Black-crowned Night Heron (Choi et al., 2007; Choi et al., 2016). Overall, water-logged rice field around breeding colony serves as an artificial wetland (Fasola et al., 1996), and its size and state of irrigation have significant positive influence on breeding success and population size of herons (Ramo et al. 2013; Forti et al., 2021).

In addition to flooded rice fields, access to nearby open-water habitats may facilitate the foraging activities of breeding herons and egrets (Kelly et al., 2008). However, open-water cover was positively associated with colony occurrence only within the 500 m buffer and was not significant at broader spatial scales. This scale-dependent relationship suggests that access to water bodies in the immediate vicinity of a colony may be more important than the total extent of open water across the broader landscape. Moreover, the PFT water-cover variables quantified the proportional extent of open water but did not capture ecologically important characteristics such as water depth, hydroperiod, shoreline configuration, vegetation structure, or prey availability. Herons and egrets generally forage in shallow water, where preys are more accessible (O' Connell and Nyman, 2010; Lantz et al., 2011), and species-specific foraging depths and microhabitat use are constrained in part by tarsus length and body size (Tojo, 1996; Choi et al., 2007). Rainfall and artificial water management can further alter hydrological conditions and prey availability in foraging habitats during the breeding season (Pang et al., 2020; Essian et al., 2022). Thus, open-water extent alone, particularly at broader spatial scales, may be insufficient to explain colony occurrence. Because our analysis did not distinguish among water-body types or account for their hydrological regimes, further studies incorporating water depth, hydroperiod, shoreline characteristics, and prey availability are needed to clarify their effects on breeding-colony occurrence.

## 4.3. Colony centroid shift and urbanization

Colonial breeding Ardeidae species in temperate zones of northern hemisphere have manifested northern expansions of the breeding range during recent decades, often accompanied by population growth and increase in the number of colonies (Matsunaga et al., 2000; Zuckerberg et al., 2009; Ławicki, Ł. 2014; Shuford et al. 2020; Kalyakin et al., 2022; Fasola et al. 2023). It is evident that rising temperature caused by climate change is one of the most significant factors influencing the worldwide trend of range expansion (Nagy et al., 2022). In contrast, our result on the nest-weighted centroid shifts within South Korea did not reflect global trend of northward shift, and the core breeding area of the Eastern Cattle Egret instead shifted southward. However, this pattern does not necessarily contradict broader-scale northward expansion. The recent discovery of the northernmost breeding colony of the Eastern Cattle Egret in North Korea suggests that the northern boundary of its breeding range may be expanding at the scale of Korean Peninsula, (Yun et al., 2025), even though the breeding abundance within South Korea shifted southward. These apparently contrasting patterns could occur simultaneously if a small number of colonies became established around the northern range margin while large colonies are lost or decline declined elsewhere, or if nest abundance increased farther south. Within South Korea, the observed association between increase in urbanization and southward centroid displacement further suggests that regional land-use change may have contributed to the redistribution of breeding abundance, although

this association does not necessarily demonstrate direct causation. Nevertheless, a single breeding record is not enough to determine whether the number or size of colonies is increasing in North Korea. Structured, long-term surveys across Korean Peninsula are therefore needed to determine whether this record represents an isolated colonization event or part of a broader-scale northward expansion.

## 4.4. Management implications

Conservation of breeding ardeids in South Korea requires a multi-scale management approach to mitigate threats associated with ongoing urban expansion. At the colony scale, proximity to urbanized habitats should not necessarily be regarded as detrimental because built-up cover was positively associated with colony occurrence in our analyses. Management should instead distinguish between the potential benefits of low–intensity urban environments and the adverse effects of direct human disturbance. For colonies located near residential or developing areas, human access, construction, logging, and other disruptive activities should be restricted during the breeding season. Site-specific buffer zones between colonies and residential or construction areas may also reduce disturbance and alleviate human–wildlife conflicts, which have increased in recent years (Hwang, 2025, July 16).

At local to regional scales, conservation should extend beyond nesting sites to nearby foraging habitats. In particular, the conversion of rice fields and shallow-water habitats surrounding breeding colonies should be minimized, and suitable irrigation and water conditions should be maintained during the breeding season where practicable. At the landscape scale, western lowland core breeding areas and the connectivity between nesting and foraging habitats should be prioritized. Conservation attention should be directed particularly toward the four species that showed restricted distributions and declines in both nest counts and occupied colonies. Finally, repeated and standardized monitoring of colony occupancy, species-specific nest counts, and surrounding land-use change is needed to evaluate management effectiveness and detect the establishment, decline, or loss of colonies over time.

### Declarations

## Author Contribution

SeonYong Lee: Writing – original draft, Formal analysis. Han-I Choi: Writing – original draft. Jae-Woong Hwang: Data curation. Ji-Yeon Lee: Data curation. Dong-Won Kim: Data curation. Hyung-Kyu Nam: Writing – review & editing, Formal analysis. Yu-Seong Choi: Writing – review & editing.

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## Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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## Figures

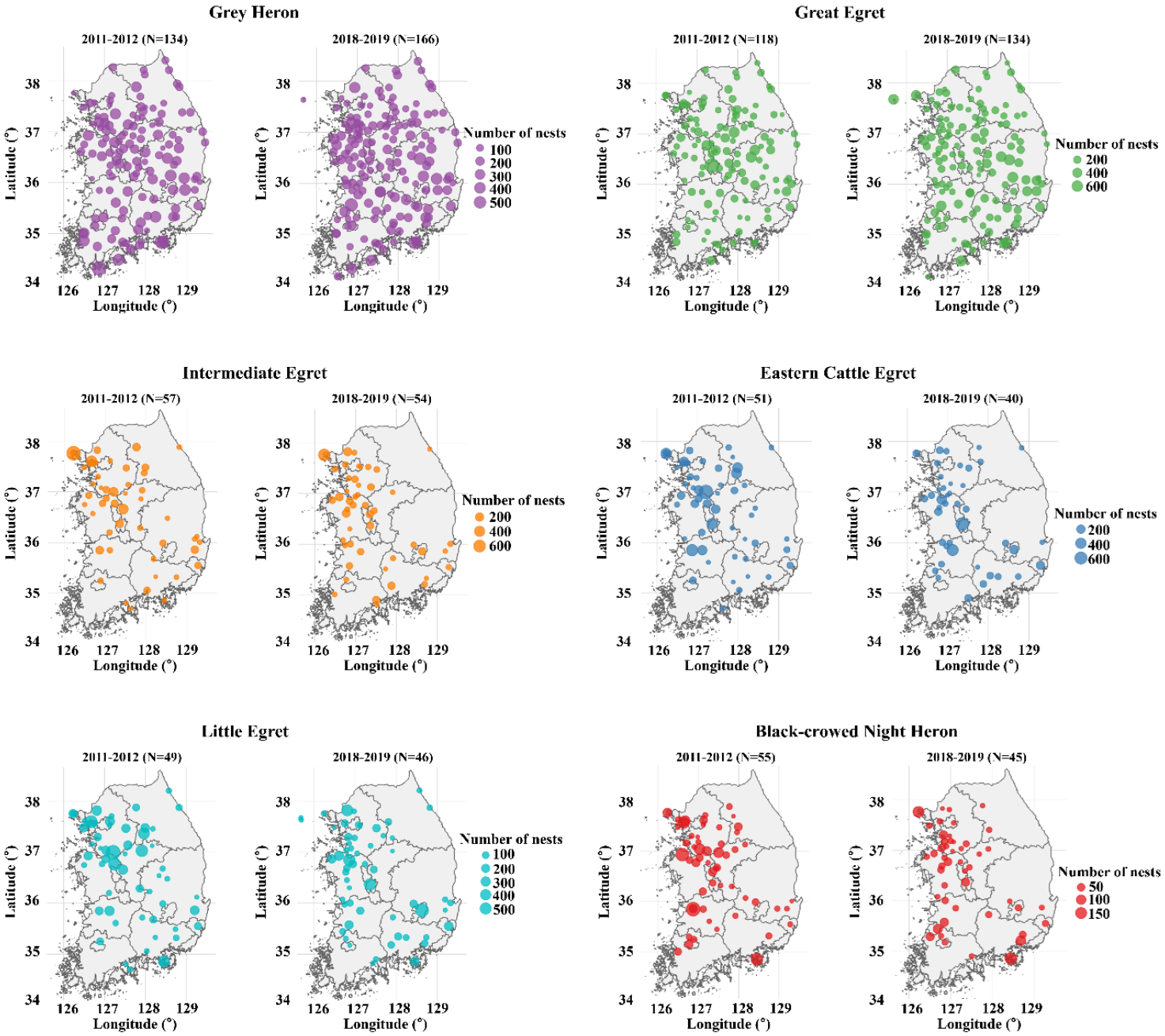



**Figure 1**

Spatial distribution of heron and egret breeding colonies across South Korea. Each panel shows breeding colony locations of each species (Grey Heron, Great Egret, Intermediate Egret, Eastern Cattle Egret, Little Egret, and Black-crowned Night Heron) at two survey periods (2011–2012 and 2018–2019) with point sizes proportional to the number of nests of the corresponding species.

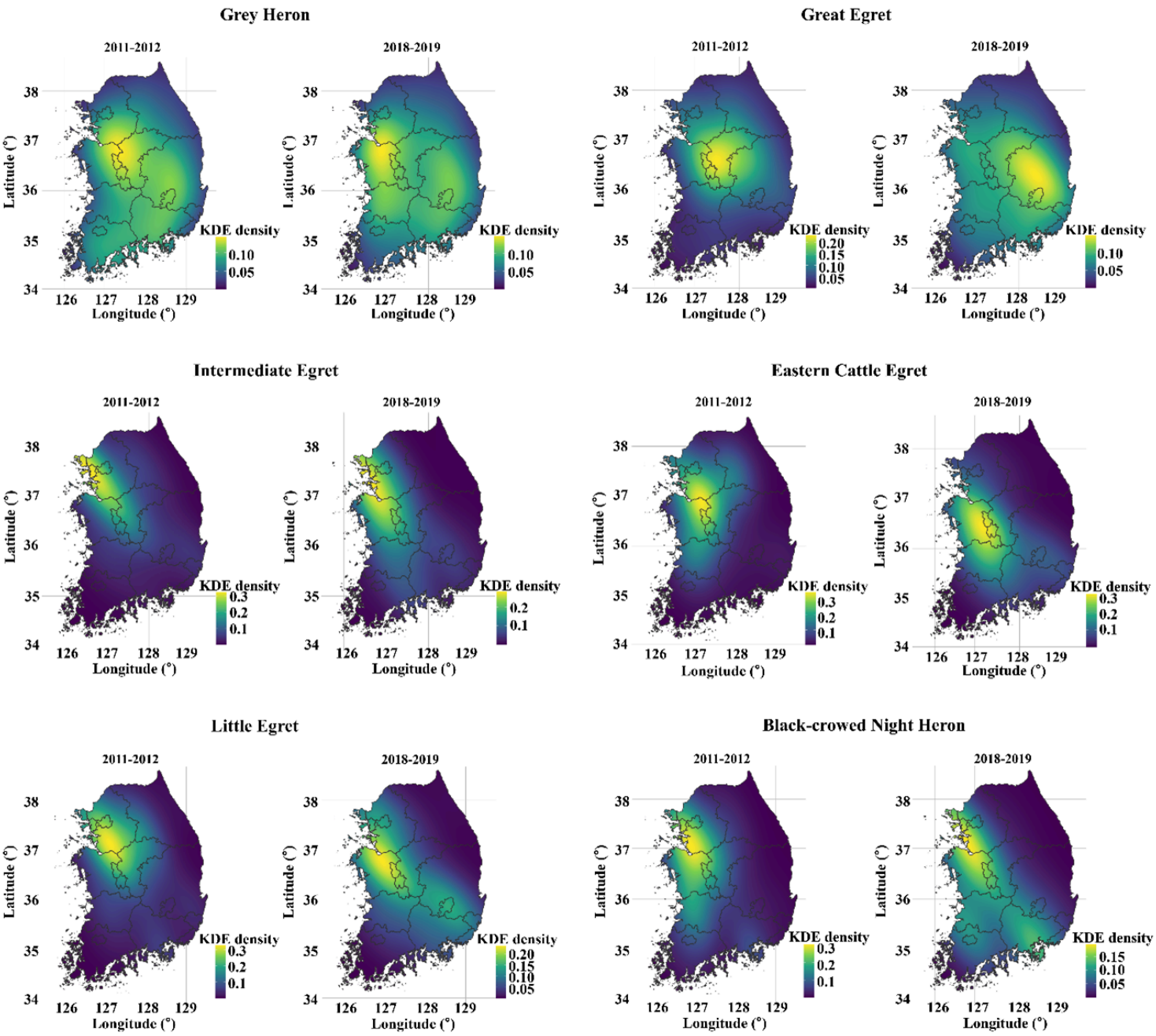



**Figure 2**

Weighted-Kernel density estimates of breeding colony distributions of each heron and egret species (Grey Heron, Great Egret, Intermediate Egret, Eastern Cattle Egret, Little Egret, and Black-crowned Night Heron) at two survey periods (2011–2012 and 2018–2019) across South Korea.

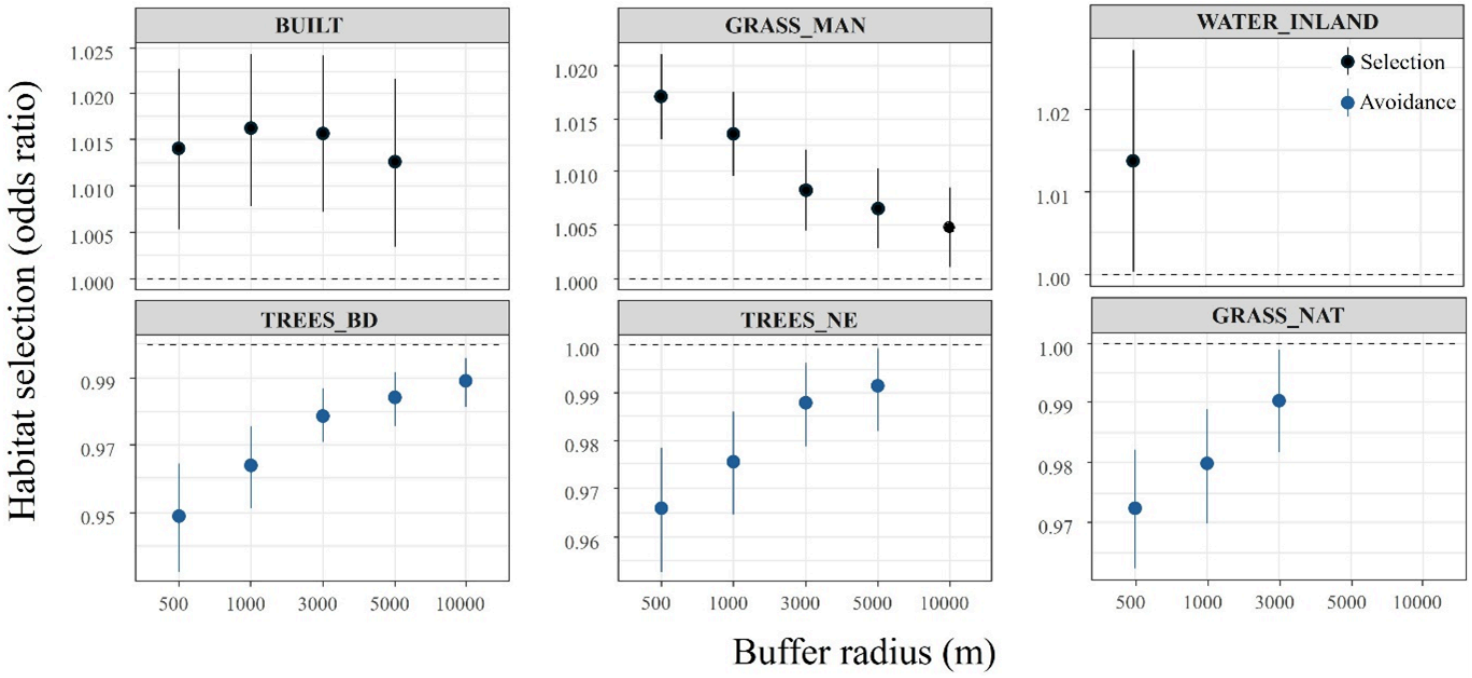



**Figure 3**

The effect size (odds ratio) of land-cover variables associated with colony site selection of herons and egrets at multiple spatial scales of 500, 1,000, 3,000, 5,000, and 10,000 m radii around each colony. Odds ratio (OR) derived from generalized linear models represents colony presence associated with habitat use (OR > 1) or avoidance (OR < 1), and only the spatial scales that showed statistical significance ($p$ < 0.05) for each land-cover variable were retained for final visualization.

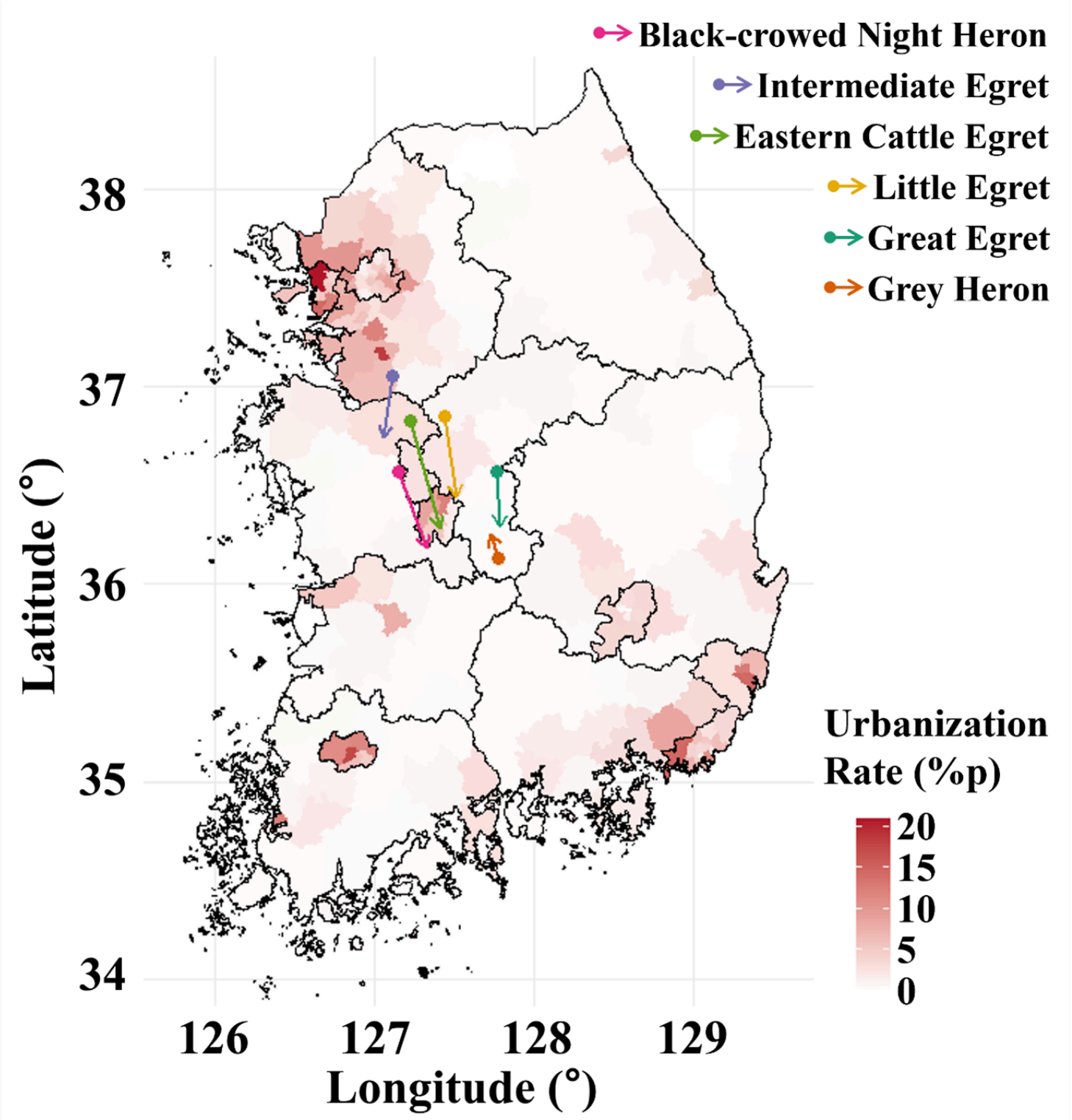



**Figure 4**

Shifts in the breeding-range centroids of heron and egret species between 2011–2012 and 2018–2019 in relation to district-level urbanization change. Arrows indicate the direction and magnitude of centroid shifts for each species, with 2011–2012 centroids shown as points and 2018–2019 centroids represented by arrowheads. Background shading