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Spatial Autocorrelation of Species Diversity and Distributions in Time and Across Spatial Scales

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ABSTRACT

Aim: Spatial autocorrelation (SAC), also known as aggregation or clumping, reflects species niche and dispersal, has conservation significance, and affects ecological models. Yet, we know little about the spatial and temporal patterns of SAC in empirical data. Here, we quantify the magnitude, spatial scaling, and temporal change of SAC in both species distributions and richness across multiple regions.

Location: Czechia, Europe, New York State, Japan.

Time Period: 1972–2017.

Major Taxa Studied: Birds.

Methods: We analysed four temporally replicated bird atlases, each aggregated to multiple spatial grains. We used Moran's I to quantify the SAC of richness and the Join count statistic (JC) for species distributions. We assessed changes in SAC across time and spatial scales, the relationship between temporal changes in SAC and occupancy, and whether habitat association, trophic level, or dispersal ability influenced temporal SAC dynamics.

Results: Species distributions and diversity consistently showed positive SAC across all regions, periods, and grain sizes, with its magnitude declining at coarser grains. SAC showed no overall temporal trend, despite varying responses across species. However, joint temporal changes in JC and occupancy revealed systematic patterns: declining species became more aggregated (clumped) while expanding species became more fragmented (disjoint) than expected from occupancy change alone. Trait effects were overall weak—dispersal ability showed no influence, whereas the ranges of open-habitat species in Japan and herbivores in Japan and Europe became slightly more fragmented than expected.

Main Conclusions: Stronger SAC at finer grains suggests greater predictability of diversity and distributions at these scales. Despite zero average change in occupancy or SAC, their coupled shifts highlight the importance of considering both jointly. We found that non-adjacent colonisations and extirpations are major drivers of range dynamics in temperate birds. The limited role of traits suggests that extrinsic environmental and spatial factors dominate large-scale SAC dynamics.

1 | Introduction

Macroecology has historically focused on static patterns of biodiversity and species distributions (Brown 1995; Rosenzweig 1995), but human-driven global change has likely been altering these patterns (IPBES 2019). Thus, research on temporal changes in species diversity and distributions has been increasing, including studies on temporal changes in single-species population abundance (Rosenberg et al. 2019; Ledger et al. 2023), occupancy (Warren et al. 2001; Klinkovská et al. 2024) and range position (Thomas and Lennon 1999; Chen et al. 2011). Multi-species studies have predominantly examined changes in species richness (Vellend et al. 2013; Dornelas et al. 2014; Blowes et al. 2019), assemblage composition (Jones et al. 2020), interspecific associations (Calatayud et al. 2019; Keil et al. 2021), and turnover (Blowes et al. 2024). The spatial structure of species diversity and distributions (i.e., their aggregation or fragmentation), which can be measured by spatial autocorrelation (SAC; Box 1), might also be affected by global change.

1.1 | Spatial Autocorrelation as an Ecological Feature

SAC, which indicates the degree of spatial dependence among values of a variable, is often considered a nuisance in ecological modelling (Lennon 2000; Dormann 2007). Autocorrelated observations are typically viewed as a form of pseudo-replication, reducing the degrees of freedom (Fortin and Dale 2005), violating the assumption of independent residuals, biasing parameter estimates, and increasing Type I error rates (Dormann et al. 2007). To account for this, methods such as conditional and simultaneous autoregressive models (Ver Hoef et al. 2018), tree-based machine learning methods, like boosted regression trees, incorporating Moran's eigenvector maps (Viana et al. 2022), or Nearest Neighbour Gaussian Processes (Doser et al. 2022) have been developed. An alternative, and less common, view is that SAC is a useful attribute of ecological systems, which can provide additional information to metrics such as species occupancy or richness, potentially informing on the processes shaping biodiversity and species distributions (Dormann et al. 2007; Hawkins 2012). Specifically, high SAC indicates higher distribution aggregation, whereas low SAC indicates increased fragmentation and reduced connectivity between populations. However, temporal changes in the SAC of species distributions and richness have not yet been quantified, and it is unclear whether these changes are consistent across regions, underscoring the value of a large-scale assessment.

BOX | 1 | What is spatial autocorrelation?

Species diversity and distributions are not random but spatially aggregated or fragmented, a phenomenon known as spatial autocorrelation (SAC; Legendre 1993). Spatial autocorrelation measures the similarity of observations as a function of spatial distance. It can be positive, where geographically close observations are more similar than those further apart, or negative, where nearby observations are more dissimilar (Legendre 1993). Positive SAC indicates clusters of species' presences or richness values, while negative SAC indicates spatial dispersion. Based on the underlying processes, the SAC of species distributions can be classified into two main types: exogenous and endogenous (Dormann 2007). Exogenous SAC arises from autocorrelated external environmental drivers such as climate, land use and topography (Fortin and Dale 2005; Dormann 2007). In contrast, endogenous SAC emerges from processes intrinsic to species, such as population dynamics, competition, dispersal or localized movement (Fortin and Dale 2005; Dormann 2007).

Several metrics have been developed to measure SAC, each addressing different aspects of spatial dependency. Global metrics, such as Moran's I (Moran 1950) and Geary's c (Geary 1954) for continuous or count variables, or the Join count statistic (Sokal and Oden 1978) for binary or categorical variables, summarise overall spatial patterns in a single number, indicating whether similar values aggregate or disperse across the study area. Local metrics, such as Local Indicators of Spatial Association (LISA, Anselin 1995) and Local Indicators for Categorical Data (LICD, Anselin and Li 2019), identify locations of high or low SAC. Additionally, correlograms and semi-variograms visualise SAC by plotting similarity (correlograms) or variance (semi-variance) against geographic distance (Dormann et al. 2007).

Multiple studies have characterised SAC patterns, ranging from the SAC of population sizes of wintering birds in North America (Koenig 2001), to the SAC of occurrences of alpine reptiles, amphibians, plants, insects, fungi and protists in Switzerland (Chevalier et al. 2021), dung beetle species distributions and diversity in southern Mexico (Moctezuma 2021), or the richness and composition of stream invertebrates (Bonada et al. 2012). SAC has also been used to disentangle exogenous from endogenous drivers of aggregation (Mielke et al. 2020), track the spread of invasive plants (Barney et al. 2008; Wang et al. 2011), and to demonstrate that climate is not the primary determinant of the structure of North American bird distributions (Rich and Currie 2018). All these examples demonstrate that SAC is an ecologically relevant characteristic of diversity and distributions, and it is thus worth studying, particularly in the context of temporal global change.

1.2 | Spatial Autocorrelation in Time

Occupancy, that is, the number (or proportion) of sites a species occupies in geographic space, is a key facet of species rarity (Crisfield et al. 2024), range size (Orme et al. 2006), and extinction risk (IUCN Standards and Petitions Committee 2024). Thus, assessing temporal changes in occupancy and identifying whether a species' occupancy is increasing ('winners') or decreasing ('losers') is highly relevant for large-scale biodiversity assessments (Warren et al. 2001; Jetz et al. 2019; Klinkovská et al. 2024).

Occupancy is closely linked to SAC: in a limited space, higher occupancy increases the likelihood that occupied sites are adjacent, even when distributed randomly. Consequently, high SAC can arise from geometric constraints rather than ecological processes. To account for this, SAC should be assessed alongside occupancy (Figure 1a; Niwa and Uno 2023) or Z-scores can be used, which quantify the deviation of the observed SAC from its expected value under randomly distributed occupied sites (Figure 1a; Lee 2003; Wang et al. 2011; Niwa and Uno 2023). However, since the relationship between occupancy and SAC is not deterministic—a single occupancy value can have multiple SAC values—observed changes in SAC can deviate from

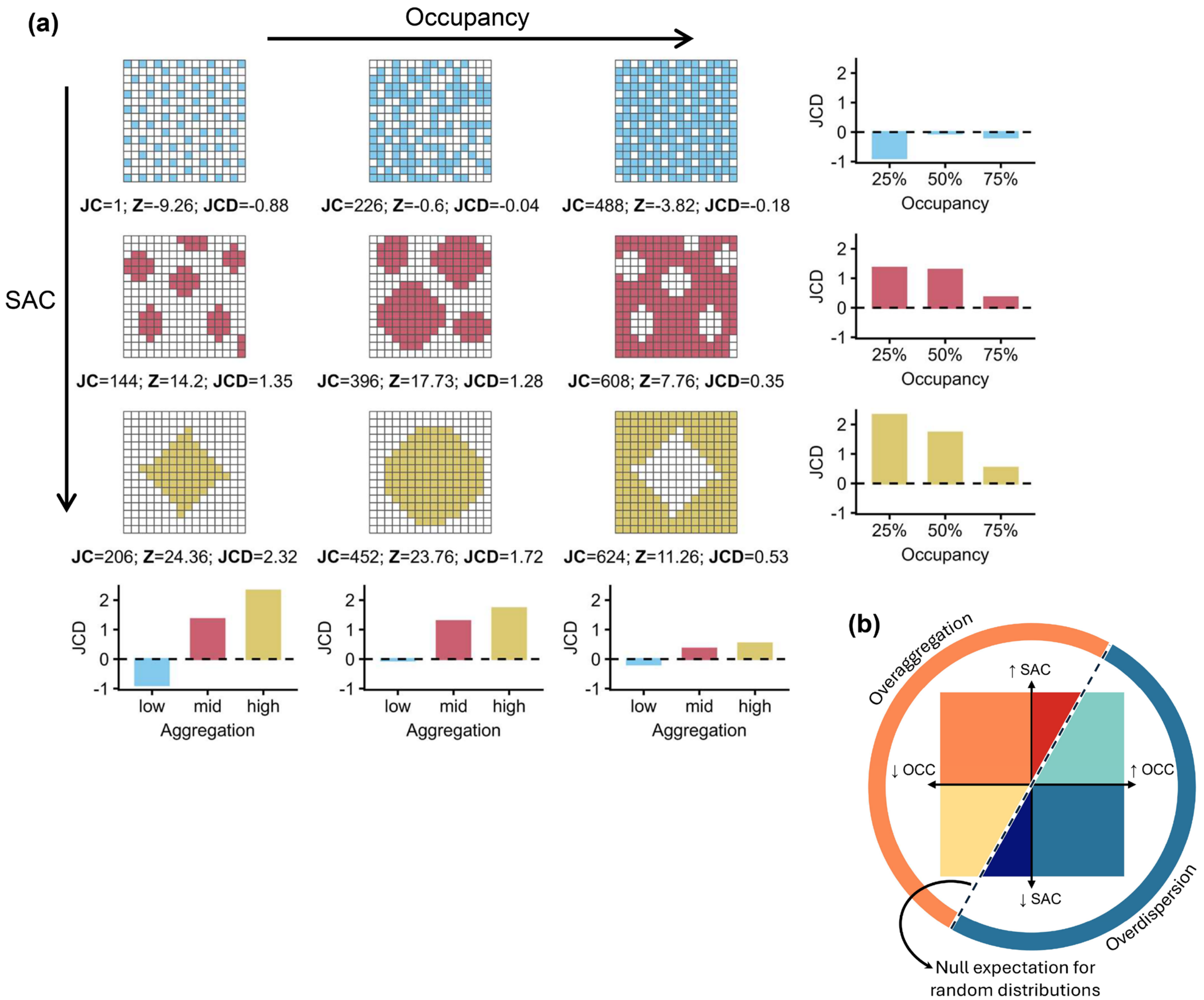

FIGURE 1 | Relationship between temporal changes in SAC and occupancy. Panel (a) shows the distribution of a virtual species, where coloured cells are presences and white cells are absences. Occupancy (columns: 25%, 50%, 75%) and aggregation levels (rows: Low in blue, medium in red, high in yellow) vary independently. Species distributions may shift along the occupancy axis (horizontal), the aggregation axis (vertical), or both. Here, spatial autocorrelation (SAC) is quantified using: Join count (JC), measuring the number of adjacent presences; Join count Z-score (Z), assessing whether presences are significantly aggregated ($Z \geq 1.96$) or dispersed ($Z \leq -1.96$) at a 95% confidence level; and average Join count difference (JCD), which accounts for occupancy and number of cells. Panel (b) decomposes the expected relationship between changes in occupancy (OCC; x-axis) and spatial autocorrelation (SAC; y-axis). The black dashed line is the expected SAC change for a given occupancy change. Deviations from this line indicate a higher increase or lower decrease in SAC (overaggregation; orange semi-circle) or a lower increase or higher decrease in SAC (overdispersion; blue semi-circle) than expected.

expectations based on occupancy change alone. This can result in *overaggregation*, where SAC increases more or decreases less than expected (e.g., extinction of isolated populations), or in *overdispersion*, where SAC decreases more or increases less than expected for the observed change in occupancy (e.g., colonisation of distant suitable locations; Figure 1b). Changes in SAC can also be independent of changes in occupancy, with species distributions becoming more aggregated or fragmented even when occupancy remains stable (Figure 1a). Therefore, solely focusing on the total area a species occupies following a disturbance may potentially obscure the existence of severe range fragmentation.

Changes in individual species distributions can also affect the spatial structure of areas of high versus low species richness, as the spatial pattern of richness results from overlaying individual distributions (Gaston 2000; Hawkins 2012). The SAC of richness can also vary independently of average richness, reflecting shifts in its spatial arrangement. If areas of high or low species richness become more clustered, SAC will increase. On the other hand, if species richness becomes more evenly or randomly distributed, SAC will decrease. We therefore argue for empirically assessing temporal trends in the SAC of both species' distributions and richness.

1.3 | Spatial Autocorrelation and Spatial Scale

Another critical gap in our understanding of SAC is its relationship with spatial grain—the average size of the elementary sampling unit (Legendre and Legendre 2012). Species occupancy scales non-linearly with grain size: as grain size increases, neighbouring cells merge, increasing the proportion of occupied cells until it levels off (the scaling pattern of occupancy, Kunin 1998; Hartley and Kunin 2003; Hui et al. 2006). Theoretical models predict that SAC decreases with increasing grain size, while the underlying spatial structure (aggregated or dispersed) remains unchanged (Hui 2009). The factors driving SAC (Box 1) are also grain-dependent: at fine-grains, endogenous processes such as population dynamics, competition, or dispersal dominate, although microhabitats may also contribute. At coarser grains, broad-scale environmental (i.e., exogenous) factors such as climate or land use become more prominent, with long-distance dispersal potentially contributing too (Fortin and Dale 2005; Dormann 2007). Figure 2 illustrates that SAC can increase or decrease with grain size, depending on the spatial pattern of the fine-scale distribution. Yet, the effect of grain size on empirical species distributions has not been studied, so it remains unclear which of these SAC patterns is most prevalent in nature. The number of available sites should also be considered, as areas with more sites have a lower expected SAC under a random distribution. Namely, clustering is more noticeable when many sites are available, and as grain size increases, the number of sites decreases.

The SAC of species richness is also expected to vary with grain size. Total richness typically increases with grain size as larger areas can host more species. This can increase SAC if smooth gradients emerge at that grain size, or decrease if richness becomes more uniform or random and less spatially structured. To the best of our knowledge, no studies have analyzed the effect of grain size on the SAC of species distributions and diversity across large geographical extents.

1.4 | Objectives

Here, we explore SAC and its relationship with occupancy, as a facet of biodiversity that can complement metrics such as species richness, occupancy or beta diversity within the context of global change. Birds are suitable study organisms because their distributions are well characterised, they are popular among the general public and ecologists, and their dispersal ability and sensitivity to environmental changes make them likely to have dynamic distributions. Using four Breeding Bird Atlases (BBAs) with continuous spatial coverage and temporal replications, we first ask whether empirical species richness and distributions are spatially autocorrelated, independent of occupancy, expecting positive SAC in both. We then examine how SAC has changed

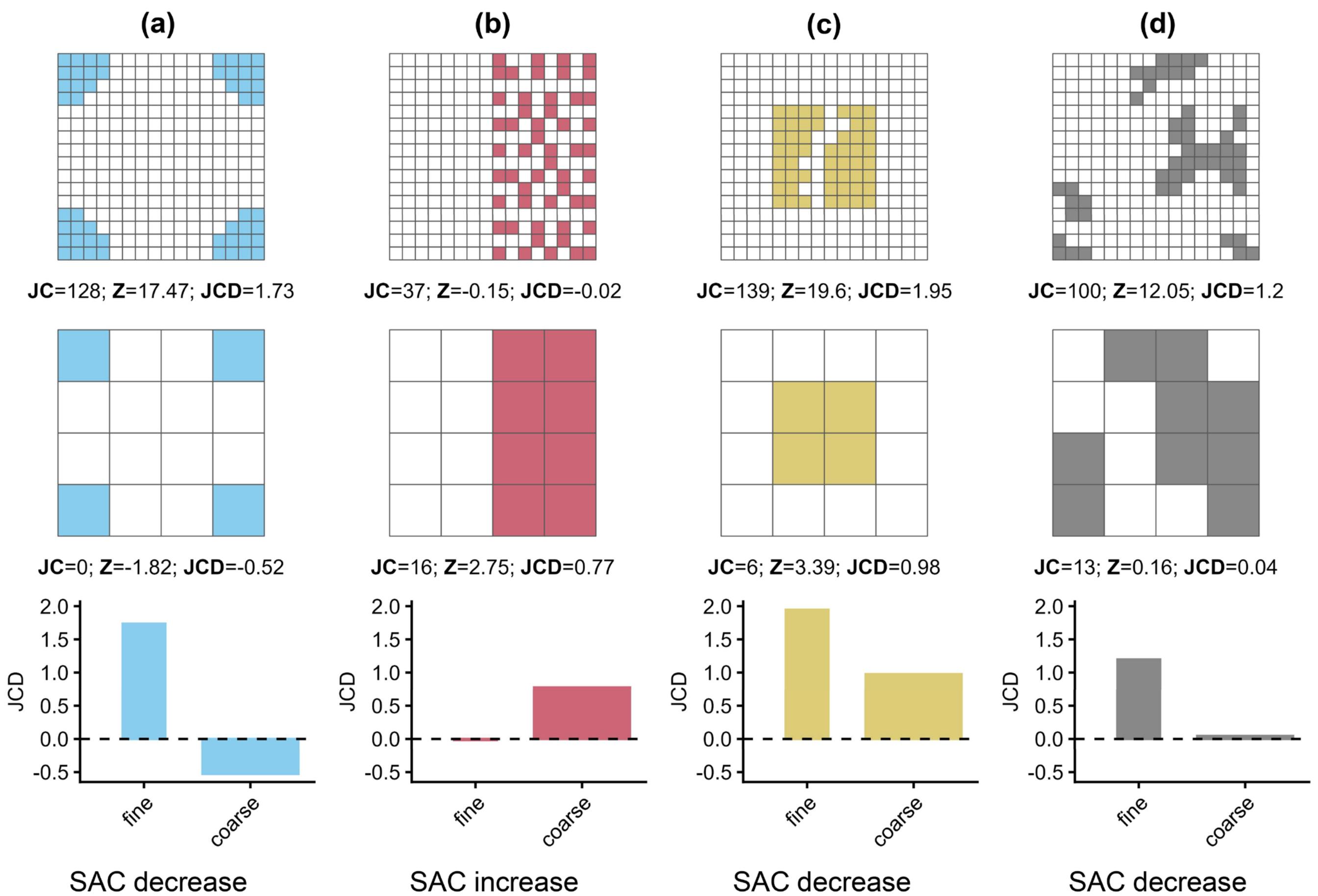

FIGURE 2 | Spatial autocorrelation (SAC) across spatial grains. The first row presents four hypothetical fine-scale species distributions, each with an occupancy of 20.31%. The second row shows the coarse-scale versions of each scenario. We quantified the SAC of species' presences for each scenario using: Join count (JC), measuring the number of adjacent presences; Z-score (Z), assessing whether presences are significantly aggregated ($Z \geq 1.96$) or dispersed ($Z \leq -1.96$) at a 95% confidence level; and average Join count difference (JCD), which accounts for occupancy and number of cells. Barplots show JCD values for each scenario grouped by distribution structure.

over time and across grain sizes, expecting species-specific variation but an overall temporal decline due to increasing habitat fragmentation (Zou et al. 2025), as well as a general decrease with coarser grains (Hui 2009). We also explore the relationship between species-level temporal changes in occupancy and SAC, expecting a positive relationship. Finally, we assess whether and how species' traits influence temporal changes in SAC and joint SAC and occupancy, expecting species with higher dispersal ability to show stronger SAC declines as they can colonise distant sites, open habitat species also to show declines due to farmland abandonment (although spatially structured habitat change may increase SAC), and omnivorous species to show smaller changes owing to diet flexibility. Overall, we expect SAC in species distributions and richness to exhibit similar spatio-temporal patterns.

2 | Materials and Methods

2.1 | Species Distribution Data

Bird distribution data were obtained from Breeding Bird Atlases (BBAs), which use standardised breeding-season surveys to provide species-level presence-absence data across grid cells covering geopolitical regions such as cities, provinces or countries. Surveys are coordinated by experts and conducted by volunteers and professionals, following a protocol established for each atlas. Each sampling period spans multiple years with repeated visits to most cells. Some regions have temporal replications of surveys, allowing for more reliable temporal comparisons than non-standardised surveys. While true absences are hard to confirm, BBAs offer one of the best large-scale approximations of presence–absence data (Pototsky and Cresswell 2023).

We utilised BBAs from Czechia, Europe, New York State (hereafter New York) and Japan (see Supporting Information S1 for details). These atlases cover diverse geographical areas in the Northern Hemisphere, species pools, time periods, survey durations, spatial extents and grain sizes (Table 1). Each region has at least two replications, enabling temporal analyses of SAC. We kept grid cells surveyed in all periods and excluded records flagged as uncertain by data curators (see Supporting Information S1). Cells were aggregated by sequentially doubling the cell side length (i.e., 2 × 2, 4 × 4, 8 × 8, etc.), considering a coarser cell as surveyed if at least one of its constituent finer cells was surveyed (see Table S21 for the number of cells per grain size). A species was considered present in the coarser cell if recorded in any of the smaller constituent cells. Species occupancy and grid cell richness were calculated for each region, period, and grain size combination. Only grain sizes with at least 30 cells were considered for SAC analysis, as this is the minimum recommended for SAC significance testing using Z-scores (Lee 2003). The approximate minimum and maximum spatial grains analysed were 11 × 11 and 44 × 44 km for Czechia, 50 × 50 and 800 × 800 km for Europe, 5 × 5 and 80 × 80 km for New York, and 20 × 20 and 160 × 160 km for Japan (Figure 3). These areas are approximate, due to the effect of irregular grid shapes and region borders, a common issue in studies examining multiple spatial scales (e.g., Hurlbert and Jetz 2007). However, this should not affect our conclusions, as we are focusing on the effects of scaling within regions rather than the effect of area itself.

2.2 | SAC in Species Diversity and Distributions

We assessed the global SAC for species richness using Moran's I and for species distributions using the Join count statistic (JC) across each combination of atlas region, replication, and grain size.

Moran's I measures SAC in continuous and count data, such as species richness (see SI for details). It ranges from −1 (perfect dissimilarity between neighbours) to +1 (perfect similarity), with 0 reflecting a random spatial pattern. We calculated Moran's I considering all immediately adjacent neighbours (first-order queen contiguity) and a row-standardised weighting scheme (Bivand et al. 2013). We tested for statistical significance using the *Z*-scores derived from a null model, which assumes that values are randomly distributed across cells (see SI for details).

The *Join count statistic (JC)* measures SAC in binary or nominal variables, such as presence-absence data. When considering species presences, a "join" occurs when two neighbouring sites are occupied (similarly, when considering absences, two neighbouring unoccupied sites constitute a join). We calculated the number of observed joins, considering first distance class queen contiguity, with a binary weighting scheme (Bivand et al. 2013), and used a null model to test for significance (see SI). A high number of joins indicates aggregation (positive

TABLE 1 | Summary of the four BBAs used in the empirical assessment of patterns of spatial autocorrelation (SAC).

Location	Replications	Periods	Original grain size	Area	References
Czechia	3	1985–1989, 2001–2003, 2014–2017	~11 × 11 km (10′ long × 6′ lat)	~78,309 km^2	(Šťastný et al. 1997, 2006, 2021)
Europe	2	1972–1995, 2013–2017	~50 × 50 km	~5,909,158 km^2	(Hagemeijer and Blair 1997; Keller et al. 2020)
New York State	2	1980–1985, 2000–2005	~5 × 5 km	~126,879 km^2	(Andrle and Carroll 1988; McGowan and Corwin 2008)
Japan	2	1974–1978, 1997–2002	~20 × 20 km	~367,613 km^2	(Biodiversity Center of Japan 2004; Environment Agency of Japan 1981)

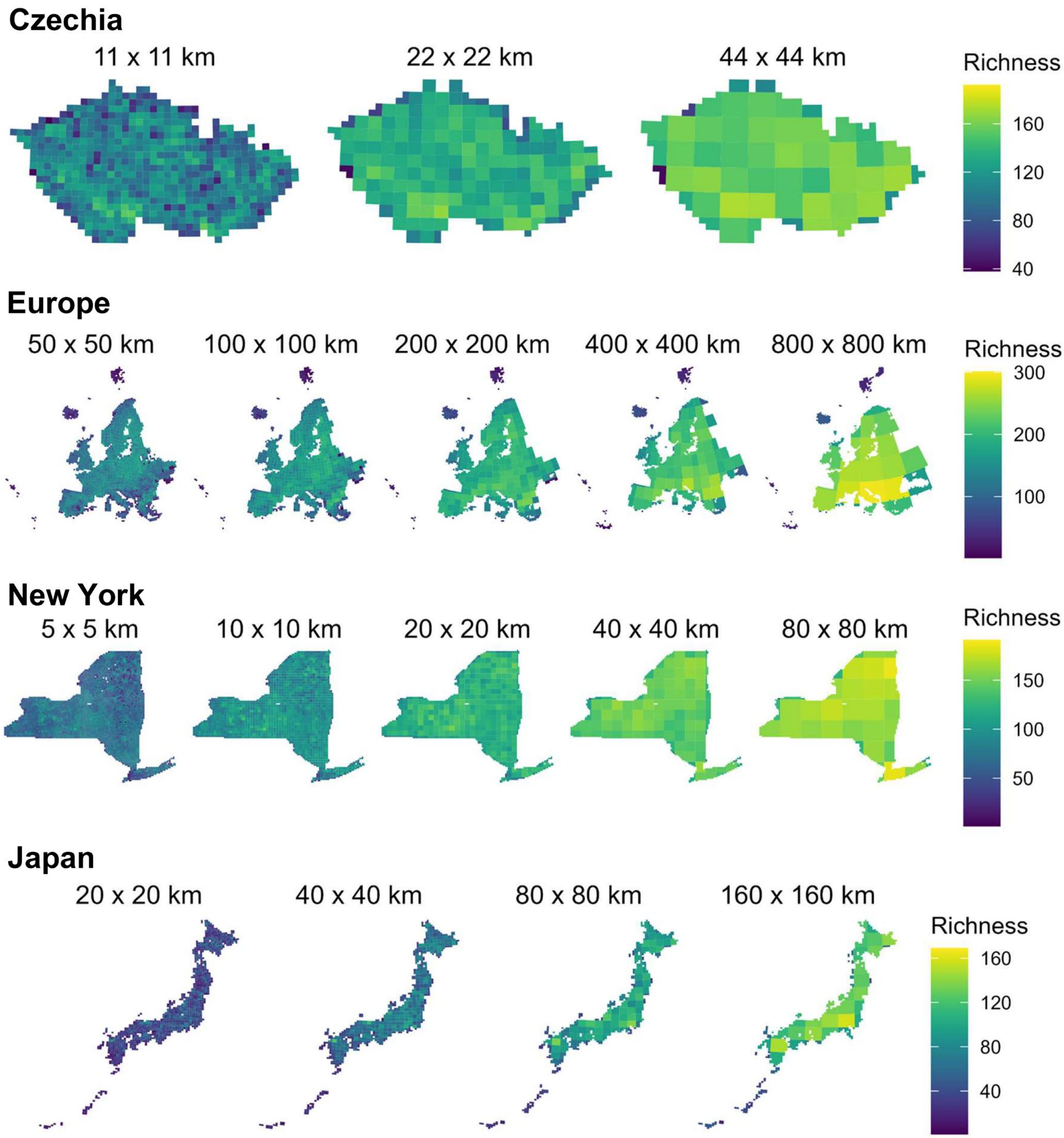

FIGURE 3 | Species richness in the first atlas period across regions and grain sizes. Richness, represented by a colour gradient, is aggregated at progressively larger spatial resolutions. The area of each grain size is indicated above each map. All maps were projected using the Lambert Azimuthal Equal-Area (LAEA) projection, with central meridians and standard parallels specific to each area to minimise distortion.

SAC), whereas a low number indicates dispersion (negative SAC), and values near the null expectation indicate no SAC. To control for occupancy and total number of available sites, we also calculated the average Join count difference (JCD), which represents the difference between the observed and the expected average number of joins (occupied neighbours) per occupied cell, with positive values indicating a higher number of average joins per cell than expected for that occupancy.

$$\mathrm{JCD} = \overline{\mathrm{JC}}_{\mathrm{obs}} - \overline{\mathrm{JC}}_{\mathrm{exp}}$$

where $\overline{\mathrm{JC}}_{\mathrm{obs}}$ and $\overline{\mathrm{JC}}_{\mathrm{exp}}$ are the observed and expected JC divided by the total number of occupied cells.

2.3 | SAC Over Time

For species SAC, we fitted individual ordinary least squares linear regressions (JCD ~ startYear) for each region and grain size, considering only species present in all periods (i.e., one regression per region, species, and grain size combination; Table S4).

To test whether JCD decreased over time, we treated period as a categorical factor and applied Wilcoxon signed-rank tests (in regions with two periods: Europe, Japan and New York) or Friedman tests (in the region with three periods: Czechia) for each region and grain size combination (17 in total), pairing by species. Significant Friedman tests were followed by paired post hoc Wilcoxon signed-rank tests with Benjamini-Hochberg correction. Effect sizes were calculated using rank-biserial correlations (r) for Wilcoxon tests and Kendall's W for Friedman tests. We did not statistically test temporal changes in richness SAC, as only one Moran's I value was available per region, period, and grain size.

2.4 | SAC Across Spatial Grains

We examined the effect of spatial scale by fitting linear models of SAC (Moran's I for richness, JCD for species) against grain size represented by the length of the side of the cell (SAC $\sim \log(\text{cellSide})$) for each region and period (9 combinations for each richness and species), pooling species within each combination (Table S7). Because grain sizes were nested and non-independent, significance and associated standard errors should be interpreted cautiously, particularly for richness, given the limited number of Moran's I values.

2.5 | Relationship Between Change in Occupancy and Change in SAC

To assess how changes in SAC relate to changes in occupancy, we calculated log ratios of occupancy and of the observed and expected JC by comparing each species' last (time 2) and first (time 1) records.

$$\text{Log ratio } X = \log\left(\frac{X_{\text{Time 2}}}{X_{\text{Time 1}}}\right)$$

where X represents occupancy, observed JC, or expected JC. Positive values indicate increases and negative values indicate decreases. We then compared observed and expected JC log ratios to assess whether distributions were becoming overaggregated or overdispersed. Expected JC values were obtained from the JC null model (see SI).

2.6 | Relationship Between Species' Traits and Changes in SAC

We explored whether species traits from AVONET (Tobias et al. 2022), namely habitat density (dense, semi-open, open), trophic level (carnivore, herbivore, omnivore), and hand-wing index (a proxy for dispersal ability; Sheard et al. 2020), influenced temporal changes in SAC and deviations from the expected SAC-occupancy relationship, at the original grain size.

Temporal changes in SAC were quantified as the slope of the linear regression of JCD over time for each species and region, considering only species present in all periods. The deviation from the expected SAC-occupancy relationship (hereafter JC-OCC residual) was defined as the residual of observed JC log ratios from values predicted by the regression of expected JC log ratios against occupancy log ratios, indicating whether species distributions are becoming more or less aggregated than expected.

For the categorical habitat density and trophic level, we tested differences in JCD slopes and JC-OCC residuals among trait categories using Kruskal-Wallis tests, followed by Dunn's post hoc pairwise tests with Bonferroni correction when significant. For the continuous hand-wing index, we fitted linear regressions within regions, with the hand-wing index as the predictor and either the JCD slope or JC-OCC residuals as the response variables. All analyses were conducted in R v4.2.3 (R Core Team 2023).

3 | Results

3.1 | How Autocorrelated Are Species Richness and Distributions?

3.1.1 | Species Richness

Richness was positively autocorrelated (Moran's I, $p < 0.05$) across all regions, periods, and grain sizes (Figures 4a and 5a; Table S1), with an overall mean Moran's I of 0.336 (SD = 0.193). The only exception was Czechia's coarsest grain size, which showed no significant SAC. Moran's I values ranged from −0.096 (Czechia 44 × 44 km) to 0.77 (Europe 50 × 50 km). Mean SAC across grain sizes was lowest in Czechia (0.153, SD = 0.185), followed by Japan (0.322, SD = 0.066), New York (0.326, SD = 0.085), and Europe (0.52, SD = 0.192).

3.1.2 | Species Distributions

Most species exhibited significant positive SAC ($p < 0.05$), ranging from 69.93% in Czechia's third BBA at 44 × 44 km to 100% in Europe's second BBA at 100 × 100 km (Table S2), with an overall mean of 88.14% (SD = 9.48) across regions, periods, and grain sizes. Mean percentages of species across grain sizes with significant positive SAC were lowest in Czechia (78.58%, SD = 11.25), followed by Japan (83.47%, SD = 2.69), New York (88.24%, SD = 5.53), and highest in Europe (91.87%, SD = 5.24). Most regions and grain sizes had no species with significant negative SAC. JCD values were predominantly positive (Figures 4b and 5b), indicating that most species distributions were spatially autocorrelated, independent of their occupancy. The percentage of species for which JC could be calculated ranged from 67.11% in Czechia's third BBA at 44 × 44 km to 100% in Europe's first BBA at 50 × 50 km (Table S2).

3.2 | SAC Over Time

3.2.1 | Species Richness

Moran's I remained largely stable over time across all regions and grain sizes, experiencing only minor changes (Figure 4a; Table S1). While in Europe and New York, Moran's I increased

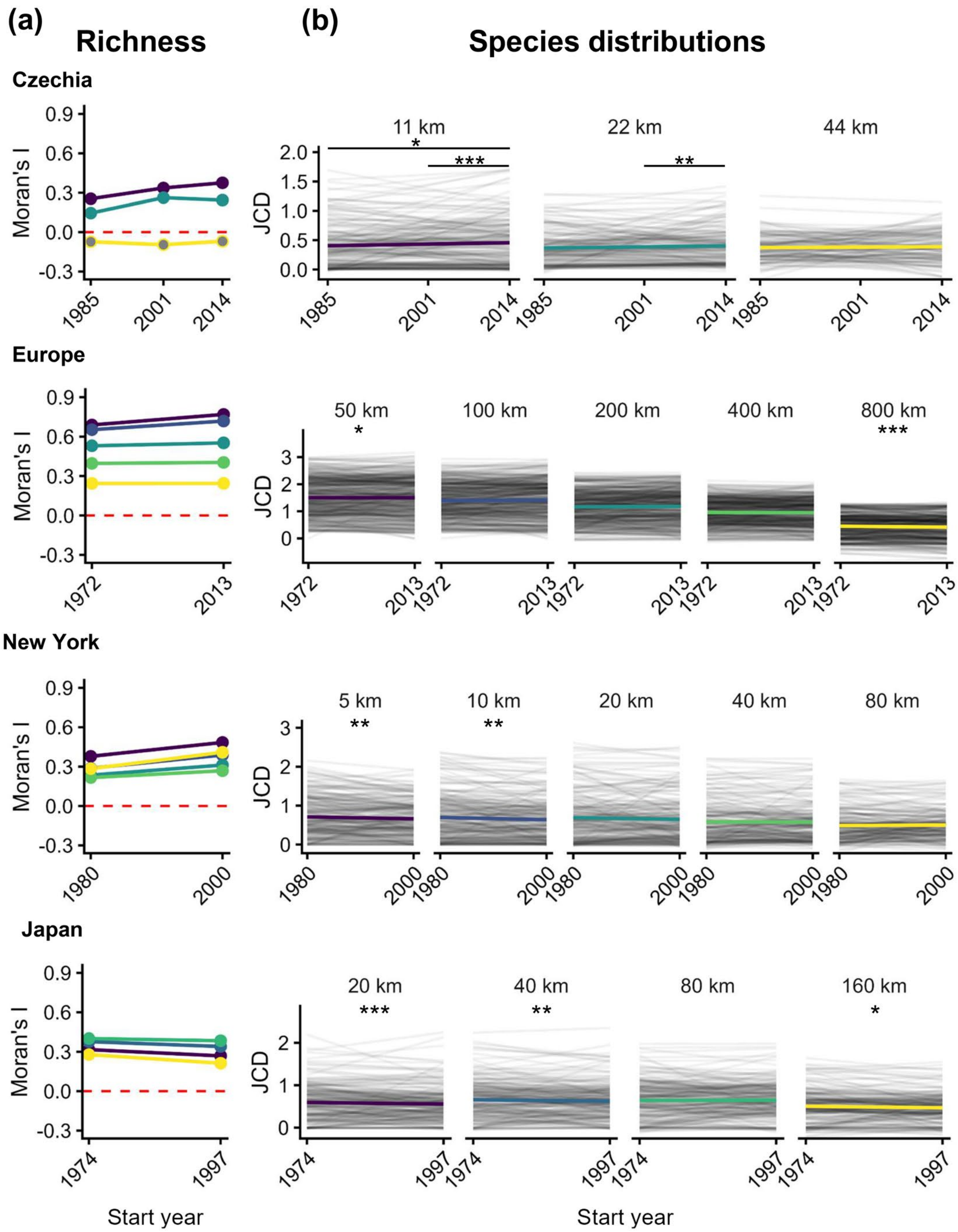

FIGURE 4 | Empirical temporal change in SAC of species diversity and distributions. Panel (a) shows Moran's I values for richness across atlas periods, with lines connecting values for each grain size. Line colours indicate grain size and correspond to those in panel (b). Points with a significant ($p<0.05$) Moran's I value are filled with the same colour as their respective line; non-significant points are filled in grey. Panel (b) shows temporal trends in species distributions' average Join count difference (JCD) across grain sizes (length of the cell side). Individual species trends are shown in grey lines, while the overall trend for each grain size is shown in colour. Asterisks indicate significant differences between time periods (*$0.05>p\geq 0.01$; **$0.01>p\geq 0.001$; ***$p<0.001$).

over time across all grain sizes, it decreased in Japan and showed varying responses in Czechia, depending on grain size.

3.2.2 | Species Distributions

Individual species distributions exhibited temporal increases (45.11% of all species across all region and grain size combinations), decreases (49.92%), or no changes (4.97%) in JCD, across all regions and grain sizes (Figure 4b, Table S3). The average temporal slopes were generally close to zero (Table S4; Figure 4b and Figure S1). Wilcoxon signed-rank test results indicate that temporal changes in SAC were generally weak ($|r|<0.3$), with significant declines in Europe at 50 ×50 km ($V=41{,}565$, $p=0.038$, $r=0.09$) and 800 ×800 km ($V=19239.5$, $p<0.001$, $r=0.2$), in New York at 5 ×5 km ($V=10{,}491$, $p<0.01$, $r=0.2$) and 10 ×10 km ($V=10{,}460$, $p<0.01$, $r=0.19$), and in Japan at 20 ×20 km ($V=8194$, $p<0.001$, $r=0.23$), 40 ×40 km ($V=8858.5$,

$p < 0.01$, $r = 0.17$) and 160 × 160 km ($V = 8109.5$, $p < 0.01$, $r = 0.14$). In Czechia, Friedman's tests results showed weak (W < 0.3) but significant temporal decreases in SAC between periods at 11 × 11 km ($\chi^2 = 22.19$, df = 2, $p < 0.01$) and 22 × 22 km ($\chi^2 = 19.29$, df = 2, $p = 0.02$). Post hoc pairwise comparisons revealed that the decrease was significant at 11 × 11 km between periods 1 and 3 ($p = 0.04$) and between periods 2 and 3 ($p < 0.001$) and at 22 × 22 km between periods 2 and 3 ($p < 0.01$).

3.3 | SAC Across Grains

3.3.1 | Species Richness

Moran's I declined with increasing grain size, with consistently negative slopes (Figure 5a; Tables S1 and S5). This decline is significant for both European BBAs (slopes = −0.197 and −0.165, $p < 0.01$, $R^2 > 0.96$). While New York and Japan had lower explanatory power ($R^2 = 0.044$ to 0.424), Czechia had a high R^2 (0.87–0.96). However, these results should be interpreted with caution given the limited number of grain sizes available ($n = 3$).

3.3.2 | Species Distributions

Species JCD also declined with increasing grain size (Figure 5b; Tables S6 and S7). Europe showed the strongest declines (slopes = −0.37, $p < 0.001$, $R^2 \approx 0.3$). In the other regions, slopes ranged from −0.085 to −0.029, and all regressions were significant ($p < 0.05$), except for the second Czech atlas ($p = 0.27$), which had a low R^2 (from 0.023 to 0.002). Mean JCD values were highest in Europe (between 0.95 and 1.5) and lowest in Czechia (between 0.27 and 0.33), while New York and Japan had similar values, ranging from 0.40 to 0.61 (Figure S2, Table S6).

3.4 | Relationship Between Change in Occupancy and Change in SAC

Changes in SAC and occupancy were strongly linked across regions and grain sizes ($R^2 = 0.79$–0.92, all $p < 0.01$; Figure 6; Figures S3 and S7; Tables S8 and S9). On average, most species exhibited congruent changes in both metrics, with an overall weighted mean of 49.91% of species increasing in both (categories Q3-Q4) and 29.18% decreasing in both (Q1-Q6). Among increasing species, most showed lower-than-expected JC increases (Q4), while declining species typically showed lower-than-expected decreases (Q1). Japan was the exception, with balanced overaggregated (Q1) and overdispersed (Q6) declines, particularly at smaller grains.

The distribution of species among change categories varied with grain size (Table S9 and Figure S7). As spatial grain increased, more species showed no change in JC and/or occupancy, while the proportion changing in both remained stable or decreased. The slopes of the regression between the log ratios of observed JC and occupancy ranged from 1.31 (Europe 50 × 50 km) to 1.27 (New York 80 × 80 km) and showed an increasing trend with grain size within each region (Figure S8). The regressions between the log ratios of expected JC and occupancy were steeper, ranging from 2.06 (New York, 5 × 5 km) to 2.27 (Europe, 800 × 800 km), with an R^2 of 0.99 (Table S10). Both marginal JC and occupancy log ratios were centred around zero, indicating little overall temporal change (Figures S9 and S10). Mean JC log ratios ranged from −0.02 (New York 10 × 10 km) to 0.31 (Japan 80 × 80 km), with SDs between 0.39 (Europe 800 × 800 km) and 1.02 (Czechia 11 × 11 km; Table S11). Mean occupancy log ratios ranged from 0.02 (New York 80 × 80 km) to 0.23 (Japan 40 × 40 km), with SDs from 0.23 (Europe 800 × 800 km) to 0.66 (Czechia 11 × 11 km; Table S12).

3.5 | Relationship Between Species' Traits and Temporal Changes in SAC

Kruskal-Wallis tests showed no significant differences in JCD slopes among habitat density or trophic level categories in any region (Tables S13 and S16, Figures S11 and S13). For JC-OCC residuals, differences among habitat categories were significant in Japan ($H = 10.31$, df = 2, $p < 0.01$) (Table S14, Figure S12), with open habitats showing lower residuals than those of semi-open habitats ($p < 0.01$; Table S15). Trophic level differences in JC-OCC residuals were significant in Europe ($H = 9.36$, df = 3, $p = 0.025$) and Japan ($H = 3.88$, df = 2, $p = 0.032$) (Table S17, Figure S14), where herbivores had marginally significantly lower residuals than omnivores (Europe: $p = 0.043$, Japan: $p = 0.044$; Table S18). We found no significant relationships between hand-wing index and JCD slope or JC-OCC residuals (Tables S19 and S20, Figures S15 and S16).

4 | Discussion

4.1 | Change in SAC and Occupancy

As expected, we found a strong positive relationship between changes in occupancy and SAC across species (Figure 6). However, the observed changes in SAC systematically deviated from what we would expect based on changes in occupancy alone. Expanding species had lower-than-expected SAC gains (Q4), while declining species had lower-than-expected SAC losses (Q1).

This suggests that 'winner' species are colonising non-adjacent cells, which contribute fewer spatial joins (overdispersion). We hypothesise that this is primarily driven by the high dispersal ability of birds, allowing them to fly over non-suitable habitat patches (Martin and Fahrig 2018). This remains consistent across spatial grains, likely reflecting a heavy-tailed dispersal distribution, where most individuals move short distances while a few disperse far, and resembles the heavy-tailed dispersal kernels found in European breeding bird ringing data (Fandos et al. 2023).

Conversely, 'loser' species are being extirpated from isolated cells, leaving the remaining populations more spatially clustered (overaggregation). This aligns with the 'rescue effect', where extirpations are more frequent in disconnected areas that receive fewer dispersing individuals (Hanski 1999). Similarly, Howard et al. (2023) found that extirpations in the European BBAs were more likely in distant cells, while colonisations occurred near continually occupied ones across the entire study area. We attribute the discrepancy in colonisation patterns to our focus on immediately adjacent cells, whereas Howard et al. (2023) considered the distance between cells. Thus, isolated populations

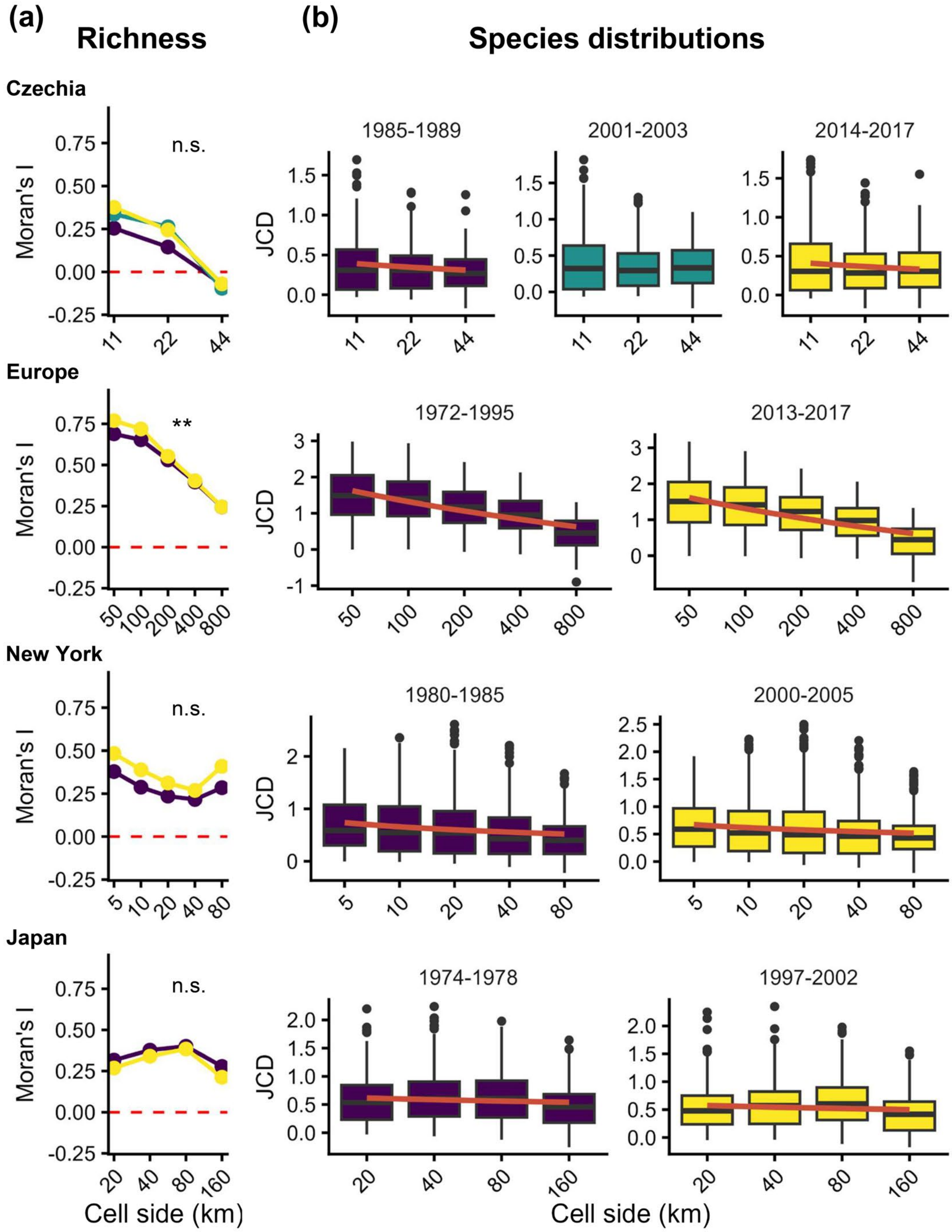

FIGURE 5 | Empirical change in SAC of species richness and distributions with increasing grain size. Panel (a) illustrates the change in SAC for species richness with increasing grain size (represented by the length of the side of the cell). Moran's I values are plotted for each grain size and region, with lines and colours representing atlas periods: Purple for the first period, yellow for the last, and green for the intermediate when available. Asterisks indicate significance between periods (**$0.01 > p \geq 0.001$) while n.s. stands for non-significant. Panel (b) shows box plots of JCD values for species distributions grouped by grain sizes and atlas periods, smoothed regression lines in orange show when the trend of change in SAC is significant ($p < 0.05$).

appear to be key drivers of range dynamics, particularly the dynamics of spatial aggregation of species distributions.

We found that changes in occupancy resulted in larger changes in join count at coarser grain sizes. This is a result of a decrease in the number of sites with increasing grain size, with colonisations and extirpations more likely to occur in neighbouring cells.

Despite observing species-level variation, mean temporal trends in JCD and the log ratios of JC and occupancy were near zero. The SAC of richness also remained largely stable, suggesting that areas of high and low diversity are not becoming more or less clumped under global change. This zero-mean trend, but large variation mirrors findings for local-scale metrics like richness (Vellend et al. 2013; Dornelas et al. 2014, 2023; Blowes et al. 2019; Crockett et al. 2022), despite increases, decreases,

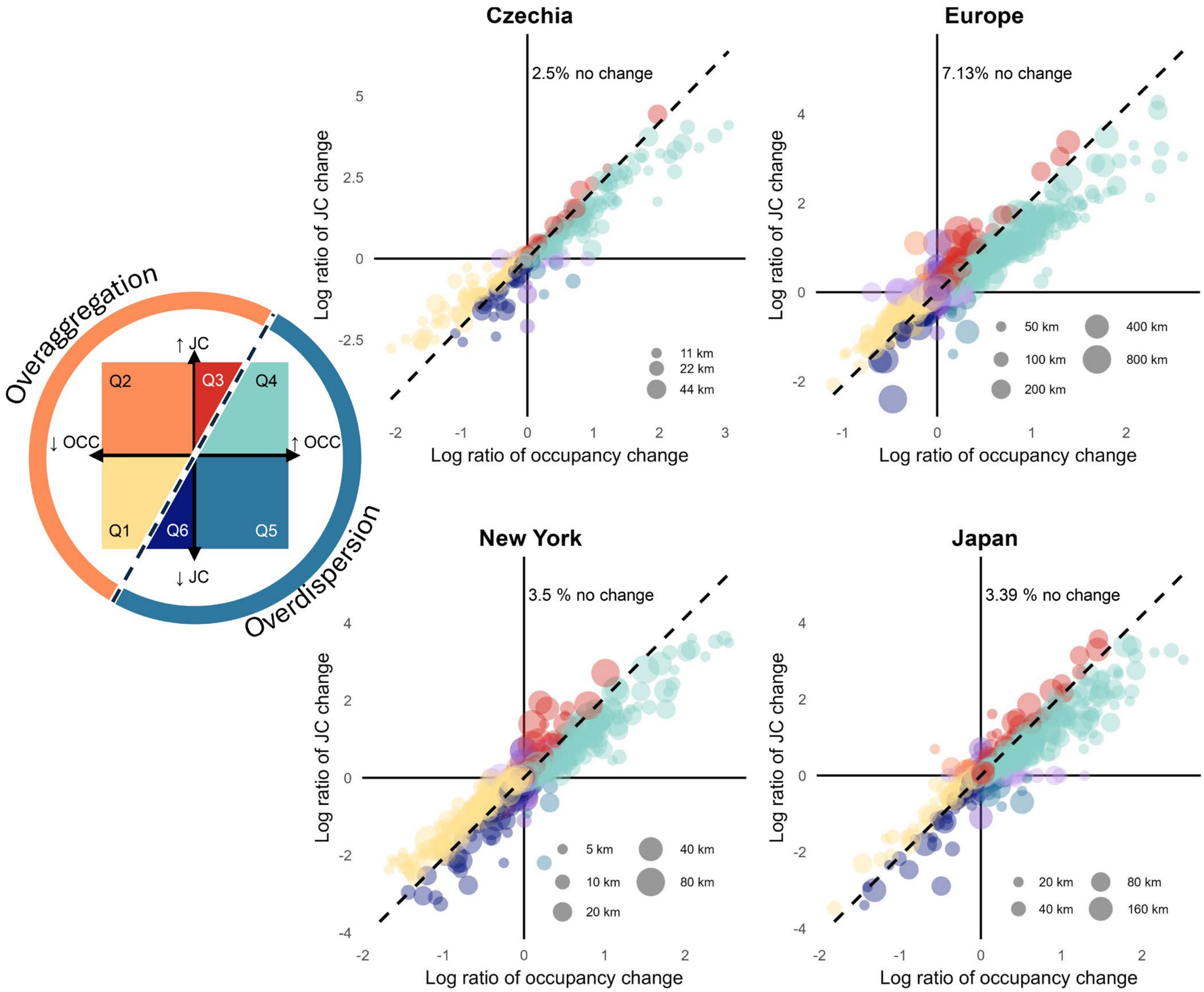

FIGURE 6 | Relationship between empirical occupancy change and Join count statistic (JC) change. The figure shows the log ratio of changes in the observed Join count statistic (JC; *y*-axis) against the log ratio of changes in occupancy (*x*-axis) across study areas. Point size corresponds to grain size, with bigger points indicating coarser grains. Colours represent quadrants, categorising the relationship between JC and occupancy changes, following the conceptual diagram on the left. The black dashed line is the linear regression of the log ratio of the expected JC as a function of occupancy change (i.e., expected JC change for a given occupancy change), pooling all grain sizes together. Observations to the left of this line indicate a greater-than-expected increase in JC (Q2 and Q3) or a lower-than-expected decrease in JC (Q1) for the observed occupancy change, while observations to the right indicate a lower-than-expected increase in JC (Q4) or a greater-than-expected decrease in JC (Q5 and Q6). Purple observations along the *x* and *y* axes are changes in the log ratio of JC independent of changes in occupancy (*y*-axis) or the reverse (*x*-axis). No changes in both occupancy and JC and transitions between zero JC and positive JC or the opposite have been removed from the plot for ease of visualisation. However, we report the overall percentage of species showing no change.

and changes in turnover (Dornelas et al. 2014, 2023; Blowes et al. 2019). Another example of this phenomenon is the relatively weak average global decline in population sizes, coupled with some extreme losses (Leung et al. 2020). This indicates that we should perhaps shift our focus from average trends to the variation around the mean. In our case, despite the overall zero net trend in SAC, some species still showed increases and decreases in both their SAC and occupancy, providing a starting point for identifying species for which we should prioritize conservation actions in follow-up studies.

Jointly analysing changes in SAC and occupancy provided deeper insights into species biodiversity change and potential conservation needs. For instance, although an increase in autocorrelation within a species' range may suggest a seemingly beneficial decrease in fragmentation, it could be due to a range contraction into one or a few patches. This emphasises the importance of jointly considering multiple metrics when studying biodiversity change, a point already highlighted by other studies (Hillebrand et al. 2018; Blowes et al. 2022, 2024).

4.2 | SAC, Grain and Extent

Most species distributions exhibited significant positive SAC across all regions, time periods and grain sizes, indicating that spatial clustering is indeed a ubiquitous feature of distributions (Figure 4; Legendre 1993). Species SAC, as well as richness SAC in Europe, decreased with increasing grain size, consistent with Hui's (2009) model of the effect of spatial scale on SAC (Figure 5). This decreasing trend likely reflects the loss of finer-scale spatial structure as species presences and richness become aggregated over larger sampling units. Coarser grains encompass a wider range of habitats, which can dilute SAC by averaging across diverse environments and reducing spatial differentiation. Given our use of presence-absence data and the spatial grain of our analyses, the SAC observed likely reflects exogenous environmental gradients (e.g., climate, land cover) rather than endogenous biological processes (e.g., competition), which are detectable at finer scales.

Among the four regions, Europe had the strongest scale dependence of SAC, which may be attributed to its larger extent, capturing entire species' ranges and broader environmental variability. This is not simply due to cell number, as New York had the most cells per all grain sizes (Table S21), yet lower SAC values. The position of each atlas within a species' range may also influence the observed SAC patterns. For instance, species' ranges are shifting towards higher altitudes and latitudes (Chen et al. 2011), and the effects of fragmentation can depend on distance from the range edge, with adverse effects occurring near the range edge (Bellotto-Trigo et al. 2023). In contrast, the weak scale dependence observed in Czechia, New York and Japan could indicate consistent spatial processes across scales or opposing species-level responses that cancel out when averaged. Future work should further explore how geographic extent and range position affect SAC metrics, and perhaps null models that go beyond spatial randomness of distributions can provide more detailed insights.

The observed scale dependency of SAC has important implications for species distribution modelling and broader ecological research. Stronger SAC at finer grains suggests species distributions may be more predictable at these scales, enabling more accurate spatial and temporal interpolations (Keil and Chase 2019, 2022). However, SAC can also bias models if not accounted for, or signal that a relevant driver of distributions is being overlooked. Coarser resolutions can reduce these biases, but at the cost of losing information (Boyd et al. 2024). These findings underscore the need to consider grain size and spatial extent carefully when interpreting SAC and its underlying drivers in ecological studies.

4.3 | Species Traits

We found no significant effect of hand-wing index on temporal changes in SAC or joint changes in SAC and occupancy, despite dispersal ability often limiting how species track suitable environments. In other words, the distributions of species with higher dispersal ability are not becoming patchier over time. This may reflect a spatiotemporal scale mismatch: while the hand-wing index informs on dispersal potential, our adjacency-based SAC was calculated over 5–50 km grids with an average 15-year interval between replications. At these scales, many species are likely able to disperse over non-adjacent cells (Fandos et al. 2023), and habitat patchiness or autocorrelated climate may thus have a stronger influence on range aggregation.

Habitat association significantly affected joint changes in SAC and occupancy, but only in Japan, where open-habitat species became more spatially overdispersed than semi-open species. This may reflect the progressive maturation of forests and loss of open habitats in Japan (Yamaura et al. 2009; Sasaki et al. 2020), which may have forced open-habitat species into isolated patches. Trophic level also marginally explained differences in joint changes of SAC and occupancy in Europe and Japan, with herbivores showing greater overdispersion than omnivores. This may be due to the greater ecological specialization and resource dependence of herbivores, in contrast to omnivores, which can maintain stable distributions due to their generalism. However, all of the abovementioned SAC-trait associations were weak, underscoring the generally observed limited explanatory power of traits for explaining large-scale spatiotemporal changes in biodiversity (Beissinger and Riddell 2021).

4.4 | Challenges and Pitfalls

We acknowledge several limitations to our work. First, unknown sampling effort and imperfect detection may influence the observed patterns, particularly at finer scales, where variations in these metrics can have a greater impact (Boyd et al. 2024). It can also result in uncertain or atypical patterns for species that are difficult to detect or live in remote areas. While methods such as the Frescalo algorithm (Hill 2012) or occupancy models account for this by incorporating spatial autocorrelation or modelling it (MacKenzie et al. 2018), this approach is challenging for studies like ours, which specifically focus on spatial autocorrelation itself. In other words, we cannot use the existing toolbox to account for sampling effort when studying autocorrelation because these methods introduce additional autocorrelation. Nonetheless, atlas coordinators make an additional effort to filter out unreliable data, and the issue of unknown sampling effort and detectability should become less pronounced at coarser scales (Hurlbert and Jetz 2007; Keil et al. 2014), making our results more robust as grain size increases. Furthermore, if the sampling process and detection are random at fine grains, they are more likely to reduce observed SAC than to inflate it. Thus, the observed patterns, particularly the increase of SAC towards finer grains, are likely genuine.

Second, global SAC metrics, like the ones we used, may mask finer-scale, localised patterns of SAC and the ecological and environmental processes that vary across space (Rollinson et al. 2021). Very different distribution configurations can have the same global SAC value. Therefore, spatially explicit maps of local SAC can provide a more informative summary of species distributions, particularly when monitored in time. Third, we focused on adjacency-based SAC (i.e., autocorrelation at first distance class), which provided a single, simple and interpretable response variable. However, distance-based SAC can characterise over which distributions are autocorrelated and can provide better insights into population connectivity. Fourth, we did not consider invasive species separately, although they may exhibit different spatial autocorrelation patterns, and SAC has already been used to study invasion processes (Wang et al. 2011). Lastly, there is a taxonomic and geographical bias, as our study is focused only on birds in the Northern Hemisphere. Thus, the patterns can vary for other taxa or in different areas.

4.5 | Future Pathways

We recommend further exploration of SAC as a biodiversity metric and support using multiple metrics to better understand and characterise biodiversity temporal dynamics. Follow-up studies should investigate local SAC dynamics using metrics such as LISA (Anselin 1995) or LICD (Anselin and Li 2019) to identify and track high and low SAC hotspots over time. Incorporating scale-dependent drivers—such as climate and land use—and examining the scales at which these drivers exhibit spatial autocorrelation and their alignment with distribution SAC patterns could provide deeper insights into the ecological and environmental processes shaping biodiversity across scales.

Exploring the SAC of other metrics, such as abundance, and at finer scales, would help detect the effects of endogenous processes driving SAC. Similarly, quantifying the SAC of sampling effort and comparing these results with ours could clarify its influence on observed patterns. Extending analyses to different taxa, geographic areas and grain sizes would help assess the generality of our findings. Finally, investigating distance-based SAC and identifying the distance-lags at which species distributions remain autocorrelated could yield valuable insights into connectivity, as well as advance the identification of the spatial extent to which biodiversity data can be interpolated in undersampled regions.

Author Contributions

Carmen D. Soria and Petr Keil conceived the original idea. Petr Keil acquired funding. Carmen D. Soria, Gabriel R. Ortega-Solís, Friederike J.R. Wölke, François Leroy, Kateřina Tschernosterová, Vladimir Bejček, Sergi Herrando, Ivan Mikuláš, Karel Šťastný, Mutsuyuki Ueta and Petr Voříšek collected, cleaned and standardised the data. Carmen D. Soria led all formal analyses with input from Gabriel R. Ortega-Solís, Friederike J.R. Wölke, Vojtěch Barták and Petr Keil. Carmen D. Soria led the writing of the manuscript. Carmen D. Soria, Gabriel R. Ortega-Solís, Friederike J.R. Wölke, Vojtěch Barták, François Leroy, and Petr Keil discussed the results. All authors reviewed the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All raw atlas data are available by request from the respective atlas coordinators. Specifically, European birds data can be obtained through data request at https://ebba2.info/data-request/, Czech birds can be requested from Karel Šťastný and Vladimír Bejček (authors of the Breeding Birds Atlases of the Czech Republic), Japanese birds data are available through request to the Japan Bird Research Association or at https://ikilog.biodic.go.jp, and the New York birds data are available at https://data.ny.gov/Energy-Environment/Breeding-Bird-Atlases/vk8g-ypxi. Data on species traits are openly available from AVONET (Tobias et al. 2022). Codes, derived data used in the analyses, and results are available in the Zenodo repository https://doi.org/10.5281/zenodo.15463597 or at the GitHub repository https://github.com/carmensoria/sac-diversity-distributions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. Breeding Bird Atlases (BBAs) information, Spatial autocorrelation metrics, Species traits details, and R packages. **Table S1:** SAC of richness across study regions, periods, and grain sizes. **Table S2:** SAC of species distributions across study regions, periods, and grain sizes. **Table S3:** Species with increasing, decreasing, and no change in SAC (JCD) over time. **Table S4:** Species temporal SAC trends. **Table S5:** Spatial trends in richness SAC (Moran's I) across study areas and periods. **Table S6:** Mean and median Join count difference (JCD) of species distributions across periods and grain sizes. **Table S7:** Spatial trends in species SAC (JCD) across study areas and periods.) **Table S8:** Relationship between the log ratios of observed JC and occupancy across regions and grain sizes. **Table S9:** Percentage of species in each quadrant of the combined temporal change in occupancy and JC per atlas location and grain size. **Table S10:** Relationship between the log ratios of expected JC and occupancy across regions and grain sizes. **Table S11:** Mean and standard deviation (SD) of observed Join count log ratios for each region and grain size. **Table S12:** Mean and standard deviation (SD) of occupancy log ratios for each region and grain size. **Table S13:** Results of the Kruskal-Wallis test assessing differences in JCD slopes among habitat associations. **Table S14:** Results of the Kruskal-Wallis test assessing differences in JC-OCC residuals among habitat associations. **Table S15:** Dunn's post hoc test results comparing JC-OCC residuals between habitat association pairs. **Table S16:** Results of the Kruskal-Wallis test assessing differences in JCD slopes among trophic levels. **Table S17:** Results of the Kruskal-Wallis test assessing differences in JC-OCC residuals among trophic levels. **Table S18:** Dunn's post hoc test results comparing JC-OCC residuals between trophic level pairs. **Table S19:** Relationship between JCD slopes and hand-wing index. **Table S20:** Relationship between JC-OCC residuals and hand-wing index. **Table S21:** Total number of cells and edge cells, as well as the proportion of edge cells in each region and grain size combination. **Figure S1:** Mean slopes of the temporal change in the Join count difference (JCD) across grain sizes. **Figure S2:** Mean Join count difference (JCD) of species distributions across grain sizes. **Figure S3:** Relationship between the empirical occupancy change and the Join count statistic (JC) change in the Czech Republic. **Figure S4:** Relationship between the empirical occupancy change and the Join count statistic (JC) change in Europe. **Figure S5:** Relationship between the empirical occupancy change and the Join count statistic (JC) change in New York. **Figure S6:** Relationship between the empirical occupancy change and the Join count statistic (JC) change in Japan. **Figure S7:** Percentage of species in each category of combined empirical occupancy and Join count statistic (JC) change. **Figure S8:** Slope of the regression of the log ratio of the Join count (JC) statistic as a function of the log ratio of occupancy. **Figure S9:** Histograms of the JC log ratio showing the marginal distributions. **Figure S10:** Histograms of the occupancy log ratio showing the marginal distributions. **Figure S11:** Boxplots of the temporal slope of JCD (JCD over time) across the preferred habitat density categories for each region. **Figure S12:** Boxplots of the residuals JC-OCC across the preferred habitat density categories for each region. **Figure S13:** Boxplots of the temporal slope of JCD across trophic level categories for each region. **Figure S14:** Boxplots of the residuals JC-OCC across trophic level categories for each region. **Figure S15:** Relationship between hand-wing index and temporal JCD slopes across regions. **Figure S16:** Relationship between hand-wing index and JC-OCC residuals across regions.