RESEARCH ARTICLE

Incongruent latitudinal patterns of taxonomic, phylogenetic and functional diversity reveal different drivers of caddisfly community assembly across spatial scales

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Abstract

Aim: Community assembly processes are difficult to observe in nature but can be inferred from species diversity patterns. However, taxonomic patterns may be consistent with multiple explanations, such as habitat filtering or biogeographical processes, which can also act differently across spatial scales. Here, we assessed multiple facets of diversity to determine the relative contributions of local versus regional processes and historical versus contemporary factors in establishing macroecological patterns.

Location: From the Mediterranean peninsulas to northern Scandinavia.

Time period: Species occurrence data gathered since *c.* 1980.

Major organism group studied: Trichoptera (Insecta).

Methods: Based on an extensive functional space and a phylogenetic tree including 197 and 509 species, respectively, and the composition of 180 communities, we assessed the distribution of taxonomic, functional and phylogenetic diversity within 18 ecoregions (local α- and β-diversity) and among those ecoregions (regional γ- and β-diversity).

Results: Local estimates of taxonomic, functional and phylogenetic α- and β-diversity were similar across Europe, which reveals that all streams have similar carrying capacity even though the local abiotic factors involved are likely different among ecoregions. In contrast, regional taxonomic and phylogenetic diversities decreased as latitude increased, whereas functional richness and functional dispersion displayed unimodal relationships. The position of species on the functional space was not conserved, while northern species pools were found to be phylogenetically clustered and southern ones overdispersed. The nestedness component mainly contributed to the taxonomic and phylogenetic β-diversity among northern communities, whereas in southern latitudes the turnover was dominant.

Main conclusions: Decoupled latitudinal patterns of taxonomic, phylogenetic and functional diversity reveal the importance of regional environmental filtering over local factors in limiting species range and shaping the regional species pool. The biogeographical signature is still present; the northern recolonizations following

the Pleistocene glaciations originated exclusively from central regions, instead of Mediterranean refugia, as was previously accepted.

1 | INTRODUCTION

Biodiversity is defined as the variety and variability of life on Earth and is often quantified by the total number of species (Gaston, 2000). However, neither species richness nor taxonomic diversity (TD) capture or reflect sufficiently the differences in the evolutionary history of species and their ecological functions in the ecosystems. Moreover, community assembly processes, which are conceptualized as the accumulation of species diversity over time in a given locality, are difficult to observe using only estimates of TD (Webb et al., 2002). In order to solve these difficulties, the use of phylogenetic diversity (PD, the sum of branch lengths on a phylogenetic tree among all species within a community) and functional diversity (FD, the value and the range of variability of functional traits within a community) has been increasingly recommended (Du et al., 2021; Webb et al., 2002). Nevertheless, studies using an integrative approach of quantifying and merging TD, PD and FD along extended spatial scales to determine macroecological patterns and eco-evolutionary processes are scarce.

Species are characterized by functional traits (e.g., respiration modes, feeding strategies, body size, emergence or flight periods) that have been acquired over evolutionary time (Múrria et al., 2018). The values of FD should integrate the variation of traits among all organisms within a community; thus, its conceptual complexity makes its estimation challenging (Carmona et al., 2016). One common approach to estimate FD is based on the functional space (FS), which represents a *species × trait* matrix on a few independent functional axes that capture the range of trait variability among organisms (Mason et al., 2005; Villéger et al., 2008). Under this conceptual framework, the functional niche of a species is defined as the exact position that it occupies in the FS. Several FD metrics have been proposed to capture different aspects of the distribution of species in the FS. For instance, the functional richness (FRic) of a given community is the minimum hypervolume in the FS occupied by all species in the community (Villéger et al., 2008), whereas the functional dispersion (FDis) represents the trait differentiation and therefore the competition between or the aggregation of species in the FS (Laliberté & Legendre, 2010; Mason et al., 2005).

Diversity patterns can be shaped by both stochastic and deterministic ecological and evolutionary processes. The effect of stochastic processes would lead to communities that are random subsets of the regional species pool under the exclusive action of ecological drift and isolation-by-distance. In contrast, deterministic processes assume that there is a certain species sorting acting on the regional pool during the assembly of local communities (Webb et al., 2002). For instance, environmental filtering implies that species can arrive at a site but fail to establish due to an inability to tolerate the abiotic conditions. As a result, communities are composed of species with particular functional traits that permit them to cope with the environments that host them. If these characters are phylogenetically conserved, communities will also be clustered in terms of phylogenetic diversity, displaying low values of PD, FRic and FDis (Emerson & Gillespie, 2008; Lamanna et al., 2014). In contrast, strong competitive exclusion can lead to communities characterized by high FDis (i.e., co-occurrence of species with distinct functionality) and phylogenetic overdispersion (i.e., high values of PD) if the functional niche is conserved (Emerson & Gillespie, 2008). However, community assembly is complex and patterns observed in nature may have multiple explanations (Vellend, 2010).

Also important in determining the community and its phylogenetic structure are the factors that constrain or favour dispersion among communities. For instance, low dispersion is commonly found in long-term stable ecosystems, resulting in high phylogenetic structure, interspecific turnover among sites and communities assembled by local speciation (Múrria et al., 2015). For freshwater fishes, basins in the Mediterranean peninsulas (Iberian, Italian and Balkan) are geographically isolated from those in central Europe by high mountain chains (Pyrenees, Alps and Dinaric Alps) that promote endemism (Leprieur et al., 2009).

The effects of all these ecological and evolutionary processes may be different when measured at distinct grain sizes, and therefore, ecological patterns observed at one spatial scale often do not extrapolate to other scales. The regional species pool (γ-diversity) as well as the differences in community composition between regions (β-diversity) are determined by large-scale historical and biogeographical processes. In contrast, local patterns of α- and β-diversity within a region are influenced not only by the regional species pool but also by local abiotic conditions, dispersal limitation and species interactions (Ricklefs, 2004). Resolving the differences in diversity patterns across spatial scales and the relative contributions of local versus regional processes may be crucial to identify the causal mechanisms underlying macroecological patterns.

Here, we aim to combine the taxonomic, functional and phylogenetic attributes of diversity to assess the local and regional patterns of caddisfly diversity (Trichoptera, Insecta) across a broad latitudinal gradient in Europe covering 18 ecoregions (ERs) (Figure 1). These patterns will be explored at (a) local scale: evaluating α- and β-diversity within ERs to disentangle how local ecological processes
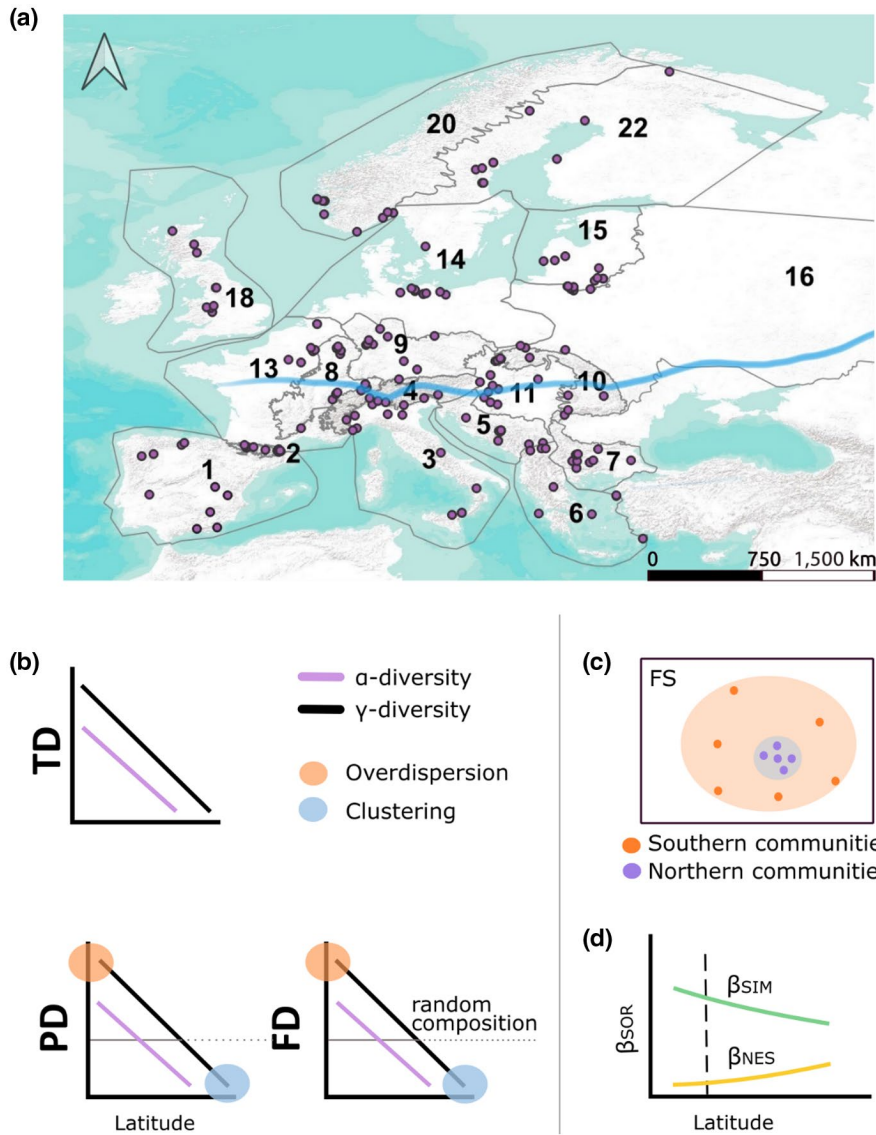
(a)

(b)

(c)

(d)

FIGURE 1 (a) Map depicting the 10 communities in each of the 18 investigated ecoregions based on Illies (1978) and the 0 °C isotherm at the Last Glacial Maximum (bold blue line) following Hortal et al. (2011). 1. Iberian Peninsula, 2. Pyrenees, 3. Italy and Corsica, 4. Alps, 5. Dinaric Western Balkan, 6. Hellenic Western Balkan, 7. Eastern Balkan, 8. Western Highlands, 9. Central Highlands, 10. Carpathians, 11. Hungarian Lowlands, 13 Western Plains, 14. Central Plains, 15. Baltic Province, 16. Eastern Plains, 18. England, 20. Borealic Uplands, 22. Fennoscandian Shield. (b) Hypotheses on the latitudinal patterns of α- and γ-diversity and community structure. FD, functional diversity; PD, phylogenetic diversity; TD, taxonomic diversity. (c) We expect northern communities to occupy a smaller functional space (FS) that is nested within the FS of the southern communities. (d) Overall β-diversity (β_{SOR}) is expected to decrease due to high species turnover (β_{SIM}) in lower latitudes. Nestedness (β_{NES}) should subtly increase due to environmental filtering after a certain latitude (indicated with discontinuous lines)

and regional species pools have formed differences between communities within ERs; and (b) at the regional scale: assessing β- and γ-diversity among ERs to elucidate the signature of biogeography (e.g., Pleistocene glaciations) and latitudinal environmental filtering on the regional species pools. Among freshwater macroinvertebrates, Trichoptera is a good model taxon for exploring macroecological patterns because (a) the larval and pupal stages are exclusively aquatic and are important in trophic dynamics and energy flow in freshwater ecosystems, (b) they are sensitive to global changes and are considered among the most useful aquatic organisms for monitoring ecosystem health, (c) they are present in almost all freshwater habitats, with high species turnover due to the high specialization and narrow preferences in habitat use, (d) they represent a significant branch on the Tree of Life, and (e) their current distribution and biogeography can reveal past events that have shaped the distribution and diversification of freshwater biota (Conti et al., 2014; Graf et al., 2019; Kjer et al., 2001; Múrria et al., 2018).

A broad latitudinal gradient in Europe covers a complete, continuous range of environmental and biogeographical conditions.

Environmental homogeneity and climatic stress associated with cold temperatures increase with latitude, whereas aridity is spatially limited to Mediterranean regions (Bonada et al., 2007). As a result, the action of environmental filtering should restrict species ranges and diversity latitudinally to those species that have certain functional traits to cope with extreme environments (Kerkhoff et al., 2014). Moreover, the cyclic Pleistocene glaciations provoked extinctions or migration of northern species, reshaping global biodiversity (Hewitt, 2004). Consequently, northern regions have subsequently been colonized by a subset of dispersive and cold-tolerant species from the Mediterranean peninsulas and extra-Mediterranean refugia located in several high mountain ranges in central Europe (Malicky, 2006; Pauls et al., 2006; Schmitt & Varga, 2012). Generally, we hypothesize that TD, PD and FD decline with latitude at local (within ERs) and regional (among ERs) scales. We expect low α- and γ-diversity among northern ERs because these areas should be inhabited by similar communities of cold-tolerant and high-dispersive species that recolonized the area during interglacial periods. Given the short time period since the Last Glacial Maximum, only a low

contribution of local speciation is expected in northern areas (Pinkert et al., 2018). In contrast, the historical habitat stability in the southern ERs should result in high TD, PD and FD, driven by high endemism, species turnover and diversity accumulation related to high habitat heterogeneity and low dispersal (Conti et al., 2014; Hering et al., 2009; Figure 1b). Therefore, ERs that hosted Pleistocene refugia should be characterized by a high contribution of the nestedness component to β-taxonomic and phylogenetic diversity towards northern latitudes, whereas turnover should be high among isolated Mediterranean peninsulas and central European regions (Baselga, 2010; Figure 1c).

2 | METHODS

2.1 | Species data acquisition

The geographical limits of the 25 European freshwater ecoregions (ERs) analysed were defined based on the distributions of species belonging to 75 different organism groups (Illies, 1978). Currently, these ERs are incorporated into the assessment of European running waters according to the Water Framework Directive (Directive 2000/60/EC) and are also commonly applied in macroecological studies, as they follow the zoogeography of freshwater species (e.g., Hering et al., 2009; Shah et al., 2015). We divided the ERs into northern, central and southern ones based on the position of their centroid, which is the point that may be considered as the centre of an ER, in relation to the 0°C isotherm at the Last Glacial Maximum following Hortal et al. (2011).

The taxonomic data were compiled from https://www.freshwater ecology.info/ (Graf et al., 2019; Schmidt-Kloiber & Hering, 2015), including a species list and the larval distribution per ER for a total of 1,425 caddisfly species (Supporting Information Table S1). ERs 12 and 17 were excluded because of their insufficient species and traits information.

For analyses at the local scale, adult species occurrences from entire communities were provided by the Distribution Atlas of European Trichoptera (Neu et al., 2018; Schmidt-Kloiber et al., 2017). Some criteria were established for community selection for maximizing region-to-region comparability in terms of sample size, spatial extent and quality. Essentially, local communities had to contain at least five different species and 50 individuals collected on one specific date, and at least 10 communities were required inside each ER. Given that the streams in the dataset reached their diversity peaks between June and September, only occurrences sampled during the summer period of the last 60 years were considered in order to compare local data. The final dataset included 180 communities (10 communities in each of the 18 selected ERs) containing a total of 340 species belonging to 23 families.

2.2 | Phylogenetic analyses

Available DNA sequences of the mitochondrial *cytochrome c oxidase subunit I* gene (*cox1*; 658 bp, DNA barcode), the *18S ribosomal RNA* gene (*18S*; 538 bp), and three nuclear genes: *wingless* (*wg*; 472 bp), *cadherin* (*cad*; 850 bp) and *elongation factor-1 alpha* (*ef-1α*; 1087 bp) were compiled from GenBank and the DNA-barcode project 'Trichoptera Barcode of Life' (Zhou et al., 2016). All species with at least one gene were used for building the phylogenetic tree. The final genetic dataset contained 509 European species representing 23 families and also four species of Lepidoptera as outgroup taxa (Supporting Information Table S2). DNA sequences were aligned in MAFFT 7 (Katoh & Standley, 2013). To account for the base composition heterogeneity across taxa (Thomas et al., 2020), all protein-coding positions were assessed with the 'basefreq' command in PAUP*4.0b10 (Swofford, 2003), which tests for base frequency differences among taxa. Only the third-codon positions of the *cox1* gene revealed significant heterogeneity. Consequently, to remove the systematic error caused by nucleotide saturation in phylogenetic analyses (Thomas et al., 2020), all purines in third-codon positions were coded as R (which is interpreted as A or G), and all pyrimidines in third-codon positions were coded as Y (C or T). As a result, the second test for base composition heterogeneity was non-significant. To select the best-fit partitioning schemes and models of molecular evolution for phylogenetic analyses, PARTITION FINDER 2 (Lanfear et al., 2017) was used. The models of sequence evolution were implemented for different partitions of the genes, starting at different codon positions in the case of protein coding genes ('fullcodon' code). The *18S* was treated as a single partition. The best model of substitution for each partition was determined using the Akaike information criterion (AIC). The Randomized Axelerated Maximum Likelihood method for maximum likelihood based phylogenetic inference (Stamatakis, 2014) was used in 999 bootstraps to reconstruct phylogenetic relationships, under the GTRGAMMA model of evolution. As conservative measures of node support, only bootstrap values of 80% or greater were considered. A time relative ultrametric tree was obtained using PATHd8 (Britton et al., 2002).

2.3 | Functional traits

Given that an extensive functional space (FS) covering a wide range of taxa, spatial scales and trait categories provides a precise estimation of functional diversity (FD) metrics (Múrria et al., 2020), all available biological traits at species level covering all major families of European Trichoptera were extracted from the website http://www.freshwaterecology.info (Graf et al., 2019). After data compilation, species with high amounts of missing data were removed in order to maximize the number of species and the trait coverage across species. Finally, a total of six biological characteristics including 23 categories (Supporting Information Tables S3, S4) was considered. The selected traits were respiration strategy, feeding type, emergence period, maximum forewing length of males and females (considered to be indicative of active dispersion capacity), type of dispersion and oviposition. Information regarding these traits was available for 197 out of 1,425 species belonging to 21 families and occurring mainly in central Europe.

A dissimilarity matrix based on the Gower distance, which was adapted to handle fuzzy-coded, quantitative and binary traits (Pavoine et al., 2009), was derived using the trait matrix. The traits 'feeding type', 'emergence period', 'type of dispersion' and 'oviposition', which presented intraspecific variability, were handled using the 'prep.fuzzy.var' function of the 'ade4' package (Dray & Dufour, 2007) in R (R Core Team, 2019), following a fuzzy coding approach (Chevenet et al., 1994). The trait 'maximum forewing length' was considered a numerical continuous variable, while 'respiration' was codified as a multichoice nominal variable that was transformed into binary by the 'prep.binary' function. The FS was built using a principal coordinates analysis (PCoA) from which the three most explanatory axes were retained. Pearson correlation coefficients (r) were used to identify which traits were correlated with each axis in the FS. To estimate the occurrence probability of different trait combinations in the FS, the kernel density estimation method was used through the package 'ks' (Duong, 2018).

2.4 | Phylogenetic trait conservatism

To assess the phylogenetic conservatism of each trait as well as of the three most explanatory functional PCoA axes, the Blomberg's K-statistic was estimated by the function 'multiphylosignal' available in 'picante' (Kembel et al., 2010). Blomberg's K-statistic seeks to quantify the degree to which variation in a trait is explained by the structure of the phylogenetic tree compared to an expected value derived from Brownian motion trait evolution. This function also calculates a P-value based on the variance of phylogenetically independent contrasts (PICs) relative to tip shuffling randomization. Traits with PIC.variance. P < .05 have non-random phylogenetic signals. In these cases, values of $K > 1$ indicate trait conservatism, whereas values $K < 1$ indicate less phylogenetic signal than expected, which means that trait composition is unrelated to evolutionary history.

2.5 | Taxonomic diversity

Species richness (or taxonomic richness, hereafter refered to as TRic) was used to estimate the TD in a community (α-TD) and within an ER (γ-TD) because the species list was a presence/absence matrix. β-diversities among local communities within an ER and among ERs were estimated using the Sørensen dissimilarity index, which was partitioned into its turnover and nestedness components (based on '$\beta_{Sor} = \beta_{Sim} + \beta_{nes}$'; Baselga, 2010), using the 'beta.multi' (among local communities) and the 'beta.pair' (among ERs) functions of the package 'betapart', respectively (Baselga et al., 2018). A null model involving 1,000 randomizations of species occurrences in each ER, while fixing γ-diversity to the TRic in the least diverse ER, was used to remove effects of varying γ-diversity among ERs.

2.6 | Phylogenetic diversity

The mean of all pairwise phylogenetic distances (MPD; Webb et al., 2002) among species within a community and within ERs were used to measure, respectively, α-PD and γ-PD for each ER. The MPD metric was selected because it is independent of species richness within the community, sensitive to deep branching structure in phylogenetic trees and therefore less sensitive to poorly resolved phylogenies (Cadotte & Davies, 2016).

In order to distinguish between phylogenetic clustering or overdispersion, the standardized effect sizes (SES) of MPD metrics within communities (local scale) and within ERs (regional scale) were calculated by the function 'ses.mpd' using 'picante' in R (Kembel et al., 2010). The 'taxa.labels' null model was used, which shuffles the labels of a distance matrix across all taxa included in the matrix, in 9,999 iterations. To account for the phylogenetic β-diversity between localities and ERs, the β-phylogenetic Sørensen index based on Faith's PD (Faith, 1992) was discomposed into the turnover and nestedness components using the functions 'phylo.beta.multi' and 'phylo.beta.pair' of the 'betapart' package, respectively. Again, the effect of the varying γ-PD was minimized by a null model with 1,000 permutations.

2.7 | Functional diversity

The FRic was calculated by the function 'fric_3d' (Gutiérrez-Cánovas et al., 2021), which computes the hypervolume defined by all species captured within a community in the first three axes of the FS. To determine how each community fills the functional space, the FDis was calculated using the function 'fdisp_k_sub' (Gutiérrez-Cánovas et al., 2021). To remove effects of the varying number of functionally described species in the calculation of FD among localities and regions, the FRic and FDis values for each ER were calculated as the mean values of 999 iterations using the species richness of the least diverse ER in terms of species with associated traits information. Likewise, the β-FD among localities and ERs were calculated and partitioned using the functions 'functional.beta.core', 'functional.beta.multi' and 'functional.beta.pair' of the 'betapart' package. Finally, to test for functional clustering or overdispersion at the two scales, the SES of the FRic and FDis metrics were calculated using custom-made functions and the 'independent-swap' null model in 9,999 iterations (Swenson, 2014).

2.8 | Statistical analyses

The centroid of each ER's polygon was located in the centre of each ER using the function 'Calculate Geometry' in ArcGIS 10.6. To test the relationship of diversity dissimilarity and distance, the spatial distances between the centroids of each pair of ERs were measured using the function 'GeoDistanceInMetresMatrix' (Rosenmai, 2014).

All diversity metrics at the local and regional scale were correlated to the latitude of the localities and ER centroids, respectively, and linear and quadratic regression models were fitted in R using the function 'lm'. At the local scale, the estimates of 'beta.multi' within each ER were correlated to the mean latitude of all communities within a region. ER2 (the Pyrenees) was excluded from the regression models due to the high spatial aggregation of localities. At the regional scale, the pairwise Sørensen, turnover and nestedness dissimilarity and geographical distance matrices among ERs were correlated using Mantel tests. Linear and quadratic regression models were tested when a significant correlation between β-diversity and geographical distance was found.

3 | RESULTS

3.1 | Phylogenetic tree and niche conservatism

The phylogenetic tree (Supporting Information Figure S1) was concordant with previous taxonomic classifications (Garcia-Raventós et al., 2021; Thomas et al., 2020), but it contained various polytomies. The three main suborders were highly supported (Annulipalpia, Spicipalpia and Integripalpia; Kjer et al., 2001). Integripalpia can be divided into two infraorders (Plenitentoria and Brevitentoria), both well supported. Spicipalpia did not appear to be monophyletic groups, consistent with previous findings (Kjer et al., 2001; Thomas et al., 2020). Plenitentoria, the group that includes the largest family Limnephilidae, presented the most unresolved nodes, likely because of insufficient gene and species coverage (Supporting Information Table S2). Even though the phylogenetic tree contained a few unresolved basal nodes, the majority of the nodes were highly supported and therefore conclusions regarding patterns found could still be drawn.

The first three PCoA axes captured 53% of the total variance of the functional traits (PCoA1: 23.1%, PCoA2: 20.4%, PCoA3: 9.5%, Figure 2a). The traits that were significantly correlated to the first axis of the PCoA were the feeding type shredder, dispersion and respiration strategies and forewing size, while the feeding types grazer and predator as well as the oviposition type were related to the second axis (Supporting Information Table S5). In general, species within the same family were located in close proximity on the FS (e.g., all Rhyacophilidae and Ecnomidae species are predators, while Ptilocolepidae and Beraeidae seem to be grazers). However, a few families revealed high variability in trait composition, such as the Leptoceridae and Goeridae along the axis PCoA2 (Figure 2b).

The positions of the species on the first two PCoA axes were not phylogenetically conserved, indicating a recent divergence of the functional traits that determine the position on the FS within clades. Consequently, the position on the functional space is related to the recently acquired functional traits regardless of the phylogeny and therefore the patterns of PD and FD can be evaluated separately. However, each trait category showed a different signature on the phylogeny (Table 1). For instance, the respiration through gills and the feeding categories xylophagous, passive filterer and predator were highly conserved, whereas most of the oviposition and dispersion trait categories were not.

3.2 | Local patterns of diversity

At the local scale, α-TD, α-PD and α-FD were unrelated to latitude ($r^2 = .09$, $r^2 = .09$ and $r^2 = .05$, $p < .05$, respectively) and were not significantly different from the expected values (Figure 3a–d, i). Multiple-site β-TD and β-PD declined latitudinally and were mostly driven by turnover ($r^2 = .7$ and $r^2 = .66$, $p < .001$, respectively). The nestedness component of β-TD and β-PD increased with latitude ($r^2 = .65$ and $r^2 = .31$, $p < .05$, respectively), even though they maintained low values (Figure 3a–b, ii). Both the turnover and nestedness components of β-FD were unrelated to latitude ($r^2 = .21$, $r^2 = .19$, $p < .05$, respectively; Figure 3c, ii).

3.3 | Regional patterns of diversity

Regional values of TRic and MPD linearly declined with latitude ($r^2 = .35$ and $r^2 = .78$, $p < .001$, respectively; Figure 4a–b, i). Observed values of MPD were significantly higher than expected in the Mediterranean ecoregions (ER1, ER2, ER3, ER6 and ER7) indicating phylogenetic overdispersion, whereas these values were lower than expected in the northern ecoregions ER20 and ER22 revealing phylogenetic clustering (Figure 4b, i, orange and green points, respectively; Supporting Information Table S6). In contrast, estimates of FRic and FDis displayed unimodal relationships with latitude ($r^2 = .48$, $p < .05$ and $r^2 = .66$, $p < .001$, respectively; Figure 4c–d, i; Supporting Information Tables S7 and S8). Observed values of FDis were almost always higher than expected, indicating overdispersion of traits, with the exception of the central European ecoregions ER4, ER8 and ER9 (Figure 4d; Supporting Information Table S8).

Among ERs, pairwise β-TD and β-PD increased linearly with geographical distance ($r^2 = .56$ and $r^2 = .60$, $p < .001$, respectively) and were driven mostly by turnover ($r^2 = .48$ and $r^2 = .63$, $p < .001$, respectively) (Figure 4a–b, ii, iii). In contrast, β-FD among regions increased with geographical distance and decreased in distances longer than 2,000 km ($r^2 = .57$, $p < .001$). In general, values of β-FD were lower than β-TD and β-PD, revealing higher functional than taxonomic or phylogenetic similarity among regions. Moreover, the nestedness component of β-FD was more prominent than the turnover but did not follow any clear pattern ($r^2 = .33$, $p < .001$), while turnover increased with distance ($r^2 = .40$, $p < .001$) (Figure 4c, ii, iii).

When examining pairwisely β-TD and β-PD between ERs, the contributions of the turnover and nestedness components across geographical distance from each ER were different. For instance, from the Iberian Peninsula (ER1) turnover displayed a strong direct relationship with geographical distance ($r^2 = .84$, $p < .001$), while the nestedness component was unimodal ($r^2 = .37$, $p < .05$) (Figure 5a). However, the closely neighbouring ecoregions ER4, ER8 and ER9 (central Europe) held the largest residuals in the linear models
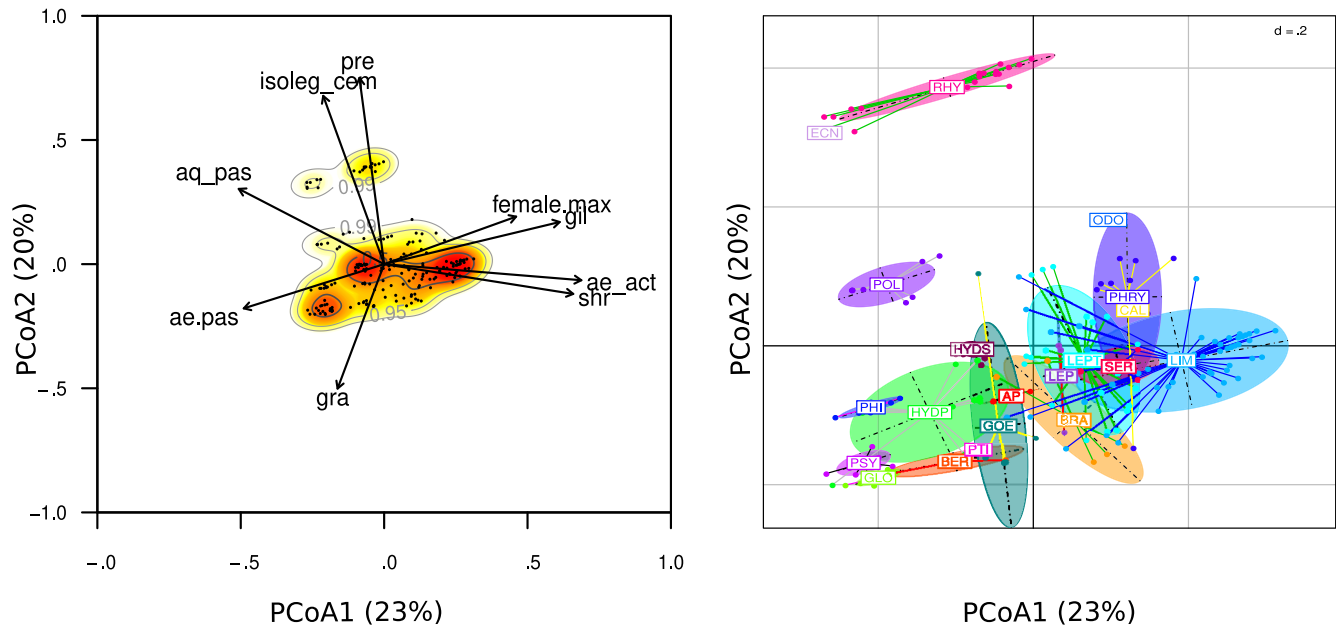
FIGURE 2 (a) Kernel density estimation plot, showing two principal coordinates analysis (PCoA) axes. ae.pas, aerial passive; aq_pas, aquatic passive; ae_act, aerial active; isoleg_cem, isolated eggs, cement; pre, predator; female.max, max. length of female anterior wing; gil, gill; shr, shredder; gra, grazer. (b) The functional space defined by the first two axes, with Trichoptera species grouped by families. Parameter '*d*' represents the proportion of the representation scale between axes 1 and 2, here *d* = .2 means that the scale of axis 2 is multiplied five times with respect to axis 1. Abbreviations of family names: AP, Apataniidae; BER, Beraeidae; BRA, Brachycentridae; CAL, Calamoceratidae; ECN, Ecnomidae; GLO, Glossosomatidae; GOE, Goeridae; HYDS, Hydropsychidae; HYDP, Hydroptilidae; LEP, Lepidostomatidae; LEPT, Leptoceridae; LIM, Limnephilidae; ODO, Odontoceridae; PHI, Philopotamidae; PHRY, Phryganeidae; POL, Polycentropodidae; PSY, Psychomyiidae; PTI, Ptilocolepidae; RHY, Rhyacophilidae; SER, Sericostomatidae

of turnover and nestedness, meaning that the Iberian Peninsula shares a high number of species with those regions (nestedness), but as distance from central Europe increases, these species are replaced by turnover. Similar patterns of dominant contribution of turnover over nestedness were observed from Italy (ER3) and the Hellenic Western Balkan (ER6) (Supporting Information Figure S2). In contrast, departing from the Central Highlands, the Alps (ER4) or the Western Highlands (ER8) (see Figure 5b, Supporting Information Figure S2 for the results of the regression models) the dominance of nestedness over turnover increased by distance between the southern and northern latitudes. Finally, departing from the Borealic Uplands (ER20) or the Fenno-scandian Shield (ER22), the turnover component was predominant, particularly in respect to Mediterranean peninsulas, whereas the nestedness component was stronger toward other northern (ER14 and ER15) and central (ER4, ER8 and ER9) ecoregions (see Figure 5c for the results of the regression models).

4 | DISCUSSION

The patterns of TD, PD and FD at the local and regional scales showed low congruence, which indicates that the underlying mechanisms that shape macroecological patterns might act differently at different scales. At the regional scale, γ-diversities as well as β-TD and β-PD among ERs were strongly correlated to

latitude, which reveals evidence for the joint effects of biogeography and environmental filtering related to climatic conditions, which is in accordance with previous findings for caddisflies (Conti et al., 2014; Hering et al., 2009). Contemporary environmental filtering by extreme climatic conditions and an incomplete re-colonization after the Last Glacial Maximum have likely restricted regional-scale species richness in the north. In southern latitudes, species accumulation over time, probably favoured by long-term habitat stability during the Pleistocene, has contributed to higher values of MPD (and FDis) than expected. As a result, northern species pools were found to be phylogenetically and functionally clustered while the southern ones were overdispersed. In contrast, at the local scale, patterns of TD, PD and FD and their similarity among communities within each ER (local-scale β-diversity) were independent of the latitude. Despite the slight decline of α-diversity towards northern latitudes, each locality hosted similar diversity, and therefore local factors (e.g., habitat heterogeneity, resource availability) seem to override the effects of regional factors (e.g., environmental conditions, biogeographical history) on current dynamics of local community assembly.

4.1 | Contemporary environmental filtering

Estimates of α-diversity were comparable across latitudes. This result supports the dependence of large-scale patterns of α-diversity

TABLE 1 Blomberg's K and PIC.variance of P. PCoA axis and trait categories with PIC.variance. P < .05 (in bold) have non-random phylogenetic signals. In these cases, values of $K > 1$ indicate trait conservatism, whereas values $K < 1$ indicate less phylogenetic signal than expected, meaning that trait composition is unrelated to evolutionary history

Traits	Categories	Blomberg's K	p-value (PIC. variance.P)
PcoA axes	PCoA-1	0.002	**.011**
	PCoA-2	0.009	**.005**
	PCoA-3	0.001	.069
Respiration	Tegument	0.201	.292
	Gills	2.292	**.001**
Forewing length	Male max.	0.013	**.001**
	Female max.	0	.577
Emergence period	Winter	0.074	.332
	Spring	0	.336
	Summer	0	.241
	Autumn	0	.113
Feeding type	Grazer	0.676	**.001**
	Xylophagous	1.266	**.001**
	Shredder	0.439	**.001**
	Gatherer	0.160	**.002**
	Passive filter feeder	1.674	**.001**
	Predator	1.251	**.001**
	Other	0.749	**.001**
Oviposition	Isolated eggs, cement	4.114	**.001**
	Clutches: cemented/fixed	0.713	**.001**
	Clutches: free	0.478	**.001**
	Clutches: terrestrial	0.408	**.001**
Dispersion type	Aquatic passive	0.519	**.001**
	Aquatic active	0.803	**.001**
	Aerial passive	10.882	**.001**
	Aerial active	2.183	**.001**

Abbreviation: PCoA, principal coordinates analysis.

upon the local habitat characteristics and heterogeneity, which determine the carrying capacities of diversity in rivers (Vinson & Hawkins, 2003). The similar values of α-diversity among ERs indicate that the community data used within ERs cover a wide range of habitat conditions and heterogeneity. This result is not entirely surprising since similar patterns of α-diversity were previously described for other freshwater macroinvertebrate groups, especially for Ephemeroptera and Plecoptera (Heino, 2011; Múrria et al., 2017). Trichoptera are commonly found across a large gradient of temperature, from thermal streams or arid-intermittent rivers to cold environmental conditions at different elevations and latitudes (Graf et al., 2007). Their diverse adaptive functional traits explain the

high diversity within the group and their presence in the majority of freshwater habitats (Morse et al., 2019). As a result, large-scale studies of caddisflies have concluded that local community composition is determined by elevation and factors related to it, such as slope, bed stability, water temperature, current velocity, substratum composition and stream hydraulics (Morse et al., 2019). Here, we confirm this result and suggest that further analyses on macroecological patterns of local diversity should take into account other types of gradients rather than only latitude, such as elevation, water temperature, disturbance (e.g., droughts or flood events, land use), acidity, habitat heterogeneity and/or productivity, because these variables strongly affect local community assembly mechanisms (Heino, 2011).

Within ERs, the fact that α-diversity did not vary with latitude implies that the decline of γ-diversity is mainly due to the decline in β-diversity among communities. Indeed, β-TD within ERs declined when moving from the Mediterranean towards central European ERs and its curve flattened after 50° of latitude. Moreover, despite the fact that β-TD and β-PD between local communities were dominated by the turnover component independently of the latitude, our results reveal a slight increase of the contribution of the nestedness component to β-diversity towards the poles. The opposite latitudinal patterns of the contribution of turnover and nestedness, which support the latitudinal decline of γ-diversity, are in accordance with previous studies using different taxa (Baselga, 2010; Soininen et al., 2018). However, ambiguous results have been found across freshwater lineages (Heino, 2011; Soininen et al., 2018). An exception is the rise of β-TD in ER22 (Fenno-scandian Shield), one of the largest areas studied, which included localities with a scattered distribution separated by longer distances compared to other regions. In large ERs, the intrinsic limited dispersion and the long topographic and environmental distances between sites increase the β-TD within ERs, which is not captured by β-PD and β-FD, and enhance isolation by distance and filtering processes, respectively (Heino et al., 2015).

Among ERs, estimates of TRic and MPD declined linearly with latitude, according to our hypotheses. This is consistent with global patterns of species richness decline for a wide range of terrestrial and freshwater biota when moving towards the poles (Gaston, 2000). Several explanations have been suggested to explain the latitudinal decrease of TRic and MPD. For instance, environmental filtering by extreme climatic conditions in the north as well as an incomplete recolonization after Pleistocene glaciations may explain the observed patterns of γ-diversity (Pinkert et al., 2018). Moreover, high speciation rates and species accumulation over time in the south, favoured by habitat stability during the Pleistocene (Hewitt, 2004), have contributed to higher values of MPD than expected, which are also reflected in the high levels of FDis. Besides, southern areas are characterized by high habitat heterogeneity and seasonal precipitation, favouring stream intermittency that may promote ecological adaptations and therefore an increase of overall TRic, MPD and FDis (Bonada et al., 2007). Hence, in long-term stable southern ERs there is a co-existence of species accumulated since the Pleistocene, comprising specialist and generalist species.
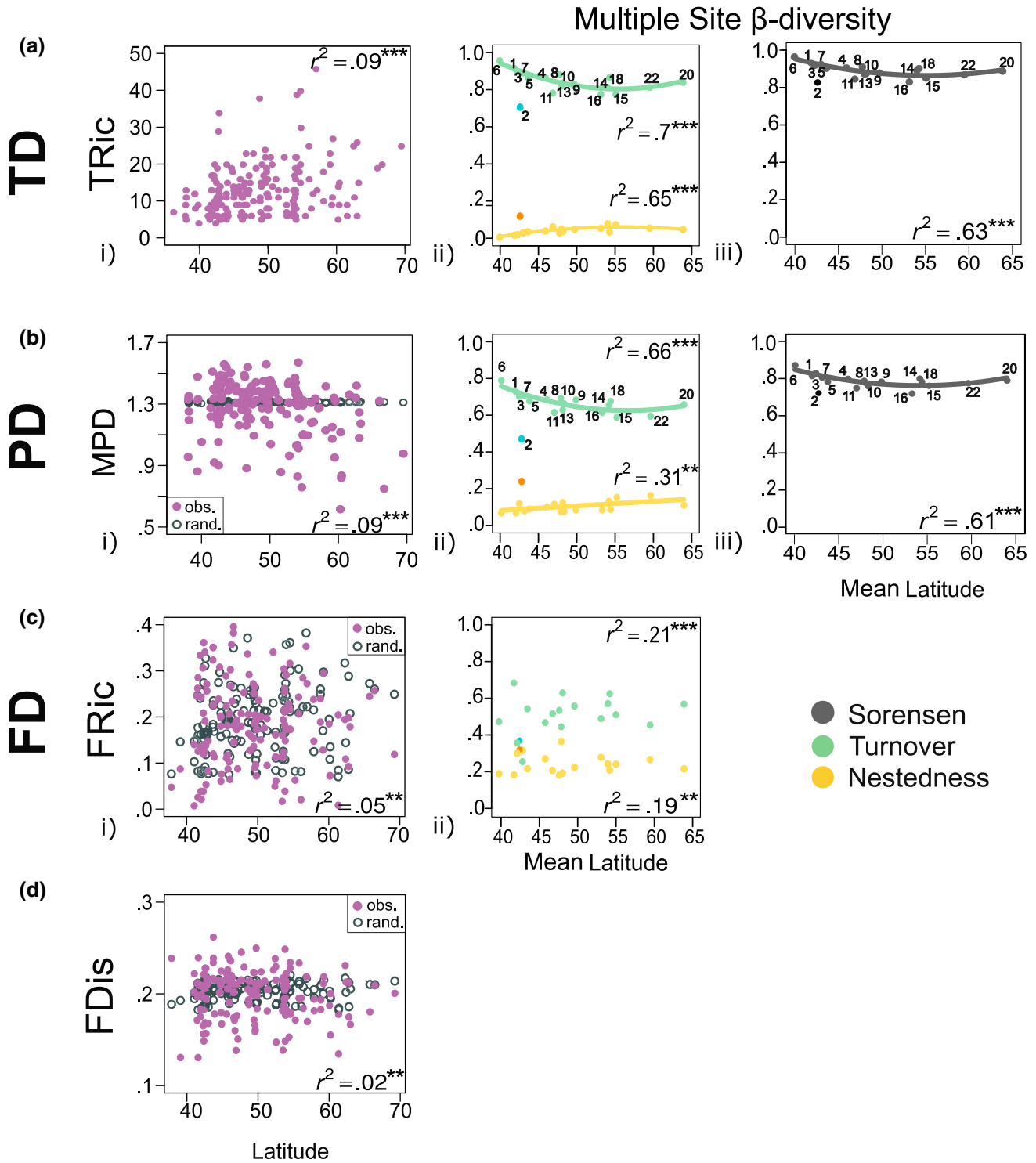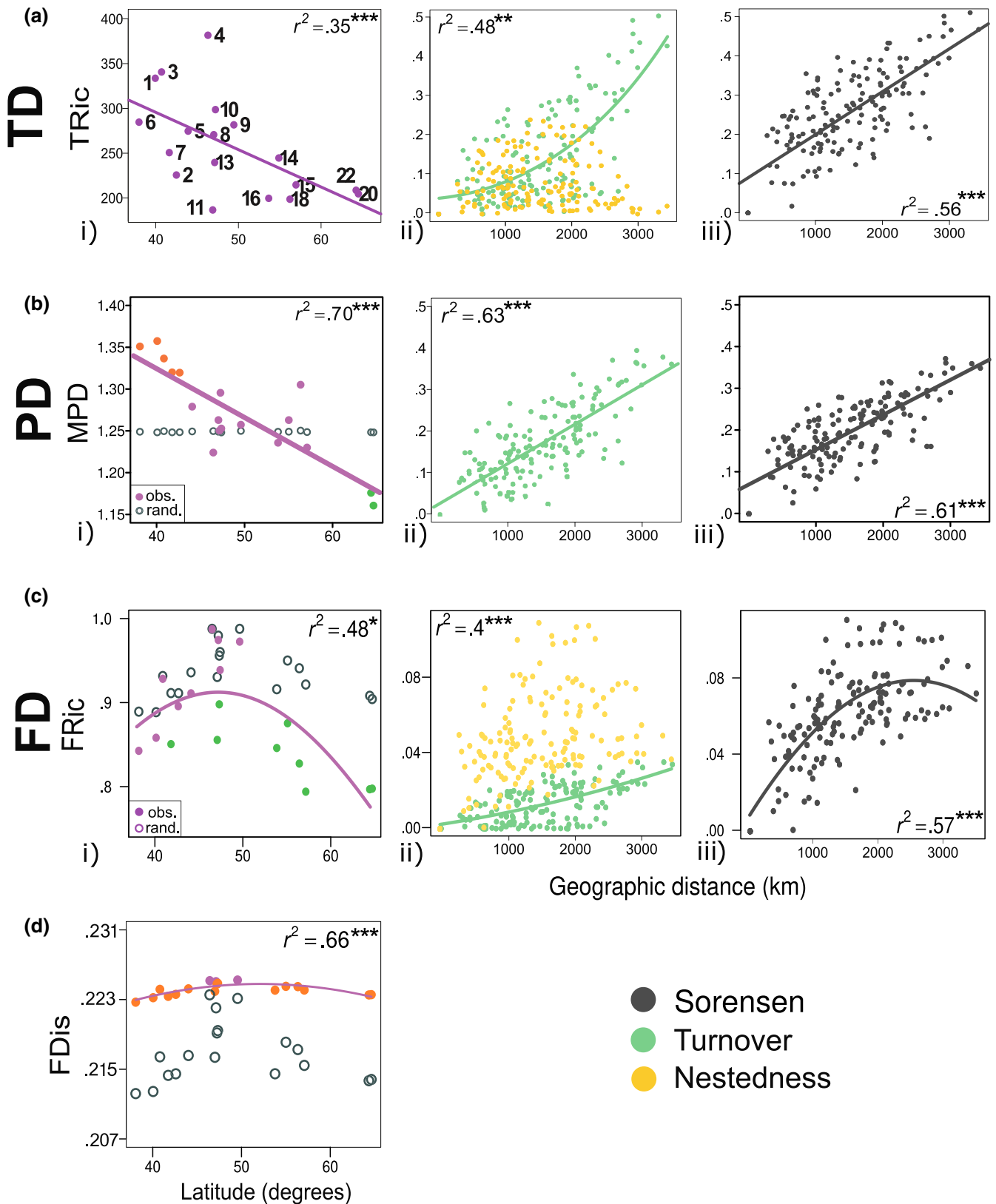
FIGURE 3 Local patterns of diversity. In each row, a different facet of diversity is shown. In the first column (i) local α-diversity with respect to latitude and in (d) the functional dispersion (FDis) also with respect to latitude. Empty grey circles are the expected values derived from a null model, while filled purple circles are the observed values. In the second column (ii) the mean multiple-site turnover (β$_{SIM}$) and nestedness (β$_{SNE}$) between communities of the same ecoregion (ER) with respect to the mean latitude of the ER are shown. The orange and blue points correspond to ER2 (excluded from the analyses). The third column (iii) shows the overall mean β-diversity (β$_{SOR}$) between communities of the same ER. ER2 is shown as the black point (***$p < .001$, **$p < .01$). FD, functional diversity; PD, phylogenetic diversity; TD, taxonomic diversity; FRic, functional richness; MPD, mean of all pairwise phylogenetic distances; TRic, species richness

Pairwise β-diversity

In contrast to patterns of TRic and MPD, FRic and FDis displayed unimodal relationships with maximum values in central Europe, instead of the predicted linear decline. This result reveals that the FD of caddisflies is not directly analogous to species richness. The low estimates of FRic in Mediterranean ERs might be attributed to the geographical isolation from central Europe by

FIGURE 4 Regional patterns of diversity. In each row, a different facet of diversity is shown. In the first column (i) linear and quadratic regressions of the regional γ-diversity with respect to latitude are shown. Empty grey circles are the expected values derived from a null model, while filled purple circles are the observed values. Orange colour indicates phylogenetic/functional overdispersion, while green indicates clustering. In the second column (ii) linear regressions of the pairwise β-dissimilarity (β_{sor}) with respect to geographical distance are depicted, while the third column (iii) shows the relationship of turnover (β_{sim}) and nestedness (β_{nes}) with geographical distance (***$p < .001$, **$p < .01$, *$p < .05$). FD, functional diversity; PD, phylogenetic diversity; TD, taxonomic diversity; FRic, functional richness; MPD, mean of all pairwise phylogenetic distances; TRic, species richness
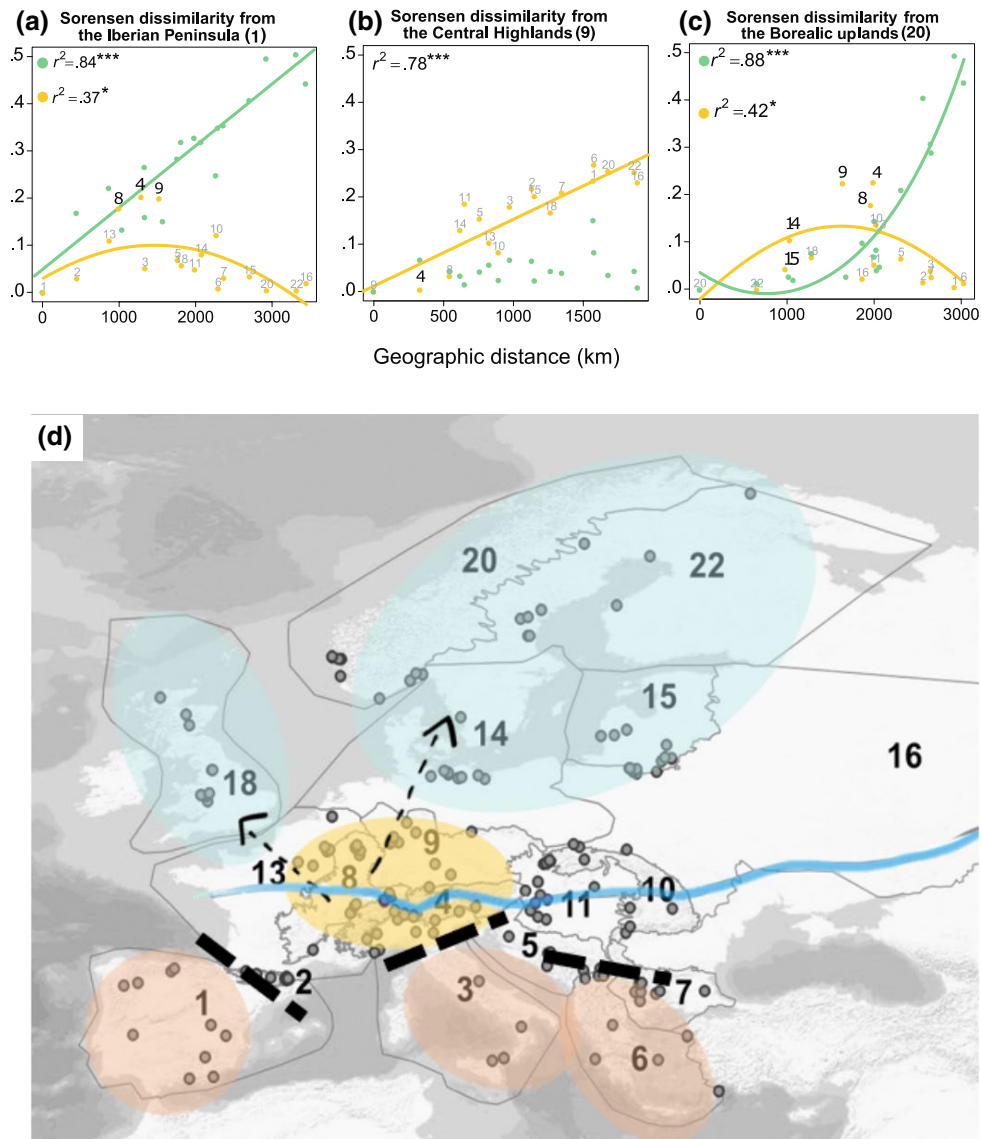

(a) Sorensen dissimilarity from the Iberian Peninsula (1)
$r^2 = .84$***
$r^2 = .37$*

(b) Sorensen dissimilarity from the Central Highlands (9)
$r^2 = .78$***

(c) Sorensen dissimilarity from the Borealic uplands (20)
$r^2 = .88$***
$r^2 = .42$*

Geographic distance (km)

FIGURE 5 (a–c) Sørensen β-taxonomic diversity (β-TD) discomposed into the turnover (green) and nestedness (yellow) components as a function of geographical distance starting from three different ecoregions (ERs), in the south (a), centre (b) and north of Europe (c). Values in black are mentioned in the Discussion (***$p < .001$, *$p < .05$). Results were the same for β-phylogenetic diversity (β-PD). (d) Possible recolonization routes (dashed arrow lines) following the Pleistocene glaciations and the 0 °C isotherm (bold blue line) at the Last Glacial Maximum, as in Hortal et al. (2011). Our findings support that northern ERs (in blue) were recolonized by species from refugia located in central Europe (yellow), while species of the Mediterranean ERs (orange) were spatially restricted by high mountain ranges (bold dashed lines)

the Pyrenees, the Alps and the Dinaric Alps, which likely impedes character enrichment through colonization (Leprieur et al., 2009; Schleuter et al., 2012). Indeed, in the Mediterranean ERs, where speciation is favoured, species are less diverse in terms of traits

(low FRic) than in central Europe, where the same number of species is reached through colonization by multiple lineages, which possess several ancestral character states (Mittelbach et al., 2007; Reyjol et al., 2007). Hence, the greater connectivity between

central European ERs by large rivers, as opposed to the isolated Mediterranean peninsulas, enhances the regional patterns of diversity (Reyjol et al., 2007). Despite the overall low FRic, the higher-than-expected FDis in the Mediterranean area implies the co-existence of species with highly variable adaptations, which is likely related to the seasonality of available resources. An exception to the general trend of higher FRic at intermediate latitudes is ER11 (Hungarian Lowlands), probably because of the homogeneity of its habitats, as indicated by its narrower elevation gradient (Frost et al., 2007). Finally, the northwards latitudinal decline in FRic is a consequence of traits being constrained by climatic stress and historical legacy. This is a common finding for northern areas, where FRic is reduced by environmental filtering due to cold temperatures and low productivity (Hortal et al., 2011; Lamanna et al., 2014) or/and an incomplete recolonization after glaciations (Hof et al., 2008). However, this pattern is not followed by FDis, which is still higher than expected. The reason behind the high values of FDis might be the functional adaptations to cold climate, likely located in extreme positions in the FS, such as wider diets, freezing tolerant eggs and larvae, reduced wing size and temporal separation of related species driven by different emergence periods (Danks, 2007).

The difference in the patterns of β-diversity at the two grain-sizes is in line with the statement that latitudinal patterns are mainly shaped by the decline of the regional γ-diversity rather than the variation in the α-diversity (Witman et al., 2004). Indeed, our results in combination with findings by Shah et al. (2015) suggest a gradual decrease in the slope of the linear model describing the relationship of caddisfly diversity with latitude in Europe; the steepest slope observed at the regional scale declines at the 1° × 1° latitudinal band scale and is completely eliminated at the local scale.

4.2 | The biogeographical signature

Patterns of β-TD and β-PD among ERs revealed that after the Pleistocene the northern areas were recolonized by highly dispersive, cold-tolerant species that came from central Europe and possess functional traits that allowed them to establish in the harsh northern environment. This is supported by the high contribution of turnover to β-diversity from the Mediterranean ERs towards northern regions, which reveals that species from the mostly isolated Mediterranean peninsulas did not overpass the extrinsic dispersal barriers (e.g., topography, abiotic factors associated with the environmental gradient) across the Pyrenees, Alps and Dinaric Alps. Moreover, moving away from the Alps, the Central or Western Highlands, the increasing contribution of nestedness to β-diversity with geographical distance suggests that the recolonization of the north could have initiated from one or more of these regions (Figure 5b and Supporting Information Figure S2). Hence, our findings are against the idea that northern communities were recolonized exclusively by species from the Mediterranean refugia (Hewitt, 2004) and support the important contribution of extra-Mediterranean refugia located

in central Europe to current macroecological patterns (Garcia-Raventós et al., 2021; Malicky, 2006; Pauls et al., 2006; Schmitt & Varga, 2012).

Using three facets of diversity simultaneously, we can suggest several recolonization routes (Figure 5d). For instance, our results suggest that a recolonization route departing from central Europe (ERs 8, 9) reached the Scandinavian peninsula (ERs 20, 22) via the Central Plains (14) and the Baltic Province (15), since they show that taxonomically ER14 is a subset of 9, ER15 is a subset of 14 and ERs 20 and 22 are subsets of both (Figure 5c and Supporting Information Figure S2). Another potential pathway of northern recolonization would originate from the Western Highlands (ER8) to reach England (ER18) through the Western Plains (ER13) (Supporting Information Figure S2). In fact, in the past 500 kyr, Britain's geographical status has fluctuated between an island and a peninsula of Europe several times as sea-levels rose and fell in response to global climate change (White & Schreve, 2000). As a result, the connection between ER8 and ER13 by the rivers Seine and Loire would favour dispersion of larvae and adults among ERs. In contrast, the expected high contribution of the Carpathians (ER10) as a refugium during the Pleistocene (Kühne et al., 2017) was surprisingly rejected here, because very low nestedness was observed from ER10 to northern ERs. The lack of big rivers connecting the Carpathians to northern ERs may explain the isolation of this mountain range. Our findings do not suggest that every caddisfly species has followed the same path, but rather provide two hypothetical recolonization routes and some insights for further research using other groups. These hypothetical recolonization routes have already been suggested for some caddisfly species (Pauls et al., 2006; Wilcock et al., 2001), Lepidoptera (Schmitt & Krauss, 2004), Coleoptera (Mayer et al., 2014) and several other taxa (Schmitt & Varga, 2012). Compared to previous studies, our approach is a paradigm of how recolonization routes can be assessed using macroecological patterns of the current diversity captured in taxonomic, functional and phylogenetic metrics.

In conclusion, this study combines data for three facets of diversity at a continental scale, assessed at two distinct range sizes. Until now the majority of macroecological studies on diversity patterns of freshwater insects have focused exclusively on the taxonomic diversity (Heino, 2011; Vinson & Hawkins, 2003). The consideration of functional and phylogenetic diversity elucidates unknown aspects of biogeographical history and can yield useful insights for freshwater conservation. Nonetheless, for performing macroecological studies that include taxonomic, functional and phylogenetic data, there is an urgent need for open-source data and across-country collaboration.

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SUPPORTING INFORMATION

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