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Regional Occupancy Is Negatively Related to Richness Across Time and Space

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ABSTRACT

Aim: Biological diversity is shaped by processes occurring at different spatial and temporal scales. However, the direct influence of the spatial and temporal scale on patterns of occupancy is still understudied. Today, occupancy is often negatively correlated with species richness, but it is unknown whether this relationship is scale dependent and consistent through time. Here, we use datasets of contemporary and paleontological communities to explore the occupancy-richness relationship across space and time, examining how scale influences this relationship.

Location: Varying spatial extents with global coverage.

Time: Varies from 7 mya to 2021 CE.

Taxa: foraminifera, mammals, birds, fish, and plants.

Methods: We gathered datasets spanning different spatial, temporal, and taxonomic extents. We binned each dataset into distinct time periods and spatially subsampled them into regional pools of varying sizes. We calculated regional occupancy and richness for each pool, measuring the strength of the relationship between the two. Using linear mixed models, we related the occupancy-richness relationship to the size of the regional pools, overall species richness, and climatic changes through time.

Results: We observed nearly ubiquitous negative occupancy-richness relationships across taxa, spatial scale, and time. The size of the regional pools and time bins had no consistent effects on the strength of the relationship, but the strength of the negative relationship varied substantially among taxa, with foraminifera and North American pollen showing weaker relationships than mammals and birds. Changes in this relationship through time were not driven by climatic perturbations but by the species richness observed across all regional pools.

Conclusions: Patterns of regional richness and occupancy are consistently negatively related and independent of spatial and temporal scale and of direct climatic changes. However, differences in the ecology of species (e.g., dispersal ability) and changes in biodiversity and community composition through time may cause fluctuations in the strength of the occupancy-richness relationship.

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1 | Introduction

Understanding how the extraordinary diversity of life on Earth is organised across space and time is one of the defining goals of ecology (MacArthur 1972; Heino 2011). For more than 100 years, ecologists have attempted to describe and predict how communities evolve, assemble, interact, and respond to external factors (Gleason 1926; Clements 1936). Debate is still ongoing on the relative roles of biotic and abiotic factors in driving patterns of evolution and community composition (e.g., the "Red Queen" vs. "Court Jester" hypotheses, Benton 2009). However, ecologists now generally accept that species arrange hierarchically and stochastically across spatial and temporal scales (Chase et al. 2018; Shoemaker et al. 2020), and different ecological and evolutionary processes tend to dominate at different spatial and temporal scales (Ricklefs 1987; Whittaker et al. 2001; Benton 2009; McGill 2010; Soininen 2010; Bino et al. 2013; Wiegand et al. 2021). At local spatial and short temporal scales, biotic interactions such as competition often govern where a species is able to establish and how they evolve (Benton 2009; Kraft et al. 2015; D'Andrea et al. 2020). In contrast, species distributions and evolutionary patterns on large spatiotemporal scales are often governed by abiotic factors such as climate or tectonics instead of particular biotic interactions (Soberón and Nakamura 2009; Fraterrigo et al. 2014; Huang et al. 2021; Benton 2009; Antell et al. 2024; but see de Araújo et al. 2014).

Processes across spatial and temporal scales combine to modify the patterns of diversity we observe today (Whittaker et al. 2001; Congreve et al. 2018). As a result, diversity patterns are often scale dependent (Stein et al. 2014; Chase et al. 2018, 2019; He et al. 2024). One of the best-known patterns in biogeography is the species-area relationship, which suggests a broadly log-linear or power relationship between the number of species in a given region and the size of the region (McGuinness 1984; Storch et al. 2012; Dengler et al. 2020). Community turnover and dissimilarity also change with spatial scale, with weaker effects of distance decay and less dissimilarity found at larger extents and finer spatial resolutions (Barton et al. 2013; Graco-Roza et al. 2022). Temporal changes in these ecological patterns often also vary with spatial scale. Jarzyna and Jetz (2018) found that modern changes in richness and functional diversity were highly scale-dependent through time, likely due to differences in environmental change and conservation management across those spatial scales.

Although biodiversity change and community assembly are clearly influenced by spatial scale, not all ecological patterns and relationships show a distinct spatial dependence (Cantor et al. 2017). For example, the relationship between site-level occupancy of a species (the number or proportion of local sites within a region the species occupies) and its abundance appears to be robust to spatial scale (Steenweg et al. 2018; Ten Caten et al. 2022). Locally abundant species tend to be more locally widespread, occupying a greater proportion of sites within the area of interest, and this positive relationship between species' abundance and site-level occupancy is maintained regardless of the spatial extent and resolution of the study (Steenweg et al. 2018; Ten Caten et al. 2022). However, research examining local vs. regional occupancy and metacommunity structure are often conducted with fixed spatial extents of the "local" and "regional" areas (White et al. 2023; but see Jarzyna and Jetz 2018). As a result, although occupancy is intrinsically linked to space (Crisfield et al. 2024), whether the patterns and drivers of occupancy vary across spatial scale is a matter of some debate.

In particular, the relationship between regional richness (the number of species in a region) and occupancy has not been thoroughly examined for scale dependence. Regions with greater numbers of species often have lower mean occupancy and a greater proportion of locally rare species (Ricklefs 1987; Hugueny et al. 2007; Belmaker and Jetz 2012). This negative relationship may be expected through neutral theory, in which each species is functionally equivalent (Hubbell 2005). According to neutral theory, species might compete with and exclude each other stochastically at local scales, leading to lower average occupancy in regions with more species. However, the extent to which biological communities actually follow these dynamics across space and time is highly debatable (McGill 2003; Dornelas et al. 2006; Chisholm and Pacala 2010; Ricklefs and Renner 2012), and the effect of spatial scale (i.e., the size of the regions) on the hypothesized negative relationship has not been studied.

We similarly do not know whether the negative occupancy-richness relationship observed today for some regions and taxa has remained stable through time or fluctuates based on external factors. Change in regional biodiversity through time does not occur uniformly across local sites. Across the tree of life, highly biodiverse local sites tend to compose broader regions of high biodiversity (Ricklefs 1987, 2000; Cornell et al. 2008; Szava-Kovats et al. 2013), but biodiversity loss on global or regional scales does not necessarily translate into biodiversity loss on local scales (Chase et al. 2019; Blowes et al. 2024). Temporal variation in dispersal rates and homogenization (Peniston et al. 2024) and an increase in rare species from disturbance and/or predation may cause changes in the relationships between regional richness and occupancy (Shurin and Allen 2001; Hillebrand 2005; Prugh et al. 2018). In particular, periods of ecological stress such as drought may substantially reorganise communities and foster transient positive interactions between species (Prugh et al. 2018; Adams et al. 2022).

Using well-sampled occurrence data over time, we examine the effects of both spatial and temporal scales on the occupancy-richness relationship and characterise the change in this relationship through time. We then examine how the relative proportion of species with high occupancy and low occupancy influence the strength of this relationship. Overall, we hypothesize a negative relationship between occupancy and richness across taxa, following the results of Belmaker and Jetz (2012) and expect this relationship to remain consistently negative through time. However, we anticipate that climatic pressures will lead to fluctuations in the occupancy-richness relationship through time by reorganising local communities, as observed by Prugh et al. (2018). Finally, we expect weaker relationships between occupancy and richness at broader spatial scales, as the heterogeneity of the landscape and dispersal processes make the regional communities less distinct from each other.

2 | Methods

2.1 | Data Acquisition and Processing

To examine the relationship between occupancy and richness across space and time, we used five sets of well-sampled time series data with varying taxonomy, temporal, and spatial extent (Table 1, Figure 1). Two of the datasets were extracted from the BioDeepTime database (Smith et al. 2023) and comprise surveys of North American breeding bird abundance originally from the North American BBS database (henceforth, "breeding bird surveys", Ziolkowski et al. 2023) and cores of lake-sampled pollen from the Neotoma database ("pollen cores", Williams et al. 2018). In addition, we used planktonic foraminifera fossils found in ocean core samples from the Triton database ("foraminifera cores", Fenton et al. 2021), surveys of river fish conducted via electrofishing from the RivFishTIME database ("fish surveys", Comte et al. 2021), and camera trap observations of mammals from Snapshot USA ("camera trap surveys", Cove et al. 2021; Kays et al. 2022; Shamon et al. 2024).

TABLE 1 | Summary of the datasets used, with the number of distinct locations, the overall richness of the dataset (after being subset to the desired time period and spatial extent, see Figure 1), the number of regional pools used for each dataset/time period, and the span of regional pool sizes. The number of regional pools and spatial scales used for the temporal analysis are in parentheses.

Dataset	Number of locations	Richness	Number of regional pools used	Regional pool radius (km)
North America Breeding Birds	439	384	20 (13)	100–1000 (250)
Pollen Cores				
North America	435	855	19 (14)	100–1000 (250)
Europe	455	1236	20 (15)	100–1000 (250)
River Fish	4197	84	20 (20)	50–500 (100)
Mammal Camera Traps	4153	118	20 (13)	100–1000 (250)
Foraminifera				
Mixed Layer	4033	19	15 (9)	200–1000 (1000)
Thermocline	3940	18	15 (9)	200–1000 (1000)

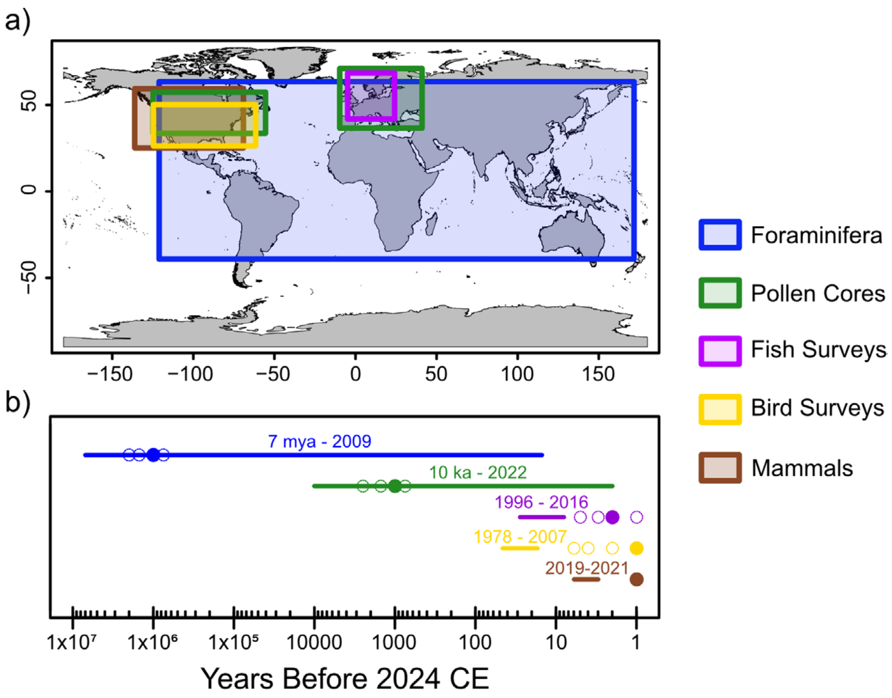

FIGURE 1 | Distribution of the data across space and time. (A) The spatial extent of the five datasets. (B) The temporal extent (lines) and resolution (precision of the temporal units, open circles) of the five datasets. Note that the x-axis is on a logarithmic scale and is defined in relation to the year 2024 CE. For clarity, only the results of the temporal resolution marked by the filled circles are presented in the manuscript; see Appendix S8 for the results of the analyses with the temporal resolutions of the open circles.

The five datasets represent series of observations conducted at the same locations through time. The observations within each dataset were gathered using consistent sampling techniques, although these techniques vary between the datasets. We therefore do not need to account for sampling changes within each dataset, only when comparing across datasets. To ensure sufficient sites to examine occupancy and richness on local and regional scales, we truncated the datasets to only include the densest time periods and study areas (Figure 1). Specifically, we subset the breeding bird surveys to an area roughly encompassing the continental United States using surveys from 1978 CE to 2007 CE (Figure 1a). We removed observations from the fish surveys older than 1996 CE and younger than 2016 CE. We divided the pollen core dataset into North American and European regions (Figure 1a), removed observations older than 10,000 years bp, and ensured that the species identifications were harmonised (see Appendix S1). For the foraminifera samples, we trimmed the data to the most recent 7 million years to capture the densest set of observations. To ensure that the species of foraminifera observed in the dataset were actually likely to encounter each other, we used the species-level functional trait data provided by Aze et al. (2011) to separate the full dataset into two functional groups: foraminifera living in the mixed layer and foraminifera living at the thermocline. We then ensured that the taxonomic identifications of each dataset were internally consistent and standardised the taxonomies if they were not (see Appendix S1). Finally, to examine changes through time, we aggregated the data into distinct time bins. The width of the time bins (temporal resolution) varied for each dataset (Figure 1b) to maximise the spatial extent and number of observations we could use. See Table 1 and Figure 1 for summary statistics of the cleaned datasets. All analyses were conducted in R v. 4.4 (R Core Team 2024) using the gtools (v. 3.9.5), lme4 (1.1–34), MuMIn (1.47.5), sjPlot (2.8.15), terra (1.7–71), vegan (2.6.4), and viridis (0.6.3) packages (Bates et al. 2015; Barton 2020; Garnier et al. 2021; Hijmans 2022; Oksanen et al. 2022; Lüdecke 2023; Warnes et al. 2023).

2.2 | Occupancy and Richness Calculations

We used a combination of two hierarchical spatial levels to explore the relationship between occupancy and richness within the datasets (Figure 2). First, we spatially subsampled the dataset into non-overlapping regions of equal area (henceforth, “regional pools”, see Figure 2) using circular radii around seed points. Each of these regional pools was required to have at least five spatially distinct sites within the circle. We varied the number of regional pools sampled between each dataset (see Table 1) so that we could include datasets that were less well-sampled; however, the number of sampled regional pools did not substantially influence the average strength of the occupancy-richness relationship (Appendix S2).

We calculated the occupancy of each regional pool by randomly sampling five sites within the regional pool and averaging the number of those sites occupied by each observed species (Figure 2a). For example, a regional pool has high mean occupancy when a large proportion of its resident species are found across all five sites (high zeta diversity sensu Riva and Mammola 2021), and low mean occupancy when dominated by species found at only one of the sites (high theta diversity sensu

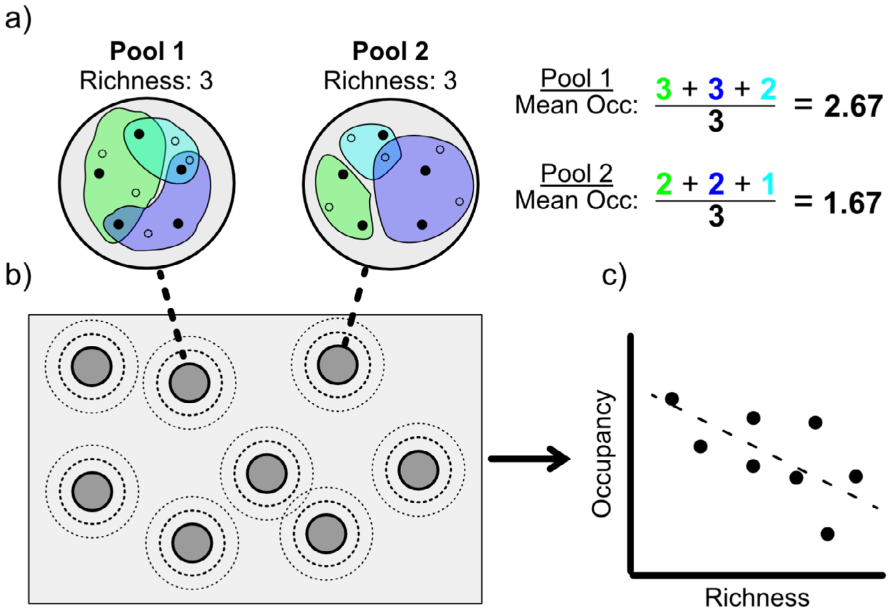

FIGURE 2 | Conceptual figure describing how we calculated the mean occupancy of each regional pool and the relationship between occupancy and richness across the study regions. (A) Two regional pools identified in the dataset, each with three species. The dots represent observation sites within the regional pool; filled dots were randomly selected to be used for this replicate of the occupancy calculation. In the pool on the left (Pool 1), each species on average occupies more of the selected observation sites than the pool on the right (Pool 2), leading to greater mean occupancy. (B) The occupancy calculation is repeated for all regional pools within the study area and several different spatial scales (dashed circles), which may include sites not present in the smaller regional pools. Note that at large spatial scales, the regional pools may overlap. (C) The relationship between richness and occupancy is calculated as the standardised effect size between richness and occupancy across the regional pools.

Riva and Mammola 2021). We then calculated the total number of species found at the five sampled sites (i.e., the species richness of the regional pool). To account for spatial variation in the datasets, we conducted 100 separate replicates of the analysis, using a different subsample of sites within each regional pool and, if possible, a different set of regional pools each time (Table 1).

After calculating occupancy and richness for each of the regional pools, we repeated the calculations for regional pools of larger sizes (Figure 2b). To avoid bias relating to the non-random spatial distribution of sites across the entire study area, we used the centroids of the smaller regional pools as the centroids of the larger regional pools. As a result, each regional pool is comparable across the spatial scale, although not across replicates. At large spatial scales (e.g., 500–1000 km), the regional pools often overlapped each other, violating the assumption of independence, although our results were similar when the larger regional pools were forced to be non-overlapping (Appendix S3). Finally, to summarise the strength of the occupancy-richness relationship, we calculated the standardised effect size between mean occupancy and richness of the regional pools within each replicate (Figure 2c) and averaged the effect sizes across the 100 replicates.

2.3 | Assessing the Influence of Scale on Occupancy-Richness Relationships

We then examined how the strength of the occupancy-richness relationship changed across time, space, and taxon. First, we explored the effect of spatial scale on the occupancy-richness relationship across all seven datasets by applying a Gaussian linear mixed model with a random slope. Using the interaction between spatial scale and dataset ID as the random effect, we regressed the standardised effect size of the occupancy richness relationship (averaged across the 100 replicates) against the size of the regional pools, species richness, and the interaction between the two. This model (henceforth, “cross-taxon mixed model”) permitted the effect of scale to vary with species group, allowing us to determine if the relationship between occupancy and richness responded similarly to spatial scale irrespective of taxon, location, and sampling method. We then examined the effect of spatial scale and total richness on each of the species groups individually. Using Gaussian generalised additive models to account for potential non-linear patterns in scale dependence, we constructed a second model (“additive model”) in which dataset ID was a fixed, intended effect. To determine whether the nonlinearity component of this model was significant, we decomposed the model into linear and smoothed components. Because quantitatively interpreting smoothing factors in a random slope model is not very informative, we only considered linear relationships in our cross-taxon mixed model.

We used results from all spatial scales (from 50-km to 1000-km regional pools) in these models. However, to compare more directly with the fish survey dataset (which has a maximum spatial scale of 500 km, see Table 1), we additionally ran the models using only 500-km regional pools or smaller (see Appendix S4). All models were fit using REML, and the mixed models were fit using the lme4 package (v. 1.1; Bates et al. 2015).

2.4 | Assessing Temporal Variation in Occupancy-Richness Relationships

To examine the drivers of temporal variation in the occupancy-richness effect across the datasets, we re-sampled each of the occurrence datasets, keeping the regional pool centroid constant across time. This method allowed us to examine changes in a single regional pool throughout the timespan of the dataset and to link these changes with changes in biotic and abiotic factors. We calculated the occupancy-richness relationship for each regional pool through time as detailed above and in Figure 2, using 100 replicates. Unlike the spatial analysis, however, we chose to use a single regional pool size for the temporal analysis to maximise the number of time series (See Table 1). Along with the occupancy and richness of each regional pool, we calculated the combined species richness of all regional pools (total species richness). In addition, we calculated two metrics describing how wide-ranging each observed species was: (i) how many of the regional pools were occupied by each species (i.e., how widespread a species was across the entire study region) and (ii) how many sites per regional pool were occupied by the species (i.e., how widespread the species was within each regional pool). We averaged these metrics across species: a high average number of occupied regional pools meant that there are relatively many large-ranged species, and a high average number of occupied sites meant that there are relatively many species that are widespread within the regional pools.

To test our hypothesis that climatic changes through time drive fluctuations in the occupancy-richness relationship, we extracted climate data for each site within the regional pools. We used different climate variables across the species groups to reflect the ecology of the taxa. Based on the results of previous literature, we used annual precipitation, minimum temperature, and maximum temperature for the bird and pollen groups (Devoto et al. 2009; Prugh et al. 2018; Gomez et al. 2020); runoff, minimum temperature, and maximum temperature for fish (Poff et al. 1997; Fox and Magoulick 2024); and sea surface temperature, salinity, and depth of the mixed layer/thermocline were used for the foraminifera datasets (Fenton et al. 2023). See Appendix S5 for a detailed description of the variables and climatic data used in this analysis. Once we had extracted the climatic data for each site, we averaged the values of the sites within each regional pool.

We first measured the temporal variation in the occupancy-richness relationship by calculating the standard deviation of the relationships across time for each replicate. Using a Gaussian linear model (“temporal variation model”), we related this temporal variation to variation in species richness and to the temporal span of each dataset. Next, we related stepwise changes in the total number of species, the average number of regional pools occupied by each species, and the average number of sites within each regional pool occupied by each species to stepwise changes in the occupancy-richness relationship using a Gaussian generalised linear mixed model with the species group as the random intercept (“stepwise mixed model”). Finally, we incorporated climatic change by relating the stepwise changes in the occupancy-richness relationship of each species group to stepwise changes in the climatic conditions of the regional pools, while accounting for changes in species richness ("stepwise climate change models"). As above, all models were fit using REML and the lme4 package. The mammal camera trap dataset had only three distinct time periods and was therefore excluded from these time-step analyses.

2.5 | A Null Model of Occupancy and Richness

A substantially negative occupancy-richness relationship may arise from statistical means, and, in particular, the highly right-skewed frequency distribution of species' geographic range sizes. Within a broad taxonomic group (e.g., birds), most species have relatively small range sizes, with only a few species having continental or cosmopolitan ranges (Gaston 1996; Takashina et al. 2022). Because broad-ranging species are more likely to occur at any given location, regional pools with few species may have a greater proportion of large-ranged species that are found throughout the regional pool. In contrast, regional pools with high species richness may be more likely to have a greater proportion of small-ranged species.

To ensure that the occupancy-richness patterns we observed were not solely artefacts of the range-size frequency distribution, we developed a null model using expert-generated range maps. We used a random subset of North American mammal range maps ($n = 200$ species) provided by the International Union on Conservation of Nature (IUCN 2020). We chose to use only the mammal dataset for this analysis because the other taxa are either predominantly migratory, complicating estimates of range size (i.e., birds) or have much sparser expert-generated range data.

First, we tested the occupancy-richness relationship generated from the expert IUCN range maps. To do so, we randomly sampled 2500 points across North America. For each point, we gathered a list of species occurrences based on which IUCN range maps overlapped the point. Next, we calculated the occupancy-richness relationships using the same methods as in the empirical data, using regional pools with 100-km radii. The occupancy-richness relationships generated from the expert range maps were strongly negative ($\mu = -0.66$; 95% CI $= -0.69, -0.63$; $n = 100$; also see Appendix S6). This relationship was, on average, slightly stronger than the occupancy-richness relationships derived from the empirical camera trap data, but there was considerable overlap between the two estimates. The concordance between the IUCN range size and camera trap observation results underscores the well-known relationship between occupancy and range size (Carotenuto et al. 2010; Di Cecco and Hurlbert 2022) and demonstrates that expert-generated range maps can make reasonable, if not exact, proxies for observation data in this study.

For the null model, we then randomly shifted each of the IUCN range polygons in space (see conceptual diagram in Appendix S6). To shift the ranges, we moved the centroid of each IUCN range polygon randomly following a normal distribution (latitudinal shift sd = 2°, longitudinal shift sd = 5°). This random shifting removed the effects of ecology and historical contingencies but kept the same right-skewed frequency distribution of range sizes. Using these new, randomly shifted species ranges, we sampled 2500 points randomly across North America once more and recalculated occupancy-richness relationships. Similar relationships between the randomly shifted polygons and true polygons would indicate that the frequency distribution of range sizes is the primary driver of the negative occupancy-richness relationship.

2.6 | Single-Biome Analysis

The regional pools we used for these analyses were distributed across the continental extents of each dataset (Figure 1a) and thus located in many different ecoregions and biomes. As a result, the relationships we calculate between occupancy and richness may be influenced by differences in the environment of each regional pool. To determine if the patterns we observe are maintained within single biomes, we re-calculated the occupancy-richness relationships for the mammal camera trap surveys and the bird surveys using only regional pools from the same biome (as defined by Olson et al. 2001). We compared these single-biome occupancy-richness relationships to the full, cross-biome relationships (Appendix S7).

3 | Results

All five species groups showed negative relationships between occupancy and richness of regional pools (Figure 3). However, the strength and significance of the occupancy-richness relationship varied significantly across the groups ($p < 0.001$). In fact, the majority of variance in the cross-taxon mixed model (93.0%) derived from differences between datasets instead of scale and species richness. Although the relationship between richness and occupancy was always negative, the relationship was strong for breeding birds, mammals, fish, and European pollen and only weak or marginally insignificant for North American pollen cores and global foraminifera (Figure 3). Whether weak or strong, the consistent negative relationship between richness and occupancy was not reconstructed in our null model despite the similar strength of occupancy-richness relationships observed in mammalian camera trap data and the sampled IUCN range maps (see Methods, Appendix S6). Instead, the null model results centered near 0 ($\mu = -0.06$; 95% CI $= -0.11, -0.01$; $n = 100$), with little relationship between occupancy and richness (Appendix S6).

When considering all species groups at once, the size of the regional pools was insignificantly related to the strength of the occupancy-richness relationship (measured as standardised effect size; cross-taxon mixed model, $t = 0.11$, $n = 722$ in 7 groups). However, regional pool size influenced the occupancy-relationship in different ways for each species group. When considering the species group as a fixed effect and accounting for non-linearity (using our additive model), we found distinct non-stationary scale dependence in breeding birds, mammals, North American pollen (negative relationship), and fish (positive relationship, Figure 4; cross-taxon additive model adjusted $r^2 = 0.84$, $n = 722$, $k = 6$). In contrast, European pollen and the two foraminifera groups had no substantial scale dependence ($F < 0.32$, $p > 0.08$, Figure 4). All taxa aside from the two foraminifera groups showed significant non-linearity, but only mammals and birds showed a linear change along with the non-linear relationships (Figure 4). When the regional pools were forced

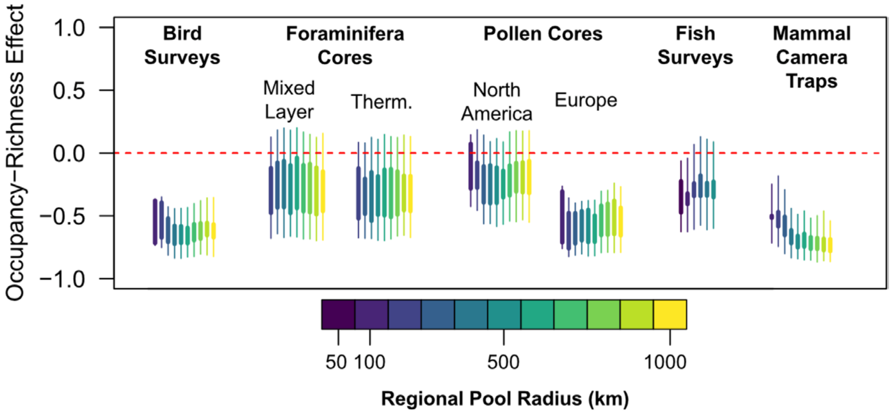

FIGURE 3 | Summary of the relationships between occupancy and richness for all seven datasets. The vertical bars show the range of standardised effect sizes for each dataset and spatial scale: Thick bars show the total range of aggregated effect sizes (average of 100 replicates) for each time period, and the thin bars show the 5% and 95% quantiles of each replicate's effect size. Colour denotes the size of the regional pools from which the occupancy-richness relationship was calculated.

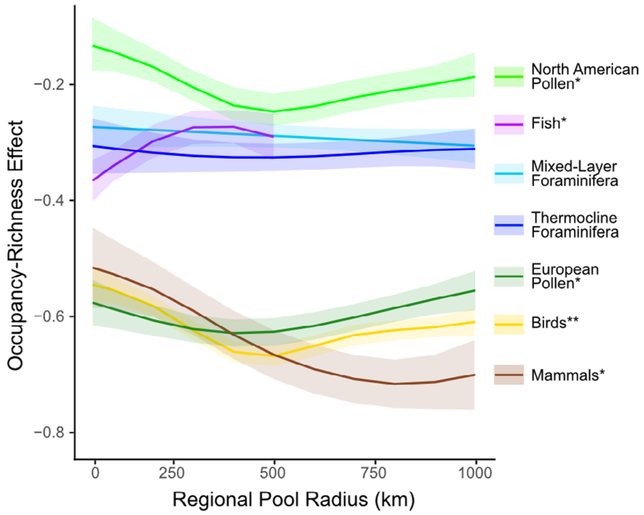

FIGURE 4 | Results of the generalised additive model predicting occupancy-richness effect size as a function of regional pool sites, incorporating species group as a fixed effect. Dark lines indicate the model coefficient, and the lightly shaded areas indicate the 95% confidence intervals. One asterisk indicates that the non-linear terms in the model are significant for that species group, and two asterisks indicate that both the linear and non-linear terms are significant for that species group.

to be non-overlapping at larger sizes, the overall results did not change substantially (Appendix S3). Moreover, the results of our analyses were only marginally influenced by temporal scale (i.e., the width of the time bins; Appendix S8, Figure 1b), and the taxonomic level of identification (i.e., identification to species level vs. genus level; Appendix S9).

For nearly all time periods, the relationships between occupancy and richness remained weakly or strongly negative across species groups. However, the strength of the occupancy-richness relationship (measured as standardised effect size) did vary through time (Figure 5). Averaged across the 100 replicates, the occupancy-richness relationship varied the most in thermocline foraminifera ($\text{sd}=0.33$, $n=7$ time periods) and the least in European pollen ($\text{sd}=0.11$, $n=10$ time periods). Variation in the occupancy-richness relationship was strongly associated with dataset timespan, with datasets spanning longer times having greater variation through time (temporal variation model, $\beta=0.64$, $t=17.93$). For foraminifera and pollen (the two datasets with the longest extents), the standardised effect varied from moderately strong ($\beta=-0.5$ to -1) to negligible ($\beta\approx 0$). In addition, time-step changes in the occupancy-richness relationship were significantly related to changes in species richness across species groups ($\beta=-0.06$, $t=-4.48$), the average number of regional pools occupied by the species ($\beta=-0.05$, $t=5.35$), and the average number of sites within the regional pools that were occupied ($\beta=-0.22$, $t=24.64$). Therefore, as expected, the occupancy-richness relationship strengthened when there were more species across the regional pools and when there were fewer widely distributed species (both at the site level and across regional pools). In contrast to the moderate effect of overall richness change in the time-step mixed model ($t=-4.48$), climate change through time was only weakly related to change in the occupancy-richness relationship (stepwise climate change models; all $r^2<0.19$, mean r^2 for all seven datasets $=0.07$); each dataset was affected differently by the climatic predictors (see Appendix S6).

Using non-overlapping regional pools with varying centroids, we observed a slight negative relationship between standardised effect size and regional pool size across species groups, in contrast to when the centroids of the regional pools were fixed in space. At larger spatial scales, regional pools were forced to be farther apart to avoid overlapping. Therefore, the non-overlapping regional pools may be more distinct environmentally from each other and have greater differences among communities than the pools that were allowed to overlap. However, the overall occupancy-richness relationships were similarly negative across groups, and the distributions of effect sizes overlapped in nearly all cases (Appendix S3).

3.1 | Breeding Bird Surveys

For North American breeding birds, the relationship between the richness of the regional pool and mean occupancy remained

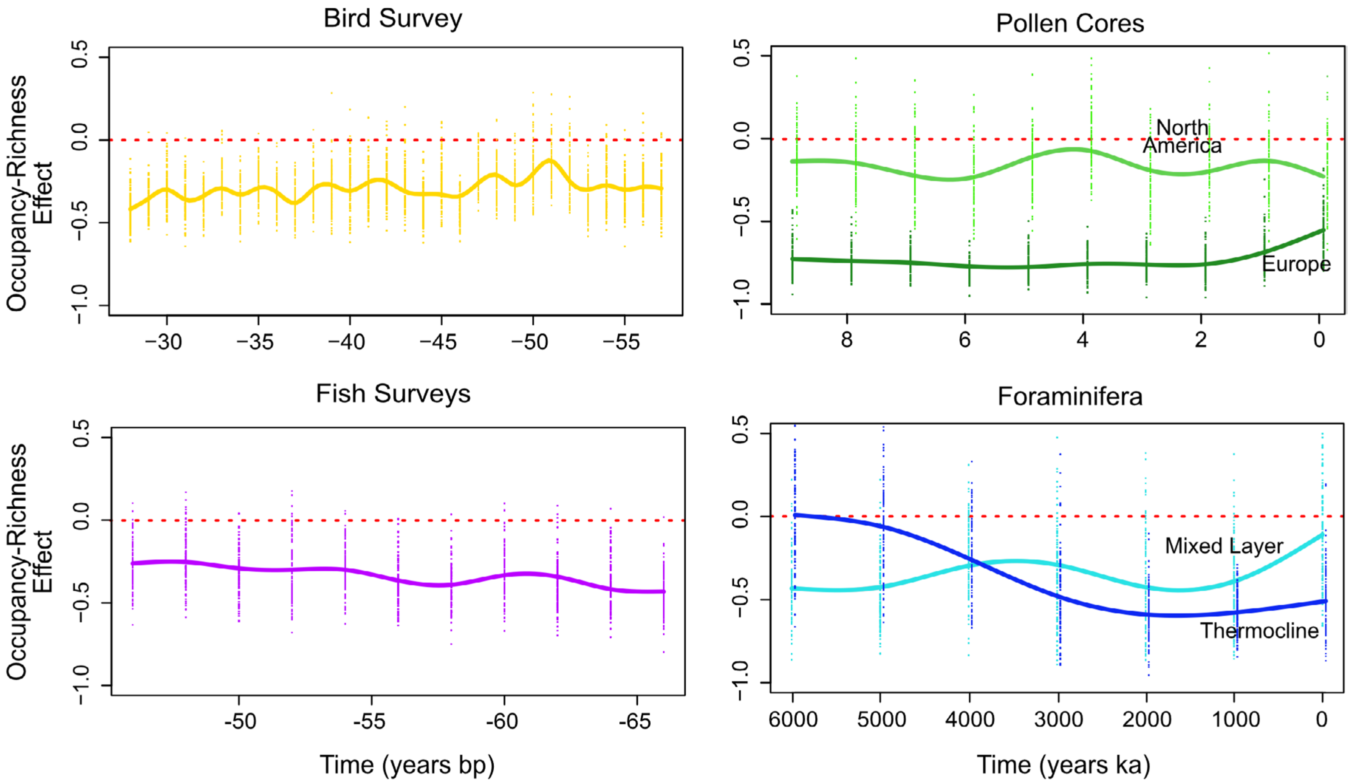

FIGURE 5 | Time series of the occupancy-richness relationship in which the regional pools were held constant through time. The thick lines indicate the average occupancy-richness relationship (across 100 replicates, shown here by the individual points). The red dashed lines indicate $\beta = 0$ (i.e., no relationship between occupancy and richness). Time series were smoothed using generalised additive modelling ($k = 0.8 \times$ number of time periods) for clearer visualisation. Note that the time axes for the pollen cores and foraminifera (right column) are in thousands of years (ka), whereas the time axes for the bird and fish surveys are in years before present (bp).

strongly negative regardless of the spatial extent of the regional pools and the year the surveys were taken (Figures 3 and 5). Averaged across the 100 replicates, the relationship ranged from $\beta = -0.720$ to $\beta = -0.361$. At smaller regional pool sizes, the distribution of standardised effect sizes across the 100 replicates was more clustered than at larger regional pool sizes, but the median effect sizes did not change substantially across spatial scales. The occupancy-richness relationship remained strongly negative through time, although we observed a slightly weaker relationship near the year 2000 CE (Figure 5).

When relating occupancy to richness of breeding birds within only broadleaf and mixed forests, we again observed strong negative relationships between occupancy and richness, although the strength of this relationship was slightly weaker than in the cross-biome analysis (Appendix S7).

3.2 | Pollen Cores

We divided the pollen data provided by the Neotoma database geographically into two species groups (North America and Europe; Figure 1a). Although the two groups have similar taxa and were constructed using similar methods, the occupancy-richness relationship differed strongly between them. Both pollen groups showed a negative relationship between occupancy and richness (Figure 3), but in North America, the effect was weak, with average effect sizes ranging from $\beta = -0.396$ to 0.079. In contrast, European plant species showed a stronger negative relationship, ranging from $\beta = -0.715$ to -0.302. In North America, smaller regional pools were associated with lower variance in effect sizes across replicates, but the effect sizes of the European data showed consistent variance from 100-km to 400-km regional pools. Through time, the European pollen showed a consistent, strongly negative occupancy-richness relationship ($\beta = -0.75$) until roughly 2000 years bp, when it weakened ($\beta = -0.25$, Figure 5). In contrast, the occupancy-richness relationship in North American pollen was consistently weakly negative, except around 4000 years bp, when it weakened before recovering.

The differences found in the relationship between occupancy and richness in the European and North American pollen may be caused by a variety of factors, including variation in environment conditions and the hierarchical structure of the plant communities. Therefore, we directly compared the European and North American communities, finding that (1) the individual regional pools and the study area as a whole were significantly more biodiverse in Europe than North American ($t > 68.1$ for both; also see Gordon et al. 2024); (2) the sites in Europe experienced significantly milder temperature extremes than the North American sites ($t > 11.9$ for all three environmental variables); and (3) changes in regional pool richness reorganised communities more completely in North America than Europe (see Appendix S10). Furthermore, North American species, on average, occupied more regional pools and more sites within each regional pool than European species ($t > 83.8$ for both comparisons; Appendix S10).

3.3 | Foraminifera Cores

The two foraminifera groups (divided by ecology into the mixed layer and thermocline species) both showed a weakly negative effect between occupancy and richness (Figure 3). The effect sizes for the thermocline foraminifera ranged from $\beta = -0.536$ to -0.118, and the effect sizes for the mixed layer foraminifera ranged from $\beta = -0.491$ to -0.040. The size of the regional pools had little effect on the average effect sizes of either ecogroup. In contrast, the effect sizes changed substantially through time in both ecogroups. The two taxa showed diverging temporal trends, with a relationship oscillating from moderately strong ($\beta \approx -0.5$) to negligible ($\beta = 0$). The mixed layer foraminifera showed a weakening trend through time, whereas the thermocline foraminifera showed a strengthening trend (Figure 5).

3.4 | Fish Surveys

For European fish, the occupancy-richness effect averaged across the 100 replicates ranged from $\beta = -0.470$ (2004 CE, 50 km regional pools) to $\beta = -0.174$ (2004 CE, 300 km regional pools), indicating a moderate relationship between occupancy and richness. Like the other species groups, this relationship was somewhat robust to both spatial scale and time (Figures 3 and 5). However, at intermediate spatial scales (200-km to 300-km regional pools), the relationship weakened. Through time, the occupancy-richness relationship remained stable, with a slight weakening trend towards the present day (Figure 5).

3.5 | Mammal Camera Trap Observations

In mammals, we observed a strong negative effect between richness and occupancy at all spatial scales across the 3 years examined, with the strongest effect found in 2019 ($\beta = -0.778$, 1000-km regional pools) and the weakest in 2020 ($\beta = -0.465$, 200-km regional pools). The effect strengthened with increasing regional pool size, especially at pool sizes greater than 400-km (Figure 3), but did not change substantially across the 3 years of the surveys. The single-biome analysis revealed similar patterns to the cross-biome analysis, with strongly negative effect sizes observed in each biome (Appendix S7).

4 | Discussion

Overall, as expected, we found negative standardised effect sizes between regional richness and average occupancy of the regional pools across time, space, and taxon, supporting previous work (Belmaker and Jetz 2012). These negative occupancy-richness relationships suggest that, in general and irrespective of differences in ecosystems and taxa, species-depauperate regions have proportionately more widespread, common, high-occupancy species than do biodiverse regions. However, the strength of the effect sizes varied through time, across space, and across species groups, with some taxa and biomes having stronger effect sizes (e.g., European pollen cores, mammal camera traps, bird surveys) than others (e.g., foraminifera, North American pollen cores, bird surveys in broadleaf forests), on average. In contrast to our hypotheses, the spatial extent of the regional pools had weak, idiosyncratic effects on the occupancy-richness relationship, and climatic change had only marginal effects on the change in the occupancy-richness relationship. Instead, we found that changes in diversity and the proportion of wide-ranging species within and across regional pools drove changes in the occupancy-richness relationship.

4.1 | Negative Occupancy-Richness Relationship

Negative occupancy-richness relationships may arise from several factors, both statistical and ecological. However, the results of our null model (in which the frequency distribution of range sizes remained the same, but the geographic locations of the ranges were randomised) do not support the idea that the occupancy-richness relationship derives from the shape of the range-size frequency distribution, as it did not reconstruct the observed negative relationships (Appendix S3). Negative relationships may also be expected under 'neutral' dynamics, in which species have no ecological or fitness differences and the total number of individuals in each species is limited in similar ways (Belmaker and Jetz 2012). In a perfectly neutral system, an increase in species richness (e.g., through speciation or invasion) necessarily corresponds to a decrease in regional occupancy because of random competition on local scales. It is often difficult to separate neutral and random effects on the community structure from ecological ones (see Connor and Simberloff 1979; Blanchet et al. 2020; Zhang 2020), and therefore, the influence of 'neutral' dynamics in driving a negative occupancy-richness relationship cannot be ruled out. Non-random niche partitioning based on differences in microclimate or microhabitat, and competition at small spatial scales (Mayfield and Levine 2010; Pastore et al. 2021), may also contribute to this negative relationship. However, the broad spatial and temporal scale of our analyses limited our ability to evaluate the influence of niche partitioning directly.

Whether driven by neutral dynamics or other factors, it is clear that small-ranged species and those with low regional occupancy organise non-randomly across space because of variance in environmental factors, ecological traits, and historical contingencies (Marcot et al. 2016; Shipley and McGuire 2023, 2024). Regions with high species richness tend to have greater proportions of species with small geographic ranges (Lamoreux et al. 2006; Shipley and McGuire 2022). These areas often have stable climates and rough topography, constraining the geographic ranges of species that arise due to increased niche partitioning and speciation (Antonelli et al. 2018). Range size is directly related to occupancy (Carotenuto et al. 2010; Di Cecco and Hurlbert 2022, also see Appendix S6), and thus, these highly-rich areas also have lower average occupancy.

4.2 | Taxonomic Differences and Resolution

The occupancy-richness relationship was nearly always negative, but the strength of the relationship varied substantially across species groups and through time. Differences among species groups may be partially explained by the ecology of the different taxa. The degree to which species within a clade compete with each other varies across the tree of life, with some related taxa competing strongly with each other and others coexisting (Cahill et al. 2008; Jiang et al. 2010; Mayfield and Levine 2010). For taxa that do not compete strongly with each other, we might expect weak relationships between richness and occupancy. The lack of strong intra-clade competition may explain the weak occupancy-richness relationships we observed in foraminifera, as they tend not to compete, instead structuring their communities by random, neutral processes (Rillo et al. 2019).

The dispersal ability of species within a community may also affect the occupancy-richness relationship. Dispersal rate influences patterns of richness at the site level (commonly called “alpha diversity”) and between sites (“beta diversity”) differently (Claramunt et al. 2012; Peniston et al. 2024). At low-to-intermediate dispersal rates, these two patterns oppose each other, whereas at high dispersal rates, they often correspond (Suzuki and Economo 2021). As a result, taxa that are able to disperse long distances may show a weaker relationship between occupancy and richness than those that are dispersal-limited. Both foraminifera and pollen are able to passively disperse long distances (Kremer et al. 2012; van Sebille et al. 2015) and have relatively weak occupancy-richness relationships, but more research must be done on the interaction between the dispersal rate and this relationship to support our observation.

We observed substantial differences between the two pollen species groups, separated geographically into European and North America communities. Comparing the two species groups showed differences in the community characteristics and environment. The more extreme climatic conditions of North America may have favoured habitat generalists, leading to more high-occupancy, large ranged species and greater variance in the relationship between occupancy and richness.

Finally, differences in the occupancy-richness relationship observed between taxa may stem from differences in the taxonomic scale at which the taxa were identified. For example, whereas the observations of foraminifera, birds, mammals, and fish were identified to the species level, in many cases, the pollen grains could only be identified to genus or family levels. We performed a sensitivity analysis in which we aggregated the bird data to the generic level, which suggests that coarser taxonomic resolution may lead to weaker occupancy-richness relationships (Appendix S9), but this effect did not substantially change the direction of the occupancy-richness relationships or the influence of the regional pool size.

4.3 | The Influence of Scale on Occupancy-Richness Relationship

We found little evidence for a consistent effect of regional pool size or temporal resolution on the occupancy-richness relationship in our cross-taxon analyses. However, larger regional pools have more species (the species-area effect) and lower occupancy (i.e., greater community differences between within-pool locations). The scale-dependence is a result of spatial autocorrelation in community assembly, in which communities that are close together are more similar than those that are farther apart (Graco-Roza et al. 2022). Taken together, these results suggest that the per se size of the regional pools may not have an intrinsic effect on the relationship between richness and occupancy, and the greater heterogeneity found in larger pools influences occupancy and richness similarly. Our results refine the prior literature, which found little influence of the spatial scale on species-level occupancy (Steenweg et al. 2018; Ten Caten et al. 2022) and on the effects of increasing richness on community composition (Cantor et al. 2017).

Although regional pool size did not affect the relationship between richness and occupancy consistently across datasets, the individual dataset analyses and the additive model that included dataset as a fixed effect revealed differing effects of spatial scale across datasets and species groups (Figure 4). These differences may stem from variation in the ecologically-relevant spatial scale (“scale of maximum effect”) for each taxon. For example, a study examining occurrence probabilities in North American birds found that the spatial and temporal scales of the maximum effect differed significantly across species, varying with morphological characteristics and life history strategies (Pease 2024). We observed non-linearity in scale dependence across most taxa, with stronger occupancy-richness relationships at regional pools with 500- to 700-km radii (Figure 4). The strong relationship at these intermediate-size regional pools may indicate the scale at which local processes that govern community composition (e.g., behaviour, species interactions, habitat use) give way to continental-scale processes (e.g., environmental and topographic constraints, long-term dispersal). In European pollen cores, the non-linear spatial dependence of the occupancy-richness relationship may explain the differences between the results using all regional pool sizes (50–1000 km) and those using only regional pools smaller than 500 km (Appendix S4). For all other species groups, we observed no difference in the spatial dependence of the occupancy-richness relationship, indicating that the non-linear patterns we observed negligibly affect our results. However, future research should examine these non-linear patterns more thoroughly, perhaps by comparing variance in community composition to variance in these local and continental processes across scales.

4.4 | Temporal Variation in Occupancy-Richness Relationships

The occupancy-richness relationship varied little across the spatial scale and temporal resolution, but for some taxa, we observed substantial variation across time. The datasets with the highest variation were those that had the coarsest temporal resolution (i.e., the least precise temporal units) and the longest temporal span (the foraminifera and pollen datasets). The relative dominance of temporal over spatial variability in foraminifera and pollen corroborates the results of Hodapp et al. (2018), who found temporal variability to be a stronger predictor of differences in site-level richness than spatial heterogeneity. The fluctuations we observed in the occupancy-richness relationship through time were primarily driven by changes in total species richness across all regional pools. In times of high species richness, stronger occupancy-richness relationships dominated. Times of low richness, however, led to a weakening of the occupancy-richness relationship. This weakening pattern corresponded to a relative increase in the number of high-occupancy and widespread species in areas of high species richness. In times of relatively high species richness, increased competition and niche partitioning (D'Andrea et al. 2020) may lead to stronger occupancy-richness relationships. Conversely, in times of low species richness, extirpations of specialist species (which are inherently more vulnerable than generalist ones; Chichorro et al. 2019) may allow for increased colonisation of large-ranged, high-occupancy species through ecological release (Button et al. 2017).

In the North American pollen dataset, we observed a substantial weakening in the relationship between richness and occupancy around 4000 bp, in which species-rich regions had similar mean occupancy to species-poor ones. One potential explanation for this pattern might be an increase in facultative (i.e., non-obligate), mutualistic interactions between individuals or species within a community. If these facultative interactions are sufficiently common, areas with the most species may also contain proportionally more common species, and therefore, the occupancy-richness relationship may be positive. Ecological interactions are often transient and can switch quickly from positive to negative if the ecology of the region changes (Hay et al. 2004). In times of stress, some plant communities may develop more and stronger positive interactions that disappear after the stressor is removed (the stress-gradient hypothesis; Liancourt et al. 2005; Adams et al. 2022). Positive interactions between related species have been observed in many marine, freshwater, and terrestrial plant ecosystems (Tirado et al. 2015; van der Heide et al. 2020), allowing some species to occupy regions they may not have been able to unassisted (Williams et al. 2017; O'Brien et al. 2019; Raath-Krüger et al. 2019). However, a cross-taxon meta-analysis suggests that support for the stress-gradient hypothesis is only observed in certain taxa (Adams et al. 2022). Our results are similarly equivocal: we find weakening occupancy-richness relationships in the North America pollen data around 4000 bp, roughly corresponding to a widespread, long-term drought event (Booth et al. 2005), but step changes in the occupancy-richness relationship were not driven by precipitation or any other climatic factor. As a result, more research must be conducted to examine the effects of mutualisms on the broad-scale community structure.

Even in the absence of extirpation and colonisation, interactions among a group of sympatric taxa are often affected by environmental controls (Tylianakis et al. 2007). For example, the strength of interactions between kelp and sea urchins on the southern California coast is highly influenced by the North Pacific Gyre oscillation (Liu and Gaines 2022). However, we found only weak correspondence between climatic change and change in the occupancy-richness relationship in each dataset. These results suggest that climate change does not directly drive variation in the occupancy-richness relationship. Instead, it may indirectly affect this relationship by influencing the local extirpation and colonisation of taxa (see Antell and Saupe 2021). More research parsing the relative roles of environment and consumer adaptation in driving this pattern will therefore be necessary.

4.5 | Limitations of the Study

The five datasets we used in these analyses each have their own sampling units, methods, and limitations. For example, the foraminifera and pollen cores include substantial space- and time-averaging compared to the modern survey data, as they are collected passively from a catchment or via ocean currents (e.g., van Sebille et al. 2015). Differences in observation methods (e.g., camera trapping vs. point-count observations) between the datasets may also lead to different assumptions about whether a species is present or absent at a given site. By treating datasets as a random effect in our analyses, we account for variation in sampling methods and find a consistently negative occupancy-richness relationship. However, for individual datasets, the strength and scale-dependence of the occupancy-richness relationship likely depend to some extent upon the sampling method. For example, the relatively weak occupancy-relationships in the foraminifera data may be caused by the large spatial footprint of each core (leading to apparent coexistence between taxa that may not have encountered each other). A comprehensive examination of the influence of sampling procedure on patterns of presence, richness, occupancy, and abundance is lacking and needed to identify specific differences and limitations of these methods.

Our analyses show a substantial geographic bias towards temperate areas, especially North America and Europe (Figure 1a). Although long-term (decadal) ecological data has been collected across Central and South America, Africa, and Asia (some examples of which include the work conducted at Barro Colorado Island, the Galapagos Islands, Amazonian BDFFP, Comoé National Park, Amboselli National Park, JaLTER, and Keo Seima Wildlife Sanctuary), this study required a set of at least 50 related ecological time series with a high level of spatial density and a broad extent. Unfortunately, the spatial distributions of many of the most well-sampled biodiversity surveys in these regions were not sufficient to examine patterns of both local and regional occupancy using the methods in this study. Because of this bias, our results may not be fully generalizable across continents and biomes.

The discordance between climatic change and change in the occupancy-richness relationship may be explained by methodological limitations. First, although the climate variables we selected are known to influence the distribution and richness of each taxon, they may not be the ones that influence occupancy at the scale of the regional pools, and it is possible that regional occupancy relates to environmental characteristics on finer spatial and temporal scales than we examine (e.g., microclimate). Changes in the occupancy-richness relationship may also react to climate changes on time lags, which we did not account for here. Finally, humans have affected terrestrial ecosystems on a global scale for tens of thousands of years, via agriculture, land conversion, and direct defaunation (Ellis et al. 2021; Mottl et al. 2021; Pineda-Muñoz et al. 2021; Fricke et al. 2022; Bergman et al. 2023). These anthropogenic effects may be substantially stronger than climatic effects for all species groups except the foraminifera, which we examined on timescales of millions of years. Our research did not directly account for anthropogenic influences on the communities. However, we might expect general decreases in richness and increases in occupancy for regional pools that are in areas more heavily affected by humans (i.e., agricultural or urban areas). Human-caused introductions of invasive species and may additionally lead to weaker occupancy-richness relationships on continental scales, although we did not find a monotonic weakening trend for any species group through time.

4.6 | Summary and Implications

Across our dynamic world, climate, geography, and biological communities constantly change on all spatial scales. These changes often occur in tandem, but understanding when and why they converge or diverge can provide us with greater insights into the maintenance and evolution of Earth systems. Our results indicate that patterns of regional species richness and occupancy consistently oppose each other and that this opposition is robust to spatial and temporal scales. However, changes in biodiversity and community composition through time cause fluctuations in the strength of the relationship between occupancy and richness. As Earth's biodiversity continues to be lost on global scales and communities continue to reorganise because of human-caused invasions and climate tracking, this link may weaken, complicating our ability to predict biogeographical patterns and the scale they operate on into the future.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The occurrence data used in the analyses are available online from the databases described in the Methods. All code and datasets used to conduct the analyses are provided open-access on FigShare: (10.6084/m9.figshare.26433454, https://figshare.com/s/a9096fc8aa5d2ac92133).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.