



Global quantitative synthesis of ecosystem functioning across climatic zones and ecosystem types

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Abstract

Aim: Providing a quantitative overview of ecosystem functioning in a three-dimensional space defined by ecosystem stocks, fluxes and rates, across major ecosystem types and climatic zones.

Location: Global.

Time period: 1966–2019.

Major taxa studied: Ecosystem-level measurements (all organism types).

Methods: We conducted a global quantitative synthesis of a wide range of ecosystem variables related to carbon stocks and fluxes. We gathered a total of 4,479 values from 1,223 individual sites (unique geographical coordinates) reported in the literature (604 studies), covering ecosystem variables including biomass and detritus stocks, gross primary production, ecosystem respiration, detritus decomposition and carbon uptake rates, across eight major aquatic and terrestrial ecosystem types and five broad climatic zones (arctic, boreal, temperate, arid and tropical). We analysed the relationships among variables emerging from the comparisons of stocks, fluxes and rates across ecosystem types and climates.

Results: Within our three-dimensional functioning space, average ecosystems align along a gradient from fast rates–low fluxes and stocks (freshwater and pelagic marine ecosystems) to low rates–high fluxes and stocks (forests), a gradient that we hypothesize results mainly from variation in primary producer characteristics. Moreover, fluxes and rates decrease from warm to colder climates, consistent with the metabolic theory of ecology. However, the strength of climatic effects differs among variables and ecosystem types, resulting, for instance, in opposing effects on net ecosystem production between terrestrial and freshwater ecosystems (positive versus negative effects).

Main conclusions: This large-scale synthesis provides a first quantified cross-ecosystem and cross-climate comparison of multivariate ecosystem functioning. This gives a basis for a mechanistic understanding of the interdependency of different aspects of ecosystem functioning and their sensitivity to global change. To anticipate responses to change at the ecosystem level, further work should investigate potential feedbacks between ecosystem variables at finer scales, which involves site-level quantifications of multivariate functioning and theoretical developments.

KEY WORDS

carbon cycle, climate, decomposition, ecosystem functioning, global change, meta-ecosystem, metabolic theory of ecology, multifunctionality, primary production, productivity

1 | INTRODUCTION

Ecosystems provide multiple services, such as food, carbon storage and detritus recycling, that benefit humans (Alsterberg et al., 2017; Byrnes et al., 2014; Hector & Bagchi, 2007). These services result from the functioning of ecosystems, which is often described in studies either by individual ecosystem functions (e.g., production, stability; de Mazancourt et al., 2013) or by proxies that integrate different functions mathematically but not mechanistically (e.g., indices of multifunctionality; Soliveres et al., 2016). While both approaches possess strengths to address specific questions (e.g., relationship with biodiversity, ecosystem state assessment), it is also important to consider the dynamic processes underlying ecosystem functioning, because ecosystem functions are not independent from one another. This becomes increasingly important in the context of global change, because perturbations affecting some functions of an ecosystem, for instance trophic cascades affecting primary production, might then cascade to others, such as carbon storage (Atwood et al., 2015). To better forecast ecosystem response to such change, we need a mechanistic understanding of how the multiple aspects of ecosystem functioning constrain one another. With this study, we aim to advance in this direction by providing a quantitative synthesis

of multiple measures of ecosystem functioning in a mechanistic framework allowing comparisons across major ecosystem types.

We propose to consider the loop of matter transformation as the central process driving functioning at the ecosystem level, a process fundamental enough to be common to all ecosystem types, thus allowing cross-system comparisons, and linking mechanistically different essential ecosystem functions (see conceptual framework in Figure 1). Biological communities build biomass from inorganic material, respire and produce detritus that is then decomposed and mineralized into new inorganic material. This material processing loop generates fluxes connecting the different ecosystem compartments (such as primary production, detritus production, or decomposition), occurring at different speeds, hereafter called rates (e.g., uptake or decomposition rates). In our framework, we distinguish rates – defined as mass-specific fluxes – from fluxes themselves, because rates provide discriminating information on environmental and physiological constraints driving processes among ecosystem types (e.g., organism efficiency), which is entangled with community dynamics and organism abundance in fluxes. Overall, the balance of ecosystem fluxes results in specific distributions of matter among living and non-living ecosystem compartments – the stocks (i.e., biomass, detritus and nutrients). Stocks, fluxes and rates – the three

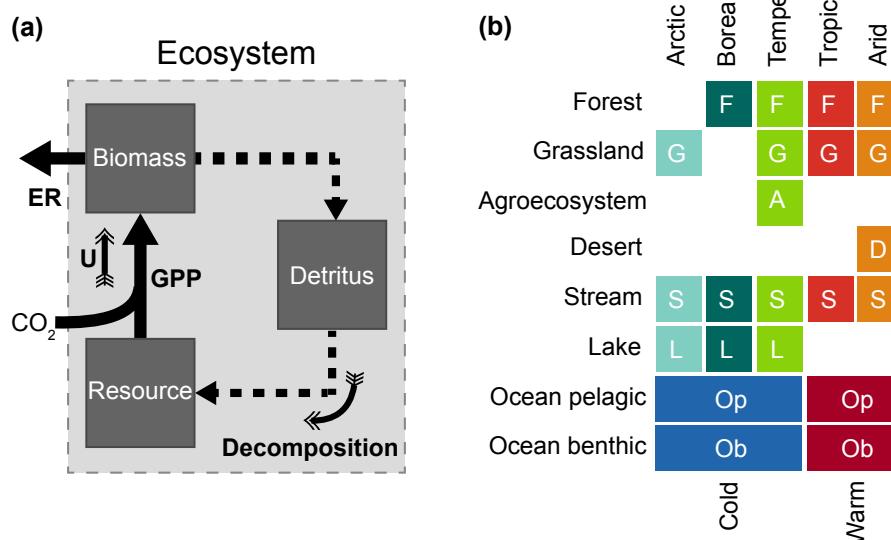


FIGURE 1 Study design. (a) Ecosystem functioning variables considered in the study for each ecosystem type \times climatic zone combination shown in panel (b). We compiled values of stocks [squares in (a)], fluxes (solid large arrows) and rates (arrows with feathers) from the literature. The dotted arrows denote production of detritus and decomposition flux, for which we did not gather estimates. For decomposition, we compiled rates (arrow with feathers) – the proportion of detritus processed per unit of time – because they were more available than fluxes. GPP = gross primary production; ER = ecosystem respiration; U = uptake rate. Note that GPP is a flux, that is, an amount of matter produced per unit of time and area, while U is a rate (i.e., mass-specific GPP), expressed in mass of carbon uptake per unit of biomass and time. In addition, we also gathered values of net ecosystem production [not shown in (a)] for all combinations displayed in panel (b). Letters in (b) stand for the ecosystem types mentioned on the left side [Colour figure can be viewed at wileyonlinelibrary.com]

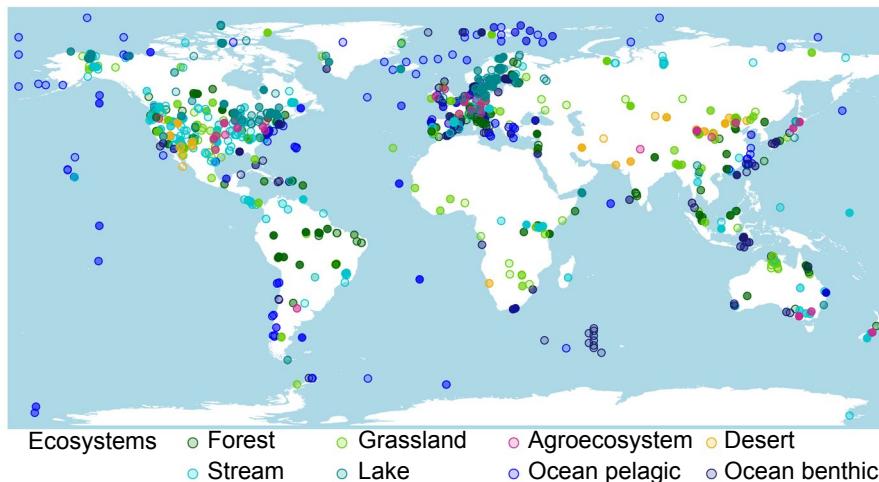


FIGURE 2 Geographical distribution of the data. Each dot shows the geographic location of sites from which we obtained data. Colours denote the different ecosystem types. Note that for about 13% of the data either the coordinates are not provided or the geographical scale given is too large or too coarse to be meaningfully reflected in the map (e.g., geographical scale in original study given as 'boreal forests of Canada'), thus these data points are not displayed here. The map is made with Natural Earth. Free vector and raster map data @ natural-earth-data.com [Colour figure can be viewed at wileyonlinelibrary.com]

dimensions of our ecosystem functioning space – link commonly used descriptors of ecosystem functioning associated with ecosystem services (e.g., biomass production, recycling of detritus, carbon storage). Their interdependency implies potential feedbacks; for instance, perturbations may increase the levels of dissolved organic carbon in lakes, which can boost phytoplankton production, and eventually lead to lake eutrophication (Brothers et al., 2014). This illustrates the need to adopt a comprehensive approach, integrating the whole loop of matter transformation when studying ecosystem functioning.

However, we still lack a general and quantitative synthesis linking stocks, fluxes and rates and comparing them across ecosystem types and climates. Knowledge on ecosystem functioning is concentrated in studies examining either individual aspects of ecosystem functioning in isolation [e.g., Biodiversity-Ecosystem Functioning approaches (Loreau et al., 2001) or cross-system comparisons of single functions (Tiegs et al., 2019)], or whole functioning in specific ecosystems [e.g., ecosystem ecology approach with fluxes and stocks budgets, for instance in Eyre and McKee (2002)]. A comparative synthesis of ecosystem functioning would reveal potential covariations among ecosystem fluxes, stocks and rates across ecosystem types, from which a holistic understanding of ecosystem functioning could emerge. Moreover, ecosystem functioning varies according to climatic constraints. For example, ecosystem processes, such as respiration or decomposition, slow down under colder climates (Tiegs et al., 2019; Yvon-Durocher et al., 2012). The metabolic theory of ecology (MTE) scales up the well-known relationship between body size and biological rates, and its dependency on temperature, to ecosystem processes (Brown, Gillooly, Allen, Savage, & West, 2004; Schramski, Dell, Grady, Sibly, & Brown, 2015). This provides predictions for changes in ecosystem fluxes and rates across temperature gradients (Schramski et al., 2015). Integrating this knowledge in a multivariate view of ecosystem functioning across ecosystem types

and climates would allow the characterization of ecosystems based on functional differences. This step is crucial to anticipate changes in ecosystem functions in response to global changes, and to upscale to global nutrient and carbon cycles.

In this study, we provide a quantified multivariate view of ecosystem functioning across major ecosystem types and climatic zones (i.e., at the biome scale; see Figure 1b). We focus on carbon, unified for stocks and fluxes across time and area, as a common currency to make the material loop comparable across systems. We assemble extensive empirical data from the literature on ecosystem carbon stocks (i.e., biomass, organic carbon, detritus), fluxes (i.e., gross primary production, ecosystem respiration), and rates (i.e., uptake and decomposition rates). We then examine the variation and co-variation of these ecosystem variables across ecosystem types and climatic zones. Our analysis characterizes broad types of functioning as well as patterns of functioning variation with climatic constraints, that we discuss in the light of the MTE.

2 | METHODS

2.1 | Study design

We collected empirical data of carbon stocks (biomass, detritus and organic carbon), fluxes [gross primary production (GPP), ecosystem respiration (ER) and net ecosystem production (NEP)] and rates (community carbon uptake rate, that is, mass-specific GPP = GPP/auto-troph biomass, and decomposition rate as described by the k constant) from the literature (Figure 1a) for eight major ecosystem types, both terrestrial [forest, grassland and shrubland (hereafter called 'grassland' for simplicity), agroecosystem and desert] and aquatic (stream, lake, ocean pelagic and ocean benthic), and for five climatic zones (arctic, boreal, temperate, tropical and arid). We lumped climatic

zones of ocean pelagic and benthic systems into 'Cold' and 'Warm' to account for lower climatic imprint on marine systems (see Figure 1b for the combinations considered and Supporting Information Table S1.1 of Appendix S1 for definitions). Note that, as rates are fluxes normalized by stocks, uptake and decomposition rates represent, respectively, the mass of carbon taken up per biomass unit, and the proportion of detritus decomposed in a given time (T^{-1} dimension). Notably, uptake rate conveys information about producers' biological efficiency and physiological constraints, while GPP also includes information on their abundance. We aimed at covering a wide range of ecosystem \times climate \times variable combinations, and retrieved at least 10 independent values for each of these combinations (see Supporting Information Appendix S1 for extended methods and a decision tree on study selection for data collection, and Supporting Information Appendix S2 for a detailed presentation of the dataset). Overall, we compiled a dataset of 4,479 data points from 1,223 individual sites (unique geographical coordinates) distributed across the globe (Figure 2), extracted from 604 published studies. The list of data sources is provided in the Appendix.

2.2 | Conversions

To make the dataset consistent, we homogenized the units of stocks, fluxes and rates into gC/m^2 , $gC/m^2/year$ and per year, respectively (noted as 'g/g/year' for uptake rates, for clarity). Data originally not provided in carbon units (21%) were converted with commonly accepted conversion factors, using preferentially the most specific one depending on the level of information available (see Supporting Information Table S1.2 for factors). Flux and rate data provided on time-scales shorter than a year (19%) were scaled up to a year assuming standardized numbers of growing days per climatic zone (Garonna et al., 2014). We also had to convert volume to areal units for some data on aquatic systems. We integrated metrics over the relevant depth of water column, which could be average depth (e.g., shallow stream) or depth relevant to pelagic production (e.g., Secchi depth for gross primary production in pelagic systems). We standardized soil and sediment organic carbon data by integrating values over the first 30 cm depth. Complete details on these unit conversions are provided in the extended methods (see Supporting Information Appendix S1).

2.3 | Data analysis

Our goal was to analyse the variation and covariation of the focal ecosystem variables across ecosystem types (E) and climatic zones (C). To reach this goal we used three complementary steps: (a) we used linear models to quantify the relative contribution of E and C in explaining the variance, and to test mean differences within each ecosystem variable; (b) then, we examined covariation between ecosystem variables with Pearson's correlation tests, using a bootstrapping procedure so that we could include the variance even

though data for the different ecosystem variables were measured in different sites; (c) finally, we used Pearson's correlation to test the relationships between ecosystem variables and latitude for each ecosystem type, to further analyse climatic modulation of ecosystem functioning. Together, these three approaches provide a holistic view on ecosystem functioning in the three-dimensional space of stocks, fluxes and rates.

2.3.1 | Differences among climatic zones (C) and ecosystem types (E)

As a first step, we ran a two-way ANOVA on each ecosystem variable to evaluate the extent to which they were explained by climatic zones (C), ecosystem type (E) and their interaction (C : E). We applied the linear model $y \sim C + E + C : E$ to log-transformed data. The few zero values of biomass, detritus and GPP (seven in total) were removed from this analysis to allow for log-transformation. NEP data were not log-transformed due to negative values. We also carried out these two-way ANOVAs on pooled categories of variables for stocks (biomass, detritus and organic carbon), gross fluxes (i.e., GPP, ER) and rates (uptake and decomposition rates). We scaled each variable between 0 and 1 before grouping to avoid giving different weights to variables among E \times C combinations due to different numbers of data points. Because the residuals were not homogeneously distributed, we repeated the model design using more conservative nonparametric Kruskal-Wallis tests on ranks, followed by post-hoc multiple comparisons based on rank sums to identify the groups that were significantly different; parametric and nonparametric tests give the same results on effect significance, so we report ANOVA results here to visualize the variance partitioning, and nonparametric tests are reported in the Supporting Information (see full statistical results in Supporting Information Appendix S3: Tables S3.1–S3.7). Finally, since C was found to be an important driver of fluxes and decomposition rate in the above analysis, and C : E interactions were significant, we investigated further climate sensitivity of these variables by comparing the variance explained by C within each ecosystem type. For that, we ran a series of one-way ANOVAs on GPP, ER and decomposition rates of each individual ecosystem type with C as the explanatory variable. Desert and Agroecosystem were excluded from this last analysis since we only had data from one climatic zone.

2.3.2 | Covariation among ecosystem variables

As a second step, we examined the correlations among ecosystem variables across ecosystems and climates. Since data were measured at different sites for each ecosystem variable, we did not have measurements of all the variables per site. We therefore adopted a bootstrapping procedure (sampling with replacement) to integrate the variability present in our data. For each pair of ecosystem variables, we randomly sampled one value of each variable in the subsets of data corresponding to each ecosystem type \times climatic zone

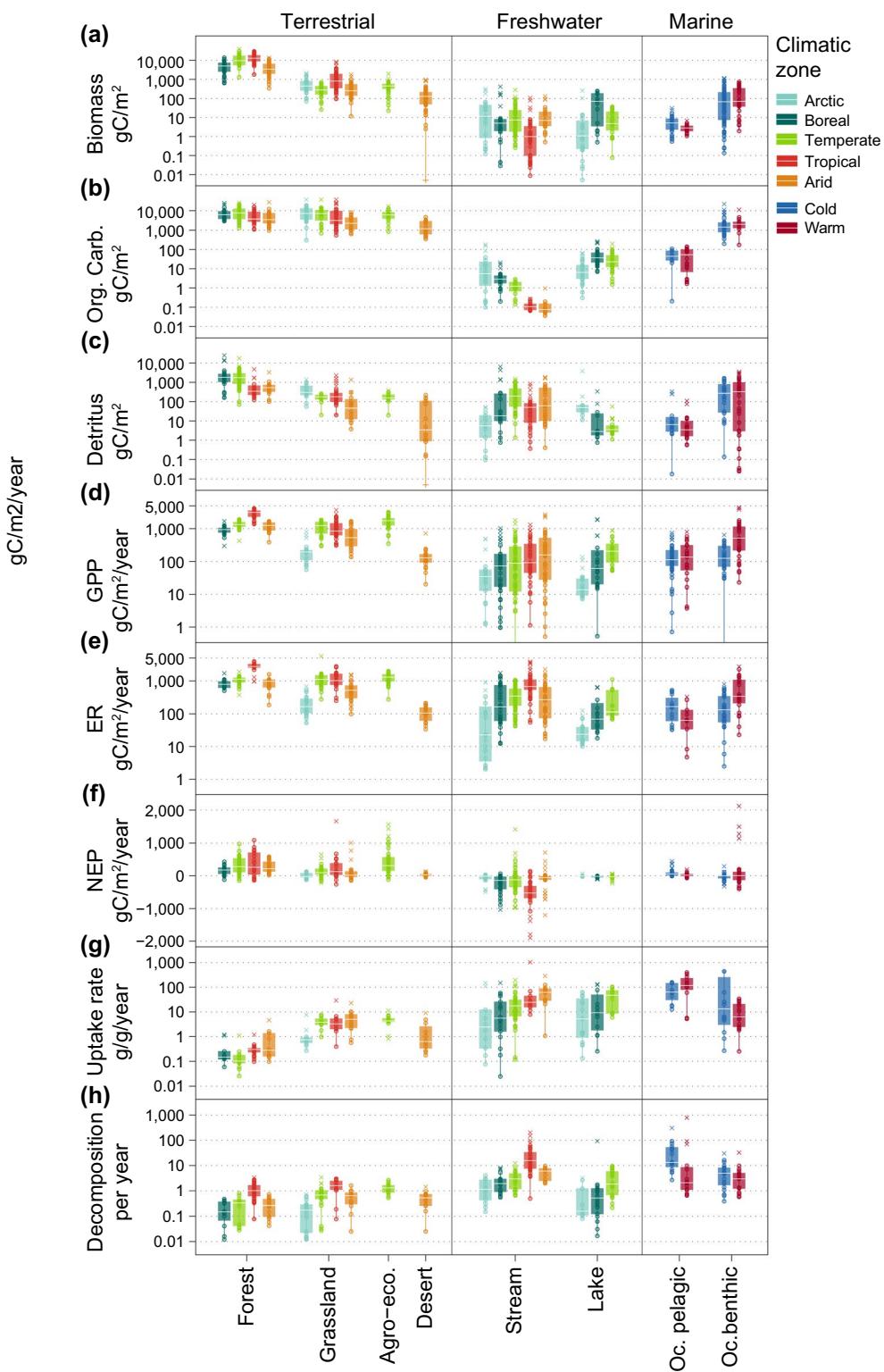


FIGURE 3 Carbon stocks, fluxes and rate across ecosystems and climates. Panels show different ecosystem functioning variables (top to bottom) across different ecosystem types (left to right) and for different climatic zones (colours). Ecosystem variables considered are (a) biomass, (b) organic carbon, (c) detritus stocks, (d) gross primary production (GPP), (e) ecosystem respiration (ER), (f) net ecosystem production (NEP), (g) uptake rate (i.e., mass-specific GPP) and (h) decomposition rate. Points give values, with 'x' denoting outliers. Zero values are replaced by 0.005 to be displayed despite log scales and are given as '+' in the figure panels (a) and (c). Boxplots give median (white line), 25 and 75% percentiles (box), extended by 1.5* interquartile range (whiskers). Scales were adapted to maximize clarity. For that purpose, three very low values of NEP in tropical streams and five null values of GPP in temperate streams and an aphotic benthic site are not displayed here (but see Figure 7). Supporting Information Tables S3.11 and S3.12 of Appendix S3 report the numbers of values of each variable \times ecosystem type \times climatic zone combination, and the groups given by nonparametric post-hoc test of multiple mean comparisons within each variable, following a significant Kruskal-Wallis test (see Methods) [Colour figure can be viewed at wileyonlinelibrary.com]

combination ($E \times C$), and tested the correlation between variables with the Pearson's test. We repeated the sampling and test 10,000 times. All values were log-transformed; therefore, we excluded the few zero values mentioned above. We display the distributions of the 10,000 Pearson correlation coefficients, and provide the mean of these distributions and the percentage of significant correlations to assess the direction and strength of the relationships between ecosystem variable pairs. Correlations on subsets of data in which pairs of variables were available per site confirm that the bootstrapping approach is conservative (Supporting Information Appendix S2.4: Figures S2.10, S2.11 and Table S3.13). Finally, we synthesize the average trends in ecosystem functioning by displaying the median values of each $E \times C$ combination in the 3-D space defined by stocks (biomass, organic carbon and detritus), gross fluxes (GPP and ER) and rates (uptake and decomposition). We scaled the values of each ecosystem variable between 0 and 1 before pooling them in broader categories (i.e., stocks, fluxes and rates) to avoid biases due to different numbers of data points per $E \times C \times V$ combination (V for ecosystem variable).

2.3.3 | Latitudinal trends

As a third and final step, we analysed the correlations between ecosystem variables and latitude for each ecosystem type covering multiple climatic zones (agroecosystem and desert were excluded) using Pearson's two-sided correlation tests (Supporting Information Table S3.8). This analysis was carried out on the 87% of the data for which we could obtain geographical coordinates. The rest of the data originate from sites with unspecified coordinates, or were estimated at scales too broad (e.g., GPP of boreal forest in Canada) for coordinates to be meaningful.

2.4 | Software

We analysed the data and plotted the figures with the open source software R version 3.6.1 (R Core Team, 2019), using the R packages *maps* (Becker & Wilks, 2018), *vioplot* (Adler, 2018), *minpack.lm* (Elzhov, Mullen, Spiess, & Bolker, 2016), *plot3D* (Soetaert, 2017) and *dunn.test* (Dinno, 2017). See Supporting Information Appendix S1 for more details. Final artwork was realized with Illustrator CC 22.0.1 (Adobe Inc. San Jose, CA).

3 | RESULTS

3.1 | Variance explained by ecosystem types (E) and climatic zones (C)

All stocks, gross fluxes (GPP and ER) and rates vary significantly among ecosystem types (E) and climatic zones (C), (see Figure 3) according to both parametric and nonparametric tests (see Supporting Information Tables S3.1–S3.5). Main and interactive effects (C, E

versus C : E) for each ecosystem variable are all highly significant (Supporting Information Table S3.1). The ANOVAs on pooled categories (stocks, fluxes and rates) show that E, C and E:C explained about 58% of the total variance (Supporting Information Table S3.2). When considering individual ecosystem variables, the two-way ANOVAs show that more variance is explained for organic carbon (91%) and biomass (78%) and less for NEP (39%), GPP (57%) and detritus (55%) (Figure 4a). On average across the different ecosystem variables, C, E and C : E represent 18, 71 and 11% of the variance explained, respectively. While ecosystem type (E) corresponds to most of the explained variance, notably for stocks (91%), climatic zones also modulate ecosystem variables, especially fluxes and decomposition rates (C effect represents 42 and 27% of the explained variance, respectively, compared to 5% in stocks). This climatic modulation, however, is highly variable among ecosystem types for some variables, for instance for GPP, which depends strongly on climatic zones for forests (where climate explains 66% of the variance) but not for streams (where climate is not significant). By contrast, the climatic effect on ER is relatively homogenous across ecosystems (see Figure 4c and Supporting Information Tables S3.6 and S3.7). Finally, interactive effects between ecosystem types and climatic zones appear to be especially important for NEP and detritus (27 and 22% of explained variance, respectively; see Figure 4a and Supporting Information Table S3.1), indicating that the direction of climatic effects varies across ecosystem types.

3.2 | Variation in stocks, fluxes and rates across ecosystem types

Stocks, fluxes and rates vary widely but consistently among ecosystem types. Moreover, ecosystem types cluster at distinct positions in the space defined by ecosystem variable pairs, and this clustering drives most of the correlations observed between variables (Figure 5 and Supporting Information Figure S4.1). On a log-log scale, stocks, fluxes and rates correlate positively within each category. For instance, ecosystem types displaying high biomass also have high organic carbon stocks (Figure 5a), and those displaying high GPP also show high ER (Figure 5b). While such a relationship between GPP and ER is expected in systems where productivity is driven by autotrophic organisms like in terrestrial ecosystems (Chen et al., 2015; see Supporting Information Appendix 2 discussion section S2.4 and Figure S2.10), it could be assumed to be disconnected in heterotrophic ecosystems where production is mainly driven by the detritivore biotic loop (e.g., in freshwater ecosystems). Surprisingly, we observe it across all ecosystem types regardless of their average auto- or heterotrophic status. On the whole, correlations we observe within stock, flux and rate categories emerge mainly from differences among ecosystems types: globally, terrestrial ecosystems have high stocks and fluxes and low rates while aquatic ecosystems have low stocks and fluxes and high uptake and decomposition rates. Looking more into detail, stocks and fluxes decrease from forests to agroecosystems, grasslands, deserts and benthic marine systems, to finally be the lowest in streams, lakes,

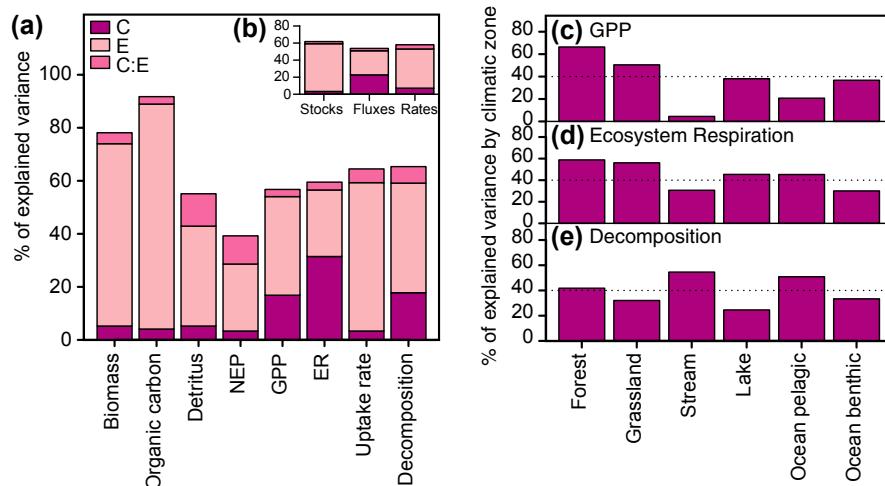


FIGURE 4 Variance of ecosystem variables explained by climatic zone and ecosystem type. (a) Proportion of variance explained in a series of two-way ANOVAs performed on log-transformed values of each individual ecosystem variable, with climatic zone (C) and ecosystem type (E) as explanatory variables; model: $y \sim C + E + C : E$. NEP = net ecosystem production; GPP = gross primary production; ER = ecosystem respiration. One null value of biomass and of detritus in a desert and five of GPP were removed to allow log-transformation. In (b), stocks (biomass, organic carbon and detritus), fluxes (GPP and ER) and rates (uptake and decomposition) are pooled into broader categories after the individual ecosystem variables are individually scaled. Panels (c), (d) and (e) show the variance explained by climatic zone in a series of one-way ANOVAs performed individually on GPP, ER and decomposition rate for each ecosystem type (18 models). Agroecosystem and desert ecosystems are removed because they are represented in only one climatic zone (temperate and arid, respectively). See full statistical results in Supporting Information Tables S3.1, S3.2 and S3.6 [Colour figure can be viewed at wileyonlinelibrary.com]

and pelagic marine systems (Figure 5a,b), while rates are higher in streams and pelagic marine ecosystems than in the other ecosystem types (see Figure 5c; see significantly different groups in Supporting Information Table S3.4). Stocks generally correlate positively with fluxes, such as biomass with GPP, but negatively with rates, such as biomass with uptake rate (Figure 5d,e, and Supporting Information Figure S4.1), the latter relationship also being strongly conserved within ecosystems (Supporting Information Figure S2.10). Thus, in systems sustaining more standing biomass, more biomass is produced in total but at a lower rate. The negative stock–rate relationship, however, does not hold for detritus and decomposition rates [Figure 5f; but see the relatively opposed directions of these variables in a principal component analysis (PCA) on median ecosystems in Supporting Information Figure S4.2].

Overall, positioning median ecosystems in the 3-D space of stocks, fluxes and rates results in a gradient of functioning types (Figure 6): forest ecosystems have the largest stocks and fluxes but low rates. Grasslands also have relatively slow biological processes, but with lower stocks and fluxes than forests. Agroecosystems position close to grasslands but with noticeably higher rates. This is followed by deserts and benthic marine systems with intermediate stocks and fluxes. Finally, freshwater and pelagic marine ecosystems cluster in the region of lower stocks and fluxes but higher rates. In addition, fluxes and rates in freshwater and terrestrial ecosystems display a marked climatic-induced secondary gradient ranging from low values in arctic/boreal zones to higher values in temperate and arid zones, and highest values in tropical zones (see shapes in Figure 6).

3.3 | Climatic modulation

A climatic imprint is most visible on fluxes and decomposition rates (Figure 4a,b and Supporting Information Tables S3.1 and S3.2). In comparison, stocks vary less, and less consistently, with climate (Figure 4b and Supporting Information Figure S4.3). For instance, while we note a significant decrease in biomass with latitude in forests, an opposing trend can be found in marine pelagic ecosystems (Supporting Information Figure S4.3 and Table S3.8). By contrast, GPP, ER and rates systematically decrease with latitude (Figure 7 and Supporting Information Figure S4.4), although the relationship is not significant in all ecosystem types: for instance, GPP does not correlate with latitude in streams (Figure 7a). This absence of a climatic effect was also apparent when using discrete climatic zones (see Figure 4c and Supporting Information Table S3.6). Moreover, different responses of GPP and ER to latitude within ecosystem types might result in an opposite response of NEP to latitude, for instance in grasslands versus streams: NEP decreases significantly with latitude in grasslands, while it increases in streams (Figure 7d), a pattern confirmed with discrete climatic zones when comparing mean NEP of these systems in arctic and tropical zones (Supporting Information Table S3.9).

4 | DISCUSSION

By integrating quantifications of ecosystem functioning in the 3-D space of stocks, fluxes and rates, this synthesis provides a global

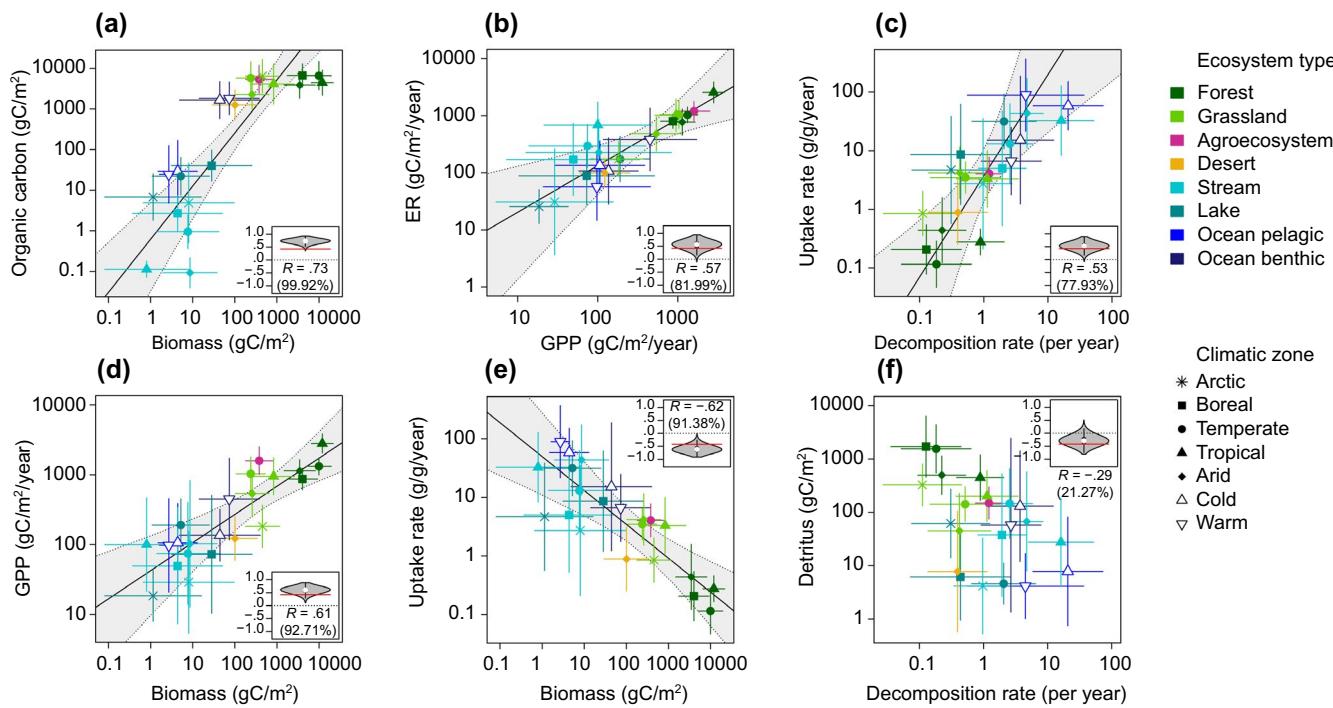


FIGURE 5 Relationships between ecosystem variables from bootstrap procedure. Points and bars give mean and standard deviation values, respectively, for the given ecosystem variables in each ecosystem type (colours)–climatic zone (shapes) combination. GPP = gross primary production; ER = ecosystem respiration. Black lines and grey areas give the mean linear regressions and the 95% confidence interval, respectively, of regressions realized in 10,000 iterations of bootstrapped values for each ecosystem \times climatic zone combination (see Methods and Supporting Information Appendix S1). The violin plots within panels show the distributions of Pearson's correlation coefficients for these 10,000 series of bootstrapped values; the numbers give the mean value of this distribution and the percentage of significant correlations in parentheses. The red lines show the limit value above and below which the correlation is significant, for positive and negative coefficients, respectively. Mean and quantile regressions are not displayed when less than 75% of the correlations are significant (d). The equations for the mean regressions in log-log space are: (a) $y = 1.31x - 0.48$, (b) $y = 0.82x + 1.13$, (c) $y = 1.72x + 1.31$, (d) $y = 0.4x + 3.75$, (e) $y = -0.58x + 3.91$. See relationships from bootstrap procedure between other pairs of ecosystem variables in Supporting Information Figure S4.1; correlations for subsets of empirical data for which pairs of variables are available per site are shown in Supporting Information Table S3.13, Figures S2.10 and S2.11; see Supporting Information Appendix S2.4 for discussion [Colour figure can be viewed at wileyonlinelibrary.com]

overview of ecosystem functioning, its characteristics and variability within and among ecosystem types. Compared to previous work, our comparative and multivariate approach reveals a gradient of functioning. Analogous to r-K ecological strategies at the species level, ecosystems have different typologies, either with fast biological processes and low storage (e.g., freshwater and pelagic systems), or slower processes but with large storage and production capacity (e.g., forests). Climate regulates the speed of this processing, modulating the position of ecosystems in the functioning space.

4.1 | Ecosystem functioning types in a multidimensional space

Functioning types – how material is stored and processed within ecosystems – align on a gradient from terrestrial ecosystems with high storage capacities, high fluxes, but slow biological rates, to aquatic ecosystems with low stocks and fluxes but fast biological rates. Forests versus streams and pelagic marine systems occupy the respective extremes of this gradient.

We interpret these functioning differences observed at the ecosystem level as originating from fundamental differences in the type of organisms dominating resource use and primary production. Notably terrestrial versus aquatic physical conditions have selected contrasting producer types, especially in terms of individual size (Kenrick & Crane, 1997). Terrestrial systems are dominated by large primary producers (trees and grasses), harbouring complex structures to access light and take up nutrients from soil (roots and stems). In pelagic waters of freshwater and marine systems, carbon enters through microscopic producers (phytoplankton), whose small sizes are optimized for osmotrophic nutrient uptake mode (larger surface to volume ratios of small organisms) and sinking avoidance. These differences in producers primarily impact carbon uptake and decomposition rates. We observe higher uptake rates in systems having small producers than in those having large ones (e.g., forest versus stream in Supporting Information Table S3.4), in line with the MTE and previous data compilations (Brown et al., 2004; Cebrian, 1999; Schramski et al., 2015): smaller organisms grow faster (Gounand et al., 2016). Along with increasing size, which imposes energetic constraints on production rates, primary producers'

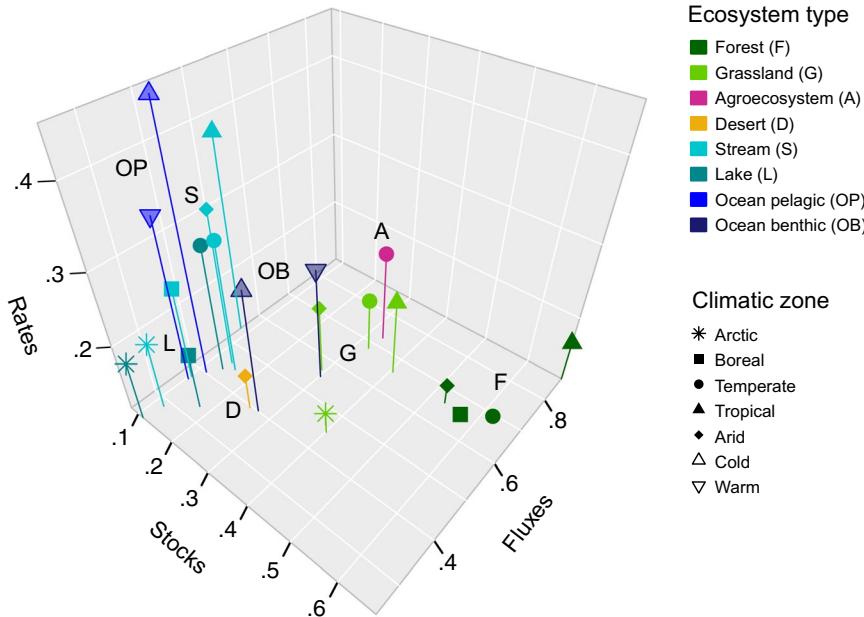


FIGURE 6 Relative positions of median ecosystems in the ecosystem functioning space. Ecosystem types (colours, labels) in each climatic zone (shapes) according to the medians of stocks (biomass, organic carbon, detritus), fluxes (gross primary production, ecosystem respiration) and rates (mass-specific uptake and decomposition rates). Values are scaled between 0 and 1 within each ecosystem variable before pooling them into broader categories (i.e., stocks, fluxes and rates) to avoid biases resulting from different numbers of data points among ecosystem \times climate \times variable combinations. Note that in each category, variables are pooled and not summed because it would only be meaningful for stocks. This makes each variable to have the same weight within each category of stocks, fluxes or rates. For the purpose of clarity, scaled median values are double square root-transformed [Colour figure can be viewed at wileyonlinelibrary.com]

stoichiometry shows increasing C : N ratios (Elser et al., 2000; Sitters, Atkinson, Guelzow, Kelly, & Sullivan, 2015), leading to decreasing decomposability from aquatic to lignin-rich terrestrial systems (Cebrian & Lartigue, 2004; Shurin, Gruner, & Hillebrand, 2006; Tiegs et al., 2019). Since aquatic conditions also favour decomposition, decomposition rates decrease from aquatic to terrestrial systems and indirectly correlate positively with carbon uptake rates (Figure 5c; e.g., between forest and pelagic marine ecosystems; Supporting Information Table S3.4); both ecological processes go faster in streams and pelagic marine systems, and slower in forests, with benthic and grassland systems processing material at intermediate speed.

Contrary to rates, stocks are higher in terrestrial than in aquatic systems. This necessarily results from among-ecosystem differences in input-to-output ratios for the different stocks. Indeed, forests accumulate more biomass and detritus than streams and pelagic systems, due to higher production to loss ratios, which could have several origins. Terrestrial systems experience less herbivory and slower decomposition due to a higher proportion of structural tissues and dry conditions (Cebrian, 1999; Cebrian & Lartigue, 2004). By contrast, biomass and detritus in aquatic communities experience higher output fluxes of consumption, mortality, respiration, and export by currents or sinking (McCoy & Gillooly, 2008). In benthic sediments, however, carbon could accumulate in large stocks when detritus production rates and sinking input exceed local mineralization (Duarte & Cebrián, 1996; Fourqurean et al., 2012).

Ecosystems harbouring higher stocks also have higher fluxes (GPP and ER), resulting, for instance, in biomass correlating positively with GPP (Figure 5d), as previously found for different community types (Hatton et al., 2015); the regression slope lower than 1 on the log-log scale indicates, however, that mass-specific uptake rates decrease with biomass across ecosystems (Figure 5e). This second relationship also holds with a surprising consistency within ecosystem types (Supporting Information Figure S2.10), but explanations of change in uptake rates based on individual size variation fail because community biomass rarely correlates with mean individual body mass (Hatton et al., 2015). In similar ecosystems, slower uptake rates with increasing biomass are better explained by variation in competition: if biomass raises with abundance of primary producers, then shading would reduce community uptake rate in high biomass ecosystems. Across broad types of producers, however, differences in size in itself could drive negative biomass–uptake rate relationships because size does not only integrate differences in uptake efficiency, but also corresponds to structural and stoichiometric differences. This likely explains much of the differences in stocks, fluxes and rates at the ecosystem scale (Allen, Gillooly, & Brown, 2005; Schramski et al., 2015). For instance, trees build structural biomass involving complex molecules such as lignin and cellulose to optimize access to light and therefore production capacity, compared to algae, but this also lowers uptake and decomposition rates (Cebrian, 1999). In aquatic systems, uptake rate is fast but production capacity (GPP) is limited by access to light (Krause-Jensen & Sand-Jensen, 1998), notably in deep or turbid waters (84% of freshwater and 63% of benthic marine ecosystems in our data are net heterotrophic: more carbon is respired

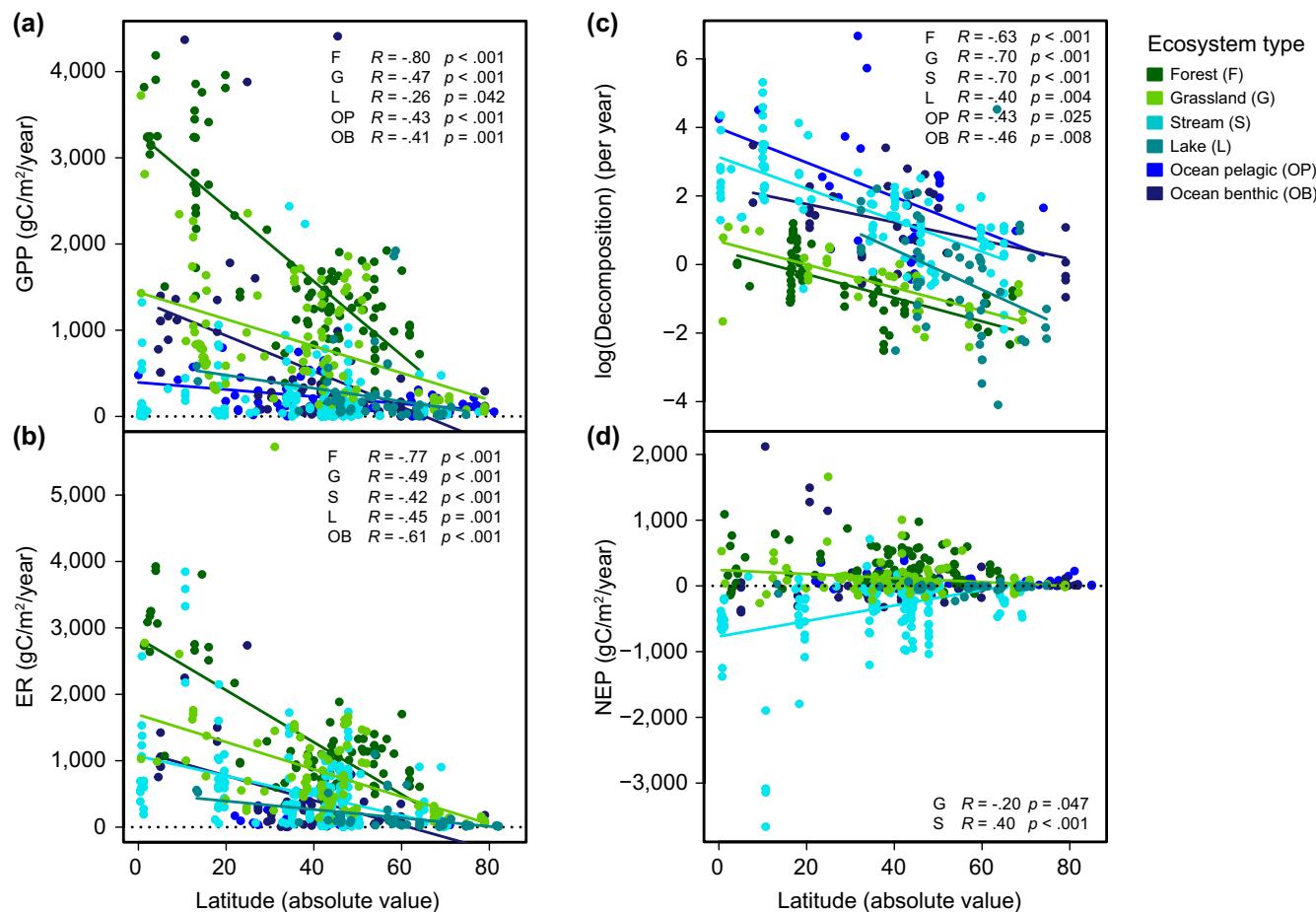


FIGURE 7 Latitudinal trends in decomposition rates and net ecosystem production (NEP). Regression lines for significant correlations between latitude and (a) gross primary production (GPP), (b) ecosystem respiration (ER), (c) decomposition rates (log-transformed values) and (d) NEP, based on two-sided Pearson's two-sided correlation tests. Solid circles show the data points. Colours denote ecosystem types. Pearson correlation coefficients and p -values are provided for the significant relationships (see colour legend for abbreviations of ecosystem types, and full details on statistical tests in Supporting Information Table S3.8). Significant correlations of stocks, uptake rates and GPP/ER ratios with latitude are available in Supporting Information Figures S4.3, S4.4 and S4.5, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

than locally produced). This interpretation is congruent with observations of strong positive correlations between carbon residence time and producer individual body mass across broad types of autotrophic ecosystems (Schramski et al., 2015).

Overall, despite considerable variability in our dataset (see presentation in Supporting Information Appendix S2), functioning types emerge that we hypothesize are driven by both the dominant primary producer categories (e.g., tree, grass, alga), which would determine stocks' general magnitude and potential activity rates, and by environmental constraints modulating the realized activity (e.g., water turbidity, water availability, temperature).

4.2 | Variation of ecosystem functioning with climatic constraints

The high variance observed in ecosystem variables at the broad organizational scale considered here must arise from variation in

species' functional traits or food web structure (Cornwell et al., 2008; Datry et al., 2018), or different availability in nutrients, which we do not examine explicitly, and also in response to climatic constraints. In particular, rates and fluxes of production and respiration (GPP and ER) consistently decrease from warmer to colder climates (see Figure 7 and Supporting Information Figure S4.4 and Tables S3.3, S3.8) as predicted by the MTE (Brown et al., 2004; Clarke, 2006; Gillooly, Brown, West, Savage, & Charnov, 2001), and in line with the nearly universal temperature-dependency of biological rates observed across many taxa and systems (Gillooly et al., 2001; Yvon-Durocher et al., 2012). Slowing down of biochemical reactions with decreasing temperature results in a relatively conserved decrease of biological rates along latitudes within ecosystems (see decomposition and uptake rates in Figure 7 and Supporting Information Figure S4.4). While the flux decrease with latitude is well quantified in some ecosystems, for instance thanks to the FLUXNET program (Yu et al., 2013), our results also show that the strength of the response to latitude might also vary among processes and ecosystems,

such as with production (GPP) and respiration (ER). As a result, net ecosystem production can respond to latitude in opposite directions among ecosystem types. In grasslands, NEP decreases with latitude (Figure 7d) meaning that ER decreases less rapidly than GPP (Yu et al., 2013), maybe due to differences in soil and air temperatures. Conversely, NEP increases with latitude in streams (Figure 7d and Supporting Information Table S3.8), and between temperate and arctic lakes (Supporting Information Table S3.9). In fact, by slowing down detritivore activity (ER), cold temperatures make fresh water less heterotrophic, as found by Demars et al. (2011) in Icelandic streams of different temperatures, even in the absence of any significant GPP decline.

Stocks also vary among climates (see Supporting Information Tables S3.1–S3.3) but not in a systematic way across ecosystem types (Supporting Information Figures S4.3, S4.6 and Table S3.8). Environmental constraints that do not follow a latitudinal gradient, such as water availability in terrestrial systems, also affect the balance between input and output fluxes regulating stocks (Anderson-Teixeira, Delong, Fox, Brese, & Litvak, 2011; Yang et al., 2011). For instance, drought limits more GPP than it limits ecosystem respiration, as observed in Europe during the exceptionally warm summer of 2003 (Ciais et al., 2005), and is associated with specific output fluxes such as erosion, depleting stocks in arid zones (Ravi, Breshears, Huxman, & D'Odorico, 2010). This illustrates how different constraints affecting fluxes in different ways might induce shifts in ecosystem functioning.

4.3 | Perspectives: ecosystem functioning facing changes

Integrating ecosystem stocks, fluxes and rates in a single framework allows us to characterize a gradient of broad functioning types. Environmental constraints, such as climate, move the cursors of ecosystem within the functioning space, but the fine directions and possible magnitude of these movements are still to be investigated. To develop fine predictions of process changes at the ecosystem level, we need more complete quantification of ecosystem functioning at the site level. The main limitation of our study is that not all variables are available for each site. Our bootstrapping procedure does not include constraints linking ecosystem variables within specific sites. Observing relationships despite this limitation demonstrates the strength of feedbacks between variables at the cross-ecosystem level. A more mechanistic understanding of these feedbacks would require examining systematically the persistence of these relationships within ecosystem types, which we were able to do for GPP–ER and biomass–uptake rates variable pairs (Supporting Information Figure S2.10). Quantification of multivariate functioning at the site level would further allow us to define reference states in the functioning space, and to analyse deviations from these states with changes in environmental constraints or in community composition. This would be a necessary step for early detection and prediction of ecosystem functioning

changes (Petchey et al., 2015). To go further, simple models using this general framework of matter transformation should allow comparison of the responses to perturbations of different ecosystem types and identification of testable mechanisms for potential variations. In this respect, incorporating the decomposition process would constitute an interesting mechanistic expansion of the trophic-level-focused 'Madingley' model (general ecosystem model; Harfoot et al., 2014) to investigate indirect feedbacks of perturbations on the structure of ecosystems. Moreover, the absence of negative relationships between decomposition and detritus in our data (Figure 5f) might be the imprint of cross-ecosystem linkages playing a significant role in ecosystem functioning: the signal is blurred by the high variability of detritus stocks and decomposition in freshwater ecosystems, likely because detritus in these systems often comes from terrestrial inputs (Collins, Kohler, Thomas, Fetzer, & Flecker, 2016; Gounand, Little, Harvey, & Altermatt, 2018). Thus, anticipating changes in ecosystem functioning and in the global carbon cycle could necessitate consideration of ecological processes at both local and meta-ecosystem scales (Gounand, Harvey, Little, & Altermatt, 2018; Gounand, Little, et al., 2018). Overall, the patterns emerging from such global data synthesis could help to evaluate mechanistic ecosystem models (e.g., Madingley) to generate hypotheses on dominant processes and factors driving ecosystem functioning.

5 | CONCLUSION

Acknowledging the multi-faceted nature of ecosystem functioning and the feedbacks linking these facets is crucial to develop a mechanistic understanding of ecosystems' response to change. Our quantified comparison of ecosystem functioning among broad ecosystem types and climatic zones integrates previous knowledge into a coherent framework based on material flow, and sets the basis for a mechanistic investigation of ecosystem multifunctionality.

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DATA ACCESSIBILITY

The dataset is available in xlsx file format from a Zenodo public repository, <https://doi.org/10.5281/zenodo.3644247>. R scripts to reproduce the figures and statistical results are available upon request.

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BIOSKETCH

The authors are part of the EMERGE (Eawag Meta-Ecosystem Research group) initiative. We are interested in bridging community- and ecosystem-level processes through the lens of spatial ecology. Collectively, our current research aims at understanding the main spatial constraints on biodiversity and how those effects scale-up to influence ecosystem functioning in the landscape. (More on each author – I.G.: <https://isabellegounand.wordpress.com>, C.J.L.: <https://chelseajeanlittle.com>, E.H.: <http://metecolab.org>, F.A.: <https://www.altermattlab.ch>).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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APPENDIX

DATA SOURCES

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