



The relationships between biotic uniqueness and abiotic uniqueness are context dependent across drainage basins worldwide

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Abstract

Context Global change, including land-use change and habitat degradation, has led to a decline in biodiversity, more so in freshwater than in terrestrial

ecosystems. However, the research on freshwaters lags behind terrestrial and marine studies, highlighting the need for innovative approaches to comprehend freshwater biodiversity.

Objectives We investigated patterns in the relationships between biotic uniqueness and abiotic environmental uniqueness in drainage basins worldwide.

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Methods We compiled high-quality data on aquatic insects (mayflies, stoneflies, and caddisflies at genus-level) from 42 drainage basins spanning four continents. Within each basin we calculated biotic uniqueness (local contribution to beta diversity, LCBD) of aquatic insect assemblages, and four types of abiotic uniqueness (local contribution to environmental heterogeneity, LCEH), categorized into upstream land cover, chemical soil properties, stream site landscape

position, and climate. A mixed-effects meta-regression was performed across basins to examine variations in the strength of the LCBD-LCEH relationship in terms of latitude, human footprint, and major continental regions (the Americas versus Eurasia).

Results On average, relationships between LCBD and LCEH were weak. However, the strength and direction of the relationship varied among the drainage basins. Latitude, human footprint index, or

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continental location did not explain significant variation in the strength of the LCBD-LCEH relationship. **Conclusions** We detected strong context dependence in the LCBD-LCEH relationship across the drainage basins. Varying environmental conditions and gradient lengths across drainage basins, land-use change, historical contingencies, and stochastic factors may explain these findings. This context dependence underscores the need for basin-specific

management practices to protect the biodiversity of riverine systems.

Keywords Context dependence · Biodiversity · Ecological uniqueness · Environmental uniqueness · Freshwaters · Streams · Aquatic insects

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Introduction

Global change has had major impacts on biodiversity in different ecosystem types and at multiple spatial scales (Butchart et al. 2010; Ceballos et al. 2017). For example, land-use change along with increasing demands on natural resources have induced habitat destruction, degradation, and fragmentation which, in turn, have accelerated biodiversity loss especially in freshwater ecosystems (Reid et al. 2019; Maasri et al. 2022). Freshwaters provide pivotal ecosystem services and support a considerable amount of Earth's biodiversity, despite their relatively small areal coverage (Strayer & Dudgeon 2010; Wiens 2015; Albert et al. 2021; Lynch et al. 2023). Not surprisingly, the pace of biodiversity loss in freshwater environments therefore exceeds that in terrestrial environments (Wiens, 2015). However, research on freshwater environments has lagged behind that in the terrestrial and marine environments, and new ways to contribute to understanding freshwater biodiversity are needed (Maasri et al. 2022). For example, it is crucial to find potential indicators of freshwater biodiversity change (e.g., Heino 2015). Moreover, understanding biodiversity change across multiple spatial scales (e.g., from local to continental scales) can provide new insights into guiding conservation and restoration planning, thus paving the way for better safeguarding of freshwater organisms, habitats, and ecosystems (e.g., García-Girón et al. 2023).

Freshwater ecosystem characteristics are often associated with landscape position and between-site connectivity (Lindholm et al. 2020; Heino et al. 2022). For example, stream site position can reflect anthropogenic land use, as anthropogenic impacts are typically stronger in downstream than upstream locations, owing to human settlements and cities having been founded close to river mouths in prehistorical and historical times (e.g., Vianello et al. 2015). Historically, surrounding anthropogenic land use is often related to long-term nutrient conditions in freshwaters, and agricultural activities tend to increase nutrients in streams (Allan 2004; Varanka & Luoto 2012; Scotti et al. 2020; Haase et al. 2023). Consequently, stream site position in anthropogenically disturbed drainage systems can also be associated with particular abiotic characteristics, such as water chemistry, with water quality being different in downstream locations (e.g., high levels of nutrients) compared

with upstream locations (e.g., often low levels of nutrients closer to the source of the stream). In addition, abiotic characteristics of streams also show natural changes along altitudinal and longitudinal gradients, with headwater streams being colder and more shaded than larger mainstem rivers (Vannote et al. 1980).

Land use has intensified and habitat degradation has increased in the Anthropocene (Ellis 2021), and this trend has rapidly influenced biodiversity patterns in freshwaters in recent decades (Stendera et al. 2012; Gossner et al. 2016; Petsch et al. 2021; García-Girón et al. 2022). These changes suggest substantial threats to freshwater biota, unless negative effects can be counteracted by management, restoration, and conservation efforts (Heino & Koljonen 2022). However, land use type and its intensity vary in space and time, as different cultures and societies have had their own practices related to land use, and these typically change through time (Ellis 2021). These practices are thus likely to vary geographically with latitude and between continental land masses. In addition, anthropogenic land use has a high potential to create novel habitats (Bucher et al. 2016), which can increase or decrease biodiversity depending on the nature of the change and the measure of biodiversity (Siqueira et al. 2015).

Spatial beta diversity is one of the components of biodiversity (Whittaker 1972). It has been defined as between-site differences or variation in the species composition across sites in a particular area (Anderson et al. 2011). Among different measures associated with beta diversity is ecological uniqueness (sensu Legendre & de Cáceres 2013). Legendre and de Cáceres (2013) proposed an approach where the relative contribution of each sampling site to total beta diversity in a region can be used as an index of a site's ecological uniqueness. This index is called 'local contribution to beta diversity' (LCBD), and it is a measure that can reveal sites that are unique (i.e., have unique biotic communities in terms of composition) compared with other sites studied within a region. This index can be further used to detect sites that have high or low importance for conservation or restoration (Legendre & de Cáceres 2013), considering their environmental settings in natural or managed areas, respectively (Heino et al. 2022).

Previous studies have mainly focused on ecological uniqueness (LCBD) and its correlation with single

environmental variables (da Silva et al. 2018; Vilmi et al. 2018; Pozzobom et al. 2020; Schneck et al. 2022). This is because spatial variation in ecological uniqueness is thought to be associated with environmental factors, yet the correlations between LCBD and local environmental factors are typically weak (Heino & Grönroos 2017; Landeiro et al. 2018; Sor et al. 2018; da Silva et al. 2018). Moreover, the relationships between LCBD and single environmental factors may vary between study areas (Tonkin et al. 2016). Hence, it could be assumed that LCBD-environment relationships are context dependent, especially if single local environmental variables are used. However, a question arises whether LCBD, a composite measure of an assemblage, could be more strongly correlated with a composite measure of environmental features.

If single local environmental factors are not sufficient to account for entire abiotic variation in the system studied, we should examine more holistic measures of abiotic uniqueness (e. g., Castro et al. 2019). In this context, Castro et al. (2019) proposed that overall abiotic uniqueness of study sites can be calculated following an approach that is similar to calculating LCBD. This measure of local contribution to environmental heterogeneity (LCEH) reveals the sites with high abiotic uniqueness. In other words, a high LCEH value indicates that the site has dissimilar or unique environmental conditions compared to the typical environmental conditions of the study area. Testing the relationship between LCBD and LCEH

would therefore offer novel insights into biodiversity, which would help in guiding conservation and land-use management efforts. A positive relationship between abiotic and biotic uniqueness would mean that environmentally distinct sites, in general, support unique biotic assemblages. This approach could reveal the sites that require restoration or conservation based on both biotic and abiotic uniqueness (e.g., Heino et al. 2022), especially if associated with variables describing land cover and land use (e.g., Schneck et al., et al. 2022).

In this study, we focused on both elevation and landscape features, whereby the properties of a sampling site in terms of its catchment characteristics and altitude were considered potential correlates of ecological uniqueness of stream insect assemblages. We chose to use catchment features because they could be identically measured for each site based on the same environmental datasets and because catchment features are assumed to better capture environmental variation compared with local-scale snapshot physio-chemical samples (Soininen et al. 2015). Spatial variation in catchment features can create differing environmental conditions between sites, thus generating differences in abiotic uniqueness of sites. We used a two-stage analysis to test the effects of the abiotic uniqueness (LCEH) on biotic uniqueness (LCBD) of stream insect assemblages. *In the first stage*, we tested the strength of the LCBD-LCEH relationship *within* each of the 42 drainage basins scattered across four continents

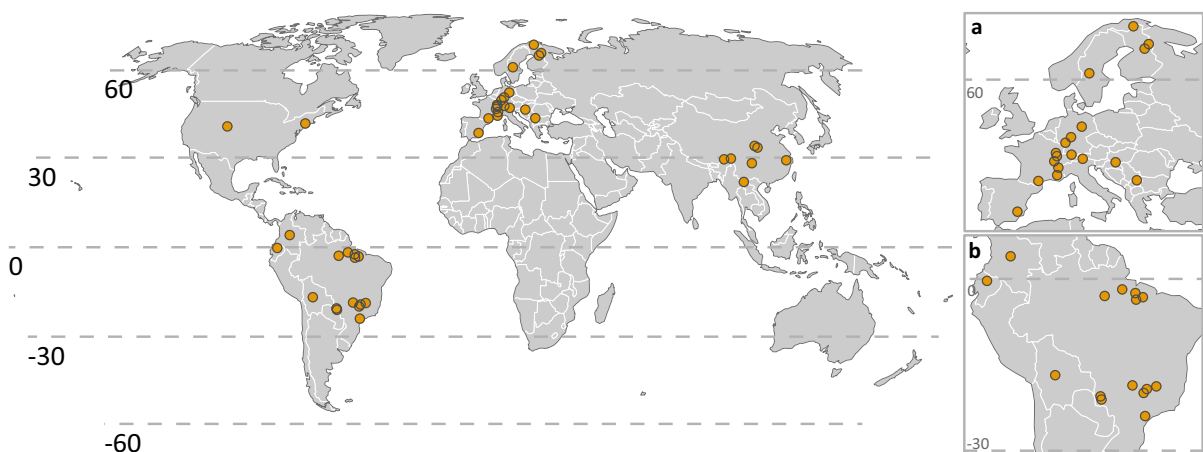


Fig. 1 Location of the studied drainage basins (N=42). Insets represent the studied drainage basins in **a** Europe and **b** South America in greater detail

Table 1 Environmental variables and their ecological impact in river systems. Dataset name and spatial resolution are defined under LCEH variable

LCEH variable and data source	Environmental variable	Ecological effects in river systems
Land use <i>European Space Agency Land Cover (300 m)</i>	Proportion (%) of different land uses in the upstream catchment	Effects on water quality (Wang & Tan 2017; Shehab et al. 2021), Indirect effects on macroinvertebrate richness, taxonomic (Nessimian et al. 2008; Scotti et al. 2020), and functional (García–Girón et al. 2022; Scotti et al 2020) community composition
Landscape position <i>GeoFRESH (Dominich et al. 2023)</i> <i>Hydrography90 (90 m)</i>	Upstream catchment area (km ²) Elevation	Environmental conditions and resource availability (Vannote et al. 1980; Soininen et al. 2015)
Atmospheric climate <i>TerraClimate (~4 km)</i>	Temperature (°C) Annual precipitation (mm) Annual evapotranspiration	Behaviour, physiology, metabolism, fitness, phenology, and community ecology and evolution (Bonacina et al. 2022) Runoff and flow conditions (eg, drying, flooding, and discharge) (Allan & Castillo 2007; Carvallo et al. 2022). Community structure and functional composition (Carvallo et al. 2022) Hydrologic cycle and flow conditions (Allan & Castillo 2007)
Upstream catchment chemical soil properties <i>SoilGrids (250 m)</i>	Nitrogen pH Organic carbon	Water quality and eutrophication (Allan 2004), trough cross-system flows (Soininen et al. 2015) Community assemblages (Wang & Tan 2017) Water quality, eutrophication, and acidification (Wade et al. 1989) Water quality and eutrophication. Community composition (Wang & Tan 2017)

and covering a wide range of variation in climate and land cover features (Supplementary Information 1). To do so, we calculated LCEH in four different ways: (1) stream site landscape position (in terms of elevation and upstream catchment area), (2) upstream land cover, (3) upstream chemical soil properties, and (4) climate. Thus, there were four separate tests of the LCBD-LCEH relationship within each drainage basin. We relied on a correlative approach because experiments were not feasible at the spatial scales examined. In this first stage of the analysis, we assumed that the LCBD-LCEH relationship is positive within each drainage basin. This is because stream sites with unique environmental conditions should harbour unique stream insect assemblages, which is based on the assumptions of the niche theory that each species prefers a certain set of environmental conditions (Hutchinson 1957). *The second stage of analysis* was a meta-analysis across drainage basins. Here, we explored the variation in the strength of relationship between

LCBD and LCEH *across* the 42 drainage basins. As predictor variables, we used mean latitude of sampling sites in each drainage basin, major continental realms (here, the Americas *versus* Eurasia), and human footprint index (HFPI) as a proxy for anthropogenic alteration and pressures in each drainage basin. In this second-stage analysis, we explored the hypotheses: (a) the strength of the LCBD-LCEH relationship varies with latitude, (b) the strength of the LCBD-LCEH relationship varies with the degree of human impact at the scale of entire drainage basins, and (c) the strength of the LCBD-LCEH relationship differs between the Americas and Eurasia because of their distinct biogeographic histories.

Materials and methods

Datasets

We compiled data from 42 drainage basins scattered across four continents (Fig. 1).

These data came from published case studies focusing on one or more drainage basins. In each drainage basin, we randomly chose 20 stream sites from larger datasets if the original studies had included more sites to guarantee the same sampling effort for the across-basins analysis. As many basins had only 20 or a little more than 20 sites sampled (mean no. sites sampled per basin was 39, range 20 to 95), we could not test the effects of resampling, for example, 80 sites on the LCBD-LCEH relationships in all basins. Moreover, as environmental heterogeneity increases with the number of sites sampled or the area covered (Stein et al. 2014), using 20 sites from each basin was considered the most feasible approach. The study drainage basins include a diverse set of streams, covering a vast range of environmental conditions, ranging from nearly pristine to heavily anthropogenically disturbed catchments (Supplementary Information 1).

Within each drainage basin, at least mayflies (Ephemeroptera), stoneflies (Plecoptera) and caddisflies (Trichoptera) (EPT) were originally sampled. Genus-level taxonomic harmonization was done to guarantee comparability between the 42 drainage basins and to ensure the same level of identification in all study regions. These three insect orders also include most of the functional variation exhibited by stream insects and cover a large range of lineage origins, thereby providing a potential proxy for wholesale stream insect biodiversity (Vinson & Hawkins 2003; Brito et al. 2018). EPT taxa were sampled using standardized methods within each study area, but not among them, as it would be impossible to obtain global broad-scale data with the same sampling methods used across all basins (e.g., Eriksen et al. 2021). We used the correlation coefficients obtained from within-basin analyses in the across-basins analyses (see below), which ensured the comparability of the different datasets. The surveys were conducted between 1998 and 2020, with all within-basin samples being collected in the same year. Moreover, all sites in a drainage basin were sampled within a period of less than 4 months to avoid excessive

temporal variation and to ensure comparability across the drainage basins. More information about the drainage basins and data collection is available in Supporting Information 1.

Environmental variables were obtained to explore the differences in abiotic conditions within drainage basins and to assess abiotic uniqueness of sites (Table 1). These environmental variables were chosen based on their ecological importance to stream insects (see Table 1 for examples), as well as practical reasons to guarantee directly comparable environmental data for each drainage basin and each stream site within each basin.

Climate variables were obtained from TerraClimate (*resolution ~4-km*) (Abatzoglou et al. 2018). Average values of atmospheric minimum and maximum temperature, annual precipitation, and annual evapotranspiration were calculated for each study site from a 30-year standard reference period (1981–2010), defined by the World Meteorological Organization (WMO), which is the latest climatic normal in use. Environmental variables were derived from the Hydrography90 dataset (*resolution 90 m*) (Amatulli et al. 2022), along with ancillary environmental variables (Domisch et al. 2023). These variables included local elevation and upstream catchment area. Upstream-catchment land cover data (*resolution: 300 m*) were obtained from European Space Agency (ESA 2017; see Supplementary Information 3). Upstream catchment chemical soil properties were derived from SoilGrids 2.0 (*resolution 250 m*) (Poggio et al. 2021). Chemical soil properties included in this study are nitrogen, pH, and soil organic carbon. We used the 0–5 cm depth layer, which likely has the greatest impact on water chemistry due to surface runoff. Additional details regarding the variation of these environmental variables can be found in Supplementary Information 3 (S2). We also used the 2009 Human Footprint index (HFPI), which is a global map of the cumulative human pressure on the environment calculated for the year 2009 (*resolution: ~1 km*) (Venter et al. 2016, 2018). We chose to use HFPI because it could be calculated for all basins and is thus comparable in the context of our global study.

The environmental variables used in this study are considered as proxies for local environmental conditions in streams. We used this proxy-based approach, as such variables were the only consistent ones

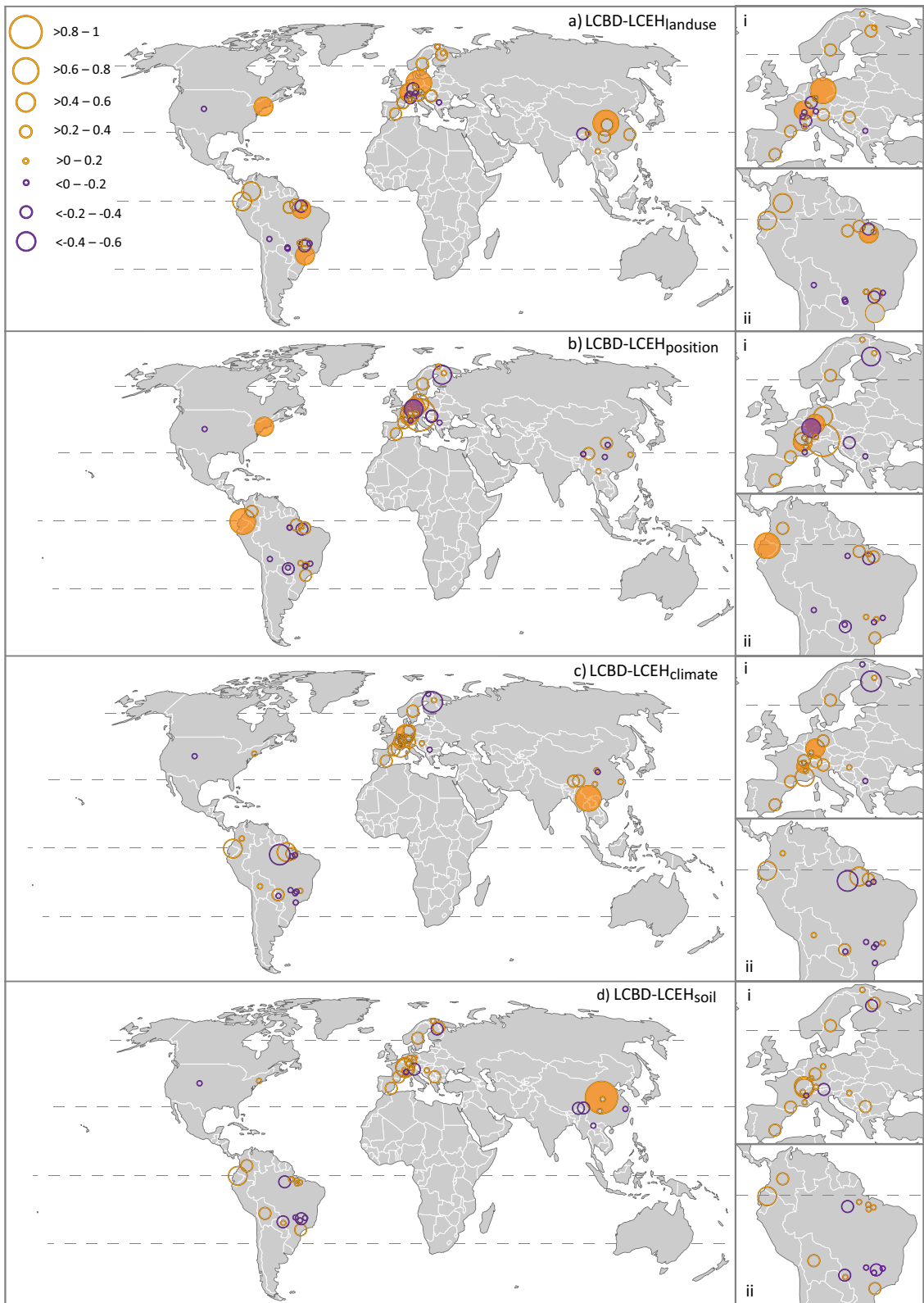


Fig. 2 World maps illustrating the correlation between local contribution to beta diversity (LCBD) and local contribution to environmental heterogeneity (LCEH). Key: **a** LCBD-LCEH_{landscape}, **b** LCBD-LCEH_{position}, **c** LCBD-LCEH_{climate}, **d** LCBD-LCEH_{soil}. The size of the circle represents the strength of the correlation, and the colour represents the direction (negative [orange] versus positive [violet]) of this relationship. Filled circles represent statistically significant ($p < 0.05$) correlations according to modified t -tests to account for spatial autocorrelation. The insets are (i) Europe and (ii) South America, with several drainage basins located relatively close to each other

available for each site across all drainage basins. We acknowledge that local environmental factors, such as water chemistry and habitat conditions, are important in affecting the biodiversity of aquatic macroinvertebrates in general, yet even their explanatory power may be low in studies of stream insects (Heino et al. 2015a, b). This may be due to these local variables being strongly affected by recent changes in weather conditions and may hence describe only a snapshot of chemical features in time. Catchment level variables, on the other hand, are more stable compared to local environmental variables and could thus more reliably describe environmental conditions in time (Soininen et al. 2015).

Statistical methods

We calculated the total beta diversity and biotic uniqueness of the sites in each basin (LCBD) according to Legendre & de Caceres (2013). LCBD values vary between 0 and 1, and a higher value indicates a higher contribution of the site to total beta diversity. LCBD was calculated for presence-absence data using the Jaccard coefficient. The abiotic uniqueness of the sites (LCEH) was calculated separately in each drainage basin based on standardized variables describing (1) stream site landscape position, (2) upstream catchment land cover, (3) upstream basin soil chemistry, and (4) climate data following the approach suggested by Castro et al. (2019). Additionally, we calculated LCEH using all environmental variables combined in the same analysis (LCEH_{total}). LCBD and all LCEH variables were calculated separately for each of the 20 sampled sites in all 42 drainage basins.

In the *first stage* of our analytical workflow, we used Moran's I tests to measure the spatial autocorrelation in LCBD and LCEH values for each dataset separately. Since these tests revealed statistically

significant spatial autocorrelation in some datasets (Supplementary Information 2 S1), we tested correlations between LCBD and different classes of LCEH using modified t -tests (Dutilleul 1993). This allowed us to control for the spatial non-independence when calculating the significance of the correlation between LCBD and LCEH.

In the *second stage* of the analysis, the correlation coefficient between LCBD and LCEH, separately for each type of environmental variable, was transformed in Fisher's Z_r scale (Borenstein et al. 2021) for each drainage basin. To calculate the variance of Z_r , while taking spatial autocorrelation into account, we used the estimated effective sample size (ESS) provided by the function `modified.ttest` of the R package `SpatialPack` (Vallejos et al. 2020). After calculating ESS, we fitted mixed-effects meta-regression (MEMR) to the Fisher's Z_r using the "`rma.mv`" function in the R package `metafor` (Viechtbauer 2010). Thus, there were four separate tests of the LCBD-LCEH relationship within each drainage basin. A meta-analytical approach is a useful tool to summarize diverging results from multiple datasets, sources, or sites, thereby clarifying findings of large-scale ecological research (Koricheva & Gurevitch 2014).

MEMR weights each effect size by the inverse of its sampling variance (calculated using the "`escalc`" function in the R package `metafor`) plus the amount of residual heterogeneity not explained by moderators (i.e., explanatory variables). To account for the non-independence among the 42 drainage basins, we included geographic coordinates as random factors using different correlation structures (here, exponential, gaussian, linear, spherical, and rational quadratic; Viechtbauer 2010). We selected the most parsimonious models in terms of predictive power using the Akaike Information Criterion corrected for small sample size (AICc). Estimates of mean effect sizes (μ) and variance between studies (τ^2) were obtained using restricted maximum likelihood (REML) estimations, and MEMRs were fitted separately with the Broyden-Fletcher-Goldfarb-Shanno (BFGS) optimisation to improve model convergence. We also illustrated the MEMRs by back-transforming Z_r into correlation coefficients (r) for interpretability (Cohen 1992).

Finally, we tested the differences in environmental heterogeneity between catchments using permutational tests of homogeneity of dispersion

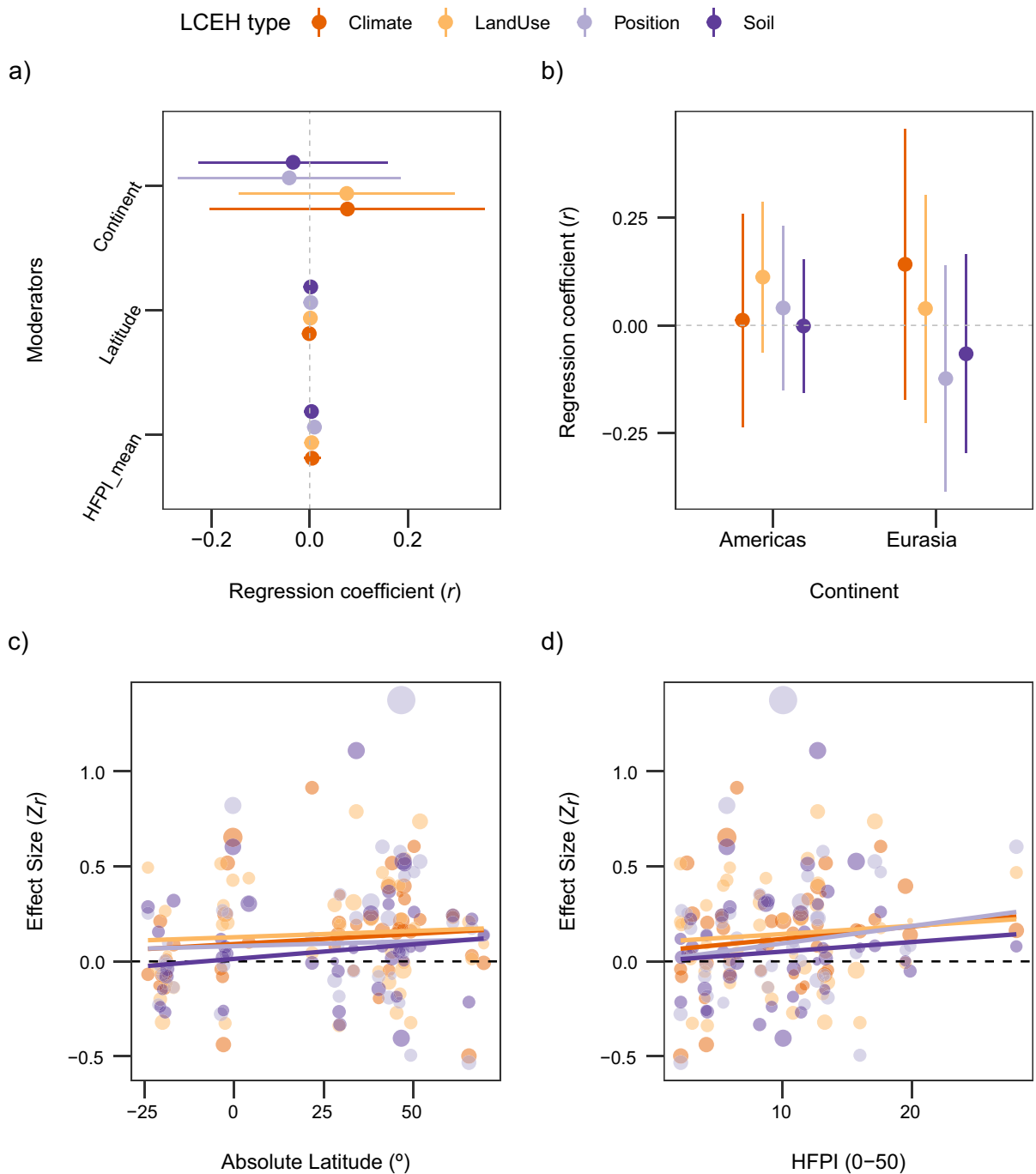


Fig. 3 Mixed-effects meta-regression (MEMR) results for the variation in the strength of the local contribution to beta diversity (LCBD)—local contribution to environmental heterogeneity (LCEH) relationships. **a** Regression coefficients evaluating the effects of moderators (continental realm, latitude, and human footprint index (HFPI)) on the relationship between biotic uniqueness (LCBD) and different types of abiotic uniqueness ($LCEH_{climate}$, $LCEH_{landuse}$, $LCEH_{position}$ and $LCEH_{soil}$). The

bars represent the 95% confidence levels. **b** Mean effect sizes (back-transformed to r) measuring the relationship between LCBD and LCEH in Eurasia and the Americas. **c** Changes in the strength of relationships (as given by Z_r) between LCBD and different types of LCEH with absolute latitude. **d** Changes in the strength of relationships (as given by Z_r) between LCBD and different types of LCEH with HFPI. The size of the data points is proportional to the inverse of variance

(PERMDISP; Anderson 2006). We used standardized environmental variables and Euclidean distance to calculate mean distance to centroid, which was used as a measure of environmental heterogeneity within each drainage basin. PERMDISP was conducted using “betadisper” function in R-package *vegan* (Oksanen et al. 2020).

All statistical analyses were run in R version 4.0.2 (R Core Team 2021). R packages and the scripts used in this study will be included in Zenodo.

Results

On average, correlations between biotic uniqueness (LCBD) and different measures of abiotic uniqueness ($LCEH_{landuse}$, $LCEH_{soil}$, $LCEH_{position}$, and $LCEH_{climate}$) were mainly low but varied widely from $r = -0.487$ $LCEH_{position}$ in the Iijoki basin, Finland, to $r = 0.880$ $LCEH_{position}$ in the Adige basin, France, (Supplementary Information 2 S3). Only a few of these results were statistically significant ($P < 0.05$), which was possibly due to the small sample sizes within each drainage basin. For $LCEH_{soil}$, only the Wei River basin, China, showed a strong, statistically significant association with LCBD ($r = 0.804$, $p = 0.002$). The correlation between $LCEH_{climate}$ and LCBD was also mainly weak, and it was statistically significant in only three of the drainage basins examined (the River Ain basin, France: $r = 0.341$, $p = 0.006$; the River Thur basin, Switzerland: $r = 0.377$, $p = 0.013$; and the River Mekong basin, China: $r = 0.723$, $p < 0.001$). The correlations between LCBD and $LCEH_{position}$, and between LCBD and $LCEH_{landuse}$ were statistically significant in six and seven drainage basins, respectively. The relationships between LCBD and $LCEH_{total}$ varied similarly across the basins as the LCBD-LCEH relationships calculated with subsets of the environmental data included in the same analysis (Supplementary Information 2 S3).

More importantly, however, both the strength and the direction (negative *versus* positive r -values) of the relationship between LCBD and different measures of LCEH varied considerably across the drainage basins (Fig. 2).

Additionally, the strength and direction of these correlations varied even between drainage basins

located geographically close to each other, and within continental realms with similar biogeographic and land-use histories. For example, the strength and direction of the correlation between LCBD and LCEH varied considerably within both the Americas and Eurasia, regardless of the LCEH measure used (Fig. 2). Similar degrees of variation can be seen even between drainages located within similar climates, freshwater ecoregions, and biomes, such as the Koutajoki and Iijoki River basins in Finland, the Ain, Saône, and Doubs River basins in France, and the Acará, Gurupi and Capim basins in Brazil.

Considering the meta-regression models, all the spatial structures tested yielded the same results for the strength of the LCBD-LCEH_{soil} relationship because spatial autocorrelation between drainage basins was low. Gaussian, spherical, and linear spatial structures provided the best model fits respectively for the LCBD-LCEH_{climate}, LCBD-LCEH_{landuse}, and LCBD-LCEH_{position} relationships, but were only marginally better compared to other spatial structures for a given measured of LCEH ($\Delta AICc > 2$ according to Burnham & Anderson 2002). In general, variation in the strength of the relationships between LCBD and LCEH measures was not significantly influenced by any explanatory variables (Fig. 3a–d).

More specifically, the effect size (Z_i) did not vary remarkably with any of the moderators used (LCBD-LCEH_{climate} QM(df=4)=4.033, $p = 0.488$, LCBD-LCEH_{landuse} QM(df=4)=12.282, $p = 0.015$, LCBD-LCEH_{position} QM(df=4)=6.470, $p = 0.167$, LCBD-LCEH_{soil} QM(df=4)=4.199, $p = 0.380$). Slightly stronger LCBD-LCEH correlations tended to be found in drainage basins with higher levels of human impact (Fig. 3d), and the direction (positive *versus* negative) of the effect size between LCBD and LCEH varied across different measures of LCEH in relation to major continental realms (Fig. 3a, b). For example, we found a tendency for negative relationships between LCBD and $LCEH_{position}$ and LCBD and $LCEH_{soil}$ in the Americas, but not in Eurasia. Overall, however, latitude, major continental realms, and HFI showed mostly marginal correlations with LCBD-LCEH relationships (in most cases, $r < 0.3$). PERMDISP results showed that there was relatively high variability in environmental conditions between sites *within* basins (Supplementary Information 2 S6), but the level of environmental heterogeneity did not differ strongly *across* basins.

Discussion

We studied the relationship between biotic uniqueness (LCBD) and four measures of abiotic uniqueness ($LCEH_{landuse}$, $LCEH_{soil}$, $LCEH_{position}$, and $LCEH_{climate}$) in river basins across most of the world. Contrary to our expectations, relationships between the uniqueness of stream insect assemblages and abiotic uniqueness were not positive in most of the drainage basins studied. Instead, these correlations varied considerably on a basin-by-basin basis, pointing to strong context dependence in the relationship between LCBD and LCEH. The results of meta-regressions also contradicted our expectations, as (1) we did not find clear patterns in the variation of the LCBD-LCEH relationship and latitude, and because (2) the strength of this relationship did not vary with the human footprint index, or (3) between the Americas and Eurasia. We did not find any reasonable explanations for the variability in the LCBD-LCEH relationship using the meta-analysis, as none of the predictor variables significantly affected this relationship. Thus, our meta-regression models suggest that there is strong context dependence in this relationship worldwide (Heino et al. 2012; Catford et al. 2022), which has been previously detected for the relationships between the LCBD of entire stream macroinvertebrate assemblages and single environmental variables across a few German drainage basins (Tonkin et al. 2016). In other words, the relationship between biotic uniqueness and abiotic uniqueness varies depending on the geographical and environmental settings studied. This is a plausible finding, as the drainage basins we studied ranged from the Tropics to the Arctic, from moist to dry regions, and from highly impacted to near-pristine areas (Supplementary Information 1).

Context dependence in ecology could result from several reasons, ranging from mechanistic context dependence related to interaction effects and apparent context dependence associated with confounding factors and methodological issues (Catford et al. 2022). Even though the biological data were harmonized and standardized, and the environmental data were comparable across the river basins, the datasets were not originally collected for the present purpose. Therefore, spatial variability in different environmental aspects was not the same across drainages, i.e., gradients in land cover, elevation, and climate

differed considerably among the river basins. This can complicate the interpretation of the relationship between biotic uniqueness and abiotic uniqueness across river basins, and even more so across continents. Datasets that are not collected for the very purpose of a study are common in large-scale ecological and biogeographical studies (e.g., Heino et al. 2015a, b; Alahuhta et al. 2017), as simultaneous sampling in multiple geographical regions is expensive, if not impossible, making it reasonable to utilize datasets collected during earlier research efforts. Differences in the local environmental factors used (e.g., Tonkin et al. 2016) and different levels of environmental heterogeneity in the studied river basins may also cause context dependence (e.g., Grönroos et al. 2013). Additionally, there could be a disparity between the scales of observation for biological and environmental data. This is because the environmental variables were measured at the catchment scale and biological data were derived from local reach-scale surveys. Therefore, we may not have captured environmental conditions (e.g., microhabitat features) as perceived by stream insects. However, as there is a paucity of comparable local-scale environmental data, we had to rely on catchment-scale environmental variables. In addition, environmental variables measured at the catchment scale might better reflect the long-term environmental conditions within river basins (see Table 1), considering that local environmental variables tend to fluctuate continuously (e.g., due to changing weather conditions) and might only reflect short-term environmental conditions of the stream and the entire catchment (Soininen et al. 2015). These factors could, in turn, explain the context-dependent findings pertaining to different relationships between biotic LCBD and abiotic LCEH, even when based on the same environmental variables measured in all drainage basins. Context dependent findings could be also explained by a possible scale disparity between the resolution of environmental and biological data (i.e., two sampling points can fall within same environmental variable pixel and thus be assigned with same value). However, there is an unfortunate lack of high-resolution datasets at global scale, which could be used in studies like ours. Context dependence in environmental features could be the underlying cause of the variability of LCBC-LCEH relationships we detected in this study. However, it is unlikely that the level of overall environmental heterogeneity caused

context dependence, as overall environmental heterogeneity did not vary considerably across basins (as revealed by PERMDISP results).

Even though we did not find generally strong relationships between biotic uniqueness and abiotic uniqueness, the few significant LCBD-LCEH correlations detected within drainage basins should be considered when designing conservation and restoration programs. For example, in the River Wei basin in China, biotic uniqueness was strongly related to the uniqueness of both soil properties and land use. This may be due to the spatial positioning of the land use in this basin (see also Sponseller et al. 2001). The calculation of the land use uniqueness in this study was based on proportion of different land use types in the upstream basin but did not consider their spatial positioning. Land use is often related to the soil chemical properties, and thus these two measures of uniqueness could be interlinked.

Land use intensification can change the physical and chemical characteristics of streams (Allan & Castillo 2007), often decreasing environmental heterogeneity among sites (Gossner et al. 2016). This can have a negative influence on the diversity and structure of biological assemblages (García-Girón et al. 2022; Larsen & Ormerod 2014). Anthropogenic land use can, however, sometimes benefit biodiversity (Schneck et al. 2022). This is because it does not necessarily homogenize landscapes but can also create novel habitats and niche opportunities (Sévêque et al. 2020). In addition, anthropogenic land use may modify landscapes and habitats in such a way that it does not instantly decrease biodiversity in a certain area (e.g., adding nutrients in an oligotrophic environment, species composition can be altered but overall richness is not affected or may even initially increase) (Jeppesen et al. 2000). Land-use practices within river basins can have a strong impact on macroinvertebrate assemblages, but the spatial positioning of different land uses in a catchment can be a key factor defining how strong its influence on streams is (Sponseller et al. 2001). For example, if land cover in the basin is overall heterogeneous but anthropogenic land uses are situated close to a stream, the positive effect of land-use heterogeneity in the basin could be compromised (Scotti et al. 2020).

Current land-use change may hamper our understanding of biodiversity patterns, as the abiotic nature context for biotic nature is constantly changing, and

the pace of change is faster than ever (Ellis 2021). The natural features of the studied river systems are spatiotemporally variable (e.g., Li et al. 2021), which also applies to human land use. Therefore, anthropogenic pressures are not constant across the studied river basins (see Supplementary Information 1). The intensity and type of human-induced pressures were different across the river basins and differing regional histories regarding land-use practices may complicate our understanding of the consequences of land cover change (Ellis 2021). Such among-region differences could account for the context dependence we detected in the LCBD-LCEH relationships and explain why we did not find any ecological correlates for the among-river basin variation in effect sizes. We accounted for the variation in anthropogenic pressures by including the human footprint index as an explanatory variable, yet our results were not statistically significant. This could also be due to using a composite index describing human pressure, as such indices can be (1) either limited in the sense of measuring only a small portion of overall anthropogenic stressors, or (2) that the indices overweight some individual factors that are important in some regions but not in the others.

The tendency for negative relationships between LCBD and $LCEH_{\text{position}}$ and LCBD and $LCEH_{\text{soil}}$ in Eurasia but not in the Americas could be explained by longer history of intensive agriculture and industry in Eurasia compared to the Americas (Ellis 2021). Historically pervasive anthropogenic land use can have long-lasting effects on biodiversity (Harding et al. 1998; Maloney et al. 2008; Santos et al. 2020; Linares et al. 2023), and therefore land-use legacy can also be assumed to influence the LCBD-LCEH relationship. For example, sites that now drain catchments with agricultural fields may have been within forests in the past, and this historical constraint could still be affecting the diversity and structure of stream insect assemblages.

Counteracting the negative effects of land-use intensification and stream degradation by management, restoration, and conservation practices (Heino & Koljonen 2022) requires that researchers can provide clear guidelines and indicators of biodiversity change. Moreover, acquiring adequate knowledge of indicators of change should be associated with alteration of natural landscapes and land-use intensification in recent decades. If one can find associations between land-use intensity and features of biotic

communities (e.g., species richness, biotic uniqueness, or presence of rare species), practical guidelines for environmental managers and conservation practitioners can be more easily established. Measures such as local contribution to beta diversity (LCBD) and local contribution to environmental heterogeneity (LCEH) based on environmental features, show some promise in this regard (e.g., Heino et al. 2022), but they should be considered in each drainage basin separately. A step forward to apply the indices of LCBD and LCEH to river basin conservation is to examine how the summed LCBD or LCEH values of a subset of surveyed sites can incorporate total beta diversity and environmental variation within a basin, as has been recently proposed for lake biota and environments (Heino et al. 2022) and abiotic features in terms of geodiversity (Alahuhta et al. 2023).

In summary, we found strong context dependence between biological uniqueness of stream insect assemblages and abiotic uniqueness of sites' catchment features. Hence, we propose considering the specific land-use histories and examining each drainage basin separately if the relationship between biotic uniqueness and abiotic uniqueness is used as the basis of conservation and restoration programs of river systems. Our present analysis, therefore, warns that any attempt of using relationships of biotic uniqueness and environmental uniqueness from single drainage basins or few drainage basins as a cure-for-all in designing conservation and restoration of world's river systems should be avoided. However, differences in the abiotic environmental factors and different levels of environmental heterogeneity in the studied river basins may also cause context dependence, and it could be the underlying cause of the variability in the LCBC-LCEH relationships detected in this study. Thus, although large-scale ecological and biogeographical studies are rarely based on datasets collected for a particular purpose, we believe that this effort would be of great value to identify the type of context dependence—mechanistic or apparent context dependence (Catford et al. 2022)—underlying the LCBC-LCEH relationship.

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Author contributions HS and JH: devised the original study idea and led the writing. JH, JGG, LMB and HS: planned

the statistical analyses. JGG: wrote the R scripts and HS: ran the analyses. PB, LSB, MC, DMPC, KC, ZC, MF, NF, BAG, JDGT, EG, PH, NH, MJH, LJ, JFJ, APJF, ZL, RL, MSL, ALA, DRM, KLM, AMD, DM, NM, NLP, RJR, FOR, VSS, LS, RBS, AS, TS, RTM, FVN, BW, JW, ZX, and JH: provided field data. SD and JRG: provided catchment environmental variables. All authors, including JA, JH, TD, and NB: contributed to revising the manuscript drafts and accepted the final manuscript version.

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Data availability Fully editable R code will be published on Zenodo upon acceptance. Some of the observations are from third parties and are thus not available to the public. The data used in this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

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