Scale Dependence of Bird Distributions in London

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Jacob Douglas Dein

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ABSTRACT

Understanding how spatial scale influences bird diversity and species-environment relationships is fundamental to effective conservation in increasingly urbanized landscapes, yet multiscale approaches remain underutilized in practice. Urban ecological studies often search for a single "scale of effect"—the spatial scale at which environmental factors best explain species occurrence. However, both theory and empirical evidence suggest that species respond to factors at multiple scales simultaneously, where single-scale perspectives may limit our understanding. To address this challenge, we examined bird diversity and occurrence over a range of scales across Greater London's urban-rural gradient through three complementary studies. Using crowdsourced (eBird) observations that included 279 species, we first applied scale variance analysis to identify how diversity variance changes across scales from 500m to 32km. We then modeled 65 species from the British Breeding Bird Survey using joint species distribution models with factors quantified across 5 scales (1,000m-16km) to assess how species-environment relationships change with scale (Part 2). Finally, we assessed factors across 10 scales (125m-64km) to determine which factors at which scales best explain occurrence for each species using a systematic selection model (Bayesian latent indicator scale selection). Scale variance analysis (Part 1) revealed that approximately two-thirds of bird diversity variance occurred at scales below 4,000m, with variance shifting from London's urban core to the rural periphery as scale increased. Joint species distribution modeling (Part 2) demonstrated that factors were highly scale-dependent, with at least one factor reversing direction across scales for 40% of the modeled species. Systematic factor selection (Part 3) revealed that environmental factors at local scales (125-500m) best explained occurrence for habitat specialists, while synanthropic species showed meaningful responses across all spatial scales, suggesting broader niche breadths. Collectively, the results illustrate that urban bird communities are structured hierarchically across scales, challenging the common practice of seeking a single best explanatory scale while supporting theories of hierarchical habitat selection. These findings provide both methodological advances for multiscale ecological analysis and practical guidance for designing urban conservation policies that better coordinate habitat management from individual properties to regional initiatives.

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INTRODUCTION

Human development is linked to changes in biodiversity through numerous pressures, with the changes highly dependent on spatial scale (Grimm et al. 2008; Keck et al. 2025). Connecting disparities between apparent increases and decreases across scales requires multiscale understanding of species interactions with their environment across diverse landscapes (Chase et al. 2018). Similarly, translating ecologic knowledge into effective management likewise demands coordination across efforts at different scales (Guisan et al. 2013; Hobbs 2003). Management is urgently needed in the face of recently documented global loss of many taxonomic groups, such as insects and birds (e.g., Burns et al. 2021; Gregory et al. 2023; Hallmann et al. 2017; Rosenberg et al. 2019). These challenges are particularly pressing in urban environments, where human and ecological needs intersect in complex ways.

Urbanized landscapes are diverse environments, affecting species differently by both hindering and enhancing biodiversity (McKinney 2008). However, efforts to improve cities for human quality of life and biodiversity do not need to be mutually exclusive goals (Oke et al. 2021). Intentional development practices and conservation initiatives can benefit public health while also supporting biodiversity and ecosystem services (Fuller et al. 2007; Miguez et al. 2025). Urban environments can actually even serve as important refuges for certain species under targeted management actions (Ives et al. 2016). For birds, overall species abundance may increase in urban areas due to a few well-adapted species thriving, while others cohabitate with humans only if specific resources are available (Evans et al. 2009; Michael et al. 2024; Narango & Proppe 2022). This variation underscores the importance of understanding urban biodiversity patterns in greater detail to inform conservation efforts.

Birds are a well-studied taxonomic group, globally widespread, easily identifiable, and often used as biodiversity indictors (Federico et al. 2021; Fraixedas et al. 2020). Despite extensive research on birds, many questions remain about effective management strategies, partly because findings often depend on specific contexts and may lack transferability (Isaksson 2018; Narango & Proppe 2022). Varying scales of observation and analysis—or vague definitions thereof—pose a significant challenge for synthesizing knowledge and integrating it into conservation and management initiatives at multiple levels, from individual backyards, to neighborhoods, to cities and regions (Hostetler 2001; Jackson & Fahrig 2015). Resolving these issues requires approaches that explicitly incorporate multiple spatial scales.

Multiscale and systematic modeling of species diversity and occurrence can help address this challenge (Stuber & Gruber 2020). Multiscale approaches better reflect our hierarchical understanding of ecosystems and how interactions at different scales shape observed patterns, which vary based on the scale(s) of observation (Levin 1992; Wiens 1989). However, although species observation data and modeling tools have expanded rapidly, relatively few studies (McGarigal et al. 2016) have fully implemented concepts like hierarchy theory to better manage ecosystem complexity—a major foundation of landscape ecology (O'Neill 1986; Urban et al. 1987). This gap highlights the need for research that applies multiscale methods to real-word landscapes.

This research addresses these gaps through three complementary multiscale analyses of bird communities across London's urban-rural gradient. We first identify the spatial scales at which bird diversity patterns exhibit the greatest variation. We then examine how environmental relationships change across scales using joint species distribution models. Finally, we implement systematic multiscale factor selection to determine which environmental factors at which scales best explain species occurrence. Together, these analyses advance both methodological tools for multiscale ecological research and offer practical insights for scale-aware urban conservation strategies that can coordinate habitat management from individual properties to landscape-scale initiatives.

Study area: London

We assessed bird diversity and occurrence across an area encompassing the full urban-rural gradient from the dense city center to surrounding rural landscapes. While we reference the Greater London administrative boundary to aid interpretation of our spatial results, this boundary has no ecological definition. However, the boundary aligns with the transition from London’s suburbs to rural areas interspersed with smaller towns and villages.

London provides an appropriate study area for examining scale-dependent relationships between birds and urbanized environments for three reasons. First, the region offers suitable physical characteristics. The area encompasses a complete urbanization spectrum, from dense urban core to large natural areas, including significant water features such as the River Thames running east-west through the city center. The relatively low topographic relief (elevations ranging 66-270m above sea level with mild hills, ridges, and plains) minimizes elevation effects,

which can significantly influence bird distributions but were not the focus of our research questions.

Second, two complementary bird observation datasets cover the study area, allowing us to leverage the strengths of each for different analytical approaches. The eBird dataset provides extensive spatial and temporal coverage through crowdsourced observations from bird enthusiasts and researchers. While eBird data are opportunistic and exhibit biases toward human activity patterns, the platform's popularity generates rich datasets that can be analyzed effectively when these biases are properly addressed. Species observations are submitted as checklists where unchecked species are recorded as not detected, providing semi-structured presence-absence data (Sullivan et al. 2014).

The British Breeding Bird Survey (B-BBS) offers a complementary structured dataset through systematic sampling by trained volunteers at stratified sites. Unlike the North American Breeding Bird Survey (NA-BBS), which uses 24.5-mile road transects across large geographic extents (Ziolkowski et al. 2024), the B-BBS randomly selects 1km grid squares throughout the United Kingdom. Surveyors traverse each square using two transects, often finding pathways to adequately sample the landscape without depending on major roads, resulting in observations well-suited for modeling species relationships in diverse urban environments (Massimino et al. 2025).

Third, London's role as a major academic center has generated substantial previous biodiversity research that provides context for our results. Although ecology would benefit from more studies in other regions and on other taxa (Litteral & Shochat 2017), the concentration of research in Europe and North America offers opportunities for comparison. Our work builds on prior research, including the study by Evans et al. (2009), which examined habitat influences on bird communities in urbanized environments across Great Britain using BBS data. Additional studies, such as those by Rosenfeld (2013) on habitat configuration effects in Birmingham, U.K., and Plummer et al. (2020) on relationships between urban environmental factors and species abundance across Great Britain, further inform the context around our research.

Theoretical concepts

Understanding how bird communities respond to environmental gradients across urban landscapes requires a theoretical framework that can accommodate the complex, multiscale nature of species-environment relationships. This work integrates species observations with

environmental data to test hypotheses about the ecological processes that shape urban bird distributions. Rather than assuming species respond to their environment at a single scale, our approaches test environmental relationships across a wide range of scales. Additionally, our studies are designed to capture both species-specific differences and broader trends between guilds. To accomplish this, our methods draw on three complementary theoretical foundations: the species niche from ecology, scale dependence and hierarchy theory developed from landscape ecology, and spatial dependence from geography. Together, these concepts enable us to systematically explore how species distributions vary across urban landscapes and spatial scales, moving beyond single-scale analyses toward a more comprehensive understanding of multiscale ecological processes in heterogeneous urban environments.

Species niche

The modern ecological niche concept, established through G. Evelyn Hutchinson's work in the 1950s, provides the mathematical foundation for understanding how species respond to environmental variation (Hutchinson 1957). Hutchinson developed an n-dimensional hypervolume framework that distinguishes between the fundamental niche—all environmental conditions where a species can survive—and the realized niche—the actual and more limited conditions where the species is found due to competition and other biological interactions. This framework allowed researchers to quantify how environmental conditions shape species occurrence patterns (Chase & Leibold 2003). This framework also laid the groundwork for modern approaches to species distribution modeling, which explicitly link environmental tolerance limits to the spatial arrangement of suitable conditions across landscapes, establishing the theoretical foundation for contemporary species distribution modeling (Elith & Leathwick 2009).

Building upon Hutchinson's framework, landscape ecologists have recognized that niche relationships often operate through environmental filtering. Such filtering determines which species can establish and persist in specific locations (Keddy 1992; Kraft et al. 2015). Environmental filtering selects for species with appropriate trait combinations from the regional species pool, predicting that species occurrences will be non-randomly associated with certain environmental conditions based on their niche requirements (Bazzaz 1991). However, contemporary research reveals substantial variation in how rigid or flexible species' niches can be. Some species show niche conservatism—maintaining similar environmental associations

across regions—while others exhibit plasticity, shifting their environmental associations depending on local conditions and biotic interactions (Wiens & Graham 2005). This variation in niche flexibility has important implications for species distribution modeling, as high plasticity can challenge assumptions that niche relationships remain constant across geographic regions (Pearman et al. 2008).

Modern applications of niche theory increasingly emphasize scale-dependent processes in shaping species-environment relationships. Environmental variables that strongly predict distributions at broad scales may become less relevant at finer scales, where local habitat features and biotic interactions play a more dominate role (Chase 2014). This scale dependence necessitates careful consideration of spatial grain and extent when developing species distribution models. Niche relationships identified at one scale may not reliably transfer to other scales, complicating ecological predictions and conservation planning. As a result, incorporating multiple spatial scales into niche-based modeling remains a central challenge and an active area of research, with hierarchical and multiscale modeling approaches offering promising avenues for progress (Mertes et al. 2020). Such approaches are particularly valuable for understanding species responses in heterogeneous urban environments, where scale-dependent habitat selection operates across multiple spatial hierarchies, creating complex patterns that demand multiscale analysis.

Scale dependence

Understanding how perspectives on scale have developed helps informs the context for this research. Many foundational concepts about scale, now widely recognized and applied in ecology and physical geography, arose from the field of landscape ecology. Carl Troll, a German geographer, first introduced the term Landschaftsökologie in 1939 while analyzing aerial imagery. He further refined the term in the 1950s and beyond, early recognizing scale and heterogeneity as central concepts. Landscape ecology then began to take shape in North America during the 1970s, where researchers discovered and adapted concepts from the European work in the early 1980s, culminating in a thriving international community by the late 1980s (Forman 2015). These developments laid the groundwork for today's multiscale approaches in ecological research.

Studies examining ecological patterns at different scales revealed that correlations and observed phenomena often shift—or even disappear—depending on the scale of observation

(Meentemeyer 1989). For example, predators and prey may appear to spatially overlap at one scale, yet actively avoid each other when viewed at a finer resolutions (Hobbs 2003). Therefore, the scale chosen for observation must align with the ecological process being investigated. Yet researchers also recognized that ecological patterns rarely stem from single-scale processes alone. Instead, many phenomena arise from multiple processes operating simultaneously at different scales, often interacting in complex ways. Scale serves as a lens imposed by human observers—a necessary but partial view into a complex system (Levin 1992).

Hierarchy theory emerged as a key framework for tackling these challenges, conceptualizing scales as nested elements within ecosystems (O'Neill 1986). This framework emphasizes that any ecological process should account for constraints imposed by higher scales, as well as emergent behaviors arising from finer-scale processes (Urban et al. 1987). In response to this complexity, researchers developed various multiscale tools—including fractal analysis, hierarchical models, and wavelet analysis—to disentangle patterns across scales (Bradshaw & Spies 1992; Lookingbill et al. 2011; Mandelbrot 1983). These tools have become increasingly vital for studying large-scale issues such as climate change and biodiversity loss, where understanding processes across multiple scales is essential for effective species conservation and ecosystem management.

Spatial dependence

Spatial dependence plays a major role in this work, as it simultaneously presents modeling challenges while also carrying valuable information that can be leveraged. Spatial clustering of similar properties represents a fundamental organizing principle in geographical analysis. Tobler (1970) described this phenomenon while investigating population growth in Detroit, stating: "everything is related to everything else, but near things are more related than distant things" as the first law of geography. This principle indicates that geographically proximate objects or phenomena are more likely to be similar compared to those that are farther apart (Miller 2004).

Spatial dependence manifests across scales from local microenvironments to global patterns, challenging the independence assumptions underlying traditional statistical approaches and creating methodological obstacles for researchers studying species distributions (Miller 2004). Ecological data collected across landscapes consistently violate the assumption of independent observations that classical experimental designs require. When observations are

spatially autocorrelated, they contribute little independent information while artificially increasing sample sizes and degrees of freedom. This often causes confidence intervals around parameter estimates to be artificially narrow, underestimating true uncertainty and leading to overconfident conclusions or spurious statistical significance (Dormann et al. 2007).

However, the same spatial structure that complicates statistical inference contains valuable ecological information about unmeasured processes and environmental factors (Warren et al. 2014). By including spatial effects in species distribution models (SDMs), researchers can accommodate spatial structure unaccounted for by measured covariates. Residual spatial autocorrelation—the spatial pattern remaining after accounting for measured environmental variables—reflects the influence of unmeasured or poorly characterized factors that contribute to species distributions. Analyzing the spatial structure of model residuals allows researchers to identify the scales at which unmodeled factors operate and generate hypotheses about driving processes and their importance (de Knegt et al. 2010).

We apply spatial dependence concepts across all three parts. In Part 1, we argue that areas of high variance revealed within each scale may be more useful than aggregate variance attributed to each scale, as the latter can be sensitive to changes in extent. In Part 2, we leverage the spatial structure of random effects—variance not explained by fixed effects—to inform scale-specific latent factors that indicate what the model might be missing. In Part 3, we extend the factor selection approach to model spatial autocorrelation in observations, revealing the scales at which unmodeled variation exists alongside identified scale-specific factors.

Current challenges

Diversity variation across scales

Urban biodiversity research has traditionally focused on analyzing patterns at specific and limited spatial scales, with individual studies examining diversity drivers within constrained spatial extents. While these investigations provide valuable insights into local processes, scaling ecological mechanisms to broader extents remains problematic because driving processes likely change across scales (Swan et al. 2021). This challenge has prompted researchers to develop conceptual frameworks that propose multiple mechanistic drivers of urban biodiversity, incorporating biotic, abiotic, and socio-economic factors (e.g., Aronson et al. 2016; Uchida et al. 2021). These frameworks commonly employ alpha, beta, and gamma diversity concepts to

describe how community composition varies across space in response to different urban habitat types and management regimes.

However, these diversity concepts lack explicit scale definitions, operating as relative concepts whose spatial boundaries depend entirely on investigator choice of sampling design and extent (Dale & Fortin 2014). This scale ambiguity prevents systematic testing of proposed mechanistic frameworks because the spatial scales at which different processes operate remain undefined. Do diversity patterns exhibit consistent variation across all spatial scales, or do critical scales exist where variation concentrates? The absence of systematic methods for decomposing biodiversity variance across multiple and specific spatial scales may lead to contradictory conclusions (Chase et al. 2018) and limit the development of scale-appropriate conservation strategies in urban environments.

Inadequate treatment of scale in species distribution Modeling

Joint species distribution models (JSDMs) represent significant advances in community ecology by modeling multiple species simultaneously, yet they typically impose unrealistic assumptions about scale-dependent environmental relationships. Most implementations assume that all species within a community respond to environmental factors at one or multiple identical spatial scales—a simplification contradicted by extensive ecological theory and empirical evidence (McGarigal et al. 2016). This constraint is particularly problematic in heterogeneous urban environments where species with varying dispersal abilities, body sizes, and habitat requirements likely perceive and respond to environmental gradients at fundamentally different scales.

Current practice in environmental factor quantification reveals systematic inadequacies in scale consideration. Researchers frequently select scales based on data availability, computational convenience, or precedent from poorly related studies rather than ecological justification (Jackson & Fahrig 2015). When multiple scales are considered, analyses typically examine only coarse distinctions between "local" and "landscape" scales—vague categorizations that vary between studies and lack species-specific relevance. The full continuum of potentially relevant scales remains unexplored, potentially missing critical scale-dependent relationships that influence species distributions.

Absence of systematic multiscale factor selection

The scale of effect concept, while advancing understanding of species-environment relationships, increasingly appears oversimplified for complex ecological systems (Miguet et al. 2016). Accumulating evidence demonstrates that species often respond to the same environmental factor at multiple scales simultaneously, with responses sometimes reversing direction across scales (Pease 2024). These multi-scale responses likely reflect how organisms integrate environmental information across their life histories—from daily foraging movements to seasonal migrations and dispersal events.

Analytical frameworks in practice lack systematic approaches for identifying which environmental factors operate at which scales for different species. The absence of formal multi-scale factor selection methods forces researchers to rely on separate univariate analyses for each factor-scale combination, ignoring potential interactions and failing to account for the multivariate nature of species-environment relationships (Stuber & Gruber 2020). Furthermore, this methodological gap widens when considering how landscape variability itself may modulate scale-dependent responses, with some species potentially changing the scale at which they use their environment as heterogeneity manifests across a landscape.

Research outline

We designed our research to address these challenges through three studies that build upon each other. We start in Part 1 by decomposing the variance structure of bird diversity across multiple spatial scales, identifying where diversity patterns exhibit the greatest variation, providing insights into the scales at which environmental processes are most likely operating. We then shift our focus to environmental factors in Part 2, evaluating how their effects on species occurrence vary across scales when modeling multiple species jointly. Finally, Part 3 implements a systematic multiscale factor selection approach to determine which factors at which scales best explain species occurrence patterns, revealing the complex multi-scale relationships that single-scale approaches typically miss. This integrated analytical framework not only advances methodological tools for multiscale ecological research but also provides practical, scale-aware insights for improved urban planning and conservation practices.

Part 1 – Scale variance of biodiversity

Part 1 asks how the variance of London's bird diversity depends on scale. In other words, does the diversity vary consistently, or are there scales at which diversity changes more relative to other scales. High variance at a scale(s) can suggest hypotheses about which environmental factors, or the layout of those factors across the landscape, may be most relevant in influencing species diversity. We quantified several different aspects of taxonomic diversity, considering richness (total species), evenness, and Simpson's diversity index, taking care to overcome sampling biases in the dataset of crowdsourced bird observations, which included 279 different species.

Part 2 – Scale dependence of environmental factors

Part 2 assesses the scale dependence of environmental factors for 65 species that were observed in at least 10% of the BBS squares, ensuring sufficient observations to model their occurrence. Our analysis implements a common method in landscape ecology that aggregates environmental factors within buffers of increasing distance—representing scale—around each sampling location. Fitting a series of models with the same factors but sampled at different scales can be used to determine the so-called "scale of effect", or scale at which the strongest relationship exists. Because the scale of factors is often not considered or based on limited data, we assessed model performance across each scale to see how the relationship changed for different groups of species.

Part 3 – Varying relationships between species and across scales

Part 3 compares scale-specific relationships between species guilds defined by primary habitat type. We implemented a systematic multiscale factor selection model that identified the factors that best explain the occurrence of each species from 10 candidate factors quantified across 10 scales. In addition to comparing how the results differed between habitat specialists and synanthropic species, we partitioned the explained variance among the selected factors to across scales, further assessing the validity of the single best "scale of effect" approach.

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PART 1

Scale dependence of bird diversity in London

A version of this chapter was originally published by Jacob Dein and Liem Tran:
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My use of "we" in this chapter includes my co-author Liem Tran. As first author, I led experimental design, data analyses, and writing the manuscript.

Abstract

Understanding drivers of biodiversity in cities can be mutually beneficial for ecosystems and people. Crowdsourced bird observations provide an opportunity to assess how patterns of bird diversity change across observation scales and suggest driving processes. We assessed the scale dependence of bird diversity within a 64 x 64km extent over London's urban-rural gradient to suggest scales at which key drivers may be operating. We quantified scale variance of bird diversity across scales from 500m to 32,000m for three groups of species (All, Passeriformes, and Anseriformes and Charadriiformes combined). We estimated diversity by aggregating observations into a series of grids and computed comparable diversity estimates within each cell using interpolation and rarefaction. We calculated the variance explained by each scale for common diversity metrics. The results show that bird diversity patterns around London vary by scale, and that the location of high variance shifts across the study area depending on both scale and species group. The variance of Passeriformes diversity gradually shifted from the urban core to the periphery, while variance of Anseriformes and Charadriiformes diversity occurred near water features. The results suggest that the urban-rural gradient and location of water are two properties of the study extent around London influencing the scale dependance of bird diversity that could be used to ground scale considerations of further modeling efforts.

Introduction

Understanding the appropriate scale of observation is a fundamental challenge in landscape ecology. As ecological processes operate and manifest in patterns at different scales, changing the scale of observation can impact resulting conclusions (Levin 1992; Wiens 1989b). As the resolution and extent of environmental data available increase, determining the most informative scales for specific ecological questions remains an important yet complex task (Miguet et al. 2016; Pease 2024). One approach towards addressing this challenge is to investigate the scales at which a phenomenon exhibits high variance to understand its

dependence on scale—suggesting where to search for important underlying processes before assessing specific relationships (Stoms 1994; Wu & Loucks 1995). Put simply, understanding how patterns depend on scale informs relevant analyses.

In urban ecology, exploring multiscale patterns of biodiversity is essential for understanding the complex interplay of influential factors (e.g., Callaghan et al. 2020; Mao et al. 2023; Shanahan et al. 2011), where the size of the city and the scale of observation play important roles (Swan et al. 2021; Uchida et al. 2021). Understanding why biodiversity is hindered or enhanced in different urban environments is key knowledge for both conservationists and urban planners aiming to support biodiversity for ecosystem and health and public well-being (Kirk et al. 2021; Michael et al. 2024). Effective strategies to integrate biodiversity considerations into urban design—such as creating green spaces and habitat corridors—rely on knowledge of what impact these actions will have and how to optimize investments for ecological and societal benefits (Kowarik 2023; Norton et al. 2016; Oke et al. 2021).

However, evidence suggests that multiscale studies often miss the most ecologically relevant scale(s), termed the scale of effect (or also intrinsic or characteristic scale), potentially resulting in conflicting species-landscape relationships (Jackson & Fahrig 2015). While the concept of the scale of effect is useful towards improving the understanding of how species respond to landscapes, recent studies have pointed out two main limitations. First, landscape variables must be defined by the researcher, which may vary in ability to capture aspects of the environment important to species distributions (Miguet et al. 2016). Second, the scale of effect may vary across space influenced by myriad factors, leading to context-dependent (i.e. nonstationary) relationships (Pease 2024; Pease et al. 2022).

Changing environmental relationships across scale and space complicate species distribution models (SDMs) and, consequently, conservation and urban design decisions based on them (Miller 2012). Improving the quality and reliability of SDMs would inform more effective and scale-appropriate management strategies (Araújo et al. 2019). Leveraging multiscale analytics before modeling relationships could allow researchers to identify how ecological patterns, such as bird diversity, depend on scale, but also change across space. The unconstrained view of multiscale patterns provided by these approaches can serve as an initial exploratory step to guide modeling assumptions.

Multiscale analytics are widely used in landscape ecology, particularly to quantify landscape patterns (e.g., land cover indices), where the availability of high-resolution land cover data across large extents has played a key enabling role (Frazier & Kedron 2017). However, data on animal biodiversity, particularly at fine spatial scales, have been significantly less available. Earlier studies, such as Stoms (1994), assessed the scale dependence of vertebrate diversity using predicted species ranges as a proxy to estimate species richness, which was the best available data at the time. With the advent of crowdsourced species observation programs like eBird (Sullivan et al. 2014) and automated methods like passive acoustic monitoring (e.g., Ross et al. 2023), more extensive data are now available. Leveraging these large datasets with multiscale analytics can improve biodiversity and species distribution models by incorporating better scale considerations, which have potential to significantly alter results and conclusions (Chase et al. 2019; Miller 2012).

Various multiscale analytics have been applied in ecology, including fractal (e.g., Milne 1991), Fourier (e.g., Lundquist & Sommerfeld 2002), and wavelet analysis (e.g., Keitt 2007). Among these, scale variance analysis is notable for its simplicity and its flexibility in handling diverse and incomplete data (Zhang & Zhang 2011). Initially proposed by Moellering & Tobler (1972), this approach partitions total variance across hierarchically nested levels corresponding to different scales (i.e. grain size), in essence identifying "where the action is" (Moellering & Tobler 1972).

Despite its utility in remote sensing applications (see Justice et al. 1991; Townshend & Justice 1988), scale variance has curiously been seldomly applied in ecology. Wu et al. (2000) tested its effectiveness in identifying patterns at specific scales using simulated and real land cover data. Zhang & Zhang (2011) further demonstrated its utility on real land cover data by leveraging complimentary metrics like Moran's I to assess the significance of variance peaks at specific scales. While these applications have focused on land cover data, scale variance analysis is broadly applicable to a variety spatial data (Moellering & Tobler 1972).

In this study, we aim to assess the scale dependence of bird diversity across an urban-rural gradient around Greater London, U.K. Specifically, we hypothesize that 1) the variance of bird diversity changes between observation scales, that 2) the variance at each scale also changes across the extent, and 3) that the results, considered together with the species included, can suggest scales at which dominant processes influencing urban bird diversity operate.

Methods

We quantified scale variance of bird diversity across a 64 x 64km extent around Greater London, UK (**Figure 1-1**a, see Appendix for all figures and tables). We choose this study area because of London's large size, with the extent containing a 2022 population of approximately 12.5 million people (Esri 2022), the availability of numerous bird observations through the eBird platform, and the availability of data on a range of potential influencing factors to enable further modeling efforts to leverage this study's results. We organized our analysis into three parts:

1. creating a hierarchical series of grids with varying grain size over the study area, starting with the highest resolution supported by the data;
2. estimating bird diversity within each grid cell, using species interpolation and rarefaction to standardize sample coverage;
3. computing and analyzing scale variance across all grid resolutions (scales).

Hierarchical grids

We created a series of regular grids necessary to compute the variance of bird diversity at multiple scales across the study area (**Figure 1-1**b). While holding the extent constant, we created grids that divide the study area into a series of progressively larger scales, each increasing by a power of two (e.g., 500m, 1000m, 2000m, etc.), where the cell's size equals the scale of computed variance (**Figure 1-1**c).

We aimed to set the starting grain size at the highest feasible resolution provided by the observations to maximize the range of scales we could analyze. While varying the grain size, we counted the number of complete checklists within each cell and observed at what grain size the percentage of cells with observations started to significantly increase. Because this determination includes several factors with uncertainty, we ran our analysis using a series of grids with varying starting grain sizes to assess the impact on the results.

Estimating bird diversity

We used species rarefaction and extrapolation methods to estimate bird diversity using Hill numbers, which are a set of metrics that quantify different aspects of diversity and are differentiated by an order parameter q:

- At q = 0, the Hill number represents species richness, effectively counting the number of distinct species present.

- At q = 1, the Hill number considers both species richness and evenness, evaluating not only how many species are present, but also how evenly their individual counts are distributed.
- At q = 2, the Hill number is the Simpson diversity index, which measures diversity by squaring the proportion of each species to the total number of individuals, placing more weight on dominant species.

As q increases, the influence of rarer species in the calculation decreases (Chao et al. 2014), and likewise places more weight on abundant species. As q approaches infinity, the metric approaches the abundance of the most common species (Hill 1973).

We used observations from the eBird dataset (EBD) to estimate Hill number diversity at the highest resolution of each grid series we created. eBird records all bird observations from a user's session as a checklist, containing a list of all species and their count at the observation location. Fields describing the amount of time spent and number of observers present are also recorded to quantify sample effort (Sullivan et al. 2014). We downloaded the EBD containing observations through December 2023 and filtered the checklists to only include those captured over 10 years between 2014-01-01 and 2023-12-31 while the observer was stationary or traveled 2km or less, along with these additional filters recommended by eBird (Strimas-Mackey et al. 2023):

- number of observers less than or equal to 10; and,
- observation duration less than or equal to 6 hours.

We joined taxonomic data from the AVONET dataset (Tobias et al. 2022), namely the family and order of each species, to be able to compute the scale variance for three different groups of species:

- Group 1 – All species
- Group 2 – Passeriformes
- Group 3 – Anseriformes and Charadriiformes

Passeriformes are the largest and most diverse order of species in the dataset, consisting mostly of songbirds and representing approximately half of the total observations. Anseriformes and Charadriiformes are water-dependent (e.g., waterfowl or shorebird) species and are the next two largest groups of species observed in the study area. We selected these groups due to their

large number of observations (enabling more and better diversity estimates) and for the significant difference in habitat.

While crowdsourced observations can increase the amount of available data, they contain many biases that need to be removed to not influence the results. While we have taken measures to control for taxonomic bias, temporal bias, and class imbalance, we have applied the concept of species interpolation and rarefaction (Chao et al. 2014), as implemented in the R package iNEXT (Hsieh et al. 2016), to control for spatial bias. This approach, which is similar to that applied by Callaghan et al. (2022), leverages the concept of sample coverage to calculate comparable diversity estimates for each grid cell across the study area.

To calculate the true diversity within a sample area, all species that inhabit the area must be observed. However, this is often not feasible, which is why rarefaction and interpolation methods were developed. Work initially developed by Alan Turing and I. J. Good to decipher encrypted communication during World War II was later applied to reliably estimate the degree to which a population has been sampled, referred to simply as sample coverage (Good 2000). While the level of sampling effort (i.e. number of complete checklists, number of observers, and total time observing) varies across space, sample coverage represents the probability that a random individual from the true inhabiting population of an area belongs to one of the species already observed in the same area (Chao et al. 2020).

Using this approach, we used iNEXT to compute estimated diversity at q = 0, 1, and 2 at a standardized 95% sample coverage for each cell containing complete checklists at the lowest level (highest resolution grain size) (**Figure 1-2**). We excluded estimates where the 95% confidence interval (implemented in iNEXT by bootstrapping 100 times) was greater than the estimate itself, indicating high uncertainty generally correlated with lower sample coverage. This approach allowed the cells included in the scale variance calculation to vary by q value, as lower orders of q, particularly q = 0, require more observations to be accurate, where estimates at q = 1 and q = 2 can be stable after fewer observations (Chao et al. 2020).

While each checklist contains the species observed and their abundance, the additional user error in observing abundance is not known, and only incidence data is required for the sample-based coverage approach. Following Callaghan et al. (2022), we converted the species abundance data (i.e. number of individuals observed) to incidence data (i.e. observed or not observed) and then listed how many times a species was observed within each grid cell.

Computing scale variance

Scale variance analysis is founded on a model where a variable X depends on its global mean plus effects from specific scales. For an example three-level hierarchy, the model can be expressed as:

$$X_{ijk} = \bar{X} + \alpha_i + \beta_{ij} + \gamma_{ijk} \quad \text{(equation 1)}$$

where X_{ijk} is the value at the lowest level, which equals the global mean ($\overline{X}$) plus the effect from the containing unit at levels α, β, and γ, where i, j, and k index the containing unit at each respective level. However, because the variance at each scale is the focus, the model is rewritten in terms of variance by subtracting the grand mean and squaring both sides (equation 2). Then, the total sum of squared deviations from the mean equals the sums of the squared deviations from the containing mean (from one level above) for all levels (equation 3).

$$(X_{ijk} - \bar{X})^2 = +(\bar{X}_i - \bar{X})^2 + (\bar{X}_{ij} - \bar{X}_i)^2 + (X_{ijk} - \bar{X}_{ij})^2 \quad \text{(equation 2)}$$

$$\sum(X_{ijk} - \bar{X})^2 = SS_{total} = SS_\alpha + SS_\beta + SS_\gamma \quad \text{(equation 3)}$$

The scale variance component is the sum of squares at each level l divided by the level's degrees of freedom (equation 4). The sum of all scale variance components is 1, meaning each component effectively represents the proportion of total variance in the dataset attributable to each respective level (Moellering & Tobler 1972).

$$SV_l = SS_l / dF_l \quad \text{(equation 4)}$$

Based on this foundation, we developed an analysis pipeline written in the R programming language to compute scale variance from the diversity estimates (**Figure 1-3**). To assess the sensitivity of the results to starting grain size, we ran the analysis a total of six times, assigning an "R#" label to each, with starting grain sizes: 500m (R1), 750m (R2), 1000m (R3), 1500m (R4), 2000m (R5), and 3000m (R6).

With our approach of determining the level of geographic support to enable the highest reasonable resolution, the resulting grain size of the lowest level grid results in many cells without any checklists and thus no diversity estimate. While the scale variance components can be computed, they might not fully capture variance at that level if actual diversity differs greatly between cells with and without diversity estimates. To assess the effect of cells without diversity estimates, we estimated diversity for all cells at the lowest level with two kriging methods. We performed ordinary kriging (OK) using the R gstat package (version 2.1-1) using an exponential

class/stable model ("Exc") with lag size equal to the starting grain size and nugget equal to 0 (to force predicted values to match estimated values) (Gräler et al. 2016). Additionally, we performed empirical Bayesian kriging (EBK) as implemented in the Geostatistical Analysis toolbox in ArcGIS Pro (version 3.1) using a Log-Empirical transformation, 100 maximum local points, overlap factor of 1, 1,000 semivariograms with a K-Bessel model, standard circular search neighborhood with radius of 1,000 and full sector type. While EBK likely results in less error overall as it accommodates for nonstationary spatial dependence, we wanted to compare the scale variance results from EBK and OK estimates, as the EBK smooths the values at the cells with original observation estimates where we set OK to not alter the estimates at cells with observations.

Results

We present the full results of analysis for All orders, R1 (starting cells size of 500m), and q = 1, which are representative of all results provided in the Appendix. At a grain size of 500m, the number of cells with observations started to significantly increase, and we used this as the starting scale. Out of 16,384 cells (128 x 128 500m cells over the 64 x 64km extent) at the lowest level, approximately 18% contained at least one complete checklist from 40,287 in total (**Table 1-1**).

Upon visual inspection, the checklists were clustered around more populated areas and popular bird watching locations (**Figure 1-4**a). Within those cells the number of complete checklists resembled a Pareto distribution where approximately two-thirds of cells with observations contained less than 13 checklists, with the remaining third ranging up to a maximum of over 5,000 checklists likely overlying popular birding hotspots (**Figure 1-9**). Estimated diversity showed a statistically significant but weakly positive correlation with number of complete checklists (Pearson correlation $r = 0.09$, $p < 0.001$).

Filtering out estimates with 95% confidence intervals greater than the estimate itself resulted in 1,171, 1,423, and 1,472 reliable estimates for q = 0, 1, and 2, respectively. The diversity estimates were normally distributed (mean = 30.8, sd = 11.3) with a slight right skew. The skew towards higher diversity values represents that relatively few sites have unusually high values of diversity, representing diversity hotspots. The distributions of diversity from OK and EBK are also normally distributed, with similar mean values (OK mean = 31.5, EBK mean = 31.8) but with less variation (OK sd = 6.0, EBK sd = 5.9).

Visually, the spatial distribution of estimated diversity across scales (**Figure 1-4**a) shows that the center of the study area is heavily sampled and in general contains less diversity than at locations outside of the Greater London boundary for all but the largest scale. However, within the boundary, there are clearly small areas with high diversity, and this pattern is most noticeable at and below 2,000m. A diversity hotspot is noticeable in the center east end of the study area between scales of 1,000m to 8,000m. At a scale of 16,000m, the pattern of generally lower diversity within the boundary than outside begins to fade, where at the highest scale of 32,000m only the northeast quadrant of the study area contains relatively higher diversity.

Comparatively, the spatial distribution of diversity across scales for EBK (**Figure 1-4**b) shows similar patterns, though some notable differences exist. With all cells across the study area containing a kriged value, the large area of high diversity at the center east end of the study area is immediately perceptible at a scale of 500m. Also more apparent is a general area of low diversity along a north-east – south-west axis, which is also apparent at scales of 8,000m and 16,000m for the observed estimates. The tendency of kriging to predict values within one standard deviation below or above the mean is perceptible, indicated by large homogenous areas between local low and high values where checklists were submitted. The results from OK are provided in the Appendix and show similar results, with one notable difference being that the OK results show sharp changes at the locations with observations because we forced the predictions to match the observations (nugget = 0).

The squared deviations at each scale show that initially much of the variance stems from within the boundary of Greater London at scales of 500m and 1,000m, but then shits to outside the boundary, where variance is generally evenly distributed at 2,000m and minimal variance occurs within the boundary at 4,000m and above (**Figure 1-5**).

For all species (group 1), roughly two-thirds of the total variance occurs at scales of 2,000m and below, with variance dropping significantly after 4,000m (**Figure 1-6**a). The pattern is similar for Passeriformes (group 2), though there is a notable increase at 16,000m after a sharp decline at 8,000m. Anseriformes and Charadriiformes (group 3) exhibit a gradual increase to peak variance at 4,000m, and drop significantly at higher scales, consistent with the patterns of Passeriformes and all species.

The results are largely consistent across q value, with scale dependence slightly increasing with decreasing q value, with q = 0 results generally having the greatest change across scales. However, the patterns are similar for all values of q in general.

Altering the starting grain changes the composition of relative variance, as the number of scales included varied from seven for R1 (500m to 32,000m) to five for R6 (3,000m – 48,000m), but the patterns remained the same, with a large drop in variance after 4,000m for all groups, as well as a notable peak at 4,000m (though ranging between 2,000m – 8,000m depending on q) for Anseriformes and Charadriiformes.

Scale variance on the kriged estimates are similar for EBK and OK, but the variance is shifted to higher scales in comparison to the observed estimates (**Figure 1-6**b). For Passeriformes, a large peak, with approximately one-third of the total variance, occurs at 16,000m, which appears in the observed estimates but is only a local peak and accounts for approximately 10% of total variance.

Several patterns in the spatial arrangement of square deviations are apparent when comparing group 2 (Passeriformes) and group 3 (Anseriformes and Charadriiformes) to all species. At 4,000m, for example, Passeriformes variance is widely distributed across the study extent, while variance of Anseriformes and Charadriiformes is mainly localized to the eastern and southern areas (**Figure 1-6**c).

Discussion

The two types of results presented—squared deviations and scale variance components—reveal scale-dependent patterns across the tested species groups and diversity metrics. Although each can be interpreted independently, a more comprehensive understanding emerges when they are considered together. The scale variance components capture the overall nature of scale dependence across the study extent, while the squared deviations indicate the location of scale variance within the extent. Two scales might show similar contributions to total variance, but the location of variance could differ across the study area. While this study's focus on scale-dependence of bird diversity does not establish direct links with environmental relationships, it offers a basis for hypotheses about how scale influences species responses and diversity to changing environments across landscapes.

The results suggest two main properties of the study area's environment that may be influencing diversity: 1) the differences within and outside the boundary of Greater London, and

2) location of water features (**Figure 1-7**). The patterns for all species and Passeriformes are similar, which is not surprising as Passeriformes account for approximately two-thirds of the total observations in the study extent. While the scale with maximum variance generally occurs between 1,000m and 2,000m depending on q, the variance components at scales 4,000m and below are similar. More notably, the variance for these two groups drops significantly at 4,000m and above. Looking at the square deviations for location of variance, Passeriformes have less variance within the Greater London boundary at 4,000m and 8,000m, which could be the reason for the local increase in variance at 16,000m. This may capture a broad trend of urban-adapted species occurring within Greater London, while other Passeriformes species less suited to urban environments generally occurring outside the boundary, illustrated by a "green ring" around the edge of the study area for mean Passeriformes diversity at scales 4,000m–16,000m (see **Figure 1-14**, **Figure 1-15**, and **Figure 1-16**).

Looking at the results from the combined diversity of Anseriformes and Charadriiformes, we can see that variance appears to be correlated with the location of water features, which we expect given that the group consists of waterfowl, wetland, and shorebird species. The peak q1 variance at 4,000m likely matches the dominant scale of environmental factors defining the transition between habitable and inhabitable areas for these species at the large area of high diversity on the east end of the study area over the mouth of the River Thames. This result is not surprising, but it serves as an illustrative example of scale variance results for species dependent on a specific habitat.

Because the results from the kriged diversity estimates appear to shift the portion of variance to higher scales, they may be biased and likely unable to reliably represent variance at smaller scales. Because kriging relies on a model of the data's spatial autocorrelation, the kriged estimates by definition depend on nearby values, effectively smoothing the resulting diversity surface (Chilès & Delfiner 2012), which is apparent when comparing the maps of observed and kriged diversity at scales below 4,000m and is why we do not consider the kriging results to be reliable. One notable exception, however, is the local increase in variance of Passeriformes diversity at 16,000m. Kriging the Passeriformes data changes the local increase in variance at 16,000m into the scale with the maximum variance, which makes sense if the difference in diversity within and outside of Greater London is strongest for Passeriformes. So, while it is

unlikely that 16,000m would contain the most variance, the result is further evidence of generally greater Passeriformes diversity outside the Greater London boundary.

Comparing estimates across q value, even though the number of reliable estimates decreased with q value, the similarity of the results for q = 0, 1, and 2 is notable. In general, the results show a slight increase of scale dependence with decreasing q, which makes sense that less common species are likely sensitive to specific environmental factors than more common species that are more adaptable (McKinney 2006). Further investigations to see if this scale dependance increases in extents with more data would be a valuable pursuit.

Because the scale variance components are the sum of squared deviations, which vary over space as demonstrated by the results, adjusting the study extent will likely change the scale dependance pattern, because influential patterns are likely to be nonstationary across the landscape (Miller 2012). Similarly, if additional observations were collected in areas of the study area, like the northeast corner for example, the scale variance components would likely change. However, this would not affect the noted patterns in the squared deviations, but rather add to them. This further speaks to the importance of considering both the scale variance components and squared deviations.

Likewise, including additional scales would influence the results, and evidence suggests that many birds experience their environment at scales less than 500m (Hostetler 2001; Melles et al. 2003). Existing literature typically distinguishes between local scales (approximately 50–500 m) and broader landscape scales (greater than 500 m). The scale range of this study, therefore, does not encompass the finer local scales that have been shown to be influential for many species. While our findings are consistent with previous research suggesting that landscape-scale factors between 500m – and 2,500m are often influential (Litteral & Shochat 2017), they do not provide evidence to compare the relative importance of local versus landscape scales. Incorporating data that support analysis at local scales would likely alter the distribution of scale variance; however, the spatial patterns of squared deviations would remain valid, with their relative importance possibly adjusted.

Analyzing scale variance over large extents and ranges of scales requires lots of data, which is why we aggregated observations over time. Considering temporal variations in diversity may add further insight, as the available evidence suggests seasonal changes may have different effects depending on the diversity metric (e.g., richness versus evenness) (Wiens 1989a);

however, urban environments tend to reduce temporal variation (Leveau et al. 2021). An additional limitation of scale variance analysis is the need to define scales a priori, thereby limiting the attribution of variance to those specific points rather than along a continuum. If observations were sensitive to a highly specific scale, a peak in variance may occur between these points and be missed. By varying the grain sizes of different analysis runs, we reduced the chances of failing to identify a peak in variance; however, future efforts to improve this workflow may also be valuable.

The quantification of biodiversity also carries limitations, and in this study we have only investigated species (taxonomic) diversity using the conventional Hill number diversity metrics. However, two sites may present similar diversity values despite having vastly different species compositions (Dale & Fortin 2014). Considering this limitation, incorporating alternative measures of diversity, such as functional diversity (e.g., as in Wu et al. 2024), may also be a helpful metric to analyze with scale variance.

Overall, the results from this study illustrate an approach to explore variance in ecological observations, or in the original words of the Moellering & Tobler (1972) study, to identify "where the action is". Because this technique identifies relevant scales without assumptions of the driving factors, researchers could leverage scale variance to better justify factors they select for subsequent modeling. Additionally, because the variance components are sensitive to both the included extent and number of scales included, we highlight that it is critical to also understand where the variance is located at each scale by exploring the squared deviations. We believe this intermediate step of scale variance analysis may actually be the most useful part of the technique, and we hope this realization, as illustrated in this context of urban bird diversity, can contribute towards better determining scales of effect and uncovering connections between patterns and processes more broadly.

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Appendix

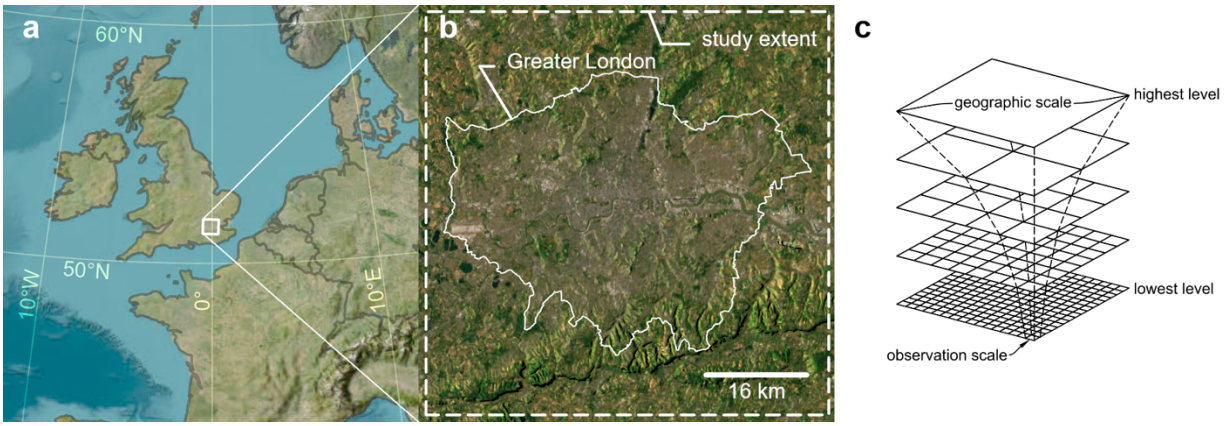
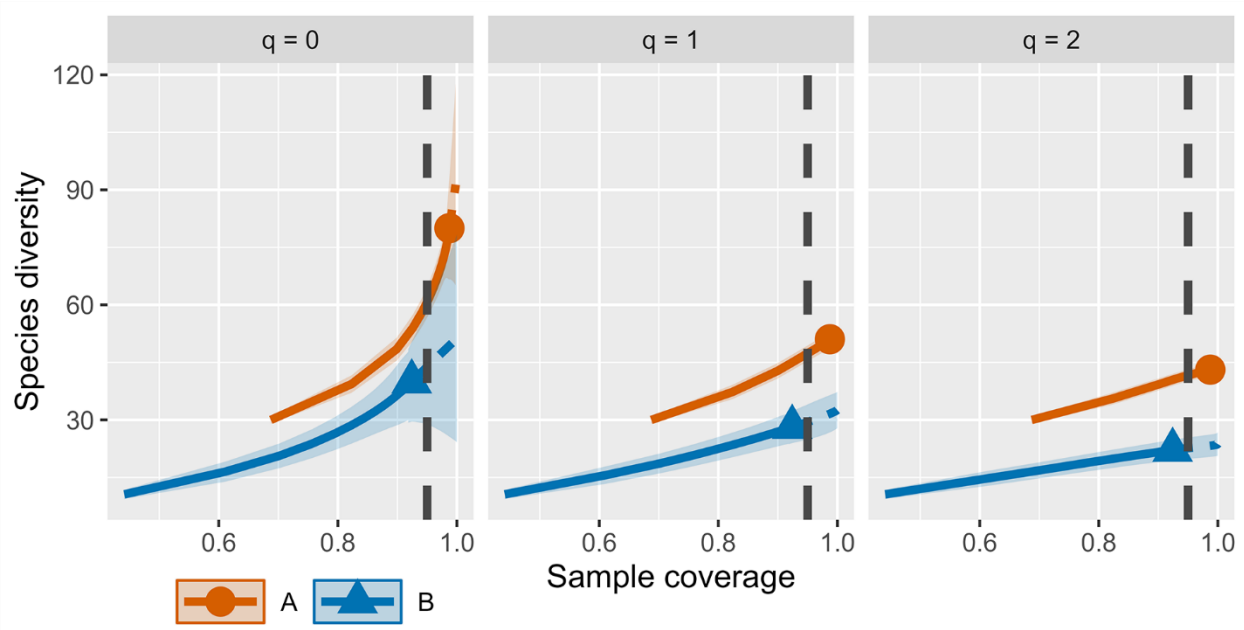


Figure 1-1: Study location, extent, and hierarchical grid illustration

a) The study location on the island of Great Britian, U.K. and surrounding region, b) the study extent around Greater London, U.K., and c) a conceptual illustration of hierarchical series of grids defined at specified scales, with scale doubling at each level from the lowest level up to the full geographic scale at the highest level



site	observations	checklists	species	coverage	estimated diversity at 95% coverage		
					q0	q1	q2
A	1080	36	80	0.987	60.7	47.4	41.6
B	159	15	40	0.924	43.8	29.5	22.6

Figure 1-2: Estimated diversity by sample coverage

Example iNEXT plots of diversity for q = 0, 1, and 2 with 95% confidence intervals for two sites "A" (higher estimated diversity) and "B" (lower estimated diversity), where the gray dashed line indicates a standard 95% sample coverage. The orange circle for site "A" and blue triangle for site "B" represent the estimated sample coverage resulting from each site's observations.

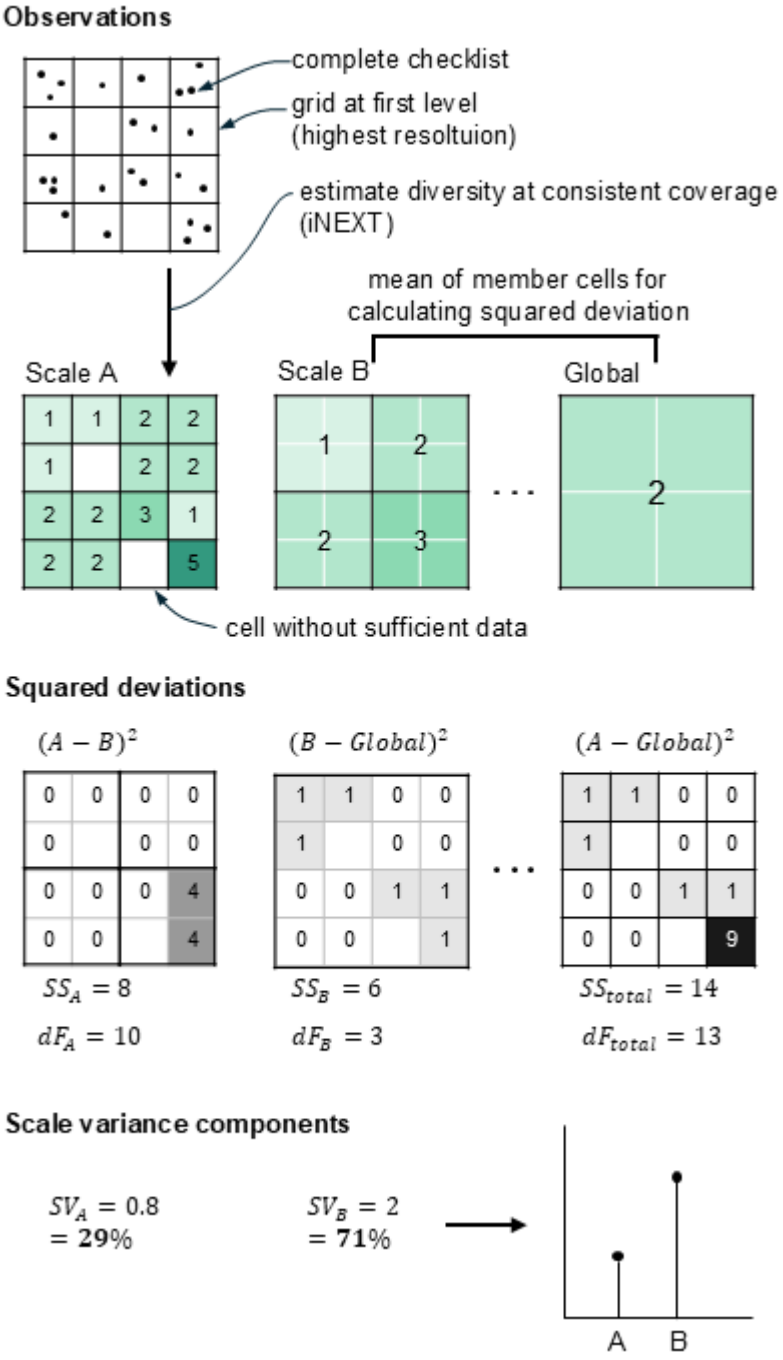


Figure 1-3: Scale variance analysis workflow

Two-scale example illustrating the main steps of the analysis workflow, where we first estimated diversity at the lowest level using the eBird observations and then applied scale variance analysis to yield the squared deviations and resulting variance components. Note that diversity is only estimated at the first scale for cells with sufficient observations.

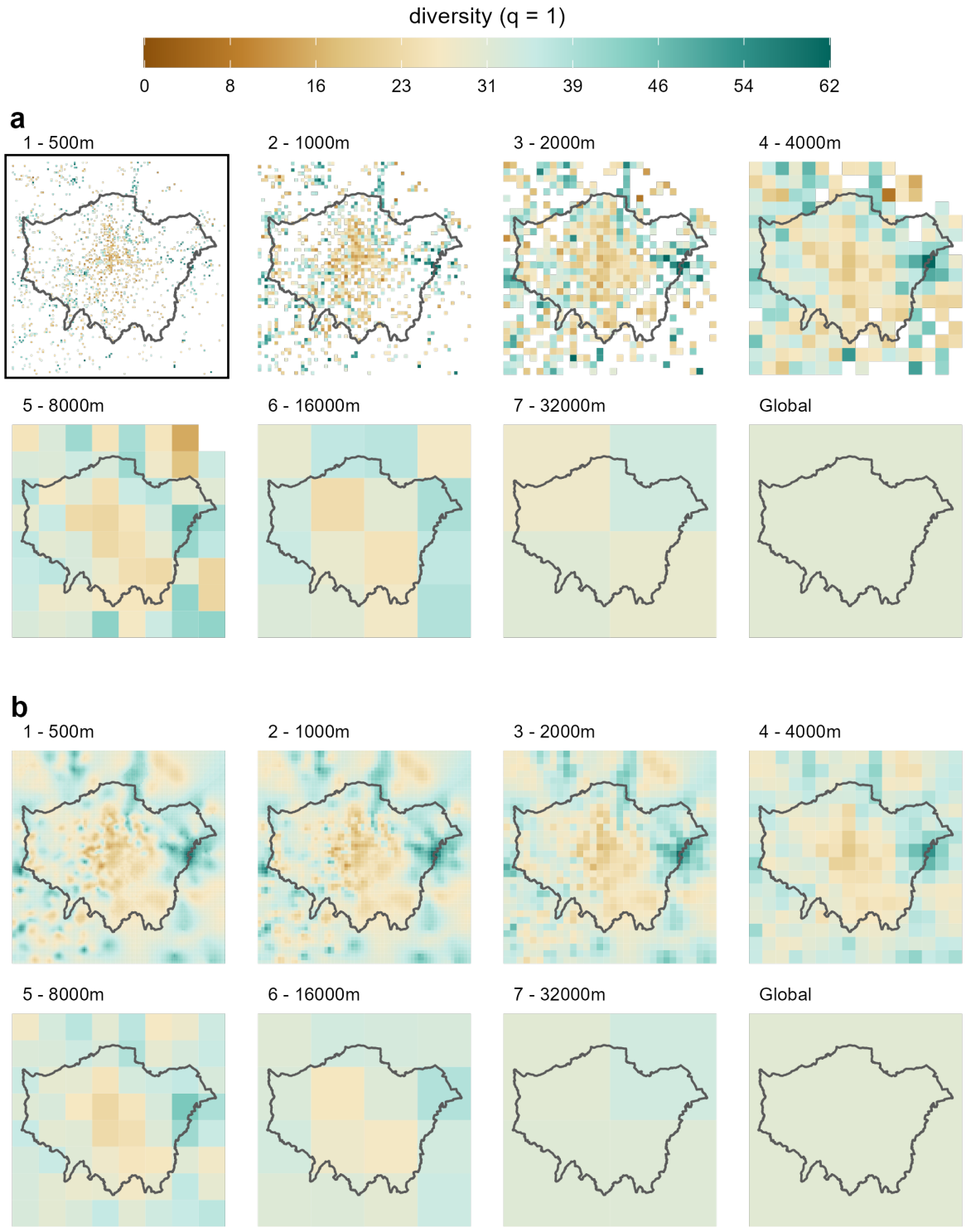


Figure 1-4: Mean diversity at assessed scales

a) Diversity from scales 1 (500m) to the full extent (64,000m), where the lowest level (1 – 500m with black boarder) shows estimated diversity (iNEXT output) and all remaining levels show the mean of member cells from the level below needed to compute the squared deviation, and b) diversity from EBK from scales 1 (500m) to the full extent (64,000m)

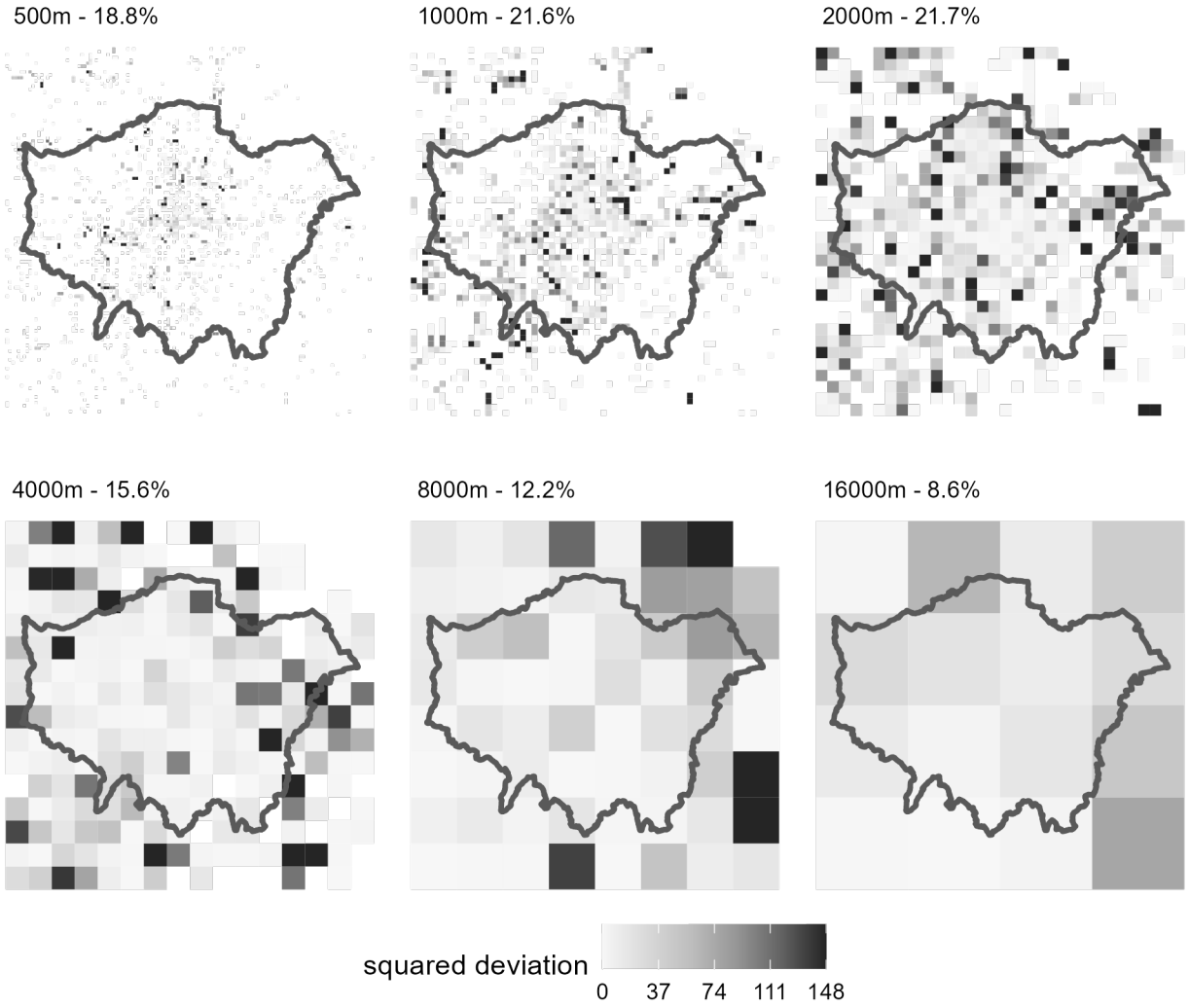


Figure 1-5: Squared deviations from mean diversity

Maps of the squared deviations for all species at each scale showing the location of all values that sum to the scale's variance component. The squared deviations at 32,000m are minimal (<2% of total variance) and are not shown.

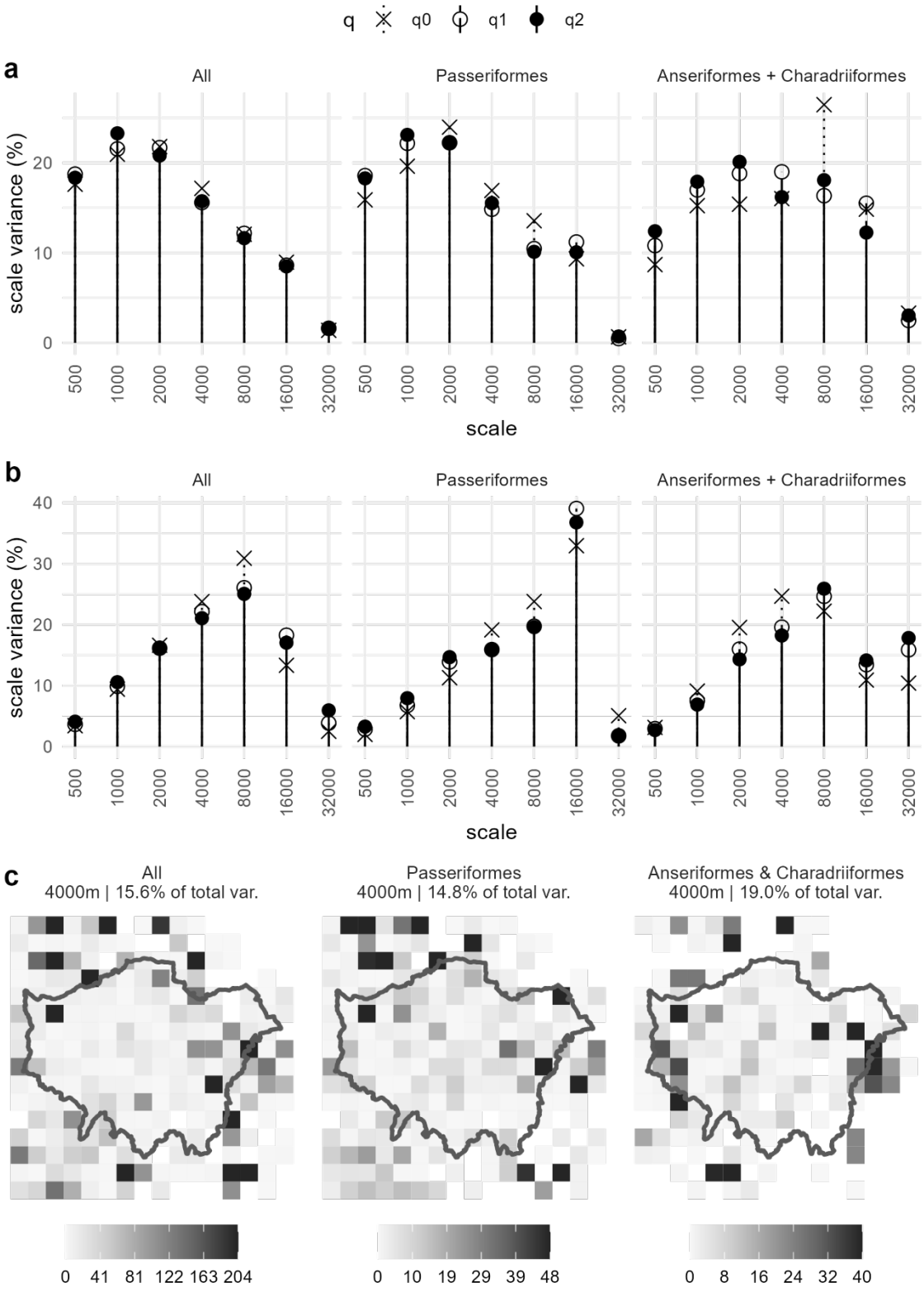


Figure 1-6: Scale variance components with squared deviations at 4,000m

Scale variance components (R1) for each species group from a) OBS diversity, b) EBK diversity, and c) squared deviations at 4,000m for each species group illustrating differing areas of high variance

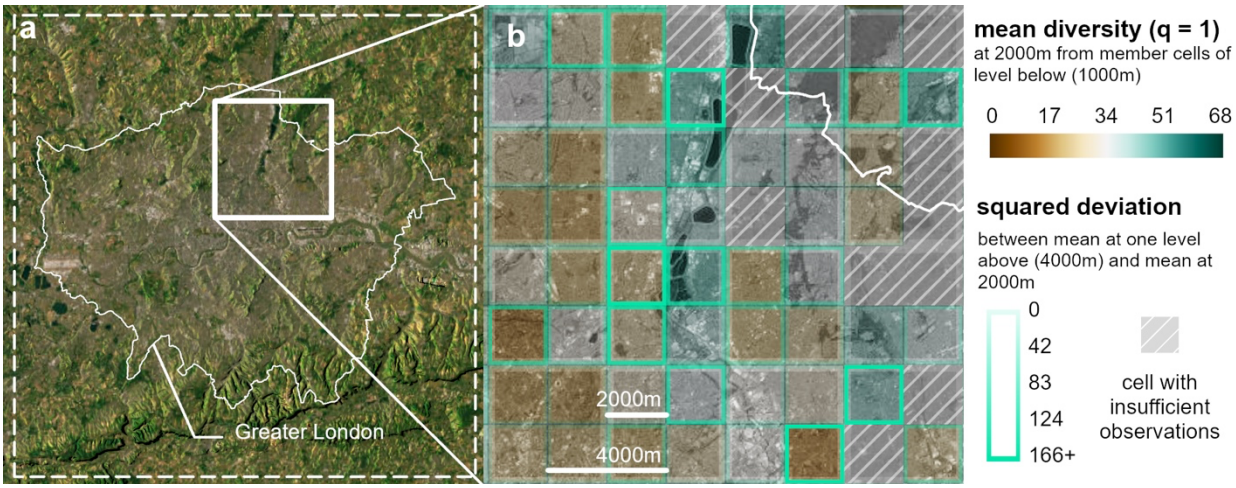


Figure 1-7: Diversity scale variance at 2,000m at the boundary of Greater London

a) Area of interest along the northern boundary of Greater London, and b) mean diversity and squared deviations at 2,000m overlaid over aerial imagery highlighting variance near water features and decreasing intensity of urban development

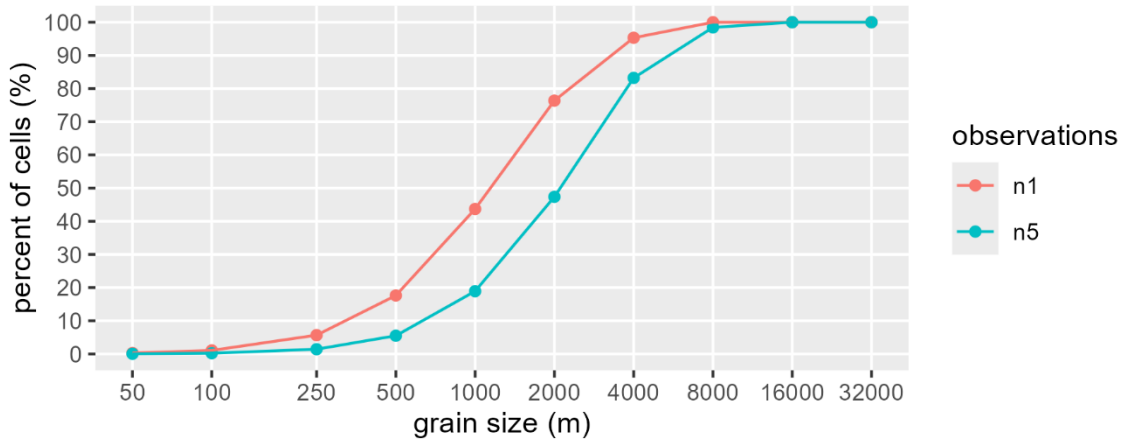


Figure 1-8: Sampled cells by grain size

Percent of cells containing at least one observation (n1) or five observations (n5) with increasing grain size

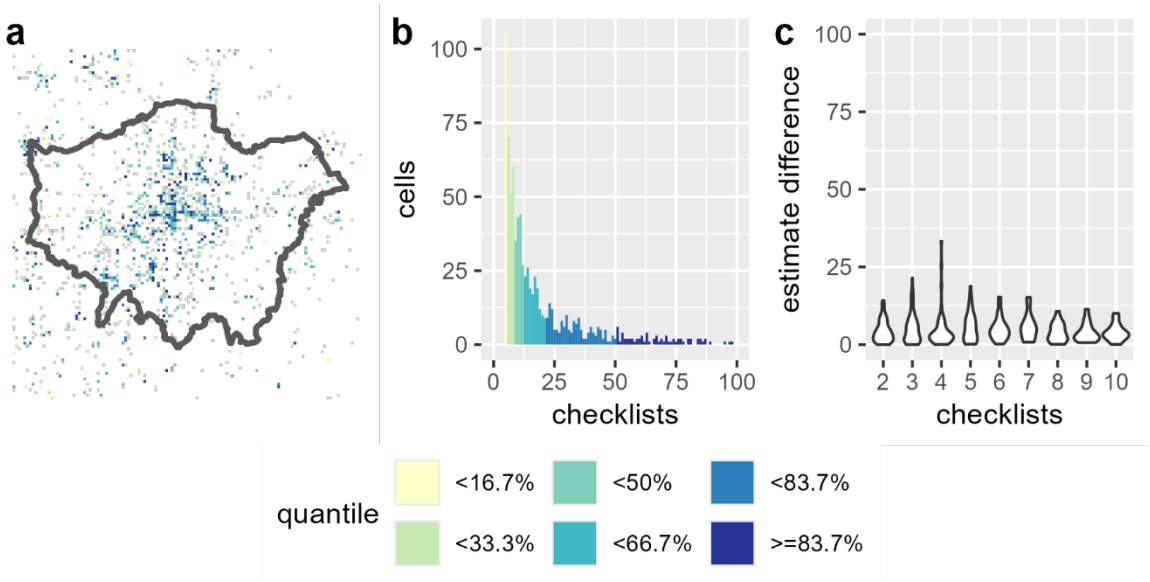


Figure 1-9: Observation statistics

a) Map showing cells with complete checklists (all species) with the boundary of the Greater London area shown for reference. b) Distribution of cells with number of checklists equal to or greater than five colored by quantile. c) Variation in the difference between observed and Empirical Bayesian kriging (EBK) diversity estimates (R1, q = 1) by number of complete checklists.

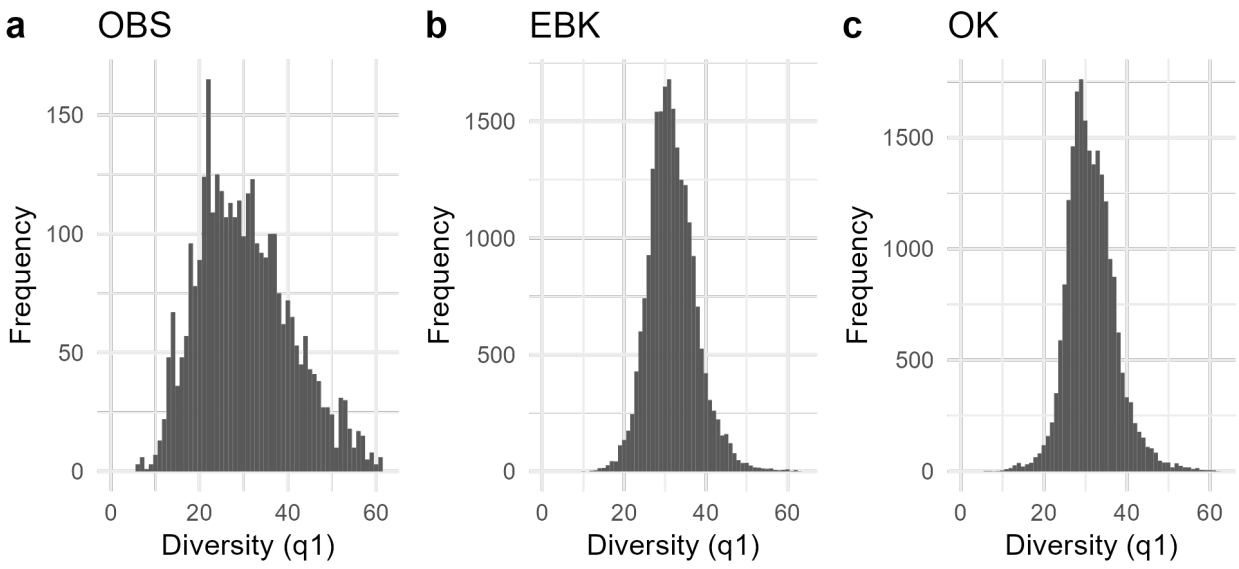


Figure 1-10: Diversity distributions by estimate type

Diversity histograms (R1, q = 1) from a) observed b) empirical Bayesian kriging and, and c) ordinary kriging diversity estimates

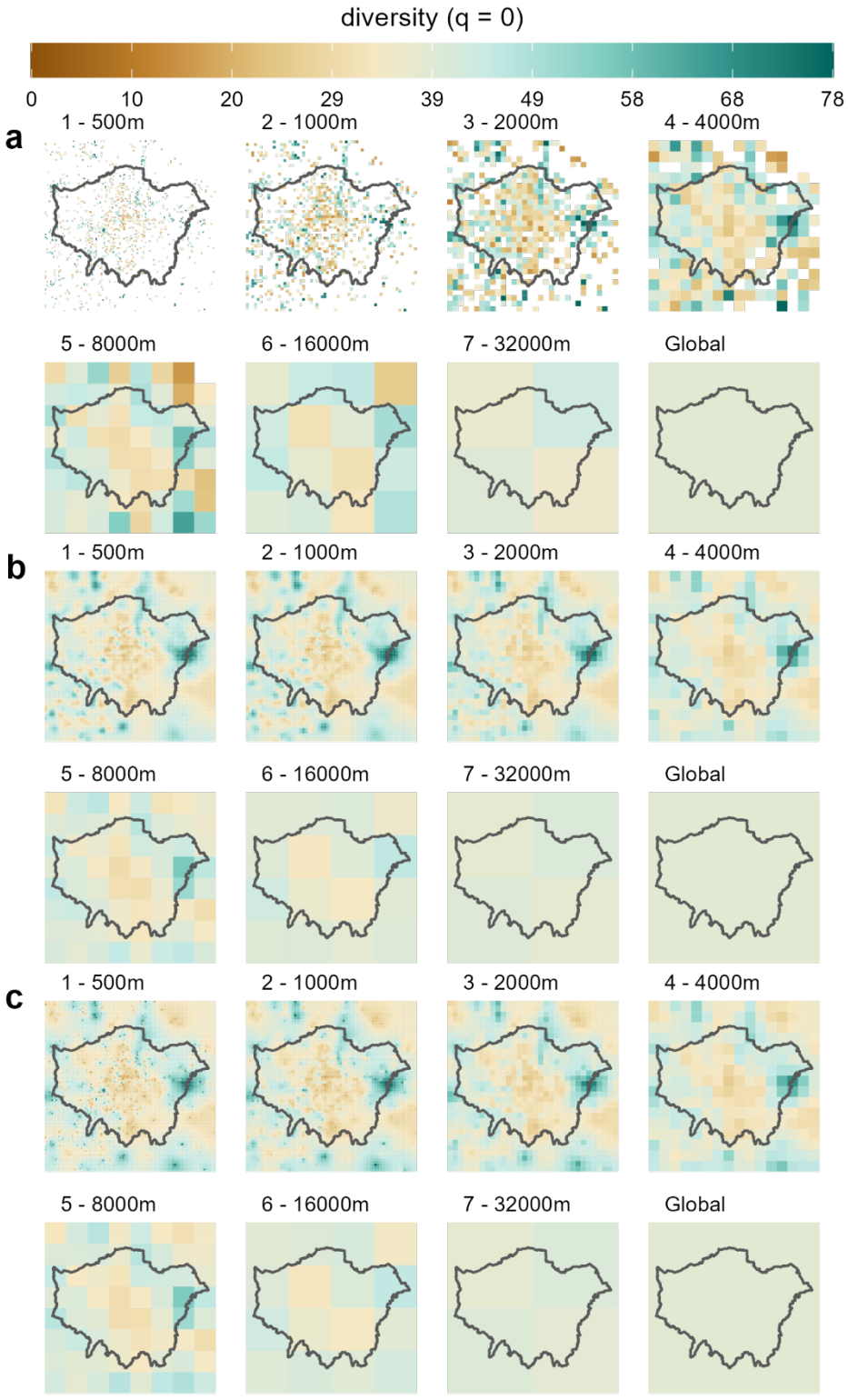


Figure 1-11: All species diversity, q0

Diversity (all species, R1, q = 0) from a) observed, b) empirical Bayesian kriging, and c) ordinary kriging from scales 1 (500m) to the full study extent (64,000m)

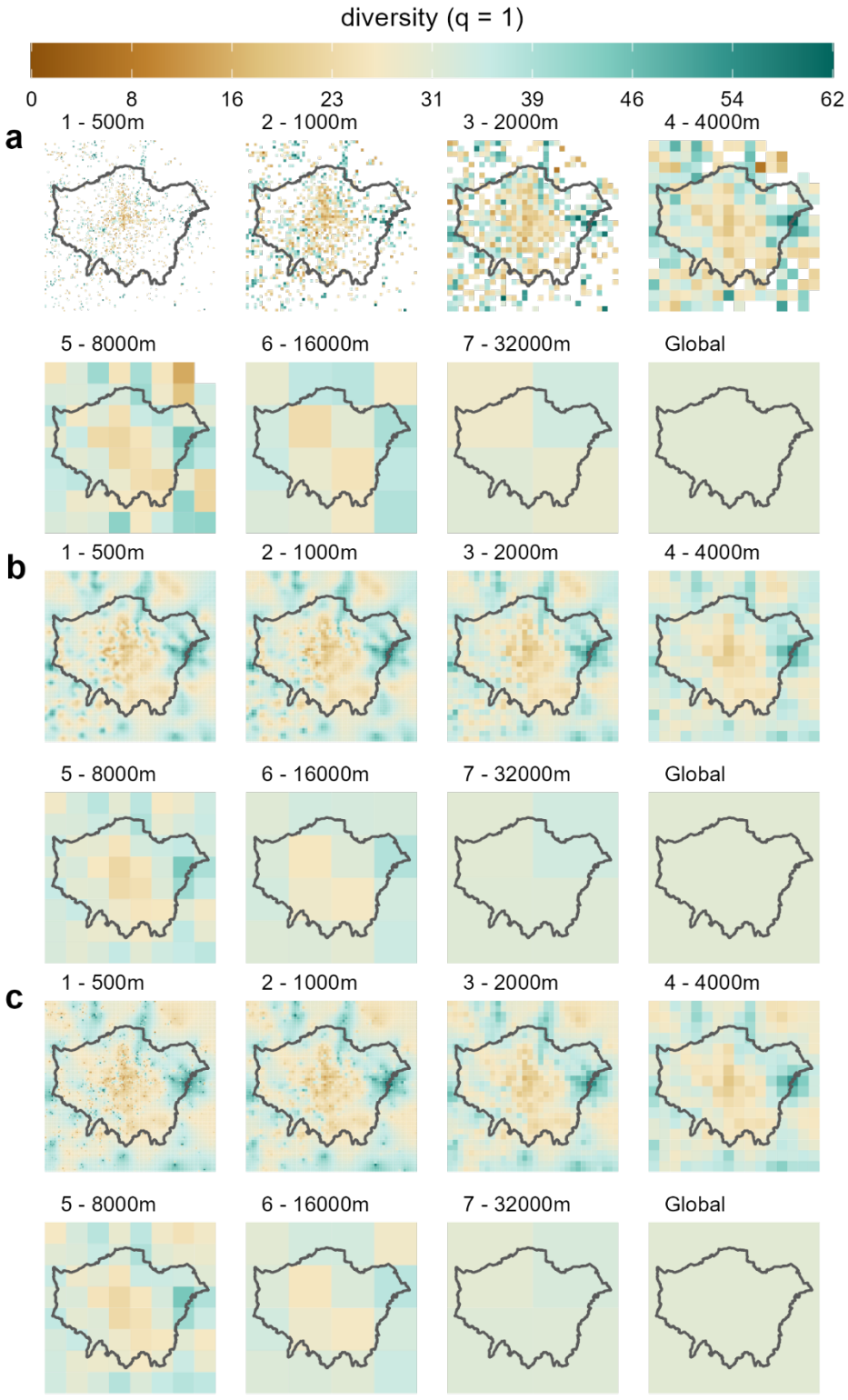


Figure 1-12: All species diversity, q1

Diversity (all species, R1, q = 1) from a) observed, b) empirical Bayesian kriging, and c) ordinary kriging from scales 1 (500m) to the full study extent (64,000m)

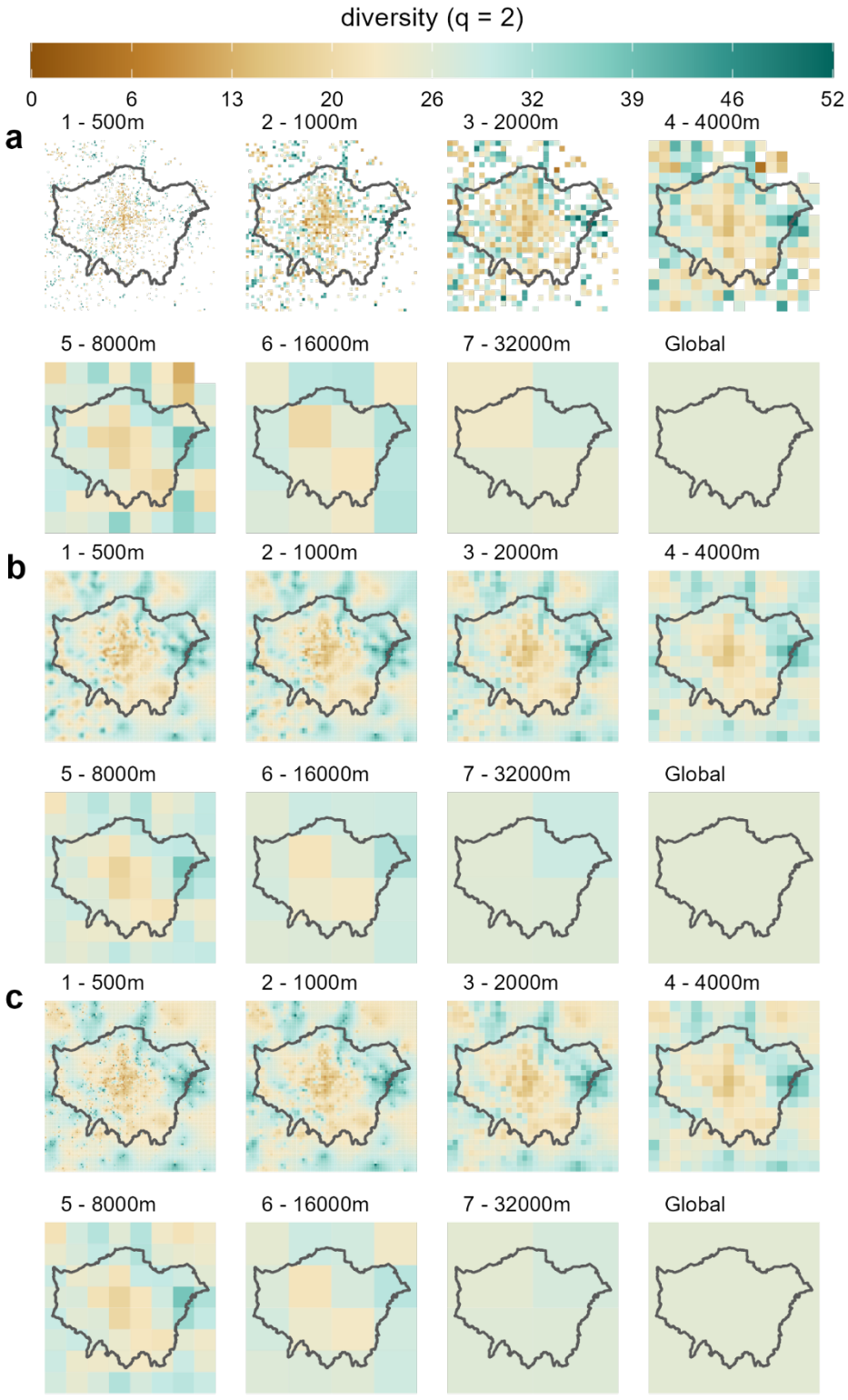


Figure 1-13: All species diversity, q2

Diversity (all species, R1, q = 2) from a) observed, b) empirical Bayesian kriging, and c) ordinary kriging from scales 1 (500m) to the full study extent (64,000m)

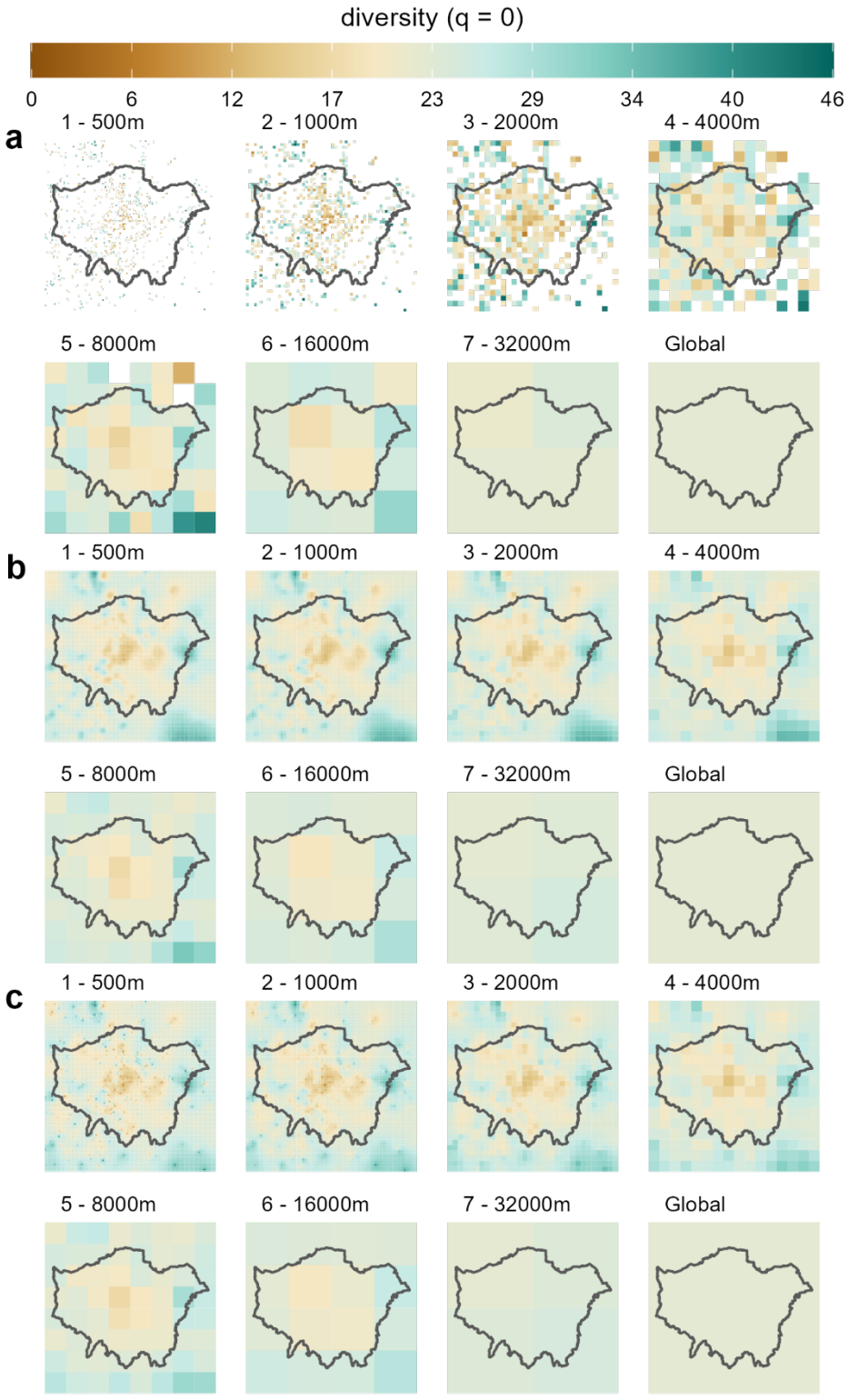


Figure 1-14: Passeriformes diversity, q0

Passeriformes diversity (R1, q = 0) from a) observed, b) empirical Bayesian kriging, and c) ordinary kriging from scales 1 (500m) to the full study extent (64,000m)

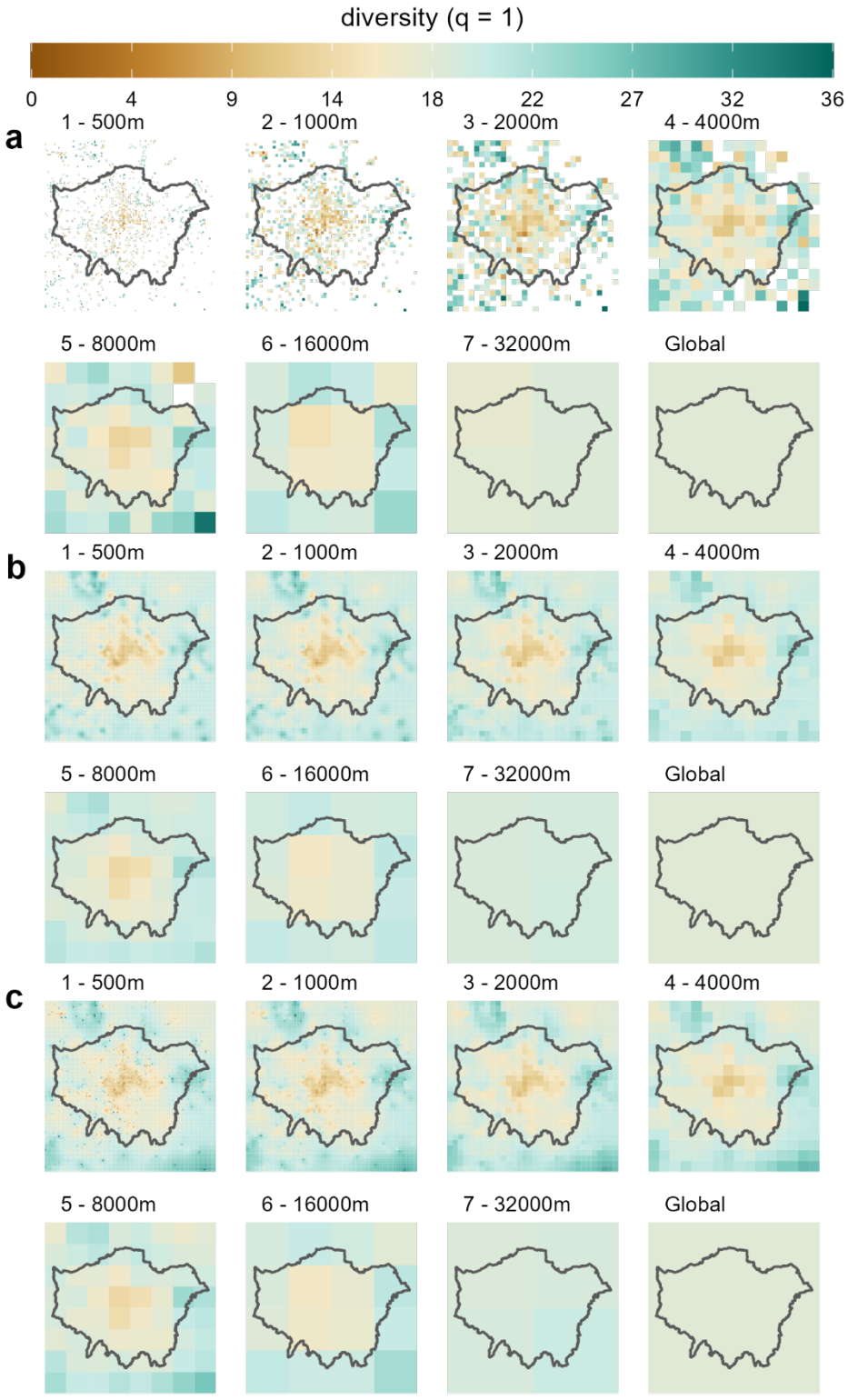


Figure 1-15: Passeriformes diversity, q1

Passeriformes diversity (R1, q = 1) from a) observed, b) empirical Bayesian kriging, and c) ordinary kriging from scales 1 (500m) to the full study extent (64,000m)

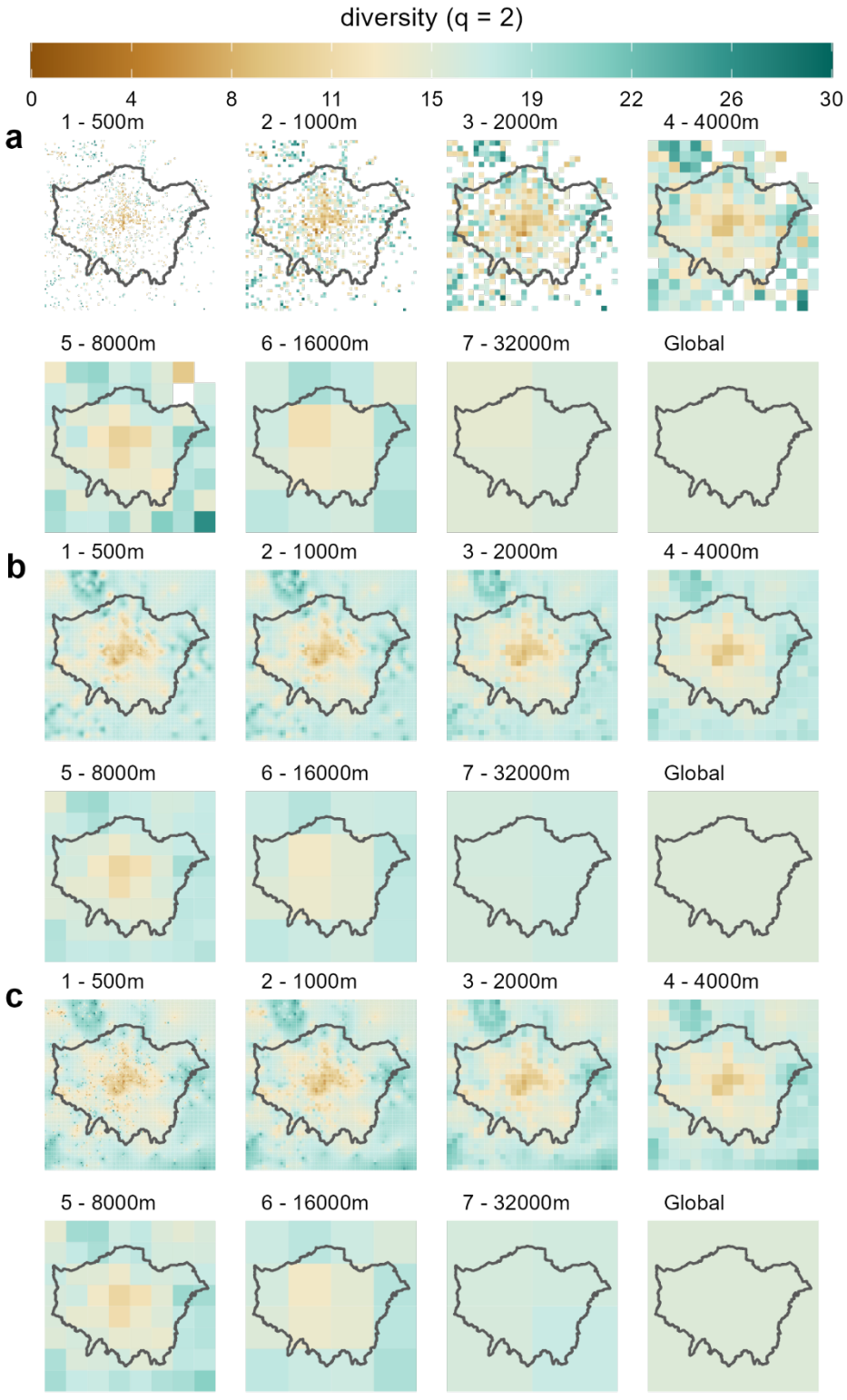


Figure 1-16: Passeriformes diversity, q2

Passeriformes diversity (R1, q = 2) from a) observed, b) empirical Bayesian kriging, and c) ordinary kriging from scales 1 (500m) to the full study extent (64,000m)

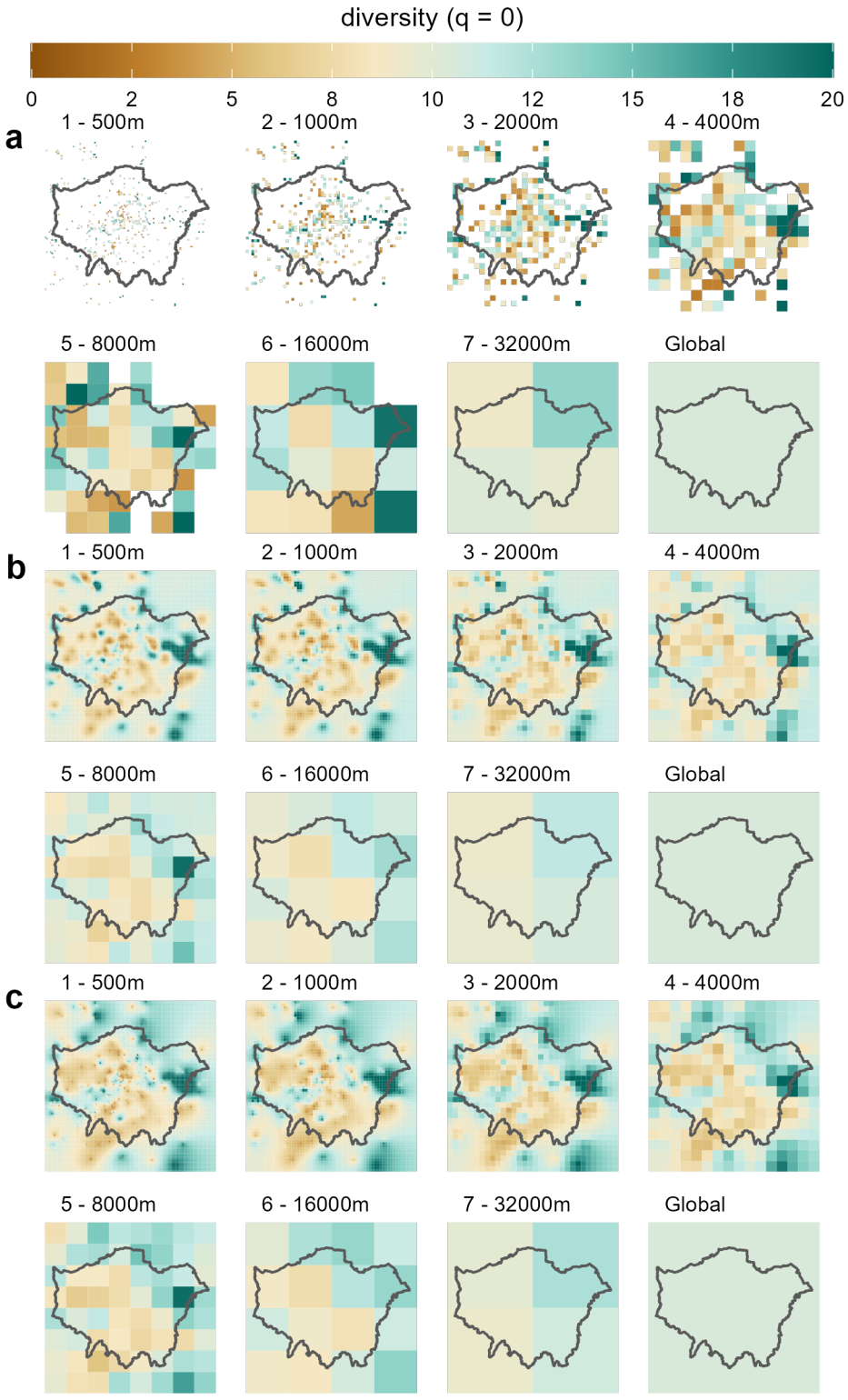


Figure 1-17: Anseriformes + Charadriiformes diversity, q0

Anseriformes + Charadriiformes diversity (R1, q = 0) from a) observed, b) empirical Bayesian kriging, and c) ordinary kriging from scales 1 (500m) to the full study extent (64,000m)

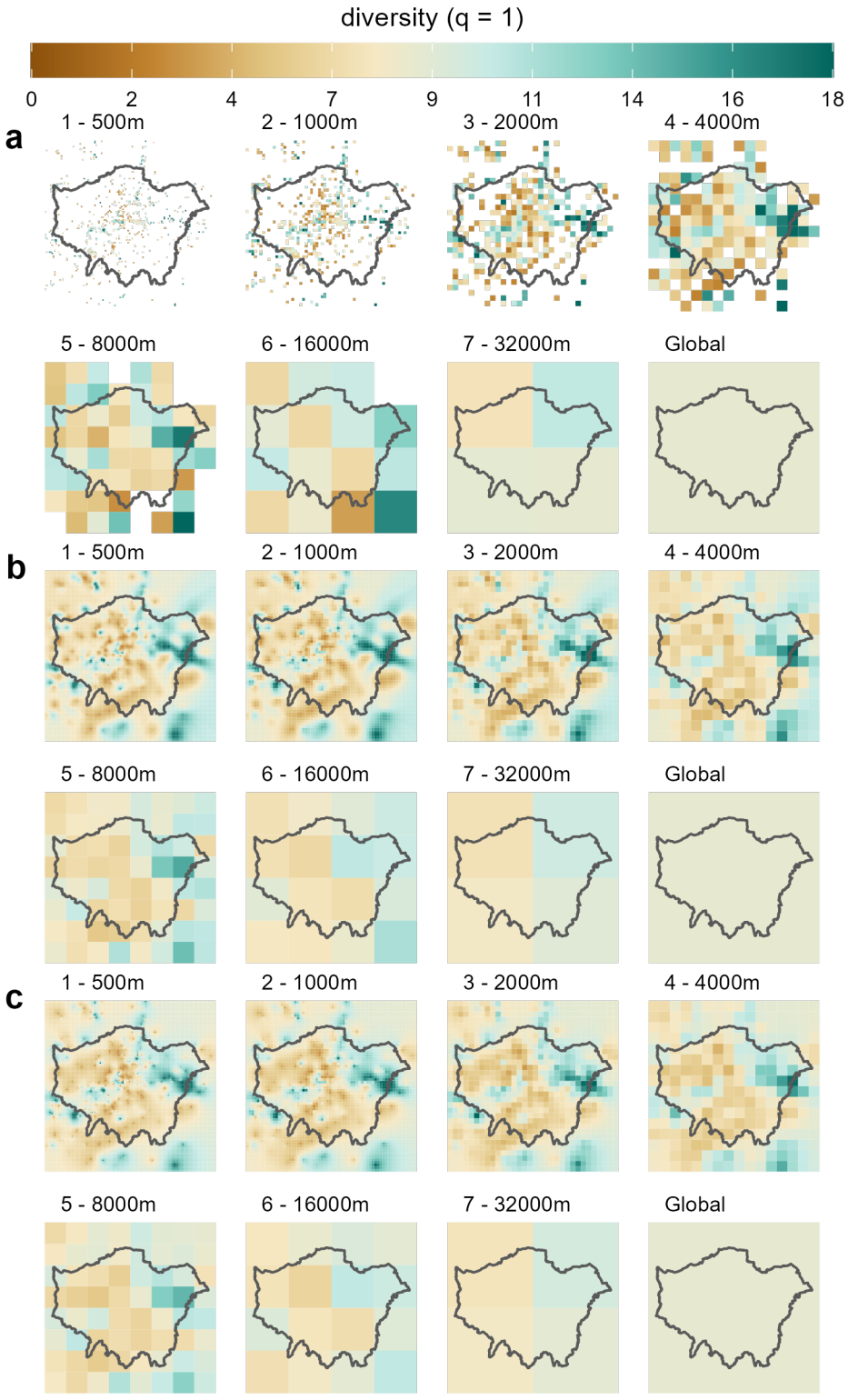


Figure 1-18: Anseriformes + Charadriiformes diversity, q1

Anseriformes + Charadriiformes diversity (R1, q = 1) from a) observed, b) empirical Bayesian kriging, and c) ordinary kriging from scales 1 (500m) to the full study extent (64,000m)

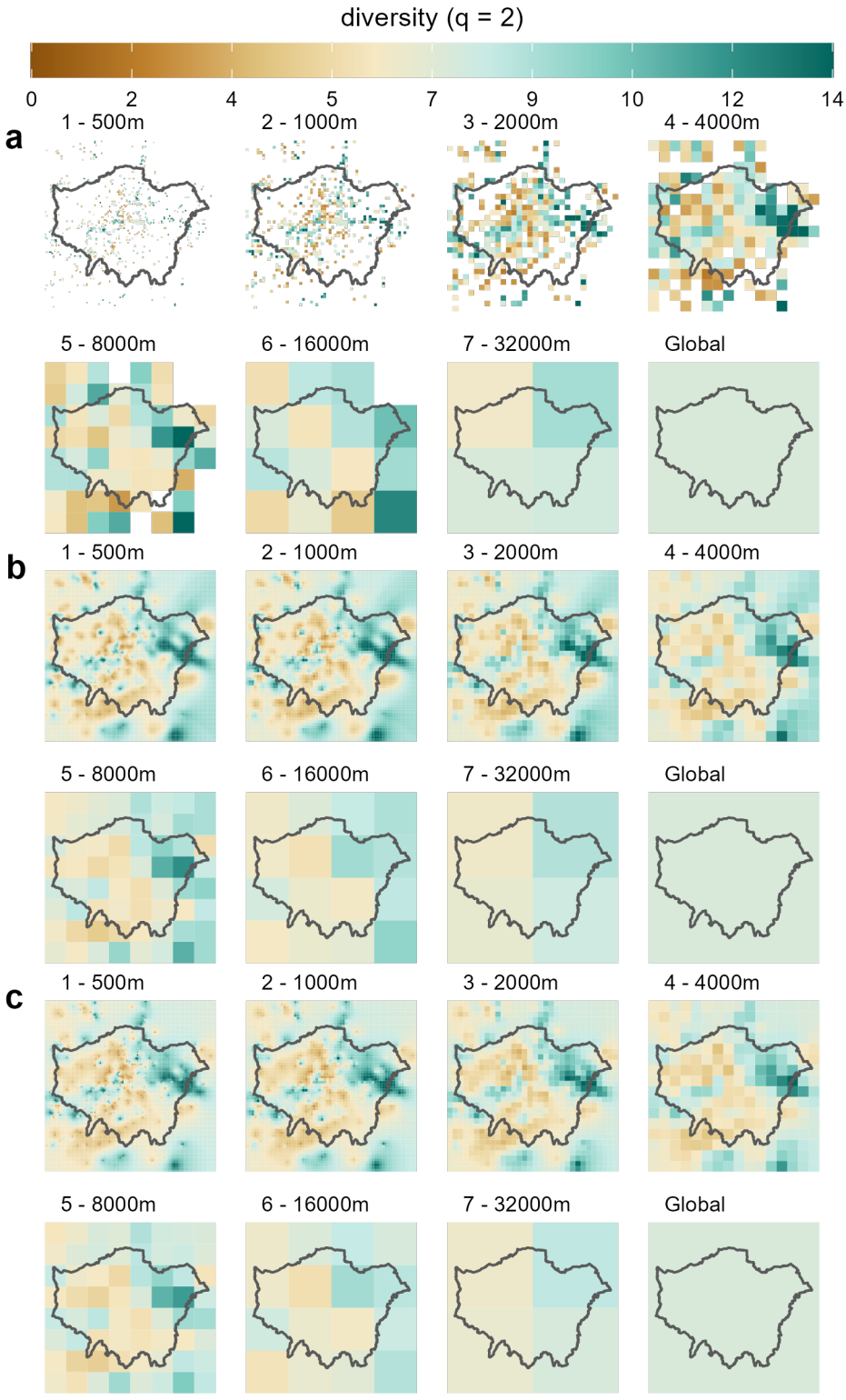


Figure 1-19: Anseriformes + Charadriiformes diversity, q2

Anseriformes + Charadriiformes diversity (R1, q = 2) from a) observed, b) empirical Bayesian kriging, and c) ordinary kriging from scales 1 (500m) to the full study extent (64,000m)

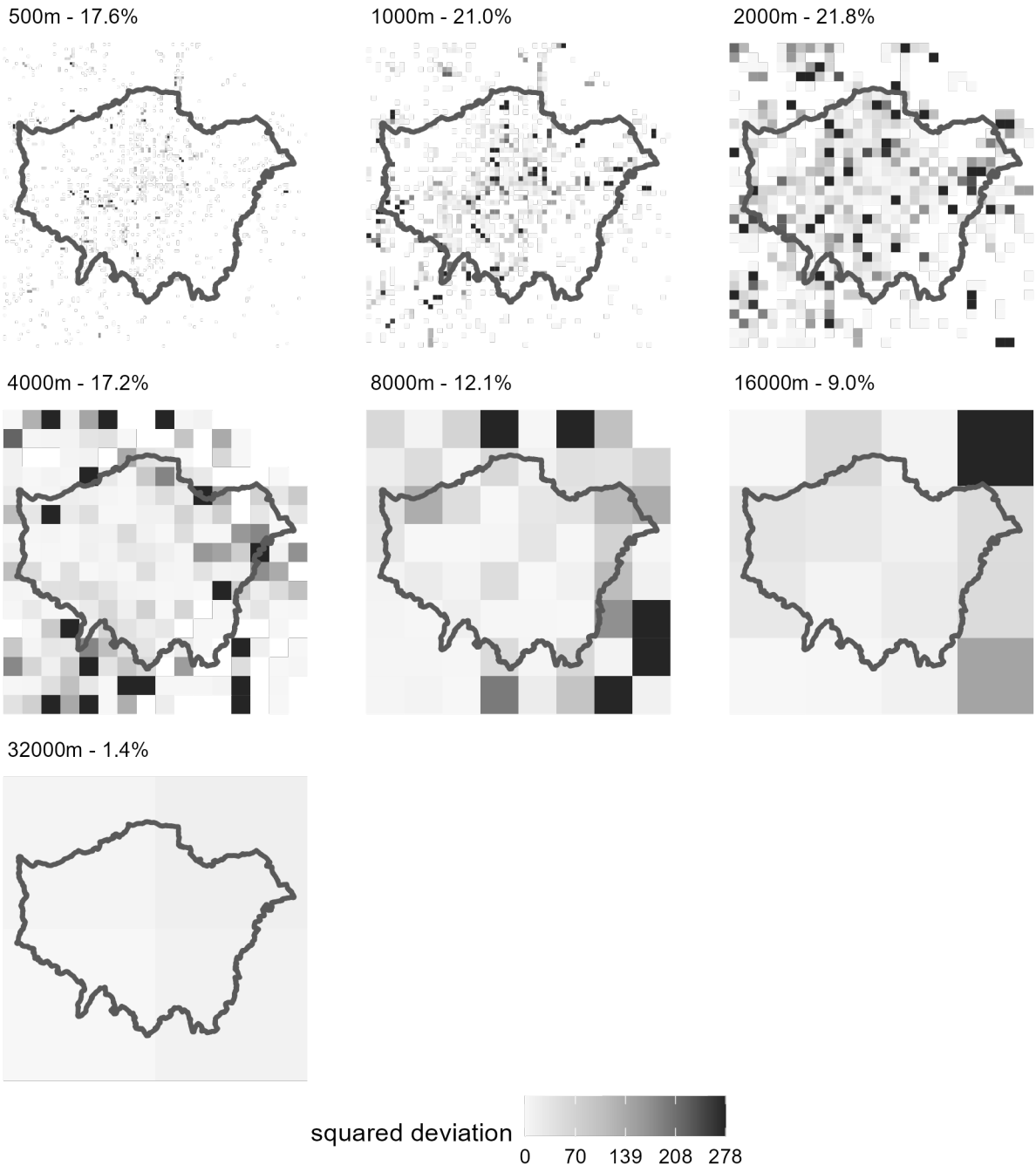


Figure 1-20: All species squared deviations, q0

Diversity (q = 0) squared deviations for all species from scales 1 (500m) to 7 (32,000m)

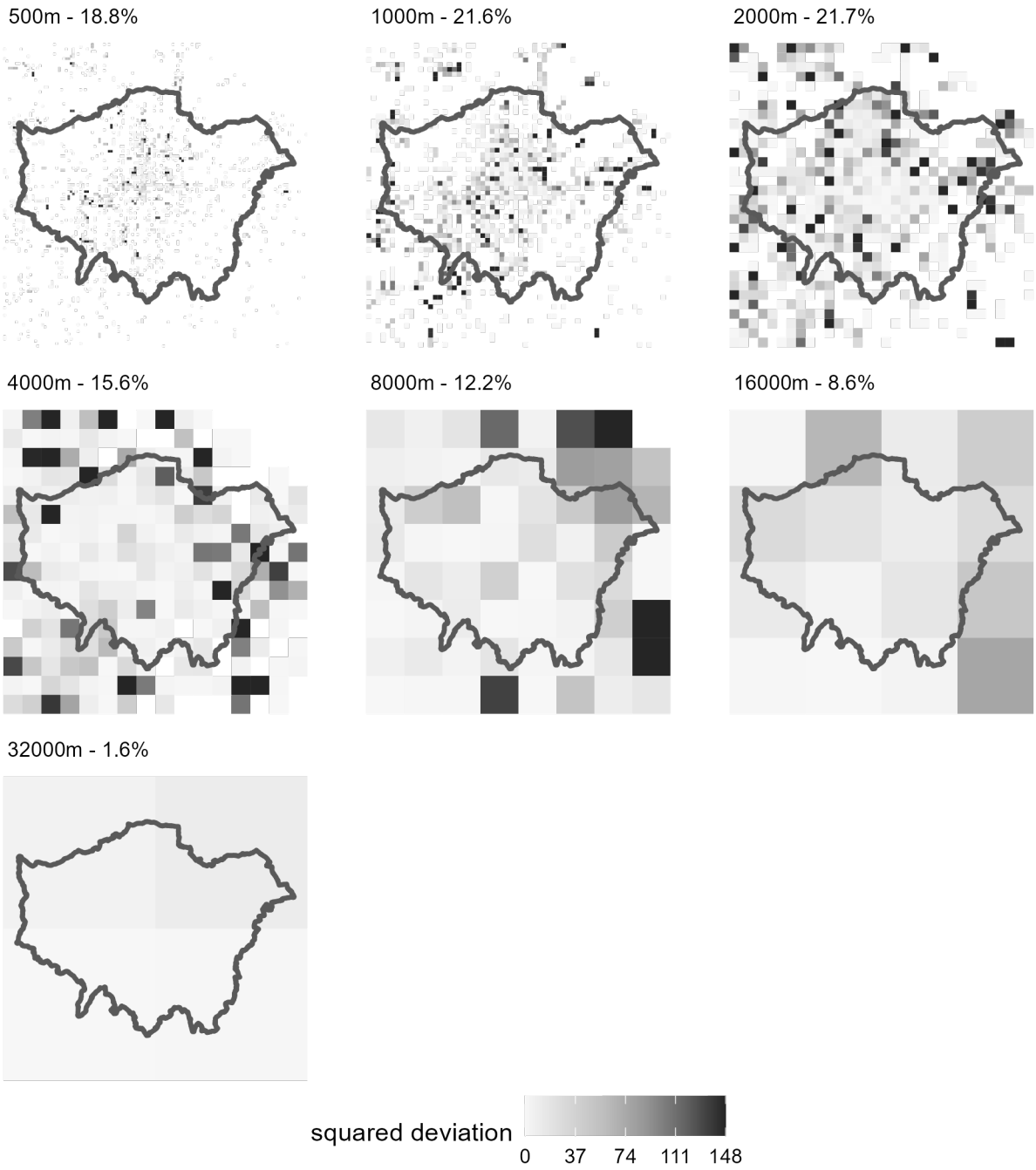


Figure 1-21: All species squared deviations, q1

Diversity (q = 1) squared deviations for all species from scales 1 (500m) to 7 (32,000m)

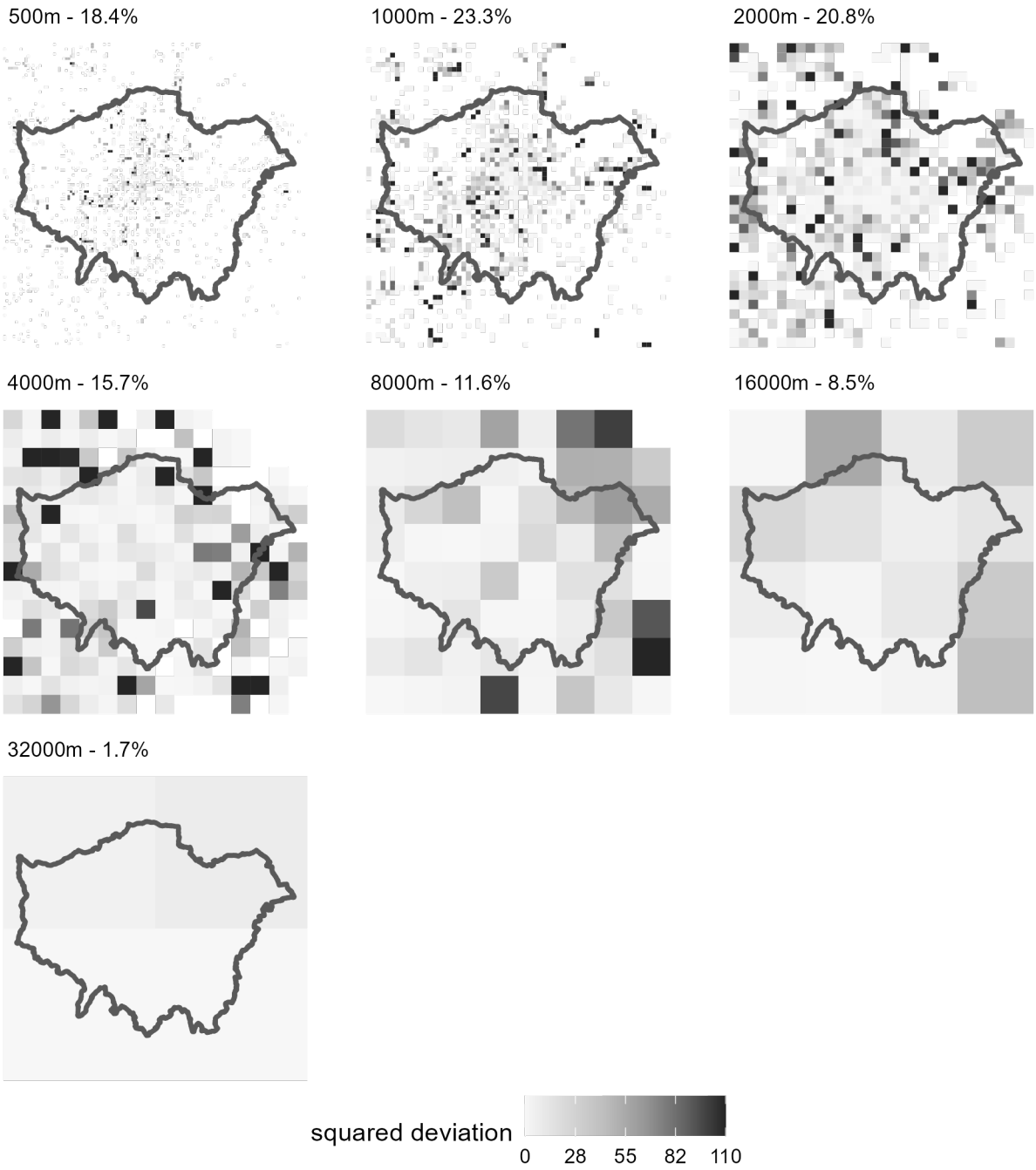


Figure 1-22: All species squared deviations, q2

Diversity (q = 2) squared deviations for all species from scales 1 (500m) to 7 (32,000m)

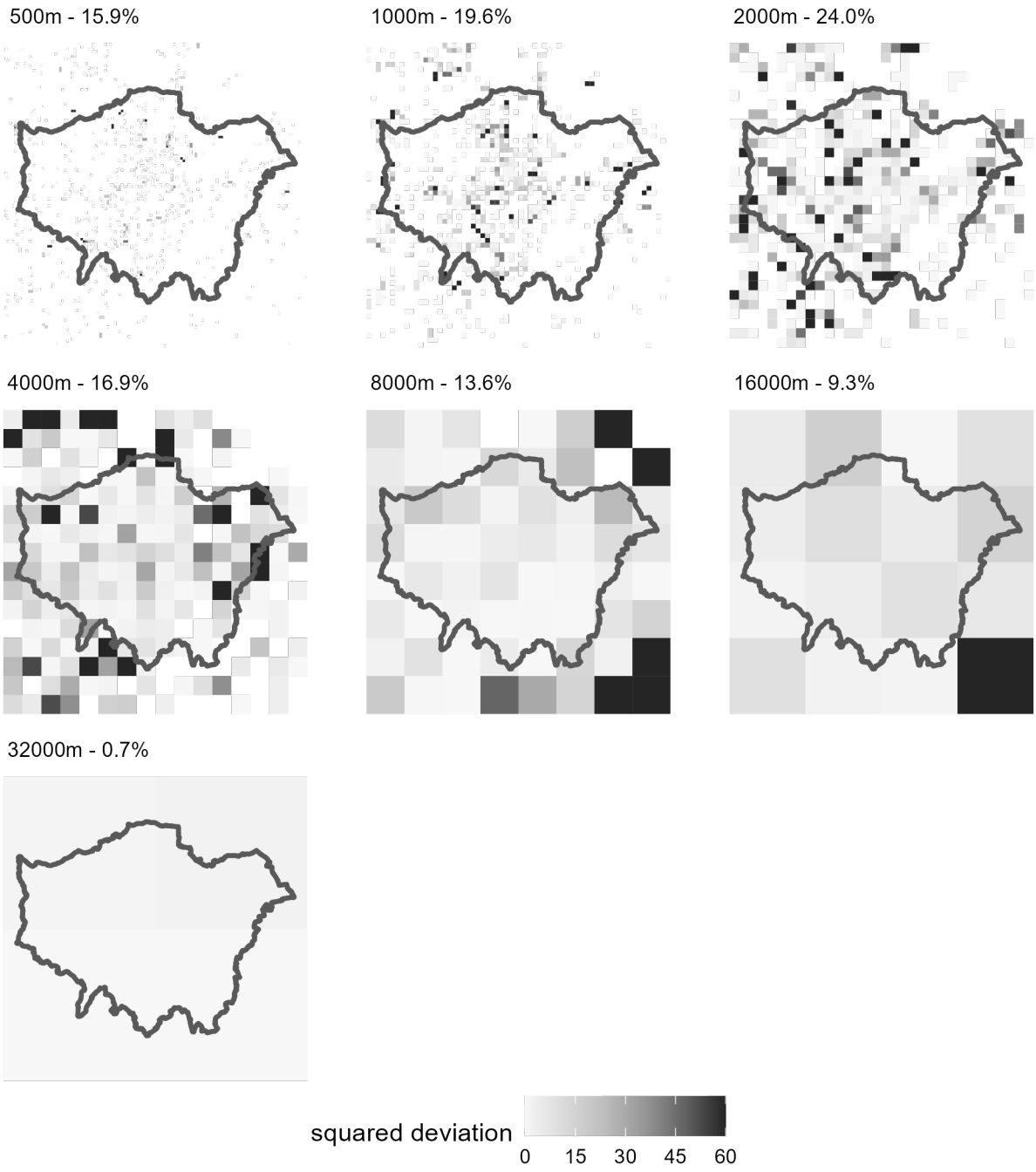


Figure 1-23: Passeriformes squared deviations, q0

Passeriformes diversity (q = 0) squared deviations from scales 1 (500m) to 7 (32,000m)

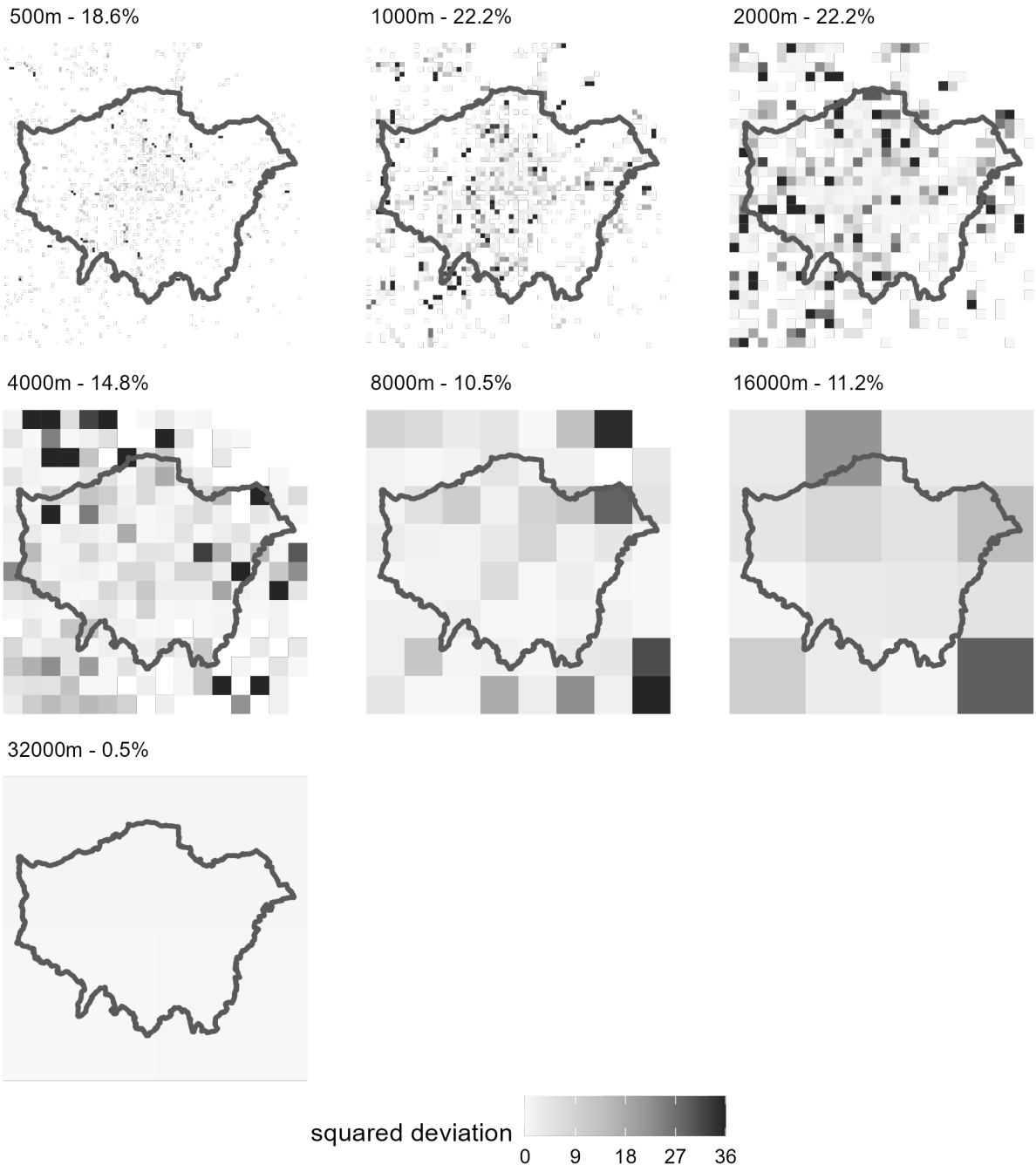


Figure 1-24: Passeriformes squared deviations, q1

Passeriformes diversity (q = 1) squared deviations from scales 1 (500m) to 7 (32,000m)

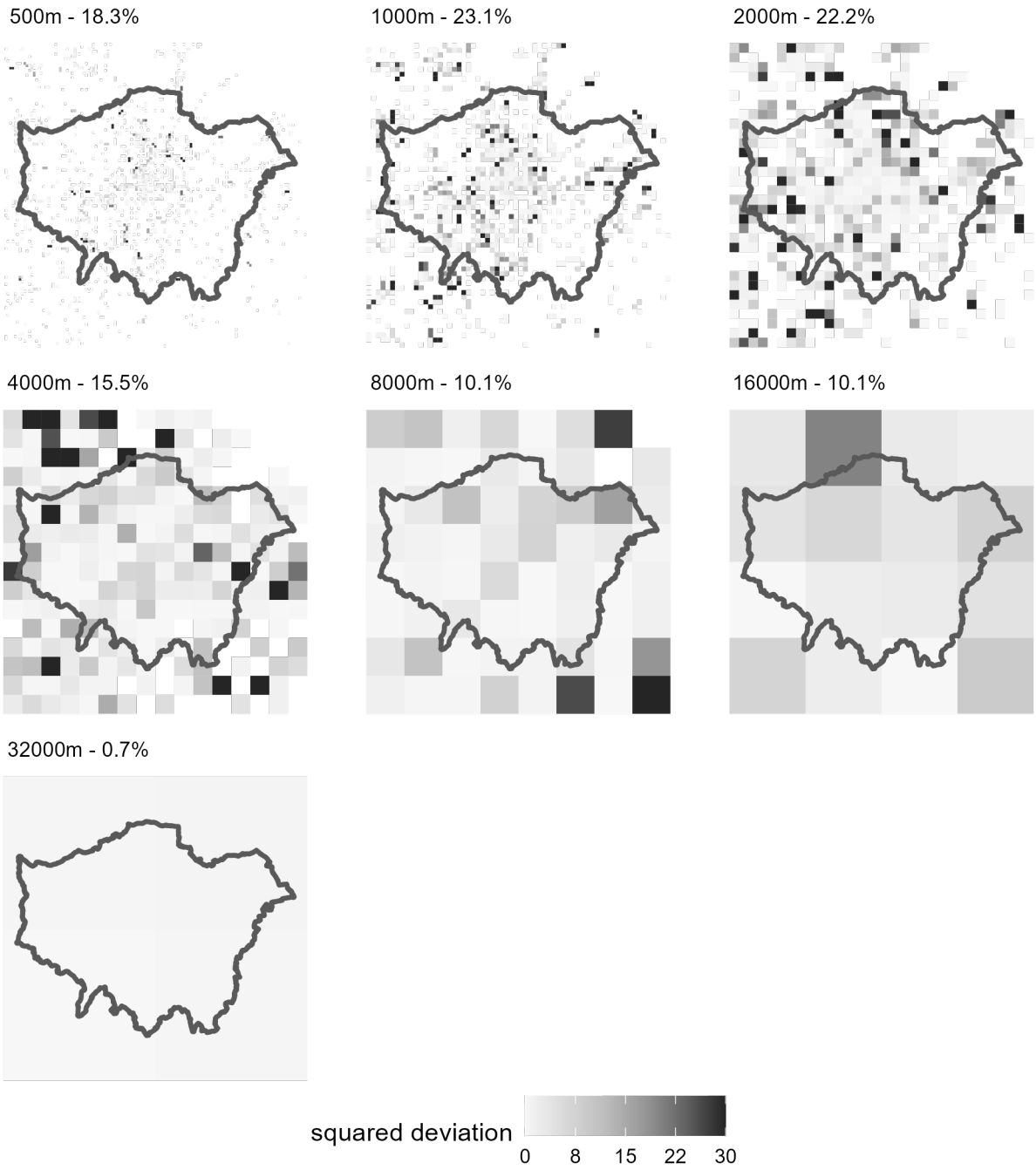


Figure 1-25: Passeriformes squared deviations, q2

Passeriformes diversity (q = 2) squared deviations from scales 1 (500m) to 7 (32,000m)

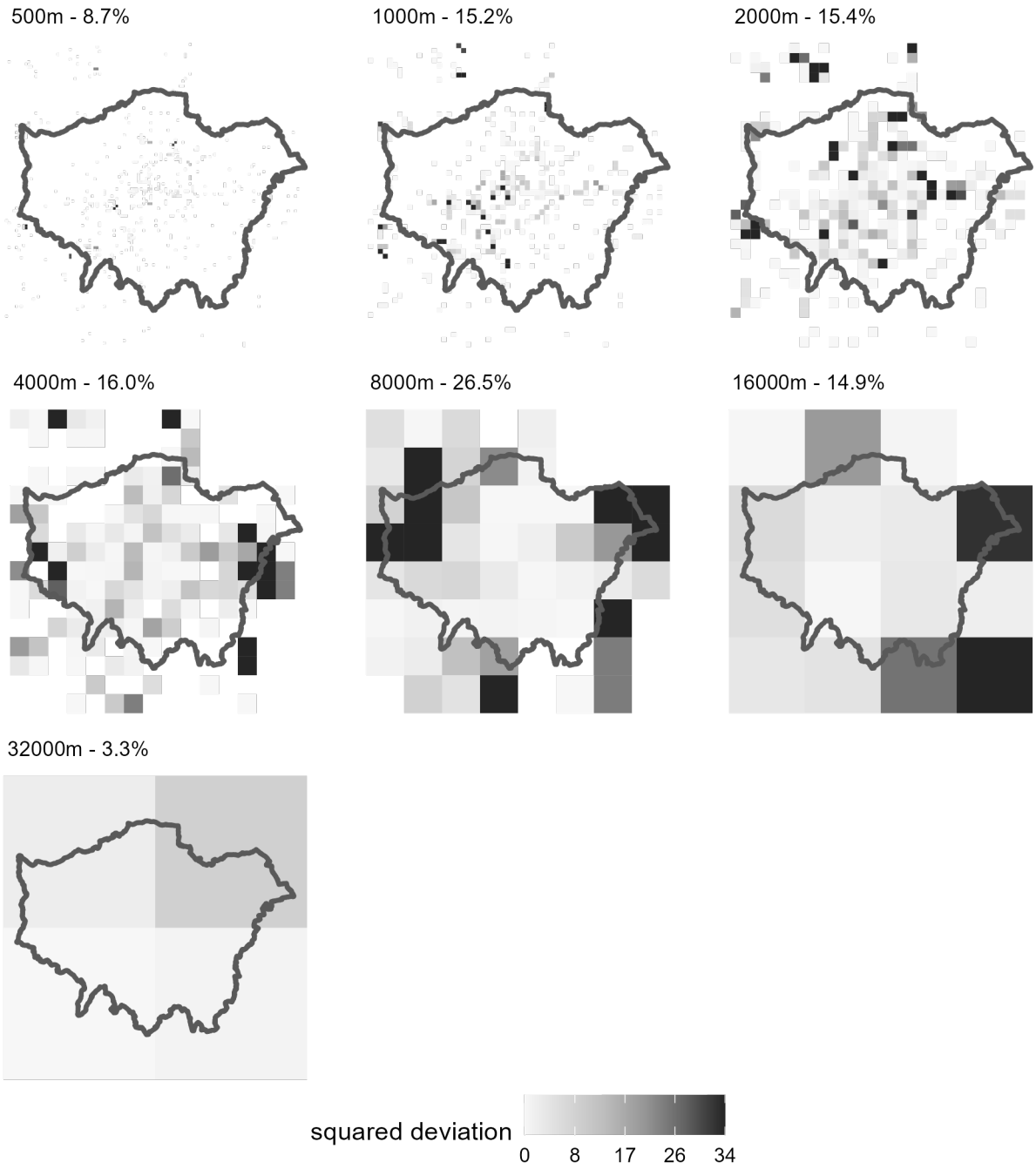


Figure 1-26: Anseriformes + Charadriiformes squared deviations, q0

Anseriformes + Charadriiformes diversity (q = 0) squared deviations from scales 1 (500m) to 7 (32,000m)

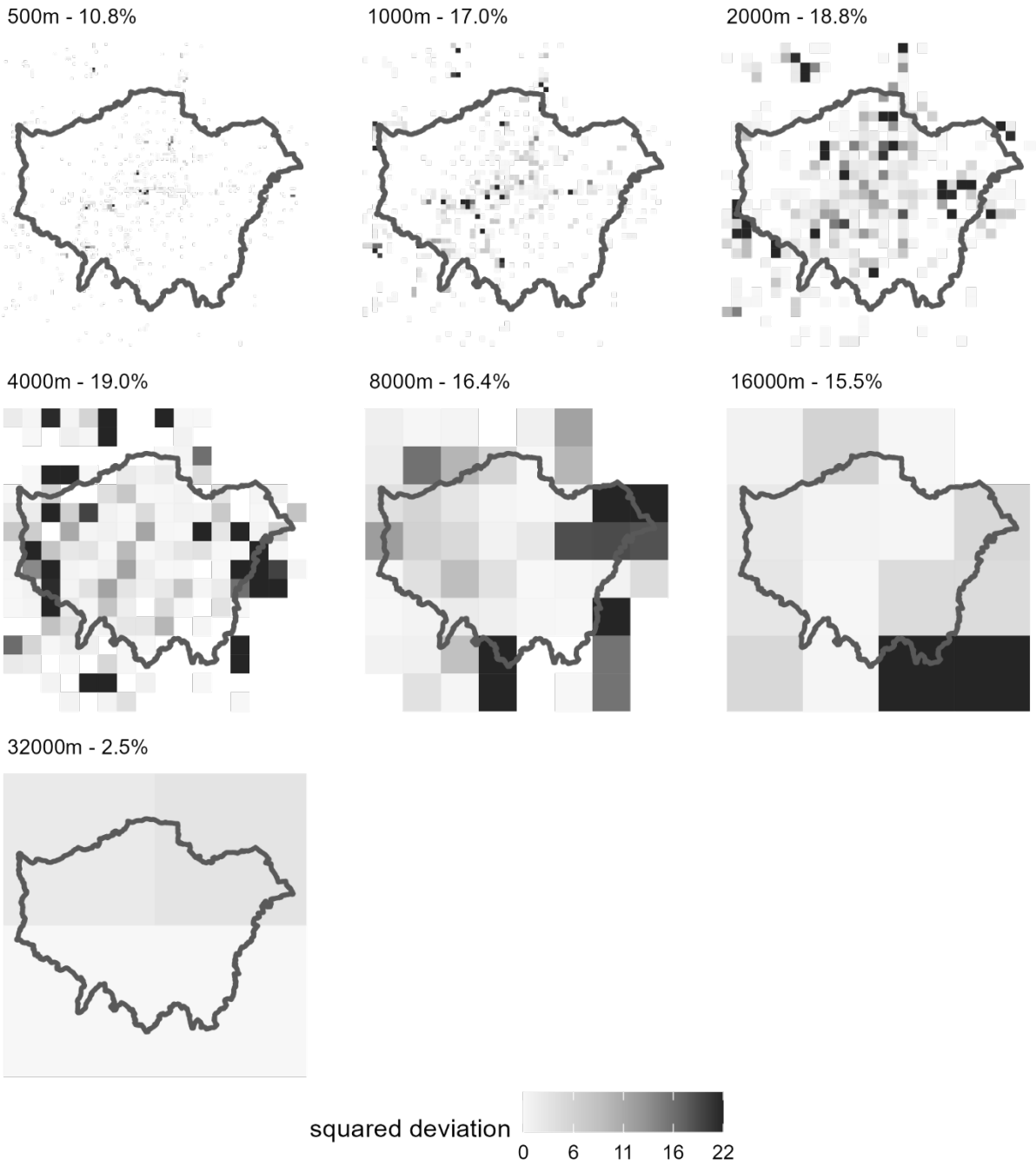


Figure 1-27: Anseriformes + Charadriiformes squared deviations, q1

Anseriformes + Charadriiformes diversity (q = 1) squared deviations from scales 1 (500m) to 7 (32,000m)

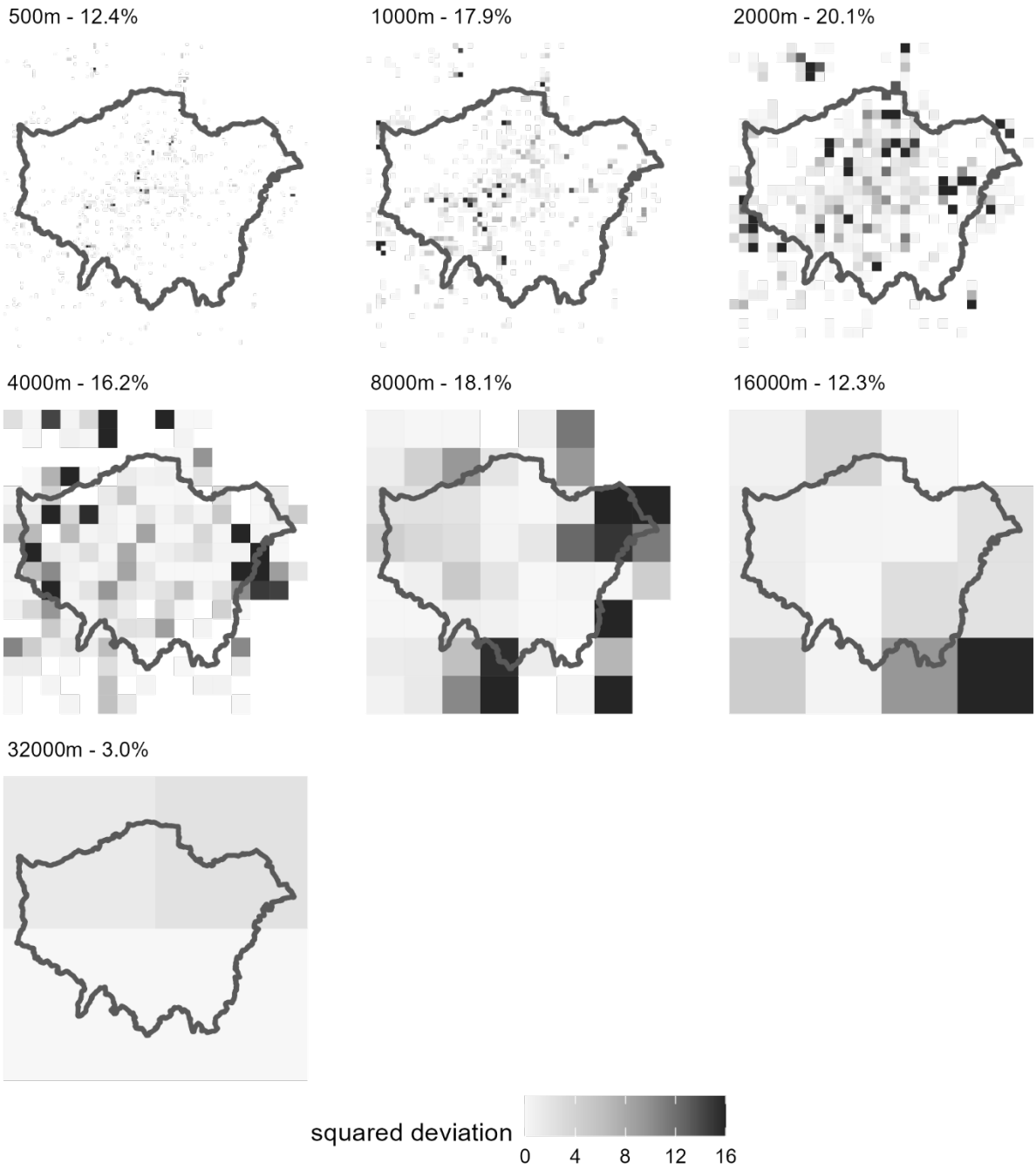


Figure 1-28: Anseriformes + Charadriiformes squared deviations, q2

Anseriformes + Charadriiformes diversity (q = 2) squared deviations from scales 1 (500m) to 7 (32,000m)

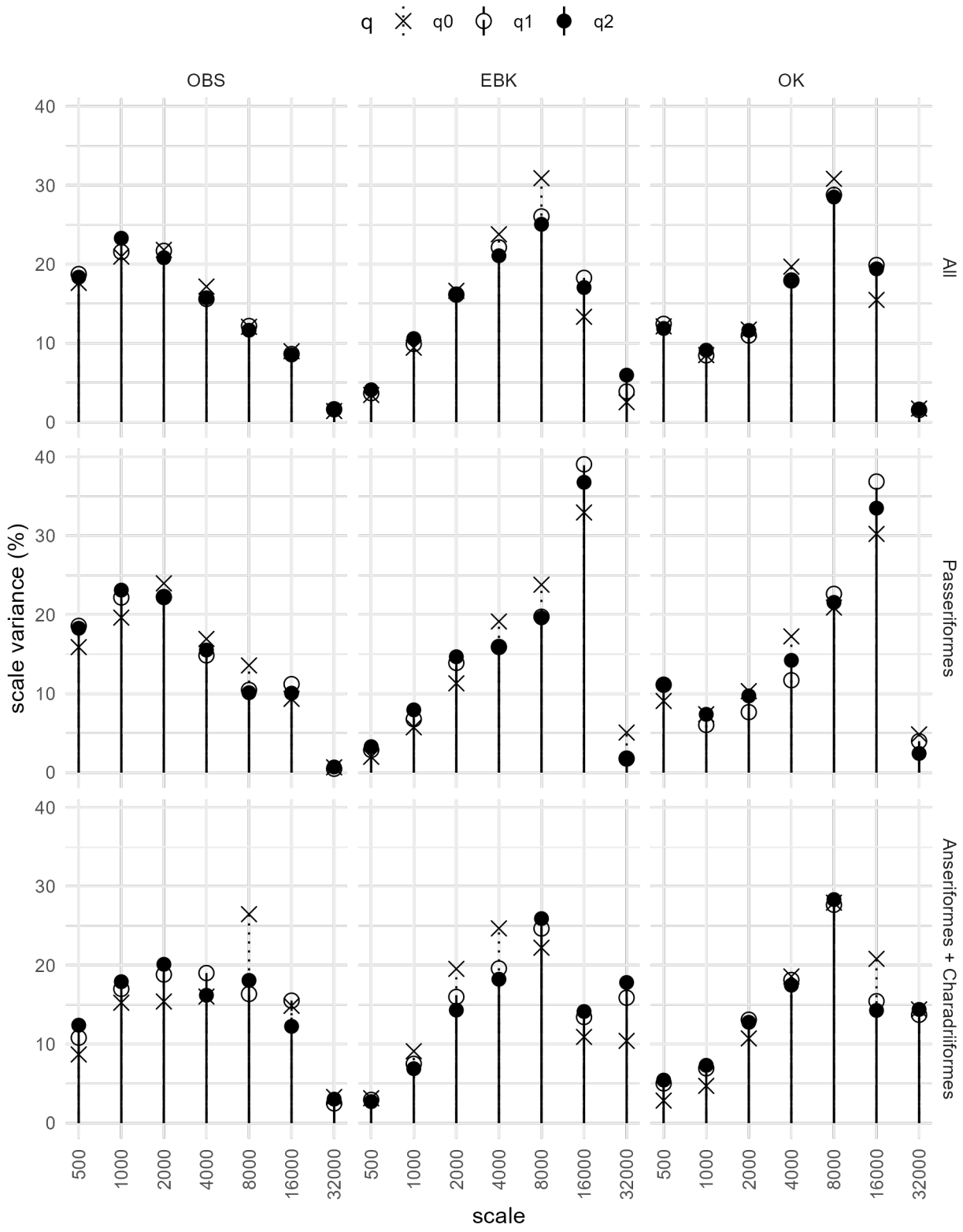


Figure 1-29: Scale variance components for run R1

(starting scale = 500m)

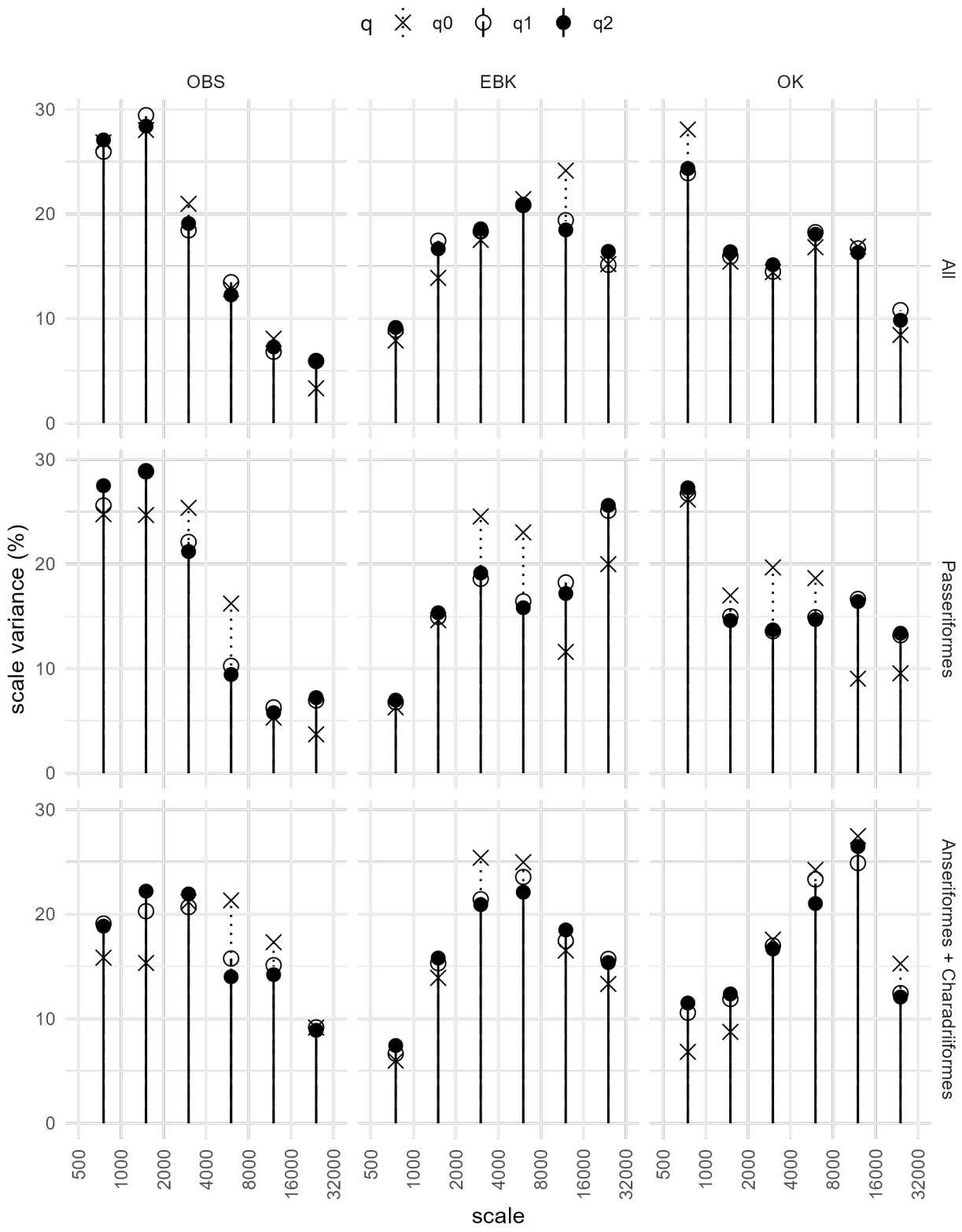


Figure 1-30: Scale variance components for run R2

(starting scale = 750m)

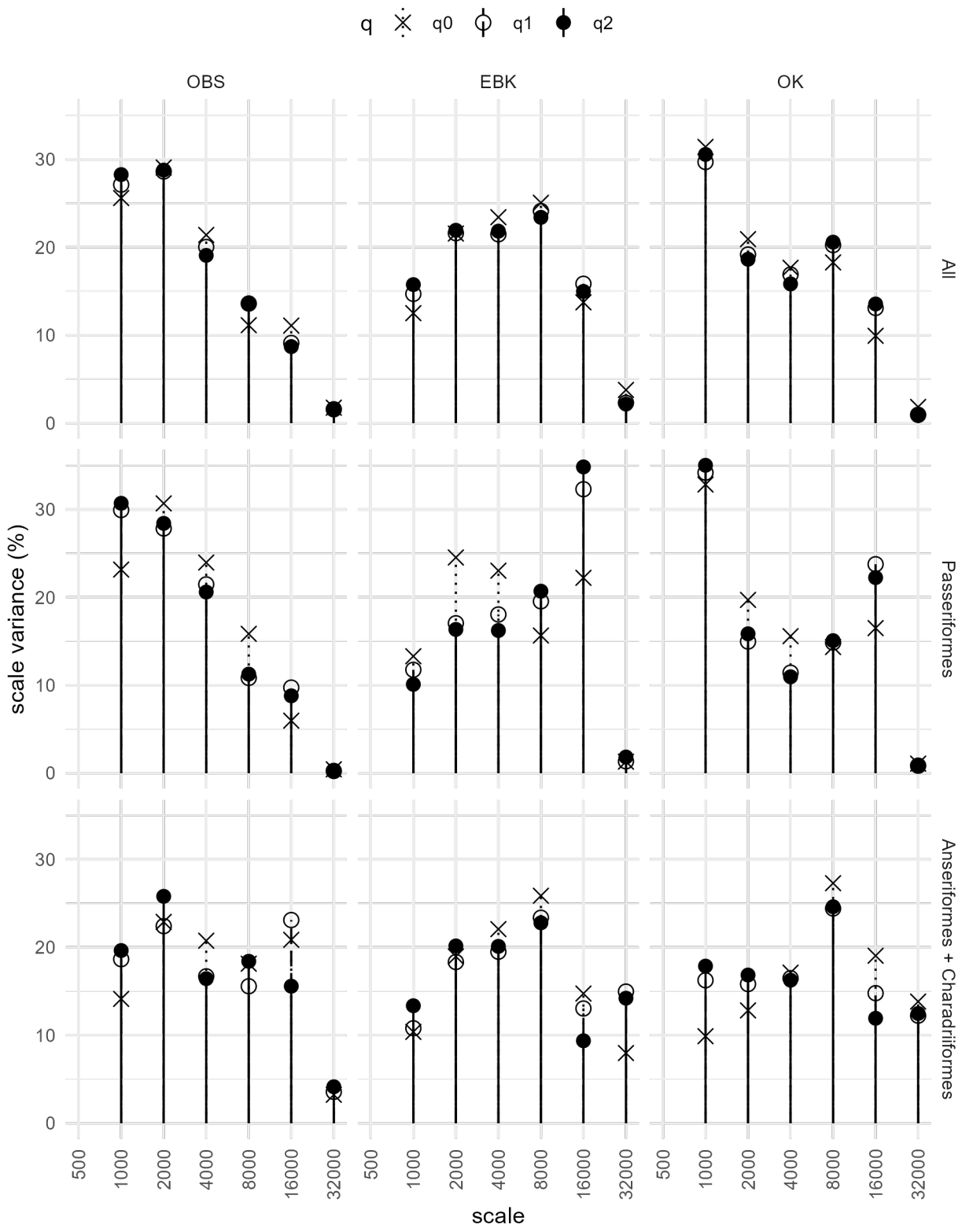


Figure 1-31: Scale variance components for run R3

(starting scale = 1,000m)

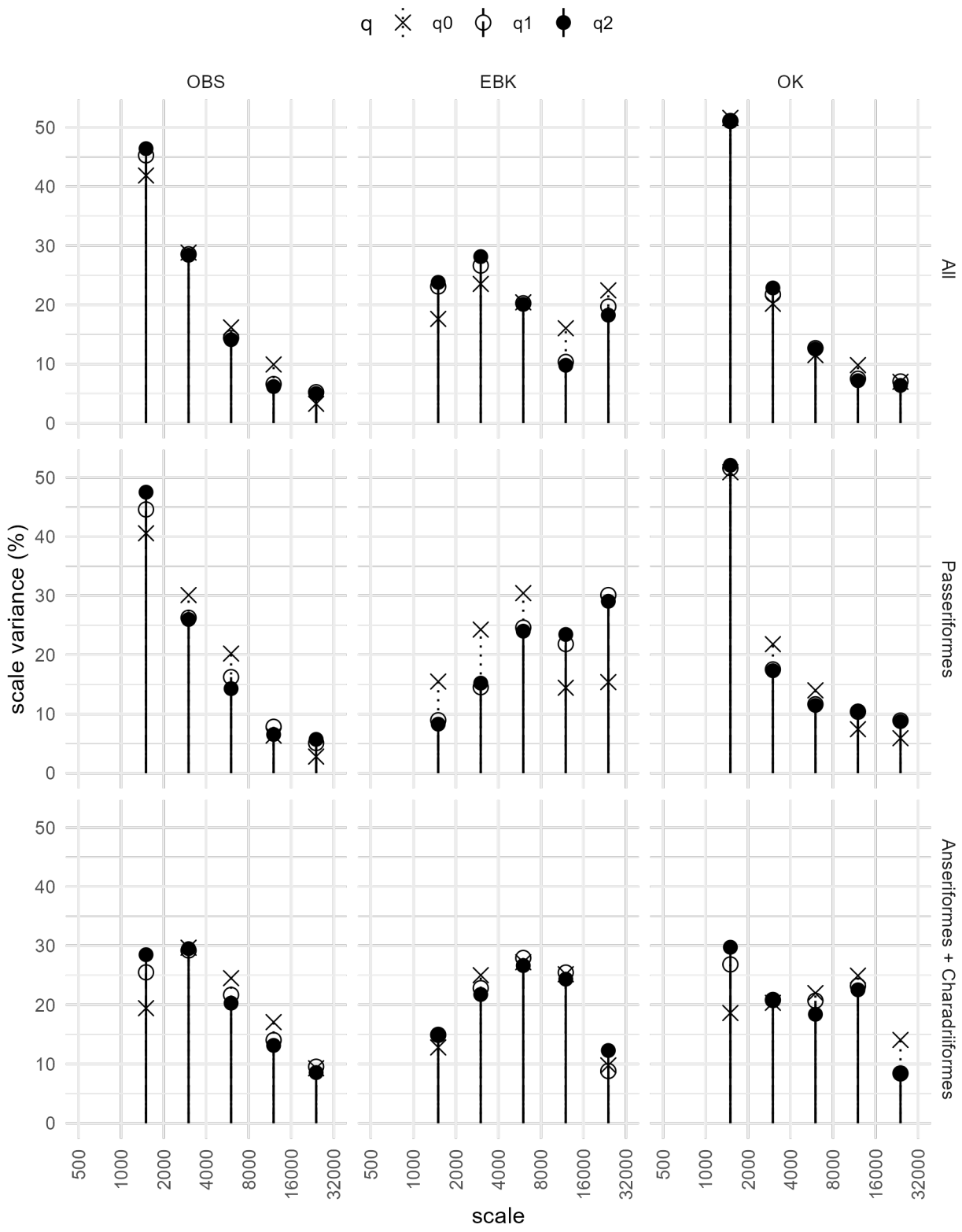


Figure 1-32: Scale variance components for run R4

(starting scale = 1,500m)

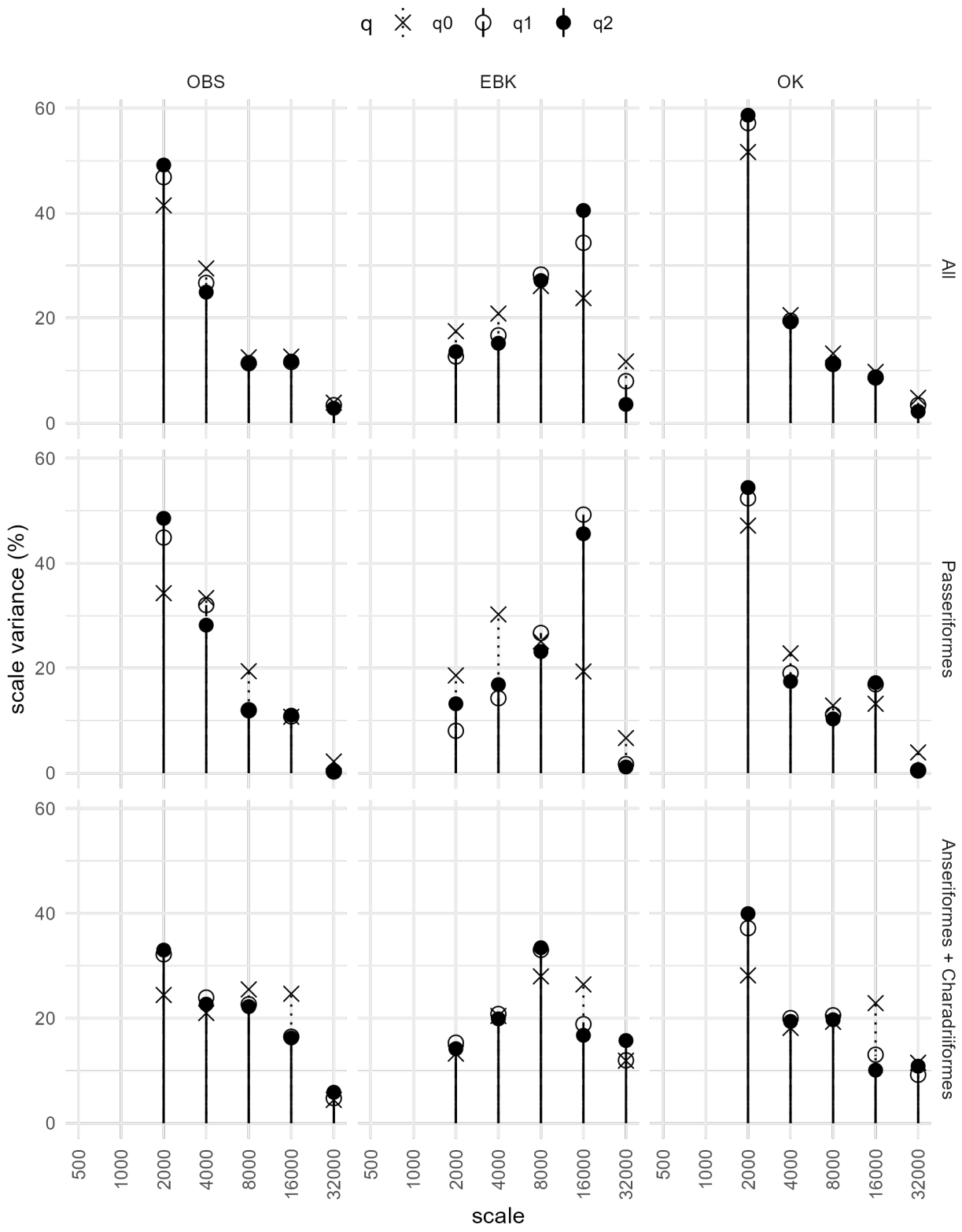


Figure 1-33: Scale variance components for run R5

(starting scale = 2,000m)

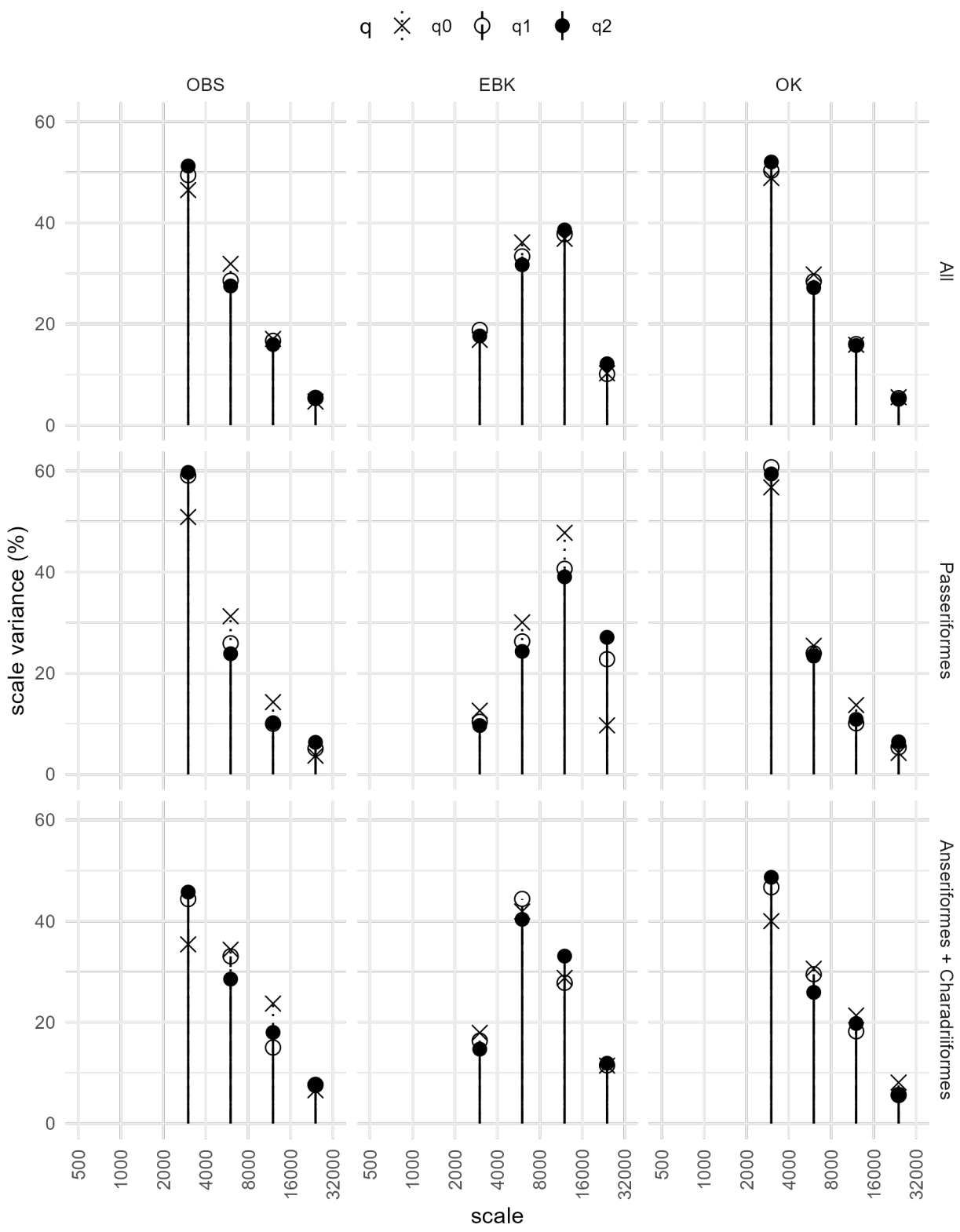


Figure 1-34: Scale variance components for run R6

(starting scale = 3,000m)

Table 1-1: Observation statistics for each group of species

Group	Order	Observations	Observers	Checklists	Species
1	All	672,316	4,006	40,287	279
2	Passeriformes	331,973	3,704	38,697	96
3	Anseriformes + Charadriiformes	155,950	3,505	30,051	112

Table 1-2: Included eBird observations within study area

Obs. = Number of observations

Species	Obs.	Common name	Order	Family
Corvus corone	29212	Carrion Crow	Passeriformes	Corvidae
Pica pica	27176	Eurasian Magpie	Passeriformes	Corvidae
Erithacus rubecula	26327	European Robin	Passeriformes	Muscicapidae
Cyanistes caeruleus	22608	Eurasian Blue Tit	Passeriformes	Paridae
Parus major	21324	Great Tit	Passeriformes	Paridae
Turdus merula	20131	Eurasian Blackbird	Passeriformes	Turdidae
Troglodytes troglodytes	17698	Eurasian Wren	Passeriformes	Troglodytidae
Carduelis carduelis	15469	European Goldfinch	Passeriformes	Fringillidae
Sturnus vulgaris	14172	European Starling	Passeriformes	Sturnidae
Prunella modularis	11191	Dunnock	Passeriformes	Prunellidae
Aegithalos caudatus	10091	Long-tailed Tit	Passeriformes	Aegithalidae
Corvus monedula	9869	Eurasian Jackdaw	Passeriformes	Corvidae
Passer domesticus	8806	House Sparrow	Passeriformes	Passeridae
Phylloscopus collybita	8075	Common Chiffchaff	Passeriformes	Phylloscopidae
Garrulus glandarius	7143	Eurasian Jay	Passeriformes	Corvidae
Fringilla coelebs	6910	Common Chaffinch	Passeriformes	Fringillidae
Turdus philomelos	6739	Song Thrush	Passeriformes	Turdidae
Sylvia atricapilla	6607	Eurasian Blackcap	Passeriformes	Sylviidae
Motacilla alba	6395	White Wagtail	Passeriformes	Motacillidae
Chloris chloris	5580	European Greenfinch	Passeriformes	Fringillidae
Regulus regulus	5043	Goldcrest	Passeriformes	Regulidae
Turdus iliacus	4624	Redwing	Passeriformes	Turdidae
Periparus ater	4443	Coal Tit	Passeriformes	Paridae
Motacilla cinerea	3629	Gray Wagtail	Passeriformes	Motacillidae
Cettia cetti	3093	Cetti's Warbler	Passeriformes	Scotocercidae
Sitta europaea	3067	Eurasian Nuthatch	Passeriformes	Sittidae
Turdus viscivorus	2400	Mistle Thrush	Passeriformes	Turdidae
Anthus pratensis	1876	Meadow Pipit	Passeriformes	Motacillidae
Linaria cannabina	1870	Eurasian Linnet	Passeriformes	Fringillidae
Hirundo rustica	1802	Barn Swallow	Passeriformes	Hirundinidae
Curruca communis	1770	Greater Whitethroat	Passeriformes	Sylviidae
Acrocephalus scirpaceus	1542	Common Reed Warbler	Passeriformes	Acrocephalidae
Alauda arvensis	1426	Eurasian Skylark	Passeriformes	Alaudidae
Emberiza schoeniclus	1418	Reed Bunting	Passeriformes	Emberizidae
Delichon urbicum	1399	Western House-Martin	Passeriformes	Hirundinidae
Riparia riparia	1074	Bank Swallow	Passeriformes	Hirundinidae
Spinus spinus	992	Eurasian Siskin	Passeriformes	Fringillidae
Turdus pilaris	973	Fieldfare	Passeriformes	Turdidae
Certhia familiaris	909	Eurasian Treecreeper	Passeriformes	Certhiidae
Phylloscopus trochilus	816	Willow Warbler	Passeriformes	Phylloscopidae
Corvus frugilegus	683	Rook	Passeriformes	Corvidae
Saxicola rubicola	623	European Stonechat	Passeriformes	Muscicapidae

Table 1-2: Continued

Species	Obs.	Common name	Order	Family
Acrocephalus schoenobaenus	513	Sedge Warbler	Passeriformes	Acrocephalidae
Sylvia borin	436	Garden Warbler	Passeriformes	Sylviidae
Acanthis cabaret	421	Lesser Redpoll	Passeriformes	Fringillidae
Curruca curruca	372	Lesser Whitethroat	Passeriformes	Sylviidae
Pyrrhula pyrrhula	325	Eurasian Bullfinch	Passeriformes	Fringillidae
Motacilla flava	299	Western Yellow Wagtail	Passeriformes	Motacillidae
Regulus ignicapilla	262	Common Firecrest	Passeriformes	Regulidae
Corvus corax	248	Common Raven	Passeriformes	Corvidae
Oenanthe oenanthe	247	Northern Wheatear	Passeriformes	Muscicapidae
Emberiza citrinella	223	Yellowhammer	Passeriformes	Emberizidae
Anthus spinoletta	222	Water Pipit	Passeriformes	Motacillidae
Fringilla montifringilla	183	Brambling	Passeriformes	Fringillidae
Muscicapa striata	151	Spotted Flycatcher	Passeriformes	Muscicapidae
Saxicola rubetra	143	Whinchat	Passeriformes	Muscicapidae
Poecile palustris	111	Marsh Tit	Passeriformes	Paridae
Phoenicurus phoenicurus	64	Common Redstart	Passeriformes	Muscicapidae
Anthus petrosus	61	Rock Pipit	Passeriformes	Motacillidae
Phoenicurus ochruros	58	Black Redstart	Passeriformes	Muscicapidae
Turdus torquatus	55	Ring Ouzel	Passeriformes	Turdidae
Emberiza pusilla	46	Little Bunting	Passeriformes	Emberizidae
Phylloscopus ibericus	46	Iberian Chiffchaff	Passeriformes	Phylloscopidae
Coccothraustes coccothraustes	42	Hawfinch	Passeriformes	Fringillidae
Passer montanus	42	Eurasian Tree Sparrow	Passeriformes	Passeridae
Ficedula hypoleuca	41	European Pied Flycatcher	Passeriformes	Muscicapidae
Phylloscopus inornatus	41	Yellow-browed Warbler	Passeriformes	Phylloscopidae
Emberiza calandra	39	Corn Bunting	Passeriformes	Emberizidae
Panurus biarmicus	35	Bearded Reedling	Passeriformes	Panuridae
Luscinia megarhynchos	34	Common Nightingale	Passeriformes	Muscicapidae
Bombycilla garrulus	31	Bohemian Waxwing	Passeriformes	Bombycillidae
Loxia curvirostra	30	Red Crossbill	Passeriformes	Fringillidae
Eremophila alpestris	24	Horned Lark	Passeriformes	Alaudidae
Anthus trivialis	23	Tree Pipit	Passeriformes	Motacillidae
Phylloscopus fuscatus	19	Dusky Warbler	Passeriformes	Phylloscopidae
Locustella naevia	15	Common Grasshopper Warbler	Passeriformes	Locustellidae
Lanius collurio	13	Red-backed Shrike	Passeriformes	Laniidae
Lullula arborea	10	Wood Lark	Passeriformes	Alaudidae
Emberiza rustica	9	Rustic Bunting	Passeriformes	Emberizidae
Serinus serinus	7	European Serin	Passeriformes	Fringillidae
Loxia pytyopsittacus	5	Parrot Crossbill	Passeriformes	Fringillidae
Phylloscopus sibilatrix	4	Wood Warbler	Passeriformes	Phylloscopidae
Remiz pendulinus	4	Eurasian Penduline-Tit	Passeriformes	Remizidae
Carpodacus erythrinus	3	Common Rosefinch	Passeriformes	Fringillidae
Motacilla citreola	3	Citrine Wagtail	Passeriformes	Motacillidae
Acanthis flammea	2	Common Redpoll	Passeriformes	Fringillidae

Table 1-2: Continued

Species	Obs.	Common name	Order	Family
Acrocephalus arundinaceus	2	Great Reed Warbler	Passeriformes	Acrocephalidae
Curruca nisoria	2	Barred Warbler	Passeriformes	Sylviidae
Euplectes afer	2	Yellow-crowned Bishop	Passeriformes	Ploceidae
Junco hyemalis	2	Dark-eyed Junco	Passeriformes	Passerellidae
Lanius excubitor	2	Great Gray Shrike	Passeriformes	Laniidae
Linaria flavirostris	2	Twite	Passeriformes	Fringillidae
Calcarius lapponicus	1	Lapland Longspur	Passeriformes	Calcariidae
Cecropis daurica	1	Red-rumped Swallow	Passeriformes	Hirundinidae
Pastor roseus	1	Rosy Starling	Passeriformes	Sturnidae
Serinus canaria	1	Island Canary	Passeriformes	Fringillidae
Chroicocephalus ridibundus	18602	Black-headed Gull	Charadriiformes	Laridae
Larus argentatus	15474	Herring Gull	Charadriiformes	Laridae
Larus fuscus	10401	Lesser Black-backed Gull	Charadriiformes	Laridae
Larus canus	4614	Common Gull	Charadriiformes	Laridae
Vanellus vanellus	2035	Northern Lapwing	Charadriiformes	Charadriidae
Larus marinus	1646	Great Black-backed Gull	Charadriiformes	Laridae
Sterna hirundo	1323	Common Tern	Charadriiformes	Laridae
Gallinago gallinago	903	Common Snipe	Charadriiformes	Scolopacidae
Tringa ochropus	523	Green Sandpiper	Charadriiformes	Scolopacidae
Actitis hypoleucos	517	Common Sandpiper	Charadriiformes	Scolopacidae
Tringa totanus	478	Common Redshank	Charadriiformes	Scolopacidae
Haematopus ostralegus	458	Eurasian Oystercatcher	Charadriiformes	Haematopodidae
Charadrius dubius	391	Little Ringed Plover	Charadriiformes	Charadriidae
Larus michahellis	303	Yellow-legged Gull	Charadriiformes	Laridae
Limosa limosa	181	Black-tailed Godwit	Charadriiformes	Scolopacidae
Recurvirostra avosetta	177	Pied Avocet	Charadriiformes	Recurvirostridae
Calidris alpina	172	Dunlin	Charadriiformes	Scolopacidae
Numenius arquata	151	Eurasian Curlew	Charadriiformes	Scolopacidae
Larus cachinnans	133	Caspian Gull	Charadriiformes	Laridae
Lymnocryptes minimus	132	Jack Snipe	Charadriiformes	Scolopacidae
Ichthyaetus melanocephalus	119	Mediterranean Gull	Charadriiformes	Laridae
Hydrocoloeus minutus	112	Little Gull	Charadriiformes	Laridae
Charadrius hiaticula	95	Common Ringed Plover	Charadriiformes	Charadriidae
Tringa nebularia	79	Common Greenshank	Charadriiformes	Scolopacidae
Chlidonias niger	58	Black Tern	Charadriiformes	Laridae
Calidris pugnax	48	Ruff	Charadriiformes	Scolopacidae
Numenius phaeopus	47	Whimbrel	Charadriiformes	Scolopacidae
Sterna paradisaea	44	Arctic Tern	Charadriiformes	Laridae
Scolopax rusticola	39	Eurasian Woodcock	Charadriiformes	Scolopacidae
Pluvialis apricaria	33	European Golden-Plover	Charadriiformes	Charadriidae
Limosa lapponica	30	Bar-tailed Godwit	Charadriiformes	Scolopacidae
Tringa glareola	29	Wood Sandpiper	Charadriiformes	Scolopacidae
Calidris alba	27	Sanderling	Charadriiformes	Scolopacidae
Calidris minuta	25	Little Stint	Charadriiformes	Scolopacidae
Larus glaucoides	24	Iceland Gull	Charadriiformes	Laridae

Table 1-2: Continued

Species	Obs.	Common name	Order	Family
Pluvialis squatarola	22	Black-bellied Plover	Charadriiformes	Charadriidae
Phalaropus fulicarius	19	Red Phalarope	Charadriiformes	Scolopacidae
Arenaria interpres	17	Ruddy Turnstone	Charadriiformes	Scolopacidae
Rissa tridactyla	17	Black-legged Kittiwake	Charadriiformes	Laridae
Calidris canutus	14	Red Knot	Charadriiformes	Scolopacidae
Calidris melanotos	13	Pectoral Sandpiper	Charadriiformes	Scolopacidae
Thalasseus sandvicensis	13	Sandwich Tern	Charadriiformes	Laridae
Sternula albifrons	10	Little Tern	Charadriiformes	Laridae
Calidris ferruginea	8	Curlew Sandpiper	Charadriiformes	Scolopacidae
Tringa erythropus	7	Spotted Redshank	Charadriiformes	Scolopacidae
Chlidonias leucopterus	6	White-winged Tern	Charadriiformes	Laridae
Stercorarius longicaudus	6	Long-tailed Jaeger	Charadriiformes	Stercorariidae
Larus hyperboreus	5	Glaucous Gull	Charadriiformes	Laridae
Chroicocephalus philadelphia	4	Bonaparte's Gull	Charadriiformes	Laridae
Burhinus oedicnemus	3	Eurasian Thick-knee	Charadriiformes	Burhinidae
Phalaropus lobatus	2	Red-necked Phalarope	Charadriiformes	Scolopacidae
Stercorarius skua	2	Great Skua	Charadriiformes	Stercorariidae
Uria aalge	2	Common Murre	Charadriiformes	Alcidae
Calidris temminckii	1	Temminck's Stint	Charadriiformes	Scolopacidae
Stercorarius parasiticus	1	Parasitic Jaeger	Charadriiformes	Stercorariidae
Sterna dougallii	1	Roseate Tern	Charadriiformes	Laridae
Tringa stagnatilis	1	Marsh Sandpiper	Charadriiformes	Scolopacidae
Anas platyrhynchos	18649	Mallard	Anseriformes	Anatidae
Branta canadensis	13673	Canada Goose	Anseriformes	Anatidae
Cygnus olor	11910	Mute Swan	Anseriformes	Anatidae
Aythya fuligula	11744	Tufted Duck	Anseriformes	Anatidae
Alopochen aegyptiaca	8896	Egyptian Goose	Anseriformes	Anatidae
Anser anser	6479	Graylag Goose	Anseriformes	Anatidae
Aythya ferina	5122	Common Pochard	Anseriformes	Anatidae
Mareca strepera	5121	Gadwall	Anseriformes	Anatidae
Spatula clypeata	3929	Northern Shoveler	Anseriformes	Anatidae
Anas crecca	3093	Green-winged Teal	Anseriformes	Anatidae
Mareca penelope	1630	Eurasian Wigeon	Anseriformes	Anatidae
Tadorna tadorna	1547	Common Shelduck	Anseriformes	Anatidae
Aix galericulata	1432	Mandarin Duck	Anseriformes	Anatidae
Netta rufina	1068	Red-crested Pochard	Anseriformes	Anatidae
Bucephala clangula	602	Common Goldeneye	Anseriformes	Anatidae
Anas acuta	282	Northern Pintail	Anseriformes	Anatidae
Branta leucopsis	208	Barnacle Goose	Anseriformes	Anatidae
Mergus merganser	179	Common Merganser	Anseriformes	Anatidae
Aythya marila	135	Greater Scaup	Anseriformes	Anatidae
Spatula querquedula	100	Garganey	Anseriformes	Anatidae
Cygnus atratus	95	Black Swan	Anseriformes	Anatidae
Aythya collaris	64	Ring-necked Duck	Anseriformes	Anatidae

Table 1-2: Continued

Species	Obs.	Common name	Order	Family
Anser albifrons	59	Greater White-fronted Goose	Anseriformes	Anatidae
Mergellus albellus	40	Smew	Anseriformes	Anatidae
Aix sponsa	34	Wood Duck	Anseriformes	Anatidae
Aythya affinis	32	Lesser Scaup	Anseriformes	Anatidae
Clangula hyemalis	27	Long-tailed Duck	Anseriformes	Anatidae
Anser indicus	26	Bar-headed Goose	Anseriformes	Anatidae
Melanitta nigra	26	Common Scoter	Anseriformes	Anatidae
Aythya nyroca	19	Ferruginous Duck	Anseriformes	Anatidae
Tadorna ferruginea	18	Ruddy Shelduck	Anseriformes	Anatidae
Branta bernicla	15	Brant	Anseriformes	Anatidae
Anser serrirostris	14	Tundra Bean-Goose	Anseriformes	Anatidae
Oxyura jamaicensis	14	Ruddy Duck	Anseriformes	Anatidae
Lophodytes cucullatus	12	Hooded Merganser	Anseriformes	Anatidae
Branta ruficollis	9	Red-breasted Goose	Anseriformes	Anatidae
Callonetta leucophrys	7	Ringed Teal	Anseriformes	Anatidae
Mergus serrator	7	Red-breasted Merganser	Anseriformes	Anatidae
Spatula discors	5	Blue-winged Teal	Anseriformes	Anatidae
Cygnus cygnus	4	Whooper Swan	Anseriformes	Anatidae
Marmaronetta angustirostris	4	Marbled Duck	Anseriformes	Anatidae
Dendrocygna viduata	3	White-faced Whistling-Duck	Anseriformes	Anatidae
Oxyura leucocephala	3	White-headed Duck	Anseriformes	Anatidae
Branta sandvicensis	2	Hawaiian Goose	Anseriformes	Anatidae
Cygnus columbianus	2	Tundra Swan	Anseriformes	Anatidae
Dendrocygna bicolor	2	Fulvous Whistling-Duck	Anseriformes	Anatidae
Melanitta fusca	2	Velvet Scoter	Anseriformes	Anatidae
Netta peposaca	2	Rosy-billed Pochard	Anseriformes	Anatidae
Anas bahamensis	1	White-cheeked Pintail	Anseriformes	Anatidae
Anser caerulescens	1	Snow Goose	Anseriformes	Anatidae
Aythya novaeseelandiae	1	New Zealand Scaup	Anseriformes	Anatidae
Bucephala albeola	1	Bufflehead	Anseriformes	Anatidae
Mareca sibilatrix	1	Chiloe Wigeon	Anseriformes	Anatidae
Oxyura vittata	1	Lake Duck	Anseriformes	Anatidae
Somateria mollissima	1	Common Eider	Anseriformes	Anatidae
Ardea cinerea	9964	Gray Heron	Pelecaniformes	Ardeidae
Egretta garzetta	2171	Little Egret	Pelecaniformes	Ardeidae
Botaurus stellaris	113	Great Bittern	Pelecaniformes	Ardeidae
Ardea alba	75	Great Egret	Pelecaniformes	Ardeidae
Bubulcus ibis	29	Western Cattle Egret	Pelecaniformes	Ardeidae
Platalea leucorodia	21	Eurasian Spoonbill	Pelecaniformes	Threskiornithidae
Nycticorax nycticorax	17	Black-crowned Night Heron	Pelecaniformes	Ardeidae
Plegadis falcinellus	9	Glossy Ibis	Pelecaniformes	Threskiornithidae
Ixobrychus minutus	1	Little Bittern	Pelecaniformes	Ardeidae
Pelecanus onocrotalus	1	Great White Pelican	Pelecaniformes	Pelecanidae
Milvus milvus	2805	Red Kite	Accipitriformes	Accipitridae

Table 1-2: Continued

Species	Obs.	Common name	Order	Family
Buteo buteo	2239	Common Buzzard	Accipitriformes	Accipitridae
Accipiter nisus	1918	Eurasian Sparrowhawk	Accipitriformes	Accipitridae
Circus aeruginosus	150	Western Marsh Harrier	Accipitriformes	Accipitridae
Pandion haliaetus	7	Osprey	Accipitriformes	Pandionidae
Accipiter gentilis	6	Eurasian Goshawk	Accipitriformes	Accipitridae
Circus cyaneus	3	Hen Harrier	Accipitriformes	Accipitridae
Buteo lagopus	1	Rough-legged Hawk	Accipitriformes	Accipitridae
Milvus migrans	1	Black Kite	Accipitriformes	Accipitridae
Columba palumbus	30821	Common Wood-Pigeon	Columbiformes	Columbidae
Columba livia	23201	Rock Pigeon	Columbiformes	Columbidae
Psittacula krameri	19896	Rose-ringed Parakeet	Psittaciformes	Psittaculidae
Columba oenas	6524	Stock Dove	Columbiformes	Columbidae
Streptopelia decaocto	3844	Eurasian Collared-Dove	Columbiformes	Columbidae
Myiopsitta monachus	40	Monk Parakeet	Psittaciformes	Psittacidae
Streptopelia turtur	11	European Turtle-Dove	Columbiformes	Columbidae
Ara ararauna	1	Blue-and-yellow Macaw	Psittaciformes	Psittacidae
Melopsittacus undulatus	1	Budgerigar	Psittaciformes	Psittaculidae
Nymphicus hollandicus	1	Cockatiel	Psittaciformes	Cacatuidae
Psittacula eupatria	1	Alexandrine Parakeet	Psittaciformes	Psittaculidae
Streptopelia orientalis	1	Oriental Turtle-Dove	Columbiformes	Columbidae
Fulica atra	17073	Eurasian Coot	Gruiformes	Rallidae
Gallinula chloropus	16389	Eurasian Moorhen	Gruiformes	Rallidae
Podiceps cristatus	6776	Great Crested Grebe	Podicipediformes	Podicipedidae
Tachybaptus ruficollis	3713	Little Grebe	Podicipediformes	Podicipedidae
Rallus aquaticus	590	Water Rail	Gruiformes	Rallidae
Podiceps nigricollis	323	Eared Grebe	Podicipediformes	Podicipedidae
Podiceps grisegena	24	Red-necked Grebe	Podicipediformes	Podicipedidae
Podiceps auritus	12	Horned Grebe	Podicipediformes	Podicipedidae
Porzana porzana	10	Spotted Crake	Gruiformes	Rallidae
Grus grus	2	Common Crane	Gruiformes	Gruidae
Dendrocopos major	7545	Great Spotted Woodpecker	Piciformes	Picidae
Picus viridis	4751	Eurasian Green Woodpecker	Piciformes	Picidae
Falco tinnunculus	2768	Eurasian Kestrel	Falconiformes	Falconidae
Phasianus colchicus	1514	Ring-necked Pheasant	Galliformes	Phasianidae
Falco peregrinus	856	Peregrine Falcon	Falconiformes	Falconidae
Falco subbuteo	407	Eurasian Hobby	Falconiformes	Falconidae
Athene noctua	311	Little Owl	Strigiformes	Strigidae
Strix aluco	237	Tawny Owl	Strigiformes	Strigidae
Tyto alba	150	Barn Owl	Strigiformes	Tytonidae
Alectoris rufa	111	Red-legged Partridge	Galliformes	Phasianidae
Asio flammeus	62	Short-eared Owl	Strigiformes	Strigidae
Dryobates minor	31	Lesser Spotted Woodpecker	Piciformes	Picidae
Jynx torquilla	14	Eurasian Wryneck	Piciformes	Picidae
Falco columbarius	8	Merlin	Falconiformes	Falconidae
Coturnix coturnix	3	Common Quail	Galliformes	Phasianidae
Pavo cristatus	2	Indian Peafowl	Galliformes	Phasianidae

Table 1-2: Continued

Species	Obs.	Common name	Order	Family
Gavia immer	101	Common Loon	Gaviiformes	Gaviidae
Gavia arctica	42	Arctic Loon	Gaviiformes	Gaviidae
Gavia stellata	4	Red-throated Loon	Gaviiformes	Gaviidae
Phalacrocorax carbo	11239	Great Cormorant	Suliformes	Phalacrocoracidae
Apus apus	3690	Common Swift	Caprimulgiformes	Apodidae
Tachymarptis melba	13	Alpine Swift	NA	NA
Caprimulgus europaeus	5	Eurasian Nightjar	Caprimulgiformes	Caprimulgidae
Morus bassanus	3	Northern Gannet	Suliformes	Sulidae
Menelikornis leucotis	1	White-cheeked Turaco	NA	NA
Alcedo atthis	1501	Common Kingfisher	Coraciiformes	Alcedinidae
Cuculus canorus	195	Common Cuckoo	Cuculiformes	Cuculidae
Ciconia ciconia	40	White Stork	Ciconiiformes	Ciconiidae
Upupa epops	3	Eurasian Hoopoe	Bucerotiformes	Upupidae
Puffinus puffinus	1	Manx Shearwater	Procellariiformes	Procellariidae

PART 2

Consistent bird occupancy model performance across scales from scale-dependent relationships

Abstract

The scale of environmental factors to species distribution models can meaningfully impact the output; however, the most relevant scale or multiple scales are often not considered. Using structured bird observations from the British Breeding Bird Survey, we analyzed the output from spatial factor joint species distribution models (JSDMs) with the same environmental factors quantified at scales between 1,000m and 16,000m for 65 bird species in a 64km x 64km extent centered around Greater London, U.K. Model performance as measured by WAIC and Tjur R^2 varied little between scales, for both the community as a whole and for each species, as the latent spatial factors were able to explain residual variance in the observations. However, the environmental relationships were scale dependent, with at least one effect changing direction (i.e., positive to negative or vice versa) for 26 species. The responses and scale dependence patterns were similar between four species clusters and help to identify common patterns. Common model performance metrics for JSDMs leveraging latent spatial factors may mask poor model specification, where multiple species are influenced by environmental factors at multiple scales, and these results illustrate the importance of quantitatively assessing scale dependence.

Introduction

Understanding species distributions is fundamental to ecology, as it can help connect observed patterns to underlying processes (Elith & Leathwick 2009). Species distribution models (SDMs) are valuable tools used to explore species relationships with their environment, as well as with other species. Consequently, SDMs have many practical applications, including testing biogeographical theories, assessing impact to climate and land-use change, and supporting conservation planning (Guisan & Thuiller 2005). However, the results and conclusions drawn from these models depend critically on the scale at which observations are recorded and on the scale at which environmental factors are quantified (Levin 1992; Wiens 1989).

Ecological theory emphasizes that species perceive and respond to environmental conditions across multiple spatial scales (Hostetler 2001; Turner & Gardner 2015), including actions that relate to geographic range, home range, suitable habitat, and available or preferred resources (Johnson 1980). Varying traits between species, such as body size, dispersal, and specialization lead to different decisions and thus different distributions at different scales

(McGill 2010; McGill et al. 2006). Furthermore, individuals within the same species can exhibit variable scale-dependent responses due to differences in behavior, life history stage, or local adaption (Bolnick et al. 2003; Takola & Schielzeth 2022). Contextual factors, including spatial heterogeneity, temporal dynamics, and community interactions further modulate these responses, making the relationship between species and spatial scale inherently dependent and dynamic (Mertes & Jetz 2018; Pease 2024). Therefore, recognizing scale-specific perception and its variability is critical for understanding ecological patterns and informing conservation strategies (Mayor et al. 2009; Wheatley & Johnson 2009).

Despite this theoretical recognition of the importance of multiple scales, SDMs surprisingly often lack a robust consideration of scale and commonly use environmental factors at a single scale, often based on default resolution convenience (McGarigal et al. 2016; Mertes & Jetz 2018; Stevens & Conway 2019). When multiple scales are considered, a full assessment across all possibly relevant scales is rare, which may often lead to false or limited conclusions (Jackson & Fahrig 2015). Much of the work relating to how environmental effects change across scales falls under the concept of determining the scale of effect, or characteristic scale, which is designed to identify the scale at which a factor has the strongest relationship with the modeled species response. While these studies are helpful and able to help test theories of why different species respond to factors at different scales, the limited consistent empirical evidence to support these theories leaves SDM modelers with little information to justify a relevant scale choice and may indicate the dominating impact of context (Miguet et al. 2016; Zipkin & Doser 2024).

This issue compounds when multiple species are modeled together. Joint species distribution models (JSDMs) include concepts from community ecology and are designed to elucidate community dynamics and improve individual species predictions compared to traditional single-species models (Doser et al. 2023; Ovaskainen et al. 2017). JSDMs can account for interspecific associations, capturing ecological processes such as competition, predation, mutualism, and shared environmental responses (Pollock et al. 2014; Warton et al. 2015). Modeling species together can enable valuable insight into the community and constituent species groups, though by default the effects are estimated at the same scale for all species in the model (Ovaskainen & Abrego 2020).

While studies incorporating JSDMs have utilized environmental factors at multiple scales, this approach typically employs only a limited combination of predefined local and

landscape scales deemed ecologically relevant (e.g., Ovaskainen et al. 2016a). König et al. (2021) aimed to systematically assess scale dependance and evaluated a set of JSDMs fit across a range of spatial grain sizes for woodland birds in Switzerland. Their results showed clear scale dependence of the model output based on factor scale. While a valuable first step, the study focused on model performance with respect to varied grain size of the environmental factors, leaving questions about how effect magnitudes and directions might change when environmental factors are quantified across different spatial extents.

The inherent capacity of JSDMs to utilize species correlations and spatial autocorrelation patterns for prediction can help identify unmodeled environmental influences (e.g., Ovaskainen et al. 2016b). However, when evaluating models solely through predictive performance metrics (e.g., when determining a scale of effect), the unmodeled latent factors may be able to compensate for lack of signal in the fixed effects. Systematically assessing scale dependence from multiple perspectives of the model are needed to better understand how different model specifications may impact its intended application. In other words, how useful is the model for performance versus inference (i.e., revealing accurate species-environment relationships).

In this study, we fit a JSDM with environmental factors quantified across a range of spatial scales to examine:

1. the performance of the model across scale (overall and for each species); and
2. the variance explained by both the fixed and latent effects across scale (overall and for each species).

Through this analysis, we seek to discover common patterns between species that could be used to develop improved JSDM that better consider scale and thereby increase their utility for ecological research and conservation.

Methods

We specified a JSDM for bird species occurrence around a 64km x 64km area centered over Greater London, U.K (**Figure 2-1**a, see Appendix for all figures and tables). While bird observations and data on environmental factors are available across the entire extent of the U.K., we limited the extent to the chosen study area for several reasons: 1) to fit the models in a reasonable amount of time given the available computing resources, and 2) to reduce broad scale nonstationary while being able to capture how difference species respond to London's large urbanization gradient.

Species observations

We used species observations from the British Breeding Bird Survey (BBS), a structured monitoring program active throughout the U.K. since 1994 (Massimino et al. 2025). In this survey, trained volunteers record bird observations within randomly selected 1km squares, chosen through a stratified sampling design. Each square is surveyed twice annually, between April and June, coinciding with the breeding season. Over its 30-year operation, approximately 7,000 squares have been surveyed, though the specific squares included vary each year due to volunteer availability. For our study, we selected data from the most recent 10-year period (2013–2024) within our study area. This selection included observations from 289 squares, each surveyed for at least one year during this period, with the number of years surveyed per square ranging from one to all ten years (**Figure 2-1**b).

During each survey visit, the observer follows two transects within the square designed to approximately divide the square into thirds, running either north-to-south or east-to-west (**Figure 2-1**c). The actual transects vary based on available linear routes within the landscape.

The transects are divided into 200m sections, where the observer records all species seen or heard within three distance bands: < 25m, 25m-100m, and >100m. Birds in flight are recorded regardless of their distance (Massimino et al. 2025). We filtered the data to include only 65 species that were detected at more than 10% of the sites. While the observations record species counts, we converted the data to binary species detection/non-detection, though an alternate analysis to model abundance is possible and could be insightful. We believe that first understanding scale dependent relationships between the environment and species occurrence is an important first step.

We organized the species into four clusters to aid in organizing the results and summarizing consistent scale-dependent patterns between different niches. We first computed Jaccard dissimilarity between all species based on their detection at each site (Legendre & Legendre 2012). We then hierarchically clustered the pairwise dissimilarities using Ward's method and plotted the resulting dendrogram. We identified isolated clusters near the leaves of the dendrogram tree with relatively large differences in height between the next highest node and assigned the resulting cluster id to each species.

Environmental factors

We computed environmental factors from land cover (LC) and normalized difference vegetation index (NDVI) layers (**Figure 2-2**). We used the latest land cover map (LCM2023) produced by the UK Center for Ecology & Hydrology that classify the landscape of the U.K. into 21 classes at a 10m resolution (Morton et al. 2024). We reclassified the LCM2023 into six classes (see **Figure 2-2**a) to reduce collinearity and improve stratified sampling of environmental factors across all survey locations.

We computed the NDVI derived from Sentinel-2 Surface Reflectance imagery. NDVI is a widely adopted metric for assessing vegetation, with values typically ranging between -1 and 1—where higher values indicate more robust, healthy vegetation, values near zero denote barren or built-up areas, and negative values generally correspond to water bodies. We generated the NDVI composite using Google Earth Engine by taking the maximum annual value for 2023, minimizing cloud contamination and other atmospheric effects (Gorelick et al. 2017).

We derived a set of landscape metrics from the LC and NDVI layers to quantify distinct aspects of landscape composition and configuration (**Table 2-1**). Following an exploratory correlation analysis, we selected a parsimonious set of metrics with minimal multicollinearity. Although initial model iterations included percent area calculations for various land cover classes, we later excluded them because exploratory model runs indicated they lacked statistical support (i.e., their 95% confidence intervals overlapped zero) and were correlated with the retained metrics.

We calculated each selected metric within circular buffers with progressively doubling diameters, representing a range of spatial scales: 1,000m, 2,000m, 4,000m, 8,000m, and 16,000m. This methodical scaling approach allowed for comprehensive assessment of environmental effects across multiple ecological domains. All code to quantify the environmental factors was performed in R, leveraging the terra (Hijmans 2025) and landscapemetrics packages (Hesselbarth et al. 2019).

Model specification

We modeled the joint distributions of all included species with a single model specification and separately fit the model with environmental factors quantified at each assessed scale. We specified and fit the models using the spOccupancy R package, using a multi-species

multi-season spatial occupancy model (stMsPGOcc function). This modeling approach specifically addresses the hierarchical nature of species distribution data by separating the ecological process (species occurrence) from the observation process (species detection), thus accounting for imperfect detection that varies by species (for model details see Doser et al. 2023; Doser et al. 2022).

The model structure incorporated year as an unstructured random effect for the occurrence process, capturing annual variability in species distributions independent of measured environmental factors. For the detection component, we implemented a simplified approach using only species-specific random intercepts rather than including observation covariates. This decision was necessitated by substantial missing values in potential detection covariates (e.g., time of day, survey date) in the BBS dataset. Preliminary model evaluations confirmed that including available detection covariates produced only marginal improvements in model performance over the random intercept approach.

To fit the model, we ran 300,000 chains with a burn in of 100,000 using three chains and saving every 400th sample (i.e. thinning = 400), resulting in 1,500 posterior samples (500 from each chain). We fit the models on the ISAAC computing cluster at the University of Tennessee, resulting in a run time of approximately 50 hours for each model. We specified weakly informative priors as exploratory runs of the model did not indicate convergence issues.

We assessed the resulting model output both for the entire community (mean of all species), as well as for each species, considering both model performance and the direction, size, and support level of the environmental effects. Additionally, we investigated the amount of variance explained by the fixed (environmental) effects versus the random (spatial latent) effects to understand how each signal varies with scale. We assessed model convergence using:

- effective sample size (ensuring sufficient samples for posterior estimates); and
- the Gelman-Rubin convergence diagnostic (Gelman & Rubin 1992), ensuring values close to 1 for all parameters.

We evaluated model performance across spatial scales using:

- the Widely Applicable Information Criterion (WAIC) (Vehtari et al. 2017) to compare model predictive capacity; and
- Tjur's R2 (Tjur 2009) to assess predictive performance for each species, which is an easily interpretable metric defined as:

$$R^2_{Tjur} = \bar{p}_1 - \bar{p}_2$$

where $\bar{p}_1$ is the mean predicted probability where the observed response = 1 (i.e., the species was detected), and $\bar{p}_0$ is the mean predicted probability where the observed response = 0 (i.e., the species was not detected).

To summarize the variability of species responses between different classification schemes, we implemented complementary multivariate statistical tests, PERMANOVA and Mantel, across three organization categories: co-occurrence clusters, taxonomic orders, and taxonomic families. The PERMANOVA analysis quantifies between-group differences in parameter space, while the Mantel test assesses correlation between distance matrices derived from estimated species parameters and group membership. While more complex trait-based or phylogenetic analyses could potentially yield additional insights in subsequent investigations, these metrics provide an efficient assessment of how effectively different classifications capture variation in the estimated species responses.

To assess how the environmental factors changed across scale, we calculated the percentage of species within each co-occurrence cluster with an estimated positive or negative effect for each factor. We further summarized the statistical support of each effect at the 95% and 75% levels (i.e., the respective confidence intervals that did not include zero), as well as those that were not supported below the 75% level. We additionally computed the maximum change in effect across scales for each factor and species, and we then listed each change that switched from an estimated positive effect to a negative effect supported at the 75% level across scales.

The model incorporated spatially structured random effects implemented as latent spatial factors, which capture the residual spatial autocorrelation after accounting for the environmental (β) effects (Ovaskainen et al. 2016b). These factors may represent either unmeasured environmental conditions not included in the model or biotic interactions between species (e.g., competition or facilitation) (Ovaskainen et al. 2016b; Poggiato et al. 2021). We modeled the spatial random effects as a nearest-neighbor Gaussian process using 15 neighbors using the Matérn covariance function. The number of spatial latent factors can range up to the number of species in the model, and some studies have shown that relatively few factors can sufficiently capture residual spatial information (Thorson et al. 2015; Warton et al. 2015) while other studies suggest more are required for larger more diverse communities (Tikhonov et al. 2020; Tobler et

al. 2019). We included three latent factors based on exploratory runs of the model that indicated diminishing returns in model performance with large increases in computation time.

Because we specified the model to use the Matérn covariance function, the model estimates two parameters that each describe the nature of the spatial autocorrelation captured by each latent factor, namely ϕ that estimates how fast spatial autocorrelation decays over distance (i.e. fast versus slow), and ν that estimates how quickly spatial autocorrelation changes over distance (i.e. smooth versus rough). With these estimated parameters, we calculated the effective spatial range at which the spatial correlation between two points falls below approximately 0.1, given by the empirically derived formula $\sqrt{8\nu}/\phi$ (Fuglstad et al. 2019; Lindgren et al. 2011). We interpreted the effective spatial range as an estimate of the scale over which each latent factor varies. We investigated how each species responded to each latent factor, commonly referred to as the species loadings, to understand what each factor might represent, as well as how latent responses varied between co-occurrence clusters.

To improve parameter identifiability, the spOccupancy package constrains the loadings of specific species on each spatial latent factor. Specifically, it fixes the loading of the first species to 1 for the first factor, the second species to 1 for the second factor, and the third species to 1 for the third factor, and so on for as many factors included (Doser 2022). Because we included three spatial factors, we intentionally selected the 1) House Sparrow (*Passer domesticus*), 2) Eurasian Skylark (*Alauda arvensis*), and 3) Mallard (*Anas platyrhynchos*) as the first three species in our model based on our a priori assumption that their occurrence patterns would be different. This selection influences the interpretation of the spatial latent factors, as each factor primarily reflects the distribution patterns of species similar to its representative anchor species (for more details see Doser 2022).

Results

Hierarchical clustering of the 65 species based on co-occurrence data produced four distinct clusters (**Figure 2-3**a). The initial split in the dendrogram divided species between relatively prevalent species (clusters 1 and 3) and relatively rare species (clusters 4 and 2). Subsequent splits further refined these groupings. Cluster 1 contains generalist and urban-adapted species, where most (> 50%) of the species were observed at every site across the study area. In contrast, cluster 4 contains rural and suburban edge species, or urban avoiders, that show

a strong preference for less urbanized peripheral areas, with only a few species observed at more urbanized areas within the boundary of Greater London. Cluster 3 contains moderate urban adapters and some common wetland species that were often observed in some urban areas but less widespread than cluster 1 species. Cluster 2 includes species associated with water or wetland habitat near the major wetlands and waterways (e.g., the River Thames) in the study area (**Figure 2-1**b, also see **Figure 2-8** through **Figure 2-15** for predicted occurrence for all species).

The performance of the model on average across all species as measured by WAIC varied minimally across scales (ranging from 151,659 to 153,598). Likewise, overall Tjur R^2 remained approximately constant at 0.57, indicating that the model was consistently able to distinguish well between occurrence and non-occurrence for the community as a whole (**Table 2-2**). For individual species, Tjur R^2 does indicate improved model performance at specific scales, but for the majority and on average there is little evidence of scale dependance on model performance.

In contrast, the partitioning of explained variance between fixed (environmental) effects and spatial latent factors showed a clear scale dependence. At a scale of 1000m, fixed effects accounted for 25% of the explained variance, with spatial latent factors explaining the remaining 75%. As the scale increased to 16000m, the fixed effects explained 51% of the variance indicating increasing signal from environmental factors quantified at greater scales.

Viewing variance partitioning by cluster, the generalist (cluster 1) and urban avoider (cluster 4) species had a larger proportion of variance explained by fixed effects compared to the urban adapter and water-associated species (clusters 2 and 3) where the model relied more on the latent spatial factors to model occurrence (**Figure 2-4**).

Among the three species classification methods (co-occurrence clusters, taxonomic order, and taxonomic family), all three successfully captured significant differences in the estimated species parameters according to PERMANOVA analysis. However, the Mantel test revealed a different pattern: only the co-occurrence cluster grouping showed a meaningful correlation (statistic = 0.32, p = 0.001) between species parameters. This indicates that species within the same co-occurrence cluster had moderately positively correlated model parameters, while species grouped by taxonomic order or family did not show significant parameter correlations. These results suggest that ecological associations based on shared habitat preferences (reflected in co-occurrence patterns) may better capture similarities in species' responses to environmental factors than taxonomic relationships (**Table 2-3**).

The environmental effects reveal distinct scale-dependent patterns that vary by both factor type and species group (**Figure 2-5**). Among the 65 bird species studied, 11 showed a complete reversal in effect direction (from positive to negative or vice versa) for at least one environmental factor with 95% statistical support. An additional 15 species showed similar reversals at the 75% support level.

The generalists (cluster 1) and urban avoiders (cluster 4), which represent the largest species groups, demonstrated relatively stable responses across scales with a mix of both positive and negative effects within each group. In contrast, the water-associated species (cluster 2) and urban adapters (cluster 3) exhibited more pronounced changes across different spatial scales. Examining specific environmental factors across groups:

- Edge (edge habitat): Shifted from predominantly negative to positive effects for water-associated species, urban adapters, and urban avoiders as scale increased
- ENN (habitat connectedness): Remained relatively constant for urban avoiders, but shifted toward positive values for generalists, urban adapters, and water-associated species, whose positive effect peaked at the 4000m scale
- Vegetation intensity (NDVI): Urban avoiders maintained consistently positive relationships across all scales, while generalists and urban adapters shifted toward more negative effects at larger scales. Notably, water-associated species exhibited a clear shift from predominantly positive effects at 1000m to entirely negative effects at 16000m
- LC diversity (SHDI): Showed consistently positive effects across all clusters, with particularly strong statistical support for urban adapter species

The latent spatial factors capture residual patterns in species occurrence that remain after accounting for the measured environmental factors (**Figure 2-6**). Recall that each factor is anchored to a representative species whose loading was fixed at 1 during model fitting. L1, anchored to the House Sparrow (*Passer domesticus*), a cluster 1 generalist species, displays a strong urban-rural gradient with predominantly negative values inside Greater London and positive values in surrounding areas, likely capturing broad urbanization effects not fully measured by the environmental variables. L2, anchored to the Eurasian Skylark (*Alauda arvensis*), a cluster 4 urban-avoiding species, shows positive values concentrated in the central-southern region corresponding with large natural areas, likely capturing residual effects of species that avoid urban environments. L3, anchored to the Mallard (*Anas platyrhynchos*), a

cluster 3 water-associated species, exhibits a more localized pattern unrelated to the urban-rural gradient, likely representing water features and wetland habitats important for this species group. The estimated species loadings to each factor shows similar responses within each species cluster.

While the general pattern of each latent spatial factor remains consistent between models as the scale of environmental variables increases, the effective spatial scale of the latent factors generally decreases. L1 decreases substantially from 8200m to 1700m, L2 decreases moderately from 4000m to 2000m, and L3 remains relatively stable between 1700m and 1400m. This declining trend suggests that as environmental variables capture more broad-scale patterns at larger scales, the latent factors increasingly represent finer-scale processes not captured by the environmental variables. This shifting balance between fixed effects and latent factors explains how the model maintains consistent predictive performance despite the changing scales of environmental variables.

Discussion

The estimated environmental effects support the fundamental understanding in ecology that environmental relationships are scale dependent, illustrated most clearly by the fact that at least one parameter for 26 species reversed direction across scales. Modeling the community of 65 bird species together shows how the responses between different species groups vary—ranging from the generalists (cluster 1) to the water-dependent specialists and urban adapters (clusters 2 and 3) to the urban avoiders (cluster 4).

However, despite the scale dependence of the environmental relationships, the overall predictive performance of the JSDMs remained consistent across all the scales we assessed. This stability emerged from the model's ability to leverage the spatially structured latent information, which was able to maintain predictive performance across scales while the signal from fixed effects varied. This finding highlights an important nuance of JSDMs that incorporate both species correlations and spatial autocorrelation: while scale selection may not critically impact prediction accuracy, it remains fundamentally important for ecological inference and understanding the mechanisms driving species distributions (Turner & Gardner 2015).

Conservation and management decisions based on misinterpreted scale relationships could lead to ineffective or counterproductive interventions (Cumming et al. 2006), despite insignificant differences in model scale performance metrics, like WAIC and Tjur R^2. While our

findings may not generalize to all study extents or species communities, they highlight the importance of understanding how explained variance is partitioned between fixed and random effects—in this case between the environmental and latent spatial factors—which informs where a model is most useful.

For example, the full model output and predictive performance is largely similar for the Eurasian Skylark (*Alauda arvensis*) across all assessed scales. However, the modeled relationship with the environmental factors differs significantly between scales, where Edge has an estimated negative effect when sampled at 1000m and a positive effect when sampled at 4000m (**Figure 2-7**), which are within the range of scales often cited as being most relevant for modeling the distribution of various bird species (Litteral & Shochat 2017). Understanding how the environment influences the Skylark at different scales is needed for effective conservation (Andreatta et al. 2025; Loretto et al. 2019).

Likewise, the shift in variance partitioning on the surface supports the argument that scale helps connect two ecological paradigms on species distributions: neutral theory emphasizing stochastic processes and niche theory emphasizing deterministic environmental context (Chase & Myers 2011; Ricklefs 1987). At smaller scales (1,000m), the latent spatial factors dominate, explaining 75% of model-predicted variance, while environmental variables account for only 25%. This relationship gradually shifts as spatial scale increases, with fixed environmental effects explaining 51% of variance at 16,000m. The scale-dependent transition we observed supports the argument by Chase (2014) that scale connects the two competing theories, where demographic stochasticity and dispersal limitation exert stronger influence at smaller scales, while niche differentiation and environmental filtering become increasingly relevant at broader scales. These results corroborate those found by König et al. (2021), who also found that the amount of variance explained by fixed environmental effects increased with scale.

However, JSDMs cannot distinguish between stochastic biotic interactions and unmodeled environmental effects (Blanchet et al. 2020; Poggiato et al. 2021). The higher variance explained by latent factors at smaller scales likely represents a composite influence of both mechanisms. This is particularly evident in clusters 2 and 3 that both include water-associated species that respond strongly to latent factors 2 and 3, which are correlated with water features in the study area. Including an environmental factor such as distance to water would have likely increased the variance explained by fixed effects for cluster 2 and 3 species. While

precise interpretation of the latent factors remains ambiguous, they can with careful inspection provide clues to unmodeled factors.

The environmental response patterns observed across clusters align with the ecological characteristics of their constituent species. Not surprisingly, the cluster 1 generalists, comprising 27 species, exhibit the most varied responses to environmental factors. The varied responses represent different ways in which the species niches are supported across the entire study extent. For example, some cluster 1 species occur only in large green spaces within Greater London, while others show an opposite pattern, occurring only in lightly to moderately developed areas. Summarizing responses in more specific subgroups, indicated by the co-occurrence dendrogram (**Figure 2-3**), would likely capture the different ways in which the generalist species occur over the large Greater London urbanization gradient.

In contrast, the cluster 4 urban avoider species demonstrate a consistently positive association with NDVI, reflecting their sensitivity to urbanization. Their scale-dependent response to Edge is also informative—showing negative associations at smaller scales—indicating preference for larger, unfragmented habitats. This preference is further supported by their consistent negative response to ENN.

The responses of clusters 2 and 3 reveal how the spatial configuration of urban green and blue spaces strongly influence their scale-dependent patterns. For the exclusively water-associated species in cluster 2, the notable shift in NDVI response from positive at small scales to negative at larger scales reflects the configuration of suitable habitat within the study area. At smaller scales, their water-associated habitats exhibit high NDVI values (even though water has negative NDVI the percent area of water is generally small compared to the surrounding habitat); however, these sites are predominantly located within Greater London's urbanized boundary. This spatial arrangement explains the shift to negative NDVI associations when analyzed at broader scales. Cluster 3, containing more prevalent urban adapters, exhibits a similar but less pronounced response shift. However, these species demonstrate stronger relationships with Shannon’s diversity index (SHDI), a metric that reaches high values in the heterogeneous suburban and diverse water/wetland interfaces characteristic of their preferred habitats.

A natural question that is the aim of many studies is to relate varying scale-specific environmental responses to species traits. This effort first relies on determining the single optimal scale, also termed the characteristic scale or scale of effect, with the strongest response

to environmental factors (Brennan et al. 2002; Jackson & Fahrig 2012). The difference in responses is then related to functional traits to determine if they explain meaningful differences between species and responses (Miguet et al. 2016). While there is some empirical evidence for varying traits leading to different responses at different scales, a general lack of consistency suggests that the spatiotemporal context may predominate rather than—or in addition to—different traits (e.g., see Pease 2024). While the Mantel test we performed indicated that taxonomic order and family do not explain the differences between model responses for this study, further exploring trait-scale perception relationships using JSDMs, beyond the general co-occurrence clusters we used remains a valuable pursuit (Ovaskainen & Abrego 2020).

While the concept of scale of effect is helpful for advancing ecological modeling toward multiscale approaches, it may in practice oversimplify reality by identifying only a single scale for all environmental factors. Our results challenge this simplification as many estimated factors both explained high proportions of variance and differed significantly (with many switching sign) across scales, indicating both are relevant to those species' distributions. These findings align with Stuber & Fontaine (2019), who found that 86 bird species responded to different factors at different scales, and often at multiple scales for each factor, challenging the notion of a single best scale of effect.

For researchers applying joint species distribution models, our findings indicate that although JSDMs can mitigate scale issues through spatial latent factors when the goal is prediction, the interpretation of environmental drivers remains highly scale dependent. We therefore recommend a systematic approach for multiscale modeling. First, assess variability of the environmental factors across scales by analyzing a variogram or through scale variance analysis (e.g., Mertes & Jetz 2018; Wheatley & Johnson 2009; Wu et al. 2000). Second, fit exploratory models considering multiple scales and investigate if variability of the environmental factor results in meaningful relationships with the species, and if these relationships are scale dependent or act on multiple scales. Finally, use variance partitioning and estimated scales of latent factors to identify potentially missing environmental variables and appropriate scales for inclusion in the final model (e.g., as suggested in Stuber & Gruber 2020).

Our results emphasize that while the predictive power of JSDMs may remain consistent across scales, understanding the true ecological mechanisms driving species distributions requires careful consideration of how environmental effects vary with scale. This approach is

essential for translating species distribution models into effective conservation and management actions in an increasingly human-modified world.

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Appendix

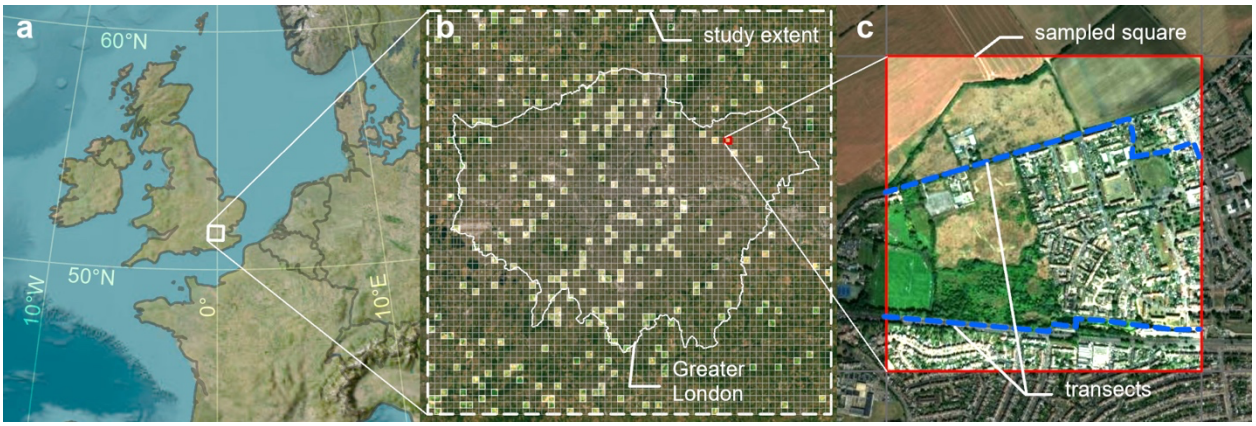


Figure 2-1: Study location, extent, and example BBS square

a) Study location within Great Britain, b) 1km squares sampled in the British Breeding Bird Survey (BBS) during the study's 2014-2023 time period, and c) example 1km square and transect lines surveyed as part of the BBS.

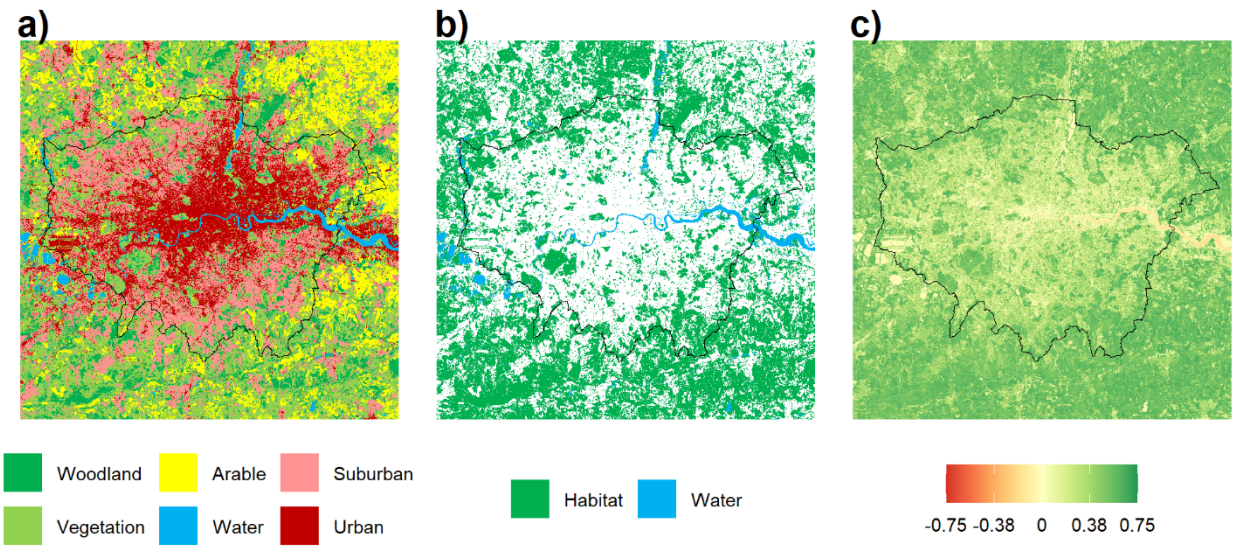


Figure 2-2: Environmental data sources

a) Land cover, b) habitat (woodland and vegetation land cover), and c) maximum 2023 NDVI in the study extent. The black outline shown in all layers is the boundary of Greater London for reference.

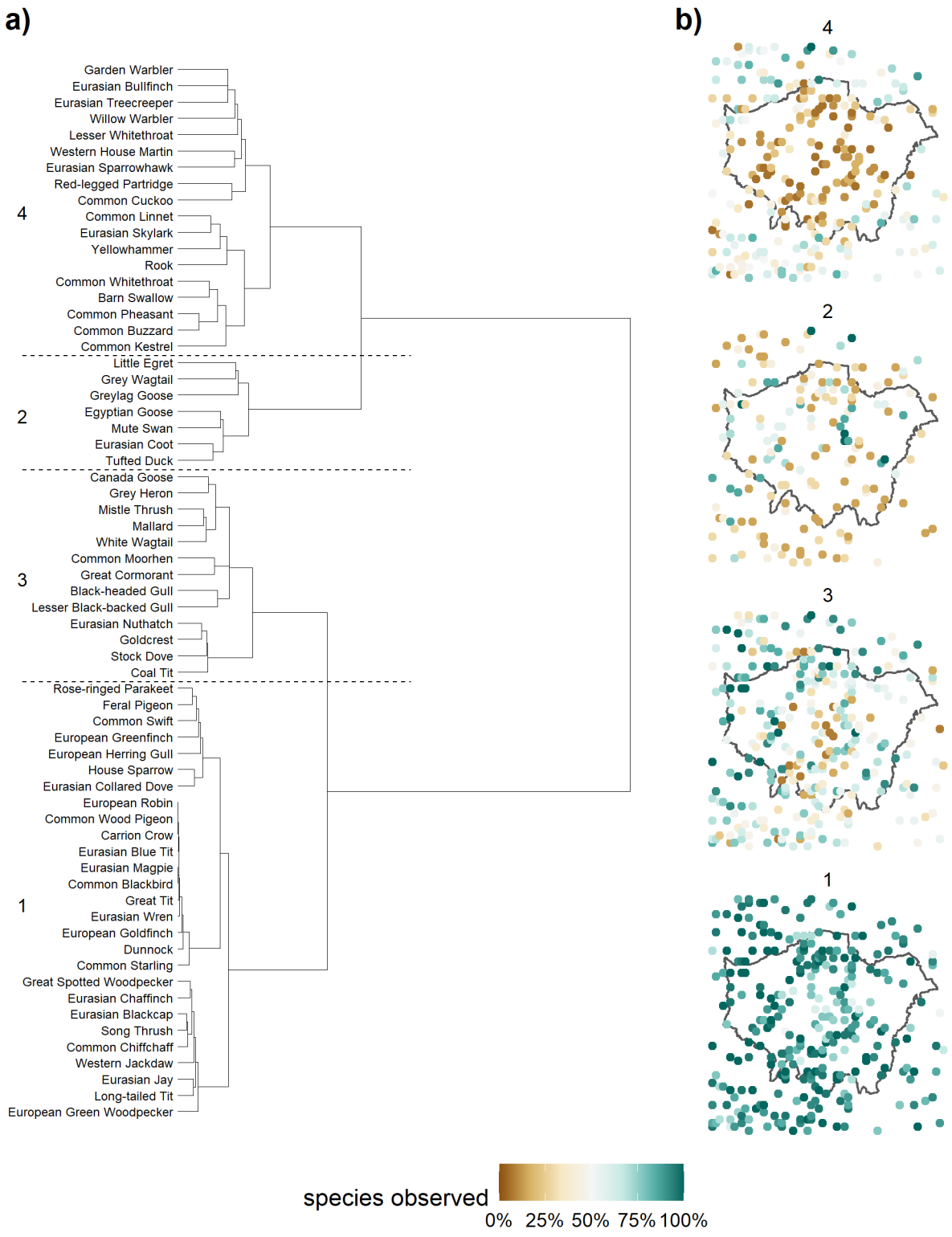


Figure 2-3: Species co-occurrence clusters

a) Dendrogram showing hierarchical clustering of species co-occurrence with height corresponding to Ward's distance between pairwise Jaccard dissimilarity, and b) maps showing the percentage of species detected at least once at each site within each cluster between 2014-2023

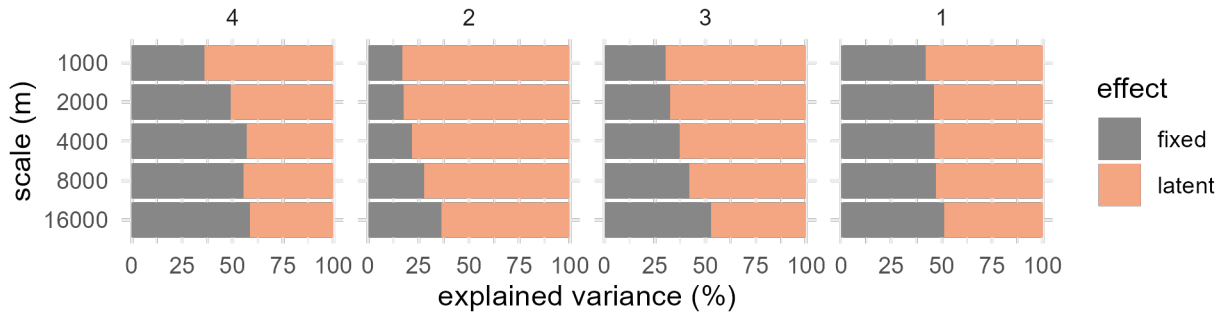


Figure 2-4: Variance partitioning

Percent of variance explained by fixed (environmental) and latent (random spatial) effects at each assessed scale grouped by cluster

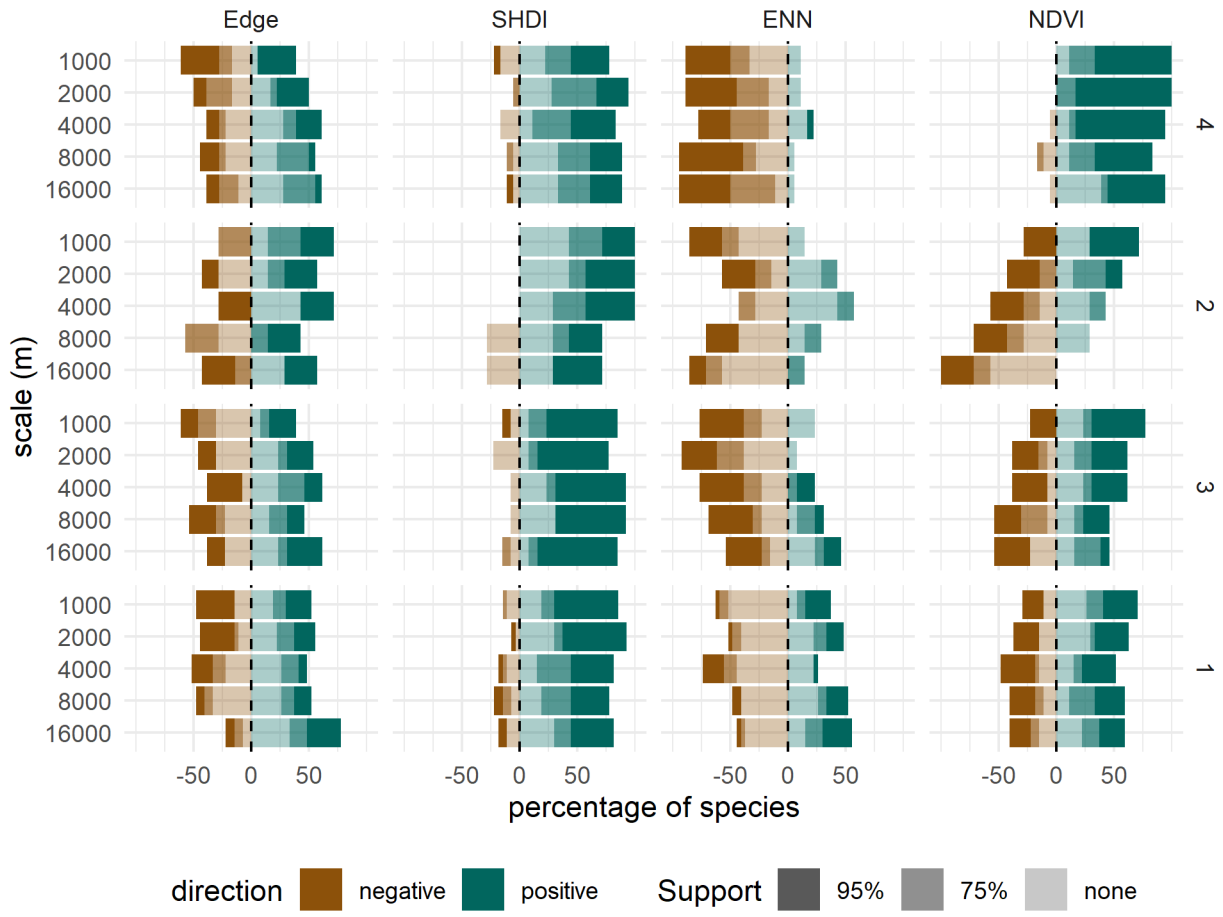


Figure 2-5: Environmental effects across scales

Environmental factor effects summarized by species cluster across all scales

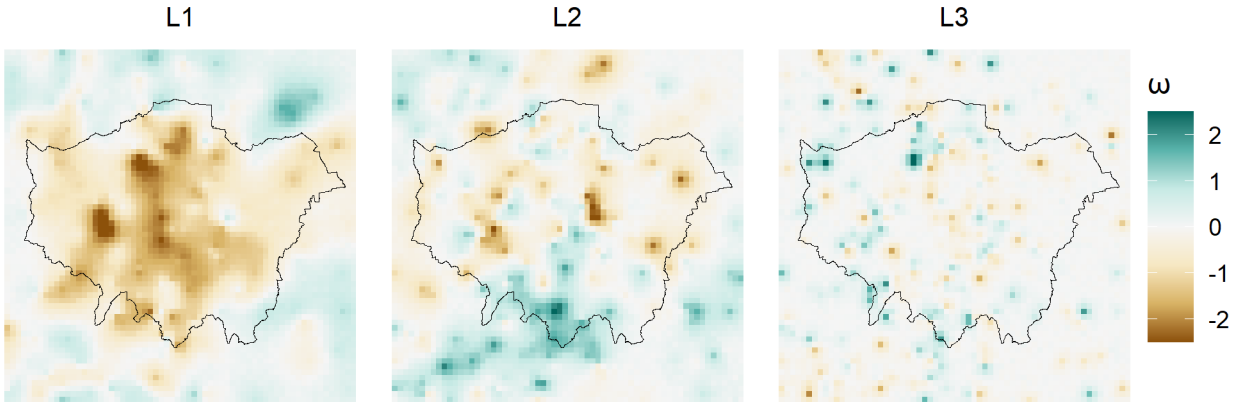


Figure 2-6: Spatial latent factors

Mean estimate of each spatial latent factor (ω) from the model fit with environmental factors sampled at 1,000m

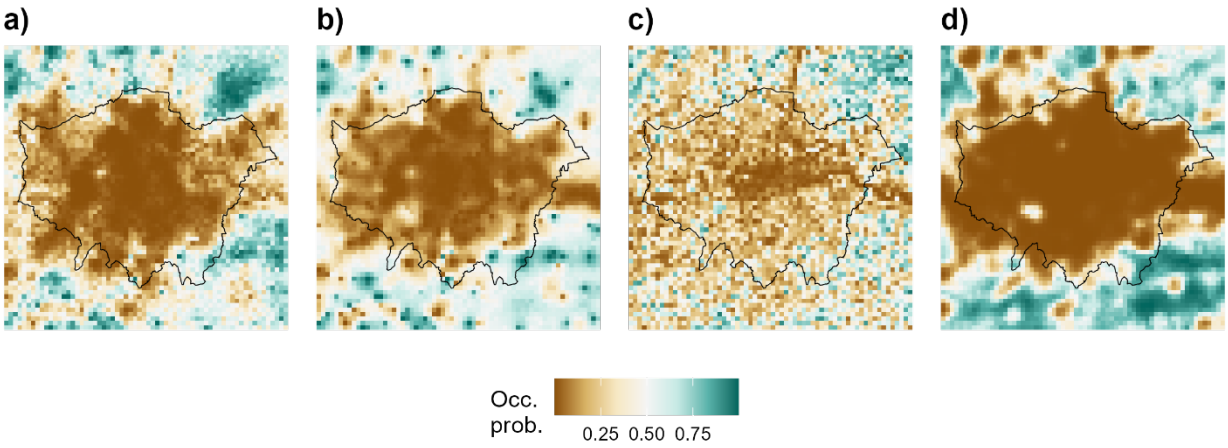


Figure 2-7: Eurasian Skylark occurrence probability

Maps showing predicted occurrence probability for the Eurasian Skylark across the study extent, with the Greater London region outlined in black for reference. When both fixed (environmental) and latent (spatial random) effects are included, predictions remain relatively consistent between a) 1,000m and b) 4,000m sampling scales. In contrast, the modeled relationships with the environmental factors differ substantially when sampled a c) 1,000m and d) 4,000m.

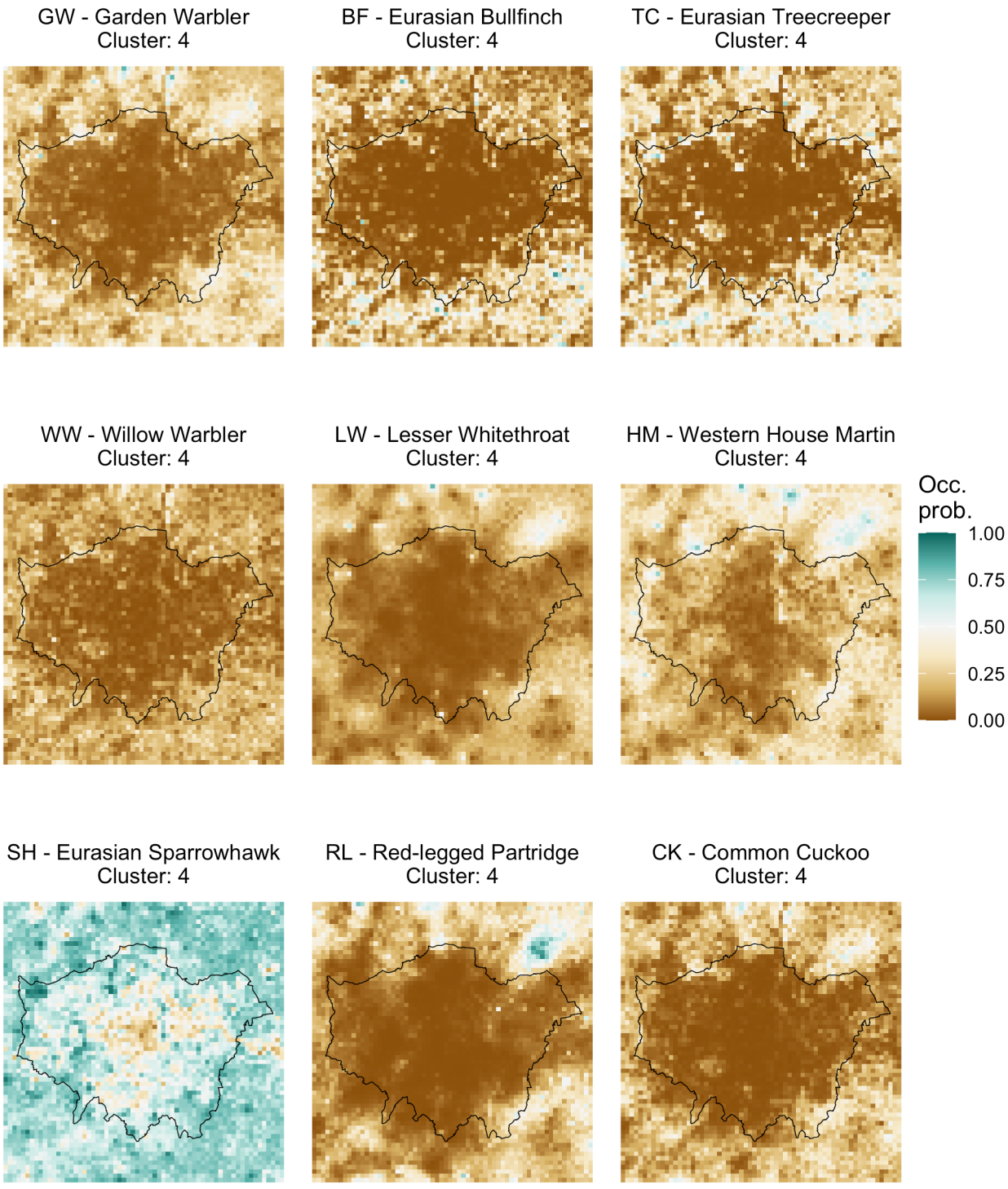


Figure 2-8: Predicted species occurrence at 1,000m (species 1-9)

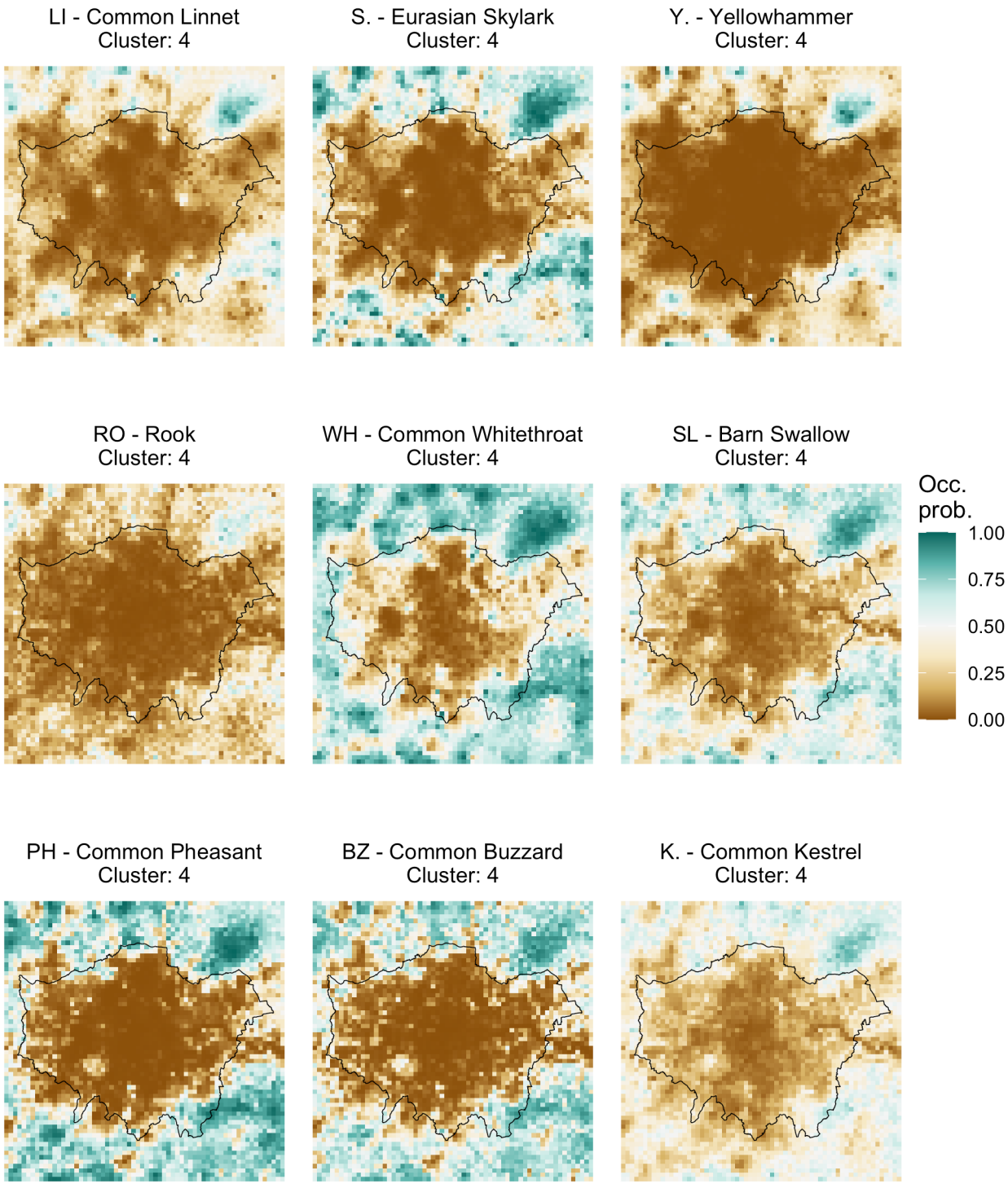


Figure 2-9: Predicted species occurrence at 1,000m (species 10-18)

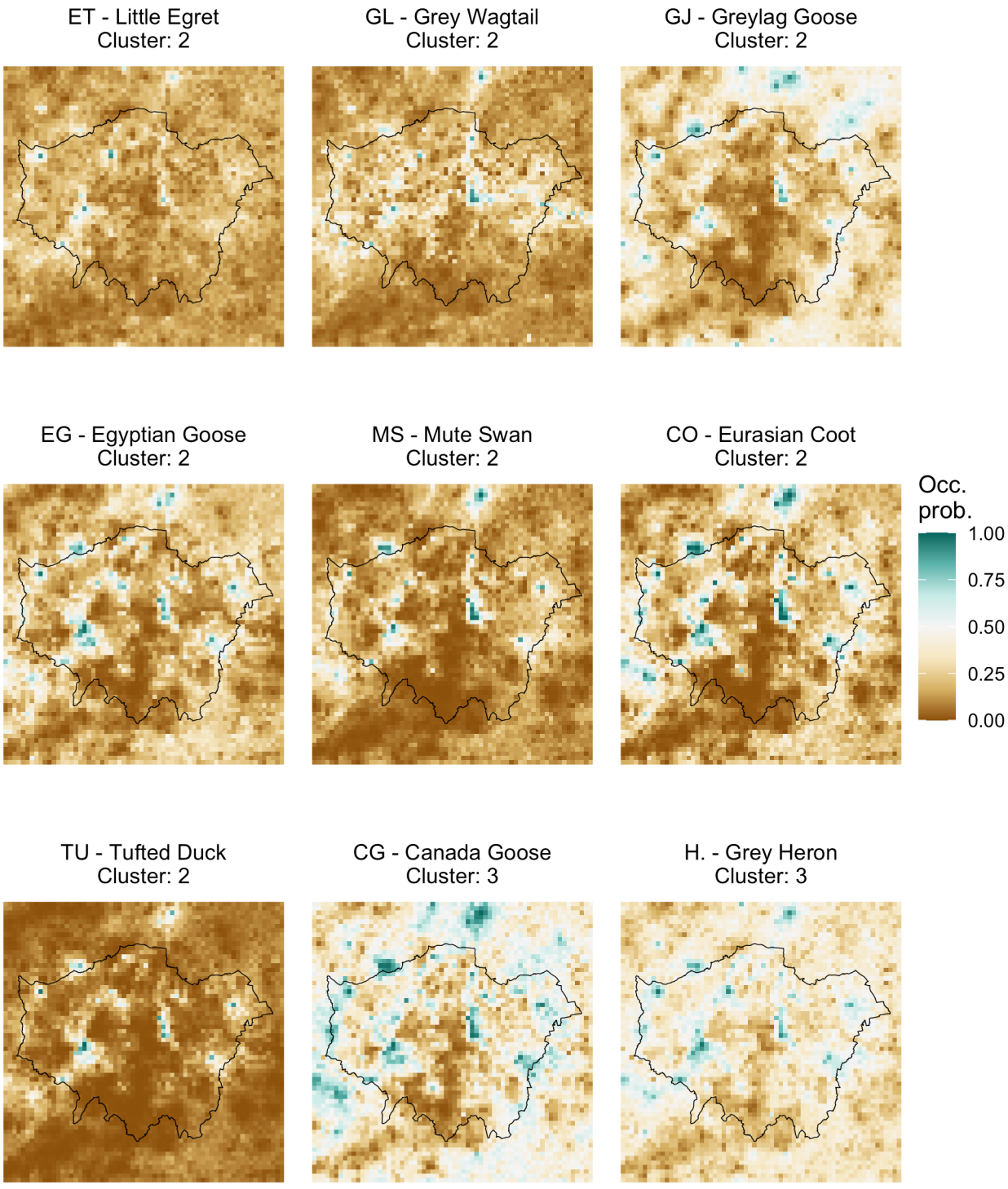


Figure 2-10: Predicted species occurrence at 1,000m (species 19-27)

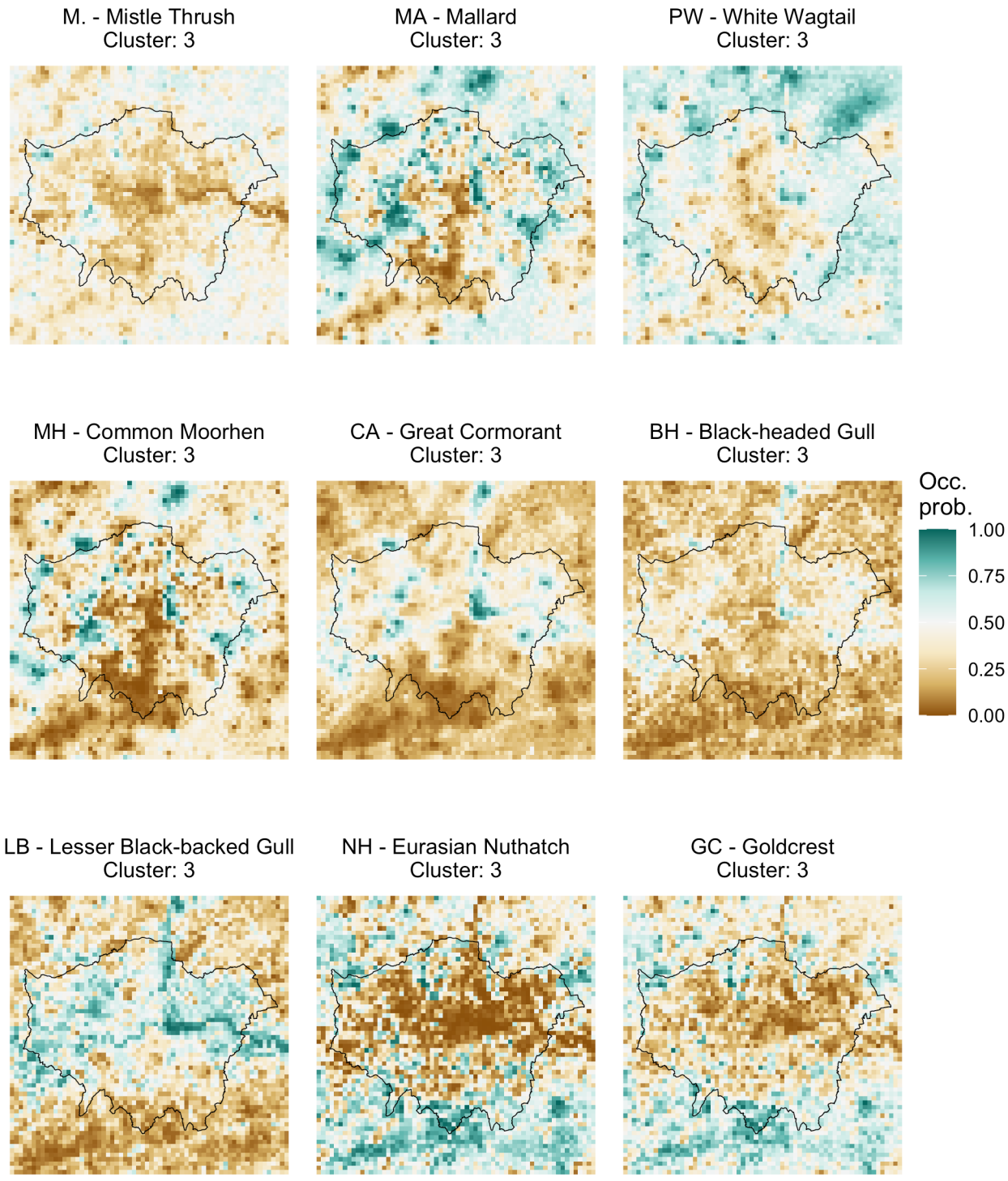


Figure 2-11: Predicted species occurrence at 1,000m (species 28-36)

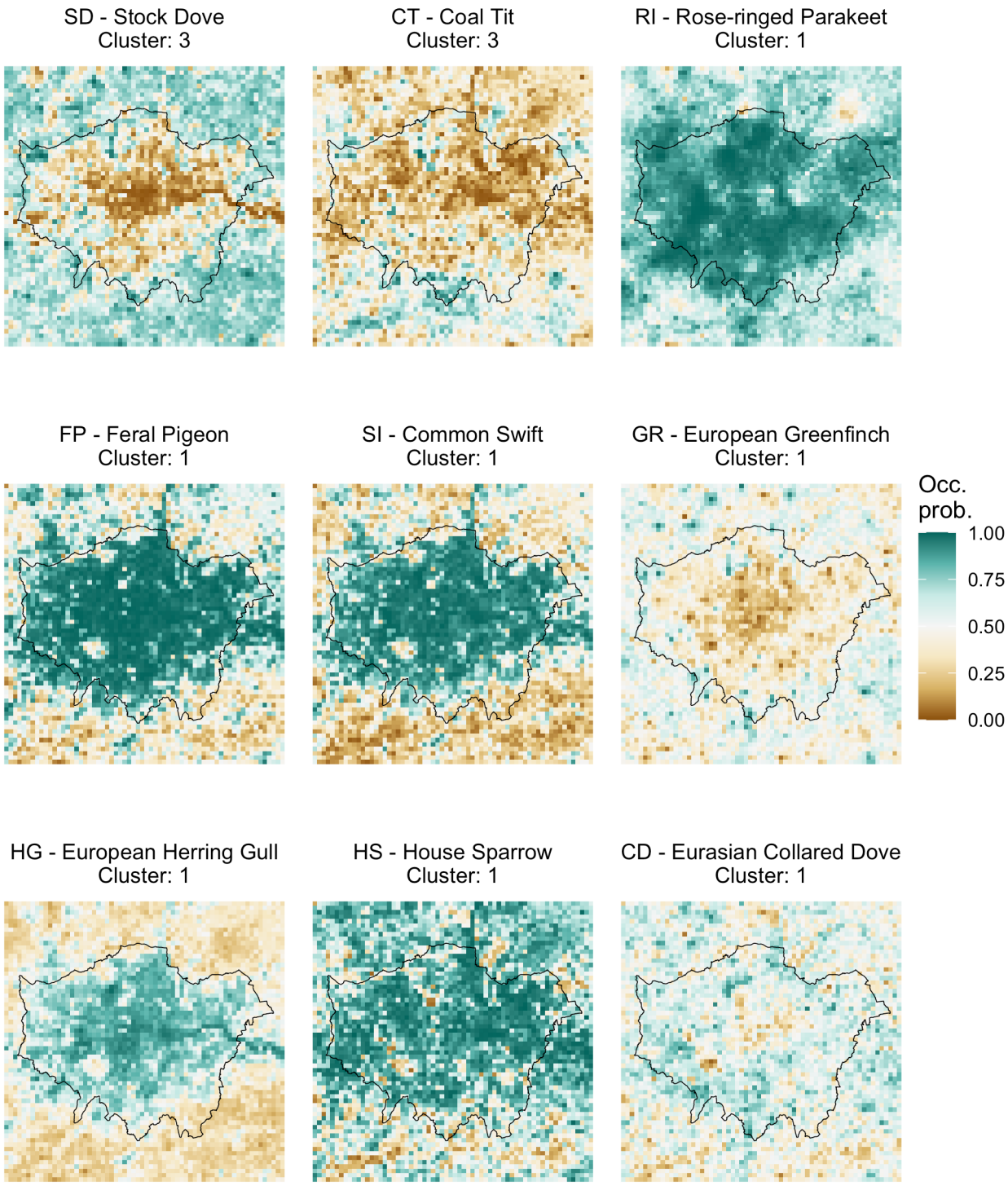


Figure 2-12: Predicted species occurrence at 1,000m (species 37-45)

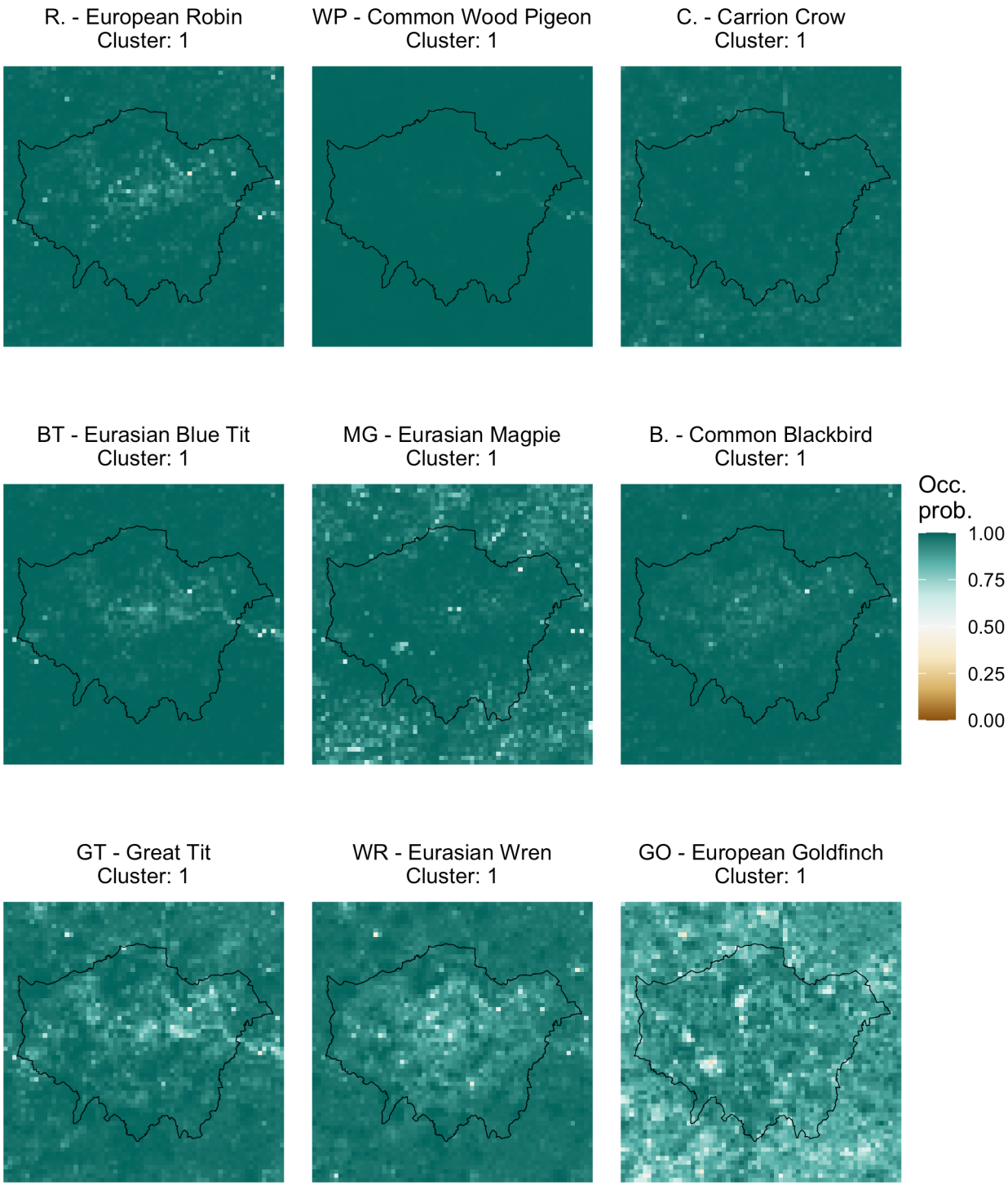


Figure 2-13: Predicted species occurrence at 1,000m (species 46-54)

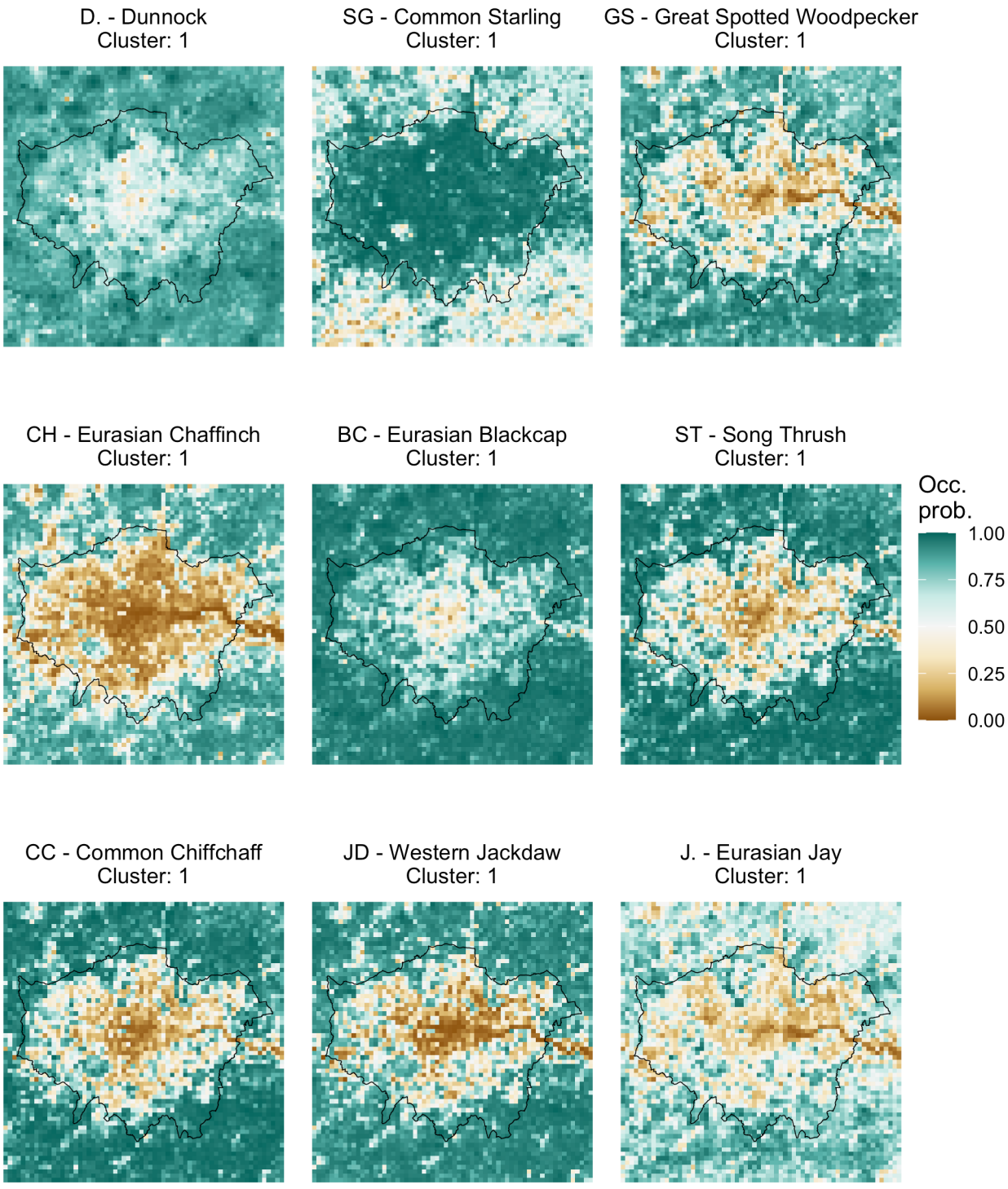


Figure 2-14: Predicted species occurrence at 1,000m (species 55-63)

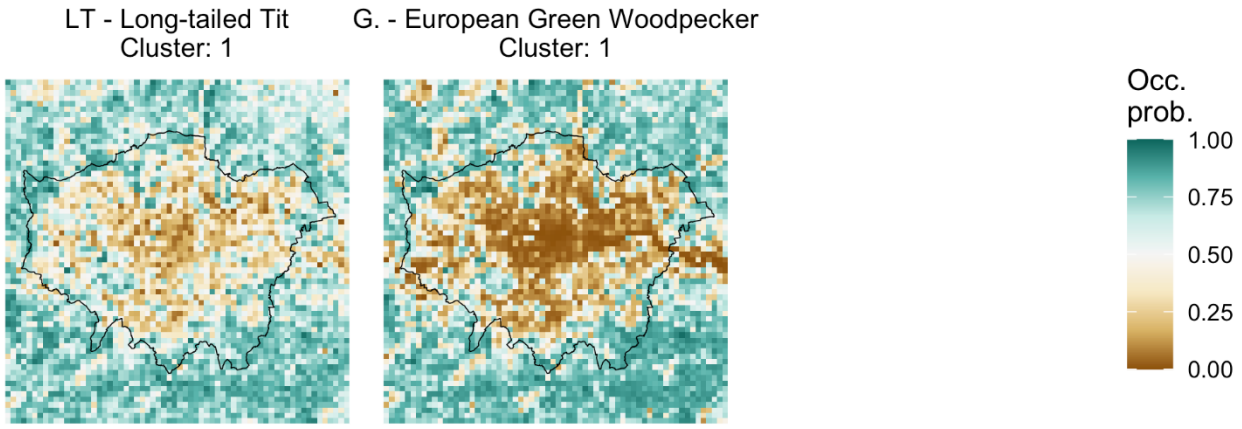


Figure 2-15: Predicted species occurrence at 1,000m (species 63-65)

Table 2-1: Environmental factors (JSDM)

Name	Metric	Category
SHDI	Shannon's diversity index	Land cover diversity
Edge	Habitat edge density	Edge habitat
ENN	Habitat mean Euclidean nearest neighbor distance	Habitat connectedness
NDVI	NDVI mean value	Vegetation intensity/urbanization

Table 2-2: Model performance summary

scale (m)	WAIC	Tjur R^2	variance explained (%)	
			fixed	latent
1000	151,891	0.57	25%	75%
2000	151,694	0.57	33%	67%
4000	151,659	0.57	39%	61%
8000	153,598	0.57	40%	60%
16000	153,570	0.56	51%	49%

Table 2-3: Model group explanatory power

Metrics are shown only for the 1,000m scale but are representative across all scales.

	Cluster		**Order**		**Family**	
	statistic	**Pr(>F)**	**statistic**	**Pr(>F)**	**statistic**	**Pr(>F)**
PERMANOVA	0.54	0.001	0.30	0.047	0.64	0.013
Mantel	0.32	0.001	-0.01	0.538	0.05	0.021

PART 3

Multiscale factor selection reveals differences between avian guilds in an urbanized landscape

Abstract

Conserving bird biodiversity in human-altered landscapes requires a multiscale understanding of how different species perceive environmental factors. The "scale of effect" is an approach commonly used to determine the most relevant scale at which to model species distributions. However, empirical evidence and theory suggest that processes at multiple scales shape the patterns of species occurrence we observe, where identifying only a single best scale may be misleading. To understand how relevant factors explain bird occurrence simultaneously across scales, we implemented a multiscale environmental factor selection approach for 65 bird species around Greater London to determine the factors at specific scales that best explain species occurrence. We included environmental factors at 10 spatial scales—from 125m to 64km around each observation location. Our analysis shows that environmental factors quantified at a scale of 125m, the smallest we tested, best explained species occurrence for habitat specialists (woodland, aquatic, and open habitat species). However, model performance for synanthropic species was lower overall, where factors were not biased towards smaller scales, suggesting less dependence on specific habitat needs and wider niche breadth. Across all species, responses often showed similar effects across ranges of scales, as well as reversing direction, suggesting hierarchal processes and the importance of implementing the multiscale perspective.

Introduction

Bird diversity patterns across urbanization gradients reflect how different species respond to human-modified landscapes (Lepczyk et al. 2008; McKinney 2008). Different species are known to have different abilities to adapt to urbanization, ranging from those that can thrive in urban environments, species that can adapt to moderate human modification, and species that avoid dense urbanization, but may persist in remaining patches of natural habitat (Geschke et al. 2018). Urban environments create complex spatial heterogeneity (Gill et al. 2008), with each species responding differently based on their specific ecological requirements and adaptive capacity (i.e. their niche) (Callaghan et al. 2019). Effective conservation planning across multiple scales depends on understanding these varied species responses and their combined effects on bird communities. While individual conservation efforts may target single species, the broader goal of increasing biodiversity requires knowledge of how these efforts will influence overall community composition and structure (Litteral & Shochat 2017).

Birds are among the best-studied taxonomic groups due to their widespread distribution and the relative ease and enjoyment of observing them (Fraixedas et al. 2020). Traditional long-term monitoring programs have generated high-quality datasets for environmental modeling, including the Breeding Bird Survey across North America (Ziolkowski et al. 2024) and similar initiatives in Europe, such as the British Breeding Bird Survey in the United Kingdom (Massimino et al. 2025). More recent data sources have expanded our understanding through acoustic detection methods that identify species by their vocalizations (Kahl et al. 2021). Additionally, crowdsourced observations from platforms like eBird (Sullivan et al. 2014) and iNaturalist provide spatially and temporally rich datasets that complement traditional survey methods.

However, regardless of the dataset, scale plays a crucial role in observing, analyzing, and interpreting information from ecological datasets (Turner & Gardner 2015; Wiens 1989), yet multiscale approaches remain underutilized in practice (McGarigal et al. 2016). Although theoretical frameworks can guide researchers toward scales that may be relevant for specific research questions, systematic data-driven methods for scale selection are rarely implemented. This gap between theory and application means that species distribution models likely fail to capture important scale-specific environmental factors to comprehensively interpret their outputs (Jackson & Fahrig 2015).

In practice, quantitatively selecting appropriate scales for environmental factors when modeling species distributions presents several challenges, namely the high computational demands and collinearity issues that arise when sampling and fitting models with environmental factors across multiple scales. The most common approach involves systematically fitting separate models for each environmental factor at different scales, then selecting the model that performs best according to metrics such as Tjur's R^2, RMSE, AUC, or WAIC (McGarigal et al. 2016; Stuber & Gruber 2020). The scale associated with the best-performing model is typically interpreted as the "scale of effect" for that factor (Brennan et al. 2002; Jackson & Fahrig 2012). However, this conventional method has notable limitations: it lacks integration across variables, potentially overlooks important multi-scale interactions, and fails to account for the biological reality that species may perceive and respond to the same environmental factor operating simultaneously at multiple scales (Kristan 2006; Stuber & Fontaine 2019).

Therefore, to understand how relevant factors explain bird occurrence simultaneously across scales, we implemented a multiscale factor identification model across Greater London, U.K. Our analysis examined 65 bird species using environmental factors quantified across 10 scales, from the lowest scale permitted by our data to the broadest scale constrained by our study extent. This approach allowed us to first identify the most relevant factors for each species, as well as the proportion variance in species occurrence that each factor explained at specific scales. The results enabled us to answer:

1. Which spatial scales best explain occurrence across an urbanized landscape, and does this vary between different bird guilds (woodland, aquatic, synanthropic, and open habitat species)?
2. Do synanthropic species (i.e., species that are well-adapted to human-modified environments) show different scale-response patterns compared to habitat specialists?

Previous work has shown that local habitat characteristics best explain diversity (Callaghan et al. 2018; Fairbairn et al. 2025), and that composition generally explains more variance than configuration (Litteral & Shochat 2017; Rosenfeld 2013). While synanthropic species have been shown to be less predictable than habitat specialists (Morelli et al. 2024), further consideration of scale dependance is needed. Previous studies have not systematically applied a systematic scale selection approach varying between and within factors to assess how relationships may vary across scales resulting from hierarchical decisions made by species in their environment (Johnson 1980).

Methods

We modeled the occurrence of 65 species within a 64 x 64km boundary centered over Greater London, U.K. with 10 environmental factors sampled across 10 spatial scales (**Figure 3-1**, see Appendix for all figures and tables). Because the environmental factors are sampled within buffers with radii of 32km (64km/2), the data extent of the environmental factors extends 32km around the study area, or a full extent of 128 x 128km. The study area contains a strong urban gradient sounded by rural open space and arable landscapes intermixed with smaller towns and villages. The south-central perimeter area is largely forested with increased topographic relief. The River Thames flows west to east, flowing through the center of the study area and draining to the North Sea. The Greater London boundary, while administrative, approximately delineates a dominate suburban landscape with rural surroundings.

Species observations

We used bird observation data from the British Breeding Bird Survey (BBS), a systematic monitoring initiative that has operated across the United Kingdom since 1994 (Massimino et al. 2025). This program employs trained volunteer observers who conduct standardized surveys within 1 km squares that are randomly selected using a stratified sampling approach. Survey activities occur twice each year during the April-June period to align with avian breeding activity. While the program has encompassed over 7,000 squares throughout its three-decade span, the squares monitored fluctuate annually based on volunteer participation rates. For this analysis we used observations from the most recently three years available, 2021-2023, which included 234 surveyed squares (**Figure 3-1**b).

The survey protocol requires observers to traverse two linear transects positioned within each square to create an approximate three-way division of the area, approximately oriented either in north-south or east-west directions (**Figure 3-1**c). The precise routing of these transects depends on the linear features present in the local landscape. Observers segment these transects into 200-meter segments and document all seen or heard species within each segment. We considered each 200-meter segment as a separate site (2,721 in total within our extent), each with two replicates, with the midpoint of the segment taken as the site's coordinates. Although the original survey data captures species abundance information, we transformed these records into binary presence-absence data for our analysis, though a similar modeling approach focused on abundance could complement this this study.

We included 65 bird species that occupy a range of niches within the study area (**Table 3-1**) that were selected because they occurred at more than 10% of the sites allowing for sufficient data for modeling. We classified each species into four guilds based on their primary habitat, based on the AVONET dataset classification (Tobias et al. 2022), which we modified based on the relevant land cover (LC) classes within the study area.

Environmental factors

We derived environmental variables from the LC and normalized difference vegetation index (NDVI) datasets. Our analysis utilized the most recent LC mapping product (LCM2023) developed by the UK Center for Ecology & Hydrology, which categorizes the British landscape into 21 distinct classes at 10m spatial resolution (Morton et al. 2024). To minimize collinearity

issues and enhance stratified sampling of environmental variables across survey sites, we consolidated the LCM2023 classification scheme into six broader categories: Woodland, Vegetation/Open, Arable, Water, Suburban, and Urban.

We based NDVI calculations on Sentinel-2 Surface Reflectance data. This vegetation index serves as a standard measure for evaluating plant health and density, with typical values spanning from -1 to 1—where elevated values reflect vigorous, healthy vegetation cover, values approaching zero represent bare soil or urban surfaces, and negative values usually indicate water features. We generated a cloudless NDVI composite using the max value for each pixel during 2023. Google Earth Engine facilitated the processing and extraction of annual NDVI composites for each year encompassed in our study (Gorelick et al. 2017).

From the LC and NDVI datasets, we extracted landscape metrics designed to capture different dimensions of landscape structure and arrangement (**Table 3-2**). For each metric, we performed calculations within circular buffers using a systematic sequence of doubling spatial extents: 125m, 250m, 500m, 1,000m, 2,000m, 4,000m, 8,000m, 16,000m, 32,000m, and 64,000m in diameter. This structured multi-scale approach enabled thorough evaluation of environmental influences spanning various ecological scales. We quantified environmental variables in R using the terra (Hijmans 2025) and landscapemetrics packages (Hesselbarth et al. 2019). Because we held grain constant when aggregating the metrics, calculating the derived landscape metrics of Edge, SHDI, and ENN was not computationally feasible above a scale of 16,000m.

Factor selection

We implemented a Bayesian hierarchical occupancy model that estimates species-environment relationships across multiple spatial scales while accounting for imperfect detection and spatial autocorrelation. Our implementation is based on the Bayesian latent indicator scale selection (BLISS) originally developed by Stuber et al. (2017), who demonstrated the approach for abundance with observations at sites presumably located far enough apart where spatial autocorrelation had little effect. BLISS leverages reversable-jump Markov Chain Monte Carlo (RJ-MCMC) to explore all variable combinations simultaneously in a single model (Green 1995). RJ-MCMC adds and removes variables between samples, where the proportion of samples that included a specific variable represents the probability that the variable should be included in the model. BLISS is able to handle moderately high collinearity between

environmental factors sampled across a range of scales, resulting in the identification of the most relevant environmental factors and the scales at which they operate.

The model consists of an ecological process that models the latent (unobserved) true occupancy state of the species, the observation process that models the observation process (i.e., probability that the species was detected if present), as well as a spatially structured random effect, or spatial latent effect, to account for spatial autocorrelation.

The model links the ecological and observation processes to model the observed data y_i for observation i following a Bernoulli distribution:

$$y_i \sim Bernoulli\left(z_{j[i]} \times p_i\right)$$

where:

z_j is the true occupancy state at site j

p_i is the detection probability for observation i

Ecological process

The true occupancy state z_j at site j is modeled as a Bernoulli distribution:

$$z_j \sim Bernoulli(\psi_j)$$

$$\text{logit}\left(\psi_j\right) = \beta_0 + \sum_k \sum_s I_{k,s} \times \beta_{k,s} \times X_{j,k,s} + \eta_j$$

where:

β_0 is the intercept

$X_{j,k,s}$ is the value of environmental variable k at scale s for site j

$\beta_{k,s}$ is the effect coefficient for variable k at scale s

$I_{k,s}$ is a binary indicator (0 or 1) determining whether variable k at scale s is included in the model

η_j is a spatially structured latent effect

Observation process

The probability of detection p_i for observation i is modeled as:

$$\text{logit}(p_i) = \alpha_0 + \sum_d \alpha_d \times W_{i,d}$$

where:

α_0 is the detection intercept

α_d is the estimated detection effect for variable d

$W_{i,d}$ is the detection covariate for variable d

Spatial structure

The spatial latent effect η_j for site j follows a conditional autoregressive distribution:

$$\eta_j \sim \mathrm{CAR}(\gamma, \tau_j)$$

where:

γ is the strength of spatial dependence, and

τ_j is the precision parameter

We implemented distance-based weights with exponential decay for all neighbors within 2,000m of each site. This represents twice the scale of each BBS 1km square, resulting in consideration of all transect segments in the same square, plus additional segments in any adjacent squares when estimating the spatial latent effect for each site.

We assigned weakly to moderately informative priors to aid in model convergence without overriding the data. We assigned the regression coefficients normal distributions with mean 0 and variance 2, and gamma distributions for precision parameters. We implemented the model using the NIMBLE framework (de Valpine et al. 2017) and ran four parallel MCMC chains for 100,000 iterations each (30,000 burn-in, thinned by 70). We assessed convergence using the Gelman-Rubin statistic to ensure all values were < 1.1 and effective sample sizes were > 200. We configured the reversable jump sampler to initially equally sample all factor parameters with 50% inclusion probability. We considered any factor as meaningful if it was included (i.e. not set to zero) for at least 60% of all samples.

The multiscale factor selection results from BLISS cannot be directly applied for predictive inference because factors identified as meaningful may represent alternative rather than additive effects. This limitation arises from the variable selection process, where factors at different scales for the same environmental variable (e.g., woodland cover at 1,000m versus 2,000m) may capture similar ecological processes and thus represent competing explanatory variables rather than cumulative effects. In such cases, including both factors simultaneously in a single predictive model could lead to overfitting and unrealistic parameter estimates, as these variables likely capture overlapping aspects of the same underlying habitat relationship.

To address this limitation and validate our BLISS results through species-specific interpretation, we conducted a focused analysis on three representative species that exemplify distinct ecological strategies within our study system: House Sparrow (*Passer domesticus*) representing a synanthropic species, Coal Tit (*Periparus ater*) representing a woodland specialist and urban adapter, and Eurasian Skylark (*Alauda arvensis*) representing an urban avoider dependent on open habitats.

For each focal species, we identified meaningful factors using two criteria: those with posterior inclusion probabilities exceeding 60% in the BLISS analysis, or alternatively, the five factors with the highest inclusion probabilities if fewer than five factors met the 60% threshold. When the same environmental variable appeared as meaningful across consecutive spatial scales (e.g., woodland cover at both 500m and 1,000m), we retained only the factor with the highest posterior inclusion probability to avoid collinearity issues and ensure model identifiability.

We then fitted separate occupancy models for each focal species using a selected subset of the BLISS-identified factors. This approach allowed the intercept to vary spatially while maintaining the same underlying model structure as our BLISS implementation. We implemented these models using the spOccupancy package (svcTPGOcc function) (Doser et al. 2022) with model configurations, prior distributions, and MCMC settings to match the original BLISS analysis as closely as possible. This validation step enabled us to examine species-specific responses in detail while confirming that the multiscale patterns identified through BLISS translate into coherent ecological interpretations for individual species.

Results

Environmental factor responses across scales

Environmental factors quantified at the smallest spatial scales (125-500m) provided the strongest explanatory power for species occurrence patterns, with 125m being the most frequently selected scale across all species and environmental factors (**Figure 3-5**). However, the most meaningful factors and scales varied between the four guilds with notable scale and direction (i.e., positive versus negative) patterns (**Figure 3-2**). Overall, configuration metrics remained less influential than composition metrics across all guilds, though water-associated species showed notable responses to edge and connectivity measures at intermediate scales.

Woodland species (n=26) showed the most pronounced scale-dependent responses, with woodland cover exhibiting strong positive associations concentrated at the 125-250m scales across approximately 12 species. This guild demonstrated secondary peaks at broader scales (8-16km) for woodland cover, suggesting that both immediate habitat availability and landscape-scale forest connectivity influence occurrence. Suburban land cover generated mixed responses across scales, with both positive and negative effects occurring primarily at local scales (≤1km), while open habitat showed consistent negative responses at the finest scales.

Water-associated species (n=15) displayed the strongest and most consistent positive responses to water features, with peak associations at 125m involving nearly all species in this guild. Edge habitat effects were more variable, showing both positive and negative responses distributed across intermediate scales (1-8km), while connectivity metrics (ENN) showed sporadic but meaningful effects primarily at local scales.

Synanthropic (urban) species (n=13) had meaningful responses across all scales for the top factors, without strong evidence of a bias towards smaller scales. Suburban environments positively influenced species occurrence at smaller scales, with some negative associates at larger scales. Urban land cover produced predominantly negative responses concentrated at 125-500m scales, suggesting that even urban-adapted species are negatively affected by intense urbanization in their immediate vicinity. Woodland cover showed primarily negative responses at local scales, reflecting these species' adaptation to more open, human-modified environments.

Open habitat species (n=11) demonstrated strong positive associations with arable land at local scales (125-500m), with responses declining sharply at broader scales. This guild showed consistently negative responses to both suburban and woodland cover at fine scales, reflecting their specialization for extensive open landscapes and sensitivity to habitat fragmentation or encroachment by developed areas.

Species-specific multiscale responses

The multiscale responses of the three focal species, House Sparrow (urban generalist), Coal Tit (woodland specialist and urban adapter), and Eurasian Skylark (open specialist and urban avoider), further illustrate differences between guilds (**Figure 3-3**).

The House Sparrow demonstrated the most complex multiscale response pattern among the three species examined. Suburban land cover showed a scale-dependent shift from positive effects at local scales (250m and below) to negative effects at broader scales (1,000m and

above), suggesting that while House Sparrows benefit from suburban environments in their immediate vicinity, extensive suburban development at the landscape scale may be detrimental. Woodland cover exhibited consistently negative effects across all meaningful scales (≤500m), reflecting this species' preference for more open, human-modified environments. Additional meaningful relationships emerged for arable and open/vegetation land cover types at scales ≤500m, with negative effects for arable land and a transition from negative to positive effects for open/vegetation areas across increasing scales.

The Coal Tit responses aligned with its woodland specialist classification and adaptation to lightly developed areas. The species showed positive associations with suburban land cover at 125m and with woodland at 250m and 500m scales. This pattern reflects the Coal Tit's ability to exploit wooded areas in suburban settings.

The Eurasian Skylark exhibited response patterns consistent with its open habitat requirements and rural associations. The species demonstrated positive relationships with arable land at local scales (≤250m) and negative responses to both suburban and urban land cover at broader scales. This pattern reflects the Skylark's dependence on extensive open agricultural landscapes and its sensitivity to urban development.

Partition of variance across scales

Variance explained by the selected factors were also proportioned differently across scales, showing that while the fixed environmental effects generally explained variance at scales at and below 2,000m, the latent unmodeled (spatially structured site effects) variance occurred at scales at or above 2,000m (**Figure 3-4**).

The variance of suburban and woodland land cover explained approximately a third of the variance of House Sparrow occurrence at a scale of 250m, plus a small edge effect at 1,000m, while an additional (but opposite) suburban effect and a large latent effect explained the remaining two-thirds of variance around a scale of 2,000m. The large explanation of variance by the latent effect further illustrates a muted signal to the included environmental effects relative to species from other guilds.

The variance explaining Coal Tit occurrence showed a large contribution from woodland landcover at 500m, with environmental factors in total explaining 40% of variance, with the remaining explained by latent effect estimated around a scale of 4,000m. In contrast, environmental effects explained approximately 60% of variance for the Skylark, with 50%

attributed to open habitats (open and arable cover) at and below 250m, showing specific habitat needs. The remaining latent effect was estimated to occur at a larger scale between 8,000m and 16,000m.

Discussion

These results illustrate that environmental factors quantified at scales less than 1,000m, particularly at 125m, were the most frequently identified factors explaining species occurrence patterns for woodland, aquatic, and open-habitat species. In contrast, synanthropic species showed meaningful responses distributed across all spatial scales, suggesting reduced dependence on specific natural habitat features and more generalized associations with human-modified environments across wider range of scales. Across all species, meaningful responses were often identified across multiple scales for the same factor, suggesting similar responses to factors across a range of scales, or hierarchical effects where a factor at a smaller scale is degraded or enhanced depending on the broader context. The ability of this systematic multiscale approach to identify correlations across scales between and within factors enables ecologists to more realistically study species distributions and diversity through the lens of hierarchy theory. Capturing multiple environmental relationships at specific scales—rather than a single best scale—could reconcile previously contradictory evidence of how species traits influence their interaction with the environment, leading to more effective conservation.

The pronounced small-scale responses observed for woodland, grassland, and aquatic species highlight the importance of habitat for specialist species, likely representing the scale at which specific resources are required for occupancy. Likewise, the strong positive response of aquatic species to water features at 125m serves as an important validation that our BLISS model successfully recovered expected ecological signals in the data.

Synanthropic species exhibited markedly different patterns, with meaningful responses occurring across all spatial scales rather than concentrating at local scales. This pattern suggests that urban-adapted species benefit from their ability to exploit resources distributed across multiple spatial scales within human-modified environments. The generally lower model performance for these species indicates their capacity to successfully inhabit diverse environments across the urban landscape, making their occurrence patterns more difficult to predict based solely on environmental factors (Morelli et al. 2024). This supports the evidence

from other studies that avian species that thrive in urbanized environments have wider or more flexible niches (Isaksson 2018; Mazza & Šlipogor 2024; Sol et al. 2013).

Composition metrics (e.g., percent area of woodland, suburban, or water cover) consistently outperformed configuration metrics (SHDI, Edge, and ENN) in both the frequency of meaningful responses as well as size of effect. This finding aligns with previous studies demonstrating that habitat amount often trumps habitat arrangement in determining species occurrence patterns (Litteral & Shochat 2017). However, this result may also indicate that commonly used configuration metrics fail to accurately capture habitat and resource arrangement as perceived by birds, suggesting a need for more ecologically meaningful measures of landscape structure (Rosenfeld 2013).

Two response patterns in the data illustrate the need to move away from models that assume a single best scale for modeling species-environmental relationships (Stuber & Fontaine 2019). The first pattern involved BLISS identifying meaningful responses in the same direction across consecutive scales, such as the positive effect of arable land cover on Skylark occurrence at 125m–250m scales, and the negative effect of woodland on House Sparrow occurrence across 125m–500m scales. This pattern likely does not indicate hierarchical effects but rather suggests that habitat composition within this range of scales consistently meets or fails to meet species requirements. These responses may reflect the grain at which landscapes vary relative to species' perceptual abilities and resource needs.

The second pattern involved directional changes in factor effects across scales, exemplified by House Sparrow responses to suburban land cover: positive effects at 125m–250m, no meaningful response at 500m, and negative effects at 1,000m–2,000m scales. These scale-dependent reversals more convincingly suggest hierarchical effects, perhaps a reflection of different habitat selection processes, such as home range versus resource availability (Johnson 1980). House Sparrows may thrive in suburban areas when these represent isolated neighborhoods or edge habitats of small towns, but suffer in extensive homogeneous residential developments characteristic of London's urban core. Such patterns indicate that species may simultaneously require specific local conditions that are enhanced or degraded depending on the broader landscape context.

The multiscale perspective enabled by systematic multiscale factor selection provides new opportunities to test theoretical relationships between species traits and scale sensitivity,

particularly dispersal ability and morphological characteristics like hand-wing index (HWI), which reflects wing pointedness and flight efficiency in forest birds (low HWI, rounded wings) versus migratory and open-habitat species (high HWI, pointed wings) (Pease 2024). While previous studies linking traits to scale effects have been constrained by single best, or characteristic, scale approaches (Miguet et al. 2016), the BLISS results allow for simultaneous effects across multiple scales, providing a more realistic foundation for testing trait-scale relationships (Stuber & Fontaine 2019).

Furthermore, our finding that synanthropic species showed the most dispersed responses across scales supports evidence linking behavioral flexibility and niche breadth to urban tolerance. Generalists appear more capable of exploiting resources distributed across multiple spatial scales, while specialists concentrate their responses at scales matching their specific resource requirements (Alba et al. 2025; Callaghan et al. 2019). Future analyses incorporating comprehensive trait databases could reveal whether the scale dispersion patterns we observed correlate with established measures of ecological flexibility, including relative brain size, dietary breadth, and behavioral plasticity.

Multiscale analysis is able to connect separate conservation initiatives for different species on different scales (Hobbs 2003), which is especially relevant in urbanized landscapes (Aronson et al. 2016; Uchida et al. 2021). Individual landowners can provide food and habitat in their backyards, providing for more species, such as the Coal Tit, that are not as well adapted as flexible synanthropic species (Fuller et al. 2008). Parks can coordinate designated breeding areas for sensitive species, such as the Skylark holding onto large urban parks (Loretto et al. 2019; Parks 2024). City and regional government can manage large scale programs reducing the impact of intensive agriculture and protect key wetlands. Furthermore, a hierarchical approach can be used to optimize resources, where candidate areas with similar characteristics could be differentiated based on its broader context, as well as the potential for meaningful actions within each area at smaller scales. This requires both leveraging multiscale model output for understanding species requirements, as well as integrating across species to understand the impact on biodiversity.

While the BLISS approach more accurately reflects ecological theory and multiscale habitat selection, our results require careful interpretation. Allowing effects across all scales for each factor increases vulnerability to spurious correlations with landscape patterns, particularly

given the nested nature of our buffer design. However, this concern is partially offset by our conservative inclusion criteria (60% posterior probability) and the biological plausibility of many identified relationships. Approaches to understand the thresholds of species responses to habitat, and how that is influenced by the heterogeneity of the landscape across scales, represents a valuable avenue for future research. Further insights could inform more nuanced habitat management strategies that consider both local habitat quality and landscape context.

Overall, these results are at step towards understanding the processes at multiple scales that contribute to the spatial variation of biodiversity across urbanized landscapes. Multiscale factor selection enables us to estimate the contribution of meaningful responses for factors at multiple scales and represents a valuable improvement over the helpful but overly simple single best scale of effect approach. Allowing environmental relationships to be systematically identified at multiple scales is necessary to enable more effective species conservation and urban development policies.

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Appendix

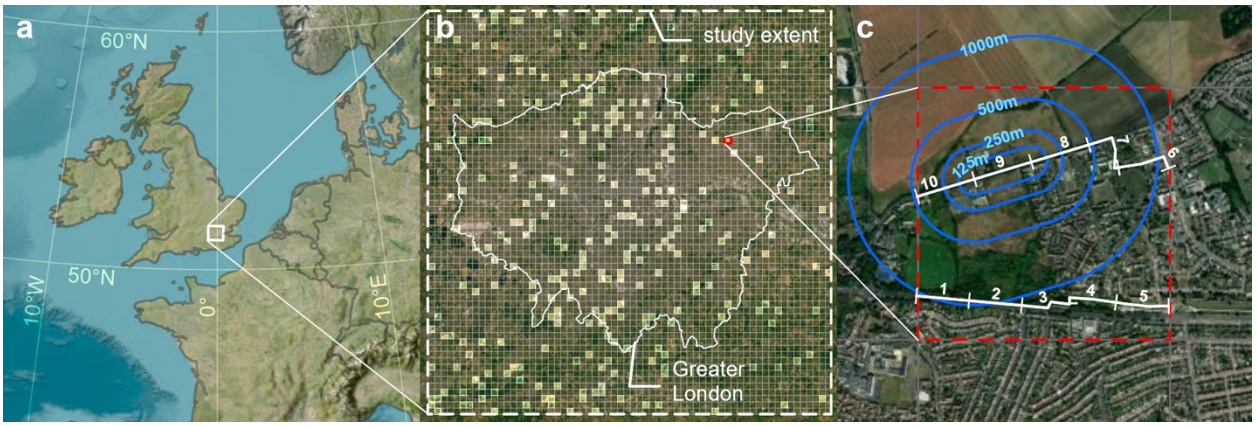


Figure 3-1: Study location, site extent, and example BBS segments

a) Study location within Great Britain, b) 1km squares sampled in the British Breeding Bird Survey (BBS) during the study's 2021-2023 time period, and c) example 1km square and transect lines surveyed as part of the British Breeding Survey

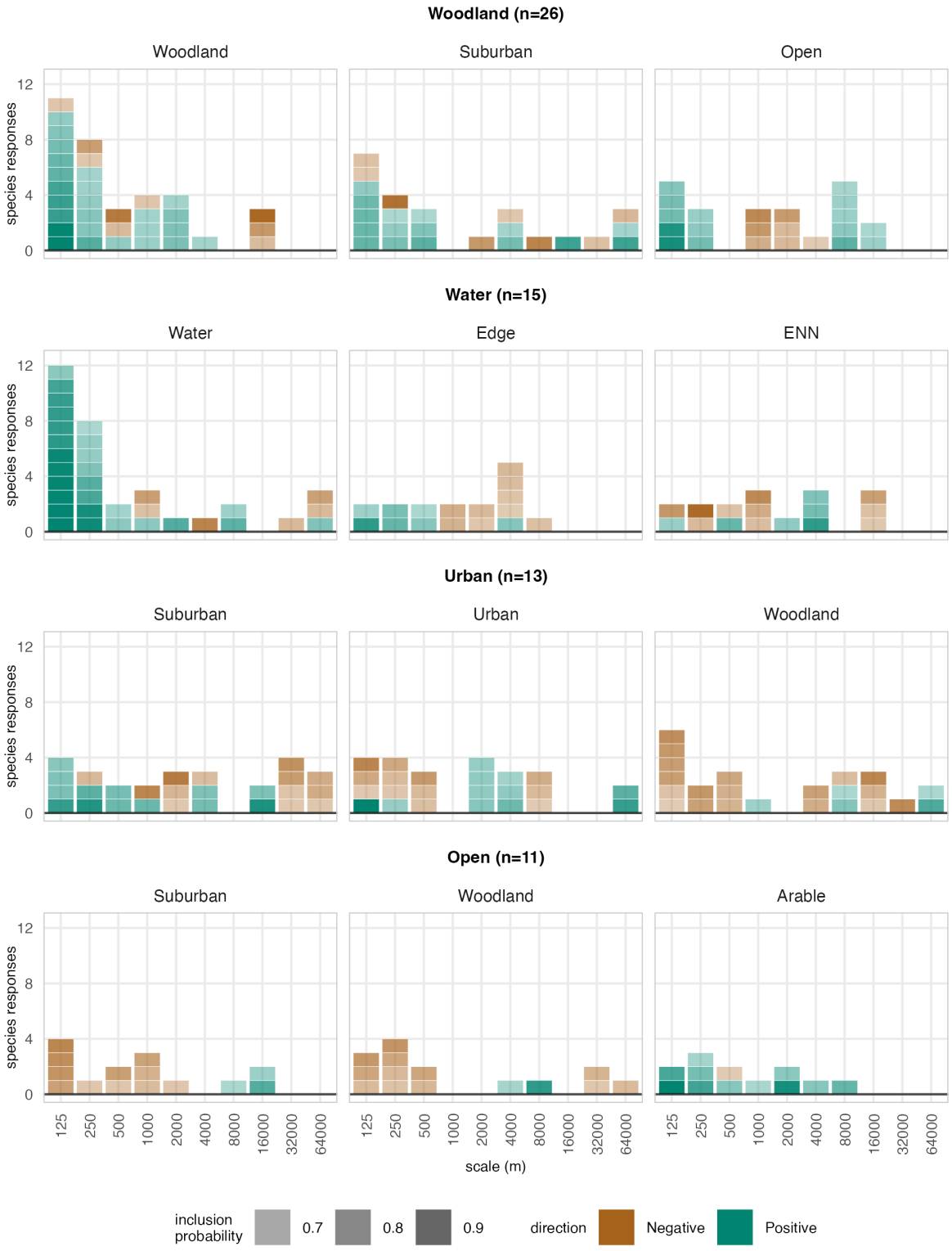


Figure 3-2: Identified relationships

Response of species to environmental factors across scales, with each box representing a factor for one species that was included in the model for at least 60% of MCMC samples. For each guild, the factors are ordered by total number of meaningful responses in descending order.

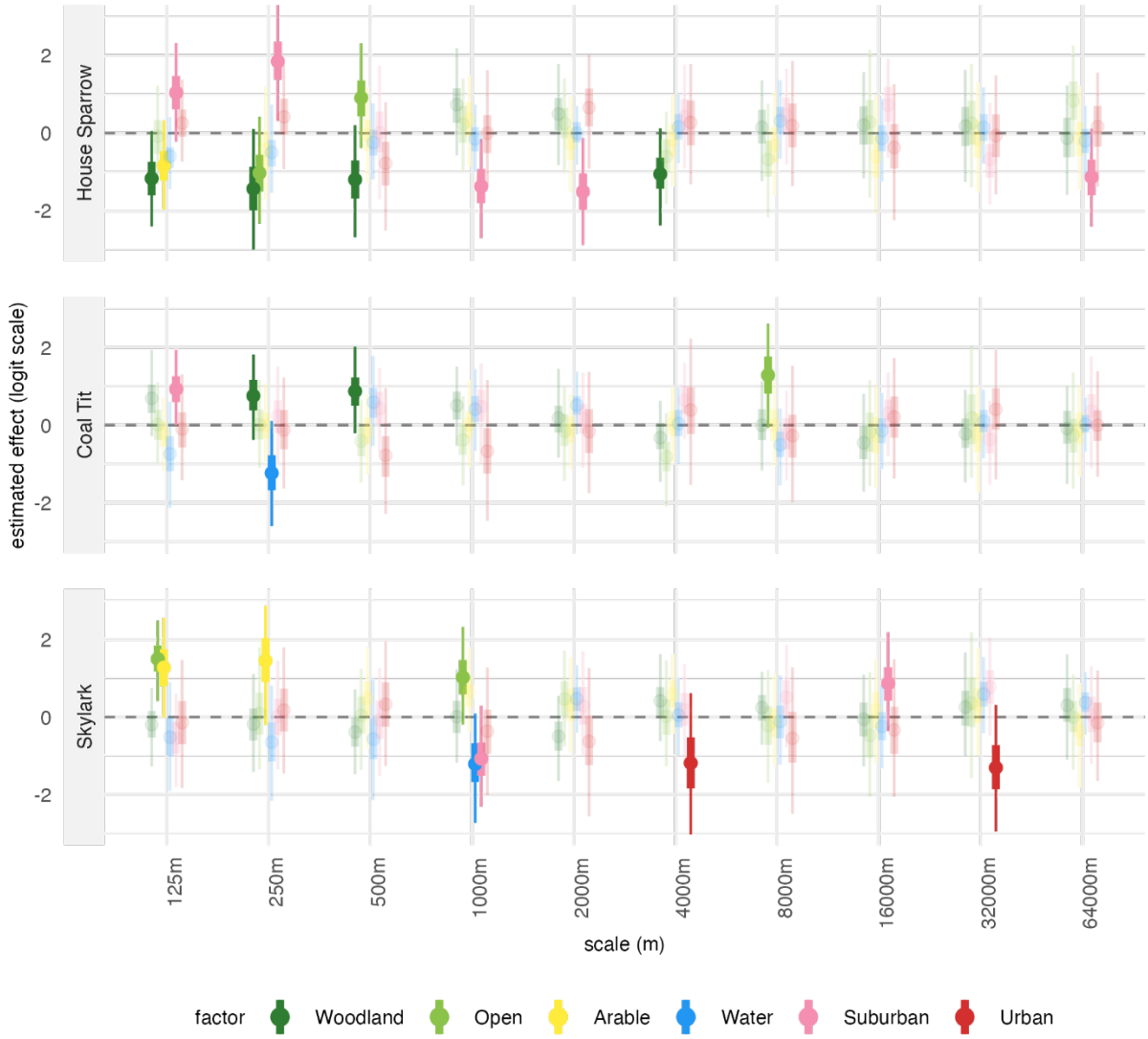


Figure 3-3: Varying responses across scale for three species

Responses to environmental factors representing composition metrics (configuration metrics not shown for clarity) of select species across scales (opaque responses are those that were included for at least 60% of the total MCMC samples)

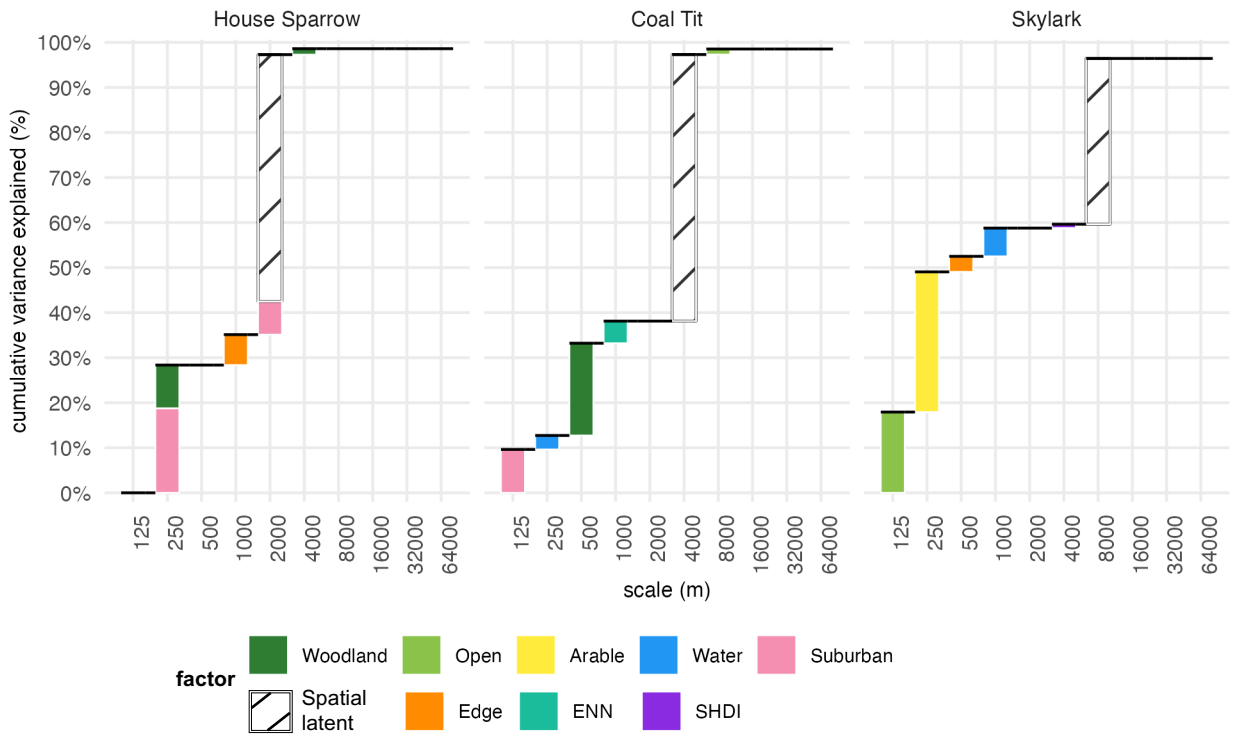


Figure 3-4: Variance partitioning for three species

Variance explained by each factor across scales from selected species models

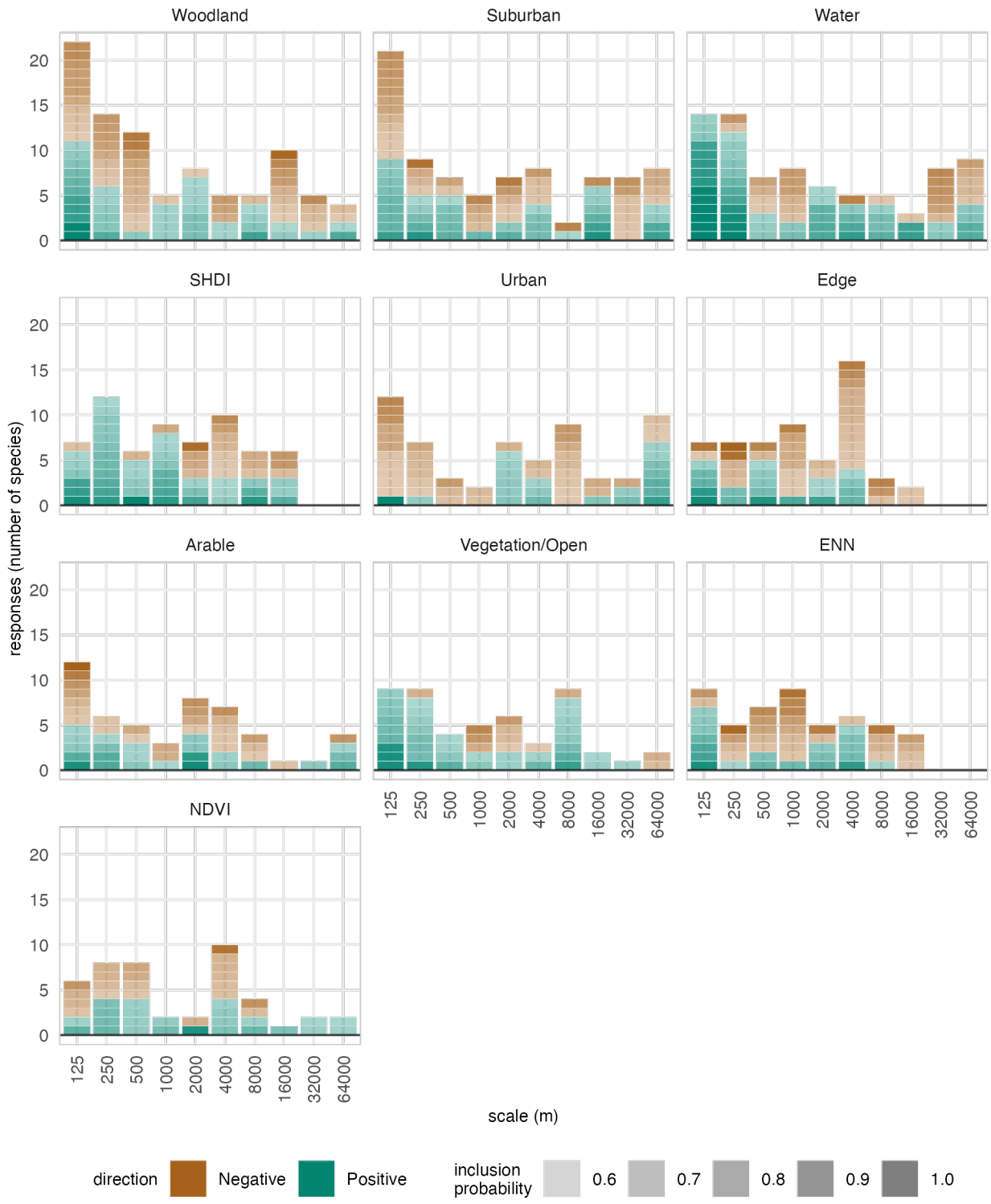


Figure 3-5: Identified relationships for all species and factors

Table 3-1: Modeled species primary habitat and detection rate

Common name	Scientific name	AVONET habitat	Classified habitat	Detection rate
European Robin	*Erithacus rubecula*	Forest	Woodland	35.4%
Eurasian Wren	*Troglodytes troglodytes*	Forest	Woodland	33.2%
Eurasian Blue Tit	*Cyanistes caeruleus*	Forest	Woodland	31.2%
Common Blackbird	*Turdus merula*	Forest	Woodland	25.6%
Great Tit	*Parus major*	Woodland	Woodland	21.1%
Eurasian Blackcap	*Sylvia atricapilla*	Woodland	Woodland	17.1%
European Goldfinch	*Carduelis carduelis*	Woodland	Woodland	14.3%
Common Chiffchaff	*Phylloscopus collybita*	Forest	Woodland	13.4%
Dunnock	*Prunella modularis*	Forest	Woodland	12.7%
Song Thrush	*Turdus philomelos*	Forest	Woodland	11.9%
Eurasian Chaffinch	*Fringilla coelebs*	Forest	Woodland	8.3%
Great Spotted Woodpecker	*Dendrocopos major*	Woodland	Woodland	7.5%
Goldcrest	*Regulus regulus*	Forest	Woodland	4.6%
Eurasian Nuthatch	*Sitta europaea*	Forest	Woodland	4.6%
European Greenfinch	*Chloris chloris*	Woodland	Woodland	4.5%
Eurasian Jay	*Garrulus glandarius*	Forest	Woodland	4.2%
European Green Woodpecker	*Picus viridis*	Forest	Woodland	3.9%
Long-tailed Tit	*Aegithalos caudatus*	Forest	Woodland	3.7%
Coal Tit	*Periparus ater*	Forest	Woodland	3.6%
Mistle Thrush	*Turdus viscivorus*	Forest	Woodland	2.0%
Garden Warbler	*Sylvia borin*	Woodland	Woodland	0.9%
Eurasian Treecreeper	*Certhia familiaris*	Forest	Woodland	0.8%
Eurasian Sparrowhawk	*Accipiter nisus*	Forest	Woodland	0.6%
Willow Warbler	*Phylloscopus trochilus*	Forest	Woodland	0.5%
Eurasian Bullfinch	*Pyrrhula pyrrhula*	Forest	Woodland	0.5%
Common Cuckoo	*Cuculus canorus*	Forest	Woodland	0.4%
European Herring Gull	*Larus argentatus*	Coastal	Water	6.2%
Mallard	*Anas platyrhynchos*	Wetland	Water	5.1%
Common Moorhen	*Gallinula chloropus*	Wetland	Water	4.0%
Lesser Black-backed Gull	*Larus fuscus*	Coastal	Water	3.5%
Canada Goose	*Branta canadensis*	Grassland	Water	2.9%
Eurasian Coot	*Fulica atra*	Wetland	Water	2.8%
Black-headed Gull	*Chroicocephalus ridibundus*	Wetland	Water	2.2%

Table 3-1: Continued

Common name	Scientific name	AVONET habitat	Classified habitat	Detection rate
Great Cormorant	*Phalacrocorax carbo*	Wetland	Water	1.9%
Grey Heron	*Ardea cinerea*	Wetland	Water	1.7%
Egyptian Goose	*Alopochen aegyptiaca*	Wetland	Water	1.3%
Mute Swan	*Cygnus olor*	Wetland	Water	1.1%
Grey Wagtail	*Motacilla cinerea*	Riverine	Water	0.9%
Tufted Duck	*Aythya fuligula*	Wetland	Water	0.7%
Greylag Goose	*Anser anser*	Wetland	Water	0.7%
Little Egret	*Egretta garzetta*	Wetland	Water	0.3%
Common Wood Pigeon	*Columba palumbus*	Woodland	Urban	33.1%
Carrion Crow	*Corvus corone*	Human Modified	Urban	22.3%
Eurasian Magpie	*Pica pica*	Human Modified	Urban	20.3%
Rose-ringed Parakeet	*Psittacula krameri*	Forest	Urban	14.6%
Feral Pigeon	*Columba livia*	Human Modified	Urban	14.4%
House Sparrow	*Passer domesticus*	Human Modified	Urban	14.2%
Common Starling	*Sturnus vulgaris*	Human Modified	Urban	13.2%
Western Jackdaw	*Corvus monedula*	Human Modified	Urban	13.1%
Eurasian Collared Dove	*Streptopelia decaocto*	Human Modified	Urban	6.4%
Stock Dove	*Columba oenas*	Woodland	Urban	5.7%
Common Swift	*Apus apus*	Human Modified	Urban	4.6%
White Wagtail	*Motacilla alba*	Human Modified	Urban	2.2%
Western House Martin	*Delichon urbicum*	Human Modified	Urban	0.7%
Eurasian Skylark	*Alauda arvensis*	Grassland	Open	5.6%
Common Whitethroat	*Curruca communis*	Shrubland	Open	5.5%
Common Pheasant	*Phasianus colchicus*	Human Modified	Open	5.1%
Barn Swallow	*Hirundo rustica*	Human Modified	Open	2.6%
Common Buzzard	*Buteo buteo*	Grassland	Open	1.8%
Yellowhammer	*Emberiza citrinella*	Shrubland	Open	1.6%
Common Linnet	*Linaria cannabina*	Shrubland	Open	1.6%
Rook	*Corvus frugilegus*	Grassland	Open	1.1%
Common Kestrel	*Falco tinnunculus*	Shrubland	Open	1.0%
Red-legged Partridge	*Alectoris rufa*	Shrubland	Open	0.7%
Lesser Whitethroat	*Curruca curruca*	Shrubland	Open	0.4%

Table 3-2: Environmental factors (BLISS)

Factor	Description	What it quantifies
Wood	percent woodland area	land cover composition
Open	percent open/vegetation area	
Arable	percent arable area	
Water	precent water area	
Suburban	percent suburban area	
Urban	percent urban area	
Edge	vegetation/open edge density	edge habitat
SHDI	Shannon's diversity index	land cover diversity
ENN	Euclidean nearest neighbor distance[1]	habitat connectedness
NDVI	normalized-difference vegetation index	vegetation density

[1] computed on two-class land cover: habitat and background

CONCLUSION

This work examined how bird diversity patterns and species-environment relationships change with scale across Greater London's urban gradient. Through three complementary studies—scale variance analysis of diversity patterns, modeling how environmental factors change across scale, and comparing differences between species through multiscale factor selection—the research furthers insight for understanding bird occurrence in urbanized areas, while demonstrating improved multiscale approaches. In this conclusion, we first synthesize the main results across all three parts, review the contributions to theory and species management, as well as discuss several limitations and outline directions for future work.

Summary of key results

Scale-dependent patterns across London

Our analyses revealed consistent scale-dependent structuring of bird communities across London's urban gradient. Scale variance analysis (Part 1) showed that approximately two-thirds of bird diversity variance concentrated at scales ≤2,000m for the 279 total species observed in the eBird data, with variance dropping significantly above 4,000m across all three taxonomic groups analyzed. The urban-rural gradient and river system configuration—particularly the River Thames and River Lea—seem to significantly drive the observed multiscale structure. Below 4,000m, most variance occurs within the Greater London boundary, while above 4,000m the majority shifts to the rural periphery where transitions between agriculture, woodland, and suburban land uses dominate.

Environmental modeling across scales (Part 2) revealed that 40% of modeled species (26 of 65 with sufficient BBS data) showed at least one effect reversing direction across scales. While such scale-dependent relationships align with widespread evidence (Chase et al. 2013; Turner & Gardner 2015), the consistent model performance across scales highlights how spatial latent effects capture residual information, suggesting that assessing models from multiple perspectives beyond performance metrics remains critical. Even seemingly minor scale differences (e.g., NDVI at 1,000m versus 2,000m) produced significantly different effects, challenging the common practice of including factors at single "local" and "landscape" scales (Litteral & Shochat 2017; Wheatley & Johnson 2009).

Systematic factor selection across scales (Part 3) revealed that habitat composition at local scales (125-500m) best explained occurrence for many species. However, synanthropic species showed evenly dispersed responses across the entire scale range (125m-64km), potentially reflecting their broader niche breadths and ability to exploit diverse habitats across the urban landscape (Callaghan et al. 2019a). These species also showed larger spatial latent effects on average, indicating less signal from the environmental factors included (Morelli et al. 2024).

Group-specific scale signatures

Different species guilds exhibited distinct scale signatures reflecting their varying relationships with urban environments. We grouped species differently in each study to address specific research questions—taxonomic orders (Part 1), co-occurrence clusters (Part 2), and primary habitat guilds (Part 3). While each grouping offers a unique perspective, several themes are consistent when the results are considered together.

Passeriformes—the largest and most diverse order of avian species directly assessed in Part 1 but represented across all co-occurrence clusters and habitat guilds in Parts 2 and 3—showed variance shifting from urban core to periphery with increasing scale. A notable "green ring" of high diversity surrounds Greater London, only perceivable at scales of 4,000-16,000m. While these scales illustrate commonly documented declines in biodiversity with increasing urbanization (McKinney 2008), many areas inside Greater London contained equally high diversity when viewed at smaller scales. This suggests species persist where suitable habitat exists (Chamberlain et al. 2007; Evans et al. 2009), bringing enhanced ecosystem function and services including birdsong and connection to nature (Fuller et al. 2007). Further work should assess whether these urban populations are sustainable or function as population sinks drawing from regional populations.

Water-associated species (the combined Anseriformes and Charadriiformes orders from Part 1, the dedicated cluster 2 from Part 2, and the water-dependent guild from Parts 3) showed peak variance at 4,000m and expected strong relationships with water bodies at small scales. Studies commonly include water-related factors in bird diversity models (e.g., Plummer et al. 2020), which makes sense. However, our results suggest that simple presence of water and its spatial arrangement may dominate other factors. The overlapping occurrence of freshwater and

shorebird species where the River Lea empties into the widening River Thames Estuary likely accounts for the variance peak at 4,000m.

Synanthropic species demonstrated responses dispersed across scales rather than concentrated around any specific scale range, with meaningful environmental relationships from 125m to 64km (Part 3). These species range from those that depend on urbanization, those that can exploit it, and those that are able to adapt. The predicted occurrence maps from Part 2 illustrate this range of patterns (**Figure 4-1**). While urban-dependent species show reliance on habitat within the Greater London boundary, exploiters and adapters show less dependence on specific urban areas, with equal probability of occurrence throughout the boundary.

Habitat specialists showed strong fine-scale associations—especially at 125m (the smallest scale tested)—with woodland, suburban, open, and arable land cover depending on their niche. However, these associations account for only approximately 50% of explained variance. Further investigation of patterns captured by spatial latent effects at their estimated scales would likely reveal additional meaningful factors. These species offer the greatest potential to increase urban biodiversity if the urban mosaic can be modified to meet their niche requirements (Buxton & Thomas 2016; Elliot Noe et al. 2022).

Theoretical contributions

Improving multiscale methods

Scale variance analysis applied to biodiversity data represents a methodological advance, providing a hypothesis-generating framework for identifying scales of ecological significance before imposing modeling assumptions. This straightforward technique, which essentially

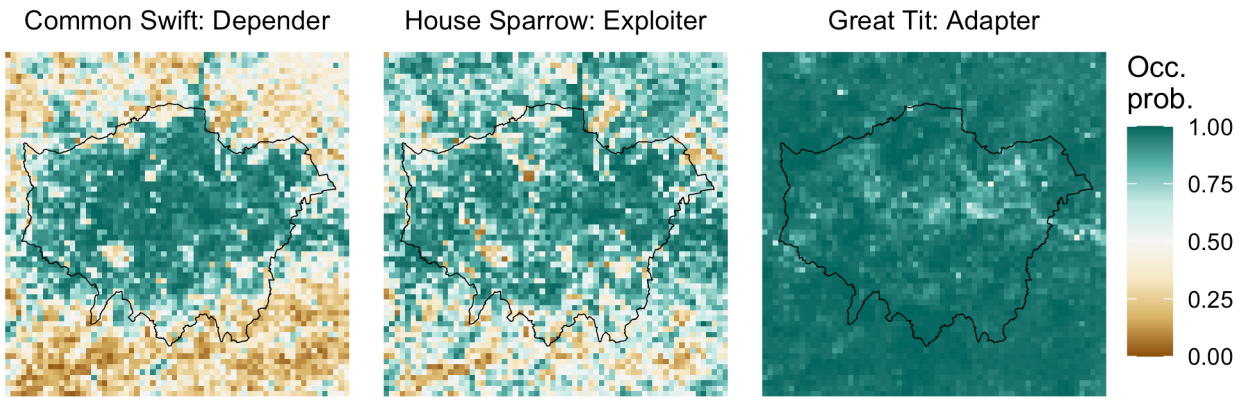


Figure 4-1: Different occurrence patterns of synanthropic species

extends analysis of variance to geographic hierarchies, may have seen limited ecological application because the results can be sensitive to the defined data extent. However, as demonstrated in Part 1, the spatial patterns of variance at each scale—revealed only when viewing intermediate computations across the entire extent—detail not just at what scale, but also where in space, high variance occurs. These spatial patterns are less sensitive to extent changes and likely more insightful for identifying "where the action is" (Moellering & Tobler 1972)—and then generating hypotheses to find out why.

Testing environmental relationships across scales with jointly modeled species revealed that while scale differences translate into different model relationships, model performance may remain unaffected due to spatial latent factors capturing residual patterns. This finding means that common scale selection approaches based on comparing performance between scales—embodied by the scale of effect concept—may be ineffective or misleading for similar JSDMs or even spatially structured models, which are important components for accounting for spatial autocorrelation (Doser 2022; Ovaskainen & Abrego 2020). Examining the pattern and scale of each latent factor should become routine model assessment to identify what the model might have missed.

We enhanced a systematic and useful factor selection method, BLISS originally proposed by Stuber et al. (2017), by incorporating spatial latent effects and demonstrating how explained variance can be partitioned across both factors and scales. This shows not only which factors matter at what scales, but also how much they matter. This scale-specific variance partitioning provides a more realistic foundation for testing mechanistic explanations of species occurrence drivers.

Advancing multiscale ecology

Our results provide evidence that the assumption of a single best scale of effect fails to align with ecological theory, showing how this assumption can miss many meaningful relationships. While the practice of quantifying the surrounding environment within spatial buffers has long been used in landscape ecology (e.g., O'Neill et al. 1991), applying it to find a single best scale for species modeling seems problematic. The terms "characteristic scale" and "scale of effect" are sometimes used interchangeably, and while the concept of characteristic or intrinsic scales may be able to describe one specific process influencing process, our results

show that species occurrence results from many influences, thus highlighting an important distinction.

For example, a bird may forage within its territory at a scale of 100m, interact with conspecifics and heterospecifics in the local community at a scale of 1,000m, and disperse or migrate over tens to thousands of kilometers (Hostetler 2001; Narango & Proppe 2022). While each process can be delineated at a hierarchical level (holon) operating at a characteristic scale, or within an intrinsic scale range, the resulting occurrence is the sum aggregate of all processes. The numerous directional changes in relationships between scales from Part 2, supported by variance partitioning across scales in Part 3, illustrate that while a single scale may explain a third or more of total variance of occurrence, the remaining variance is explained by factors operating at different scales. Similar to the results by Stuber & Fontaine (2019), our results suggest that attempting to identify a single characteristic scale that best captures environmental relationships may only be reasonable for a few select species and highly suboptimal in many cases.

This shift in perspective demonstrated by our approaches potentially reopens questions about species traits that may explain scale-factor differences. Miguet et al. (2016) reviewed 14 proposed hypotheses potentially driving differences in scales of effect, including species traits, landscape factors, biological responses, indirect influences, and regional context. However, empirical evidence shows only 5 hypotheses have received some limited support. For example, Tittler (2008) tested for relationships between bird dispersal distance and scale of effect, finding no correlation, but rather that the landscape structure (gap distance) better predicted scale relationships.

Likewise, Pease (2024) found that scales of effect or bird species were partially explained by hand-wing index (HWI), a common proxy of dispersal distance, and migration behavior (i.e. resident versus migratory). However, because multiple scales likely need to be considered, these results warrant reconsideration. Since the hypotheses remain ecologically grounded, our results suggest reexamining these questions using variance partitioning across scales instead of selecting only a single dominant scale. For example, relating HWI to differences in variance explained across different scale ranges, such as local (<1,000m) versus landscape (≥1,000m), may provide a more realistic approach that could unify previously contradictory evidence.

Conservation and urban design implications

Many cities are in constant tension between development pressures and biodiversity conservation. For example, London's 2021 City Plan identifies a need for 66,000 new housing units annually, while new developments are simultaneously required to achieve an urban green factor score and meet national biodiversity net gain (BNG) policy requirements (Marshall et al. 2024; Pipe et al. 2021). These policies rely on standardized scoring systems to integrate green infrastructure into urban planning, yet recent assessment by Marshall et al. (2024) of BNG outcomes revealed only modest plant diversity increases with no measurable improvements for butterflies or birds (which leveraged BBS observations). The authors called for modifications including consideration of known key habitat for critical species, as well as non-linear effects. Furthering this discussion, our results suggest that these current policies (which are widely adopted by many countries and large cities across the globe) fail to account for multiscale and hierarchical factors, where mechanisms to integrate conservation efforts across spatial scales could significantly add value.

The results from Part 3 suggest that many synanthropic species or urban adapter species could benefit from green habitat at any scale, which is also suggested by the negative response of even these species to urban land cover at small scales. Yet, this may do little to increase diversity if these species are already present in adjacent small green areas. Linking the effects of new developments with existing properties to create larger habitat may be necessary to support more specialized species, that may require, for example, woodland patches adjacent to open areas with native species to support both nesting and foraging (Plummer et al. 2020; Pollock et al. 2017).

Additionally, the modeling approaches offer a pathway to enhance existing biodiversity policies by explicitly incorporating multiscale effects. The BNG metric could be redesigned as a scale-aware assessment system, where habitat value reflects both local site quality and broader spatial context across multiple scales. Under this approach, habitat creation projects would receive biodiversity credit values based on their connectivity functions. For instance, initiatives that connect habitat patches at 250-500m scales—important scales for many urban adapter species—would earn higher credit values than isolated sites of similar local quality. By incorporating explicit scale considerations, policies could coordinate existing conservation initiatives hierarchically from neighborhood to citywide levels to serve different species needs. For example, additional woodland species with some degree of urban adaptability could be

supported, while also creating larger or specific habitats like undisturbed open areas for ground nesters such as the Skylark. In London's context, this could connect local sites to the royal parks or through major landscape features like the Rivers Thames and Lea, ultimately linking to the metropolitan green belt, aligning with London's goals in the 2021 plan (Pipe et al. 2021).

Limitations and considerations

Temporal dynamics

Our analyses focused on spatial scale, and while and we subsequently controlled for temporal variation over the time periods analyzed, we were unable to extract insights into temporal patterns that likely also exhibit scale dependence. While overall bird population trends across the United Kingdom have stabilized since 1990 (Gregory et al. 2023), many included species show concerning declines. House Sparrow abundance, for example, has declined by approximately 60% overall since the late 1970s, potentially declining by up to 90% in urban areas including London (De Laet & Summers-Smith 2007).

Additionally, the BBS data by design only include detections during the breeding season. Breeding season represents peak observable diversity, where all migratory species are present and birds are most likely to be detected by observers. While breeding represents a main and important life stage, varying behavior during other periods or life stages (e.g., during migration or as a juvenile) may result in different relationships with environmental factors at different scales. Some evidence suggests that climate buffering of urbanized areas may attenuate seasonal differences of bird behavior for some species (Leveau et al. 2021), while other studies illustrate the need for more information on drivers of urban bird distributions during the non-breeding season (Alba et al. 2025).

Data constraints

The eBird dataset provides spatially dense observations compared to structured surveys; however, rural areas remain under-sampled, which is noticeable around our study extent's periphery such as the largely agricultural region in the northeast corner. Programs to incentivize or gamify citizen science observations, shifting effort from over-sampled to under-sampled regions (Callaghan et al. 2019b), could improve the utility of approaches like scale variance analysis for decomposing multiscale structure in these rich datasets.

Because the BBS aggregates observations within 200m transect sections, we were limited to assess relationships at small scales (i.e., <100m). Even eBird data would likely add limited signal at smaller scales because many eBird checklists are performed while moving, recording only a single centroid coordinate. Traveling checklists far outnumber stationary checklists globally, as well as in our Greater London study area (Pipe et al. 2021). Strategically located passive acoustic recording devices (e.g., evenly stratified across environmental factors and spatially balanced) could be integrated with structured data like BBS to assess finer scale relationships while improving detection probability modeling through increased replicates. The spOccupancy modeling framework (Doser et al. 2022) we used is well suited for this integration, and the BirdNET algorithm (Kahl et al. 2021) could reliably automate species detection, even on existing datasets available in the study area, such as the CitySounds project conducted by Fairbrass et al. (2019).

Computing constraints

While we tried to keep the scales and time periods of all three studies extensive and consistent, we were unable to match 10 years of data across 10 scales across all three studies, as well as 10 factors across Parts 2 and 3, because of data and computing limitations. Initial exploratory models in Part 2 indicated limited signal for the land cover area (e.g., percent area of woodland) factors. For this reason, we excluded them from the analysis, which also helped achieve feasible model fit times. However, the results from Part 3 indicate that including them may add further insight, especially if the model could be optimized (or sufficient computing resources acquired) to leverage observations at the BBS segment level (rather than the square level) to assess scale dependence over the same range of scales from 125m to 64,000m.

Future research

Expanding to different cities

While maintaining a consistent study area across these three studies was essential for identifying reliable patterns, applying these analyses to other urban landscapes would significantly advance our understanding. Although species distribution models have been implemented in numerous cities, few studies have systematically compared how scale-specific relationships remain consistent across different urban environments for the same species or species groups.

Testing our scale variance analysis in cities with different urban layouts would be particularly valuable. This approach could help determine whether the defining features observed in London—such as the distinctive green ring pattern or water-associated diversity hotspots—represent general characteristics of large metropolitan areas or unique features specific to London's urban landscape.

Validating and integrating approaches

Staying within London, an important next step would be to test whether the scale-specific environmental factors identified in Part 3 can accurately reproduce the diversity patterns observed in Part 1. This validation would serve two purposes: confirming the reliability of our species distribution models and strengthening the connection between multiscale bird observation patterns and their underlying ecological drivers.

This validation process would involve several steps:

- Refining species-level relationships: The environmental factors identified in Part 3 would need detailed examination for each individual species
- Creating integrated models: Individual species occurrence models could then be overlayed or modeled jointly if a parsimonious set of driving factors exists
- Comparing predicted and observed patterns: Scale variance could be calculated on the resulting predicted species diversity surface and compared directly with Part 1 results

This approach would demonstrate how these methods can be broadly applied for biodiversity assessments that integrate multiple, disparate data sources.

Broader implications

This research contributes to the growing recognition that effective conservation in human-dominated landscapes requires embracing the multiscale nature of ecological systems. By identifying where variance in bird communities concentrates across spatial scales and pinpointing the scale-specific environmental factors that shape species distributions, our work provides theoretical insights and practical conservation tools. The multiple scale perspective we advance—finding "where the action is" and understanding how patterns emerge from multiscale processes—helps bridge ecological theory with the complex realities of urban biodiversity management. As cities continue to grow, a multiscale understanding becomes increasingly important for creating environments that support both human wellbeing and ecological diversity.

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VITA

Jacob Dein was born and raised in northeastern Pennsylvania and studied civil and environmental engineering together with German at Lafayette College. He became interested in geospatial information systems through his engineering studies at Lafayette and leveraged spatial analysis to complete his undergraduate thesis. He briefly worked as a consulting engineer in New York City before conducting a research project in Austria on a Fulbright grant that again leveraged spatial theory and techniques to investigate a major burden of infrastructure on ecosystems and public health: noise pollution. He later moved to Knoxville, Tennessee with his wife, Melissa Dein, who was beginning graduate school, and he soon began graduate studies in the geography department at the University of Tennessee, Knoxville. He continued his research that began in Austria, focusing on spatial analysis and landscape ecology, while concurrently working as a geospatial software developer at a local engineering firm, Barge Design Solutions. He is excited to continue grounding practical engineering solutions in the spatial theory that he enjoyed exploring while a PhD student. He is grateful for his wonderful colleagues at Barge, several of whom are UTK geography alums, all the brilliant and friendly geographers at UTK, and especially his supportive family.