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Exploring the Spatial Relationship Between Carbon Storage and Biodiversity: A Systematic Review and Meta-Analysis

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ABSTRACT

Climate change and biodiversity loss are severe and intertwined global threats. Land-based efforts to address both require an understanding of the spatial relationships between carbon storage and biodiversity. Here, we present a systematic review and meta-analysis of the strength of these spatial relationships across the literature. We synthesize the estimated spatial correlations and infer how different factors (spatial scale, metrics, biome, human pressure) impact these strengths using linear mixed-effect models. Our results show that spatial scale is a significant factor, and the combination of metrics used to express carbon storage and biodiversity plays a more important role. While relationships are moderately positive across all conditions, the strength of the relationships decreases significantly from global to local scales. We find large variations in the strength for different metrics, across different biomes, and in the presence or absence of human pressure. We find a stronger relationship in natural rather than human-dominated landscapes for temperate forests, grasslands, and deserts, but the opposite for tropical and subtropical forests. Ecosystem-level biodiversity proxies (habitat quality) show strong relationships to the total carbon pool, while taxonomic metrics (species richness) show a weaker relationship. The largest negative relationship is between total carbon and flora and fauna species richness. Our results suggest different synergies for different dimensions of carbon storage and biodiversity and shed light on where further effort is needed.

1 | Introduction

Climate change and biodiversity loss are deeply intertwined, sharing common drivers that can amplify one another (Mori 2020). Substantial anthropogenic land impacts have driven climate change, with land-use change alone accounting for over 14% of total carbon emissions between 2009 and 2019 (Allan et al. 2017; Friedlingstein et al. 2020). Land use has also been the main driver of terrestrial biodiversity decline (Bongaarts 2019; Newbold et al. 2016). Habitat loss, degradation, and fragmentation, along with human-induced climate change, jointly contribute to unprecedented levels of modern extinction estimated to be a hundred times higher than the background rate over the last century (Ceballos et al. 2015; Kremen and Merenlender 2018). Climate change is playing an increasing role in biodiversity loss and is estimated to overtake land-use change to become the greatest threat to biodiversity by 2070 (Newbold 2018). Meanwhile, biodiversity loss has been causing a rapid deterioration in ecosystem functioning, which is, in turn, affecting carbon cycles and impeding our effort to stabilize emissions (Díaz et al. 2019; Leclère et al. 2020; Mace et al. 2018).

Urgent and coordinated land-based action is required to limit overall temperature rise while simultaneously halting biodiversity loss (Dinerstein et al. 2020; Pörtner et al. 2021; Thomas et al. 2013). However, climate and biodiversity targets are

generally treated separately, and their outcomes may not always be aligned (Beaudrot et al. 2016; Paoli et al. 2010; Potts et al. 2013; Sabatini et al. 2019). There are concerns about how well nature-based solutions (NbS), such as REDD+ and natural climate solutions more generally, address biodiversity issues (Gardner et al. 2012; Seddon et al. 2019; Smith et al. 2022). Though protecting areas with large carbon stocks will directly protect biodiversity within the conservation region, there may be an underappreciation of high-biodiversity but low-carbon areas at a high risk of habitat conversion and biodiversity loss. It is important to avoid such direct "bio-perversity" in carbon sink conservation (Lindenmayer et al. 2012). Given the evidence that biodiversity collapse and ecosystem destruction can amplify climate risks (Mori 2020), comanagement should be grounded in an understanding of the spatial relationship between carbon storage and biodiversity.

Spatial correlation analysis is an important approach for quantifying spatial relationships (Cord et al. 2017). It helps reveal the underlying causation behind relationships and indicates the magnitude and direction of synergies/trade-offs across spatial scales (Schober et al. 2018; Vallet et al. 2018). Specifically, a positive and strong relationship suggests that a biodiversity and climate target could simultaneously benefit one another, and a negative one implies trade-offs. This method has been widely used to examine the association between carbon stocks and biodiversity, mainly based on two types of datasets: plot data and distribution data. Plot-based correlation studies (Beaudrot et al. 2016; de Lima et al. 2013; Flores-Rios et al. 2020; Sullivan et al. 2017) provide valuable ecological insights into the site-level mechanisms underlying the relationships but are limited in revealing wider spatial relationships (van der Sande et al. 2017). In parallel, the rapid development of earth observation technologies and breakthroughs in spatial modeling has led to increasing interest in quantifying carbon–biodiversity relationships using distribution data (Armenteras et al. 2015; Di Marco et al. 2018; Lecina-Diaz et al. 2018; Murray et al. 2015; Strassburg et al. 2010). Such distribution-based correlations, albeit the results of modeling studies, can inform opportunities for aligning carbon and biodiversity objectives at the large scale (Ricketts et al. 2016; Strassburg et al. 2012; van der Sande et al. 2017; Visseren-Hamakers et al. 2012).

As yet, the scientific evidence for distribution-based carbon–biodiversity relationships is scattered and mixed in terms of study contexts and results, limiting the comprehensive understanding of their interactions as well as the ability to deliver co-benefits. Synthesizing the available knowledge across broad literature is urgently needed but challenging, as the relationships are likely to be mediated by a wide variety of factors. However, investigating the main factors and quantifying their impacts on carbon–biodiversity relationships can serve as a starting point. Positive correlations at the global scale are not always seen at the national or subnational scale (Paoli et al. 2010; Sollmann et al. 2017; Visseren-Hamakers et al. 2012), and there is some evidence suggesting that the spatial extent of the study area influences relationships (Armenteras et al. 2015; Di Marco et al. 2018; Roces-Diaz et al. 2018). There is also evidence that the choice of different metrics for carbon and biodiversity can impact relationships (Egoh et al. 2009; Locatelli et al. 2014; Strassburg et al. 2010). Nevertheless, it is still unclear which factor is more important in determining the relationship: the spatial scale or the metrics used and how much the variations are across different conditions. From a local perspective, different relationships have been found for Mediterranean forests and boreal forests with the same carbon and biodiversity metrics (Lecina-Diaz et al. 2018). As earth's natural communities vary by biome (Olson et al. 2001) and human activities have clear impacts on local biodiversity and ecosystem services (Newbold et al. 2015; Vačkář et al. 2016), local relationships can also result from differences in the local biota and the intensity of human pressure (Osuri et al. 2020). Yet, we also lack knowledge of the biome-specific relationships and potential influences of human impacts thereon.

In this study, we explored how main study factors may influence the spatial relationship between ecosystem carbon storage and biodiversity using a systematic review and meta-analysis. We aimed to summarize carbon–biodiversity correlations across studies and to explore how factors (spatial scale, metrics, local biome, human pressure) and their interactions impact the strength of the relationships using linear mixed-effect models. We reflected on our main findings and important areas for future investigation.

2 | Methods

2.1 | Literature Search

We followed the PRISMA protocol for systematic reviews and meta-analyses (Moher et al. 2009, 2019; Siddaway et al. 2019). The literature search was conducted via the Web of Science in September 2022. We included synonyms and related concepts of spatial relationships in the search terms (e.g., spatial correlation, spatial congruence, spatial concordance, spatial coincidence, and spatial association). Similarly, we used "biological diversity" and "species" as synonyms and related concepts of biodiversity, and widely used concepts for carbon storage (e.g., "carbon stock," "carbon sequestration," and "carbon density"). With no time limitation, the search returned 504 papers (see Table S1 for the full search protocol).

We first filtered the literature based on three criteria: (1) the article includes a spatial assessment of carbon and biodiversity; (2) the article reports a correlation of the carbon–biodiversity relationship; (3) the paper is peer-reviewed, and the study area is nonurban (given the high heterogeneity and small area of urban studies). After the screening, 37 papers were identified (32 from the initial list and 5 after snowball sampling). To ensure that relationships are comparable, we included papers reporting Pearson's or Spearman's rank correlation. Articles reporting correlations only based on intentional selection were not included. For example, Vijay et al. (2022), Izquierdo and Clark (2012), and Chan et al. (2006) were excluded, as correlations are reported only for the noncontiguous areas selected by return on investment criteria or hotspot prioritization. We also considered temporal differences. Papers obtaining correlations based only on potential maps of future scenarios were excluded (e.g., Reside et al. 2017), whereas Carvalho-Santos et al. (2016) was kept, as they reported three correlations, one of which is based on contemporary data. Overall, 7 papers were excluded during

eligibility checking, and 30 papers, published between 2009 and 2020, were finally included in this review (see Figure 1 for an overview of the searching, screening, and eligibility checks, Table S2 for the final selected paper list).

2.2 | Data Processing

We collected correlation coefficients across studies and extracted all relevant information, such as the metrics used to characterize carbon storage and biodiversity. Some studies present more than one relationship, as they cover multiple research areas or target one study area but report both the overall relationship for the whole area and multiple relationships for regions within that area. Some studies obtain multiple relationships by adopting different pairs of metrics or present different relationships at different spatial resolutions. In those cases, we included all the reported results and treated each relationship as a separate record while tracking where that record came from. Statistically insignificant relationships were included if the authors provided the correlation coefficients.

We analyzed spatial relationships at two scales: global and local. We merged non-global relationships into "local" throughout our analyses. We accounted for the different metrics used to characterize carbon storage and biodiversity. To ensure a sufficient sample size for each metric category (at least 5, based on McNeish and Stapleton 2016), we included commonly used metrics and grouped them into categories with meaningful ecological distinctions. Given that studies considered different compartments of the total carbon in an ecosystem (e.g., vegetation stocks or soil stocks or both), and soil carbon is generally not spatially congruent with vegetation carbon (Soto-Navarro et al. 2020), we divided carbon metrics into three main categories: vegetation, soil, and vegetation and soil. For vegetation carbon, we did not distinguish between above-ground and below-ground biomass carbon, as the latter is often inferred from the former with a specific "root-to-shoot" ratio at the same location (Mokany et al. 2006). We did not account for the depth of soil organic carbon due to insufficient samples. For instance, Murray et al. (2015) reported relationships for two different depths (100 and 30 cm); we treated them equally and categorized them only by the main carbon metric classification. As the concepts of carbon storage and carbon sequestration are often used loosely in reporting correlations, we did not separate them in our statistical modeling.

Species assemblages and habitat types vary substantially from place to place, as do biodiversity metrics in the reviewed literature. Habitat quality (HQ) is an ecosystem-level measure and accounts for both habitat suitability and anthropogenic threats to the habitat (Terrado et al. 2016). We included it based on the general evidence that biodiversity is higher in locations with higher HQ (Poniatowski et al. 2018; Thomas et al. 2011). We also included species richness (SR) as a biodiversity metric,

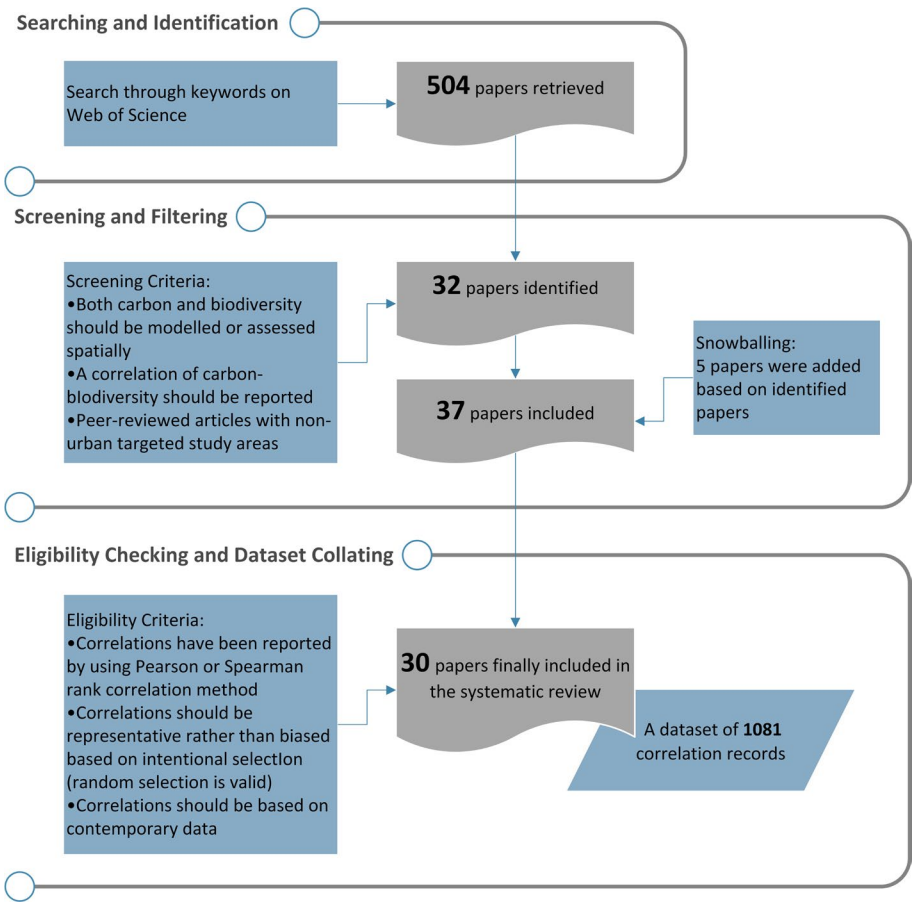

FIGURE 1 | Literature search flow chart. Blue rectangles represent the search processes and filtering criteria. Gray documents denote the identified papers after each step, and the blue parallelogram shows the final dataset. [Colour figure can be viewed at wileyonlinelibrary.com]

which is very common in the literature. Considering the literature's non-standardized taxonomic coverage of SR metrics, we aggregated SR metrics using general taxonomic differences (flora, fauna, or flora and fauna). Although this classification may obscure some details (e.g., SR-fauna does not differentiate the SR of vertebrates from that of invertebrates), it provides increased resolution beyond ecosystem-level metrics while keeping sufficient observations per category. Overall, we distinguished four biodiversity metrics: habitat quality (HQ), flora species richness (SR-flora), fauna species richness (SR-fauna), and flora and fauna species richness (SR-flora & fauna).

We classified the local relationships by biome and human pressure. Biomes are large areas characterized by a similar climate, flora, and fauna and can span multiple continents. They were taken from World Wildlife Fund definitions that divide the world into 14 biomes (Olson et al. 2001) (see Table S4 for classifications). When the study area (non-global study) contains more than one biome type, the biome covering the largest area was used to represent the local biome type of this relationship. Human pressure was categorized into human-dominated landscapes (HDL) and nonhuman-dominated, natural landscapes (NDL). One study (Di Marco et al. 2018) with a large number of results reported ecoregions in its results, so to include this information in our work, we first overlaid the human footprint map of 2009 (Venter et al. 2018) with terrestrial ecoregions (Olson et al. 2001) and calculated the average human footprint value for each ecoregion. We then defined the ecoregions of an average human footprint value ≤ 2 as NDL and others as HDL (following Venter et al. 2016). For other relationships for which we were generally unable to obtain the accurate spatial boundary of the study area, we qualitatively determined human pressure by its local land use. Relationships derived from study areas dominated by anthropogenic land use (e.g., agriculture, forestry, build-up areas) were grouped into HDL, while those from more natural regions (e.g., protected areas, conservation regions, reserve areas) were defined as NDL.

Overall, our quantitative synthesis comprises a dataset of 1081 correlation records (see Table S3 for the full dataset). It is worth noting that Di Marco et al. (2018) contribute 875 relationship records, which account for 81% of our dataset. As such, we perform our modeling twice, with Di Marco et al. (2018) included and excluded, to ensure that our findings are robust to this large contribution. We report findings for the total dataset.

2.3 | Linear Mixed-Effect Modeling

To account for multiple observations from the same individual study, we applied mixed-effect modeling to infer the impacts of factors on carbon–biodiversity relationships while explicitly accounting for the nonindependence in our data (Harrison et al. 2018; Zuur et al. 2009). The correlation coefficients are the response variable in our models. For global and local correlations, there are three categorical predictor variables, each with multiple levels: spatial scale (global, local), carbon metric (vegetation, soil, vegetation and soil), and biodiversity metric (HQ, SR-flora, SR-fauna, SR-flora & fauna). There are two additional factors for local correlations: biome type (7 biome types) and human pressure (HDL, NDL). As this information is not available for global correlations, we built two models: one for the overall dataset with three factors (spatial scale, carbon metric, and biodiversity metric) and one for the local dataset with four factors (biome type, human pressure, carbon metric, and biodiversity metric). As our dataset is normally distributed (see Data S2 for more details, Tables S12 and S13) we used linear mixed-effect models throughout our inferential analysis.

As we have unbalanced data, we simplified the random effect structure in our models by considering only the random intercepts of studies. That is, we assume study means can vary, but all studies have a common slope for the fixed effects in our investigation. We tested the dependence among studies by Intra-Class Correlation (Kreft and de Leeuw 1998) and confirmed that a random effect of studies is present in our data. For the fixed effect structure selection, we made a compromise between model fit and model complexity. We started with the simplest model, including only one main effect, and added more main effects and two-way interactions until we considered every possible combination of factors. To capture the most influential interaction (if there was one) and reduce the risk of multicollinearity among model variables, we followed the principle that in one single model structure, if one factor was already involved in one interaction term, it was not to be added to another interaction. For model comparisons, we held the random effects term constant and used maximum likelihood estimation to select the best model structures based on the lowest Akaike information criterion (AIC). We assessed the multicollinearity among categorical variables by using Generalized Variance Inflation Factors (Fox and Monette 1992) and did not detect multicollinearity in our best models (Table S15). Following the protocol suggested by Zuur et al. (2009), we refitted the selected best two models (for both the overall model and the local model) using the restricted maximum likelihood method to predict model parameters and carried out variance analyses. This results in unbiased estimates of the variance. We made post hoc comparison tests (p-value adjusted by Tukey) based on the best models to identify significant differences among levels in each factor (or interaction).

To account for the uncertainty in the estimation of each correlation from primary studies and to assess the robustness of our models, we conducted an additional sensitivity analysis. As direct measurements of uncertainty (e.g., standard error, standard deviation, or confidence interval) were missing from most primary studies, we collected the number of observations (n) the primary studies used to calculate correlation coefficients as a proxy of uncertainty. This proxy assumes that the larger the number of observations, the lower the uncertainty in the estimate, and we used the square root of n as weight in our linear mixed-effect models. We assessed model robustness by comparing non-weighted and weighted results. In the weighted models, we excluded 31 correlation records that did not report the number of observations and for which we were unable to estimate the number of observations. Our sensitivity analysis shows that the two best models (the best overall model and best local model) and our findings remain the same, demonstrating the high robustness of our conclusions (see Tables S7–S11 and Table S17 for detailed results

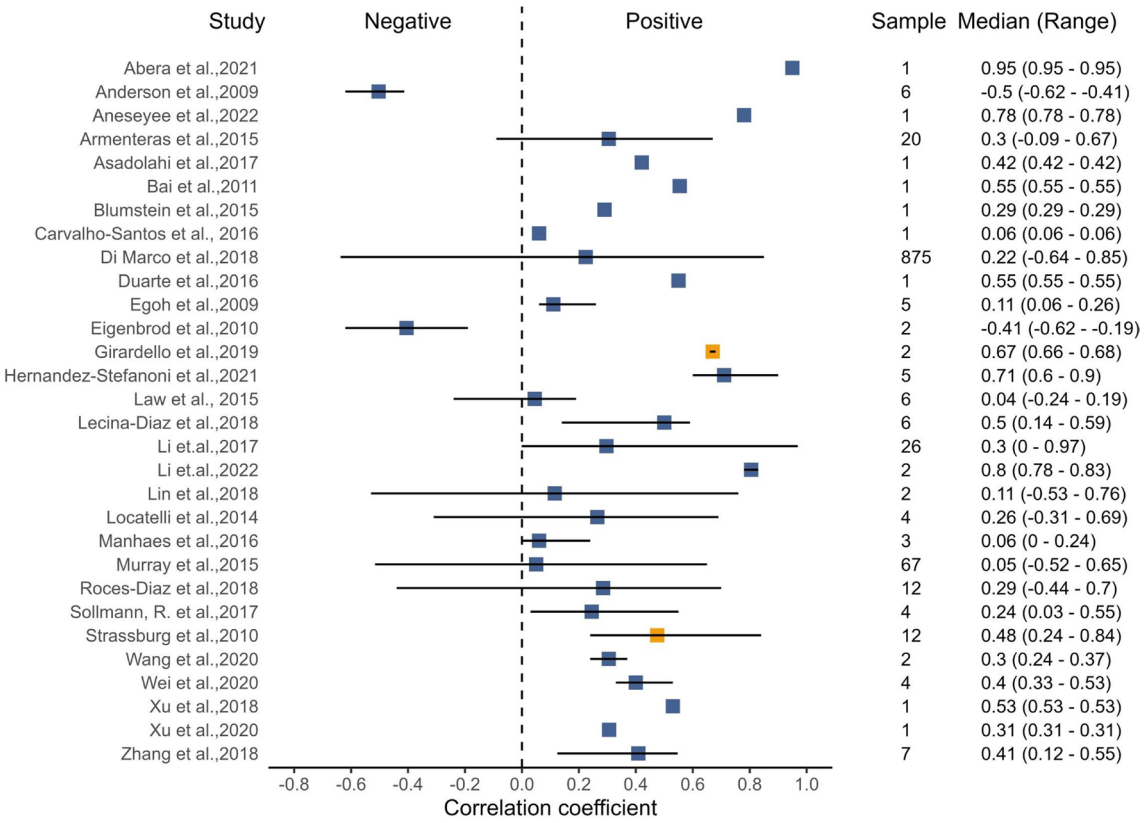

FIGURE 2 | Forest plot of relationships reported in included studies. The lines represent the ranges of the correlation coefficients reported in each study. Blue squares mark the median values of correlation coefficients from non-global studies, and orange squares show median values from global assessments. [Colour figure can be viewed at wileyonlinelibrary.com]

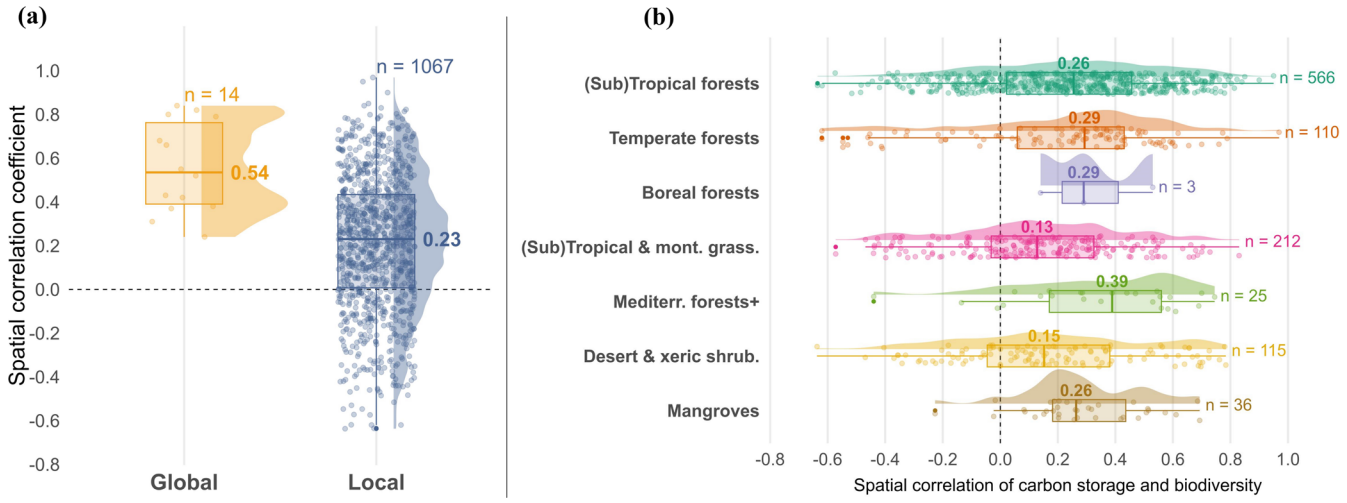

FIGURE 3 | Carbon–biodiversity relationship across global and local scales (a) and across biomes (b). The half-violins outline the distribution of each group. The boxes represent the range from the first to the third quartile of each group, and the horizontal lines within show the group median. Dots with different colors represent correlation samples collected based on the classifications. Annotation texts (n=) show the sample size of each group. [Colour figure can be viewed at wileyonlinelibrary.com]

for weighted models). Given that we can include more studies when not using weighted models, with larger geographic scope, we reported results based on the original full dataset (the non-weighted models) in the main text.

We conducted all the analysis in R version 4.3.3. The best-fit distribution for our data was selected by using the fitdistrplus package in R (Delignette-muller and Dutang 2015). We used the lme4, lmerTest, jtools, and effectsize packages (Bates et al. 2015, 2022; Ben-Shachar et al. 2020; Kuznetsova et al. 2022; Long 2022) for model fitting, selection, variance decomposition, and parameter estimation (see Data S2 for detailed statistical modeling). We used the car package (Fox and Weisberg 2019) for assessing multicollinearity, the emmeans package (Lenth 2022) for

multiplecomparisons, and the ggplot2 package (Hadley 2016) for data plotting.

3 | Results

Along with two global studies, 28 local studies have been conducted in 23 countries across six continents (Figure S1). The reported relationships vary considerably within and among studies, in both direction and magnitude (Figure 2). The global assessments (Girardello et al. 2019; Strassburg et al. 2010) present uniformly positive relationships, while local studies report diverse relationships. The median correlation coefficients from each individual study are all positive except for two nationwide studies in the UK (Anderson et al. 2009; Eigenbrod et al. 2010). In total, 24% of correlations in our dataset are negative, of which 95% are significant.

3.1 | Global and Local Difference

Global correlations present a higher median value (+0.54) and smaller variation (SD = 0.21), while local correlations show a substantially lower median value (+0.23) and larger standard deviation (SD = 0.31, Figure 3a). Negative correlations were only found in some local studies. When the original studies subdivided a larger study area, only a few of the subunits presented negative relationships (Armenteras et al. 2015; Di Marco et al. 2018; Li et al. 2017).

When considering the random effect of primary studies, our overall baseline model (intercept-only) shows that, on average and across all systems, there is a moderate positive correlation of 0.30 (SE = 0.06, p-value << 0.01, Table S14). The best model for our overall dataset includes spatial scale and the interaction term of metrics. As we described above, the study of Di Marco et al. (2018) contributes over 80% of the correlations. Therefore, we tested its impact on our modeling. The best models were shown to be robust when removing all the data points from this study (see details in Tables S7 and S8).

Decomposition of the variance based on our best overall model shows that the spatial scale significantly impacts correlations (F-value = 5.84, p-value = 0.03, Table S16). Specifically, when holding the metric type constant, correlations at the local scale are significantly lower than those at the global scale by 0.38 (p-value << 0.01, Table S9).

3.2 | Biome Differences

When examining local relationships within the seven biome types, relationships within each biome are still mixed (SD = 0.20–0.34, Figure 3b, Table S5), but median correlations are all positive. More than half of the correlations in our local dataset are from tropical and subtropical forests, reflecting the high level of research interest. In contrast, we see very limited (only three data points) relationships reported for boreal forests. Mediterranean forests show the highest median correlation (+0.39), and boreal forests present the smallest variation (SD = 0.20), both with a relatively smaller sample size. Tropical and subtropical forests, temperate forests, and mangroves show similar median correlations (+0.26 to +0.29), while temperate forests represent considerably larger variation (SD = 0.34). Grasslands show the lowest median correlation (+0.13), lower than deserts and xeric shrublands (+0.15).

3.3 | Impact of the Metric Used

The most frequently used carbon metric is vegetation carbon (n = 977), with a median correlation of +0.25 and the smallest variance (SD = 0.30). A small proportion of relationships (n = 8) are with soil carbon only. The soil metric shows the highest variation (SD = 0.45), with the highest median of +0.32. The remaining relationships (n = 96) use the total mass of carbon in vegetation and soil and yield the lowest median of 0.11 and a moderate standard deviation (SD = 0.34).

Over 92% of the relationships are based on animal species richness (SR-fauna, n = 997), while roughly 2% target woody plants (SR-flora, n = 21), and another 2% consider both animal and woody species (SR-flora & fauna, n = 22). Different taxonomic coverage results in different medians and variances. The lowest median and largest variance can be observed for relationships using SR-flora & fauna as a biodiversity proxy (median = −0.15, SD = 0.33). Nonetheless, SR-fauna (median = 0.23, SD = 0.30) and SR-flora (median = 0.28, SD = 0.32) alone represent substantially higher positive medians. Roughly 4% of relationships are based on HQ, and these have the highest median value (+0.34) with the smallest variance (SD = 0.29). Weaker and sometimes even negative correlations appear when focussing on a subset of species of special interest, such as threatened or endemic species. This also applies to the two UK studies reporting only negative relationships; they focus on target species in the UK Biodiversity Action Plan scheme or "species of conservation concern."

Among all metric pairs (Figure 4, Table S6), vegetation carbon and SR-fauna are the most frequently used combination (n = 929, median = 0.24) (both when including and excluding Di Marco et al. 2018). The soil and SR-fauna pair show the highest median correlation (+0.69), yet with the largest variation (SD = 0.47). The vegetation and soil carbon and HQ pair express a similar

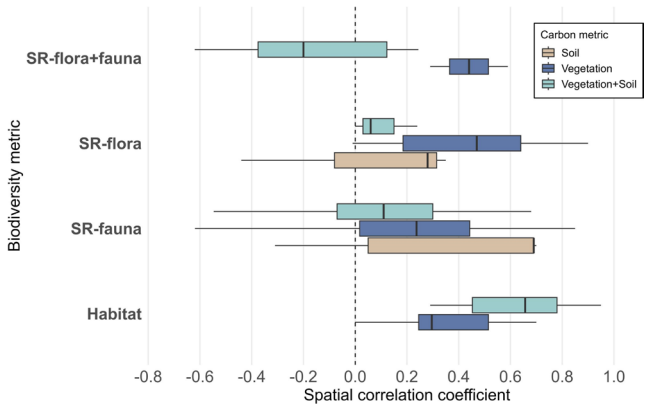

FIGURE 4 | Carbon–biodiversity relationship under different metric combinations. The boxes represent the range from the first to the third quartile of each group. The vertical lines in the boxes show the median of each group. [Colour figure can be viewed at wileyonlinelibrary.com]

high median value (+0.66) while having a much smaller variation (SD = 0.22). The only negative median correlation (−0.2) is the linkage between vegetation and soil carbon and SR-flora & fauna. The two UK studies reporting only negative relationships also used the metric pair. The most stable relationship is from vegetation and soil carbon and SR-flora (SD = 0.12). For all SR measures, a consistent pattern can be observed that vegetation carbon presents a higher median correlation than vegetation and soil carbon. However, this is not the case for the habitat metric.

Our overall model indicates that the metric used significantly influences correlations (F-value = 4.47, p-value << 0.01, Table S16). Effect sizes measured by partial eta-squared for the spatial scale and metric type are 0.28 (95% CI: 0.02–1.00) and 0.37 (95% CI: 0.16–1.00), respectively. That is, the metric combination is more influential than the spatial scale. Multiple comparison tests based on our two best models (the best overall model and the best local model) together show that the correlations between total carbon storage and HQ are significantly higher than those with SR-fauna and SR-flora & fauna (Table S10). That is, with the total carbon pool, the ecosystem-level metric (HQ) generates considerably stronger relationships than taxonomic metrics (SR). We also find that correlations between vegetation carbon alone and SR-fauna and SR-flora are significantly higher than correlations between the total carbon pool and SR-flora & fauna (Table S10).

3.4 | Local System and Human Impact

For local relationships only, the best model includes the interaction term of biome and human pressure and the interaction term of metrics. Our analysis shows that the metric choice is still a predominant factor in local systems (F-value = 4.52, p-value << 0.01, partial effect size = 0.34, Table S16). Despite a smaller effect size, the interaction term of biome and human pressure also significantly affects local relationships (F-value = 8.41, p-value << 0.01, partial effect size = 0.16, Table S16). Among the four biomes with relationships in both HDL and NDL, we find an inconsistent trend in terms of median correlation difference (Figure 5). We see higher median relationships in NDL than in HDL for temperate forests, grasslands, and deserts, whereas the opposite pattern occurs in tropical and subtropical forests. Our post hoc test based on the best local model (with Di Marco et al. 2018 included) shows that, in tropical and subtropical forests, relationships for NDL and HDL are significantly different, with HDL 0.29 (p-value << 0.01) higher than NDL (see Table S11 for more details).

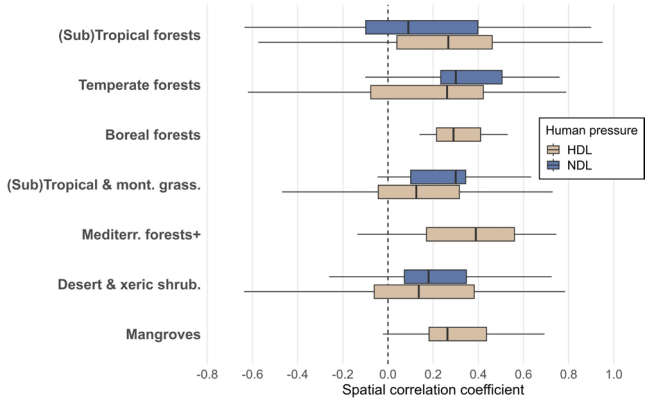

FIGURE 5 | Relationship between carbon storage and biodiversity under combinations of different biomes and levels of human pressure. The boxes represent the range from the first to the third quartile of each group. The vertical lines in the boxes show the median correlations of each group. [Colour figure can be viewed at wileyonlinelibrary.com]

4 | Discussion

By conducting a systematic review of carbon–biodiversity relationships, we find that global relationships are uniformly positive, while local relationships can be negative and have a larger variation. Negative relationships occur in smaller study areas, for specific combinations of metrics, and for a small group of species. Relationships within each biome are still mixed, but the median correlations are all positive.

4.1 | Spatial Scale as a Significant Factor

Our finding that there is a significant impact of spatial scale on correlations is in line with the increasing recognition of the spatial dependence between biodiversity and ecosystem services/functioning, including carbon storage (Cardinale et al. 2012; Ricketts et al. 2016; Thompson et al. 2018). Although others have suggested that spatial scale is an important factor in determining carbon–biodiversity correlations (Di Marco et al. 2018; Roces-Diaz et al. 2018), their conclusions are limited to their specific study. Our study moves beyond the current literature by generalizing conclusions via a meta-analysis, accounting for both the within-study and between-study variations. This spatial-scale effect is partly explained by the differences in the ecological processes driving the biodiversity–carbon relationship at different scales. There is a positive relationship between productivity and terrestrial carbon stored across scales (Field et al. 2009; Steffen et al. 1998), at least up to a certain level of productivity (Keeling and Phillips 2007). In contrast, the biodiversity–productivity relationship varies between conditions even though it tends to follow a unimodal (hump-backed) curve (Graham and Duda 2011). In addition, empirical evidence shows that scale consistently impacts the SR–productivity relationship (Graham and Duda 2011). For larger spatial scales, Chase and Leibold (2002) found that greater species diversity was associated with higher productivity, while Field et al. (2009) found that productivity shows a higher correlation with SR than other variables they tested, particularly for connected (i.e., non-insular) terrestrial habitats. In combination, these ecological patterns may explain the lower strength of the carbon–biodiversity relationship at a local scale. Another explanation could also be purely statistical, as a smaller study area implies a smaller range of sampled values, which makes it more difficult to detect a relationship (Bland and Altman 2011).

4.2 | Difference Between Global and Local Correlations

The grand mean of carbon–biodiversity correlations from the overall modeling is moderately positive (+0.3, SE = 0.06, p-value << 0.01), indicating a general opportunity for addressing

both issues simultaneously across all conditions. However, the significantly higher global relationships than local ones could mislead both global and local policymakers. Global analyses can inform worldwide prioritization and targets, but they may not accurately reflect local conditions. Local policymakers should be aware of local heterogeneities to better identify potential trade-offs. When linking the same aspects of carbon storage and biodiversity, local correlations were 0.38 (p-value = 0.03) lower than the global results. This gap is large enough to reverse strong global relationships to weak or even negative associations in the local context, suggesting that the local scale implies a lower probability of achieving synergies between carbon and biodiversity targets than the global picture. Although time-intensive for policymakers, this emphasizes the need to carry out location-specific and biome-specific analyses to inform local policies or to consider the estimated differences here to extrapolate local relationships from global analyses if local studies are not readily available.

4.3 | Importance of Considering the Biodiversity Metric

The importance of biodiversity metrics on the relationships highlights different interactions that may exist for different aspects of biodiversity and carbon storage. Biodiversity is multidimensional in nature, primarily composed of three aspects (taxonomic, structural, and functional diversity) and has different scales, from genes, populations, species, and communities to ecosystems (Lyashevska and Farnsworth 2012). Ideally, metrics should capture this complexity. In practice, the most widely used metrics in our review are SR and HQ. We find that the ecosystem-level metric (HQ) shows stronger correlations with the total carbon pool, while taxonomic metrics correlate weakly. This suggests that a taxonomic perspective alone may not be able to capture all influences of an ecosystem on carbon storage, while HQ captures more of those characteristics. In addition, we find that SR data often focus on narrower taxonomic categories, such as woody plants and vertebrates, overlooking other important categories, such as invertebrates and soil biodiversity (Oberprieler et al. 2019). These taxonomic biases in SR and potential observation biases in natural areas could misrepresent overall biodiversity impacts (Cardoso et al. 2012).

4.4 | Different Biodiversity Impacts for Different Carbon Pools

Our modeling results show that correlations with the total carbon pool (vegetation and soil) can be considerably different from the ones with vegetation carbon alone (e.g., when comparing the total carbon pool to vegetation carbon alone for SR-flora & fauna, although the difference is not significant due to a small sample size). The predictive power (i.e., the correlation coefficient) of the total carbon pool is lower than that of the vegetation pool alone (and to some extent, the same applies to patterns for the species richness of flora). These findings suggest that vegetation and soil carbon are likely to have different impacts on biodiversity, which could be due to the spatial incongruence (Cameron et al. 2019; Guerra et al. 2022; Soto-Navarro et al. 2020) and temporal asynchrony (Hong et al. 2023) in the development and effects of the two carbon pools. Soil carbon pools may also be related to a different component of biodiversity than vegetation carbon, with concomitant different correlation coefficients. Although soil carbon is the largest terrestrial carbon reservoir, holding about three times as much carbon as vegetation (Friedlingstein et al. 2020), correlations with soil carbon alone account for less than 1% of the data points in the dataset used here and demonstrate a larger variation in values compared to vegetation carbon. We find that the soil and SR-fauna pair shows the highest median correlation (+0.69), but we fail to obtain statistical evidence for its significant difference. We cannot say whether it is because of the small sample size or whether it indeed implies an inherently stronger relationship than other linkages. More work targeting soil carbon is needed to understand the differences in correlations between the two carbon pools with biodiversity metrics.

4.5 | Local Relationships and Human Impacts

More attention on some biomes across the world is necessary to understand local relationships and human impacts on them. While tropical and subtropical forests are global hotspots of carbon storage and biodiversity (Sullivan et al. 2017) and have long attracted particular attention, our synthesis shows they do not always express exceptionally high positive relationships. We see less attention on boreal forests (only three data points in our dataset), a biome that contains more than 30% of global forest carbon stocks and faces faster-rising temperatures than average (Bradshaw and Warkentin 2015; Pan et al. 2011). More evidence is also needed for assessing human impacts on carbon–biodiversity relationships in different biomes. For temperate forests, grasslands, and deserts, higher correlations in NDL than in HDL imply adverse consequences of human activities on the inherent carbon–biodiversity relationships. But this is not the case for tropical and subtropical forests. This inconsistency might be partly due to a biodiversity data bias for NDL in tropical and subtropical forests. Those natural forests tend to be inaccessible for scientific studies and species observations. Yet, more evidence is still needed to explore the human impact on biome-specific relationships.

4.6 | Limitations

There are several limitations of this study. First, we formulated our exclusion criteria for primary studies such as to minimize the chance of selection bias, but we cannot fully prevent it. For instance, species abundance was not included as a biodiversity metric due to insufficient sample size. Since species abundance may have effects on carbon storage (Conti and Díaz 2013), and species abundance can be assumed to be more sensitive than SR, as changes in the number of individuals are a prerequisite for changes in the presence or absence of species, not including it might underestimate the strength of the relationship. Second, our study might not be able to cover all potentially relevant factors mediating these relationships. For example, climate will impact the relationship at a large scale (Fei et al. 2018), while general ecosystem disturbances could impact local relationships (i.e., human disturbances, as broadly already considered, but also natural disturbances).

Thirdly, the categorization of metrics is likely to introduce some uncertainty. For example, we did not distinguish carbon sequestration from carbon stocks, and above-ground carbon from below-ground carbon. Similarly, we did not distinguish invertebrates from vertebrates, and general species from threatened/endemic species. Since more broadly defined biodiversity may have a stronger ecological connection with carbon storage, targeting a subset of species, such as species of high conservation importance, increases the likelihood of obtaining weaker or even negative relationships.

There are also uncertainties surrounding the human impact, given we were only able to use a two-level categorical variable based on local land use. We recommend that correlation studies also report detailed spatial data for the locations, which would enable future meta-analyses to include greater detail on the impact of human pressures. Moreover, we simplified the random effect structure of our models by considering only the random intercepts of studies. Increased size of datasets (particularly the coverage of observations for different metric combinations) would allow researchers to reduce this uncertainty.

Our results are also unavoidably influenced by the inherent uncertainties in the included primary studies (e.g., measurement uncertainty in biodiversity or carbon storage, which could cause noise and thus reduce the correlation coefficients). The potential publication bias of these studies could have influenced our results, given that studies reporting non-significant correlations may not be published, and for any given sample size, the result is more likely to be statistically significant if the correlation (effect size in general) is larger (Borenstein et al. 2009). This tendency means the resulting correlation mean from our models is potentially higher than in reality.

5 | Conclusions

The interdependence of climate and biodiversity strategies requires a holistic land-based comanagement, in which the spatial relationship between carbon storage and biodiversity is essential to the magnitude of potential synergies. Through a systematic literature review and meta-analysis on spatial correlations, we enhance the understanding of the multifaceted relationships across different conditions. We find that the choice of metric consistently plays a predominant role in defining the strength of global and local relationships, which highlights different levels of synergies that may exist for different aspects of carbon storage and biodiversity. We also find biome and human pressure jointly affect local relationships, but the human impacts are not consistent across biomes. Negative relationships happen in smaller study areas, for specific combinations of metrics, and for a small group of species. Our results suggest a lower probability of achieving synergies between carbon and biodiversity targets at the local scale than the global picture. Nonetheless, with a better global representation of relevant biomes and assessments on the role of soil carbon, human impacts, and broad biodiversity metrics, opportunities for creating local synergies in carbon storage and biodiversity conservation may be optimized.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article. The research code is available in Zenodo (DOI: https://doi.org/10.5281/zenodo.14870192).

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Supporting Information

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